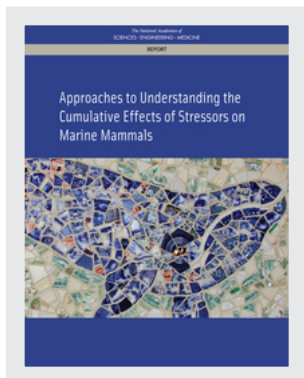


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## Approaches to Understanding the Cumulative Effects of Stressors on Marine Mammals (2017)

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# Approaches to Understanding the Cumulative Effects of Stressors on Marine Mammals

Committee on the Assessment of the Cumulative Effects of Anthropogenic Stressors on Marine Mammals

Ocean Studies Board

Division on Earth and Life Studies

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## Preface

Assessing the cumulative effects of multiple stressors is a top-priority problem in marine ecology. An important marine policy paper by Rudd (2014) surveyed more than 2,000 ocean scientists and policy makers from nearly 100 countries, asking them to prioritize the most important questions for the ocean environment. Out of 67 questions, the top priority was “How will the individual and interactive effects of multiple stressors (e.g., ocean acidification, anoxia, warming, fishing, and pollution) affect the capacity of marine ecosystems and species to adapt to changing oceans?” The topic of cumulative effects was chosen by the federal agencies that funded this report because assessing cumulative effects has been an important part of U.S. regulations protecting marine mammals since the 1970s, but the approaches used have little predictive value. Marine mammal populations are affected by a large number of natural and anthropogenic stressors. This report was tasked with focusing on sound and other stressors when evaluating cumulative effects on marine mammals. If cumulative effects cannot be accounted for, then unexpected adverse impacts from interactions between stressors pose a risk to marine mammal populations and the marine ecosystems on which people and marine mammals depend.

Assessing cumulative effects is not only important, it is also a problem that has proven nearly impossible to solve. Scientists and managers involved in these assessments confront data gaps concerning the dosages of all stressors to which marine mammals are exposed, and a lack of dose–response functions to predict effects of single stressors. For ethical and practical reasons, there are no studies in marine mammals on interactions between stressors. Studies in other marine organisms show that these stressors often interact, but their cumulative effects are extremely difficult to predict.

The audience intended for this report includes stakeholders, managers, policy makers, and scientists. This report has developed approaches to analyze how stressors exert their effects on individuals, populations, and ecosystems to help guide research on cumulative effects in the future. The report aims to help managers decide when cumulative effects are particularly important, and to help guide decisions about which stressors or combinations of stressors to reduce when this is necessary to protect marine mammal populations.

Recognizing that quantitative prediction of cumulative effects of stressors on marine mammals is not currently possible, this committee developed a conceptual framework for assessing the population consequences of multiple stressors. The framework uses indicators of health that integrate short-term effects of different stressors that affect survival and reproduction. The report explores a variety of methods to estimate health, stressor exposure, and responses to stressors. The committee also developed a decision tree for determining when cumulative effects are particularly important for managing a marine mammal population.

Many stressors that affect marine mammals are themselves affected by larger-scale ecological drivers. For example, ocean climate is an ecological driver that changes the exposure of marine life to the stressors of warming and ocean acidification. Similarly predators, prey, and competitors of marine mammals are potential stressors whose distributions are affected by ecological interactions. The committee explored the use of interaction webs to help ensure that important ecological interactions, including indirect interactions, are included in assessments of cumulative effects.

Cumulative effects must be evaluated in environmental assessments of planned activities, but this evaluation is equally important for selecting management actions once populations or ecosystems are found to be at risk of adverse impacts. In this case, the critical issue is to decide what



combination of stressors to reduce in order to bring the population or ecosystem into a more favorable state. Whatever increases in stressors may have created the risk, the best management action may require reducing a different combination of stressors. For example, if a persistent toxicant increases mortality of a species but cannot be removed from the ocean, the best management action might involve reducing fishing bycatch, which can be controlled. This broadening of management approaches could be a particularly important result of assessing cumulative effects.

Recognizing difficulties with measuring trends in marine mammal populations, the report explores early warning indicators for adverse impacts, including health and population measures. Measures of health that indicate which stressors caused an effect would be particularly useful for managing the effects. The committee hopes that this report may help direct the development of methods to identify when cumulative effects pose a risk of driving a population or ecosystem into an adverse state, and to develop management strategies that can select stressors whose reduction will minimize this risk. The committee recognizes the enormous scientific challenge posed by these two problems, but their importance justifies significant effort to solve them.

This committee met four times and held a workshop in the National Academies of Sciences, Engineering, and Medicine's Beckman Center in Irvine, California. On behalf of the committee, I would like to thank the speakers invited to the

workshop and audience members who shared their insights with the committee. On behalf of the committee, I would also like to thank the study directors who oversaw this report, first Deborah Glickson and then Kim Waddell, and the director of the Ocean Studies Board, Susan Roberts, along with other members of the staff whose contributions were essential for our meetings and development of the report.

Academies reports are designed to address problems that are both important and difficult, but this committee was tasked with a more difficult and broad-ranging problem than I have encountered in previous studies on marine mammals and sound. The committee explored many approaches to evaluating cumulative effects, and, in response to this task, this report is more extensive than the others on marine mammals and sound. The committee members and members of the National Academies staff working on this report not only had to write about and review a large body of information, but were all stretched to work outside of their disciplines. I would like to thank the committee members for their generosity in working together so well to meet the challenge of the statement of task, exploring creative solutions while providing a broad and critical review of the problem of evaluating cumulative effects in marine mammals.

Peter L. Tyack, *Chair*  
Committee on the Assessment of the Cumulative  
Effects of Anthropogenic Stressors on Marine Mammals

## Acknowledgments

This report was greatly enhanced by discussions with participants at the committee's meetings as part of this study. The committee would like to acknowledge, especially, the efforts of those who gave presentations at the committee meetings: Kim Anderson (Oregon State University), Jesse Barber (Boise State University), Steve Beissinger (University of California, Berkeley), Shekhar Bhansali (Florida International University), Tiffini Brookens (Marine Mammal Commission), Mitch Eaton (U.S. Geological Survey), Tim Essington (University of Washington), Jason Gedamke (National Oceanic and Atmospheric Administration), Horst Greczmiel (Council on Environmental Quality), Carrie Kappel (University of California, Santa Barbara), Sara Maxwell (Old Dominion University), Jonna Mazet (University of California, Davis), Jim Price (Bureau of Ocean Energy Management), and Mike Weise (Office of Naval Research).

This report has been reviewed in draft form by individuals chosen for their diverse perspectives and technical expertise. The purpose of this independent review is to provide candid and critical comments that will assist the institution in making its published report as sound as possible and to ensure that the report meets institutional standards for objectivity, evidence, and responsiveness to the study charge. The review comments and draft manuscript remain confidential to protect the integrity of the process. We wish to thank the following individuals for their review of this report:

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Although the reviewers listed above have provided many constructive comments and suggestions, they were not asked to endorse the report's conclusions or recommendations, nor did they see the final draft of the report before the release. The review of this report was overseen by Andrew R. Solow, Woods Hole Oceanographic Institution Senior Scientist, and John Dowling, Harvard University Professor of Neurosciences. They were responsible for making certain that an independent examination of this report was carried out in accordance with institutional procedures and that all review comments were carefully considered. Responsibility for the final content of this report rests entirely with the authoring committee and the institution.



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# Summary

Marine mammals face a large array of stressors, including loss of habitat, chemical and noise pollution, and bycatch in fishing, which alone kills hundreds of thousands of marine mammals per year globally. To discern the factors contributing to population trends, scientists must consider the full complement of threats faced by marine mammals. Once populations or ecosystems are found to be at risk of adverse impacts, it is critical to decide which combination of stressors to reduce to bring the population or ecosystem into a more favorable state. Assessing all stressors facing a marine mammal population also provides the environmental context for evaluating whether an additional activity could threaten it. Under the National Environmental Policy Act of 1969 (NEPA), federal agencies are directed to assess the environmental impacts of their actions, considering direct, indirect, and cumulative effects. Cumulative effects are defined by the U.S. Council on Environmental Quality as “the incremental impact of the action when added to the other past, present and reasonably foreseeable actions” that might interact with a proposed action. Although significant progress has been made in understanding the responses of marine mammals to specific stressors such as noise and toxins, it is not yet possible to provide quantitative estimates of the impact of repeated exposure to a stressor or to predict how different stressors will interact to affect individuals and populations of marine mammals.

The Office of Naval Research, the National Marine Fisheries Service, the Bureau of Ocean Energy Management, and the U.S. Marine Mammal Commission funded the present study in order to review the understanding of cumulative effects of anthropogenic stressors, including sound, on marine mammals and to identify new approaches that may improve the ability to estimate cumulative effects. The statement of task is detailed in Box S.1.

## CUMULATIVE EFFECTS

The definition of *cumulative effects* under the implementing regulations for NEPA focuses on the incremental effect of a proposed human action when added to those of other human actions. In contrast, most biologists view cumulative effects similarly to the U.S. Environmental Protection Agency’s view of cumulative risk, which focuses on the individual animal or population, with effects accumulating when animals are repeatedly exposed to the same or different stressors. In this ecotoxicology-type approach, a noise source would be considered one of a number of stressors experienced by marine mammals and one component of an overall aggregate exposure to noise. Cumulative risk would derive from the combination of noise and other anthropogenic stressors, such as chemical pollution, marine debris, introduced pathogens, fishing, and warming or lower pH induced by carbon dioxide emissions, as well as natural stressors, such as increased presence of predators, pathogens, parasites, or reduced availability of prey due to natural ecological interactions.

In this report *aggregate exposure* is defined as the combined exposure to one stressor from multiple sources or pathways and *cumulative risk* as the combined risk from exposures to multiple stressors integrated over a defined relevant period: a day, season, year, or lifetime.

Cumulative risk from exposure to multiple stressors cannot be predicted based on existing scientific theory and data for individual marine mammals or their populations. The Committee developed a Population Consequences of Multiple Stressors (PCoMS) model to provide a conceptual framework for the challenging task of assessing the risks associated with aggregate exposures to one kind of stressor, such as sound, and the cumulative exposure associated with sound and other stressors. To broaden the analysis of cumula-

### BOX S.1 Statement of Task

The National Academies of Sciences, Engineering, and Medicine's Ocean Studies Board has previously convened four highly successful panels on the subject of biological effects of manmade underwater sound, which produced a progressive series of reports published in 1994, 2000, 2003, and 2005, with the latest report focusing on the potential for biologically significant effects on marine mammal populations. Sound, however, is only one of a variety of potential anthropogenic or natural stressors that marine mammals encounter, and it is often evaluated in isolation without consideration of the effects of other stressors (e.g., fishing, climate change, pollution, etc.), or consideration of how these other stressors may affect an animal's response to sound exposure. The committee will conduct a workshop and review the present scientific understanding of cumulative effects of anthropogenic stressors on marine mammals with a focus on anthropogenic sound. The committee will assess current methodologies used for evaluating cumulative effects and identify new approaches that could improve these assessments. The committee will examine theoretical and field methods used to assess the effect of anthropogenic stressors for

- short or infrequent exposure in the context of other known stressors (i.e., multiple stressors, both natural and anthropogenic) and
- chronic exposure in the context of other known stressors.

The review of methodologies will begin by focusing on ways to quantify exposure-related changes in the behavior, health, or body condition of individual marine mammals and assess the potential to use quantitative indicators of health or body condition to estimate changes in vital rates and, in turn, estimate the potential population-level effects.

tive effects to include multiple species and ecosystems, the concept of interaction webs was introduced.

The report distinguishes between two kinds of stressors: an *intrinsic stressor* (e.g., fasting), which is an internal factor or stimulus that results in a significant change to an animal's homeostatic set points,<sup>1</sup> and an *extrinsic stressor* (e.g., noise or a pathogen), which is a factor in an animal's external environment that creates stress in an animal. It also

<sup>1</sup> Homeostasis is a characteristic of a system that regulates its internal environment and tends to maintain a stable, relatively constant condition of properties. The normal value of a physiological variable is called its set point.

distinguishes between stressors, defined by how they influence an individual animal, and ecological drivers, which affect levels of organization from populations to ecosystems. An *ecological driver* is defined as a biotic or abiotic feature of the environment that affects multiple components of an ecosystem directly and/or indirectly by changing exposure to a suite of extrinsic stressors. Ecological drivers for marine mammals include loss of keystone or foundational species, variations in ocean climate (such as El Niño events), and climate change.

### Effects of Sound

In this study, the committee was asked to place sound in the context of other stressors to which marine mammals may be exposed. The National Research Council (NRC) report *Marine Mammal Populations and Ocean Noise* (NRC, 2005) noted that “[n]o scientific studies have conclusively demonstrated a link between exposure to sound and adverse effects on a marine mammal population.” That statement is still true, largely because these impacts are so difficult to demonstrate, but the intervening decade has seen an increasing number of studies showing the effects of ocean noise on individual marine mammals. Under the U.S. Marine Mammal Protection Act (MMPA), regulation of the effects of human activities on marine mammals requires determining the number of individual animals expected to be “taken”<sup>2</sup> lethally, by injury or by harassment. One current method is to set an all-or-nothing threshold at the sound pressure level corresponding with an estimated probability of response of 50% from the dose–response function. However, the radiation of sound from point source emissions typically exposes many more animals at sound levels below this threshold compared with the number exposed to higher sound levels. Hence, using this threshold leads to potentially significant underestimates of the total number of animals taken. An “effective received level” can be calculated that gives a more realistic take estimate. Still, the effects of sound on marine mammals cannot reliably be condensed into a single estimate of the number of animals affected by a given exposure. Changes in transmission patterns of sound in the ocean, distribution of animals, variable responsiveness of individual animals, and temporal, spatial, and social determinants of response all create uncertainty in the number of animals that will respond behaviorally or physiologically to any defined sound stimulus. Including measures of uncertainty, such as confidence intervals for estimates of predicted take, would be more consistent with the state of knowledge than providing a single number for the MMPA take estimates.

Estimating the effect of sound on marine mammals requires understanding the relationship between acoustic dosage and the probability of behavioral or physiological

<sup>2</sup> A marine mammal “take” is the act of hunting, killing, capture, and/or harassment of any marine mammal, or the attempt at such.

## SUMMARY

responses of varying degrees of severity. The criterion used under the MMPA for injury induced by sound is noise-induced hearing loss. The distribution of sound exposures that cause permanent hearing loss is estimated from studies of noise levels that cause the onset of temporary shifts in the hearing threshold (temporary threshold shift [TTS] onset) followed by the increase in the amount of TTS with increasing levels of noise. Currently, data on this relationship exist for one species of fur seal, two species of true seals, two species of mid-frequency dolphins, and two species of high-frequency porpoises. Only a few individuals (one to five) of each species have been tested, and within hearing groups there is wide variation in TTS onset and growth with increasing levels of noise. This variation indicates that the physiological effects of sound cannot be generalized based on testing of a few species of marine mammals but will require studies in more individuals of more species. Understanding how the physiological effects of sound become permanent hearing loss requires audiogrametric measurements. Because there are no audiograms available for baleen whales, physiological sound impacts are estimated based on indirect evidence, such as modeling how sound interacts with tissues in the head, estimated historical ocean noise thresholds, and data from other cetacean hearing groups.

For the recommendations that follow, the chapter number is given where supporting text for a particular recommendation can be found.

**Recommendation: Uncertainties about animal densities, sound propagation, and effects should be translated into uncertainty on take estimates, for example, through stochastic simulation. (Chapter 2)**

**Recommendation: Additional research will be necessary to establish the probabilistic relationships between exposure to sound, contextual factors, and severity of response. (Chapter 2)**

Significant progress has been made in developing experiments that can estimate acoustic dose–behavioral response relationships in marine mammals. The response criteria selected for dose–response studies have typically had low severity so as not to harm the subjects, but high enough to act as indicators of harassment under the MMPA. However, in the course of these studies some high-severity responses have been observed for signals that were barely audible. The severity levels were established based on assumed effects on individual fitness, and thus severe responses to low sound levels raise concerns regarding population consequences. This will require research to establish (1) the relationship between levels of exposure and the severity of response, (2) the role of behavioral context in determining the dose–response relationship and the response severity, and (3) the most appropriate acoustic dosage measures for sound exposure.

## EFFECTS OF MULTIPLE STRESSORS

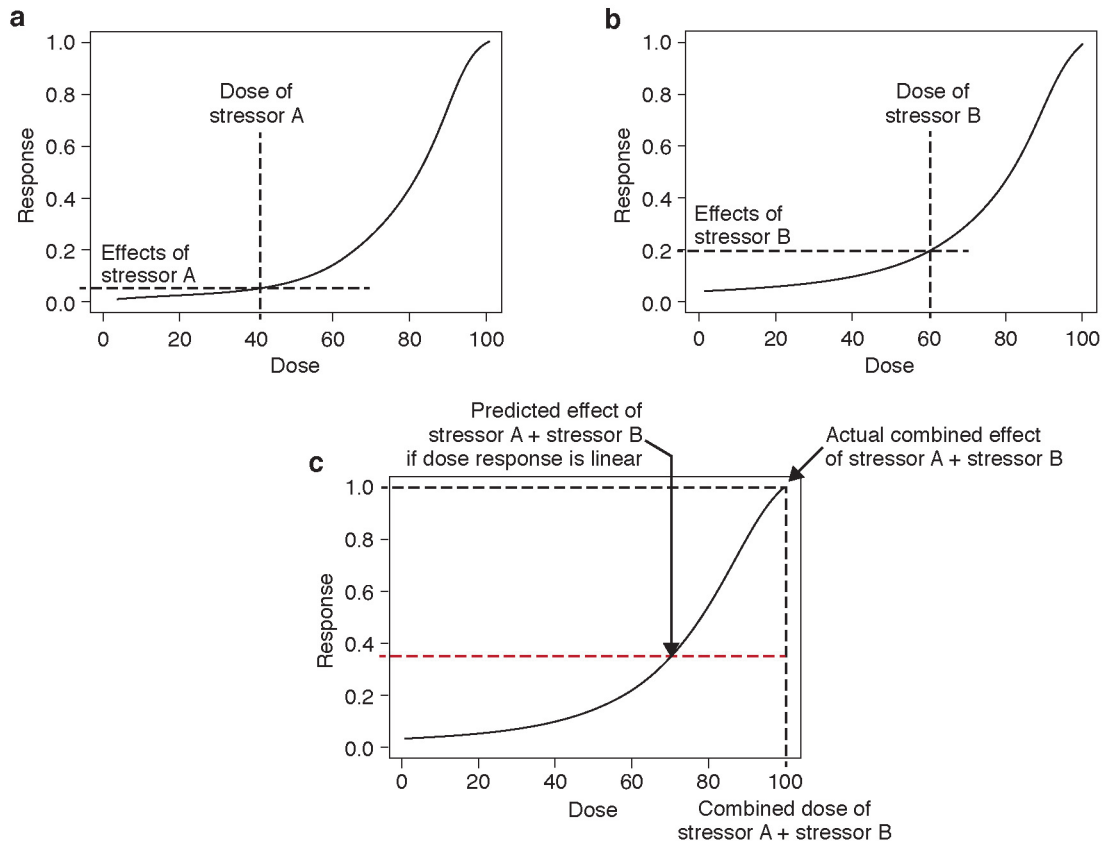
There is considerable evidence for single-factor stressor effects on marine mammals. Most of these involve physiological and behavioral responses. Dose–response functions have been estimated for a limited number of single stressors. Particular progress has been made in understanding the effects of anthropogenic sound on behavior. Experiments on a few species have estimated dose–response functions, and, once responses have been characterized in this way, monitoring can be used to estimate the scale of effects from sound-producing activities. Studies of effects of pollutants on marine mammal health and reproduction have also estimated dose–response functions, but there are fewer data on dose–response relationships for other stressors.

While the relationship between the dose of a single stressor and the response of an individual animal is relatively straightforward to predict given sufficient data, the addition of a second stressor can add considerable complexity due to the potential for interaction between the stressors or their effects. Stressors may interact in a synergistic or antagonistic manner, where the resulting response is larger or smaller, respectively, than the sum of the individual stressor responses.

Insight about cumulative effects in the individual can be gained by considering mechanisms at the molecular, cellular, and organ system levels. When stressors act through a common pathway, this provides a high potential for interaction because the stressors may provoke physiological perturbations within the same organ or neuroendocrine system. One common assumption of ecotoxicologists is that, if two or more stressors act through a common molecular mechanism, then their doses can be summed to provide a cumulative dose that can then be used with a single dose–response function (dose addition). Many dose–response functions are sigmoidal in shape or are otherwise nonlinear, and in these cases the sum of two doses may produce a response that is greater or less than the added responses to each stressor alone (response addition). A simple example to illustrate the complexity introduced when a dose–response function is nonlinear is discussed below.

Consider two stressors that act through a common molecular mechanism and are therefore considered eligible for dose addition. After correcting for different strengths (e.g., a toxicity factor for chemical stressors), the doses of the two stressors can be added to give a combined dosage and compared to a dose–response function (see Figure S.1). Stressor A has an effect of 0.10 given a dose of 40 units (see Figure S.1a), and stressor B has an effect of 0.20 given a dose of 60 units (see Figure S.1b). If the responses were additive (response addition), then the response to stressor A and B combined is expected to be 0.30. However, due to the sigmoidal shape of the dose–response function, the added doses of the two stressors (100 units) produces an effect of 1.0, more than threefold higher than the sum of the





**FIGURE S.1** This figure illustrates how the potential for interaction between two stressors (A and B) that share a common mechanism of action depends on the form of the dose–response relationship. (a) Effect of stressor A alone. (b) Effect of stressor B alone. (c) Effect of a combined dose of stressor A and stressor B, obtained by adding the dose from stressor A to that of stressor B (dose addition). The effect predicted from the dose–response relationship shared by the two stressors is more than three times higher than the prediction if their effects are assumed to be additive (red line).

individual responses (see Figure S.1c). Therefore, although these stressors are considered additive in terms of dosage (dose addition), they produce a synergistic response. Note that this same phenomenon could also occur with aggregate exposure to a single stressor. Even for this simple situation, a prediction cannot be made of the effects of most stressors unless the dosages, the relative strengths of the stressors, and the dose–response functions are known.

The interaction of stressors that act through different mechanisms but still involve a common adverse outcome pathway may be more difficult to predict due to the complexities of signaling pathways and the existence of feedback loops. For example, stressors such as noise, prey limitation, and some chemical pollutants can induce responses involving the neuroendocrine system known as the hypothalamic-pituitary-adrenal (HPA) axis that controls reactions to stress and regulates many body processes, albeit potentially

through differing mechanisms. Chronic activation or perturbation of the HPA axis may be an important mechanism through which cumulative effects arise, and the nature of these effects will be difficult to predict. In cases such as this where there are common adverse outcome pathways but potentially differing mechanisms, the form of interaction between two stressors could be estimated by determining the dose–response relationships for one stressor at different dosages of the second stressor. However, this type of study would be extremely difficult if not impossible to conduct, particularly when more than two stressors are involved, and mechanistic models may be a more appropriate approach to elucidate potential effects. Unfortunately, mechanistic models generally require a detailed understanding of the biochemical and physiological systems, and this is often lacking for marine mammals.

A review of the literature revealed that many stressors

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whose effects are mediated through common adverse outcome pathways are therefore more likely to interact. The examination of common adverse outcome pathways underscores the importance of understanding and detecting changes at lower levels of biological organization, such as at the cellular or organ response level, before they exert potentially irreversible effects at individual or population levels. However, it is also imperative to collect information to understand the linkages and processes by which such lower-level responses eventually translate into individual or population-level impacts.

The influences of multiple stressors on marine mammals might be inferred from studies of other species, such as nonmammalian marine species or terrestrial mammals. However, this can be problematic because marine mammals have evolved unique morphologies, behaviors, and physiologies as adaptations for life at sea.

Most existing research on interactions between effects of stressors on marine systems involves factorial experiments with species or systems in settings where treatments can be replicated and controlled. Factorial experiments are useful for detecting the presence of interactions but, because such systems are usually only exposed to one level of each stressor, they rarely provide sufficient information to predict responses at varying levels of stressors present in nature. Meta-analyses of results from studies of multiple stressors on various marine species have been conducted, but no general pattern has emerged for predicting how the effects of stressors will interact. Findings from each specific study were categorized as additive (i.e., noninteractive), synergistic, or antagonistic. One review paper reported that synergy is more common when more than two stressors are added to a system; another study found no evidence of antagonistic interactions between physiological responses. Beyond these generalities, the committee found no information to help predict the influences of multiple stressors on marine mammals. Given the difficulty in predicting interactions, cumulative effects assessments often assume that stressor effects are additive. However, work on other species indicates that this assumption is often wrong.

A rigorous approach for testing interactive effects of multiple stressors involves factorial experiments using a range of levels of each stressor coupled with some tests of mixtures of stressors. But for both practical and ethical reasons, such experimental approaches are often not possible for marine mammals, in which case inferences must be based on quasi-experiments: patterns associated with stressor variation in space or time. Although such data are subject to confounding and thus multiple interpretations, reasonably strong inferences are often possible from time-series analyses and weight of evidence approaches.

One type of single-stressor experimental study design could select subjects from the wild population to sample the cumulative effects of exposure to sound along with the combination of stressors currently found in that population.

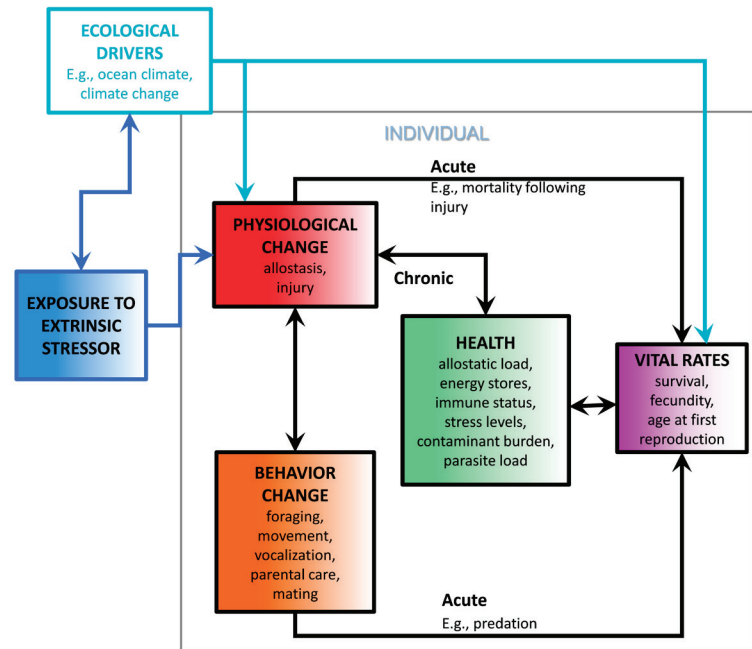
If this type of study adds one stressor to subjects in the wild whose exposure to other stressors can be documented, the cumulative effects of the single stressor then can be evaluated in the context of the full complement of environmental stressors. The interpretation of these single-stressor experiments in terms of cumulative effects is difficult because the exposures to preexisting stressors are difficult to quantify. Also experimental addition of a stressor is limited for ethical reasons to stressors such as sound, where the added stressor can be controlled in terms of both intensity and duration of exposure. In situations where the current pattern of exposure to stressors is expected to change in the future beyond the levels currently experienced, such as those caused by changes in ocean climate, this approach for studying cumulative effects will be inadequate.

The exposure of marine mammals to stressors has been estimated by mapping stressors in both space and time. However, in order to understand cumulative effects, mapping of stressors needs to be accompanied by mapping the distribution of marine mammal species of concern, because stressors must overlap with the species to exert an effect. Another approach, which is common for chemical stressors, is to sample tissue from a marine mammal to characterize its dosage of the stressor. Biopsies are now a standard remote sampling method for marine mammals that cannot be handled. The development of new methods for remote sampling of blood and other tissues for estimating dosage of stressors from marine mammals at sea are included in a recommendation later in this summary. On-animal dosimeters could also provide a time series of stressor exposure measurements for individual animals.

## A MODEL FOR HEALTH AND POPULATION CONSEQUENCES OF MULTIPLE STRESSORS

The PCoMS model (see Figure S.2) developed in this report provides a framework for exploring pathways from stressor exposure to effects on health to effects on populations. Following the general structure of the Population Consequences of Acoustic Disturbance model developed in NRC (2005), PCoMS documents the pathways from exposures to stressors through their effects on physiology, behavior, and health to their effects on vital rates and population dynamics. A key component of this framework is an assessment of the health of individuals. A variety of health indices, including allostatic load, energy stores, immune status, organ status, stress levels, contaminant burden, and parasite load, are discussed. Appropriate health indices integrate the potential effects of physiological and behavioral responses to multiple stressors on fitness over a time scale that is longer than the duration of the responses themselves but shorter than the response time of vital rates. Such indices can provide early indicators of risk of reduced survival and reproduction before an actual alteration in these rates and can increase

**FIGURE S.2** The Population Consequences of Multiple Stressors (PCoMS) framework for a single individual exposed to one stressor. Each compartment in the framework represents one or more quantities (variables) that evolve over time. Compartments are connected by arrows that represent causal flows (“transfer functions” in the terminology of NRC [2005]). For each individual, changes in physiology may result in changes in behavior (such as movement away from a sound source and cessation of feeding), which may in turn affect physiology.



understanding of the mechanisms by which these stressors affect fitness.

The committee developed a number of research recommendations that are designed to address the PCoMS model and measures of stressors and health:

**Recommendation: Future research initiatives should include efforts to develop case studies that apply the PCoMS framework to actual marine mammal populations. (Chapter 5)**

These studies will need to estimate exposure to multiple stressors, predict changes in behavior and physiology from those stressors, assess health, and measure vital rates in order to parameterize the functional relationships between these components of the framework. Where possible, the data on changes in demography, population size, and the health of individuals collected in these studies should be used to improve estimates of the parameters of the PCoMS model and reduce uncertainty.

**Recommendation: Future research initiatives should support evaluation of the range of emerging technologies for sampling and assessing individual health in marine mammals, and identification of a suite of health indices that can be measured for diverse taxa and that best serves to predict future changes in vital rates. (Chapter 8)**

Potentially relevant measures include hormones, immune function, body condition, oxidative damage, and indicators of organ status, as well as contaminant burden

and parasite load. New technology for remotely obtaining respiratory, blood, and other tissue samples and for remote assessment (e.g., visual assessment of body condition) should also be pursued.

Comprehensive health assessments are not only a critical component of the PCoMS framework, but they can also be used to serve as early warning indicators of risk before the consequences have population-level effects. There are some populations of marine mammals where periodic health assessments can include a sufficient sample of individuals to assess population health. To optimize usefulness for management, there is a need to develop databases of stressors and effects measured using established standards. For species that cannot be handled, methods are not currently available to obtain the samples used to assess health.

Establishing baseline values of health indices and their associations across life history stages in marine mammal species will provide critical information for assessing individual and population health. Cross-sectional sampling and repeated sampling from the same individuals of blood or other tissues during critical life-history phases can help to document exposure to and health effects of extrinsic stressors within the context of annual cycles and life cycles of intrinsic stressors. Long-term studies of known individuals are required for longitudinal studies.

**Recommendation: Agencies charged with monitoring and managing the effects of human activities on marine mammals should identify baselines and document exposures to stressors for high-priority populations. (Chapter 8)**

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High-priority populations should be selected to include those likely to experience extremes (both high and low) of stressor exposure in order to increase the probability of detecting relationships. This will require stable, long-term funding to maintain a record of exposures and responses that could inform future management decisions. Information on baselines and contextual variables is critically important to interpreting responses.

**Recommendation: A real-time, nationally centralized system for reporting marine mammal health data should be established. (Chapter 7)**

**Recommendation: Standards for measurement of stressors should be developed along with national or international databases on exposure of marine mammals to high-priority stressors and associated health measures that are accessible to the research community. (Chapter 8)**

**Recommendation: Techniques should be developed that will allow historical trajectories of stress responses to be constructed based on the chemical composition of the large number of baleen whale earplugs and baleen samples in museums or similar natural matrices in other species. Artificial matrices should be studied for their potential to absorb materials (hormones or chemical stressors) and thereby provide a record of exposures and responses to stressors. (Chapter 8)**

Recent work on baleen whales has shown that some tissues that lay down layers with time, such as baleen or a waxy earplug, can provide a record of stress, reproductive hormones, and some contaminants for up to the entire lifespan. Large archival collections of such tissues could be analyzed to provide time series of data that could yield critical information on the relationships between contaminants, stress, and reproductive intervals in baleen whales. Other materials that lay down semiannual layers, such as teeth, could be assessed for their potential to record stressor and life-history information over long periods of time. In addition, artificial materials could be tested for their capacity to store chemical stressors and hormones over long enough time periods to test the relationship between exposure to the stressors and response in terms of health or vital rates.

## ECOSYSTEM-LEVEL EFFECTS

The committee broadened its review from cumulative effects of stressors on marine mammals to consider how interactions among stressors may affect entire ecosystems. The distribution and abundance of species in an ecosystem are determined by the interactions among and between species and abiotic environmental elements, which together define an interaction web (see Figure S.3).

In an interaction web, species or abiotic elements that affect the distribution and abundance of a selected species are called drivers of the recipient species. When a driver affects the recipient directly, for example, when gill nets entangle and kill marine mammals, this is called a direct effect. When a driver affects a second driver that in turn affects the recipient, this is called an indirect effect. For example, human fisheries might reduce the population of a fish species that feeds on the same prey as a marine mammal. If this reduction in the competitor species increased the abundance of prey for the marine mammal species, it might have an indirect positive effect on the recipient species. Known or suspected drivers for marine mammals include ocean climate, prey limitation, predators, fishing bycatch, toxins, and pathogens. Interaction webs can help identify the suite of factors that need to be considered in evaluating cumulative effects on populations and ecosystems. As with the PCoMS model, interaction webs do not provide an algorithm for predicting cumulative effects; they serve primarily to identify the most important components of any comprehensive model of cumulative effects, including indirect effects. Interaction webs and the PCoMS model would need to include mathematical functions that describe the relationships between the different compartments before they could be used to predict those effects. Estimating these functions will be extremely challenging.

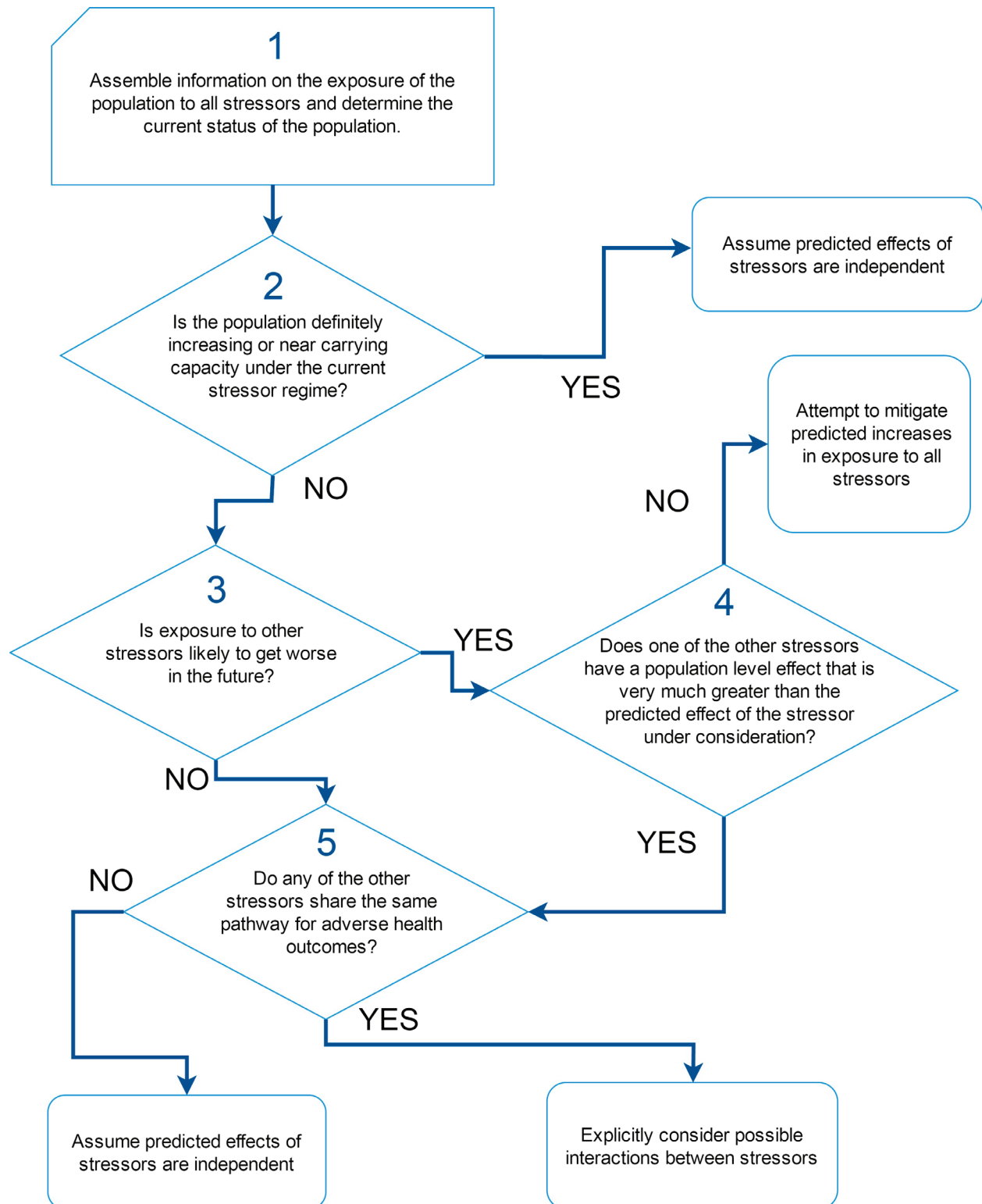
## MANAGEMENT OF CUMULATIVE EFFECTS

The critical question for predicting risk of cumulative effects asks what combinations of stressors dosages elevate the cumulative effect enough to pose a risk to populations and ecosystems. The committee's review indicates that the strength of effects cannot currently be predicted based on specific levels of exposure to multiple stressors for marine mammals. Once populations or ecosystems are found to be at risk of adverse impacts, the critical issue for selecting management actions is to decide what combination of stressors to reduce in order to bring the population or ecosystem into a more favorable state. The committee concluded that current scientific knowledge is not up to the task of predicting cumulative effects of different combinations of stressors on marine mammal populations. Even though exposure to multiple stressors is an unquestioned reality for marine mammals, the best current approach for management and conservation is to identify which stressor combinations cause the greatest risk. The committee developed a decision tree that can be used to identify situations where a detailed study of potential cumulative effects should be given a high priority (see Figure S.4). The decision tree was applied to three case studies demonstrating its utility.

**Recommendation: Situations where studies of cumulative effects should be prioritized can be identified using tools such as the decision tree developed by the committee**



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**FIGURE S.4** A decision tree for identifying situations where studies of the possible interactions between stressors should be given a high priority when considering the effect of a focal stressor on a population.

**Recommendation: Responsible agencies should develop relatively inexpensive surveillance systems that can provide early detection of major changes in population status. (Chapter 7)**

Surveillance systems should be developed first for populations that currently lack adequate stock assessments. To be most effective in providing an early warning, the variables monitored will depend on the species and situation, and may change over time with development of new technology and increasing ecological knowledge. Indices of population health, such as mother-to-calf ratios and body condition, are potentially sensitive measures. Abundance indices, such as calibrated acoustic detection rates, may also be appropriate in some circumstances. All measures considered should be evaluated in the context of their ability to inform alternative hypotheses about the mechanisms underlying population changes so that, if a negative change is detected, an early start on evaluating the possible cause could be made. For example, declines in population health indices may indicate increases in exposure to anthropogenic stressors, but they may alternatively be caused by an increase in population size approaching carrying capacity.

**Recommendation: Adaptive management should be used to identify which combinations of stressors pose risks to marine mammal populations, and to select which stressors to reduce once a risk is identified. (Chapter 6)**

Once a population of marine mammals has been found to be at risk, managers need to identify a stressor or suite of stressors whose reduction can reduce this risk. It may not be possible to reduce some stressors or ecological drivers that contribute to risk. For example, it simply may not be possible to remove persistent toxicants or reverse warming in the ocean due to climate change. This leaves those stressors that in practice can be mitigated within a time period consistent with the population's rate of decline or recovery. Among these remaining stressors, or combination of stressors, it will be important to next identify those whose reduction would be most effective at decreasing the risk. These considerations can be used to establish research priorities for estimating dose–response functions. This approach suggests a new form of effect study—experiments that remove or reduce one or more stressors to study effect of reduction. This experimental design may be more appropriate for adaptive management than the more traditional experiments that add stressors to the current baseline.

The committee recognizes that the state of the science of cumulative effects has low predictive power compared to regulatory demands to assess these effects. The most important goals for managing cumulative effects are (1) identifying when the cumulative effects of stressors risk transitioning a population or ecosystem to an adverse state and (2) identifying practical reductions in stressors to reduce this risk.

## 1

## Introduction

**ORIGIN OF THE REPORT AND STATEMENT OF TASK**

Four previous reports of the National Research Council (NRC)<sup>1</sup> have documented effects of anthropogenic sound on marine mammals. It is now recognized that intense sounds from human activities such as seismic air guns can have direct physiological effects on marine mammals, and naval sonar triggers behavioral reactions that can lead to death by stranding. However, nonlethal behavioral disturbance is the most common effect of anthropogenic noise on marine mammals. Rather subtle behavioral changes experienced by many marine mammals may have greater population consequences than occasional lethal events. Environmental reviews of human activities that make noise<sup>2</sup> in the ocean routinely assess the number of animals that may be injured or disturbed, and researchers have started to develop methods to estimate effects on populations.

Noise is a stressor for humans and wildlife, and its effects can interact with those of other stressors. Marine mammal populations exist in environments that are being altered simultaneously by various combinations of human activities and their effects, such as pollution and habitat degradation and loss. Natural factors interact in complex ways with effects of human activities to alter climate, the numbers of prey, competitors, pathogens, and predators, potentially contributing to the mix of threats that populations must withstand to remain viable.

Scientists, regulators, and managers have long recognized that the complexity of these interactions must be better understood in order to ensure that marine mammals will con-

tinue to be functioning components of their ecosystems. This has led to a strong desire to better understand marine mammal responses to cumulative effects of multiple stressors.

Terminology in the area of cumulative effects in scientific literature has been driven primarily by considerations of environmental chemicals. The U.S. Environmental Protection Agency (EPA, 2007) defines aggregate exposure as the combined exposure of a receptor (individual or population) to a single chemical. The chemical can originate from multiple sources and be present in multiple media, and exposures can occur by different routes and over different time periods. Cumulative risk is defined as the combined risk to a receptor (individual or population) from exposures to multiple agents (here, chemicals) that can come from many sources and exist in different media, and to which multiple exposures can be incurred over time to produce multiple effects. More than one chemical must be involved for the risk to be considered cumulative.

The term *cumulative effect* has been used in marine mammal literature to encompass both aggregate exposure and cumulative risk. For example, noise has been considered to have cumulative effects when an animal is exposed to multiple noise sources, such as shipping plus seismic. To be consistent with the much larger field of environmental chemical exposure, noise should be considered one of a number of stressors experienced by marine mammals. As such the effects of various noises on an individual or a population would be considered components of an overall aggregate exposure to noise. Cumulative effect would derive from the combination of noise and other anthropogenic stressors, such as chemical pollution, marine debris, introduced pathogens, and changes in temperature or pH induced by climate change, and also natural stressors, such as presence of predators, pathogens, parasites, or reduced availability of prey.

The committee defines *aggregate exposure* as the

<sup>1</sup> Until 2015, reports were published under the authorship of the National Research Council.

<sup>2</sup> Noise refers to sounds that are unwanted or are not useful for a receiver.



combined exposure to one stressor from multiple sources or pathways and *cumulative effect* as the combined effect of exposures to multiple stressors integrated over a defined relevant period: a day, a season, a year, or a lifetime.

When assessing cumulative effects, biologists focus on cumulative effects on an individual animal or population when they are repeatedly exposed to the same or different stressors. By contrast, definitions of “cumulative effects” used in relevant laws and regulations, particularly the National Environmental Policy Act of 1969 (NEPA) and the Endangered Species Act (ESA), focus on the effects of multiple “actions.” In addition to NEPA and ESA, there are a number of other acts and implementing regulations dealing with environmental impacts on marine mammals, which are summarized in Appendix B.

**Finding 1.1:** There is an important difference between the definition of cumulative effects as used by most biologists and cumulative effects as defined under the implementing regulations for the National Environmental Policy Act and the Endangered Species Act. The regulatory definition focuses on the incremental effect of a proposed human action when added to those of other human actions. Most biologists think of effects accumulating when individual animals or populations are repeatedly exposed to the same or different stressors, taking into consideration natural factors that may affect the response to human activities.

NEPA recognized the importance of these interactions by requiring all federal agencies to assess the environmental impacts of their actions. At the heart of NEPA is a requirement that federal agencies “include in every recommendation or report on proposals for legislation and other major Federal actions significantly affecting the quality of the human environment, a detailed statement by the responsible official on—(i) the environmental impact of the proposed action, (ii) any adverse environmental effects which cannot be avoided should the proposal be implemented, (iii) alternatives to the proposed action, (iv) the relationship between local short-term uses of man’s environment and the maintenance and enhancement of long-term productivity, and (v) any irreversible and irretrievable commitments of resources which would be involved in the proposed action should it be implemented.”<sup>3</sup> The detailed statement called for in NEPA is termed an Environmental Impact Statement (EIS). NEPA regulations require agencies to include in each EIS an evaluation of direct, indirect, and cumulative impacts associated with the action and proposed alternatives. *Cumulative impact* is defined for these purposes as “the impact on the environment which results from the incremental impact of the action when added to the other past, present, and reasonably foreseeable future actions regardless of what agency (federal or non-federal) or person undertakes such other actions.” The

regulations add that “[c]umulative impacts can result from individually minor but collectively significant actions taking place over a period of time.”<sup>4</sup>

Section 7 of the ESA directs federal agencies to carry out programs for the conservation of threatened and endangered species. It further requires federal agencies to ensure that their actions (i.e., all actions authorized, funded, or carried out by the agency) are not likely to jeopardize the existence of a listed species or adversely modify the critical habitat of a listed species. As part of these assurances, Section 7 also requires agencies to consult with the U.S. Fish and Wildlife Service (FWS) or National Marine Fisheries Service (NMFS) (Steiger, 1994) regarding any activities that may affect listed species.<sup>5</sup> “Procedurally, before initiating any action in an area that contains threatened or endangered species, federal agencies must consult with the FWS (for land based species and selected marine mammals) or NMFS (for all other marine species) to determine the likely effects of any proposed action on species and their critical habitat.”<sup>6</sup>

The text of the ESA does not directly address cumulative impacts or effects, but the implementing agencies (FWS and NMFS) and the courts have interpreted Section 7 as to require consideration of cumulative effects during the consultation process. The regulations promulgated under the ESA define “cumulative effects” as “those effects of future State or private activities, not involving Federal activities, that are reasonably certain to occur within the action area of the Federal action subject to consultation.”<sup>7</sup> Guidance produced by the FWS and NMFS regarding Section 7 consultations specifically states that this more narrow definition should not be conflated with the broader definition of “cumulative impacts” used in NEPA and pertains only to ESA Section 7 analyses.<sup>8</sup>

The science is not currently in place to allow quantitative estimates of how different stressors will interact as they impact individuals and populations or what the impact will be of repeated exposure to stressors. For federal agencies that seek to continue to improve their consideration of cumulative effects, such as the U.S. Navy, the U.S. Department of the Interior’s Bureau of Ocean Energy Management (BOEM), and the National Oceanic and Atmospheric Administration’s

<sup>4</sup> 40 C.F.R. § 1508.7.

<sup>5</sup> 16 U.S.C. § 1536(a). The agency first determines whether their proposed action “may affect” a listed species or its habitat. If the agency determines it may, then formal consultation with either FWS or NOAA Fisheries is automatically required. If the agency determines that the action is not likely to affect a listed species or its habitat and the consulting agency agrees with this assessment, then further formal consultation is not necessary. If, however, the consulting agency does not agree with the assessment, then a formal consultation is required. *Conservation Congress v. USFS*, 720 F.3d 1048 (9th Cir. 2013).

<sup>6</sup> *Conservation Congress v. USFS* 720 F.3d 1048 (9th Cir. 2013) citing *Natural Resources Defense Council v. Houston*, 146 F.3d 1118, 1125 (9th Cir. 1998) and *Forest Guardians v. Johanns*, 450 F.3d 455, 457 n.1.

<sup>7</sup> 50 C.F.R. § 1508.7.

<sup>8</sup> See [https://www.fws.gov/ENDANGERED/esa-library/pdf/esa\\_section7\\_handbook.pdf](https://www.fws.gov/ENDANGERED/esa-library/pdf/esa_section7_handbook.pdf).

<sup>3</sup> 42 U.S.C. § 4332(2)(C).

(NOAA's) NMFS, this presents a challenge. The U.S. Navy, BOEM, and NMFS each either fund and conduct noise-making activities, issue authorizations and permits for such activities, or regulate impacts of sound on most marine mammals. These agencies, along with the U.S. Marine Mammal Commission, funded the present study in order to review current understanding of cumulative effects of anthropogenic stressors, including sound, on marine mammals, to assess current methodologies, and to identify new approaches that may improve the ability to estimate cumulative effects.

## REVIEW OF PREVIOUS NRC REPORTS ON MARINE MAMMALS AND SOUND

There has been a consistent expansion of focus in the series of NRC reports on marine mammals and sound from 1994 to 2005. Aside from scientific concern that noise from shipping might reduce the range over which whales may communicate (Payne and Webb, 1971) and studies on the impact of noise from offshore oil industry activities (Malme et al., 1983, 1984), there was little interchange before 1990 between marine mammal biologists and the ocean acoustics community, which understood how well low-frequency sound propagates in the deep ocean. The first NRC report on low-frequency sound and marine mammals (NRC, 1994) was motivated in large measure by a single ocean acoustics experiment designed to monitor changes in ocean temperature by measuring the speed with which a sound travels across ocean basins (Baggeroer and Munk, 1992). Four federal agencies funded a \$1.7 million feasibility test for this project, which would involve sending a ship with powerful underwater loudspeakers to a site in the Indian Ocean where a low-frequency sound projected from the ship could be heard in Bermuda and California. When a report in *Science* (Gibbons, 1990) showed how the sound could be detected over much of the global oceans, the executive director of the U.S. Marine Mammal Commission could not understand how this federal action had not required permitting for effects of sound on marine mammals, because it covered such large ranges. His concerns led to the addition of a program to monitor effects on marine mammals, and the transmissions were permitted as marine mammal research (Cohen, 1991). This feasibility test succeeded in precisely timing how long sounds took to travel as far as 16,000 km (Munk et al., 1994). This success led to plans to operate a low-frequency source over a decade or more to measure changes in ocean temperature (in a project called Acoustic Thermometry of Ocean Climate, or ATOC). The long period of operation of such a long-range sound source raised concern about the impact of ATOC on marine mammals. The 1994 NRC report was tasked to review the effects of these kinds of low-frequency sounds on marine mammals and “to consider the trade-offs between the benefits of underwater sound as a research tool and the possibility of its having harmful effects on marine mammals” (NRC, 1994, p. 1). The NRC (1994) report addressed

the state of knowledge on the effect of low-frequency sound on marine mammals and found very little relevant data. The 1994 report provided a number of research recommendations to close these data gaps.

The second NRC report, *Marine Mammals and Low-Frequency Sound* (NRC, 2000), was specifically tasked with assessing progress in research on effects of low-frequency sound on seals and cetaceans since 1994, with an evaluation of the marine mammal research program associated with ATOC. Given that the Marine Mammal Protection Act was coming up for reauthorization, NRC (2000) made specific recommendations for changes in the Act, along with recommendations to NOAA for setting priorities for regulating effects of noise, and recommendations for research sponsors. The 2000 report made a suite of recommendations calling for research that could address the uncertainty around the effects of different types and sources of sound on various marine mammal species, both in the context of biological consequences and for monitoring and regulatory purposes (NRC, 2000).

The third NRC report was tasked to evaluate all frequencies and sources of anthropogenic sound that could affect marine mammals, rather than simply low-frequency sound, to identify data gaps in ocean noise databases, and to recommend research to develop a model of ocean noise (NRC, 2003a). Consistent with this charge, the NRC (2003a) expanded the work of prior committees to recommend monitoring noise and marine mammal populations globally. This NRC report (2003a) also recommended that research on effects of sound on marine mammals be structured to test for population-level effects. This latter problem became the primary focus of the fourth NRC report (NRC, 2005), titled *Marine Mammal Populations and Ocean Noise: Determining When Noise Causes Biologically Significant Effects*. In order to begin to address the question of when a behavioral response will become significant to the individual animal, and, more importantly, significant to the population, the NRC (2005) developed a conceptual heuristic<sup>9</sup> model that outlined how behavioral changes could have population consequences. This model, named the Population Consequences of Acoustic Disturbance (PCAD) model, identified a series of stages for relating the effects of acoustic disturbance on the life history of marine mammals, through to the impact on populations. The only stressor this model focused on was sound, and the model recognized that population-level consequences would be likely only when the stressor was repeatedly encountered. Specifically it looked at the aggregate effect of anthropogenic noise as a stressor over a sufficient period—a season or year—that could result in changes in life-history parameters for the exposed animals. These

<sup>9</sup> A qualitative model informed by expert opinion that links processes and states, in this case the linking of acoustic disturbance through behavior and physiology to its impact on individuals and populations. The heuristic model informs research that can quantify the processes so the qualitative model is turned into a predictive model.

### BOX 1.1 Statement of Task

The National Academies of Sciences, Engineering, and Medicine's Ocean Studies Board has previously convened four highly successful panels on the subject of biological effects of manmade underwater sound, which produced a progressive series of reports published in 1994, 2000, 2003, and 2005, with the latest report focusing on the potential for biologically significant effects on marine mammal populations. Sound, however, is only one of a variety of potential anthropogenic or natural stressors that marine mammals encounter, and it is often evaluated in isolation without consideration of the effects of other stressors (e.g., fishing, climate change, pollution, etc.), or consideration of how these other stressors may affect an animal's response to sound exposure. The committee will conduct a workshop and review the present scientific understanding of cumulative effects of anthropogenic stressors on marine mammals with a focus on anthropogenic sound. The committee will assess current methodologies used for evaluating cumulative effects and identify new approaches that could improve these assessments. The committee will examine theoretical and field methods used to assess the effect of anthropogenic stressors for

- short or infrequent exposure in the context of other known stressors (i.e., multiple stressors, both natural and anthropogenic) and
- chronic exposure in the context of other known stressors.

The review of methodologies will begin by focusing on ways to quantify exposure-related changes in the behavior, health, or body condition of individual marine mammals and assess the potential to use quantitative indicators of health or body condition to estimate changes in vital rates and, in turn, estimate the potential population-level effects.

aggregate effects were modeled on the concept of allostatic load/overload (McEwen and Wingfield, 2003).

The model has subsequently been expanded to consider the population consequences of all forms of disturbance (PCoD). New et al. (2014) describe the PCoD model and present an early attempt to quantify fitness effects of behavioral disturbance. The recognition of the importance of identifying intermediate scales between short-term disturbance and population effects was a key element of the 2005 report that is taken up again by this report.

This report develops a metric of health of the individual

that can integrate effects which can be related to survival or reproduction over periods of seasons up to the lifetime. The model defines how the distribution of the health of individuals can be used to determine the cumulative risk to the stock, population, or species.

The statement of task for this report is provided in Box 1.1.

### REPORT OVERVIEW AND ORGANIZATION

Nine committee members were selected, representing a broad range of expertise (marine mammalogy, ecology, animal behavior, biostatistics, physiology, global change biology, zoology, and bioacoustics). Beginning with its first meeting in June 2015, the committee held four meetings and a workshop. The workshop, held in October 2015, was an information-gathering opportunity designed to survey approaches and methodologies that have been developed to identify and measure animals' exposure to stressors and their responses. The committee was particularly interested in efforts developed for human and terrestrial ecosystems because they wanted to hear how other disciplines addressed these same challenges and questions of assessing cumulative impacts. The workshop discussions also helped the committee members identify innovations (in thinking and application) that they could consider in their review of the current approaches and methods.

In this chapter, the committee begins by defining some of the terminology associated with cumulative effects and the contrasts in their interpretation by biologists and regulators. This is followed by a brief introduction of select U.S. legislation that provides the general legal framework for addressing impacts to marine mammals that the sponsors of this report also use to guide their programmatic activities and responsibilities relevant to marine mammals. The chapter closes with a review of earlier NRC studies that looked at marine mammals and sound.

The effects of sound on wildlife are the focus of Chapter 2 and the committee examines the various sources and the variations in time, frequency, and intensity of sound. Both terrestrial and marine studies are reviewed, and particular attention is given to the perception of or responses to sound by animals. The chapter discusses auditory sensitivities, shifts in hearing (both temporary and permanent), and dose-response relationships in the context of stressors. Characterizing these relationships is an essential step in understanding exposure and outcomes, an approach that is revisited in the remaining chapters in the reviews of other types of stressors and their effects. The chapter includes an explanation of how dose-response functions, properly obtained, can provide much more accurate estimates and variances of marine mammal "take" in association with sound-generating activities.

Chapter 3 transitions away from sound to explore the current state of knowledge regarding the many other types

and sources of stressors, with a particular focus on extrinsic stressors (factors in the animal's external environment that create stress). The committee reviewed the effects of extrinsic stressors associated with anthropogenic activities, such as pollutants or ship strikes, and ones that are associated with natural factors. The chapter concludes with a discussion of how the spatial and temporal variation among stressors affects the potential for cumulative effects of individual and combined stressors.

Understanding how the effects of extrinsic stressors might interact to create cumulative effects is the focus of Chapter 4. The committee reviewed studies of interactions of multiple stressors and discussed the challenges of applying the findings from these studies to management of marine mammals and their environment. The chapter examines how multiple stressors are likely to interact, and then identifies approaches for prioritizing stressors for cumulative effects analysis with the use of a decision tree. The committee also explored a set of case studies involving marine mammal population declines that illustrate the difficulty of inferring causes—but also provided the committee an opportunity to investigate what conclusions might have been drawn if the decision tree had been used with these case studies.

Chapter 5 provides a conceptual framework via a new model, titled Population Consequences of Multiple Stressors (PCoMS), developed for assessing the risks associated with aggregate exposures to one kind of stressor, such as sound, and the cumulative exposure associated with sound and other stressors. The PCoMS model documents the pathways from exposure to stressors through their effects on health to their effects on vital rates and population dynamics. A key component of this framework is an assessment of the health of an individual. The chapter discusses a suite of measures that the committee identifies as useful for assessing health in the target populations.

In Chapter 6 the committee broadened its review from cumulative effects of stressors on individuals and populations to consider how interactions among stressors may affect multiple species and entire ecosystems. In doing so, committee members review the components of an interaction web and the various species or abiotic elements that affect the distribution and abundance of species of interest, and specifically how interaction webs can help identify the factors that need to be considered in evaluating cumulative effects on populations and ecosystems.

Chapter 7 acknowledges the challenges of detecting and anticipating the cumulative effects of multiple stressors on marine mammal populations and discusses a suite of population-monitoring parameters that could facilitate the early detection of unexpected population declines and, where possible, the rapid diagnosis of the main factors contributing to them.

In the final chapter of the report (Chapter 8), the committee reviews a broad range of approaches for assessing cumulative impacts that include approaches with limited use for marine mammals as well as those with more utility. The committee identifies the use of comprehensive health assessment as a broadly applicable approach that can serve as a key component of the PCoMS model framework as well as an early warning indicator of population risk prior to population decline.

The tasks asked of this committee span a broad range of scientific disciplines from toxicology to marine ecology. Terms such as *interaction* have different meanings to different specialties, and the dose–response functions discussed in the report span many levels of biological organization from molecules to ecosystems. Nearly every reader may have questions about the usage of some terms. The committee has included a glossary of important terms used throughout this report (Appendix D).



## 2

## Estimating Exposure and Effects of Sound on Wildlife

### INTRODUCTION

The world is a cacophony of sounds—from natural sources such as wind-blown vegetation and ocean waves or calling insects, birds, fish, and whales—so all animals have evolved mechanisms to modify their vocalizations to compensate for noise and to focus as listeners on relevant sounds (Tyack and Janik, 2013). However, the increasing levels of anthropogenic noise create acoustic conditions unprecedented in the evolutionary record (Swaddle et al., 2015). Worldwide expansion of human activities and infrastructure is increasing the exposure of terrestrial and marine environments to anthropogenic sound (Hildebrand, 2009; Barber et al., 2010; Shannon et al., 2015). Recent estimates suggest that more than 88% of the contiguous United States experiences elevated sound levels due to anthropogenic activities (Mennitt et al., 2013) and that the propulsion noise from ships elevated ocean sound levels in the 25-50 Hz band by 8-10 decibels (dB) from the mid-1960s to the mid-1990s, which then remained constant or showed a slight decline in the next decade (Andrew et al., 2011).

Most of the human activities that produce noise are common to terrestrial and marine ecosystems. These include transportation, exploration for and extraction of oil and gas, construction, mining, and military operations. Sounds from these sources can influence terrestrial and marine animals in similar ways. Although this report focuses on the cumulative effects of anthropogenic stressors, including sound, on marine mammals, recent terrestrial studies have evaluated consequences of noise exposure in ways that have not been thoroughly investigated in marine mammals, such as declines in foraging efficiency (owls [Mason et al., 2016; Senzaki et al., 2016] and bats [Siemers and Schaub, 2011; Bunkley and Barber, 2015]), heightened vigilance (prairie dogs [Shannon et al., 2014, 2016] and songbirds [Quinn et al., 2006; Ware

et al., 2015]), declines in reproductive success (Halfwerk et al., 2011), and altered predator–prey relationships (Francis et al., 2009). Insights from such terrestrial research help point to potential effects that deserve more attention in marine studies, and these studies can serve as guides for future efforts to determine whether noise affects marine mammals in similar ways.

Because research on land and at sea has largely progressed in isolation, we summarize the research status of each ecosystem separately below. Nevertheless, research in these disparate ecosystems provides a general framework for investigating how diverse noise stimuli present a multitude of challenges to wildlife.

When assessing the potential influence of a sound stimulus on an animal, determining whether the stimulus is within the organism’s sensory capabilities is critical. Most animals have developed sensory organs that allow them to detect either pressure waves or particle motion in the environment somewhere in the range of frequencies from below 10 Hz to above 180 kHz. They use this sensory input to communicate, orient, avoid predators, detect prey, and monitor their environment. If the stimulus falls outside of an animal’s sensory capabilities, i.e., higher or lower in frequency than its sensory organs can detect, the stimulus is likely not to have a direct effect (Francis and Barber, 2013), although indirect consequences of noise exposure are possible (e.g., Francis et al., 2009, 2012a).

There is a diverse array of anthropogenic sound sources, which vary in time, frequency, and intensity. Variation along these axes is not only relevant to the detection capabilities of an organism’s sensory system, but is also relevant to how organisms perceive sound stimuli. Sounds that are sudden, unpredictable, and loud often generate startle responses that can be similar to those associated with predation risk (see Figure 2.1). Sounds with these characteristics need not be

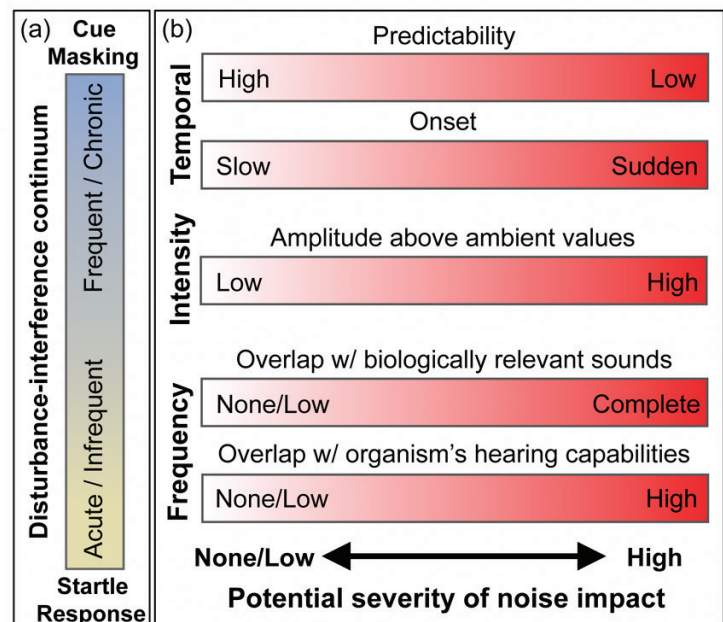
associated with real threats to elicit strong responses. For example, the acoustic startle response in mammals is stimulated by sounds that increase to 80-90 dB above the threshold of hearing in 15 milliseconds (Fleshler, 1965). Götz and Janik (2011) demonstrated that the startle responses triggered by these stimuli are aversive enough to lead grey seals (*Halichoerus grypus*) to show fear conditioning with strong flight responses. Other sounds that animals interpret as originating from either predators or aggressive conspecifics may evoke disturbance responses similar to those that function to defend against risk of predation (Frid and Dill, 2002) or potential intraspecific confrontation. Beaked whales (*Mesoplodon densirostris*) respond to military sonar through antipredator behavior in a manner similar to, albeit less intense than, their responses to playback of predator calls (killer whales [Tyack et al., 2011]). Military sonar sounds in the 1-10 kHz band are well below the frequencies used in beaked whale vocalizations and those at which they hear best, but these sonar signals share a similar duration and frequency structure with the stereotyped calls of killer whales. The stronger response of killer whales (*Orcinus orca*) than that of sperm whales (*Physeter macrocephalus*) or long-finned pilot whales (*Globicephala melas*) to playbacks of sonar signals (Miller et al., 2012; Harris et al., 2015) suggests that killer whales also perceive the sonar as threatening.

Sounds that are frequent, continuous, or chronic may not be perceived as threatening but nonetheless can affect animals by interfering with their ability to detect acoustic signals or cues, such as calls from conspecifics or sounds made by predators or prey (see Figure 2.1). The more overlap there is in spectral bandwidth between anthropogenic sounds and

those used by an organism, the more likely they are to interfere with detecting biologically important signals. Masking of relevant sounds has the potential to reduce an organism's auditory perceptual range, or listening area (Payne and Webb, 1971; Clark et al., 2009; Barber et al., 2010), and can interfere with an organism's abilities to detect, interpret, and respond to cues in their environment. As early as 1971, Payne and Webb (1971) suggested that shipping noise could have reduced by a factor of 6 the range over which one fin whale could hear another vocalizing at 20 Hz. Male fin whales (*Balaenoptera physalus*) repeat series of 20 Hz songs that can be detected at ranges of hundreds of kilometers (Croll et al., 2002). During the 20th century, when shipping noise increased, commercial whaling also reduced fin whale populations to 10% or less of their original numbers (Rocha et al., 2014). If females listen to these 20 Hz songs to find and select a mate, then this reduction in the range could interact with the decrease in abundance of whales to reduce the reproductive rate of this endangered species (Croll et al., 2002).

Anthropogenic sounds can also distract animals (Chan et al., 2010), causing them to divert their attention to a sound stimulus away from other important environmental stimuli, whether acoustic or via another sensory modality. For example, exposure to shipping noise disrupts feeding in shore crabs (*Carcinus maenas*) and causes them to take longer to find shelter after a simulated predatory attack, even if the attack does not involve acoustic cues (Wale et al., 2013). Finally, in addition to the sound characteristics, the behavioral context of the animal is critical to understanding how and why organisms respond to various anthropogenic sounds (Ellison et al., 2011).

**FIGURE 2.1** (a) The disturbance–interference continuum can range from acute or infrequent noise stimuli that will likely trigger startle, flight, or hide responses to frequent or chronic noises that interfere with cue detection. (b) The severity of an impact from a noise stimulus will depend on the temporal, intensity, and frequency features of the stimulus. SOURCE: Francis and Barber (2013).



## TERRESTRIAL STUDIES

The most extensive research on the effects of noise has been conducted on humans where noise has been shown to have cardiovascular, endocrinological, neurological, and auditory effects (Basner et al., 2014). Cognition is also impacted; chronic noise at levels typically found in residential areas can impair cognitive processes in children (Lercher et al., 2003). Whether marine mammals and other nonhuman animals experience similar consequences of noise exposure is less well known. Research in the last decade demonstrates many effects of noise for taxonomically diverse wildlife, but many potential consequences have not been adequately investigated.

Researchers have known for decades that acute intense sound events, such as those generated by aircraft overflight, gunshot, or chainsaws, can trigger immediate behavioral responses, such as hiding or fleeing (reviewed by Ortega [2012]). Additionally, early road ecology studies suggested that traffic noise reduces the density of vertebrates, especially birds, near roads (e.g., van der Zande et al., 1980; Reijnen et al., 1995; Kuitunen et al., 1998). However, these early studies were viewed with skepticism because confounding factors also associated with roads (e.g., mortalities from collisions with vehicles, changes in predator densities, and land cover changes) could also explain observed changes. Recent work has bolstered these early studies; research that isolates noise as a single environmental stimulus or introduces noise experimentally demonstrates that noise alone can explain declines in bird abundance and species richness (Bayne et al., 2008; Francis et al., 2009). More recently, experimental approaches that broadcast playbacks of traffic noise (McClure et al., 2013; Shannon et al., 2014) or energy-sector noise (Blickley et al., 2012a) over large areas have supported earlier observational studies and “natural” experiments. For example, at an important migratory bird stopover site McClure et al. (2013) constructed a 0.5 km “phantom road” where they simulated 12 vehicle pass-by events per minute for vehicles traveling ~70 km/h and alternated 4 days of noise “on” and 4 days of noise “off.” Noise “on” periods resulted in a one-quarter decline in bird abundance, and several species avoided areas exposed to the playback entirely. Another study experimentally introduced traffic noise via playback to prairie dog (*Cynomys ludovicianus*) colonies such that received levels at the center of colonies were approximately 52 dbA  $L_{eq}$  (re 20  $\mu$ Pa; Shannon et al., 2014).<sup>1</sup> In response to exposure, prairie dogs significantly reduced aboveground activity, and those that remained above ground increased visual vigilance at the expense of active foraging. There was no evidence of habituation to repeated exposure to the stimulus across the 3-month study period. Prairie dogs respond to an approaching human at greater distances in the presence of road noise than during quieter control periods (Shannon et al., 2016).

<sup>1</sup> See Box 2.1 for acoustic terminology.

### BOX 2.1 Acoustic Terminology

The decibel (dB) is a logarithmic scale for measuring a quantity with respect to a specified reference level.

The sound pressure level (SPL) in dB is equal to  $20 \log_{10}$  (sound pressure/reference pressure).

In water the reference pressure is 1  $\mu$ Pa and in air it is 20  $\mu$ Pa, where Pa is an abbreviation for a pascal or newton per square meter.

The sound energy level ( $SEL_{cum}$ ) is the cumulative sound energy level over the time interval of interest. The reference value for  $dB_{SEL}$  is 1  $\mu$ Pa<sup>2</sup>-s.

$SPL_{pk}$  is the peak SPL encountered over the time interval of interest.

$SPL_{p-p}$  is the maximum difference between the compression and rarefaction phases associated with an impulsive sound source.

$SPL_{RMS}$  (reported in  $dB_{RMS}$ ) is the root mean square SPL measured over an appropriate time interval. The value of a  $SPL_{RMS}$  for a transient signal is influenced by the time interval over which the  $SPL_{RMS}$  is calculated.

dba is a measure of the SPL with different frequencies weighted by the frequency-dependent sensitivity of human hearing.

$L_{eq}$  is the steady SPL that over a given period of time has the same total energy as the energy in the varying sound of interest. It can be reported as either dB or dba.

Impulsive noise is defined by short duration, rapid rise, and broad frequency content.

The costs in reduction of habitat are obvious for species that avoid noisy areas entirely or that decline in abundance with noise exposure, but there also may be costs for those individuals that remain in noisy areas. For example, the number of males in courtship displays (leks) of greater sage-grouse (*Centrocercus urophasianus*) declines in response to experimental playback of natural gas compressor noise or energy-sector truck traffic (Blickley et al., 2012a). Individuals that remain in the leks exposed to noise experience elevated stress hormone levels relative to those in leks that were not exposed to playbacks (Blickley et al., 2012b). Experimental playback of traffic noise also increases stress hormones in



female wood frogs (*Lithobates sylvaticus*) and appears to impair navigation toward chorusing males at breeding ponds (Tenessen et al., 2014). Whether mediated by physiological stress responses or due to other factors, avian reproductive success can decline in response to noise. The most obvious of these declines in success include examples in which male birds occupying noisy territories have lower pairing success than individuals in areas that are less noisy (Habib et al., 2007; Gross et al., 2010). In other cases, birds breeding in noisy areas lay fewer eggs (Halfwerk et al., 2011) or fledge fewer young (Kight et al., 2012). It is unclear whether the lower breeding success is due to the influence of noise on these pairs or if the lower success is due to less fit birds being marginalized to the noisy habitat. If the latter, and if there remain better territories for the more fit pairs, then it likely will not lead to population-level effects.

Even relatively short exposure (i.e., approximately 4 days) to experimentally introduced traffic noise causes declines in a body condition index (i.e., mass-to-wing chord length ratio) among migrating songbirds (Ware et al., 2015). This decline in health appears to be mediated by a foraging–vigilance trade-off; in noisy conditions, birds increase visual vigilance in response to impaired acoustic surveillance capabilities, but decrease time spent actively foraging. Frid and Dill (2002) argue that disturbance generally causes animals to reduce time allocated to other critical activities, such as foraging, which may pose increasing fitness costs as disturbance increases. Noise can also directly impair foraging by masking the acoustic cues used by predators to locate prey, such as in gleaning bats (e.g., Schaub et al., 2008; Siemers and Schaub, 2011). Additional evidence from a comparative study examining responses of 183 bird species suggests that birds with animal-based diets are more sensitive to human-made noise than birds with plant-based diets, perhaps due to an underappreciated use of hearing alongside vision when hunting (Francis, 2015). Regardless of the precise mechanisms responsible for predator sensitivities to noise, decreases in predator abundance, or decreases in predator efficiency, can have broader ecological consequences. For example, declines in common nest predators in areas exposed to energy-sector noise results in higher nesting success among several songbird species that persist in noisy areas (Francis et al., 2009). Similarly, noise-induced declines in the abundance of species that perform key ecological functions, such as the seed-dispersing activities of Woodhouse’s scrub-jay (*Aphelocoma woodhouseii*), can trigger the reorganization of foundational species (Francis et al., 2012b; see “Indirect Effects of Sound on Marine Mammals” on p. 31).

## MARINE STUDIES

This section provides a selection of studies showing the anatomical, physiological, and behavioral responses of marine mammals to different intensities of sound. It begins with an overview of U.S. regulations that established criteria and

thresholds for various levels of acoustic disturbance of marine mammals that correlate with the legal definition of a take.<sup>2</sup>

### Criteria, Thresholds, and Takes

While shock waves from underwater explosions have resulted in mechanical trauma in whale ears (Ketten et al., 1993), the most severe acoustic injury associated with intense sound waves is a permanent hearing threshold shift (PTS)—a loss of hearing within a particular frequency range that is not reversible. Sounds not intense or energetic enough to cause PTS can cause a temporary threshold shift (TTS)—reduced hearing sensitivity within a particular frequency range that lasts for a period of minutes to hours, but recovers to its prior level of sensitivity. Sounds at all levels can cause behavioral changes as long as they are audible. Animals can reduce the physiological impact of sound through behaviors in which they move down the sound gradient. They can also respond to noise masking relevant sounds through behavioral changes.

The prohibitions against taking marine mammals under the Marine Mammal Protection Act described in Appendix B focus on two kinds of takes: Level A takes that have the potential to injure an animal, and Level B takes that harass animals by disrupting behavior. In spite of the early focus on the global scales at which shipping noise might mask fish and whale communication, these regulatory definitions led research in the United States to focus on identifying how intense sounds may injure animals or disrupt their behavior. The National Marine Fisheries Service (NMFS) has defined acoustic injury as a PTS. Studies of the toxic effects of chemicals typically determine the dose that kills half of a sample, whereas studies that involve intentional injury or death of marine mammals are rarely permitted. This led to the development of experiments that use TTS as a reversible indicator of risk of injury.

For sound sources, two critical measures are sound pressure level (SPL) measured in dB re 1  $\mu$ Pa, a measure of sound intensity, and sound exposure level (SEL) measured in dB re 1  $\mu$ Pa<sup>2</sup>-s, a measure of the energy received due to the aggregate exposure to all sound sources over a defined interval of time. SEL accumulates the energy in short, intense sounds, such as pile driving, with longer, lower-level sounds, such as shipping. One critical decision for SEL calculations is the duration over which energy is accumulated. Several different integration times are important for marine mammals. The mammalian ear integrates sound energy over a period of about 200 milliseconds (msec) (Green, 1985), so 200 msec can be used as a maximum integration time to estimate apparent loudness of a sound. The animals are more likely to react behaviorally to short, intense sounds,

<sup>2</sup> Defined in the Marine Mammal Protection Act as “harass, hunt, capture, or kill, or attempt to harass, hunt, capture, or kill” (16 U.S.C. § 1362; see also 50 C.F.R. § 216.3), and in the Endangered Species Act as “harass, harm, pursue, hunt, shoot, wound, kill, trap, capture or collect” (16 U.S.C. § 1532 (19)).

whereas physiological effects are greater for equivalent energy delivered as long, less intense sounds. To estimate effects of noise exposure on the sensitivity of hearing, longer integration times are required. For humans, the 8-hour daily exposure in a workplace is commonly used as an integration time. There is no obvious equivalent for marine mammals in the wild, but the longer SEL accumulates sound energy, the higher the value. Most animals go through daily cycles of behavior, so a 24-hour integration time has been adopted (e.g., Southall et al., 2007; NMFS, 2016a), but the critical point for assessing noise impact on hearing is whether the animal has long enough time at low enough exposure levels for the auditory system to recover from any temporary effects of noise exposure (Ward et al., 1976). Thus, although there is an appropriate energy metric for aggregate exposure to sound sources, it is more effective as a physical measure than as a predictor of aggregate impact on marine mammals. Predicting impacts on hearing requires integrating SEL until the animal has a long enough period of relative quiet to recover.

Southall et al. (2007) conducted a very thorough study of the available science and laid the groundwork for more recent updated approaches to determining onset of TTS and PTS (e.g., Finneran, 2016). They categorized marine mammals into five hearing groups: low-, mid-, and high-frequency cetaceans; pinnipeds in water; and pinnipeds in air. For each hearing group, they established the SPL and the SEL that would result in PTS or behavioral disturbance for three categories of sounds: single pulses, multiple pulses, and non-pulses. NMFS recently published acoustic thresholds for the onset of TTS and PTS (NMFS, 2016a) that aim to be based on the best current available science. These guidelines have separate PTS thresholds for impulsive and nonimpulsive sounds for five categories of marine mammals: low-, mid-, and high-frequency cetaceans; phocids; and otariids.<sup>3</sup> For each marine mammal category two thresholds are given for impulsive sounds: one for peak sound pressure level ( $SPL_{pk}$ ) and one for cumulative sound exposure level ( $SEL_{cum}$ ) accumulated over 24 hours; and one threshold is given for nonimpulsive sounds: the cumulative sound exposure level ( $SEL_{cum}$ ) accumulated over 24 hours. The  $SPL_{pk}$  ranges from 202 dB re 1  $\mu Pa$  for high-frequency cetaceans to 232 dB re 1  $\mu Pa$  for otariid pinnipeds in water. The SEL values for impulsive sounds range from 155 dB re 1  $\mu Pa^2$ -s for high-frequency cetaceans to 203 dB re 1  $\mu Pa^2$ -s for otariids, and the threshold values for nonimpulsive sounds range from 173 dB re 1  $\mu Pa^2$ -s for high-frequency cetaceans to 219 dB re 1  $\mu Pa^2$ -s for otariids.

The Level B behavioral harassment criteria used by NMFS for most situations are thresholds of  $SPL_{RMS}$ <sup>4</sup> of 160

dB re 1  $\mu Pa^5$  for impulsive sounds and 120 dB<sub>RMS</sub> for non-impulse sounds.<sup>6</sup> NMFS classifies a variety of sonar signals as impulsive for Level B criteria, but as nonimpulsive for Level A criteria (NMFS, 2016a). These thresholds are treated as all-or-nothing thresholds, with all animals exposed above the threshold treated as harassed and no animals below the threshold considered to be harassed. The primary exception involves estimates of “takes” by Navy sonar, which are estimated using a behavioral response function developed by Finneran and Jenkins (2012) to estimate the proportion of animals receiving a given sound level that will show the criterion behavioral response. This response function has a sigmoidal shape in which the probability of response varies more gradually as a function of dosage than in the step function threshold. The Navy has adopted more conservative criteria for behavioral response thresholds for beaked whales (all-or-nothing threshold of 140 dB<sub>RMS</sub>) and for harbor porpoises (all or nothing threshold of 120 dB<sub>RMS</sub>) exposed to sonar (Finneran and Jenkins, 2012).

In order to determine received sound levels, the propagation of a sound from a point source can be modeled to determine the spatial distribution of the sound field. The level of exposure can then be determined by combining this with an estimate of the animals’ distribution. There is generally much greater uncertainty associated with estimating the distribution of animals than the sound field. The principles of underwater sound propagation are relatively well understood (Keenan, 2000), whereas the information available on the movements and distribution of marine mammal species is highly variable geographically and by species. Spatially explicit marine mammal density estimates have been calculated based on transect-based (typically visual) surveys (Hammond et al., 2002; Redfern et al., 2006; Roberts et al., 2016) and telemetry data (Aarts et al., 2008; Whitehead and Jonsen, 2013), as well as through the use of habitat-based models (Forney, 2000; Redfern et al., 2006). More complex individual-based animal three-dimensional movement models have also been used to estimate the  $SEL_{cum}$  for individuals (Frankel et al., 2002; Gisiner et al., 2006; Donovan et al., 2013).

Takes have typically been calculated based on determining the 190 dB<sub>RMS</sub> or 180 dB<sub>RMS</sub> (Level A) or the 160 dB<sub>RMS</sub> or 120 dB<sub>RMS</sub> (Level B) isopleth<sup>7</sup> and moving that area through space as the source moves. The total area encompassed over the course of 24 hours is multiplied by the density of a given marine mammal species in that general geographical area at the time of year of the activity to produce a single value take estimate for that species for that 24-hour period. However, a hard threshold typically based

<sup>3</sup> Low-frequency cetaceans are all the baleen whales. High-frequency cetaceans are all porpoises, river dolphins, pygmy and dwarf sperm whales, all dolphins in the genus *Cephalorhynchus*, and two species of *Lanenorhynchus*, *L. australis* and *L. cruciger*. Mid-frequency cetaceans are all the odontocetes not in the high-frequency group.

<sup>4</sup> RMS is root mean square.

<sup>5</sup> All underwater acoustic intensity dB are re 1  $\mu Pa$ . This reference level will not be repeated for future dB.

<sup>6</sup> See [http://www.westcoast.fisheries.noaa.gov/protected\\_species/marine\\_mammals/threshold\\_guidance.html](http://www.westcoast.fisheries.noaa.gov/protected_species/marine_mammals/threshold_guidance.html).

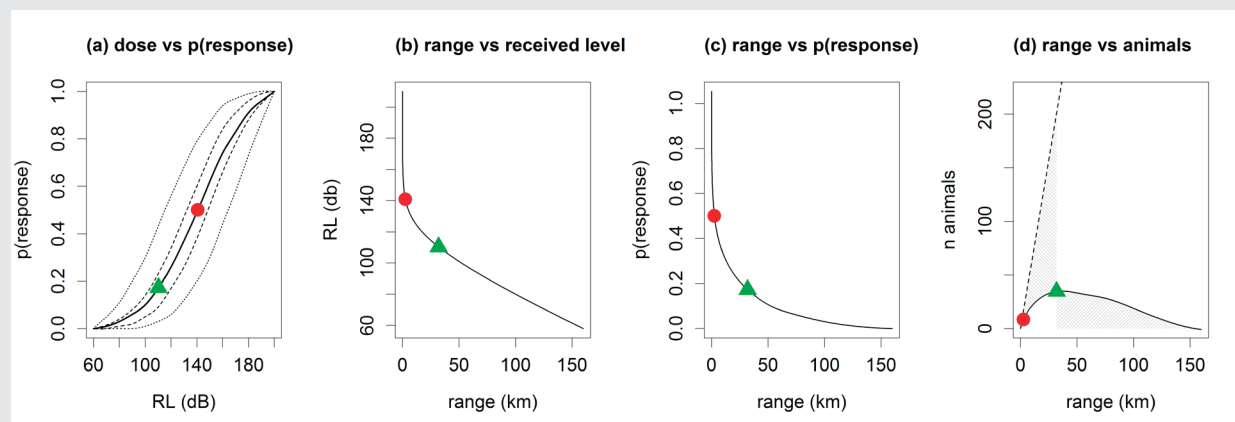
<sup>7</sup> Typically a circle centered at the source with a radius equal to the distance at which the signal falls to the criterion value.

## BOX 2.2

## Estimating the Number of Behavioral Takes from a Dose–Response Function

Behavioral dose–response functions based on experimental data are now available for a number of marine mammal species (reviewed later in this chapter). One approach for determining the threshold for response is to use the received sound pressure level (RL) at which the probability of response is 0.5, the “ $RL_{p50}$ .” For example, this is the origin of the 120  $dB_{RMS}$  Level B harassment criterion used by National Marine Fisheries Service (NMFS) for nonpulse sounds (NRC, 1994, p. 19). There are two problems with this approach. First, using  $RL_{p50}$  as a threshold typically results in a substantial underestimate of the number of takes implied by the dose–response function. Second, this procedure ignores uncertainty in the dose–response function, as well as in the source level, propagation model, and density estimate. These issues are illustrated here using the fitted dose–response function from Miller et al. (2014) for killer whales showing onset of avoidance behavior in a controlled exposure experiment that used a scaled mid-frequency sonar source as the stimulus (see Box Figure 1a).

To illustrate the first issue, the average estimated dose–response function is used (solid line in Box Figure 1a); a stationary single-frequency 6 kHz source is assumed, with a source level of 210 dB re 1  $\mu Pa$  at 1 m and a simple propagation model (spherical spreading and frequency-dependent absorption; see Box Figure 1b). The resulting probability of response as a function of range from the source is shown in Box Figure 1c. If the spatial distribution of animals is independent of the source location, then, on average, the number of animals at each range will increase linearly with range (see Box Figure 2). The expected number of animals responding is the number at each range multiplied by the probability of response at that range (see Box Figure 1d), integrated over all ranges. Assuming a density of one animal per  $km^2$  gives an expected take of 3,215 animals. If, instead, a threshold is set at  $RL_{p50} = 141$   $dB_{RMS}$  (the red dot on Box Figures 1a-d), this translates to a threshold range of 2.63 km, and an estimated take of  $\pi 2.63^2 = 21.8$  animals, more than two orders of magnitude too low.



**Box Figure 1** (a) Example dose–response function from Miller et al. (2014): solid line is posterior mean; dashed lines show 50% CI; dotted lines 95% CI. Red dot shows received level corresponding with probability of response of 0.5 ( $RL_{p50}$ ); green triangle shows effective received level (ERL; see box text). (b) Range versus received level from a simple transmission loss model. (c) Dose–response model reexpressed in terms of range. (d) Expected number of animals as a function of range in 1 km bins (dashed line); expected number of responding animals as a function of range in 1 km bins (solid line). ERL is at the range (green triangle) where as many animals are expected to fail to respond within this range as are expected to respond outside this range (i.e., the two shaded regions have the same area).

If a fixed threshold must be used (e.g., for reporting), the correct take value can be obtained by using the “effective RL” (ERL)—this is the RL corresponding to the range at which the number of animals expected to respond at larger ranges is balanced by the number failing to respond at smaller ranges (analogous to the effective detection radius in Buckland et al. [2001, Ch. 5]). In this example, the ERL is 110  $dB_{RMS}$  corresponding to a range of 32.0 km (green triangle in Box Figures 1a-d).

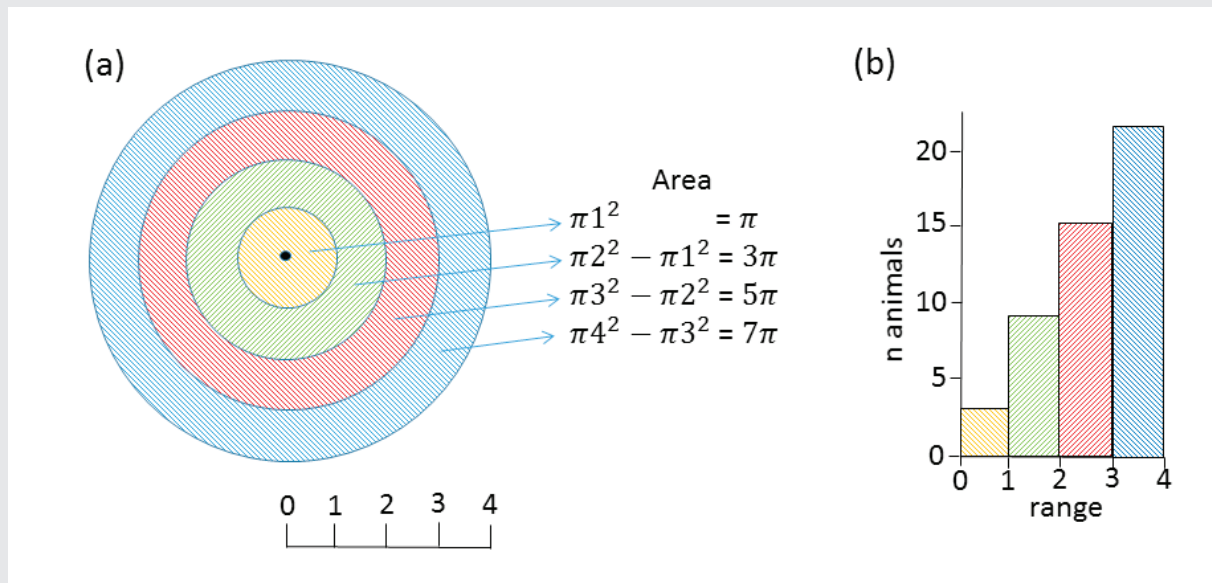
Regarding the second issue, uncertainty on inputs can be translated into uncertainty on take estimates readily through stochastic simulation. Regulators may then choose the level of risk they wish to use in deciding whether to permit an activity (e.g., Taylor et al., 2000). For simple cases, simulation is unnecessary: for example, if it is desired to include only uncertainty in the dose–response function, the above calculations can be repeated using the 2.5% and 97.5% quantiles (dotted lines in Box Figure 1a), yielding a 95% confidence interval (CI) of 313 to 9,910 takes. However, there are often multiple sources of uncertainty and other complications, making simulation the best approach.

To allow the calculations outlined here, researchers should provide sufficient information to allow reconstruction of their dose–response functions, and uncertainty about these functions. For example, Miller et al. (2014) provide a table of quantiles for probability of response over a range of doses. Unfortunately, this is not common practice, and only  $RL_{p50}$  values are reported for many studies (see main text). The current NMFS Level B harassment criterion of  $120 \text{ dB}_{\text{RMS}}$  was based on reported levels from the 1980s at which approximately 50% of gray and bowhead whales responded; Malme et al. (1984) reported dose–response functions for gray whales exposed to experimental oil exploration and production-related activity that could be used to calculate the extent to which the  $120 \text{ dB}_{\text{RMS}}$  criterion may underestimate the number of whales taken.

**Finding 2.1:** Current methods for calculating behavioral take based on animals within a range determined by the 50% probability-of-response threshold lead to potentially significant underestimates of the total number of animals taken. An “effective received level” can be calculated that corrects the take estimate.

**Finding 2.2:** Take numbers are currently requested and approved based on a point value estimate. Changes in transmission patterns of sound in the ocean, distribution of animals, variable responsiveness of individual animals, and temporal, spatial, and social determinants of response all create uncertainty in the number of animals taken by sound. Thus, any effort to include measures of uncertainty, such as confidence intervals for estimates of predicted take, as required under the Marine Mammal Protection Act, would be more consistent with the state of our knowledge than providing a single number for takes.

Calculations of take are very sensitive to the shape of the dose–response function at low levels of dose, because this corresponds to larger distances, where relatively more animals are exposed. Increased realism can be introduced by accounting for animals’ auditory sensitivity, where known (Miller et al., 2014; see next section), and by experimental information about how RL and range interact to affect animals’ responses.



**Box Figure 2** (a) The areas of rings of fixed width increase linearly with their distance (range) from a central point. (b) If the point is located at random with respect to animals then the number of animals within each ring is, on average, proportional to the area of the ring, and so also increases linearly with range.

on a 50% probability-of-response criterion can significantly underestimate the number of animals taken. Even though the probability of an exposed animal responding is smaller outside of the impact threshold than inside it, the greater number of animals experiencing low exposures may overwhelm this difference in risk and ultimately result in more animals being affected at distances that are greater than the ones currently considered for monitoring and mitigation (see Box 2.2).

Models that estimate the number of “takes” do not describe how this “taking” may affect the population, which requires further understanding how these impacts on individuals affect their survival and reproduction. Changes in these vital rates can then be incorporated into a dynamic population model to estimate population-level impacts (Thompson et al., 2013b; New et al., 2014; King et al., 2015).

### Auditory Sensitivity

Studying what sounds cause masking or TTS demands understanding how the sensitivity of hearing varies with frequency, which is achieved by measuring audiograms of different species. It has become apparent from studies on marine mammal hearing that their auditory capabilities differ considerably among species. Underwater audiograms have been determined using either behavioral or physiological methods for 18 species of cetaceans (14 in the mid-frequency hearing group, 4 in the high-frequency hearing group, and none for baleen whales) and 11 species of pinnipeds and other marine carnivores (6 phocids and 5 in the combined otariids, sea otters, and walrus) (Mooney et al., 2012; Finneran, 2016). Behaviorally determined audiograms are available for individuals from four of the five marine mammal groups (mid- and high-frequency cetaceans and phocids and otariids in water). Within each group, the audiograms were combined to arrive at a best-fit composite audiogram for that group as shown in Figure 2.2. No hearing measurements have been made on low-frequency cetaceans. Hence the estimated hearing thresholds were calculated based on data from Cranford and Krysl (2015), Houser et al. (2001), Parks et al. (2007a), and Tubelli et al. (2012) as described by Finneran (2016).

The curves for all hearing groups follow a typical mammalian pattern in which there is a best frequency of hearing. Below the best frequency there is a gradual falloff in hearing sensitivity for low frequencies and above there is a much more rapid falloff in hearing sensitivity for high frequencies. These curves represent the best available peer-reviewed data. It is recognized that the curves are based on small numbers of animals, and only a few species are surrogates for each entire hearing group. No data were available for low-frequency cetaceans, so this estimate is based on correlation and assumptions.

**Finding 2.3:** A behavioral dose–response relationship can be determined without knowing the subject’s audiogram.

However, understanding the physiological effects of sound from TTS through PTS requires an audiogram. For baleen whales physiological sound impacts are estimated based on modeling of the skull, estimated historical ocean noise thresholds, and data from other cetacean hearing groups. An audiogram from at least one species of baleen whale would be beneficial in understanding the effects of anthropogenic sound on baleen whales.

### Permanent and Temporary Threshold Shift

If sounds are loud enough, they can lead to TTS. As indicated by the name, the hearing threshold returns to baseline in minutes to hours after the cessation of the stimulus, depending on the amount of TTS. The energy in the sound that generates a TTS is expressed as the SEL and measured in dB re  $1\mu\text{Pa}^2\text{-s}$ . TTS and the growth in TTS with increasing SEL have been measured in four cetacean and three pinniped species. The weighted TTS threshold ranged from 153 dB<sub>SEL</sub> for high-frequency (HF) cetaceans to 193 dB<sub>SEL</sub> for otariids in water (Finneran, 2016). TTS can reduce an animal’s communication space and its abilities to detect predator and prey during the minutes to hours it takes for the threshold to return to its preexposure state. It is arguable whether this temporary reduction in hearing sensitivity represents an injury in itself. Kujawa and Liberman (2006) demonstrated in laboratory mice that noise exposures that cause only TTS may cause pathological changes that render the auditory system more vulnerable to age-related hearing loss. However, TTS is not considered an injury in the U.S. regulatory framework. No experiments have investigated the long-term effects of TTS in marine mammals, or have tried to create a PTS in a marine mammal (but see Kastak et al., 2008). Based on data from terrestrial mammals, the onset of PTS has been set by Southall et al. (2007) at an SEL that would produce 40 dB of TTS. Thresholds for PTS can then be calculated by knowing the threshold for onset of TTS and estimating the growth in TTS with increasing sound levels. For impulsive sounds, TTS in laboratory animals increases with a slope of 2.3 dB of TTS per dB of noise, suggesting a minimum of 15 dB SEL above TTS onset for PTS caused by impulsive sound. Similarly the slope for nonimpulsive sounds, based on human data, is 1.6 dB of TTS per dB of noise or conservatively rounded down to 20 dB SEL above TTS onset for PTS (Southall et al., 2007). The amount of sound energy required to produce injury based on TTS data has been summarized by Southall et al. (2007) and the NMFS (2016a) for each of the marine mammal hearing groups. The HF cetaceans have the lowest estimated PTS threshold, 173 dB<sub>SEL</sub> for nonimpulse sounds, but the predicted range of injury is not necessarily much less than for the higher thresholds at lower frequencies, because lower frequencies propagate better than higher frequencies. The sound energy required to cause injury judged by PTS is so great that zones of injury for even intense sound sources such as airguns and naval sonars are estimated at

less than 1 km for all but a few cases. For example, a single one-second ping from one of the loudest naval sonars, the 53C, would be above the PTS threshold for HF cetaceans out to a range of 1 km given omnidirectional propagation, while it would be above the PTS threshold for mid-frequency and low-frequency cetaceans for less than 100 m from the source. These ranges suggested monitoring and mitigation measures that focused on detecting animals close to the source ship and suggest that the probability of marine mammals experiencing PTS from anthropogenic activities will likely be sufficiently low as to preclude any population-level effects.

**Finding 2.4:** Studies of noise levels that cause TTS and the growth in TTS with increasing noise are used to predict the occurrence of permanent hearing loss. Currently data exist for one species of otariid, two species of phocids, two species of mid-frequency (delphinid) cetaceans, and two species of high-frequency (phocoenid) cetaceans. Only a few individuals (one to five) of each species have been tested and within hearing groups there is wide variation in TTS onset and growth with increasing levels of noise. This variation indicates that the physiological effects of sound cannot be generalized based on testing of a few species of marine mammals, and more species need to be studied.

### Behavioral Responses

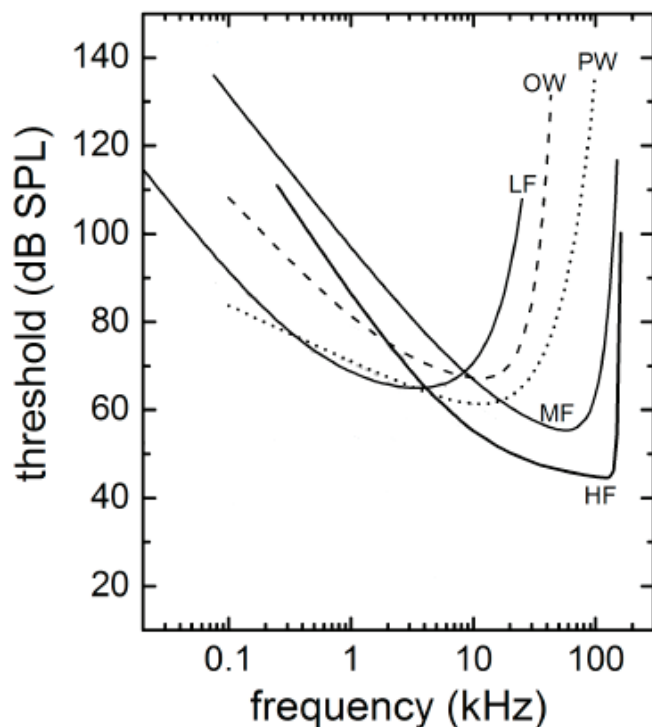
Just about the time that data from TTS studies started to suggest limits on the ranges at which sound could injure marine mammals, evidence began to accumulate that lethal strandings of a poorly known group of whales called beaked whales coincided with naval sonar exercises. Frantzis (1998) described an atypical mass stranding where 12 Cuvier's beaked whales (*Ziphius cavirostris*) stranded over 38 km of a Greek bay over 2 days when a naval sonar was being tested. Issues with mid-frequency sonar came to national attention in the United States following the stranding of 17 cetaceans and the death of 7 during a naval sonar exercise on March 15-16, 2000, in the Northeast and Northwest Providence Channels of the Bahamas Islands. A joint U.S. Navy and U.S. Department of Commerce report (Evans and England, 2001) determined that "the cause of this stranding event was the confluence of the Navy tactical mid-range frequency sonar and the contributory factors . . . a strong surface duct, unusual underwater bathymetry, intensive active use of multiple sonar units over an extended period of time, a constricted channel with limited egress, and the presence of beaked whales that appear to be sensitive to the frequencies produced by these sonars." Usually when whales mass strand, they strand together at the same time. D'Amico et al. (2009) cataloged 12 atypical mass strandings of beaked whales that coincided with naval exercises that may have transmitted sonar. These strandings represent the most obvious and clearly lethal impact of anthropogenic sound on marine mammals.

Cox et al. (2006) reported on a workshop convened by

the U.S. Marine Mammal Commission in 2004 to synthesize the current understanding of beaked whale strandings and to recommend research initiatives to determine the most probable causal pathways between transmission of mid-frequency sonar and strandings of beaked whales. The consensus from that meeting, which has not changed to date, was that a behavioral response occurring under a combination of contributory conditions was the progenitor of the strandings and the associated pathologies. Extensive behavioral, physiological, and anatomical research has been conducted over the last decade and a half to better understand not only this extreme example of the effect of anthropogenic sound on marine mammals but that of less dramatic chronic and episodic exposures. Some of the beaked whales that stranded during sonar exercises showed gas and fat emboli apparently caused by a decompression sickness (DCS) (Jepson et al., 2003; Fernández et al., 2005). Fernández et al. (2012) reported on three beaked whales that appear to have died at sea from decompression symptoms and then washed ashore, suggesting that whales do not just die from stranding, but may die directly from DCS at sea. These results have reinvigorated analysis of the diving physiology of deep-diving whales to better understand how they manage N<sub>2</sub> and other gases under hydrostatic pressure (Hooker et al., 2012). Current thinking is that anthropogenic noise can in some situations trigger behavioral reactions that may interfere with the ways whales manage gas under pressure and/or may cause whales to strand and die.

### Dose-Response Relationships

This understanding that sound can trigger behavioral responses that may lead to injury or death motivated research to better define the relationship between exposure to sound and behavioral responses that could lead to effects that regulators view as "Level B takes" under the U.S. Marine Mammal Protection Act. Managing the impacts of underwater sound requires an understanding of the effect of this disturbance on individuals and the risk to the population. Dose-response relationships have commonly been used in toxicology to relate the level of exposure to the probability of a particular response or to the elicitation of different responses with differing levels of severity. When we discuss the first case, we will call these dose-p(response) relationships, and when we discuss the latter, we will call these dose-s(response) relationships. Toxicologists typically study genetically inbred laboratory animals under conditions designed to minimize stress, narrow the diversity of subjects, and control all variables except the experimental one to provide the strongest baseline condition for experimental detection of effects of known dosages of a single stressor. Behavioral responses of marine mammals are highly context dependent, being influenced by age (Houser et al., 2013a), sex (Symons et al., 2014), behavioral state (Sivle et al., 2012; Goldbogen et al., 2013), location (Tyack and Clark, 1998),



**FIGURE 2.2** Composite audiograms obtained through behavioral testing except for LF that was calculated. NOTE: HF = high-frequency cetaceans; LF = low-frequency cetaceans; MF = mid-frequency cetaceans; OW = otariids, walrus, and sea otter in water; PW = phocids in water. Thresholds are expressed in  $\text{dB}_{\text{RMS}}$  re  $1 \mu\text{Pa}$ . SOURCE: Adapted from Finneran (2016; peer reviewed for NMFS [2016a]).

prior exposure resulting in habituation (Houser et al., 2013b) or sensitization (Kastelein et al., 2011), and individual sensitivities. Most experimental studies on the effects of an anthropogenic sound stimulus on marine mammals have been conducted with subjects drawn from wild populations. If the subjects are a representative sample of the contexts that affect responses, then the dose–response functions and other behavioral observations should be appropriate for the populations under study. Behavioral dose–response functions for three species were obtained from captive animals, and all TTS research has been done with captive animals.

One approach to estimating dose–response functions assumes a specific functional relationship between exposure and response. Many methods to estimate dose–response functions often assume a sigmoidal shape with a monotonic relationship between exposure and response. Some toxicological dose–response curves do not have this functional form (Calabrese, 2005), and we cannot assume that behavioral responses to sound will have a sigmoidal shape. Most dose–p(response) analyses assume a minimum exposure below which no response is expected and a maximum

exposure above which all of the animals are assumed to respond. In the case of behavioral responses to sound, the minimum exposure can be assumed to occur at the limits of detectability as determined by the frequency-dependent audiograms. Ellison et al. (2011) emphasize the importance of context and environment in modulating the behavioral response to a given received level. Context includes current behavioral state and past exposure to the signal, and environment includes all the environmental factors that influence the signal-to-noise ratio and may result in a masked response threshold. DeRuiter et al. (2013) provided evidence that animals are more likely to show a response to a nearby signal at lower intensity than they do to a signal coming from farther away but with a greater received level. For example, tagged Cuvier’s beaked whales responded to the simulated sonar at received levels as low as  $89 \text{ dB re } 1 \mu\text{Pa}$  but did not respond to sonar from an active naval ship farther away with a received level up to  $106 \text{ dB}$ .

Within the U.S. regulatory structure, Level A takes (injury) are equated with exposures resulting in PTS, whereas both TTS and behavioral disruption are regarded as Level B takes. Level B behavioral takes are generally considered to be less severe than Level B physiological takes (TTS). It is likely that, at the maximum exposure for behavioral response, animals may already be experiencing TTS. Note that in the case of the beaked whale strandings, exposures well below those required for PTS did disrupt behavior in a way that led to the death of the animals that stranded, so the logic of this regulatory structure is questionable for some settings.

The importance of understanding how sonar initiates a behavioral response in cetaceans has been the impetus to several studies that have developed empirical dose–p(response) curves linking the probability of a behavioral response to a given sound exposure. Finneran and Jenkins (2012) constructed a behavioral response curve that is used by the U.S. Navy and its regulator to estimate the proportion of animals receiving a given sound level that will show the criterion behavioral response. The Finneran and Jenkins (2012) curve is based on a mathematical formula following Feller (1968) and based on data from Finneran and Schlundt (2004), Fromm (2009), and Nowacek et al. (2004). The threshold response level is set at  $120 \text{ dB}_{\text{RMS}}$  and the level at which the probability of response is 0.5 is at  $165 \text{ dB}_{\text{RMS}}$ , resulting in an asymptotic value of approximately  $200 \text{ dB}_{\text{RMS}}$  for 100% response.

Another approach used to estimate probabilistic dose–p(response) functions assumes that the distribution of the probability of responses as a function of exposure is Gaussian (truncated at a lower and upper SEL) and estimates the mean and variance for this relationship (Antunes et al., 2014; Miller et al., 2014). Hierarchical Bayesian models can be used to estimate dose–p(response) functions, assuming that each individual has a response threshold, and that the distribution of thresholds across the population is (truncated)

normal. Observed levels associated with responses are then used to estimate the population mean and variance, which together with the minimum and maximum values can be used to estimate the dose–p(response) function.

Figure 1a in Box 2.2 shows the dose–p(response) function for killer whales exposed to 1–2 kHz and 6–7 kHz sonar, where the 50% response was at  $141 \pm 15$  dB<sub>RMS</sub> with thresholds ranging from 94 to 164 dB (Miller et al., 2014). Similar dose–p(response) functions have been determined for exposure to sonar for Blainville’s beaked whale (RL<sub>p50</sub> at 150 dB<sub>RMS</sub>; Moretti et al., 2014), long-finned pilot whales (RL<sub>p50</sub> at approximately 170 dB<sub>RMS</sub>; Antunes et al. 2014), a captive harbor porpoise (RL<sub>p50</sub> at 124–144 dB<sub>RMS</sub> depending on sonar type; Kastelein et al., 2013), captive bottlenose dolphins (RL<sub>p50</sub> at 162 dB<sub>RMS</sub> on first trial and 174 dB<sub>RMS</sub> by tenth trial; Houser et al., 2013b), and captive California sea lions (RL<sub>p50</sub> at 147 dB<sub>RMS</sub> increasing to 158 dB<sub>RMS</sub> when sensitive juveniles [ $<2$  years] were removed; Houser et al., 2013a). The responses used to establish the response function varied: presence or absence of a foraging dive in a 30-minute period for Blainville’s beaked whale where the stimulus was actual naval sonar operations; a change in two-dimensional movement tracks for long-finned pilot whales where the stimulus was simulated sonar in a controlled exposure experiment (CEE); an avoidance reaction as determined by an expert group consensus for killer whales where the stimulus was simulated sonar in a CEE; a sudden change in swimming speed or direction for the captive harbor porpoise where the stimulus was synthesized sonar signals; and primarily based on a statistically significant change in breathing during a 30-second period for captive bottlenose dolphins and California sea lions where the stimulus was simulated sonar. These studies have generally been based on relatively small sample sizes, in some cases a single animal, but have indicated that the responses are dissimilar enough that taxon-specific rather than a generic odontocete exposure–response relationship is necessary for impact assessments (Antunes et al., 2014; Harris et al., 2015). The responses of captive bottlenose dolphins also suggested that they may be capable of habituation to repeated exposures (Houser et al., 2013b), in contrast to California sea lions that did not demonstrate habituation under a similar experimental protocol (Houser et al., 2013a). This does not mean that pinnipeds do not habituate to sounds under other circumstances, but simply that they did not show habituation under this experimental protocol.

The responses used to establish the above-referenced dose–p(response) functions have varied in severity and most of them would be considered minor on the 10-point severity scale presented by Southall et al. (2007). The responses noted above range in severity from 2 (brief or minor changes in respiration rate) for captive bottlenose dolphins and California sea lions, to 3 (minor changes in locomotion speed, direction, and/or dive profile but no avoidance of sound source) for captive harbor porpoises and long-finned pilot whales, to 4 (moderate changes in locomotion speed, direction,

and/or dive profile but no avoidance of sound source) for Blainville’s beaked whale, to 6 (minor avoidance of sound source) for killer whales. These experiments are designed so as not to harm the subjects. In this sense the experiments have succeeded, but it may take some extrapolation to predict thresholds for more severe responses if those are more relevant for a specific regulatory regime. Miller et al. (2012a) reviewed data from dose–s(response) experiments on killer, long-finned pilot, and sperm whales and reported that there was no consistent relationship between exposure and the severity score assigned to a response. It was noted that just-audible signals could result in responses of severity levels between 0 and 7. This variation highlights how different the responses of different individuals may be to similar acoustic levels of exposure. Ellison et al. (2011) suggest that contextual factors cause variability in responsiveness at low received levels, but annoyance/disturbance responses may be evoked in most animals over a relatively narrow range of high levels of acoustic exposure. This argues against assuming that the distribution of responses is likely to fit a symmetric normal distribution around a mean, but might better be viewed as a hybrid of several distributions driven by different processes.

Harris et al. (2015) demonstrated when combined killer whale, sperm whale, and long-finned pilot whale dose–p(response) data were plotted for three different levels of severity of response, a basically sigmoidal curve was generated for each severity level. For low severity of response, the curve reached 0.5 response probability at 153 dB<sub>SEL</sub> and asymptoted at 1.0 probability at 167 dB<sub>SEL</sub>. For medium severity of response, the curve reached 0.5 response probability at 155 dB<sub>SEL</sub> and reached 1.0 probability at 180 dB<sub>SEL</sub>. For the highest severity of response, the curve asymptoted at a 0.1 probability of response at 160 dB<sub>SEL</sub>. The overall population effect will be a function of the probability of a response and the severity of the response. It is not yet possible to determine whether a greater probability of a less severe response or a lower probability of a more severe response will have the greatest population consequences.

Dose–p(response) relationships have not been estimated for the same marine mammal species in both captive and natural settings, but limited data suggest different responsiveness across these contexts, albeit using different criteria for the response. A free-ranging bottlenose dolphin tagged before the start of naval sonar exercises remained in the same general area during the 3 days of exercises and had modeled exposure levels up to 168 dB<sub>RMS</sub> (Baird et al., 2014). This value is above the RL<sub>p50</sub> for captive dolphins on the first trial at an exposure SPL of 162 dB<sub>RMS</sub>. The response of free-ranging harbor porpoises to a commercial two-dimensional seismic airgun survey in the North Sea was determined through passive acoustic tracking. The density of porpoises was unchanged at 10 km at received SPL of 148 dB<sub>RMS</sub> and reduced by 6% at 5 km at received levels of 155 dB<sub>RMS</sub> (Thompson et al., 2013a). These levels are well above the RL<sub>p50</sub> estimated for a captive harbor porpoise exposed to sonar (124–144 dB<sub>RMS</sub>),



although another captive harbor porpoise consistently exhibited an aversive behavioral reaction to seismic airgun sound at SPL above 174 dB<sub>RMS</sub> (Lucke et al., 2009). Captive studies have provided necessary first-order information on dose–response relationships for species too small or too difficult to tag under current methods, but they are an inadequate proxy for dose–response relationships determined in free-ranging animals because the context is so different, and the suite of behavioral responses available to captive animals is restricted compared to that available to free-ranging animals. This lack of dose–response data is particularly important for small pelagic odontocetes that form the majority of animals predicted to be taken in many environmental assessments (e.g., U.S. Department of the Navy, 2013). The responses observed in captivity are also low on the severity scale and would be unlikely to have population consequences in the wild.

**Finding 2.5:** The selected response criterion for dose–response studies has typically been a low-severity response, but anomalous high-severity responses have been observed during these studies. Just-audible signals have resulted in responses of severity levels between 0 and 7. The severity levels were established based on assumed effects on individual fitness, and thus severe responses to low sound levels raise concerns regarding population consequences.

**Finding 2.6:** A primary reason for having no free-ranging dose–response curves for any of the smaller cetaceans is the lack of a suitable data recording package for attachment to these animals. The development of such a data recording package that would combine GPS with a measurement of sound exposure level is essential to estimate the impact of sound on these species that constitute the vast majority of cetaceans exposed to anthropogenic sound.

Many species of marine mammals continue to occupy U.S. naval test and training ranges in Southern California, the Bahamas, and Hawaii (Falcone et al., 2009; McCarthy et al., 2011; and Baird et al., 2014, respectively). These range animals have been observed to respond to sonar activities with changes in diving patterns and movements. For example, Blainville’s beaked whales move to the periphery of the U.S. Navy’s Atlantic Undersea Test and Evaluation Center (AUTEK) range during training exercises with multiple ships operating sonar. They return to the range within a few days after the training exercises have concluded (McCarthy et al., 2011; Tyack et al., 2011). It is very difficult for observational studies to demonstrate that sonar is the cause of these reactions (see Chapter 6). A combination of controlled experiments to demonstrate causation, with opportunistic observations of actual exercises to study the scale and significance of responses (Tyack et al., 2011), has proven particularly informative. The long-term consequences of the energetic costs of displacement and changes in foraging location and potential changes

in foraging resources are not completely known, but a recent study (Claridge, 2013) has shown that the average animal abundance of beaked whales at AUTEK is lower than in an equivalent area at Abaco, an area 170 km away in the Bahamas where sonar exposure is limited. Also the female-to-calf ratio at AUTEK is higher, suggesting lower recruitment. Beaked whales have both capital and income breeding characteristics (Huang et al., 2011). New et al. (2013b) developed an energetic model that considered the impact of displacement from food resources on survival and reproduction of beaked whales. Their results showed that, while adult survival was relatively robust under reduced energy input, minor reduction in energy intake over an extended period could affect lifetime reproductive output.

Killer whales represent an existential threat to marine mammals of several species, so playback of killer whale calls has been used as a positive control in studies of responses to anthropogenic sound. Blainville’s beaked whales (Tyack et al., 2011) and gray whales (Malme et al., 1983) show behavioral responses to playbacks of killer whale vocalizations when the signal-to-noise ratio is 0 dB. Some cetaceans also respond to some anthropogenic sounds, such as sonar at levels well below the current criteria for disturbance used in the United States. The 50% probability of a startle response for a captive harbor porpoise to playback of 6-7 kHz up-sweeps mimicking naval sonar signals occurred at SPL received levels of 101 dB<sub>RMS</sub> (Kastelein et al., 2012). The minimum level for response of Cuvier’s beaked whales to playback of sonar signals occurred at SPL received levels of 89-127 dB<sub>RMS</sub>, although the whales did not respond to sonar from a distant warship at received SPL of 78-106 dB<sub>RMS</sub> (deRuiter et al., 2013). The above data show that the thresholds defining behavioral harassment used by NMFS (160 dB<sub>RMS</sub> impulsive sounds; 120 dB<sub>RMS</sub> nonimpulsive) need to be updated in light of the new data for sonar. Some harbor porpoises and Cuvier’s beaked whales respond at levels well below the 120 and 140 dB<sub>RMS</sub> response thresholds currently used for these species. Similarly, the 50% probabilities of response are in most cases below the 165 dB<sub>RMS</sub> previously used in environmental impact assessments for naval activities. As described in Box 2.2, the current method of calculating takes based on response thresholds can lead to an underestimate of the number of animals taken.

### Masking

With behavioral responses being observed at dose levels close to the limits of detectability in some cases, and with detectability used to set the minimum exposure at which the dose–response function starts, the acoustic signal-to-noise ratio needs to be considered when it limits detectability through masking. Masking occurs when the level of detectability for one sound is increased in the presence of a second sound by an amount expressed in dB. The mammalian ear

has been modeled as a bank of overlapping band-pass filters<sup>8</sup> and only energy in the band-pass filter centered on the sound being detected, the critical band, contributes to the masking of that sound (Fletcher, 1940). While this has been investigated most thoroughly for Gaussian<sup>9</sup> noise, it does not hold true for many natural and anthropogenic noises that have complex spectra and amplitude fluctuations. Through a phenomenon known as comodulation masking release (Trickey et al., 2010), the broader the frequency band of the natural noise is outside the critical band, the more the masking is reduced compared to what it would have been with Gaussian noise in the critical band. Masking has been considered primarily in the case where the second sound represents noise for the species or individual in question. For example, concern has been expressed that shipping noise, which has increased since the advent of motorized vessels, overlaps with the frequency range of important social calls of baleen whales, including blue (Mellinger and Clark, 2003), fin (Watkins et al., 1987), and right (Parks et al., 2007a) whales. The primary concern here has been that elevated ambient noise would reduce the range over which whales could detect calls of conspecifics.

Clark et al. (2009) have proposed analyzing the potential effect of masking through a calculation of the reduction in communication space for several species of baleen whales. They found the most profound reductions due to the modeled passage of two ships within 4 km of a right whale in the Stellwagen Bank National Marine Sanctuary, where the aggregate exposure resulted in an 84% reduction in the communication space for that animal. Hatch et al. (2012) calculated an overall 63% reduction in communication space for right whales in Stellwagen Bank National Marine Sanctuary compared to what they experienced in the mid-20th century, when background levels were estimated to be 10 dB below the lowest 5% of all the background levels currently recorded.

One serious problem with these predictions is that they ignore compensation mechanisms that whales use to maintain the effective range of their communication signals in noise. The natural environment in which animal communication evolved has significant variation in noise, for example from rain (heavy rain causes up to a 40 dB increase) or waves and bubbles caused by wind (8 dB increase between Beaufort 0.5 and 1.0), and most birds and mammals have evolved mechanisms to compensate for this natural variation in noise. One of the most pervasive compensation mechanisms is the Lombard effect, by which animals increase the source level of their calls in increased noise (Brumm and Zollinger, 2011). All birds and mammals tested have

shown the Lombard effect, and marine mammals are no exception. Killer whales increased their call amplitude by 1 dB for every dB increase in background noise created by motorized vessels (Holt et al., 2009). Making louder calls in increased noise can have an energetic cost; bottlenose dolphins increase their metabolic rate as the acoustic energy of their vocalizations increases (Holt et al., 2015). In the case of the right whales in Cape Cod Bay, the location modeled by Clark et al. (2009), Parks et al. (2010) showed that individual right whales elevate the source level of their calls as the noise level increases. In addition, as shipping noise chronically increased from the 1960s to the 1990s, right whales have increased the fundamental frequency of their calls by about an octave, outside of the peak frequency of shipping noise (Parks et al., 2007b). These mechanisms are not taken into account in the Clark et al. (2009) model, making it unrealistically extreme in its predictions of reduction of effective space. Other mechanisms by which human engineers compensate for noise include making signals longer and/or more redundant. These mechanisms are also used by marine mammals; humpback whales increased the duration of their songs by 29% in the presence of low-frequency active sonar, and this was produced by increasing the redundancy of the song (Miller et al., 2000).

In addition to potential effects on communication space, shipping can also act as a physiological stressor. Rolland et al. (2012) measured fecal glucocorticoids in North Atlantic right whales in the Bay of Fundy during the summers of 2001-2005. Shipping activity was reduced by 67% and the associated noise levels declined by about 6 dB immediately after the attack on the World Trade Center on September 11, 2001. This reduction in ship movement and noise was associated with a reduction in stress-related glucocorticoids compared to other years and before September 11, 2001. However, this opportunistic study lacked the controls required for standard experimental design.

### Impulsive Sources

Impulsive sources affect animals differently than relatively continuous sources. The rise time and peak pressure (measured in kPa) are more important metrics than the root mean square (RMS) value of the received level. Depending on the interpulse interval, the auditory system may have an opportunity to partially recover between pulses. As noted previously, the current NMFS threshold for behavioral response to impulsive sounds is 160 dB<sub>RMS</sub> and for nonimpulsive sounds it is 120 dB<sub>RMS</sub>. The primary sources of impulsive sounds that marine mammals experience come from seismic activity associated with oil and gas exploration; pile driving associated with construction of bridges, docks, and wind farms; and some acoustic deterrent devices associated with fishing and aquaculture.

<sup>8</sup> A band-pass filter allows a range of frequencies to pass with minimum attenuation and strongly attenuates frequencies outside that band. The width of the band-pass is typically given as the frequencies above and below the center frequency at which the attenuation is 3 dB.

<sup>9</sup> Gaussian noise has a normal distribution of instantaneous amplitudes over time.

### Seismic Surveys

Responses to seismic surveys have been studied in a variety of marine mammals. The following overview captures most of the salient results but is not a comprehensive literature review. Romano et al. (2004) sampled blood from a captive beluga whale (*Delphinapterus leucas*) and bottlenose dolphin (*Tursiops truncatus*) after exposure to underwater impulsive sounds from a seismic water gun. For the beluga whale, levels of norepinephrine, epinephrine, and dopamine were significantly higher for peak pressure levels of 116 to 198 kPa. For the dolphin, serum levels of aldosterone were significantly elevated and monocytes decreased after exposure to peak pressure levels of 146 to 220 kPa. Miller et al. (2009) conducted controlled approaches of a commercial seismic survey vessel to make pass-bys of sperm whales in the Gulf of Mexico. The whales, which were exposed to received levels varying from 120 to 147 dB<sub>RMS</sub> at ranges varying from 1.4 to 12.8 km, did not change their direction of travel or behavioral state in response to exposure, but did decrease the energy they put into swimming and showed a trend for reduced foraging. Madsen et al. (2002) studied responses of sperm whales in Norwegian waters to seismic surveys at ranges greater than 20 km and reported no responses at exposure ranging up to 123-130 dB<sub>RMS</sub>. Avoidance responses have more commonly been reported for baleen whales. Avoidance responses to airgun sounds at received levels of 160-170 dB<sub>p-p</sub> re 1  $\mu$ Pa have been reported for migrating gray whales (Malme et al., 1983), bowhead whales (Richardson et al., 1986), and migrating humpback whales (McCauley et al., 2000). Fin whales moved away from a 10-day seismic survey in the Mediterranean and were spatially displaced for at least 14 days after the seismic airgun shooting period (Castellote et al., 2012). The survey area affected was estimated to be about 100,000 km<sup>2</sup> (Castellote et al., 2012).

### Pile Driving

Pile driving is used in the construction of structures, such as piers and bridges, and the installation of oil and gas platforms and offshore wind turbines. The impact of pile driving for offshore wind turbines has been of particular concern for marine mammals because of the high source level (Madsen et al., 2006). Pile driving produces broadband, multiple pulsed sounds, similar to seismic airgun surveys, with the peak energy below 1 kHz (Bailey et al., 2010). During pile driving, hammer strikes occur about every 1-2 seconds and the piling duration is generally several hours for each pile with the interval between piles varying from minutes to days (Bailey et al., 2010; Dähne et al., 2013). Source levels vary depending on the size of the pile and method of pile driving, but have been estimated to be 226-257 dB<sub>p-p</sub> re 1  $\mu$ Pa at 1 m based on recorded levels back-calculated to 1 m (OSPAR, 2009; Bailey et al., 2010). Sound levels of 205 dB<sub>p-p</sub> at 100

m (Bailey et al., 2010) and energy up to 176 dB<sub>SEL</sub> re 1  $\mu$ Pa<sup>2</sup>-s at 720-750 m distance (Brandt et al., 2011; Dähne et al., 2013) have been reported.

In Europe, assessments of the impacts of offshore wind developments on marine mammals have focused on small cetaceans and pinnipeds (Bailey et al., 2014). The response of marine animals to the construction phase, particularly the pile-driving activity, has primarily been studied for the most abundant cetacean species in the North Sea, the harbor porpoise (*Phocoena phocoena*). Harbor porpoises have been reported to exhibit an avoidance response to the impulsive sound of pile driving at distances of 20 km or more and for up to 3 days (Tougaard et al., 2009; Thompson et al., 2010; Brandt et al., 2011). There is currently a lack of data for large whales. Large whales are classified as having low-frequency hearing (see Figure 2.2), which suggests that they may be most sensitive to pile-driving sounds. Offshore wind energy areas have been identified and leased by the Bureau of Ocean Energy Management on the U.S. Outer Continental Shelf where a number of whale species, many of which are listed as endangered species, are known to occur. As offshore wind energy facilities begin to be installed off the U.S. coast, studies on the short- and long-term responses of large whales will be particularly important for determining the potential population-level consequences.

### Acoustic Deterrent Devices

Acoustic deterrent devices (ADDs) are intentionally designed to deter wildlife such as marine mammals from depredate resources such as fish in a fish farm. A variety of different ADDs have been developed to deter seals from depredate fish farms (reviewed by Nowacek et al., 2007; Götz and Janik, 2013). Götz and Janik (2013) reviewed mixed evidence on the effectiveness of ADDs in reducing depredation by seals. Activation of ADDs in some settings was associated with increased depredation, perhaps through broadcasting the location of a food source (Geiger and Jeffries, 1987; Jefferson and Curry, 1996). In other settings, ADDs were judged by fish farmers to vary from ineffective to moderate effectiveness in different sites (Quick et al., 2004; Sepulveda and Oliva, 2005). In cases where ADDs were associated with reduced depredation, some showed a decreased effect over time, which could be due to habituation (Groves and Thompson, 1970), tolerance (Bejder et al., 2009), or hearing damage due to exposure to the ADDs (Reeves et al., 1996).

In contrast to the mixed evidence for effectiveness of ADDs on the target pinnipeds, there is strong evidence that operation of ADDs causes some odontocetes to avoid large areas of habitat. Morton and Symonds (2002) studied the presence of killer whales in inshore waters of British Columbia where their distribution had been well studied for more than a decade before four ADDs were installed. Sightings of killer whales were significantly reduced in

the roughly 10 km<sup>2</sup> area where the ADDs were installed during the 6-year period of their use, and then recovered to baseline after their use ended. Olesiuk et al. (2002) report a similar sharp decline in sightings of harbor porpoise out to their maximum sighting range of 3.5 km when ADDs were activated for periods of 3 weeks. Brandt et al. (2013) showed a similar decrease in the abundance of porpoises detected out to ranges of 7.5 km from an ADD when it was operating. None of these studies suggest much habitation in the response of odontocetes to ADD signals.

## INDIRECT EFFECTS OF SOUND ON MARINE MAMMALS

Marine mammals are among the animals with the most sensitive underwater hearing, but sound may also affect them indirectly through effects on prey, predators, or competitors. Indirect effects of stressors may be more important than direct ones (Ockendon et al., 2014).

### Effects on Prey

Some fish are specialized to hear the pressure component of sound. A few species of herring (subfamily Alosinae) can detect the ultrasonic clicks that toothed whales use to find their prey. Wilson et al. (2011) demonstrated that one of these species swims away from these clicks, in a directional antipredator response. Mann et al. (1998) showed that shad respond to echolocation clicks at received levels of 171 dB<sub>p,p</sub>. This level is high enough that few sources of noise would be likely to mask the clicks, so it is unlikely that elevated noise would make the shad less likely to escape. Most prey of marine mammals detect the particle motion component of sound rather than the pressure component. This mode of hearing limits the ability of animals to hear sounds with wavelengths smaller than roughly their body size, so these animals do not hear well above a few kilohertz. However, some low-frequency sources of anthropogenic sound, such as airguns used in seismic surveys, have been shown to affect the hearing and behavior of fish. McCauley et al. (2003) found that caged fish exposed to repeated passes of a seismic air gun (source level of 222.6 dB<sub>p,p</sub> re 1 μPa at 1 m) starting 400–800 m away and passing within 5–15 m of the cage experienced significant hair cell damage that remained unresolved 58 days later. They note that, had the fish not been caged, they would have swum away as they tried to do within the confines of the cage at first hearing of the seismic gun. Engås et al. (1996) report that the catch of cod and haddock was reduced by 50% when airguns began to transmit sound. Reductions in catch were observed 33 km away from the survey and lasted more than 5 days after the airguns stopped operating. The acoustic density of cod and haddock was reduced by 45% during the seismic survey and by 64% post survey. In contrast Løkkeborg et al. (2012) found that gillnet fisheries yields increased during a seismic

survey while longline fisheries yields decreased. Acoustic mapping of fish abundance showed only pollock were displaced from the fishing grounds in this study. Løkkeborg et al. (2012) note that the airgun discharge rate was 19 times higher in the Engås et al. (1996) study, and they point out that the lower levels of exposure could explain the lower level of response in their study. If avoidance behavior reduces the prey of marine mammals, it could affect their feeding even if the sound does not affect them directly. However, short-term displacement of prey may have few consequences for marine mammals. Prey often move considerable distances for a variety of reasons, and presumably marine mammals can usually move to relocate them.

There is evidence that continuous noise, similar to the sound of shipping, may increase the mortality of eggs and larvae of a minnow (*Cyprinodon variegatus*; Banner and Hyatt, 1973) and decrease the growth of larvae of the minnow and longnose killifish (*Fundulus similis*). Regnault and Lagardère (1983) showed that exposure to noise 30 dB above ambient increased the metabolic rate of the shrimp *Crangon crangon* in an aquarium, with a significant reduction in growth and reproduction and elevated mortality (Lagardère, 1982). If chronic exposure to noise reduces the abundance of fish and invertebrate prey of marine mammals, this could reduce the quality of their habitats, resulting in site abandonment or survival and reproductive costs for individuals that remain.

### Effects on Predators

Sharks and killer whales are some of the primary predators of marine mammals. Sharks do not have particularly sensitive hearing, so effects of noise are likely to be minimal. However, killer whales not only have excellent hearing, but have also been shown to be more responsive to low- and mid-frequency sonar than some other toothed whales, such as sperm and pilot whales (Harris et al., 2015). If killer whales avoid noise sources at greater ranges than potential prey, this could create a zone near the noise source with a lower risk of predation. Noise-mediated predator shelters or shields have been documented in terrestrial systems where songbird nest predators appear to be more sensitive to chronic noise than are their prey (Francis et al., 2009). In the same system, Francis et al. (2012b) found evidence of additional indirect effects with potential long-lasting consequences for the ecosystem. Specifically, the reduced recruitment of piñon pine (*Pinus edulis*), a foundational species, in noisy areas is linked to avoidance of noisy areas by a key seed disperser, the Woodhouse's scrub-jay (*Aphelocoma woodhouseii*), and increased abundance of important seed predators. These studies highlight how noise, like other anthropogenic stressors, can have indirect effects that reverberate throughout communities by interfering with interactions among species. Given the many pathways by which anthropogenic noise could affect marine mammals, a potential benefit from a

predator shield must be weighed against potential costs of persisting in noise-exposed zones.

### Effects on Conspecifics

Different kinds of noise can have varying effects on social cohesion in different species. Buckstaff (2004) showed that, as a motorboat approaches a group of bottlenose dolphins (*Tursiops truncatus*), the dolphins will increase the rate at which they produce signature whistles, followed by increased social cohesion (Nowacek et al., 2001). When sonar signals trigger a flight reaction, this can interfere with normal social cohesion, leading to separation of members of a group. For example, Miller et al. (2012a) report on a group of killer whales exposed to a playback of mid-frequency sonar sounds. When the received level of these sounds reached 152 dB<sub>RMS</sub>, a calf that had been in the group was seen to have separated from the group. Miller et al. (2011) notes three unique characteristics of this experiment to this exposure session: it was the only repeated mid-frequency active sonar up-sweep exposure presented to the same group of animals; the experiment was conducted in an unusually narrow fjord roughly 1 km wide; and transmissions were

started unusually close to the subjects. The calf rejoined the group after 86 minutes, and remained with the group for many hours after exposure. However, this separation was scored as quite a severe response because it could have had more serious consequences for the calf. High-latitude adult male sperm whales that are usually solitary responded to playback of killer whale vocalizations by clustering together at the surface and producing social alerting sounds (Curé et al., 2013).

### RECOMMENDATIONS

**Recommendation 2.1: Additional research will be necessary to establish the probabilistic relationships between exposure to sound, contextual factors, and severity of response.**

**Recommendation 2.2: Uncertainties about animal densities, sound propagation, and effects should be translated into uncertainty on take estimates, for example, through stochastic simulation. Regulators may then choose the level of risk they wish to use in deciding whether to permit an activity.**

## 3

## Current Understanding of Stressors

### INTRODUCTION

Although increased noise exposure is a concern for marine mammals, other anthropogenic activities also serve as potential stressors that can alter individual behavior and health and contribute to cumulative impacts. In general, a stressor can be defined as any causal factor or stimulus, occurring in either the animal's internal or external environment that challenges the homeostasis of the animal. Marine mammals are exposed to a diverse set of both intrinsic and extrinsic stressors during their lifespan (see Table 3.1).

There are short-term internal stimuli that evoke myriad physiological responses occurring daily to maintain an organism near its homeostatic set points, but these are not considered stressors. However, aspects of the life cycle that result in significant changes to the set points are considered

intrinsic stressors, and inherent in the life-history strategies of marine mammals are numerous features that constitute such stress. Many marine mammals are capital breeders that fast during reproduction or periods on shore. These species are intrinsically nutritionally stressed during reproduction and during migration away from foraging habitat. The amphibious lifestyle of pinnipeds requires that even income breeding species undergo food deprivation while on shore for breeding. Extended periods on shore have been associated with increases in stress hormones in numerous species (Champagne et al., 2012). Species that fast as part of their natural life history may exhibit intrinsic stress during or just after reproduction. During pregnancy, even species that do not fast will undergo significant physiological changes, including metabolic, cardiovascular, respiratory, immuno-

**TABLE 3.1** Definition and Examples of Types of Stressors

	Definition	Examples
Intrinsic Stressor	An internal factor or stimulus that results in a significant change to an animal's homeostatic set points	Pregnancy, lactation, migration, molting, fasting (e.g., during the breeding season in capital breeders)
Extrinsic Stressor	A factor in an animal's external environment that creates stress in an animal	<i>Anthropogenic:</i> Pollutants, ship strike, entanglement, noise, psychological factors (e.g., perceived threat)  <i>Natural, but potentially influenced by anthropogenic activity:</i> Harmful algal blooms, resource limitation, predator pressure, pathogens, temperature, salinity, naturally occurring chemicals, intra- or interspecific competition
Ecological Driver	A biotic or abiotic feature of the environment that affects multiple components of an ecosystem directly and/or indirectly by changing exposure to a suite of extrinsic stressors	Loss of keystone or foundation species, recurring climate patterns such as El Niño, climate change

logical, and hematological changes, in order to accommodate the growing fetus.

In addition, there are extrinsic stressors that arise from chemical, physical, or biological factors in an animal's external environment. Extrinsic stressors may be specifically associated with anthropogenic activities (e.g., pollutants or ship strike) and include psychological factors that occur when human activities are perceived as a threat, typically a predatory threat (e.g., sonar; Isojunno et al., 2016). Extrinsic stressors may also be prompted by natural factors, although these natural factors are often influenced by anthropogenic activities to some degree (e.g., disease or resource limitation), making it difficult to classify the extrinsic stressor as unequivocally natural. Regardless of whether causal factors are purely natural or not, these stressors have potential to influence an animal's responses to other anthropogenic stressors. In addition, how the animal responds to extrinsic stressors is dependent on its physiological capacity, which is modulated by intrinsic stressors. So long as the extrinsic stressors and intrinsic stressors do not exceed the animal's ability to maintain organismal function (i.e., allostasis; McEwen and Wingfield, 2003), effects on health and reproduction that lead to population impacts are unlikely. Numerous studies have evaluated the impact of the various extrinsic stressors on the individual health, survival, and reproduction of marine mammal species, although these studies have been biased toward pinnipeds (reviewed by Atkinson et al., 2015). At the extreme, extrinsic stressors can result in increased mortality, demographic impacts, and even cohort failures in some marine mammal species. The cumulative effect of whatever combination of these existing intrinsic and extrinsic stressors to which an individual is exposed will influence the impact of any additional anthropogenic stressors on individuals and consequently their population-level effect.

Many extrinsic stressors can be the products of larger phenomena that are identified as ecological drivers. An ecological driver is a biotic or an abiotic feature of the environment that affects multiple components of an ecosystem directly and/or indirectly by changing exposure to a suite of extrinsic stressors. Ecological drivers may operate on multiple species at varying trophic levels and may even affect multiple ecosystems.

## POTENTIAL ENVIRONMENTAL (EXTRINSIC) STRESSORS

Human activities can potentially cause mortality, injury, disturbance, and stress to marine mammals. Activities that result in immediate fatalities, such as bycatch, hunting (or other deliberate killing), and collisions with ships, will increase the population mortality rate above that caused by natural factors alone. These lethal stressors directly affect population abundance. In contrast, human activities with nonlethal effects on marine mammals may affect their behavior and physiology and lead to impacts on their health.

The cumulative effect of these human activities, along with natural extrinsic stressors, on the health of individual animals may result in changes in their reproduction and survival that then affect population dynamics. In this section the committee reviews and discusses environmental stressors and their associated effects that have been reported for marine mammals. The focus is on those stressors that have been emphasized in the literature, and/or that have strong potential to interact with other stressors due to chronicity of exposure (e.g., persistent chemical contaminants to which many marine mammals are exposed over a lifetime), or the potential for a sublethal but chronic effect (e.g., permanent damage to an organ system). This should not be considered an exhaustive list of all possible environmental stressors that have potential to affect marine mammals. A comprehensive review of all potential stressors is beyond the scope of this report.

### Physical Injury

#### *Fishery Interactions*

Entanglement in fishing gear represents an important source of injury and mortality in marine mammals. Bycatch mortality is estimated globally to exceed hundreds of thousands of marine mammals each year (Read et al., 2006). Bycatch occurs most frequently in association with gillnet fisheries. There is a strong spatial component to bycatch of marine mammals, with "hotspots" influenced by marine mammal density (Block et al., 2011), fishing intensity (Stewart et al., 2010), or both (Lewison et al., 2014). Spatial overlap between fisheries and marine mammals is often associated with coastal zones, shelf breaks, upwelling regions, and frontal zones (Hyrenbach et al., 2000; Scales et al., 2014). When not immediately fatal, entanglement or ingestion of fishing gear can impede the ability of marine mammals to feed and can cause injuries that eventually lead to infection and death (Wells et al., 2008; Cassoff et al., 2011; Moore and van der Hoop, 2012). Weakened animals may be more susceptible to predation (Moore and Barlow, 2013). There are also costs likely to be associated with non-lethal entanglements in terms of energy and stress (Moore and van der Hoop, 2012). The prevalence of scars on North Atlantic right whales (*Eubalaena glacialis*) associated with entanglements indicates the persistent and repetitive nature of this threat (Knowlton et al., 2012).

#### *Vessel Collision*

Collision with ships is a key threat to large whales (Laist et al., 2001; Thomas et al., 2016). Vessel strike also poses a risk to manatees (Runge et al., 2015) and small cetaceans in heavily populated coastal regions (e.g., Wells et al., 2008), and the risk may increase when illegal feeding has conditioned the animals to approach vessels (Donaldson

et al., 2010). Several studies have estimated quantitative relationships (i.e., dose–response relationships) between vessel speed and the lethality of collisions for large whales (Vanderlaan and Taggart, 2007; Wiley et al., 2011; Conn and Silber, 2013). Even when it is not lethal, collision with a vessel causes stress and injury, which could make individuals more susceptible to negative sequelae following exposure to subsequent stressors.

## Toxic Compounds

### *Nonbiological Toxins*

Chemical contaminants, particularly those that are persistent in the environment, are a concern for marine mammals that often occupy high trophic positions. Persistent organic pollutants (POPs), which include legacy pesticides (e.g., DDT and chlordane), legacy industrial-use chemicals (e.g., polychlorinated biphenyls [PCBs]), and emerging contaminants of concern (e.g., polybrominated diphenyl ethers and perfluorinated compounds) accumulate in fatty tissues of marine organisms and are magnified through the food chain, leading upper trophic predators to be highly exposed. High concentrations of PCBs and DDT have been reported in tissues of marine mammals in most parts of the world, particularly in coastal regions adjacent to heavy coastal development and/or industry (Ross et al., 2000; Houde et al., 2005; Kajiwara et al., 2006; Kucklick et al., 2011). These legacy POPs have been linked to a number of adverse health effects, but primary concerns relate to endocrine disruption, and specifically thyroid hormone disruption (Sormo et al., 2005; Boas et al., 2006; Tabuchi et al., 2006; Schwacke et al., 2012), reproductive impairment or developmental effects (Reijnders, 1986; Ulbrich and Stahlmann, 2004; Hall et al., 2009), and immune dysfunction or disease susceptibility (De Guise et al., 1998; Van Loveren et al., 2000; Jepson et al., 2005). Polybrominated diphenyl ethers (PBDEs), commonly used as flame retardants, are another class of POPs that have spread globally in the environment and have also been reported in a broad array of marine mammal species (Houde et al., 2009; Rotander et al., 2012). The toxicity of PBDEs has not been as thoroughly investigated in comparison to PCBs, but rodent studies have suggested developmental neurotoxicity with learning and memory impairment that can persist into adulthood, and decreased thyroid hormone production similar to the toxic effects of PCBs (Eriksson et al., 2001; Branchi et al., 2003). PBDEs can be biotransformed to hydroxylated brominated diphenyl ethers, which exhibit greater toxicity for some effect end points as compared to their parent compound, and some studies have suggested that biotransformation of naturally occurring compounds in the marine environment may be an even greater source of the hydroxylated analogues as compared to the anthropogenic flame retardants (Wiseman et al., 2011).

POPs bind to fatty tissues and as such are sequestered

in the blubber of marine mammals. Concentrations are likely maintained at equilibrium, or increase with age if the exposure continues, until an event (e.g., parturition, lactation, seasonal blubber changes, or loss of prey base) prompts blubber depletion and mobilization of the sequestered contaminants (reviewed by Houde et al., 2005). Once contaminants are mobilized, they may be more likely to reach target organs and initiate mechanistic pathways for adverse health effects. Therefore, POPs have potential to affect an individual over a lifetime, depending on life events and whether or not there is continued exposure. Neonates and dependent calves or pups may be particularly susceptible due to high concentrations of POPs that are offloaded from mother to offspring through milk (Wolkers et al., 2004; Yordy et al., 2010).

Aside from POPs, other organic compounds of concern include polycyclic aromatic hydrocarbons (PAHs). PAHs exist naturally in the environment but can also be from anthropogenic sources. Crude oil, fumes, vehicle exhaust, coal, organic solvents, and wildfires are all potential sources for PAHs. Exposure may be continual, associated with runoff from impervious cover in developed coastal regions, or natural seeps that produce low-level but steady exposure. Acute events such as oil spills may produce pulses of more significant exposure. Depending on the route of exposure (inhalation/aspiration, ingestion, or direct dermal contact), PAHs can produce a broad range of health effects. Lung disease, disruption of the hypothalamic-pituitary-adrenal (HPA) axis, and altered immune response have been reported in marine mammals as well as experimental mammal species following exposure to oil (Mazet et al., 2000; Schwartz et al., 2004; Mohr et al., 2008; Schwacke et al., 2014a) or inhalation of smoke associated with wildfires (Venn-Watson et al., 2013). Although PAHs are more rapidly metabolized and do not accumulate as is the case with POPs, the toxic effects (lung disease and HPA-axis damage) may be long lasting and initiate chronic disease conditions (Smith et al., 2017). Heavy metals, particularly mercury—which has been associated with immunological and neurotoxic effects and can cause permanent damage to the brain (Kakuschke and Prange, 2007; Farina et al. 2011)—have also been widely measured in the tissues of marine mammals (Dietz et al., 1996; Wagemann et al., 1996; Weihe et al., 1996; Seixas et al., 2008). Comparison of mercury tissue concentrations with established toxicological thresholds have indicated that some Arctic marine mammal species are at risk of neurological effects (Dietz et al., 2013), and levels of mercury in Arctic regions have been increasing in recent decades (Dietz et al., 2009; Rigét et al., 2011).

Despite the vast evidence to suggest that marine mammals are exposed to anthropogenic, as well as natural, chemicals capable of producing significant toxic effects, only a few studies have actually examined the impacts on population survival or reproductive rates (e.g., Hall et al., 2006; Lane et al., 2015). Such observational assessments are inherently challenging due to the difficulty in controlling for



confounding or interacting variables, as well as the sublethal but chronic nature of chemical contaminant effects, and the difficulty of observing mortality or reproductive end points in long-lived marine mammal species, particularly cetaceans. Even fewer studies have attempted to develop quantitative relationships relating a given dose of a chemical to changes in a vital rate (e.g., reduced fecundity) and have had to rely on data from experiments with other mammalian species (e.g., Schwacke et al., 2002; Hall et al., 2006).

### Biological Toxins

Marine algal toxins are produced by unicellular algae that are often present at low concentrations but that may proliferate to form dense concentrations under certain environmental conditions. When high cell concentrations form, the toxins that they produce can harm the health of marine life, and this is referred to as a harmful algal bloom (HAB). Marine mammals can be exposed to HAB toxins directly by inhalation or indirectly through food web transfer (Durbin et al. 2002), and these toxins can cause severe neurotoxic effects (reviewed by Van Dolah, 2005). Mortality and morbidity related to HAB toxins have been increasingly reported over the past several decades, and biotoxins has been a primary contributor to large-scale die-offs across marine mammal taxa (Van Dolah, 2005; Simeone et al., 2015). Since 1998, multiple die-offs as well as abortions and premature parturition have been reported for California sea lions (*Zalophus californianus*) in relation to domoic acid, a toxin produced by diatoms of the genus *Pseudonitzschia* (Scholin et al., 2000; Bejarano et al., 2008a). Furthermore, studies have determined that even sea lions that survive can suffer sublethal effects that could influence reproduction and longer-term survival (Gulland et al., 2002; Goldstein et al., 2008, 2009). Impacts of *Pseudonitzschia* blooms on marine mammal populations along the western U.S. coast have not been limited to sea lions; domoic acid has also been linked to mortalities of balaenopterids, delphinids, phocoenids, and mustelids (Van Dolah, 2005). Domoic acid has also been detected in tissues of marine mammals along the southeast U.S. coast (Schwacke et al., 2010; Twiner et al., 2011), but perhaps of greater concern in this area are the brevetoxins produced by Gulf of Mexico red tides. Brevetoxin has been implicated in multiple die-offs involving common bottlenose dolphins (*Tursiops truncatus*), as well as the endangered Florida manatee (*Trichechus manatus latirostris*) (Flewelling et al., 2005; Twiner et al., 2012; Simeone et al., 2015). Other HAB toxins, such as saxitoxin and ciguatera toxins, have been implicated in morbidity or mortality of other marine mammals, including humpback whales (*Megaptera novaeangliae*) and endangered monk seals (*Monachus* sp.) (Reyero et al., 1999; Bottein et al., 2011; summarized by Van Dolah, 2005).

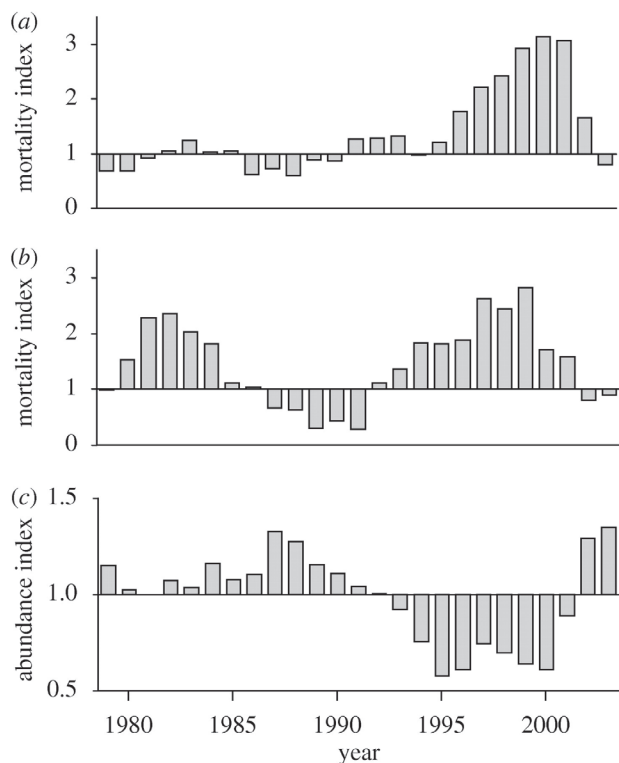
### Parasites and Pathogens

Parasites are ubiquitous. Parasites have the ability to cause disease and to function as pathogens. Microparasites, which include viruses, bacteria, fungi, and protozoa, multiply inside the host and are frequently associated with immune responses and development of host immunity in healthy animals. Macroparasites, which include helminths and arthropods, are larger in size and have complex life cycles that frequently involve more than one host for reproduction.

Microparasites can infect respiratory, central nervous, or other organ systems causing morbidity and mortality (e.g., Guzmán-Verri et al., 2012; Van Bresseem et al., 2014; Simeone et al., 2015), and in some cases have been associated with epidemics that produce significant mortality. For example, viral pathogens of the genus *Morbillivirus* have been associated with severe respiratory illness and linked to large-scale die-offs of marine mammal populations worldwide (Van Bresseem et al., 2014). Endemic microparasites may sporadically infect a smaller number of animals, but contribute to natural mortality as well as to widespread, low-level disease that in some cases may affect reproduction (e.g., *Brucella* sp.; Guzmán-Verri et al., 2012). Similarly, macroparasites may chronically infect marine mammals and contribute to low-level mortality or morbidity that reduces fitness or resilience (Simeone et al., 2015). Perrin and Powers (1980) estimated that 11-14% of natural mortality in spotted dolphins (*Stenella attenuata*) was attributable to the nematode *Crassicauda* sp. based on the prevalence of cranial lesions by age in spotted dolphins incidentally killed in the eastern tropical Pacific tuna fishery. The distribution of parasites and thus the risk of exposure and subsequent infection in marine mammals can be influenced by human activities. For example, domestic or human-managed animal populations and landscape alteration can affect terrestrial parasite distribution, and in coastal areas this can influence the risk for land-to-sea transmission. Such an influence has been supported by studies of *Toxoplasma gondii* transmission from terrestrial animals (feral cats and wildlife) to marine mammals in adjacent coastal waters (VanWormer et al., 2013, 2014).

### Resource Limitation

Competition between marine mammals and fisheries has long been recognized (Northridge, 1984), and there is little doubt that this competition can be significant. For example, Punt and Butterworth (1995) estimated that the South African west coast population of Cape fur seals consumed some 600,000 tons of commercially valuable fish, such as Cape hake—in contrast to the average annual landings of 50,000 tons of Cape hake by South African fishing fleets. Conversely, Ford et al. (2010) discovered a strong bottom-up effect on the abundance of fish-eating killer whales in the northeastern Pacific Ocean from the availability of their



**FIGURE 3.1** Mortality of (a) northern and (b) southern resident killer whales negatively covary with (c) abundance of Chinook salmon. (a, b) Values above or below 1 reflect higher or lower mortality rates than expected or (c) higher or lower abundance of Chinook salmon than the average for the time series. SOURCE: Ford et al. (2010).

preferred prey, Chinook salmon (see Figure 3.1), although there is some uncertainty about how this interaction affects population growth (Vélez-Espino et al., 2015).

However, despite this clear connection, the systems involved are complex, and unraveling the nature and extent of the competition between marine mammals and fisheries has been challenging (Matthiopoulos et al., 2008). Fisheries may also result in a variety of indirect effects by changing the ecosystem and decreasing or increasing the abundance of potential marine mammal prey such as forage fish. Analysis challenges stem from complexities in ecosystems, such as spatial heterogeneity and multispecies interactions, which constrain the ability to clearly interpret cause and effect (Harwood, 1992; Matthiopoulos et al., 2008). Other difficulties for quantifying competition emerge from the fact that many marine mammals are generalist predators. The prey consumption of generalist predators varies with the availability of all their preferred prey species (Asseburg et al., 2006; Smout et al., 2014). As a result, more data than are usually available in field studies of marine mammals are required to realistically characterize these interactions. Thus, despite the

intuitive connection between fisheries and marine mammals, there is currently no existing demonstration that resource depletion from fisheries has demographic consequences for marine mammals. Other influences of fisheries on marine mammals, such as bycatch, have been well documented.

In addition to food resources, critical marine mammal habitat can be limited by human activities. Critical habitats are areas essential to an animal's survival, such as the islands and protected beaches that grey seals (*Halichoerus grypus*) need for successful breeding (Harwood, 2001). Human disturbance may reduce the ability of seals, such as Hawaiian monk seals (*Monachus schauinslandi*), to use critical breeding beaches (Gerrodette and Gilmartin, 1990). These habitats, and others like the seagrass beds that manatees (*Trichechus manatus*) require for foraging, may also become limited by environmental drivers such as sea level rise (Burns, 1997). While some marine mammals can move to find other habitats, others such as freshwater river dolphins cannot (Harwood, 2001). Ice-associated species that rely on sea ice for pupping, molting, and transportation may be particularly vulnerable to population consequences of reduction of sea ice resulting from climate change (Kovacs and Lydersen, 2008; Kovacs et al., 2011). For example, ringed seals (*Phoca hispida*) show a decrease in body condition, ovulation rates, and recruitment that is correlated with low ice years (Harwood et al., 2000; Ferguson et al., 2005). Likewise, in polar bears (*Ursus maritimus*), decreased ice cover leads to longer periods of fasting, lower reproductive rates, declining body condition and survival, and increased contact with human settlements (Stirling et al., 1999, 2004; Stirling and Parkinson, 2006). At present, few examples exist that demonstrate direct impacts of habitat limitation on marine mammal populations, but as critical habitats become more limited by ecological drivers, this type of stress may become more apparent.

As an adaptive response to reducing intraspecific competition when prey is limited, dietary specialization may occur among individuals (Tinker et al., 2008). This can result in different exposure risks to pathogens within the population. For example, sea otter feeding on abalone, a preferred prey species, had a low risk of infection by *Toxoplasma gondii* and *Sarcocystis neurona* compared to otters feeding on small marine snails, despite foraging in the same habitat (Johnson et al., 2009). Food resource limitation can therefore lead to changes in pathogen exposure and have potential adverse effects on health as a consequence of the interaction between disease and increasing prey limitation.

### Perceived Threat

Frid and Dill (2002) made an important contribution to studies of disturbance in wildlife when they pointed out that anthropogenic disturbance stimuli may evoke responses similar to those evoked by predators or other threats, with which a species may have a long evolutionary history. Some

species with strong flight responses to threat may be at risk of acute lethal effects of disturbances. Cox et al. (2006) reviewed data on atypical mass strandings of beaked whales that coincided with sonar exercises and concluded that the most likely cause of these strandings involved sonar triggering a behavioral reaction that ultimately led to stranding. If sonar triggers a strong enough avoidance response to send beaked whales from their deep water habitat to water shallow enough to pose a risk of stranding, this suggests that the whales perceive the sonar as a potential threat. As mentioned in Chapter 2, mid-frequency sonar signals share some similarities with calls of killer whales, an important predator, and beaked whale responses to sonar share some similarities to responses to playback of killer whale sounds. These observations are consistent with the hypothesis that beaked whales perceive sonar as a threat, similar to the risk of predation.

Other forms of disturbance that evoke less drastic acute responses may have aggregate effects in wildlife populations. Wildlife tourism, which focuses on experiencing or interacting with wild animals, is a rapidly expanding industry (Newsome et al., 2002; Burgin and Hardiman, 2015). Although effects on marine mammal behavior have been documented, their impact at the population level is not well known (New et al., 2015). It appears that it is not only the sound produced by a whale-watching vessel that elicits a response, but the physical presence of a boat also plays a role in disturbance and the perceived threat risk. Pirotta et al. (2015a) found that the probability that bottlenose dolphins would engage in foraging activity declined by almost half in the presence of boats, but there was no relationship with the sound level. Various other short-term responses of marine mammals to boat traffic and swimmers have been reported. Well-documented examples include avoidance behavior by bottlenose dolphins (*Tursiops truncatus*) of swimmers (Constantine, 2001), and a reduction in resting and surface activity combined with faster swimming among southern right whales (*Eubalaena australis*), also in response to swimmers (Lundquist et al., 2013). Bejder et al. (2006) documented a significant reduction in the abundance of bottlenose dolphins in Shark Bay, Australia, when there were two or more wildlife tour operators compared to control sites with no tourism or when there was only one tour operator. Their findings indicated that the decline was due to a displacement of individuals, potentially those more sensitive, and a long-term shift in habitat use from disturbed sites with high vessel traffic to areas with lower activity. A study of bottlenose dolphins in Fiordland, New Zealand, also found that dolphins avoided areas where there was high tourism traffic (Lusseau et al., 2006; Lusseau and Bejder, 2007). A threshold of 68 minutes between boat interactions was identified below which dolphins switched from a short-term behavioral avoidance strategy to long-term habitat displacement. If this threshold was regularly exceeded, the population was predicted to decline as a result of a reduction in reproductive success, an increase in stillbirths, and decline in calf survival

(Lusseau et al., 2006; Lusseau and Bejder, 2007). However, a recent study (Brough et al., 2016) has suggested that some of the decline in reproductive success in this population may be the result of an increase in the discharge of freshwater into the system after 2002. The Lusseau and Bejder (2007) results contrast with dolphins in Sarasota Bay, Florida, where the dolphins remain even though a boat passes within 100 m every 6 minutes (Nowacek et al., 2001). One difference between these examples is that most boats in Sarasota Bay may be passing with no activity directed toward the dolphins in contrast with the tourist boat activities in Fiordland.

These studies indicate that population-level effects may be more likely to occur when individuals have small home ranges and high fidelity to sites with a high level of whale watching. In these circumstances a large number of individuals may experience repeated and long-term disturbance. In cases where individual exposure is relatively short, such as for migratory baleen whales, the effects are expected to be less. For example, Christiansen and Lusseau (2015) found that interactions between minke whales and whale-watching boats off Iceland resulted in a 42% decrease in feeding activity and an estimated 64% decrease in net energy intake. However, the aggregate exposure of individuals to whale-watching boats over the course of a summer was low (less than 450 minutes), leading to only a small decrease in female body condition that was unlikely to affect reproductive success (Christiansen and Lusseau, 2015). An examination of calving rates of humpback whales and calf survival off New England also found no evidence for negative effects of exposure to whale watching (Weinrich and Corbelli, 2009). Frameworks using individual-based models are being developed to simulate the potential effects of boat traffic and other human activities on marine mammal populations (New et al., 2013a; Pirotta et al., 2015b).

### Ocean Climate and Conditions

Oceanographic and meteorological phenomena can profoundly alter characteristics of the marine environment, which, in turn, affect the distribution and resource acquisition of marine mammals. One of the strongest is the atmospheric forcing of the El Niño–Southern Oscillation (ENSO), which results in major changes in the physical structure and productivity of the North Pacific subtropical gyre (Karl et al., 1995). These changes directly impact low-latitude and coastal upwelling zones that are important habitat for marine mammals and have time-lagged effects at higher latitudes (Brinton et al., 1987). El Niño alters water temperature and structure on large spatial scales and reduces coastal upwelling. These features are important in determining habitat use and movement patterns of marine mammals (Croll et al., 2005; Doniol-Valcroze et al., 2007), altering the range and abundance of some species and concentrating individuals in areas with high productivity (Gardner and Chávez-Rosales, 2000; Benson et al., 2002). These changes in distribution

may also influence exposure to other stressors that have geospatial components. Prey limitation associated with El Niño may have severe impacts on coastal and pelagic foraging species, reducing survivorship and reproductive rates and impacting local population dynamics of cetaceans and pinnipeds (Trillmich et al., 1991; Crocker et al., 2006; Leaper et al., 2006).

Multidecadal changes in ocean climate, or regime shifts, also influence sea surface temperature, upwelling, and biological productivity (Croxall et al., 1992; Francis and Hare, 1994). These alterations that persist over longer time scales can amplify effects of ENSO variation. The Pacific Decadal Oscillation (PDO) may influence the periodicity of El Niño events, resulting in stronger cumulative impacts on individuals and populations. Warm water regimes of the PDO are associated with increased nutritional stress in Pacific marine mammals (Le Boeuf and Crocker, 2005). Similarly, a multidecadal oscillation in the climate of the North Atlantic, the North Atlantic Oscillation (NAO), influences the distribution and foraging of numerous marine mammal species and impacts reproductive rates and population dynamics (Fujiwara and Caswell, 2001; Greene and Pershing, 2004; Jiang et al., 2007). Ocean climate is thus a major driver of distribution, abundance, and reproduction of marine mammals with enormous potential to influence the way that individuals and populations respond to extrinsic stressors. However, clear linkages between ocean climate and marine mammal population trends have not been well documented. A study on southern elephant seals spanning five decades also highlighted the importance of considering density effects in combination with environmental conditions to evaluate effects on populations because these factors can interact (de Little et al., 2007).

Besides ocean climate shifts due to ENSO, PDO, or NAO, changes in global and ocean climate that result from anthropogenic climate alteration are likely to have profound impacts on marine mammals (Moore and Huntington, 2008) that will potentially interact with other stressors. Some marine mammals associated with polar ice are already showing shifts in distribution, reduced body condition, and declines in abundance and reproduction in response to declines in sea ice (Kovacs et al., 2011). However, the quality of abundance estimates varies greatly among location and species and in most cases the data currently are not sufficient for analyzing population trends (Laidre et al., 2015). For bowhead whales, the warming Arctic regions have proved beneficial. Their axial-girth-based body condition index ( $BCI_G$ ) is positively correlated with summer sea ice loss over the past 2.5 decades, and  $BCI_G$  is significantly correlated with the duration of the melt season (George et al., 2015). Range expansions of temperate species may alter resource competition in high-latitude habitats. Long-term impacts may include alteration in oceanographic features used in foraging strategies. Changes in prey distribution and abundance may also occur as a result of disruption of ocean currents

and increases in the energetic cost of calcification caused by ocean acidification (Doney et al., 2012). Ocean warming has been implicated in reports of rising disease prevalence in marine organisms, including marine mammals (Harvell et al., 2002; Lafferty et al., 2004; Burek et al., 2008; Van Bressem et al., 2009). Emerging evidence from climate change studies (Ockendon et al., 2014) suggests that indirect effects of stressors, through the disruption of interspecific interactions, may be more important than direct ones. Apparently caused largely by increased nutrification, dead zones (hypoxic areas) have increased in recent years in many coastal areas, such as the northern Gulf of Mexico (Rabalais et al., 2002; Diaz and Rosenberg, 2008). Although the influences of dead zones on marine mammals have not been well documented, reduced production and prey availability (Grimes, 2001) almost surely are detrimental to these animals.

### SPATIAL AND TEMPORAL VARIATION AMONG STRESSORS

The range of extrinsic stressors to which marine mammals can potentially be exposed over a lifetime has been briefly reviewed, but to appreciate the potential for cumulative effects of these combined stressors, the spatial and temporal patterns of exposure should also be considered. The occurrence of individual stressors may show strong spatial variation, and their effects depend on the habitat used by a given marine mammal species. Even ubiquitous stressors, like anthropogenic noise and globally dispersed chemical contaminants, show variation in magnitude across geographic regions. Species that exhibit long-distance movements may be exposed to diverse stressors in disparate ecosystems, and consideration of cumulative effects must include stressors throughout this range. Although highly migratory species may be exposed to a wide range of stressors, the aggregate exposure of individuals may be low (e.g., Christiansen and Lusseau, 2015), affecting the overall impact at a population level. In contrast, species with smaller home ranges may potentially be exposed to fewer stressors, but with greater exposure times to those that occur in the region.

There is also a potential temporal component to variation in vulnerability to stressors related to life-history variation within species. For example, the need of capital breeding species to conserve energy may outweigh short-term costs of local stressors during breeding (Bishop et al., 2015). However, once breeding is completed they may be at an exceptionally low nutritional plane with high allostatic load that reduces their ability to respond to new stressors. Females with calves or pups may also be more sensitive to disturbance and perceived threats (Engelhard et al., 2002; Stamation et al., 2009). During key foraging periods, animals may be less vigilant in responding to threats, which may increase their vulnerability to other stressors such as predators. Some behavioral states also increase vulnerability to stressors. For example, during feeding North Atlantic right

whales spend much of their time just below the surface, increasing the risk of vessel collisions (Parks et al., 2012). Stressors that affect prey availability and predation risk on the feeding ground may directly impact animals' body condition, pregnancy rate, and survival (Williams et al., 2013). Because these life-history periods are often associated with specific habitats or spatial use, managers should consider this dimension when assessing the potential impacts of the spatial component of exposure to stressors. From this perspective, chronic stressors that impact individuals across multiple life-history stages are more likely to have deleterious effects than those that impact only one life-history stage. Species or populations that are continually exposed to stressors in a particular location with a given geospatial distribution are also more likely to suffer deleterious effects than species that migrate through that location and are only periodically exposed.

The physiological and behavioral impacts of single and multiple stressors will also vary depending on the frequency of exposure. Ongoing or continuously occurring (i.e., chronic) exposure can be associated with dysregulation of endocrine and homeostatic function and therefore have negative impacts on individual fitness. Chronic activation of generalized stress responses may be an important mechanism through which cumulative impacts arise. Conversely, when exposure to a stressor is acute, occurring for a single discrete period, or intermittent, occurring repeatedly but not necessarily at frequent or regular intervals (e.g., HABs or sonar), animals may accommodate. That is, a physiological response may be invoked but normal function is then restored or a new homeostatic set point is reached. In some cases, the resulting physiological responses may be adaptive and even enhance the ability to respond to future stressors through hormesis<sup>1</sup> (Calebrese et al., 2007). However, even if the exposure is not chronic, an alternative mechanism for cumulative impacts emerges when the adverse effect produced by the stressor persists or is irreversible (i.e., a chronic effect). For example, a permanent threshold shift in auditory sensitivity will impact behavior.

## SUMMARY AND CONCLUSIONS

Numerous studies have evaluated the impact of various extrinsic stressors on the individual health, survival, or reproduction of marine mammal species. Stressors such as fishery interaction, vessel strike, HAB toxins, and pathogens can cause acute mortality. Even when there are effects that are nonfatal, they can induce sublethal effects that continue to affect the animal's ability to maintain homeostasis and respond appropriately to other extrinsic or intrinsic stressors. The broad array of chemicals to which many marine

mammals are exposed, often chronically over their lifetime, also produce sublethal physiological effects. Such effects have been documented from observational studies of marine mammals and in many cases are supported by findings from experimental studies in other mammalian species. However, linking chemical stressors to decreases in vital rates through observational assessments is inherently challenging due to the chronic nature of many exposures or effects, the complexity involved in controlling for confounding or interacting variables, and the difficulty of observing mortality or reproductive end points in long-lived marine mammal species, particularly cetaceans. These challenges extend to other stressors that induce sublethal effects. Regardless of the stressor, few studies have explicitly defined *quantitative* relationships between varying doses and associated mortality, reproductive, or physiological effects for marine mammals.

**Finding 3.1:** Numerous studies have demonstrated direct physiological effects from a broad array of extrinsic stressors in marine mammals. However, few studies have explicitly quantified the relationship between varying doses of a given stressor and the level of mortality, reproductive, or physiological effect (i.e., defined a dose–response relationship).

Ecological drivers such as ocean climate shifts act directly or indirectly through prey or other resources to induce stress on marine mammal populations. Similarly, fisheries can directly create competition for resources, or indirectly affect prey availability through ecosystem changes. Wildlife tourism or other forms of disturbance that may be perceived as a threat evoke more acute responses but may have aggregate effects. For these stressors, analysis challenges stem from complexities in ecosystems and/or difficulties in elucidating long-term shifts in behavior or habitat use, constraining the ability to clearly interpret cause and effect at the population level.

The occurrence of some stressors may show strong spatial variation. In addition, an animal's vulnerability to stressors may vary temporally in relation to life history. Therefore, temporal and spatial variation in exposure to stressors must be considered. Ongoing or continuously occurring (i.e., chronic) exposure to a stressor can be associated with dysregulation of endocrine and homeostatic function and therefore may be an important mechanism through which a cumulative effect manifests within individuals. Even if the exposure is not chronic, an alternative mechanism for a cumulative impact emerges when the adverse effect produced by the stressor persists or is irreversible (i.e., a chronic effect).

**Finding 3.2:** The effects of stressors on marine mammals depend on temporal and spatial overlap in the distribution of stressors and the target organisms. Chronic exposure or a chronic effect resulting from an acute exposure provides mechanisms through which cumulative impacts may arise.

<sup>1</sup> A phenomenon of dose–response relationships wherein a stressor that produces harmful biological effects at moderate to high doses may produce beneficial effects at low doses.

## 4

## Assessing Interactions Among Stressors

### INTRODUCTION

As described in Chapters 2 and 3, marine mammals are exposed to a diverse set of extrinsic stressors during their lifespan. Understanding the way exposure to any one stressor may affect marine mammal populations is challenging; understanding the population-level consequences of exposure to multiple stressors is far more challenging. However, a key to understanding how the effects of extrinsic stressors might integrate to create cumulative effects is determining how specific stressors create responses, and evaluating the potential for interactions between the effects of these responses over the lifespan of an individual. It is important to be clear what is meant by an interaction between stressors. Gennings et al. (2005) reviewed the models that have been used to quantify toxicological interactions and defined an interaction between two chemicals as occurring when the shape of the dose–response relationship for one chemical is affected by the dose of the other chemical. The committee adopted the same definition for interactions between stressors. If the shape of the dose–response relationship of one stressor does not change in the presence of another stressor, then these stressors do not interact, and the responses are said to combine additively.

The impact of multiple extrinsic stressors can be studied at different levels of biological organization from molecular, cellular, or organ responses, to effects on the individual, to higher-order population- and community-level responses (see Figure 4.1). Accommodation, or recovery that restores normal function, may occur at any level of organization (e.g., Nichols et al., 2011). However, when the exposure to a stressor is sufficient, the response at one level will be propagated to the next level. For example, at the molecular level, changes in gene expression, enzymatic reactions, and receptor function may occur in response to a stressor; these

in turn may initiate cellular responses such as differentiation, proliferation, or altered hormone synthesis. When sufficient, these cellular responses can produce an injury to an organ or disruption of an endocrine axis that eventually leads to morbidity, mortality, or reproductive failure for the individual. If sufficient individual-level responses occur, there can be impacts on populations and, ultimately, communities and ecosystems. It is at these higher levels of biological organization that responses are of greatest societal relevance and greatest concern for natural resource, coastal, and ocean management.

Although the flow of responses in Figure 4.1 is depicted as moving upward through increasingly higher levels of biological organization, responses may also be introduced at a higher level (e.g., ecosystem or community) and then initiate a cascade of responses within an individual marine mammal. The El Niño–Southern Oscillation would be an example of an ecological driver initiated at the ecosystem level, which can cause prey depletion, prompting a response at the molecular level, which then propagates upward to an individual-level response.

Unfortunately in many cases, responses at the higher levels cannot be detected until the process is so far along that the change may be catastrophic and irreversible. It is therefore important to study effects of stressors at the lower levels of biological organization. However, it is imperative to supplement the information on lower-level responses with an understanding of the linkages and processes by which such responses eventually translate into higher-level impacts. The linkages and associations of responses across different levels of biological organization are considered by ecotoxicologists when describing adverse outcome pathways (AOPs) (Ankley et al., 2010; Connon et al., 2012) and by conservation physiologists when describing biological upscaling (Cooke et al., 2014). Depending on the context, an AOP may be

considered to extend from molecular-level responses all the way through to population-, community-, or even ecosystem-level responses. Similarly, the Population Consequences of Disturbance (PCoD) model structure (New et al., 2014), which is used in Chapter 5 as the basis for a model of the population consequences of exposure to multiple stressors, describes a series of compartments and transfer functions that upscale from physiological or behavioral changes to anticipated impacts on population vital rates. The series of transfer functions between compartments from the initial physiological change to the ultimate effect on individual vital rate or population dynamics in the PCoD model is essentially equivalent to an AOP. However, for this report, the committee defines an AOP to span the molecular- to individual-level responses shown in Figure 4.1.

In practice, it is extremely difficult to detect interactions between two stressors by determining the dose–response relationship for one stressor at different dosages of the second stressor. Instead, most research has focused on detecting deviations from additivity, usually by assessing the significance of the interaction term in an analysis of variance (ANOVA) or other linear model analysis of results from a

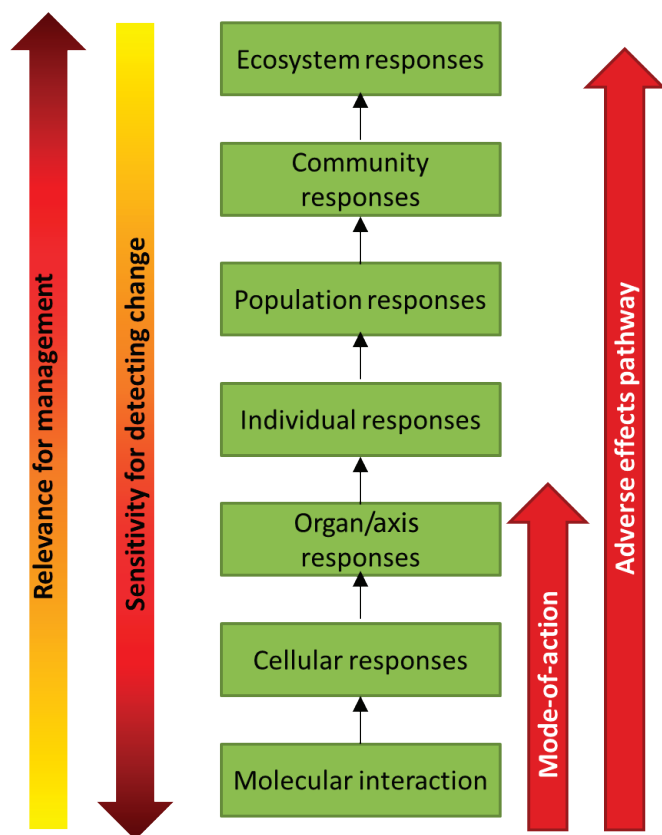
controlled factorial experiment (Folt et al., 1999), or the deviations from a null model of additive effects (e.g., Darling and Côté, 2008). However, as Greenland (2007) notes, “concepts of biologic interaction do not in general correspond to the concept of statistical interaction, because the latter is only the need for a product term in a statistical model.”

In the next section, the results of recent meta-analyses of studies of the interactions between stressor effects that have used this statistical approach are reviewed in order to assess the prevalence and nature of interactions between extrinsic stressors in marine and freshwater systems. However, as noted above, these meta-analyses only provide information on whether statistical interactions have been detected: they do not provide quantitative models of the way the stressors actually interact. In subsequent sections the committee describes how interaction effects may be quantified by considering common pathways for adverse health outcomes along which different stressors act, provides some examples of the way in which the extrinsic stressors to which marine mammals are exposed may interact, and explains how stressors might be prioritized for cumulative effects analysis. Finally, that approach is used to look at the potential causes of some unexplained declines in marine mammal populations.

## STUDIES OF MULTIPLE STRESSORS: A BRIEF REVIEW

As noted in the previous section, most studies of interactions among multiple stressors test whether the effect of the stressors together is significantly different from the combined effect of each stressor acting independently. The magnitude of effect expected depends on the mathematical operation used to combine the independent effects. For example, stressor effects may be combined additively or multiplicatively depending on the nature of the response being tested. Because a multiplicative combination of stressor effects is additive on the logarithmic scale, both methods of combination are usually referred to as “additive.” The test statistics that are most commonly used are Hedges’  $d$ , which, according to Crain et al. (2008), is “constructed similar to ANOVA where a significant interaction effect signifies deviation from the null model of additivity,” and the sum of the natural logarithms of the response ratios ( $\ln RR$ ) for each stressor. For the latter metric, an interaction is identified if the difference between the  $\ln RR$  when both stressors are present and the sum of the  $\ln RR$  values for the individual stressors is significantly greater than zero. If the combined effect of two or more stressors is greater than the combination of their individual effects, this is referred to as a synergistic interaction. If it is less than the combination of the individual effects it is referred to as an antagonistic interaction. If there is no significant difference, the cumulative effect is referred to as additive.

The complications that can arise with these simple null models are elegantly summarized by Côté et al. (2016). For



**FIGURE 4.1** The hierarchy of responses to a stressor across multiple levels of biological organization.

example, synergistic interactions are impossible to detect with these methods if the sum of the individual effects is greater than 100% (Folt et al., 1999). These issues can be overcome by using the “multiplicative risk model” as described by Sih et al. (1998). The predicted combined effect using the multiplicative risk model is less than the predicted effect from a simple additive model, and its use as the null model is therefore more likely to result in the detection of synergistic interactions. Further complications occur if the effect of one stressor is so large that it results in the death of most experimental animals before any other stressor can have an effect. This is referred to as “dominance” by Côté et al. (2016). It would be incorrectly identified as an antagonistic interaction using a simple additive model. Additional problems arise if the stressors under consideration have opposite effects. In these cases, the threshold for a synergistic or antagonistic effect is actually smaller than the effect of either of the stressors. Such effects have been referred to as “reversals” (Jackson et al., 2016). Finally, in some cases the combined effect of the two stressors is in the opposite direction to the effects of either of the individual stressors, a phenomenon called “mitigating synergism” by Piggott et al. (2015).

Crain et al. (2008) reviewed 171 studies that used factorial experimental designs to investigate the effects of two or more of 13 stressors on marine and coastal environments. About 90% of the experiments were done in the laboratory and three-quarters of the studies subjected single species rather than entire communities or ecosystems to the stressors. They detected synergistic interactions using Hedges’ *d* in 36% of the studies and antagonistic interactions in 38%. When a third stressor was added, the proportion of synergistic pairwise interactions increased from 33% to 66%. Piggott et al. (2015) reanalyzed the same data set as that used by Crain et al. (2008) to take account of comparisons in which the stressors had opposite effects and the potential for mitigating synergisms. They found fewer examples of synergistic interactions (31% versus 36%) and more examples of antagonistic interactions (43% versus 38%).

Harvey et al. (2013) analyzed 623 observations from controlled factorial studies of the cumulative effects of temperature and acidification on calcification, photosynthesis, reproduction, survival, and growth in marine organisms using lnRR as the test statistic. Their analysis found evidence for synergistic interactions between the two stressors for four of the response variables. This was the result of a greater than expected increase in photosynthesis, and a greater than expected reduction in calcification, reproduction, and survival.

Ban et al. (2014) used a parametric bootstrap approach for calculating the standard error of the interaction term in an ANOVA of the results from studies of the effects of multiple stressors on coral reefs. Their aim was to increase the statistical power of more conventional analyses, which can result in failure to detect an interaction when one is, in fact,

present. They analyzed the results of 26 fully factorial studies that investigated the cumulative effect of irradiance and temperature on photosynthesis in corals and found that the mean effect size of the combined treatments was statistically indistinguishable from a purely additive model.

Jackson et al. (2016) analyzed values of Hedges’ *d* extracted from 286 observations of the responses of freshwater ecosystems to paired stressors in controlled factorial experiments. They found that multiple stressors exerted significant antagonistic effects on animal abundance/biomass, animal condition, animal growth/size, and animal survival.

Przeslawski et al. (2015) analyzed values of Hedges’ *d* extracted from the results of 104 factorial experiments that examined the cumulative effects of temperature, salinity, and pH on growth and/or survival of the embryos or larvae of marine organisms using a generalized linear mixed-effects model. They found evidence for synergistic interactions between temperature and pH in 76% of the experiments, and for synergistic interactions between temperature and salinity in 58%.

This review of meta-analyses establishes that the cumulative effects of multiple stressors may be additive, antagonistic, or synergistic in almost every setting tested. The proportion of cases providing evidence for antagonism and synergism varied substantially among studies. As a result, the prevalence of interactions between stressors in nature remains uncertain, especially because the relatively low statistical power of most of the studies (Ban et al., 2014) will have resulted in some interactions going undetected. Nonetheless, the basic conclusion that one can take from all of these studies is that there are few situations where one can confidently assume that the effects of multiple stressors are additive. Although Côté et al. (2016) have pointed out that synergies are not the most prevalent form of interaction reported in the literature, and caution about the risks of managing antagonistic interactions as if they were synergistic, they also found that “physiological response variables have so far not yielded evidence of antagonisms.” Because physiological responses are a fundamental component of most of the observed reactions of marine mammals to extrinsic stressors, this suggests that assuming the effects of individual stressors are additive may frequently lead to an underestimation of their cumulative impact.

**Finding 4.1:** There are few situations where one can assume that the effects of multiple stressors are simply additive, and this assumption may lead to an underestimation or overestimation of their cumulative impact.

Most of the studies of cumulative effects of multiple stressors that contributed to these reviews have used factorial designs. This leads to elegant experiments with simple analyses in situations where the conditions can be replicated and controlled. However, if the factorial design does not actually provide a dose–response relationship for each stressor–effect



pair, or for any relevant combinations of stressors, then it is of little use to management. The critical questions for managers who aim to prevent threats are “What stressor effects threaten populations or ecosystems, and what combinations of dosages of stressors elevate the effect enough to pose a risk?” Given that many anthropogenic stressors have negative effects on marine mammals, simply evaluating whether their cumulative effects may be antagonistic, additive, or synergistic does not provide the information needed to decide whether specific dosages of one or more stressors are likely to cause an effect that poses a risk to species of concern. The critical point for managers in the planning phase is to define population-level effects that need to be avoided, and then to evaluate whether the cumulative impact of a planned activity, of other activities, and of the relevant array of natural stressors poses a risk of causing the deleterious effects. After it is discovered that a population or ecosystem is in danger, then the critical issue is to evaluate what changes in stressors will provide the best reduction in risk at the least disruption of other critical human priorities. Both of these problems require assessment of dose–response relationships across the relevant range of dosages and effects. Ideally this assessment should be conducted under realistic field conditions, coupled with quantitative assessments of the interaction between all stressors that may cause the effect of concern.

**Finding 4.2:** The critical question for managing risk of cumulative effects is “What combinations of dosages of stressors are likely to elevate the effect enough to pose a risk to populations or ecosystems?” Once a population is found to be at risk, then the critical issue is to determine which combination of stressors could be reduced in order to bring the population or ecosystem into a more favorable state.

## CUMULATIVE IMPACT SCORES

Halpern et al. (2008) used expert-derived vulnerability weights from Halpern et al. (2007) and a cumulative impact model to identify what they believed to be the greatest threats among 38 different stressors and ecological drivers at large or small spatial scales of marine ecosystems, and to identify the most threatened ecosystems. They used this method to create a global map of human impacts on marine ecosystems, and they argue further that this map can be used to allocate conservation resources for ecosystem-based management. Maxwell et al. (2013) adapted the methods of Halpern et al. (2007, 2008) and used them to estimate cumulative impacts for marine mammals and other marine predators. Here a critical review of this approach is provided.

Halpern et al. (2008) calculated cumulative impact scores  $I_C$  for each 1 km<sup>2</sup> of ocean using the following equation:

$$I_C = \sum_{i=1}^n \sum_{j=1}^m D_i \times E_j \times \mu_{i,j},$$

where  $D_i$  is the log-transformed and normalized value of the intensity of the driver at location  $i$ ,  $E_j$  is the presence or absence of ecosystem  $j$ , and  $\mu_{i,j}$  is an impact weighting for each driver–ecosystem pair. Drivers were allowed to have different weights for different ecosystems, but this calculation of cumulative impact assumes the effects of the drivers are additive, with no interaction between them. Maxwell et al. (2013) estimated the cumulative impact of multiple stressors (CUI) using a similar equation:

$$CUI = \sum_{i=1}^n \sum_{j=1}^m D_i \times S_j \times \mu_{i,j}$$

where  $D_i$  is the normalized and log-transformed value of intensity of an anthropogenic stressor at location  $i$ ,  $S_j$  is the probability distribution of species  $j$  being present in a given cell, and  $\mu_{i,j}$  is the impact weight, which reflects the potential effect of anthropogenic stressor  $i$  on species  $j$ . The impact weight for each stressor–species combination is calculated from expert rankings of the importance of a number of different vulnerability measures for that combination.

The determination of impact weights is a critical aspect of this approach. Halpern et al. (2007) used two numerical measures (area and recovery time) of vulnerability, and three ordinal variables (frequency, extent of ecosystem impacted, and resistance of the ecosystem to the threat). Maxwell et al. (2013) used six measures (frequency of impact, whether the impact was direct or indirect, likelihood of mortality, individual recovery time, reproductive impact, and spread of the impact across the population). These rankings are then combined into a single vulnerability score.

This kind of arbitrary tallying of ordinal scores is not uncommon in situations where, for example, a health practitioner wants a simple repeatable way to assess the cumulative risk of a series of factors for a specific adverse outcome. However, the committee thinks that the arbitrary tallying of this kind of scale requires validation. When Halpern et al. (2007) asked the experts to identify the three top threats in the ecosystems, only half of the results of the vulnerability ranking matched the judgment of the experts, indicating either that there was low confidence in the resulting rankings or that the experts suffered from perception bias.

The cumulative impact scores used by Halpern et al. (2008) and Maxwell et al. (2013) assume that cumulative effects are additive across threats within an ecosystem. As discussed above, all the reviews of the effects of multiple stressors found evidence for synergistic and antagonistic interactions, which suggests that this simple additive approach may overestimate some impacts and is likely to underestimate others. The committee recognizes the enormous amount of work that has gone into developing this approach and compiling the databases needed for its application. Determining the spatial overlap between human activities and species or ecosystems is an important first step in identifying locations where interactions between stressors

are likely to occur. However, the committee believes that a better quantitative understanding of potential exposure levels, dose–response functions, and linkages to vital rates is required to provide an adequate assessment of cumulative effects in these locations.

### **PREDICTING HOW MULTIPLE STRESSORS ARE LIKELY TO INTERACT**

A consideration of cumulative effects has been often discussed with respect to marine mammals (Wright and Kyhn, 2015), and such effects must be considered in Environmental Assessments and Environmental Impact Studies (40 C.F.R. § 1508.7). However, in spite of the large number of factorial experiments in other taxa, no experiments have examined the cumulative effects of multiple stressors on marine mammals. Quantification of the interactions between these stressors is hindered by a limited understanding of the physiological and behavioral effects of cumulative exposure, and the logistical difficulties of measuring the impacts of this exposure on free-ranging individuals over their lifespans.

Any stressor that induces effects up to at least an individual level (e.g., mortality or reproductive impairment), whether exposure is acute, intermittent, or chronic, has the potential to contribute to a cumulative population-level impact. For example, direct lethal effects may occur as a result of acute exposure to ship strike, intermittent exposure to infectious disease outbreaks or harmful algal blooms, or to the risk of bycatch in fishing gear that is left in the water for long periods (e.g., gillnets). In most cases, the acute effects of each stressor on survival can be evaluated independently and their cumulative effect calculated using a multiplicative risk model that accounts for the fact that an individual can only be killed once.

However, it is more difficult to predict the interactions that may occur among stressors that have a chronic effect on survival and reproduction, and that therefore have the potential to generate unexpected, nonadditive effects for populations and communities. These occur when a stressor affects an individual's homeostatic systems so that it can no longer respond appropriately to its environment, and its vulnerability to other stressors is increased. Interactions may also occur at the population level if the stressor effects result in demographic changes, for example, if mortality is preferentially focused on adult females. They may also occur at a higher level of biological organization (community or ecosystem level) if a tipping point (see Chapter 6) is reached because an ecological driver has, for example, caused a collapse in the prey base. In the rest of this section, approaches that can be used to improve understanding of potential interactions between stressor effects at the individual level are explored. The potential for interactive effects at higher levels is discussed in Chapter 6.

Insight for predicting cumulative effects at the individual level can be gained from the environmental health and

ecological risk assessment communities, where scientists are grappling with the complicated issue of cumulative risk assessment for chemical mixtures. There are more than a hundred million chemical substances known to date,<sup>1</sup> and a recent report from the Centers for Disease Control and Prevention provides data for 265 environmental chemicals that are a potential concern for human exposure.<sup>2</sup> People, other terrestrial organisms, and marine organisms are all exposed to this plethora of potentially toxic substances to varying degrees and are most often exposed to mixtures of these chemicals chronically or repeatedly throughout their lives.

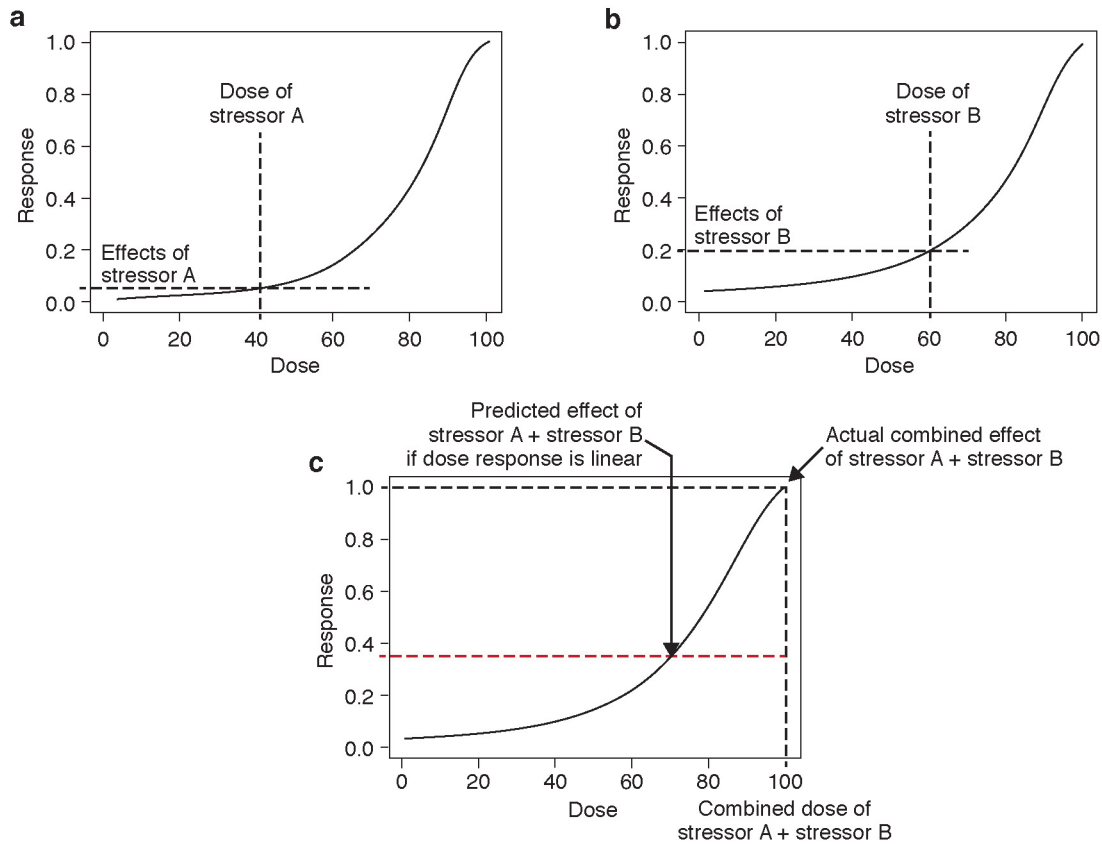
A number of different approaches have been proposed for assessing the cumulative risk for multiple chemicals. They often involve identifying a group of chemicals that can be considered collectively (EPA, 2000). One mathematical modeling approach integrates an index for chemicals that co-occur in the environment and have similar structure or mode of action in order to predict a cumulative dose (EPA, 2002; Connon et al., 2012). The index for each chemical can be based on its concentration and toxic potential; therefore, the approach is most applicable for chemicals with a well-characterized mechanism for toxicity, such as the dioxin-like compounds whose toxicity is induced through the aryl hydrocarbon receptor (Van den Berg et al., 2006). Alternative approaches have been suggested that focus on the overall physiological process, rather than mechanisms or modes of action, because there can be a multitude of underlying molecular mechanisms that contribute to a given adverse outcome. This potentially expands the array of chemicals to be considered collectively, because chemicals that have distinct modes of actions may still disrupt the same endocrine pathway or organ system and, ultimately, result in the same disease.

There are clearly limitations to the expansion of these approaches to the multitude of stressors, particularly non-chemical ones, that are of potential concern for marine mammals. However, the paradigm of using co-occurrence, and a common mechanism of action or a common outcome, may be valuable. At the molecular level, it may be possible to predict the effect of stressors that have a similar mode of action using a common dose–response relationship. The cumulative effect of these stressors will only be additive in the unlikely event that the common dose–response function is linear (see Figure 4.2).

One common assumption of ecotoxicologists is that if two or more stressors act through a common mechanism of action, then their doses can be summed to provide a cumulative dose that can then be used with a single dose–response function. Many dose–response functions are sigmoidal in shape or are otherwise nonlinear, and in these cases the sum of two doses may produce a response that is greater or less than the added responses of each stressor alone. A simple

<sup>1</sup> See <http://www.cas.org>.

<sup>2</sup> See <http://www.cdc.gov/exposurereport>.



**FIGURE 4.2** This figure illustrates how the potential for interaction between two stressors (A and B) that share a common mechanism of action depends on the form of the dose–response relationship. (a) Effect of stressor A alone. (b) Effect of stressor B alone. (c) Effect of a combined dose of stressor A and stressor B, obtained by adding the dose from stressor A to that of stressor B. The effect predicted from the dose–response relationship shared by the two stressors is three times higher than the prediction if their effects are assumed to be additive (red line).

example to illustrate the complexity introduced when a dose–response function is nonlinear is discussed below.

Consider two stressors that act through a common mechanism of action. If one of these stressors is more powerful than the other, then its dosage needs to be adjusted by a metric that corrects for the difference in their relative strengths (e.g., a toxicity factor for chemical stressors). After this correction, the doses of the two stressors can be added to give a combined dosage and compared to a dose–response function (see Figure 4.2). Stressor A has an effect of 0.10 given a dose of 40 units (see Figure 4.2a), and stressor B has an effect of 0.20 given a dose of 60 units (see Figure 4.2b). If responses were additive, then the response to stressors A and B combined is expected to be 0.30. However, due to the sigmoidal shape of the dose–response function, the added doses of the two stressors (100 units) produces an effect of 1.0, more than threefold higher than the sum of the individual responses (see Figure 4.2c). Therefore, although these stressors are considered additive in terms of dosage, they produce a synergistic response. Note that this same phenomenon

could also occur with aggregate exposure to a single stressor. Even for this simple situation, a prediction cannot be made of the effects of most stressors because the dose, the relative strengths of the stressors, and the dose–response functions are not known.

Similar interactions may occur at the organ system and individual levels if the stressors act through a common or connected pathway. This may occur if the stressors induce damage or provoke a physiological perturbation within the same organ system or endocrine axis, in which glands signal each other in sequence and/or with feedback loops, such as the hypothalamic-pituitary-adrenal (HPA) axis. In addition, effects via one cellular mechanism or component of an endocrine axis may impact the function of other components through shared signaling pathways. Due to this complexity, the overall physiological process or pathway for an adverse health outcome should be considered. Of primary concern are those pathways that lead to a permanent or at least long-lasting (persistent) adverse health condition, because co-occurrence of the health effects of multiple

stressors within an individual is necessary for an interaction to ensue. Alternatively, although the health effect associated with a particular exposure to a stressor could be transient, co-occurrence with other stressor effects is still likely if the exposure to the stressor is chronic.

**Finding 4.3:** Predicting which combinations of dosages of stressors are likely to elevate cumulative effects enough to pose a risk to populations or ecosystems will be challenging, particularly for stressors that have a chronic effect on survival and reproduction. The paradigm of using co-occurrence and a common pathway for adverse health outcomes, developed by the environmental health and ecological risk assessment communities, could be applicable for addressing this challenge.

Marine mammals are exposed to stressors that have the potential to interact as a result of chronic exposure, or because they may cause permanent or persistent health conditions. The pathways for a persistent health outcome along which each stressor may act are indicated in Table 4.1. Non-biological toxins are divided into persistent organic pollutants (POPs), inorganic pollutants, and petroleum-associated chemicals and organic solvents, because these most often exert effects through differing pathways. Note that this table is not intended to provide an exhaustive list of all the possible sublethal effects associated with each stressor. Only the principal and previously recognized pathways are indicated, with one or more illustrative references. In addition, only direct pathways are indicated as priorities for consideration. The potential for interaction between pathways should not be disregarded. For example, although the hypothalamic-pituitary-thyroid (HPT) and HPA endocrine pathways are presented separately, effects on one axis may impact the function of the other because of shared molecular substrates, enzymatic reactions, and signaling pathways (Nichols et al., 2011). Ultimately, they may impact other connected pathways, such as the immune or central nervous systems (CNS). There are strong associations in some marine mammals of contaminant burdens with suppression of sex hormones, including testosterone and estradiol. In some cases low levels of sex hormones concomitant with high POP burdens were associated with sterility or reproductive failure (Reijnders, 2003).

## POTENTIAL INTERACTIONS AMONG STRESSORS

In this section the committee reviews documented or proposed interactions between stressors, focusing on interactions that occur along the same pathways for persistent health outcomes (see Table 4.1). Most of the interactions we consider are synergistic, not only because ignoring such interactions in an assessment of cumulative impacts increases the risk of underestimating those impacts, but also because Côté et al. (2016) found no evidence for antagonistic interactions

involving physiological responses to stressors, such as those mediated by pathways for persistent health outcomes.

### Acute Mortality

A number of the stressors listed in Table 4.1 (noise, some organic chemicals and solvents, biotoxins, microparasites, prey limitation, and predation pressure) may have direct, acute effects on survival or reproduction. In some situations where marine mammals are exposed to several of these stressors there may be little opportunity for stressor effects to interact, because individuals are likely to die from the effects of one stressor before they can be affected by any of the others. In these circumstances, as noted earlier in this chapter, treating the effects of each stressor as independent can be justified. However, it should be recognized that historical exposure to other stressors may increase an individual's susceptibility to acute effects from a particular stressor. For example, Hall et al. (2006) showed that previous exposure to polychlorinated biphenyls (PCBs) increased the risk of death from infectious diseases in harbor porpoises. In addition, a multiplicative risk model should be used to account for the fact that individuals are unlikely to die from the effects of more than one acute stressor. Because acute effects are normally evaluated by attributing cause of death to a particular stressor, the simplest approach is to calculate the survival rate of individuals exposed to each stressor. The cumulative effect of all the stressors to which the population is exposed is then calculated by multiplying together the survival rates associated with each stressor.

Although there is little opportunity for interaction among the acute effects of different stressors, chronic effects caused by the same or other stressors can interact with acute effects if they alter individual exposure or susceptibility to the acute stressors. These interactions between acute and chronic stressor effects may be antagonistic. A classic example is the use of active sound emitters ("pingers") to reduce the risks of cetacean bycatch in fishing gear (Dawson et al., 2013). Noise from these emitters displaces marine mammals from the area around the gear to which they are attached, thus reducing their risk of physical injury as a result of entanglement but imposing potential energetic costs.

### Hypothalamic-Pituitary-Adrenal Axis

The HPA axis has a central role in coordinating an organism's response to stress, controlling the release of glucocorticoids into circulation and moderating levels through negative feedback (Sapolsky et al., 2000). Glucocorticoid secretion is further modulated by neuronal effects of other brain structures; also gene-environment interactions in response to stressors may have long-term impacts on subsequent secretion (Alexander et al., 2009). Disruption of the HPA axis may therefore interact with the effects of other stressors, particularly if the disruption is the result of chronic

**TABLE 4.1** Stressors with Potential for Chronic/Repeated Exposure or Persistent Effects, and Associated Pathways for Adverse Health Outcomes

Pathway for Persistent Adverse Health Outcome								
Stressor	HPA axis	HPT axis	Nutritional	Immune	Reproductive	Respiratory	Brain/CNS	Auditory (hearing loss)
Noise	<b>Rolland et al., 2012</b>		<b>Isojunno et al., 2016; Ware et al., 2015</b>	Celi et al., 2015	Halfwerk et al., 2011; Kight et al., 2012			<b>Finneran, 2016</b>
<b>Non-biological toxins: potential chronic exposure (POPs, inorganic pollutants) and/or persistent adverse health outcome</b>								
POPs (primarily PCBs)	Possible, but not well described; Harvey, 2016; <b>Oskam et al., 2004</b>	Patrick, 2009; Tabuchi et al., 2006; <b>Schwacke et al., 2012</b>		Diamanti-Kandarakis et al., 2009; <b>Ross et al., 1996a, 1996b; Lie et al., 2004, 2005</b>	<b>Reijnders, 1986; Diamanti-Kandarakis et al., 2009</b>		Developmental; Zoeller et al., 2002	Developmental; Crofton et al., 2000; Kenet et al., 2007
Inorganic pollutants				<b>Kakuschke and Prange, 2007</b>			Farina et al., 2011	
Petroleum-associated or other organic chemicals or solvents	Mohr et al., 2008, 2010; <b>Schwacke et al., 2014a</b>			<b>Schwartz et al., 2004</b>	<b>Lane et al., 2015</b>	<b>Schwacke et al., 2014a</b>		Fuente and McPherson, 2006
<b>Biological toxins: potential recurrent exposure, and potential persistent adverse health outcome</b>								
Biotoxin	Gulland et al., 2012			<b>Schwacke et al., 2010</b>	<b>Goldstein et al., 2009</b>		<b>Cook et al., 2015</b>	
<b>Pathogens: persistent adverse health outcome (microparasites) or potential chronic exposure (macroparasites)</b>								
Micro- or macro-parasites			<b>Reif et al., 2006</b>	Some, e.g., morbillivirus; Van Bresse et al., 2014	Some, e.g., Brucella; Meegan et al., 2012		Some, e.g., morbillivirus; Van Bresse et al., 2014	
<b>Other stressors with potential for chronic or repeated exposure</b>								
Prey limitation	<b>Rosen and Kumagai, 2008; Shero et al., 2015</b>	Eales, 1988; Ayres et al., 2012; <b>Gobush et al., 2014</b>	<b>Crocker et al., 2006</b>	<b>Brock et al., 2013a; Peck et al., 2016</b>	Meyer-Gutbrod et al., 2015; Ward et al., 2009; Robinson et al., 2012			
Perceived threat	<b>Spoon and Romano, 2012; Di Poi et al., 2015; Champagne et al., 2012</b>		<b>Isojunno et al., 2016</b>	<b>Brock et al., 2013b</b>	<b>French et al., 2011</b>			
Predation pressure	Newman et al., 2013; Narayan et al., 2013		Creel et al., 2009					Creel et al., 2007; 2009; Hua et al., 2014; Zanette et al., 2011
Salinity				<b>Wilson et al., 1999; Mullin et al., 2015</b>				

NOTE: Publications highlighted in bold refer to studies involving marine mammals.

exposure to a persistent chemical contaminant, because of the numerous points of regulation and complexity of the involved biochemical pathways. However, an understanding of specific mechanisms for a given set of stressors would be needed to accurately predict the consequences of any resulting interactions.

The analysis provided in Table 4.1 suggests that cumulative risk associated with sound and other stressors will occur primarily through the HPA axis. While there is some evidence that the presence of ships and their accompanying sounds affect the HPA axis (Rolland et al., 2012), no studies have looked at the cumulative risk of sound and other stressors through the HPA axis. The indirect effects of sound through prey limitation and predator response are discussed in Chapter 2.

There is strong evidence that petroleum-associated chemicals can adversely affect the HPA axis, providing a potential pathway for interactions with other stressors. Studies by Mohr et al. (2008, 2010) of mink (*Mustela vison*) as a surrogate for sea otters (*Enhydra lutris*) found that exposure to fuel oil interfered with the HPA pathway, resulting in damage to the adrenal gland and an insufficient stress response when the animals were experimentally stimulated with adrenocorticotropic hormone. Polycyclic aromatic hydrocarbons (PAHs), the predominant class of chemicals in fuel oils that are linked to adverse health effects, are more rapidly metabolized (Mohr et al., 2008, 2010) than POPs. Unless there is continuing exposure to an environmental source, exposure of marine mammals to PAHs is generally more limited than to persistent organochlorines. However, the effects on the HPA pathway as a result of acute exposure from, for example, an oil spill may persist for many years. Nearly half of the live bottlenose dolphins (*Tursiops truncatus*) sampled from a bay within the *Deepwater Horizon* (DWH) oil spill footprint approximately 1 year after the massive spill had indications of insufficient production of adrenal hormones (Schwacke et al., 2014b). Adrenal insufficiency can lead to adrenal crisis and death in animals that are challenged with other stressors, such as physical injury, microparasites, or temperature extremes, to which a healthy animal would otherwise adapt. Many of the dead dolphins that were recovered in the 1.5 years post-spill had rare adrenal gland lesions, and Venn-Watson et al. (2015) suggested that a likely cause of death for these dolphins was an adrenal crisis brought on by an interaction between the effects of petroleum-associated chemicals with the HPA axis and thermal stress (a particularly cold winter in the year after the spill) or a pathogen infection. Indications of adrenal insufficiency were found in dolphins from the same bay sampled 3 to 4 years after the DWH spill (Smith et al., 2017), suggesting that injuries to the HPA axis may be long lasting.

It has been suggested that some POPs may also disrupt the HPA axis by interfering with glucocorticoid receptors or the synthesis of adrenal steroids (Martineau, 2007; Diamanti-Kandarakis et al., 2009; Harvey, 2016), but stud-

ies to support such effects are still lacking. However, there is strong evidence for an HPA axis effect for one POP: the DDT derivative o,p'-DDD, which is a well-known inhibitor of adrenal steroidogenesis and is used in the treatment of hyperadrenocorticism (chronic overproduction of glucocorticoid) in dogs (Klein and Peterson, 2010).

Permanent or persistent adverse health outcomes, including decreased glucocorticoid measures, have also been reported in survivors of toxic algal blooms (Bejarano et al., 2008b; Goldstein et al., 2008; Gulland et al., 2012), and these provide the potential synergistic interactions with other stressors. For example, sea lions exposed to domoic acid, a potent neurotoxin, from algal blooms were found to have low serum cortisol concentrations as compared to unexposed controls (Gulland et al., 2012). This effect was seen in sea lions with indication of recent exposure (domoic acid in urine or feces sample), as well as in sea lions that were assumed to have been previously exposed (undetectable domoic acid in urine or feces sample). It is unclear whether the low cortisol concentrations were due to binding of domoic acid to glutamate receptors in the endocrine glands, adrenal gland exhaustion, or other disruption of the HPA axis (see Gulland et al. [2012] for discussion). Regardless, the low cortisol suggests that these individuals were more vulnerable to the effects of other stressors (e.g., petroleum-associated chemicals, noise, and perceived threat) that affect the HPA pathway.

### Hypothalamic-Pituitary-Thyroid Axis

The effects of prey limitation may interact with the effect of POPs via the HPT axis. The interference of POPs with the HPT pathway has been well established in terrestrial animals (Patrick, 2009), and there is evidence that similar HPT disruption occurs in marine mammals (Tabuchi et al., 2006; Schwacke et al., 2012). HPT disruption can produce adverse effects during critical stages of development and growth (see Zoeller et al. [2002] and Diamanti-Kandarakis et al. [2009] for review). There is strong evidence for the relationship of POP burdens to suppression of thyroid hormones in diverse species of marine mammals, including pinnipeds, cetaceans, and polar bears (Jenssen, 2006). These effects could potentially act synergistically with the effects of prey limitation, in times of nutritional stress or when animals are faced with other environmental challenges. Ford et al. (2010) suggest high POP concentrations in Pacific killer whales (Ross et al., 2000) may have acted synergistically with the effects of prey limitation, resulting in increased mortality during times of low prey abundance. Reduced prey availability would have resulted in the depletion of fat stores and could have led to mobilization of POPs sequestered in the blubber. The increase in circulating POPs could have interfered with metabolic processes. It could also have further increased suppression of immune responses that were

already being modulated by the nutritional stress, resulting in increased disease susceptibility.

### Immune Pathway

Numerous researchers have suggested a potential for synergistic interactions between the effects of chemical contaminants and microparasites through the immune pathway. This is based on the well-known immunosuppressive effects of many POPs. Evidence for a greater incidence of infections in relation to POP exposure has been demonstrated in human studies (reviewed by Carpenter [2006] and Gascon et al. [2013]), and effects on immunity have been demonstrated in marine mammals using indices of immune function and/or in vitro experiments using marine mammal leukocytes (Ross et al., 1995, 1996a; De Guise et al., 1998). Exposure to POPs has been considered as a potential exacerbating factor for a number of viral epidemics, including the morbillivirus epidemics of striped dolphins in the Mediterranean in the early 1990s (Aguilar and Borrell, 1994) and common bottlenose dolphins along the Atlantic coast in the late 1980s (Kuehl et al., 1991). However, the cross-sectional nature of the studies (i.e., POP concentrations were measured simultaneously with the mortality outcome) has made it difficult to demonstrate a causal link between these stressors in wild populations because disease-related weight loss may have resulted in an increased concentration of lipophilic POPs in the remaining blubber layer (Hall et al., 1992). In order to overcome this problem, Hall et al. (2006) adopted a case-control design to analyze data from a long-term study of harbor porpoises stranded around the United Kingdom. They found an increased risk of mortality from infectious disease in animals with high tissue concentrations of POPs.

Other potential synergistic interactions mediated by the immune pathway involve petroleum-associated chemicals and microparasites. Persistent adverse health outcomes involving this pathway were reported in bottlenose dolphins following the *DWH* oil spill (Schwacke et al., 2014a, 2014b; Lane et al., 2015; Venn-Watson et al., 2015). The reported immune perturbations were compatible with an increased susceptibility to intracellular bacterial infections (e.g., brucellosis) that can cause reproductive failure (S. De Guise, personal communication), and in the years immediately following the spill, a higher than expected prevalence of primary bacterial pneumonia was noted in recovered dolphin carcasses (Venn-Watson et al., 2015).

The chronic effects of one pathogen may result in a synergistic interaction with the effects of other pathogens via the immune pathway. For example, morbillivirus infection may result in residual immune system perturbations. It has been shown to erase immunological memory in laboratory animals, leading to a persistent increased susceptibility to other infectious agents (de Vries et al., 2012). Impairment of cell-mediated adaptive immunity and partially upregulated humoral immune response has been reported in bottlenose

dolphins with morbillivirus-positive antibody titers (Bossart et al., 2011). These perturbations could impact an animal's ability to mount an appropriate immune response when challenged. Furthermore, opportunistic secondary infections leading to mortality following the acute phase of morbillivirus infection have been reported following a number of cetacean morbillivirus outbreaks (see Van Bresseem et al. [2014] for review).

### Brain/CNS Pathway

Maternal exposure to POPs, and specifically PCBs, has been linked to adverse developmental effects in human offspring, including neurological effects and reduced cognitive function (e.g., Jacobson and Jacobson, 1996; Stewart et al., 2003, 2008; reviewed by Boucher et al., 2009). Such effects would produce less fit offspring, and if similar effects occur for wild marine mammals this could clearly lead to decreased survival in the earliest life stages, if individuals are exposed to other stressors that require increased foraging proficiency or rapid avoidance responses (e.g., prey limitation, perceived threat, and noise). In addition, a recent study by Cook et al. (2015) provides evidence that hippocampal lesions caused by sublethal exposure to domoic acid linked to toxic algal blooms affect spatial memory, which potentially could impair an animal's ability to navigate and forage. Such effects would be permanent for the individual and would likely interact with the effects of other stressors, such as prey limitation.

Animals that survive morbillivirus infection may be plagued with persistent chronic CNS infection. Chronic encephalitis was identified as a common cause of death in stranded striped dolphins (*Stenella coeruleoalba*) for years following a morbillivirus outbreak in the Mediterranean (Soto et al., 2011) and has also been identified in other cetacean species following morbillivirus outbreaks after the outbreak had subsided (Uchida et al., 1999; Yang et al., 2006). These chronic CNS infections could affect behavioral and physiological responses to other stressors, such as noise, particularly for deep-diving cetaceans. However, the estimated prevalence of CNS infection even following the substantial Mediterranean dolphin morbillivirus epidemic was relatively low (1-3 per 1,000 cases of infected individuals) (Soto et al., 2011) and therefore may not be a significant factor for population-level effects.

### Auditory Pathway

One of the documented developmental effects of POP exposure is hearing loss, potentially mediated at least in part through the HPT axis; it involves loss of outer hair cells (Crofton et al., 2000; Lilienthal et al., 2011) and distorted development of the primary auditory cortex (Kenet et al., 2007). Such permanent conditions could result in an interaction between POP exposure and the effects of other stressors,

such as prey availability and predation pressure, mediated by the auditory pathway.

Organic solvents may also induce permanent hearing loss by damaging the outer hair cells or through effects on central auditory pathways. Studies of other mammal species (primarily rats and humans) demonstrate that the hearing frequencies affected by solvents are different from those affected by noise (reviewed by Fuente and McPherson, 2006). Furthermore, studies in rats have reported synergistic effects between some solvents and noise, demonstrating that simultaneous exposure to both produces a more severe hearing loss than the summed hearing loss produced by exposure to either agent alone (Lataye and Campo, 1997; Brandt-Lassen et al., 2000; Lataye et al., 2000; Mäkitie et al., 2003). The timing of exposure may be important as studies have also shown that the interactive effect between toluene and noise exposure was only synergistic if the exposures occurred simultaneously, or if the toluene immediately preceded the noise exposure. When the noise exposure was prior to the toluene exposure, the effects of the two stressors were independent (Johnson et al., 1990).

### Interactions Across Pathways

All of the actual or potential interactions between stressor effects we have described above occur when the effects of different stressors act along the same pathway for persistent health outcomes. However, interactions may also occur across such pathways.

For example, interactions between the immune and reproductive pathways have been documented when prey is limited. The substantial metabolic cost of mounting an immune response has been well documented in diverse taxa, including mammals, birds, reptiles, and insects (Lochmiller and Deerenberg, 2000). Responses to moderate infections can lead to energetic costs as high as 55% increases in metabolic rate and 150-200% increases in the rates of glucose production. If prey is limited, animals can make allocation trade-offs between competing physiological processes. Ecological immunology theory predicts allocation trade-offs between reproductive effort and immune responses under conditions of energy limitation (Graham et al., 2011). When energy is limited, low-intensity infections may be allowed to persist if the energetic costs outweigh the benefits of clearing the infection (Sheldon and Verhulst, 1996; Martin et al., 2011). Individuals may prioritize innate immune responses over more expensive adaptive immune responses, despite greater potential for oxidative damage and autoimmunity (Downs and Dochterman, 2014).

During reproduction, nutrient limitation can force individuals to reduce their energy allocation to immune response so that they can support current reproductive effort in a way that may affect their future reproductive potential (Sheldon and Verhulst, 1996; Svensson et al., 1998). Thus, nutrient limitation may lead to impaired immune response especially

during periods of reproduction. Because reproduction is associated with increased potential for pathogen exposure from conspecifics (e.g., during colonial breeding), energetic impacts on immune response can influence the survival costs of reproduction in marine mammals (Peck et al., 2016).

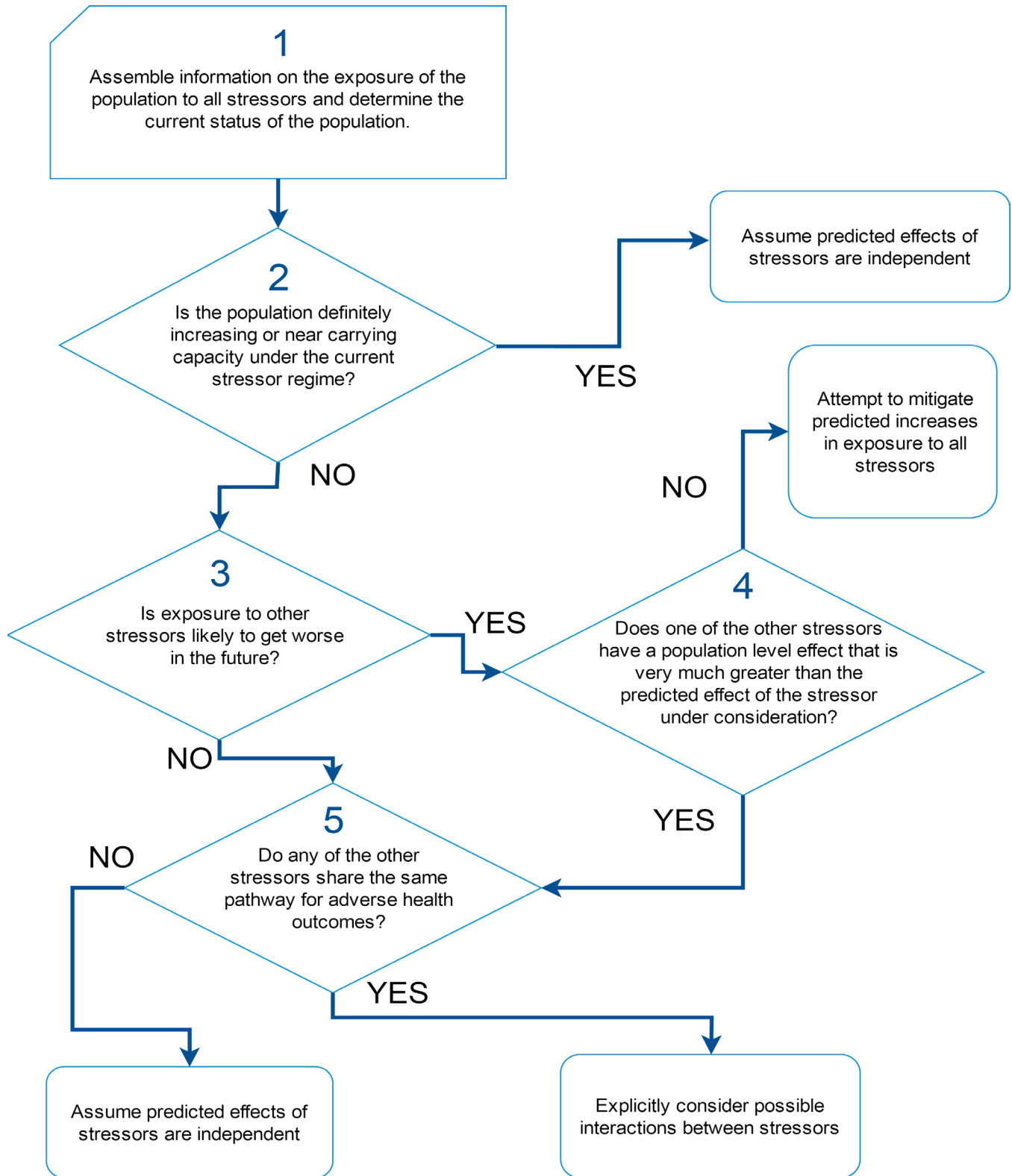
There is also potential for interactions between the HPA and immune pathways as a result of exposure to a range of stressors. Chronic elevation of stress hormones is known to downregulate immune response in wildlife systems (Sheldon and Verhulst, 1996; Råberg et al., 1998) through several pathways, including altering antibody responses (Fowles et al., 1993) and inhibiting lymphocyte proliferation (Rollins-Smith and Blair, 1993). Effects of glucocorticoid stress hormones are hypothesized to be an important mechanism underlying trade-offs between energy expenditure and immune response and may help to reduce the response to injury or infection during nutrient limitation (Sternberg et al., 1992; DeRijk et al., 1997).

There have been numerous efforts to examine the effect of stress hormones on immune responses in wildlife (Ricklefs and Wikelski, 2002; Acevedo-Whitehouse and Duffus, 2009; Peck et al., 2016). The few studies in marine mammals suggest that stress modulation of immune function in marine mammals is complex. Body reserves, foraging success, and the degree of plasticity in immune response may impact disease risk synergistically, through a trade-off between immunity and starvation resistance (Brock et al., 2013a; Peck et al., 2016). Immune investment may be directly impacted by anthropogenic disturbance. Brock et al. (2013b) revealed negative associations between body condition and immune response but only in a population exposed to anthropogenic disturbance. These findings implied energetic costs to disturbance that influenced energy allocation toward fighting infection. Finally, individual components of the immune response may be impacted differentially by elevations in stress hormones and variation in body reserves in ways that differ from biomedical model species (Peck et al., 2016).

### PRIORITIZING STRESSORS FOR CUMULATIVE EFFECTS ANALYSIS

As noted above, there is only limited understanding of how exposure to individual stressors may affect demographic rates or population dynamics in marine mammals. Yet most marine mammal populations are actually exposed to multiple stressors, and the committee's review of studies of multiple stressors indicates that they are as likely to interact synergistically or antagonistically as they are to act in a simple additive way. It is necessary to find a way to understand the nature of these interactions, while recognizing that experimental investigations of the combined effect of multiple stressors on marine mammals are unlikely to be feasible or ethical. Figure 4.3 is a decision tree that can be used to identify situations in which studies of the interactions between stressors





**FIGURE 4.3** A decision tree for identifying situations where studies of the possible interactions between stressors should be given a high priority when considering the effect of a focal stressor on a population. See text for a detailed description of the decision-making process.

should be given high priority. It is based on the assumption that interactions are most likely to occur among stressors that share a common pathway for a persistent health outcome (Côté et al., 2016).

Step 1 in the decision process is to determine the spatial and temporal overlap between each stressor and the population of interest. Geospatial approaches, such as those described by Halpern et al. (2007) and Maxwell et al. (2013), can be used to determine this overlap, although, as noted above, these approaches do not provide a rigorous assessment of cumulative impacts. However, several issues make the estimation of exposure to multiple stressors more complicated than first meets the eye. For example, many marine mammal populations are migratory and they will therefore experience considerable temporal variation in their exposure to particular stressors. Thus, the actual duration of exposure to a stressor that is present in a particular area is limited by the amount of time the population actually spends in that area. Quantifying temporal variation in stressor presence is also important for resident populations, because the presence of a stressor may not coincide with sensitive life-history stages. In addition, prior exposure to pathogens or toxins may increase an individual's sensitivity to additional stressors that are encountered in different locations or long after the initial exposure to the pathogen or toxin. Step 2 is to determine the current status of the population of interest (i.e., is it increasing, neither obviously decreasing nor increasing, or decreasing). Chapter 7 describes the methods that can be used to ascertain population status. If a population is definitely increasing, or if it is close to carrying capacity, it should be reasonably resilient (Taylor and DeMaster, 1993) to additional mortality caused by interactive effects between stressors. Large adverse population-level effects of these interactions are likely to be detected before the population has declined to levels of concern. In these circumstances, studies of possible synergies between stressors would not be a high priority.

Steps 3 and 4 allow the identification of situations in which the population is decreasing and the population's exposure to stressors is expected to increase over time. If one of the existing stressors to which the population is exposed is known to have a dominant effect (Step 4), possible interactive effects should be considered for stressors that share the same pathways for adverse health outcomes as the dominant stressor. If there is no dominant stressor, efforts will likely be required to mitigate any potential increases in stressor exposure, even if there is no evidence of interaction between the stressors.

In Step 5 the other stressors to which the population is currently exposed should be reviewed to see if they share the same pathway for adverse health outcomes. If they do, then the possibility that these stressors may interact synergistically should be investigated.

When considering the way the effects of multiple stressors may be analyzed, it is important to take account

of the lessons that have been learned from epidemiological studies, where confounding variables are known to give rise to spurious associations between exposure variables and effects of interest. This is particularly likely to be the case when the effects of one stressor operate along the same causal pathway as other variables. This situation may result in colinearity between stressor variables in linear models, or it may mask the indirect effects of stressors through other variables when fixed effects are assessed in an ANOVA. In these cases, analyses that are based on structural equation modeling or some other latent state modeling may better account for the causal pathways by which stressors impact physiology, behavior, health, or vital rates.

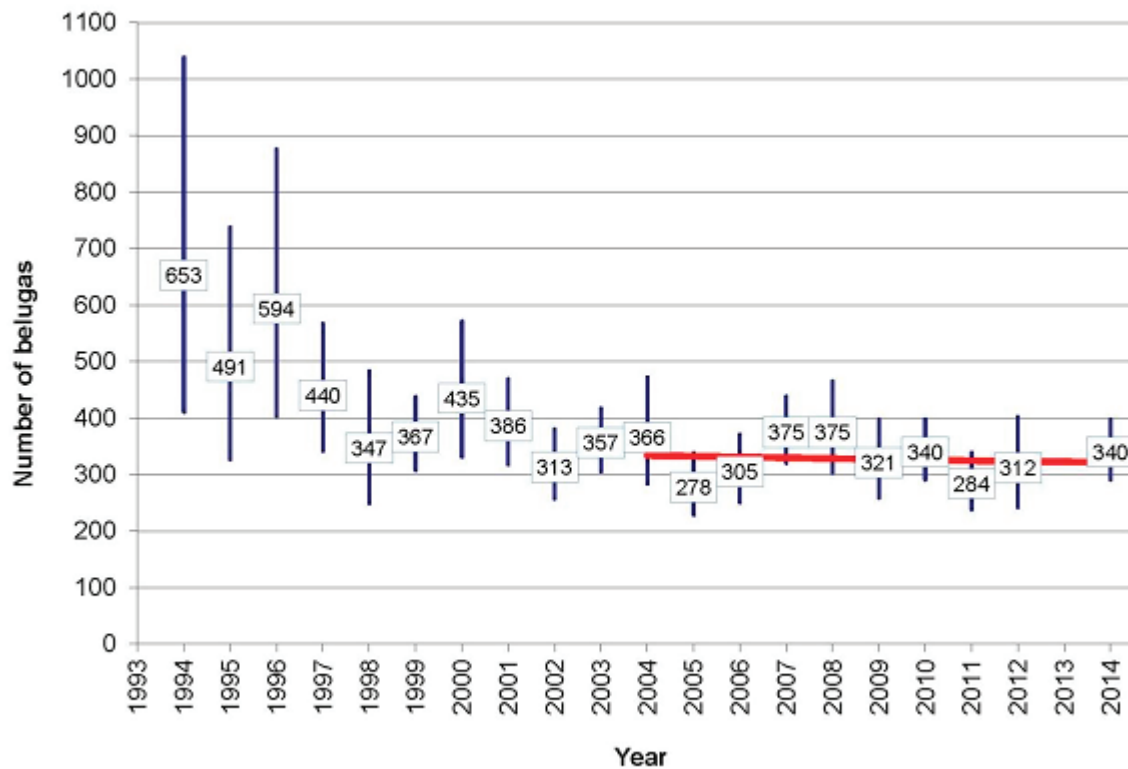
**Recommendation 4.1: Situations where studies of cumulative effects should be prioritized can be identified using tools such as the decision tree developed by the committee and testing for whether pathways for adverse health outcomes are shared across stressors.**

## CASE STUDIES: DIFFICULTIES IN INFERRING CAUSES OF DECLINES

In this section, three case studies of marine mammal populations that have either suffered a precipitous, unexplained decline, or have failed to recover following the removal of a dominant stressor are considered. This is not a critique of the work that has been done to investigate these declines, nor is it an attempt to suggest how these populations should be managed to promote their recovery. Rather, the committee's aim is to describe how the potential causes of the decline were initially identified, and to investigate what conclusions might have been drawn if the decision tree shown in Figure 4.3 had been used as part of this process.

### Cook Inlet Beluga

The Cook Inlet (CI) beluga whale (*Delphinapterus leucas*) population, which is separated by the Alaska Peninsula from other beluga populations in Alaskan waters, declined from around 1,300 whales in 1979 to 367 in 1999 (Hobbs et al., 2000; see Figure 4.4). Alaskan Native subsistence harvest between 1993 and 1998 ranged from 21 in 1994 to 123 in 1996. The most reliable data come from 1995-1997, when an average of 87 whales were taken per year (Angliss and Lodge, 2002). Including this subsistence take in models of the population's dynamics indicated that it was sufficient to account for most of the observed decline over this period. Alaskan Natives imposed a voluntary moratorium in 1999, and in 2000 the National Marine Fisheries Service (NMFS) declared the population depleted under the Marine Mammal Protection Act (65 Fed. Reg. 34590). The expectation was that with greatly reduced subsistence take the population would grow between 2% and 6% annually. Since 1999 the total subsistence harvest has been five whales, with none



**FIGURE 4.4** Figure 13 from NMFS (2015) showing abundance estimates for Cook Inlet beluga whales between 1994 and 2014. Vertical bars indicate the 95% confidence interval for each estimate. The trend from 1999 (when the hunt was managed) to 2014 was  $-1.3\%$  per year (standard error [SE] =  $0.7\%$ ).

taken after 2005 (NMFS, 2015). Nonetheless, the population has shown no sign of recovery (see Figure 4.4). The most recent estimate of population size is 340 in 2014 (Shelden et al., 2015). Based on aerial surveys and satellite telemetry data, the core summer distribution of the population has contracted from more than 7,000 km<sup>2</sup> in 1978-1979 to 2,800 km<sup>2</sup> in 1998-2008 (Rugh et al., 2010). As a result, most of the population is concentrated in upper Cook Inlet, during the summer months. This is close to the port of Anchorage, where the population is most likely to be exposed to disturbance from human activities (NMFS, 2015). Why there has been this change of distribution is not known, although several possible reasons have been suggested (Moore et al., 2000; Shelden et al., 2003; Goetz et al., 2007).

In 2010, the NMFS established a Cook Inlet Beluga Recovery Team (CIBRT). The CIBRT drew up a list of threats which they believed “might significantly impact CI recovery” (NMFS, 2015) and used their “best professional judgment” to identify the most important threats. These threats were then ranked on the basis of their extent, frequency, trend, probability of occurrence, and potential magnitude.

The 10 threats of greatest concern are listed below, with an indication (in parentheses) of which of the stressors listed in Chapter 3 might be associated with each threat:

1. catastrophic events, such as an oil spill
2. cumulative and synergistic effects of multiple stressors (primarily between noise, nonbiological toxins, and perceived threats)
3. noise (noise, perceived threat)
4. disease agents (pathogens) and harmful algal blooms (biotoxins)
5. habitat loss or degradation (habitat limitation)
6. reductions in prey (prey limitation)
7. subsistence hunting (acute physical injury)
8. unauthorized take (acute physical injury)
9. pollution (nonbiological toxins)
10. predation (acute physical injury, perceived threat)

Threats 1-3 were categorized as of “high relative concern,” threats 4-7 as “medium” concern, and threats 8-10 as “low” concern. The only threats for which data on beluga

morbidity and mortality exist were placed in the low- and medium-concern categories. The justification for this placement is that CI belugas generally have lower contaminant loads than belugas studied elsewhere, that killer whales (*Orcinus orca*) were suspected in the deaths of only three CI beluga whales in the past 17 years and that mammal-eating killer whales have not been observed in the population's core summer range, and that the subsistence hunt is suspended until at least 2018 and would be reinstated at a low level only if it did not place the recovery of the population in jeopardy.

The draft recovery plan concluded that "disease as a factor in the deaths of CI belugas appears to be low, and there is little evidence to suggest diseases of concern are present in other mammals in the area." It is therefore slightly surprising that disease was considered to be a threat of medium concern. However, this categorization may be because of the potential role of diseases in catastrophic events. In contrast, the draft recovery plan recognizes that "the trend of habitat loss or degradation . . . is . . . increasing over time," but habitat degradation was only categorized as a medium concern "due to limited understanding of how . . . habitat may be altered . . . and its resilience to perturbation." Prey limitation was also categorized as being of medium concern because "the magnitude of the impact of a reduction in prey on . . . belugas is unknown, as is the trend."

Catastrophic events are known to strongly influence extinction risk for small populations (Morris and Doak, 2002, p. 21). Such events are particularly likely to occur when a large proportion of the population is concentrated in a small area at certain times of the year. This is one of the consequences of the contraction in the summer range of CI belugas and, as a result, many animals could be exposed to episodic stressors such as spills of petroleum-associated chemicals and solvents and outbreaks of infectious disease.

There have been no documented direct or indirect effects of noise on CI belugas, and the categorization of noise as a threat of high relative concern appears to be primarily based on "evidence from other odontocete species . . . to conclude that a high potential exists for negative impacts (of noise)." As noted in Chapter 2, evidence of the effects of noise on marine mammal populations is largely circumstantial or conjectural.

When the decision tree from Figure 4.3 is applied to the CI beluga population, one can see that the population is declining, existing stressor levels are likely to get worse in the future, there is no dominant stressor, and there are a number of stressors (noise, nonbiological toxins, microparasites, and prey limitation) that share potential pathways for adverse effects. This leads to the conclusion that efforts will be required to mitigate any potential increases in stressor exposure, even if there is no evidence of interaction between the stressors.

In summary, the initial decline of the CI beluga population can be largely explained by excessive harvesting, but the reasons why the population has failed to recover remain

unknown. However, interactions between some of the many stressors to which the population is exposed may be involved in this failure. The recovery plan is primarily concerned with mitigating the threats of high and medium relative concern; this is also the recommendation that emerges from application of the decision tree in Figure 4.3. The population monitoring planned as part of the recovery plan will focus on photo-identification studies which, as we note in Chapter 7, have the potential to provide relatively precise information on many of the demographic characteristics of the population.

### **Collapse of Pinniped and Sea Otter Populations in the Northern North Pacific Ocean and Southern Bering Sea**

Once abundant populations of harbor seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubata*), and sea otters (*Enhydra lutris*) have collapsed over large areas of the Gulf of Alaska, Aleutian archipelago, and southern Bering Sea during the past four or five decades (Doroff et al., 2003; NRC, 2003b; Small et al., 2008). Despite high levels of public interest in these species and legal mandates to define and assess their various stocks under the U.S. Marine Mammal Protection Act, considerable uncertainty and scientific debate remain over the patterns, causes, and consequences of these declines.

Although there is no question that these three species have declined, data on the timing and magnitude of their declines varies in quality among the species. This is largely a consequence of when the surveys were done relative to the periods of decline. For harbor seals and Steller sea lions, rigorous monitoring programs were not initiated until the 1990s after the declines had begun (NRC, 2003b; Small et al., 2008). This shortcoming is most acute for harbor seals, which were effectively unmonitored in southwestern Alaska until after the decline had run its course. Monitoring data for Steller sea lions are better in that more systematic surveys were initiated in the 1970s while the decline was ongoing (NRC, 2003b). However, few data exist from before the decline or during its early stages, thus creating uncertainty over the onset and magnitude of the decline. This shortcoming is most severe in the central and western Aleutian Islands.

While the monitoring data range from problematic to less than ideal for pinnipeds and sea otters, they are essentially nonexistent for regional stocks of small cetaceans except for killer whales. Two species are common in this area (harbor porpoise [*Phocoena phocoena*] and Dall's porpoise [*Phocoena dalli*]), and there are a variety of rarer species (e.g., Cuvier's beaked whale [*Ziphius cavirostris*], Baird's beaked whale [*Berardius bairdii*], Stejneger's beaked whale [*Mesoplodon stejnegeri*], beluga [*Delphinapterus leucas*]; possibly striped dolphin [*Stenella coeruleoalba*], Pacific white-sided dolphin [*Lagenorhynchus obliquidens*], Risso's dolphin [*Grampus griseus*], false killer whale [*Pseudorca crassidens*]; and conceivably one or more as-yet-to-be-

described species). Part of the difficulty for monitoring these cetacean species is that they spend their entire lives in a vast oceanic environment that is difficult to access and to survey.

Except for sea otters, both the causes and consequences of the marine mammal population declines are poorly known. In the sea otter's case, the weight of available evidence points to killer whale predation as the likely cause (Estes et al., 1998; USFWS, 2013). Ecological consequences of the sea otter collapse, which also have been reasonably well documented, include a widespread ecosystem phase shift (e.g., Selkoe et al., 2015) from a kelp-dominated to a deforested, sea urchin-dominated coastal sea floor (Estes et al., 1998) and various knock-on influences of this "trophic cascade" to other species and ecological processes (Estes et al., 2009a).

In the case of pinnipeds, there are at least four reasons for the general lack of causal understanding. A primary reason, in contrast with the sea otter decline, is that none of the systems were observed closely or carefully while the declines were in the process of occurring. Other than the declines themselves, few data exist on co-occurring patterns of changes in the abundance and distribution of other species. A second reason arises from a generally poor understanding of food web structure and dynamic process that led to spatiotemporal variation in prey in the open sea. In contrast with the sea otter's food web, which is easy to observe and measure and can be studied experimentally, water column and oceanic food webs that sustain pinnipeds are difficult to observe and even more difficult to study experimentally. A third reason for the lack of understanding of the pinniped declines arises from the mobile nature of their predators and prey, which, when coupled with convective influences of ocean currents, produces an ecosystem in which meaningful measurements of the distribution and abundance of species must be done at large spatial scales. Finally, until the early 2000s, the pinniped declines were believed to have resulted from bottom-up forcing—detrimental impacts on survival or reproduction resulting from changes in the abundance or quality of food, which in turn were mostly thought to have resulted from changes in physical oceanography or competition with fisheries. This belief in nutritional limitation has been, and continues to be, embraced by many people in the local research and management communities, despite a general lack of evidence (NRC, 2003b). While the pervasiveness of bottom-up forcing processes in driving the sea lion declines has been questioned (Springer et al., 2003), there has been no concurrence and considerable debate over both the cause of the sea lion decline and the failure of the species to recover following various conservation and management actions (DeMaster et al., 2006; Trites et al., 2007; Wade et al., 2007, 2009; Springer et al., 2008; Estes et al., 2009b; and many others). These differing views are evident in the remarkably different perspectives and conclusions in two separate overview reports—one by the National Research

Council (NRC, 2003b) and the other by the NMFS (NMFS, 2008).

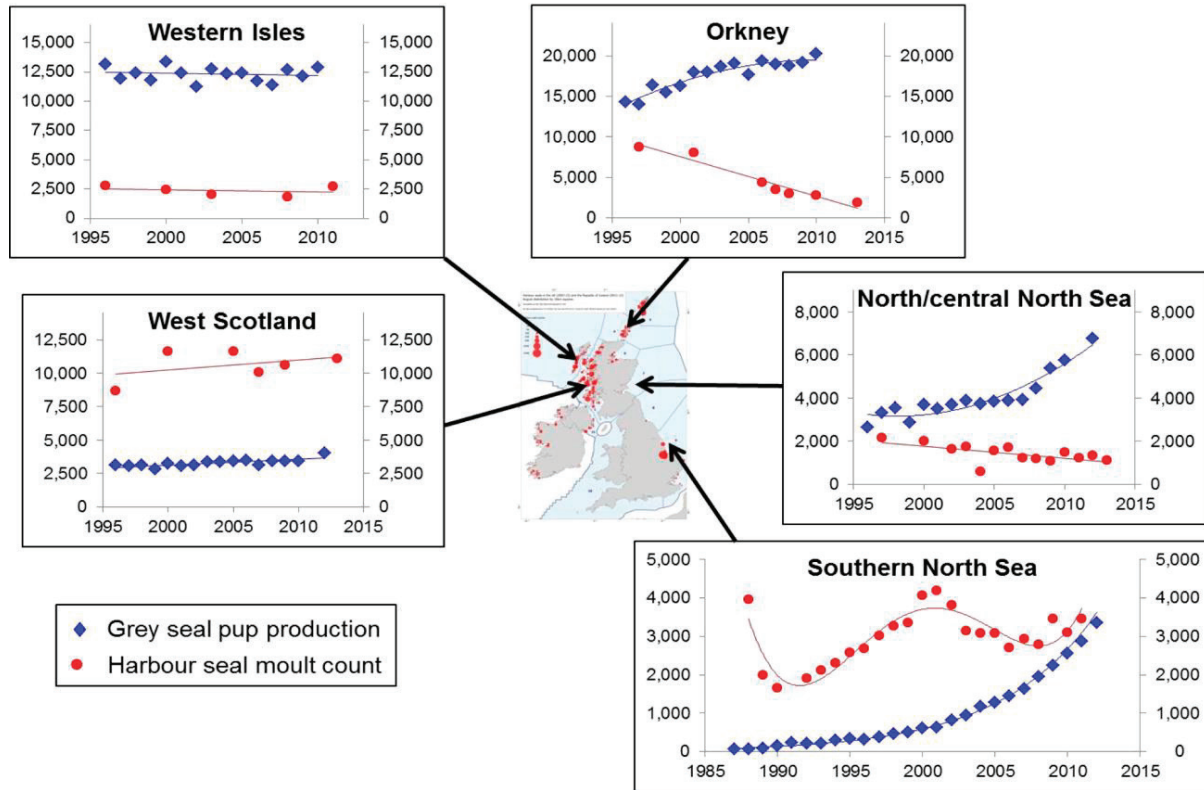
This particular case study of the causal factors for the declines in sea otters and pinnipeds illustrates how the nature of evidence, together with differences in belief and scientific philosophy (i.e., one's foundational bases for making inferences), can prevent consensus on the potential roles of even simple direct effects in marine mammal population declines. It is possible, if not likely, that sea otter and pinniped declines are the consequence of multiple stressors. However, so long as such strong debate surrounds the potential importance of the single stressors, progress in assessing the impacts of multiple stressors on marine mammals will remain an elusive goal.

Because of the lack of suitable data, it is difficult to apply the decision tree in Figure 4.3 to this case study. The two principal stressors for all species that have definitely declined appear to be food limitation, predation pressure, and (possibly) perceived threat. These do not share potential pathways for adverse effects.

### **Collapse of U.K. Harbor Seal Populations**

U.K. populations of harbor seals are monitored on a 5-year cycle using aerial surveys of haul-out concentrations conducted during the summer molt. These surveys provided evidence of declines of around 40% between 2001 and 2006 in a number of Scottish populations (Lonergan et al., 2007). The declines have continued, with an estimated decline of 65% since 2001 in Orkney (Hanson et al., 2013), and 90% since 2002 in the Firth of Tay (Hanson et al., 2015). However, the pattern of decline has not been consistent. For example, counts in the Moray Firth declined by 50% between 1993 and 2005 (Thompson et al., 2007), probably because of the effects of deliberate killing (Matthiopoulos et al., 2014); although levels of deliberate killing have been reduced, the population has continued to fluctuate in size. Populations on the west coast of Scotland and in the southern North Sea populations have shown no obvious long-term declines (see Figure 4.5).

A workshop held in 2012 identified a long list of potential causes for these declines that included almost all of the stressors listed in Chapter 3. However, by the time a second workshop was held in 2014, this list had been narrowed down to three "key potential drivers" (Hall et al., 2015): physical injury (spiral lesions; Bexton et al., 2012), prey limitation, and biotoxins. The spiral lesions, originally attributed to collisions with ducted propellers, are now believed to be the result of predatory attacks by male grey seals (van Neer et al., 2014; Thompson et al., 2015). Deaths from these injuries may be sufficient to explain the precipitous decline of the small Firth of Tay population (Hanson et al., 2015), but it is not clear whether they can explain the decline in the much larger Orkney population. Although there is evidence that harbor seals around the United Kingdom are regularly



**FIGURE 4.5** Changes in harbor seal molt counts and grey seal pup counts for the United Kingdom over the period 1996-2013. SOURCE: Taken from Figure 1 of Hall et al. (2015).

exposed to biotoxins, no deaths have actually been attributed to this cause (Jensen et al., 2015).

Application of the decision tree from Figure 4.3 indicates that the affected populations are not increasing or near carrying capacity, that some stressor levels are likely to increase (grey seal numbers, and therefore grey seal predation, are increasing, as is the incidence of toxic algal blooms in Scottish waters [Hall and Frame, 2010]), and that some of the stressors (prey limitation and biotoxins) share two pathways for adverse outcomes. There has been some preliminary work to investigate possible interactions between these stressors. Caillat and Smout (2015) modified the state-space population model developed by Matthiopoulos et al. (2014) for the Moray Firth population to include the potential effects

of prey availability, grey seal numbers, and exposure to biotoxins. They used a series of logistic equations to model the potential effects of all these stressors on fecundity and pup survival. Although the logistic equation does not explicitly include an interaction term, the predicted effects of the different stressors are not additive. In fact, Caillat and Smout (2015) found that only grey seal numbers had a significant effect on pup survival, and the only stressor affecting fecundity was prey limitation. This suggests that each of these stressors had a dominant effect on one demographic rate, and that there was no interaction between their effects. This analysis was only possible because detailed information on changes in demographic rates over time were available from photo-identification studies of the Moray Firth population (Cordes, 2011).



## 5

## Modeling the Population Consequences of Exposure to Multiple Stressors

### INTRODUCTION

A conceptual model of the Population Consequences of Acoustic Disturbance (PCAD) was first developed by the National Research Council (NRC) (2005). A working group established by the U.S. Office of Naval Research in 2009 has formalized this model structure and extended it to cover all forms of disturbance. This Population Consequences of Disturbance (PCoD) model is described by New et al. (2014). It consists of a series of transfer functions that describe how

- exposure to stressors (such as noise) affects individual behavior,
- the resulting changes in behavior can affect health (defined as all internal factors that affect fitness or homeostasis),
- variations in health may affect individual vital rates (the probability of survival, giving birth, or growth/attaining sexual maturity for an individual), and
- data on the variation in the level of exposure to the stressor experienced by different individuals can be used to scale up the anticipated changes in vital rates so that they can be used to predict population-level effects.

As noted in Chapter 4, these transfer functions and their associated causal flows correspond to the first five levels of biological organization in the hierarchy of responses to a stressor illustrated in Figure 4.1. Approaches for assessing the effects of stressors on the two higher levels of biological organization (communities and ecosystems) are described in Chapter 6.

Full PCoD models have been developed for a number of marine mammal populations (Lusseau et al., 2012; Nabe-Nielsen et al., 2014; New et al., 2014; King et al., 2015).

Ideally, the predictions of these models should be fitted to appropriate time series of empirical data obtained over a range of levels of disturbance, and the results of the fitting process used to improve the parameter estimates and quantify the uncertainty associated with the model predictions. Approaches such as Bayesian hidden-process modeling (Newman et al., 2006) may be appropriate for this purpose. However, in no case has this been possible, and such models should be considered “exploratory.” Exploratory models are most useful for comparing the possible consequences of different scenarios and for identifying priority areas for research. It is particularly important that the uncertainties associated with their underlying parameter values are documented, and that the effects of these uncertainties on their predictions are quantified.

New et al. (2014) used the PCoD model structure to investigate the potential effects of lost foraging dives on the health (measured by total lipid mass; see Schick et al., 2013) of adult female southern elephant seals, and the implications of variation in health for pup survival and population dynamics. They used information obtained from data loggers that were attached to animals immediately before they embarked on their ~240-day post-molt foraging trips. The data loggers allowed a reconstruction of their surface transit time and their foraging dive time. During portions of some foraging dives, elephant seals drift, and the rate of vertical movement during the drift is related to the ratio of lipid to lean body mass. The data logger information was calibrated against actual lipid gain during the foraging trip using measurements of body composition collected before and after the foraging trip. The results of other studies were used to link maternal mass to pup mass at weaning (Arnbom et al., 1993) and pup mass at weaning to pup survival (McMahon et al., 2000, 2003). The model was then used to determine the effect of foraging dive disturbance on pup survival. It was assumed that there



were no foraging dives for the duration of the disturbance, and surface transit time was set to the observed maximum for that individual. If animals were disturbed for 50% of their time at sea in 1 year, the predicted decline in population size was small (<1%). However, if this level of disturbance persisted for an extended period (for example, as a result of variations in the extent of the Antarctic ice sheet caused by climate change), the predicted effects were much greater (a 10% decline in abundance over 30 years). This analysis was only possible because detailed longitudinal data on the movements, health, and reproductive success of a large number of adult female seals were available. Such extensive data sets require decades of intensive research and are only available for a few marine mammal populations.

Researchers have adopted a range of techniques to build PCoD models in situations where empirical data are more limited. Nabe-Nielsen et al. (2014) used an individual-based model of the movements of harbor porpoises to estimate the potential effects of responses to the noise associated with wind turbine operation and shipping on their energy reserves. They then used a hypothetical relationship between energy reserves and survival to calculate population-level consequences. Villegas-Amtman et al. (2015) used a similar approach to predict the potential effects of reduced energy intake on reproductive success and survival for gray whales.

If empirical data are sufficient to estimate a relation between behavioral change and health, but not between health and vital rates, it may be possible to use a surrogate measure for the relevant vital rate. Christiansen and Lusseau (2015) used a bioenergetic model and empirical information on the behavioral response of adult female minke whales (*Balaenoptera acutorostrata*) to whale-watching boats on their summer feeding grounds in Iceland to estimate the effects of these responses on the whales' health (as measured by their blubber volume). They calculated how different rates of encounter with whale-watching boats would affect an individual whale's health at the end of the summer, and then used an empirically derived relation between female blubber volume and fetal length (Christiansen et al., 2014) as a surrogate for the relationship between health and the probability of giving birth. Although interactions with whale-watching boats resulted in a 40% reduction in feeding activity, the predicted reduction in a female's body condition over the course of the summer was very small (0.049%), because encounters with boats were rare. This reduction in body condition was not predicted to affect fetal survival. However, even if Christiansen and Lusseau (2015) had detected a significant effect on fetal survival, they would have been unable to forecast the population-level effects of exposure to whale-watching boats because the proportion of the North Atlantic minke whale population that feeds in Icelandic waters and the percentage that has actually encountered boats is not known.

In situations where even surrogate measures are unavailable, expert elicitation (Sutherland and Burgman, 2015) can

be used to parameterize some of the transfer functions of the PCoD model. Expert elicitation is a formal process in which a number of experts on a particular topic are asked to predict what may happen in a particular situation. The process is used in conservation science when data are lacking but there is an urgent need for management decisions (Runge et al., 2011; Martin et al., 2012). It is designed to mitigate the well-documented problems that arise when expert judgments are canvassed in an unstructured way. These include anchoring, availability bias, confirmation bias, and overconfidence (Cooke, 1991). These predictions are combined into calibrated, quantitative statements, with associated uncertainty, which can be incorporated into mathematical models (Martin et al., 2012). King et al. (2015) used this approach to parameterize relationships between the number of days on which harbor porpoises were disturbed by noise associated with the construction of offshore wind farms and their survival and reproductive success. These relationships were then used to predict the potential population consequences of different scenarios for the construction of multiple wind farms. Lusseau et al. (2012) used a similar approach to predict the potential aggregate effect of noise associated with wind farm construction, tour boat operation, and harbor expansion on the bottlenose dolphin population in the Moray Firth, Scotland.

In the remainder of this chapter, how the PCoD framework can be expanded to assess the potential population-level effects of exposure to multiple stressors is considered.

## DEFINING INDIVIDUAL HEALTH

Evaluation of the potential demographic impacts on marine mammal populations of cumulative exposure to multiple stressors requires the biological upscaling (Cooke et al., 2014) of many levels of organization, including the behavioral responses of individuals, and the effects of these responses on population dynamics, biogeography, and community ecology (see Figure 4.1 in Chapter 4). In this chapter, we consider upscaling to the level of population dynamics. One important factor that links individual behavioral and physiological responses to population dynamics is the "health" of individuals. In 1948, the World Health Organization (WHO) defined health as "a state of complete physical, mental and social well-being and not merely the absence of disease or infirmity." Similarly, definitions of "disease" in wildlife are broader than just infection by pathogens. They include the potential for cumulative impacts on health from nutrition, exposure to toxic chemicals, and climate (Wobeser, 1981). The WHO definition has been debated and criticized over the years (Jadad and O'Grady, 2008; Huber et al., 2011; Stephen, 2014), and recently it has been proposed that health be considered as "the ability to adapt and self-manage" (Huber et al., 2011), implying that a healthy organism is capable of maintaining physiological homeostasis under changing conditions. For wildlife, such definitions are effective

tively proxies for fitness, emphasizing the potential effects of health on lifetime reproductive success. The committee therefore adopts “the ability to adapt and self-manage” as the definition of health.

Given this background, an assessment of an individual’s health provides a useful integration of the way physiological and behavioral responses to multiple stressors may affect that individual’s fitness. Potential health indices include body condition, hematological and serum biochemical parameters, steroid hormone levels, and markers of immune function and oxidative stress. This approach offers some potential advantages over empirical attempts to correlate variations in demographic rates with exposure to different stressors, because it can provide an assessment of the potential for reduced survival and reproductive output *prior to* an actual alteration in these rates. In addition, the application of health-based approaches to modeling the cumulative effects of exposure to multiple stressors may increase understanding of the mechanisms by which these stressors affect fitness.

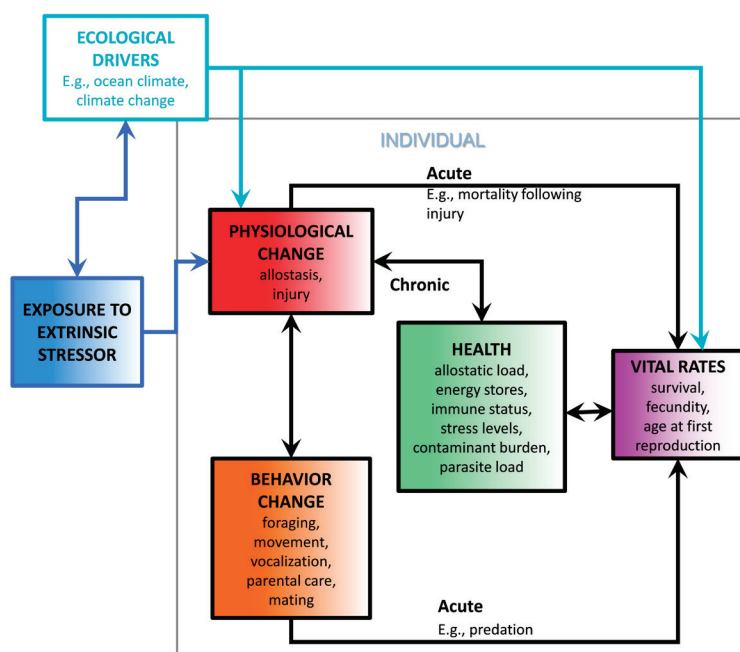
### A CONCEPTUAL MODEL FOR THE CUMULATIVE EFFECTS OF MULTIPLE STRESSORS

In this section, an expanded version of the PCoD model shown in Figure 6 of New et al. (2014) is described that can also be used to understand how specific stressors affect individual animals, how these effects can accumulate as a result of exposure to multiple stressors, and how these cumulative effects may translate into population-level consequences. This model, identified as Population Consequences of Multi-

ple Stressors (PCoMS), provides a framework around which quantitative, predictive models for particular situations can be constructed. Figure 5.1 shows the structure of this framework for a single individual exposed to one stressor. It differs from the original PCoD model in the following ways:

- It can be used to describe the effects of any dosage scenario for any stressor, not just those that cause disturbance.
- The individual-based nature of the model is made explicit.
- It includes the direct, acute effects of predation and anthropogenic causes of mortality, such as bycatch, collisions, and deliberate killing.
- Following the model outlined by McEwan (1998, Figure 1), the initial effect of any stressor is assumed to be on an individual’s physiology. The resulting physiological changes may or may not be translated into behavioral responses, depending on the context (Killen et al., 2013).
- The direct link between the behavioral change and health compartments in the PCoD model has been removed because, in practice, behavior can only affect health indirectly through its effects on physiology.

The model assumes that an individual’s response to any stressor is always mediated, at least initially, by a physiological response because the initial interaction with that stressor will always be through the nervous system. This reflects one of the fundamental aspects of the allostatic



**FIGURE 5.1** The Population Consequences of Multiple Stressors (PCoMS) framework for a single individual exposed to one stressor. Each compartment in the framework represents one or more quantities (variables) that evolve over time. Compartments are connected by arrows that represent causal flows (“transfer functions” in the terminology of NRC [2005]). For each individual, changes in physiology may result in changes in behavior (such as movement away from a sound source and cessation of feeding), which may in turn affect physiology.

load concept (McEwan, 1998): whether or not an animal exhibits a behavioral response to a stressor will depend on its internal state and a suite of intrinsic stressors. Consider a foraging individual's response to an approaching vessel. If it perceives the vessel, and its allostatic load is tolerable, it will probably take evasive action (a behavioral response mediated by a physiological response). However, if its body condition is poor, it may choose to keep feeding and may fail to evade the vessel.

Changes in behavior or physiology in response to a stressor may have a direct, acute effect on the vital rates of an individual. For example, an individual may move into an area with a high risk of predation as a result of avoidance behavior, or it may be at increased risk of mortality due to decompression sickness if it changes its diving behavior. For many marine mammal populations, the direct effects of acute stressors, such as bycatch and predation, may be more important than indirect effects. Because these acute effects operate on a short time scale, their cumulative effects are likely to be additive, as discussed in Chapter 4, so they can be modeled in a relatively straightforward way within the PCoMS framework. In this chapter, the focus is on the chronic effects of multiple stressors on health, primarily modeled using the concept of potential allostatic load (McEwan and Wingfield, 2003) that involves the adverse outcome pathways along which nonadditive effects are most likely to occur.

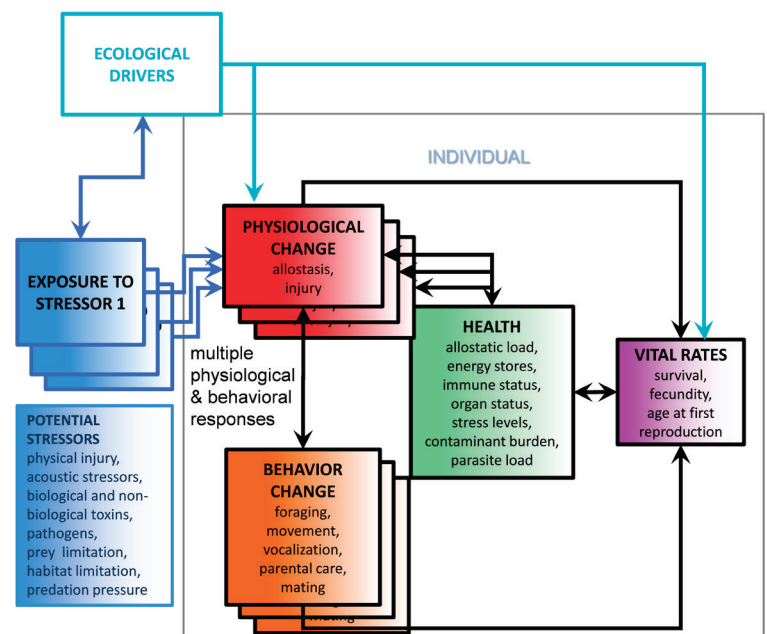
Allostatic load represents the consequences of the individual's efforts to maintain homeostasis. Examples include reduced immune status, increased long-term levels of stress hormones, and reduced body condition relative to normal levels. The allostatic load associated with exposure to a particular stressor is only "potential" because that exposure

will not necessarily have an immediate effect. However, it may have an effect on allostatic load at some later date, possibly because of the interaction with other stressors. A high allostatic load will have implications for all of an individual's vital rates. For example, an adult female may choose to forgo breeding in order to reduce her potential for allostatic overload.

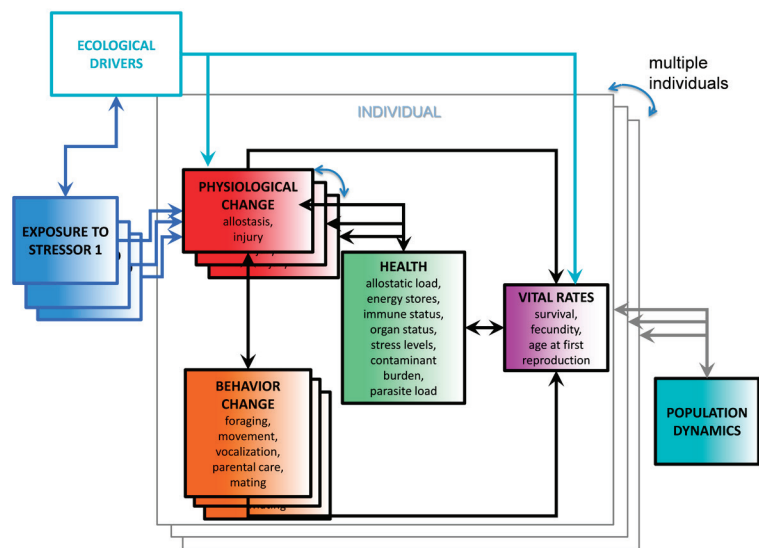
In some cases it may be sensible to combine compartments in the PCoMS model (i.e., hypothesize a transfer function that "jumps over" an intermediate compartment) if there is insufficient information to treat them separately. For example, explicitly modeling the physiological processes that occur between exposure to a stressor and a behavioral response is unlikely to be necessary.

The framework can readily be expanded to illustrate the effects of multiple stressors on a single individual (see Figure 5.2). Exposure to a particular dosage scenario for each stressor results in a unique set of physiological and behavioral responses (represented by the stack of responses in Figure 5.2, each layer corresponding to the responses to a different stressor), which may interact with the responses to other stressors. The consequences of the responses to many of these stressors are integrated through their combined effect on an individual's potential allostatic load. Although it is currently impossible to measure allostatic load directly, it may be possible to use proxy measures of health (as described below) as appropriate response variable in studies of cumulative impacts.

The effects of multiple stressors may interact internally to affect allostatic load. For example, contaminants sequestered in the blubber layer may be mobilized during lactation or as a result of elevated stress levels or reduced energy



**FIGURE 5.2** An expanded version of the framework shown in Figure 5.1 that includes the effect of multiple stressors on a single individual.



**FIGURE 5.3** An expanded version of the framework shown in Figure 5.2 that includes multiple individuals and population-level consequences.

intake that are caused by other stressors. They may then interact with an individual's immune function and affect its response if it is challenged with a novel pathogen. Similarly, the effect of macroparasite burden and dormant pathogens on health may be amplified if immune status is compromised.

The framework can be expanded to the population level if estimates of the potential exposure of each individual in the population to the suite of stressors under consideration, and the effects of this exposure on physiology and behavior, are available (see Figure 5.3). This will require information on the distribution in time and space of the marine mammal species and the stressors, which can be assembled using approaches similar to those used by Maxwell et al. (2013). However, this will also require definition of appropriate dose–response relationships for each stressor, as well as a functional representation of interactions. The committee does not underestimate the difficulties that will be involved in obtaining the information needed to parameterize these functions for even a small number of stressors. The final step is to integrate the effect of these exposures on individual vital rates across the entire population in order to estimate their population-level consequences.

As noted above, the PCoMS framework treats mortality from predation and anthropogenic activities (such as bycatch, deliberate killing, and fatal ship strikes) as acute effects of exposure to the agents of this mortality (predators, fishing gear, hunting pressure, and vessel traffic). It can also be used to model the effects of natural and anthropogenic ecological drivers. For example, as noted in Chapter 3, changes in ocean climate can have profound effects on some marine mammal populations as a result of the redistribution of prey species. In the PCoMS framework this would be modeled as a change in exposure to a prey limitation stressor. Similarly, the effects of climate change are likely to lead to shifts in

the distribution of vessel traffic, which can be modeled as changes in exposure to the risk of physical injury, toxic compounds, pathogens, and acoustic stressors. The effects of ice reduction on pagophilic species can be modeled as a habitat limitation stressor. Exposure to this stressor will result in behavioral changes, which could have acute effects (if seal species that normally breed on ice switch to breeding on land, and are therefore at greater risk of predation) or chronic effects (via the health compartment) as a result of the increased travel costs.

The PCoMS framework is similar to the framework developed by Rider et al. (2012) for assessing the role of non-chemical stressors in modulating the human risk factors associated with chemical exposure. However, Rider et al. (2012) place greater emphasis on how to predict the distribution of stressor doses across a population, and they do not consider the consequences of those doses for population dynamics.

The committee stresses that the PCoMS framework, like the original PCAD framework developed in NRC (2005), is only conceptual: it serves primarily to identify what the committee believes are the most important components of any comprehensive model of cumulative effects. The framework needs to be fleshed out with mathematical functions that describe the relationships between the different compartments, and integrated across all the individuals in the population that are exposed to the stressors under consideration. Determining appropriate forms for these functions and then parameterizing these functions will be extremely challenging. In many cases, it may be possible to ignore some of these relationships because they are not relevant to the population under consideration, but such decisions need to be carefully evaluated and fully justified. In situations where one stressor is considered to be dominant (i.e., its effects are so large that the effects of all other stressors to which the population is

exposed are negligible by comparison), use of a simplified version of the framework that considers only the dominant stressor is appropriate.

**Recommendation 5.1: Future research initiatives should include efforts to develop case studies that apply the PCoMS framework to actual marine mammal populations.** These studies will need to estimate exposure to multiple stressors, predict changes in behavior and physiology from those stressors, assess health, and measure vital rates in order to parameterize the functional relationships between these components of the framework. Where possible, the data on changes in demography, population size, and the health of individuals collected in these studies should be used to improve estimates of the parameters of the PCoMS model and reduce uncertainty.

### APPLYING THE PCOMS FRAMEWORK TO NORTH ATLANTIC RIGHT WHALES

North Atlantic right whales have been protected since the 1930s and intensively studied since the early 1980s (Kraus and Rolland, 2007), yet their population numbers remain perilously low (Kraus et al., 2005). They are exposed to a wide range of stressors on their summer feeding grounds and over their lengthy migration pathways. These include physical injury as a result of entanglement in fishing gear, collisions with shipping, strong interannual variation in prey availability, and exposure to shipping noise (Clark et al., 2009). The North Atlantic Right Whale Catalogue,<sup>1</sup> curated by the New England Aquarium, contain records of the life histories of many right whale individuals, as well as more than 700,000 photos and drawings. These records can be used to provide information on variations in the health (Pettis et al., 2004) and location of these individuals over time. Values for a set of visual health parameters are added to the catalog each time a whale is photographed. Schick et al. (2013) used these data to estimate the movements and overall health status of these individuals over time and to relate survival to health status. Rolland et al. (2016) used the same health information and model structure to link the health status of females in one year to their calving success in the subsequent year. Successful females were, on average, significantly healthier than unsuccessful ones. There was a dramatic decline in health status and calving success from 1998 to 2000 that coincided with reduced prey availability.

These relationships could be used as the transfer functions linking the health and individual vital rates compartments in a PCoMS framework that described the cumulative effects of physical injury (resulting from entanglement and collisions) and variations in prey availability on this population. Additional information in the North Atlantic Right Whale Catalogue could be used to parameterize a transfer

function that would describe the changes in health that occur as a result of different levels of exposure to entanglement over the course of an entire year.

### QUANTIFYING EXPOSURE-RELATED CHANGES IN PHYSIOLOGY AND ASSOCIATED CHANGES IN BEHAVIOR

#### Physiology

As noted above, there will be an immediate physiological response to exposure to a stressor mediated by the central nervous system. These kinds of short-term physiological responses to a stressor have evolved to reduce the risk that the animal's health is compromised. Thus, one of the critical aspects of using physiological measures to assess aggregate and cumulative impacts is the ability to detect physiological changes that actually compromise health. In many cases, the generalized endocrine response to stress can provide relevant information, if there is appropriate contextual information to differentiate between normal adaptive variation and increased allostatic load. Hematological and serum biochemical parameters can be measured from blood to help identify a wide range of disease conditions such as inflammation, liver dysfunction, or anemia. Markers of immune status can provide critical information on the health of an individual, but it may be difficult to differentiate suppression of immune function from absence of exposure to pathogens. The effects of many stressors may be integrated through their impacts on oxidative stress (OS). For example, exposure to organic and inorganic contaminants is associated with dramatic increases in OS and oxidative damage (Ercal et al., 2001; Valavanidis et al., 2006). Exposure to polychlorinated biphenyls is associated with increased OS and oxidative damage to DNA, lipids, and proteins (Stohs, 1990; Oakley et al., 1996). OS also plays an important role in the pathogenesis of viral and bacterial infections (Schwarz, 1996). Chronic activation of the hypothalamic-pituitary-adrenal (HPA) axis and the release of glucocorticoids also enhance OS (Costantini et al., 2008, 2011; Stier et al., 2009; Cote et al., 2010). Such antioxidant responses are energetically expensive and may limit investment in important life-history components (Costantini et al., 2008; Dowling and Simmons, 2009; Monaghan et al., 2009; Metcalfe and Alonso-Alvarez, 2010; Isaksson et al., 2011). Thus, evidence of oxidative damage may provide a valuable marker of the cumulative effect of multiple stressors in marine mammals.

Uses of single physiological markers have yielded strong but inconsistent links to individual and population fitness. For example, a meta-analysis (Bonier et al., 2009) found negative associations between glucocorticoid concentrations and fitness in 51% of published studies. Together, suites of physiological measures that include body condition, hematological and serum biochemical parameters, stress hormones, reproductive hormones, immune markers,

<sup>1</sup> See <http://rwcatalog.neaq.org>.

and OS markers provide the most comprehensive measures of individual health. Changes in global gene expression in tissue samples may allow development of biomarkers that integrate these parameters.

Deep-diving marine mammals are exposed to high hydrostatic pressures and must support the metabolic costs of each dive using the oxygen they bring with them on the dive. If exposure to sound or other stressors changes dive behavior, this could have energetic costs and impose risks from effects of pressure. Marine mammals that dive to 500 m or more are exposed to hydrostatic pressures of 50 atmospheres (atm) or more. This would cause high-pressure nervous syndrome in most mammals tested and it is not known how marine mammals avoid this problem (Kooyman and Ponganis, 1998). More is known about how they avoid problems such as toxicity of oxygen at high pressures. When an air-breathing mammal fills its lungs at 1 atm of pressure and then dives, the volume of air reduces under pressure following Boyle's law. The parts of the lung where gas is exchanged with the blood are the most compliant, so they contract before stiffer tissues such as the bronchi and trachea (Fahlman et al., 2009). This limits the risk that breath-hold divers are exposed to  $\text{Po}_2$  high enough to be toxic.

The shallower the depth at which diffusion stops because of alveolar collapse, the lower the  $\text{Po}_2$  to which breath-hold divers are exposed. Estimating the depth of alveolar collapse is thus an important parameter for determining change in physiology that may be stimulated by exposure to sounds that affect dive behavior. Measurement of arterial  $\text{Po}_2$  (McDonald and Ponganis, 2012) or arterial  $\text{PN}_2$  (Falke et al., 1985) in free-diving pinnipeds has proven a powerful method to estimate depth of lung collapse. The  $\text{PN}_2$  measurements were made possible by a portable blood sampling device that could be attached to freely diving seals.

The amount of oxygen available in the lungs is limited so that many marine mammal species store most of the oxygen they take on a dive in blood and muscle. The length of time a mammal can dive is limited by the oxygen available and tolerance of tissue for anaerobic metabolism, which can be detected by the presence of lactate in the blood. Thus, diving behavior represents a complex interaction of physiological adaptation and the requirements of foraging and social behaviors. Alterations in behavior in response to disturbance have the potential to create health impacts when they exceed the constraints imposed by physiology. The aerobic dive limit (ADL) has been defined as the dive duration after which there is an increase of lactate in the blood (Kooyman, 1985). Many studies have estimated the ADL by estimating the  $\text{O}_2$  store and metabolic rate, but both of these may be modulated by dive behavior, and the estimate is sensitive to assumptions about how low a  $\text{Po}_2$  an animal can tolerate. Meir et al. (2009) measured arterial and venous  $\text{Po}_2$  in freely diving elephant seals and found they tolerate unusually low  $\text{Po}_2$  in their tissues, allowing them to prolong their dives. More measurements of post-dive lactate would

improve understanding of ADL, and more measurements of arterial and venous  $\text{Po}_2$  would help to understand the physiological mechanisms affecting ADL.

Another important exposure-related change in physiology involves the regulation of  $\text{N}_2$  and managing risk of decompression. Recent evidence that exposure to sonar can cause decompression sickness (DCS) in deep-diving whales has reinvigorated analysis of risk of DCS in marine mammals (Hooker et al., 2012). When a mammal dives with lungs full, as the hydrostatic pressure increases,  $\text{N}_2$  diffuses into the blood and tissues, elevating their  $\text{PN}_2$ . As the lungs collapse under pressure, this diffusion reduces and ceases. However, as the animal ascends, with reducing hydrostatic pressure, there is a decompression, with risk that bubbles may form if tissues or blood are supersaturated with respect to the ambient hydrostatic pressure. There is evidence that chronic exposure to small bubbles may damage the bones of deep-diving sperm whales (Moore and Early, 2004) and explosive DCS has been reported for beaked whales exposed to naval sonar (Fernández et al., 2005). Models of diving physiology have been used to predict risk of gas bubbles based on the dive profiles of tagged deep-diving marine mammals (Fahlman et al., 2014), and these models help us to understand how reactions to anthropogenic noise might disrupt the mechanisms used by these animals to manage gases under hydrostatic pressure, leading to risk of DCS. Marine mammals are breath-hold divers, so rapid ascent from a single dive poses a low risk of DCS. Furthermore, once an animal dives below the depth of alveolar collapse in the lungs, there is no gas exchange. Therefore, one risk factor for DCS is time spent above the depth of alveolar collapse, but deep enough for hydrostatic pressure to increase the nitrogen tension in tissues. Another risk factor for DCS involves long-duration dives at great depth, as these may cause redistribution of dissolved gases from tissues that take up and release gas quickly (e.g., muscle) to tissues that take up and release gas more slowly (e.g., adipose tissue) (Fahlman et al., 2014).

## Behavior

The most comprehensive information on quantifying exposure-related changes in marine mammal behavior as a function of measured levels of exposure to a stressor come from studies of the behavioral responses of an increasing number of species to sounds produced by military sonars, or devices that mimic these sounds. Harris and Thomas (2015) have provided a review of these studies. Behavioral response studies are experiments designed to test the causal link between sound exposure and behavioral responses. One challenge for these studies with marine mammals is the difficulties in quantifying sound exposure at the animal and in obtaining continuous unbiased measures of behavioral responses. Johnson and Tyack (2003) describe a sound and movement recording tag that functions as an acoustic

dosimeter and as a sensitive recorder of behavioral responses. These tags have been used in experiments that record baseline behavior, then record exposure and response to controlled playback of sonar and other sounds. Use of a dose escalation design makes it possible to estimate the lowest exposure that elicits each response. Statistical methods for identifying significant changes in behavior are described by Miller et al. (2012a). Miller et al. (2014) used this approach to define the probabilistic dose–response function illustrated in Figure 1a in Box 2.2.

One common response to anthropogenic sound is a marked reduction in marine mammal vocalizations. This may be the result of animals leaving the vicinity of the sound source or ceasing vocalization. Passive acoustic monitoring can be used to derive a relationship between received sound levels and this response. For example, Moretti et al. (2014) used data from an array of hydrophones on a Navy range to derive a relationship between acoustic detections of Blainville’s beaked whales and calculated exposure level of sonar. Thompson et al. (2013b) deployed their own array of acoustic sensors to relate the detection rate of harbor porpoise clicks to distance from a seismic survey.

Controlled experiments and opportunistic monitoring of behavioral responses to anthropogenic noises can often complement one another. Controlled experiments can be critical for demonstrating that a sound causes a response, and for defining how animals respond to the sound. These results, which are often derived from a small sample of short-term experiments, can be used to design a monitoring scheme for the actual activities that produce the sounds. The Moretti et al. (2014) study showed responses to actual sonar exercises that were similar to those predicted from the experiments. Thompson et al. (2013b) were not only able to show the spatial scale of responses to seismic surveys, but were also able to demonstrate how that response reduced over the duration of the survey.

## QUANTIFYING EXPOSURE-RELATED CHANGES IN INDIVIDUAL HEALTH

### Measures of Body Condition That Are Useful for Assessing Health

Body condition is one of the few proxies for allostatic load that can be measured using conventional methods. Classic methods to measure energy stores involve separating skin, blubber, and other tissues, weighing them, and estimating their caloric values. Noninvasive measures such as ultrasound can also be used to measure blubber layers. The total amount of water in the body (total body water or TBW) can be estimated by diluting a known volume of isotopically labeled water, and total body lipid (TBL) can then be estimated by known relationships between TBW and TBL. Less specific morphometric measurements such as length, weight, and girth are also often used to estimate

body condition. These measurements do not require dead animals, but they often require handling live animals. Biuw et al. (2003) used the dilution technique to validate a method for estimating body condition on tagged elephant seals while they were at sea. They used the rate of vertical change in depth of these animals while they were drifting passively through the water column to estimate their buoyancy. The lean tissue of marine mammals is denser than seawater, but lipid stores are less dense, so that the buoyancy of an animal is largely a function of the ratio of lean to lipid tissues (Crocker et al., 1997). Schick et al. (2013) used information of this kind to estimate variations in the health of individual elephant seals over time. These health estimates were then incorporated into the PCoD model developed by New et al. (2014). Monitoring buoyancy appears to be a useful method for quantifying changes in body condition in a number of species. For example, Gordine et al. (2015) describe a filtering method that can reliably detect buoyancy changes in the dive records of drift diving species using the highly summarized data that are normally collected by most of the tags fitted to marine mammals. Aoki et al. (2011) demonstrated that estimates of the body density of elephant seals fitted with tags that could record depth, swim speed, and temperature at 1 second intervals, and three-dimensional accelerations (for detecting pitch and hind flipper movements), were within 1% of the equivalent estimates from isotope dilution from the same individuals. In addition to these detailed studies of buoyancy, information on changes in body condition may be obtained from time series of aerial photogrammetry of the same individual collected using unmanned vehicles (e.g., Durban et al., 2015).

### Measures of Organ Status That Are Useful for Assessing Health

Hematology and serum chemistry parameters are routinely used in human health care to assess physiological state and are generally organized into panels that represent specific pathological processes or organ systems. In circumstances where blood samples can be collected from marine mammals these measures can provide information on basic metabolic status, kidney function, inflammation, liver disease, or thyroid disorders.

### Measures of Immune Status That Are Useful for Assessing Health

Wild populations and individuals are constantly challenged by pathogens. The immune responses to these pathogens influence the demographic parameters of populations (Daszak et al., 2000; Morens et al., 2004). Immune responses are energetically expensive, and the ability to mount them may be influenced by nutritional state, stress hormones, and toxics exposure (Hammond et al., 2005; Peck et al., 2016). The primary difficulty of assessing immune response is

interpreting variation in markers without information on the exposure of individuals to pathogens. To date, studies on immune function in marine mammals suggest that they share all of the primary immune components identified in biomedical studies. However, it is likely that there are modifications to marine mammal immune function that serve to preserve response under the diverse environmental conditions experienced, including high pressure, cold temperatures, and extreme hypoxemia, conditions that are immunosuppressive in many human studies (Shepard and Shek, 1998; Brenner et al., 1999).

A variety of approaches have been developed to assess immune competency from cross-sectional samples. Functional immune assays have been developed for both pinniped and cetacean species that quantify the proliferative response of lymphocytes (e.g., Levin et al., 2005; Mori et al., 2006; Schwacke et al., 2012). Cytokines regulate the development of humoral and cellular immune responses. For species where blood or tissue sampling is feasible, a suite of markers are available to measure individual innate and adaptive immune responses, including circulating levels of cytokines, acute phase proteins, and immunoglobulins. Microarrays and RNA sequencing allow examination of cytokine expression in tissue. Multiplex cytokine arrays have been optimized for individual marine mammal species (Mancia et al., 2007; Vechhione et al., 2008; Eberle et al., 2013). DNA sequences for cytokines for many species have been published and can be used to develop quantitative assays (King et al., 1996; Inoue et al., 1999). Commercial assay antibodies have also been validated for use in numerous marine mammal species (e.g., Peck et al., 2016). Innate immune function can be assessed with serum from any species through simple complement killing assays, such as hemolytic complement (CH50) and bacteria killing assays. As measures of adaptive immune response, total immunoglobulin levels have been measured using species-specific and commercial antibodies (King et al., 1998; Peck et al., 2016), and pathogen-specific immunoglobulins have been measured to document exposure to a wide variety of diseases using direct agglutination assays, immunohistochemical staining, and commercial enzyme-linked immunosorbent assays. Together these measures represent a formidable arsenal of tools that could, in principle, be used to assess individual and population innate and adaptive immune function. However, collecting the appropriate samples for analysis will be challenging, particularly because large cross-sectional data sets on immune markers in populations are needed to differentiate robust and appropriate immune responses that occur as part of life-history variation from exaggerated or suppressed immune responses in individuals that indicate impaired health. The association between immunosuppression and increased infections is well documented in humans (Luebke et al., 2004), but the form of that relationship varies with life stage and the level of immune suppression. Given the well-documented expo-

sure to pathogens and parasites in wild marine mammals, it is likely that immunosuppression will lead to an increase in rates of infection.

### Measures of Stress That Are Useful for Assessing Health

One approach to measuring the cumulative physiological impact of multiple stressors on marine mammals is through the measurement of stress hormones. Physiological stress can be defined as a complex physiological response to aversive environmental stimuli that challenge fluctuating homeostatic set points. The mammalian neuroendocrine stress response is driven largely by activation of the HPA axis, which results in the release of glucocorticoids into circulation (Sapolsky et al., 2000). Glucocorticoids bind to tissue receptors and alter expression of genes affecting a diverse array of physiological processes, including metabolism. Meta-analysis has shown that anthropogenic disturbances are associated with elevation of glucocorticoids in wildlife regardless of the kind of disturbance (Dantzer et al., 2014), although the fitness impacts of these elevations are less clear. While acute stress responses are usually adaptive, and may even increase subsequent fitness through the process of hormesis (Boonstra, 2005), biomedical studies have suggested that chronic activation of stress responses can have negative effects on survival and reproduction, mainly through suppression of immune and gonad function. Thus, chronic activation of the HPA axis may be an important mechanism by which cumulative exposure to diverse stressors leads to physiological and demographic impacts. Chronic stress resulting from persistent or cumulative exposure to stressors may lead to dysregulation of the HPA axis. This dysregulation is thought to result from loss of negative feedback, when chronic elevation of glucocorticoids decreases the number of glucocorticoid receptors in areas of the brain that regulate activation of the response (Dickens et al., 2009).

Several conceptual models have been developed to represent the physiological impacts of chronic stress, including allostatic overload (McEwan and Wingfield, 2003) and homeostatic overload (Romero et al., 2009). Individuals undergoing chronic stress responses would be expected to exhibit higher baseline levels of circulating glucocorticoids, enhanced glucocorticoid responses to environmental stressors, and increased time for glucocorticoid levels to return to baseline following a stressor (Dickens and Romero, 2013). In biomedical studies, chronic elevation of glucocorticoids directly suppresses immune and gonad function (Sapolsky et al., 2000), although these relationships are less well established in wildlife species than in humans. Because the detrimental physiological effects of chronic stress are thought to result from a larger cumulative exposure to glucocorticoids and because conserved glucocorticoid stress responses can result from a wide variety of stressors, measurement of glucocorticoids represents a potentially important proxy for cumulative stress and health in marine mammals.



Unfortunately, measurement of the magnitude of stress responses and the status of negative feedback regulation is not possible for most marine mammal species, because it requires repetitive blood samples or experimental manipulations (adrenocorticotropic hormone or dexamethasone injection). Baseline (i.e., not altered by sampling) glucocorticoid concentrations can be measured in rapidly acquired blood samples, although this kind of sampling is not feasible for most species of marine mammals. For pinniped species that haul out on land, studies have suggested that chemical immobilization may ameliorate the stress response to handling, allowing measurement of baseline levels in some species (Champagne et al., 2012). Extensive work is under way to develop and validate techniques for measurement of glucocorticoids in other sample matrices that are appropriate for use in free-ranging cetaceans, including fecal samples, blow, blubber, and skin (reviewed by Hunt et al., 2013), sometimes called “integrated measures.” Measures from these matrices may be superior to blood samples in allowing identification of chronic elevation in baseline glucocorticoids. Fecal measures are the least invasive and may be more sensitive to anthropogenic disturbances (Dantzer et al., 2014) but are sometimes difficult to link to targeted individuals. Blubber samples acquired by biopsy dart have perhaps the greatest potential as a matrix for measurement of glucocorticoids in large whales. Highly fat-soluble glucocorticoid hormones dissolve in perfused blubber. Blubber samples can be targeted to specific individuals and taken prior to any alteration in glucocorticoids from sampling. In addition to measurement of glucocorticoids, blubber samples can also be analyzed for reproductive hormones, fatty acids, and contaminants, allowing increased understanding of potential integration among stressors. One key limitation in the current utility of measuring blubber glucocorticoids is understanding how blubber concentrations respond to acute and baseline changes in plasma (i.e., turnover and lag times). This issue can potentially be addressed through controlled experiments in tractable species that allow manipulation of cortisol levels and repetitive sampling. It is also important to understand how blubber cortisol levels may be influenced by important life-history events like fasting or reproduction. This need can be addressed through large sample size, cross-sectional, or longitudinal studies that measure glucocorticoids across multiple matrices. Finally, there is great potential for development of gene expression markers in marine mammal blub-

ber that differentiate between acute and chronic elevation in glucocorticoids (Khudyakov et al., 2015).

Recent developments in the technologies available for long-term time series of stress and reproductive hormones, as well as potential exposure to contaminants, have the potential to provide unique insights into the historical variation in stress responses and reproduction. Earplugs from several species of large cetaceans provide time series of hormone and contaminant data over the lifetime of the individual, as long as 65 years in currently analyzed samples (Trumble et al., 2013). These profiles potentially reveal the timing of pregnancies and lactation, baseline stress hormones, and exposure to several important classes of contaminants. Similarly, baleen samples can provide individual time series of stress and reproductive hormones lasting up to 20-25 years (Hunt et al., 2014).

Interpretation of the potential relationship between glucocorticoid levels and individual fitness requires extensive contextual data. Currently there are few large cross-sectional data sets of stress hormones from marine mammals that can be used to quantify natural variation in glucocorticoids with age, gender, season, and/or reproductive status. However, such data are critical for assessing anthropogenic impacts on stress hormone levels and their potential for health and reproductive effects as well as for determining key periods where sampling is likely to be most informative about health. A primary research need is to collect glucocorticoid measurements across life-history stages in species of interest. These data will not only provide a basis for identifying unusual glucocorticoid levels in individuals or populations but will also enhance understanding of how natural variation in glucocorticoids may regulate the allocation of energy resources between immune response and reproduction, and how intrinsic factors might modify responses to anthropogenic stressors. For example, a large literature in seabirds has focused on the roles that natural variation in glucocorticoids plays in regulating breeding decisions (e.g., Kitaysky et al., 2007), carry-over effects between stress responses at various life-history stages (e.g., Schultner et al., 2014), and the interaction of glucocorticoid stress responses with exposure to toxins (e.g., Nordstad et al., 2012; Tartu et al., 2015). Currently, no parallel literature exists for marine mammals. Understanding the adaptive uses of stress responses in marine mammal systems is critical to assessing how cumulative stress impacts might integrate and when they are most likely to have demographic consequences.

## 6

## Interactions Among Stressors and Challenges to Understanding Their Cumulative Effects

### INTRODUCTION

The assessment of aggregate and cumulative effects from stressors (anthropogenic or natural) on any particular species or stock of marine mammal involves two fundamental elements: conceptualizing the process by which the potential stressors might influence the mammal population, and designing and implementing approaches to test specific hypotheses for relationships among stressors and demographic responses. Both of these needs present particular challenges in the case of marine mammals. Chapter 6 explores these challenges in further detail.

### CONCEPTUALIZING PROCESS

Understanding the impacts of a potential stressor on any species in nature is always best served by first establishing a conceptual model that defines the pathways and processes by which that impact might occur. This general approach further involves defining the relationship between dosage of the stressor and response of the individual marine mammal, the population, or the associated ecosystem. Multiple potential stressors add to the challenge of understanding impacts. One commonly used approach to this difficulty that has been used in biomedical research involves estimating whether the impacts of two or more stressors occur via common pathways. Sharing common modes of action is thought to increase the likelihood of interaction (see Table 4.1). However, demonstrating or even predicting how the diverse set of stressors considered in this report may interact to influence marine mammals will be no mean feat. In this chapter the problem is treated in a manner that is broadly conceptual. The discussion begins by introducing the “interaction web” as a way of envisioning how the distribution and abundance of marine mammals will be influenced by stressors of any

sort. Next is a discussion of functional relationships between stressor level and marine mammal response. In the third short section of this chapter, “ecological surprises” are introduced and discussed as the likely manifestation of what science does not yet understand about the way interaction webs are assembled and how they function. The section on ecological surprises is followed by an exploration of how the understanding of stressor–response relationships for marine mammals might be improved through a discussion of the principles of experimental design and scientific inference. The chapter concludes with a section on adaptive management: how best to use the insights derived from the various studies of marine mammals, stressors, and responses for their conservation and management.

### THE INTERACTION WEB

Although various approaches have been taken to define the network of interactions among species and between species and their abiotic environments, in this report the idea of an *interaction web*, as defined by Dunne et al. (2002) is used. The older, more well-known, and more widely used notion of a *food web* (the network of trophic interactions among species [Pimm, 1979]) is embedded in the interaction web concept. The conception of the interaction web is based on a single broad premise—that the distribution and abundance of species in any ecosystem is dictated by interactions among species and between these species and their abiotic environment. In the case of food webs, abiotic factors are not considered, and species interactions are restricted to those involving consumers and their prey. The interaction web broadens the concept of interactions to include abiotic and biotic ecological drivers that have effects on populations that are broadly similar to the effects of stressors on individuals. Stated in the specific context of this report, a stressor stimulates the



negative influence on the distribution and/or abundance of a marine mammal species, population, or stock. In this context it is important to recognize that stressors at the individual level may have little or no influence, or in some cases even a positive influence, on the species or stock of interest. *Interaction strength*, defined as the magnitude of the direct effect of one node on another node, is visually characterized by line weight (see Figure 6.1).

Interaction web nodes can also affect one another via one or more intervening nodes, in which case their interplay is defined as an *indirect effect*. For example, node A might affect node D both directly and even more strongly through an indirect effect on node D via node B. Indirect effects are often imagined to be weaker than direct effects because the likelihood of a weak link occurring in the interaction chain increases with chain length, and the strength of any indirect effects will be limited by the weakest link in the chain. However, indirect effects can be as strong as or stronger than direct effects, and, in all but the simplest ecosystems, the number of potential indirect effects greatly exceeds the number of potential direct effects (Estes et al., 2013a). The net effects of anthropogenic drivers on marine mammal populations might thus be composed of either direct or indirect effects, or, most likely, both types of effects.

Interaction webs, by their fundamental nature, are exceedingly complex. Endeavors to quantify or otherwise analyze interaction web behavior have employed two broadly similar approaches, use of the community matrix (May, 1972; Yodzis, 1988) and network analysis (Proulx et al., 2005). Although these general methods of analysis will not be discussed further in this report, they may be used for further understanding the influence of anthropogenic stressors on marine mammals and their associated ecosystems.

**Finding 6.1:** Interaction webs characterize the numerous pathways in which all species within an ecosystem interact with one another and the various elements of their physical environment. This approach can be used to conceptualize the myriad ways extrinsic stressors may influence marine mammals.

**Finding 6.2:** Any two species may link together in the interaction web via direct or indirect interactions. Direct interactions are those in which there are no intervening species, whereas indirect interactions are those in which there are one or more intervening species. Indirect effects can link species with stressors via long interaction chains that may involve both bottom-up and top-down forcing processes.

## RELATIONSHIP BETWEEN STRESSOR LEVEL AND INTERACTION WEB RESPONSE

The effects of a stressor on a population or ecosystem depend on the functional relationship between stressor level and an individual's response through changes in vital rates,

the proportion of the population that is exposed to the stressor, and, for those exposed individuals, the level of exposure that each individual experiences.

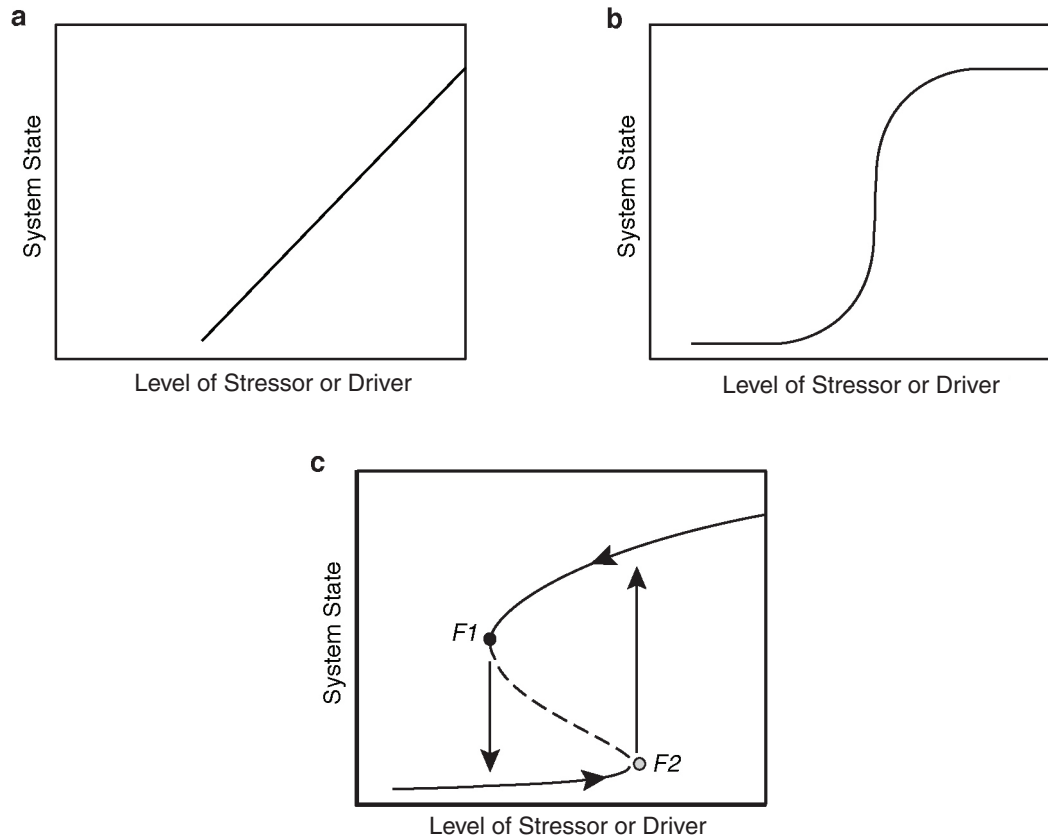
A critical question here is: How sensitive are the predictions of population- and ecosystem-level effects from stressors to the form of the mathematical function that describes these relationships? If for example this function is linear (see Figure 6.2a), then some change in stressor level is predicted to lead to a constant proportional change in the system in which it acts, whatever the specific value of the stressor. Using this simple function, the magnitude of stressor impact can be estimated from the slope of the stressor–response function and the magnitude of change in the stressor, and even very low doses will have some effect. If the stressor has a point source, large numbers of individuals may be exposed to these very low stressor levels (see Box 2.2), and this could have important population-level effects. If, however, a sigmoidal function of the form shown in Figure 6.2b is assumed, very low doses are predicted to have little or no effect, and the population-level effects associated with the linear function would be ignored. In contrast, if the true function is in fact sigmoidal but linearity is assumed, unanticipated strong effects from small increases in stressor level may occur.

There are many reasons why a nonlinear function is more likely to be appropriate. Some of the more obvious reasons at both the individual and population levels are summarized below:

- For toxicants whose effect depends on binding with a receptor, the well-developed theoretical understanding of receptor–ligand kinetics predicts a nonlinear function.
- The physiological mechanisms that animals use to maintain homeostasis in the face of stressors often mean that adverse effects may not be visible until these systems break down, after which an adverse effect can suddenly appear. This nonlinear pattern can lead to sharp thresholds for effects.
- Any pattern of threshold variation (i.e., any particular density function) among individuals in response to a stressor within a population is likely to lead to a nonlinear cumulative distribution function.
- For a noise effects example, animals are not expected to respond to sounds at levels below their hearing threshold, and responsiveness may not increase above a certain high intensity of sound.

The preceding discussion is not meant to imply that these functional relationships must be understood before stressor effects can be documented. Such functional relationships will likely remain unknown in many cases. Even under this more limiting circumstance, stressor impacts might still be detected.

As explained further in Chapter 5, the Population Consequences of Acoustic Disturbance model (NRC, 2005) aimed



**FIGURE 6.2** State-space graphs capture the functional relationships (all direct and indirect interactions) between a stressor and its effect on the state of a system. This relationship may be (a) linear or (b, c) nonlinear. The abrupt transitions depicted in (b) and (c) are often referred to as *phase shifts* or *regime shifts*. When the stressor or driver level at which a phase shift occurs is different when the stressor or driver level is increasing and when it is decreasing (c), the system is said to exhibit *hysteresis*. F1 and F2 are referred to as *tipping points* or *breakpoints*. Figures 6.2b and 6.2c adapted from Scheffer et al., 2009.

to break the causal chain from exposure to the stressor of noise to population effects into a series of sequential functional relationships. Chapter 5 describes recent applications of this model that use measures of body condition to integrate effects of stressors, from which the influences on reproduction and survival are predicted. There is evidence for nonlinear relationships between body condition, which integrates effects of many stressors, and reproduction, and this in turn varies among marine mammal species. Analysis of data from several species of pinnipeds showed that maternal state variables explained twice the variation in natality rates in capital breeders compared with income breeders (55% compared to 25%) and that the relationships between maternal state variables and pregnancy were distinctly nonlinear in capital breeders (Boyd, 2000). Thus, even if disturbance of feeding had a linear effect on body condition, the combined effect of disturbance on condition and then condition on pregnancy would be nonlinear, and the form of this function would likely vary between capital and income breeders.

Hunsicker et al. (2016) reviewed 736 relationships

between driver levels and ecosystem responses in marine pelagic ecosystems. They report that nonlinear responses are more common than linear ones. Strongly nonlinear relationships were particularly common among climate and trophodynamic variables but also were associated with anthropogenic drivers, such as overfishing and pollution. The results of their meta-analysis of ecological studies led Hunsicker et al. (2016) to suggest that “in the absence of evidence for a linear relationship, it is safer to assume a relationship is non-linear.”

The shape of the functional relationship between a stressor or driver and its effect on an individual, population, or ecosystem has significant implications for management. If managers can assume that gradual changes in intensity of the stressor or driver lead to roughly linear changes in recipients, as in Figure 6.2a, then they can aim to monitor the effects over time to make sure these effects are not becoming adverse. If the slope of this linear relationship is known at low driver levels, this relationship can be extrapolated to predict effects at higher driver levels. By contrast, if the functional relationship is as in Figures 6.2b and 6.2c, then no

effect may be seen over a considerable range of driver levels, but beyond this range effects may escalate rapidly with only a small increase in the driver. Functional relationships of this nature lead to what are called *phase shifts* or *regime shifts* (Conversi et al., 2015), defined as abrupt and sometimes catastrophic responses by a system to small changes in driver intensity. The net effects of anthropogenic stressors on marine mammal populations and their associated ecosystems might thus be small and imperceptible until some critical level is reached, at which point the effect is strong. Selkoe et al. (2015) argue that this situation is common enough that resource managers should, “[i]n the absence of evidence to the contrary, assume nonlinearity.”

In some situations, the functional relationship between the level of a stressor or driver and the state of a system may vary depending on the directionality of change in stressor or driver level (see Figure 6.2c). This phenomenon is called hysteresis. For example, an individual marine mammal that has been exposed to a sound may habituate or become sensitized, changing its responsiveness to later exposures. Similarly, the initial response of an individual to increasing numbers of a pathogen following infection will differ from the response as the body reduces the number of pathogens. In this case, the state of the organism has changed from when the infection starts to when its immune system is causing the infection to decrease. At the population level, if abundance is reduced to a very low level by a driver, the population may not recover following driver relaxation because of such factors as demographic stochasticity or inverse density dependence (Allee effect; Stephens et al., 1999). For populations governed by the generalized logistic growth equation, the rate of decline following overshoot beyond carrying capacity will be more rapid than the rate of recovery from a similarly sized reduction in abundance below carrying capacity (Gotelli, 2008, p. 30). In multispecies systems (i.e., biological communities), a driver-induced reduction in one species might alter species interactions such that the driver relaxation is not followed by a similar pattern of recovery. A critical point about hysteresis for this report is that managers should not assume the response of a system will follow the same path when the level of a stressor is reduced as it did on increase of the stressor.

Ecosystems can shift among different basins of attraction (Scheffer et al., 2001)—different configurations to the distribution and abundance of species, in which movement from one basin to another requires a strong perturbation. This situation can be likened to the behavior of a ball over a three-dimensional surface of ridges and valleys, in which the valleys are basins of attraction and the ridges are tipping points (also known as breakpoints). Perturbations (changes in driver level) that are sufficient to push the ball over a ridge and into another valley result in regime shifts. The consequences of this process for the functional relationship between driver level and system state is illustrated graphically by Figure 6.2c. When driver level changes from just

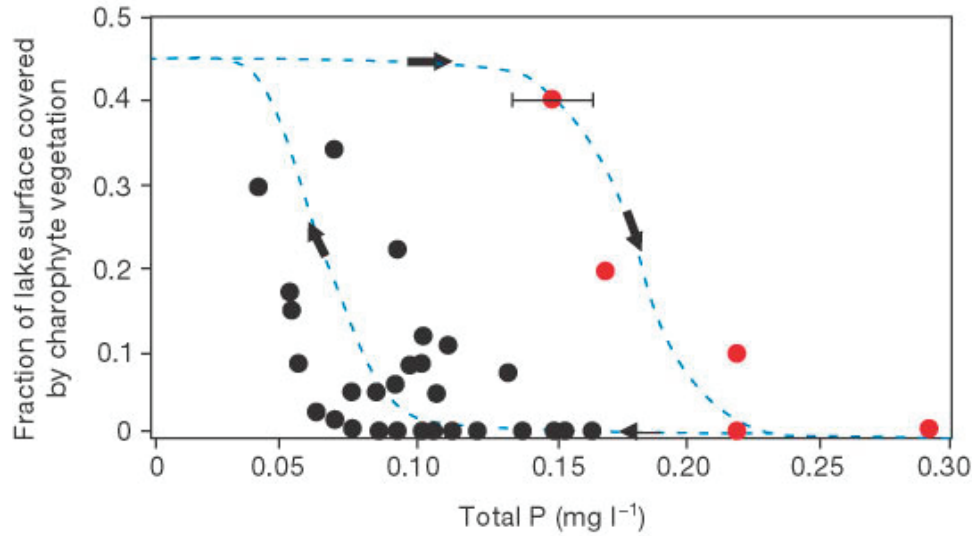
below F2 to just above F2 (a tipping point), the system jumps from one state to another (a regime shift). Once a regime shift has occurred, driver level must be reduced to below F1 for the system to return to the initial state. These breakpoints or tipping points can be thought of as unstable equilibria between alternative stable states (May, 1976). The first explorations of ecological tipping points and regime shifts were based on theoretical analyses (e.g., Lewontin, 1969; May, 1976). A large and growing body of empirical study confirms the existence of these state shifts and regime shifts in nature (Sutherland, 1974; Scheffer, 2009), including the shift from coral-dominated systems to macroalgae-dominated systems in the Caribbean (Hughes, 1994; Knowlton, 2004), changes in fishery yield (Steele, 2004; Vert-pre et al., 2013), shifts between kelp forests and sea urchin barrens (Steneck et al., 2002); and changes at larger system-wide scales (Beaugrand, 2004; Hare and Mantua, 2000; Möllman et al., 2009). Empirical evidence for hysteresis, although more limited, does exist (see Figure 6.3).

The general situation in which the state or condition of an individual, population, or ecosystem is largely unresponsive over one range of stressor or driver levels but responds strongly at other levels presents a substantial challenge to management. Under this circumstance, managers must know the range of stressor levels over which the desired state is maintained, thereby allowing them to set a threshold below which the risk of transition to the adverse state is suitably low. The actual forms of the functional relationship between stressor levels and their effects on marine mammal physiological systems, individual condition and life-history metrics, or the distribution and abundance of populations are largely undocumented. To the extent possible, the choice of such functional relationships should be based on data and/or theory, not on scientific preconceptions.

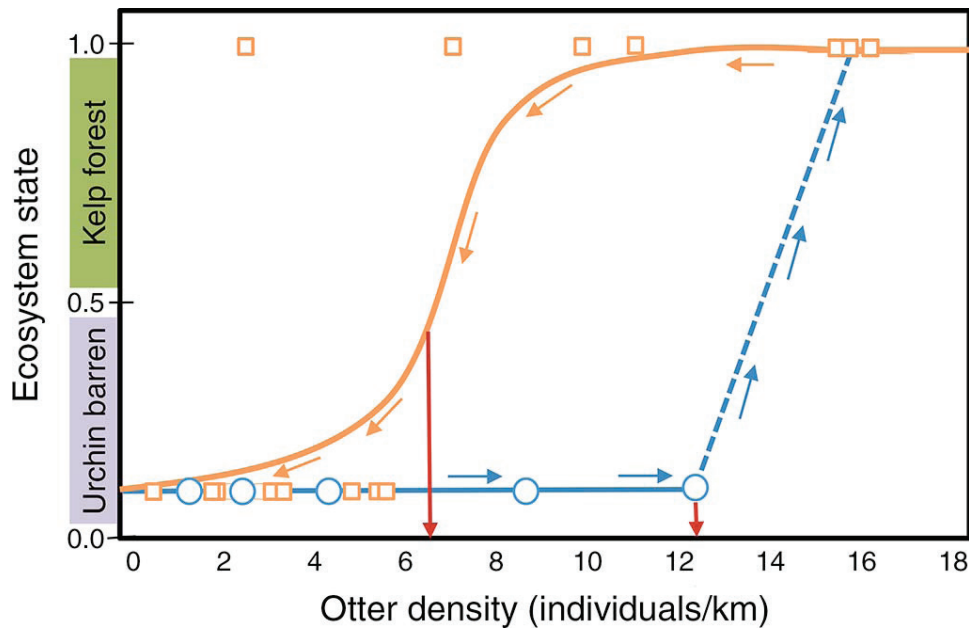
## ECOLOGICAL SURPRISES

The preceding sections of this chapter establish two key points: (1) that interaction webs are highly complex structural entities, given the great diversity of species and the even greater diversity of ways these species can interact with one another and their physical environment, and (2) that functional relationships among species and between species and their physical environments are commonly nonlinear. Given these two key points, the responses of natural systems to stressors are expected to be difficult to predict and thus often characterized by what have been referred to as ecological surprises. In a paper based on analyses of various case studies and a survey of established field ecologists, Doak et al. (2008) concluded that major surprises (defined as “a substantial change in the abundance of one or more species resulting from a previously unknown or unanticipated process of any kind,” p. 593) should be expected in any effort to understand and predict ecological dynamics (Peetchey et

## Panel A



## Panel B



**FIGURE 6.3** Two empirical examples of hysteresis: Panel A shows the differing response of charophyte vegetation in a shallow European lake to an increase (red dots) followed by a decline (black dots) in phosphorous concentration. SOURCE: Scheffer et al. (2001). Panel B demonstrates the differing sea otter densities (red arrows) required to precipitate a phase shift between kelp- and urchin-dominated phase states, depending on whether the otter population was growing or declining. SOURCE: Selkoe et al. (2015).

al., 2015). Key attributes of ecological surprises (Doak et al., 2008) include the following:

- Surprises are both dramatic and widespread in scientific studies of all kinds.
- Ecological surprises are especially common and underreported.

- Ninety percent of well-established field ecologists who responded to a questionnaire in which they were asked if they had ever been surprised (as defined above) answered in the affirmative.
- Eighty-eight percent of those who responded in the affirmative believed that they understood the reasons for having been surprised after the

fact, thus suggesting that the causes were easy to understand but previously unanticipated.

- Many of these examples remained unpublished because the individual investigators thought they were either uninteresting (scientifically) or unpublishable.
- Efforts to improve predictability and quantify uncertainty in ecological models are unlikely to reduce the frequency of ecological surprises because these modeling efforts necessarily are built around things that are known as opposed to things that are unknown.
- Sooner or later, most natural resource management strategies will not work as planned, thus reinforcing the need for management plans that are precautionary.

In keeping with this general view of nature, studies of marine mammals have resulted in numerous surprises. For example, while most populations and species of great whales recovered following protection from exploitation during the whaling era, some (like southern blue whales) have not recovered for reasons that remain unknown (Branch et al., 2007). In Chapter 4, several case studies of population decline were explored where it has been difficult to infer causes, including beluga whales in Cook Inlet, Alaska, pinnipeds and sea otters in the Northern Pacific and Southern Bering Sea, and harbor seals in the United Kingdom. Other examples of surprises involving marine mammals could be described and cited. However, the committee is not aware of any cases where these surprises were subsequently attributed to cumulative impacts or the interaction among multiple stressors. This does not imply that such cumulative or interactive effects are unimportant in causing ecological surprises, but rather that they are not well understood.

To reiterate, the basic reasons for these various surprises are (a) insufficient understanding of interaction web structure, especially with regard to the various important pathways that lead from potentially diverse drivers to marine mammals; (b) complex functional relationships in the interactions among species and between species and the abiotic environment; and (c) overly simplistic views of interaction web structure and process.

**Finding 6.3:** The functional relationships between interacting species are often nonlinear and characterized by hysteresis. These complex functional relationships, coupled with immensely complex interaction web topologies, often result in unanticipated outcomes, sometimes referred to as ecological surprises.

## DESIGNING APPROACHES TO UNDERSTANDING STRESSOR IMPACTS AND THE PRINCIPLES OF SCIENTIFIC INFERENCE

Empirically based scientific inquiry in ecology involves two main elements: a search for pattern (which is commonly based on one's view of interaction web structure and dynamics, as discussed above), and distinguishing between causation and correlation. Empirically based patterns nearly always derive from observation of variation in space or time. These two elements of scientific inquiry are in turn often challenged by two essential inadequacies: (1) inherent difficulties in observing patterns associated with purported or hypothesized causal agents (in the context of this report, stressors and drivers) and (2) the inability to distinguish between causation and correlation with a high level of confidence. These shortcomings are best overcome through the experimental method, wherein the influence of some purported causal agent or agents (e.g., anthropogenic stressors or drivers) is assessed by observing differences between experimental units (e.g., behavior or physiological parameters in the case of stressors; individuals or populations in the case of driver effects on the distribution and abundance of species) that have been treated with the purported causal agent (i.e., by adding or removing the imagined stressor or driver) and those that have not (controls).

The three basic principles of experimental design are *randomization*, *replication*, and *local control*, which exist because experimental units always contain some level of intrinsic variation, independent of that which might be caused by their experimental treatments. For example, no two individuals are exactly the same. One needs to be able to detect and measure experimental treatment effects through this intrinsic variation in experimental units. Randomization (the random matching of experimental treatments to experimental units) is done in order to ensure that intrinsic variation among the experimental units is as likely as possible to be spread evenly between treatments. Replication provides a measure of experimental error, defined as the difference among identically treated experimental units, and causes the average value of the intrinsic variation among identically treated experimental units to converge on zero with increased replicate number. Local control is accomplished by choosing and arranging the experimental units and then assigning treatments to these experimental units so as to reduce experimental error.

Scientific experiments that are conducted in accordance with these design principles have three important properties. First, they minimize the likelihood of mistaking correlation for causation. Second, they provide an inferential template for the assessment of multiple agents of causality and the interactions among these agents. Third, they often permit increased inferential efficiency through the processes of blocking, stratification, and the analysis of covariance, all



of which help reduce experimental error. These broad principles are discussed and explained in greater detail in any introductory text on experimental design (e.g., Fisher, 1937; Montgomery, 1997).

As observed in Chapter 4, the predominant approach to studying interactions between stressors uses experiments with a simple factorial design. Although this approach is both powerful and broadly applicable, it has drawbacks and limitations for answering the many questions about nature that scientists have been unable to address experimentally. This is the current state of affairs for the committee's charge in this report, which is to evaluate the cumulative influences of anthropogenic stressors on marine mammals. As noted in Chapter 3, the lack of strong evidence for an influence of fisheries on marine mammals through competition for prey or other indirect interaction web effects is due to the failure to be able to assess these effects experimentally. Instead, the conclusions are more often based on observations of individuals and populations of marine mammals between otherwise similar areas with and without fisheries effects. Other approaches have been used in an effort to make these assessments (most commonly correlative analyses or inferences based on modeling approaches), but in many cases the signal is weak, and in most cases the distinction between causation and correlation is equivocal. For example, despite the great biomass of fish removed from the North Pacific Ocean/southern Bering Sea ground fisheries, it has proven both difficult and contentious to establish whether or not these potential prey removals have contributed to the declines of fur seals, harbor seals, Steller sea lions, and sea otters in southwest Alaska (NRC, 2003b). Moreover, pinniped populations in the northwestern Atlantic Ocean have generally increased, despite the collapsed ground fisheries (Estes et al., 2013b). Similar obstacles apply in the assessment of noise on marine mammals, although in this latter case experimental or quasi-experimental approaches are less problematic because noise is more manageably controlled than fisheries in space and time. However, the assessment of noise effects in combination with other potential stressors on marine mammals is exceedingly challenging because not only is it difficult or impossible to experimentally assess most singular (main) effects, doing so in sufficiently orthogonal combinations to be able to sort out the interactive effects is vastly more challenging. This is the fundamental nature of the problem at hand.

Understanding the influence of anthropogenic or natural stressors on marine mammals can only be rigorously assessed through observations of the manner in which individuals and populations respond to changed intensities of these stressors in their surrounding environments. Such information can be obtained in two general ways—through purposeful experimentation and through correlative studies from regions in which data from marine mammals are available in areas where the purported or hypothesized stressor has also varied. The strength of the experimental method is that,

when properly done, the likelihood of misinterpreting results because of potentially confounding factors is eliminated or greatly diminished. As explained previously, the difficulty with experimental approaches for marine mammals is that they are difficult or even impossible to implement at appropriate scales of space and time for a host of fairly obvious reasons, including logistical limitations and legal, social, and economic constraints. Many of the experimental approaches that have been implemented lack sufficient samples to have the necessary statistical power or precision to detect effects. With proper planning, correlative studies are easier to conduct, but these are also usually plagued with uncertainties over whether the purported or hypothesized stressor is the cause of any marine mammal response in the face of other potential confounding variables. This fundamental limitation to correlative analyses will be greatly magnified in efforts to assess the potential influences of multiple stressors or the aggregate influences of single stressors on marine mammals.

The strength of inferences from nonexperimental information can often be improved through various analytical approaches. One of these is a weight-of-evidence analysis in which the array of relevant information is contrasted against the expectations of alternative competing hypotheses. Using this approach, it is sometimes possible to determine the most likely of two or more alternative hypotheses, or to exclude one or more of these hypotheses based on internal inconsistencies with available data. More recently, Sugihara et al. (2012) proposed a general method for distinguishing causality from correlation based on nonlinear state-space reconstruction of time-series data.

**Finding 6.4:** Controlled experiments are the most rigorous way of testing for the influences of potential stressors on any species. For marine mammals, such experimental approaches are often not possible, in which case inferences must be based on quasi-experiments. Although quasi-experimental data are subject to confounding and thus multiple interpretations, reasonably strong inferences are often possible from time-series analyses and weight-of-evidence approaches.

## ADAPTIVE MANAGEMENT

As described above, classical factorial experiments are impractical as a vehicle for evaluating potential cumulative influences of stressors on marine mammal populations, while observational (correlative) studies are more practical to undertake but are likely to result in ambiguous inferences. Despite this, regulators must make decisions on whether and where to allow potentially harmful anthropogenic activities to take place. The concept of adaptive (resource) management offers a framework for making such decisions in the situation where there is some scientific understanding of the link between management action and outcome, and where repeated decisions must be made over time (such as issuing annual permits for activities, or setting harvest limits). Key

texts describing the concept include Walters (1986) and Williams (2011a, 2011b). A brief overview is provided here.

Adaptive management involves first setting a conservation objective and then formulating multiple hypotheses about the population response to the different management options, together with an assessment of the probability of each hypothesis being correct. The optimal decision is determined (see later for how “optimal” is defined), and this action taken. The population response is monitored, and the new information gained is used to update the probabilities for each hypothesis, whereupon the process is repeated. A key concept is that “we learn more about the system as we go along” and hence can adapt management decisions in the light of the improved information. There are broadly two approaches of adaptive management, depending on how “optimal” is defined: in passive adaptive management, the optimal decision is the one most likely to bring scientists closest to the conservation objective given the current state of knowledge; in active adaptive management, determining the optimal decision also involves accounting for the learning that is anticipated to occur as a result of each possible decision. (See Williams [2011b] for a more nuanced discussion of the various closely related definitions that have been used.) Hence, in active adaptive management, it is sometimes considered optimal to take management decisions that result in moving away from the conservation objective in the short term if this means one learns more about the biological system and so can make better conservation decisions in the future. Classical experiments may be contemplated, where different management actions are assigned at random to spatially replicated regions (if possible). Active adaptive management is therefore riskier, in that it relies more on having an accurate assessment of the consequences of selected actions (in terms of how much each possible action will help us distinguish between the multiple alternative hypotheses).

Although adaptive management ideas are much discussed, they are relatively little used in practice. A recent literature review by Westgate et al. (2013) identified 1,336 articles published between 1978 and 2011 using the term “adaptive management.” Of these only 61 (<5%) explicitly claimed to enact the methods, and only 13 projects were found that the review authors felt met the criteria for actually using adaptive management. There are multiple possible reasons for this lack of usage. First, the method requires the formulation of multiple competing hypotheses, typically expressed as alternative quantitative conceptual models of the system, and it may be that there is simply not enough knowledge about most systems to do this adequately. Second, the realistic rate of learning may be too slow to be useful. This may be because there is strong natural variability (e.g., from ecological drivers such as El Niño in the Pacific or the North Atlantic Oscillation) that nearly masks any signal coming from alternative management actions; because possible management options do not generate a strong signal (e.g., if they can only be applied to a small component of the popula-

tion); because any signal may take a long time to be manifest (as will be the case for long-lived, slow-reproducing animals like most marine mammals); because standard experimental practices like replication and blocking are not possible; or because the monitoring of outcomes that are feasible is too imprecise to be useful. Third, although adaptive management is designed to cope with uncertainty about which hypothesis is correct, and with observation error in the outcome measurements (both “known unknowns” [Logan, 2009]), it is not robust to the kinds of ecological surprises that were discussed earlier in this chapter (the “unknown unknowns”); hence, focusing only on measuring the best metrics for distinguishing between alternative hypotheses risks missing other important conservation issues. The topic of monitoring is explored in the next chapter. Finally, implementing adaptive management is complex, typically requiring a team with skills in theoretical ecology, applied conservation, statistics and modeling, and, potentially, social sciences if the human aspect of management decisions is to be considered. Resources and commitment over the long term are required, and these are rarely available.

Despite these issues, there does not appear to be a superior alternative to adaptive management as a rational and structured system for making optimal conservation decisions. Trial and error, or “reactive management” (Sutherland, 2006), is clearly inferior. For this reason, the application of adaptive management principles to the management of cumulative effects is encouraged wherever this is possible.

**Recommendation 6.1: Adaptive management should be used to identify which combinations of stressors pose risks to marine mammal populations, and to select which stressors to reduce once a risk is identified.** In this approach, hypotheses are developed which guide management actions and data collection to assess the strength and impact of individual stressors and their cumulative effects.

## CONCLUSIONS

In addition to direct mortality from entanglement in fishing gear, ship strikes, and purposeful killing, marine mammals are exposed to a broad range of potential anthropogenic stressors, including but not necessarily limited to noise, prey depletion by fisheries, disease, pollutants and toxins, and a broad (but still largely unknown) array of indirect effects of these various stressors on the associated ecosystems. In particular cases, each of these direct effects is known or suspected to have negative impacts on marine mammal individuals and populations. A separate literature from experimental studies (see Chapter 4) has demonstrated the cumulative or synergistic influences of stressors on a wide range of aquatic plant and animal species. Therefore, cumulative influences of anthropogenic stressors on marine mammals are nearly a certainty.

The challenge is in conceiving of and especially then

demonstrating these effects on marine mammals. The important outstanding questions are these: For which particular stressors under what specific conditions and for which marine mammal species will cumulative effects occur, and what are the functions that relate stressor dosage to the linked effect? Answering these questions in a scientifically rigorous manner is beset by three significant challenges. The first challenge is to properly characterize a topology of influence by stressors on marine mammals. Simple direct effects of singular stressors on marine mammals are relatively easy to imagine, but the potential influences of multiple stressors, acting through both direct and indirect interaction web pathways, will be substantially more difficult. The second key challenge will be in designing studies in which the interactive influences of multiple stressors on marine mam-

mals can be evaluated. Experimental designs that are capable of demonstrating interactive effects while controlling for confounding influences are nearly impossible to carry out without purposely manipulating the purported drivers in an orthogonal manner. A final challenge is in the detection of any real impact from stressors on a marine mammal stock at the individual and especially the population level. Rigorous demonstration of population change has proven to be exceedingly difficult for most marine mammal species. Thus, even when the process by which multiple stressors might influence a marine mammal is well conceived and a study can be properly designed to put the resulting hypothesis to a test, the ability to document an effect on the marine mammal species, population, or stock of interest will often be limiting.

## 7

## Early Warning Signs of Risk to Populations

### INTRODUCTION

The previous chapters have attempted to establish that scientists may anticipate the nature of some interacting effects, but in most situations they are not currently able to forecast the cumulative effects of all stressors with any accuracy. Therefore, there is a pressing need for early detection of unexpected population declines and, where possible, rapid diagnosis of the main factors contributing to them. This requires some form of population monitoring. The parameters monitored must be informative about the status of the population; it is also helpful if they are informative about the contributing factors for any decline in status, although that could become part of a secondary, more intensive, data-gathering effort that is instigated if the first stage of monitoring indicates a problem. (An alternative view is given in the following paragraph.) Detecting a deleterious situation involves testing for long-term declines in status over time (trend analysis; see, e.g., Thomas et al., 2004), or a recent sudden drop (sequential surveillance; see, e.g., Anderson and Thompson, 2004; Frisé, 2009). Alternatively a comparison could be made with reference to populations thought to be in good status, although such comparisons need to consider natural variability. The parameters monitored must also be measured with sufficient accuracy and precision that there is a good chance a deleterious change of magnitude large enough to cause concern will be detected (i.e., good statistical power, if a statistical hypothesis test is the detection mechanism).

The above approach has been criticized as being inefficient and ineffective by Nichols and Williams (2006), who refer to it as “surveillance monitoring.” They argue that a focus on detecting declines, often using statistical hypothesis testing, is unlikely to lead to optimal conservation decisions and introduces unnecessary time lags, and that identifying

the causes of declines is less important than identifying the most effective remedy (although recognizing the cause can often help identify possible solutions). Instead, they advocate embedding monitoring within a larger framework of conservation-oriented science or management, where monitoring is used to enable discrimination between multiple competing hypotheses about the biological system being monitored and hence facilitate better management decisions. Monitoring therefore becomes an integral part of an adaptive management framework, as defined in the previous chapter. This also implies that monitoring programs will change what is measured as the scientific hypotheses under consideration are updated—a paradigm called “adaptive monitoring” by Lindenmayer and Likens (2009).

The committee believes that there is merit in both of these frameworks. Adaptive management, and hence adaptive monitoring, potentially can be effective in situations where there is enough knowledge of the system to formulate working hypotheses about the link between each potential management action and the outcome, to evaluate the *a priori* probability of each hypothesis, and where learning through focused monitoring will be useful. However, there are at least two reasons not to rely exclusively on such adaptive monitoring. First, there are many cases where the above criteria will not be met and adaptive management will not be helpful. Second, as described in Chapter 6, there is a strong potential for “ecological surprises,” for example, unexpected declines in species that had not previously been considered to be of conservation concern. Hence, a dual approach is advocated, where the principles of adaptive management and adaptive monitoring are applied where possible, but where, in addition, a “light touch” surveillance program is undertaken in order that very large changes in conservation status of species are not missed until it is too late to do anything about them. It is recognized that such a surveillance program will have low

power, but its aim is to detect only large changes in status. The chance of detecting a change in status will be improved if a sensitive indicator can be found that is also relatively inexpensive to monitor.

The committee has previously recommended the use of adaptive management (Recommendation 6.1) to focus data collection and guide management actions. The following recommendation concerns a “light touch” surveillance program.

**Recommendation 7.1: Responsible agencies should develop relatively inexpensive surveillance systems that can provide early detection of major changes in population status and health.** Surveillance systems should be developed first for populations that currently lack adequate stock assessments.

In the following sections, the population parameters that might best be measured in either of the above frameworks are discussed. One form of ecological surprise described earlier is that of an ecological tipping point. In the last section, suggestions from the literature on the early detection of a species or system approaching a tipping point are described.

## MONITORING POPULATION SIZE

Population size is the most basic measure of population state. However, for most marine mammal species, monitoring total population size (or density) over time or space is not a sensitive way to obtain early warning of problems (for surveillance monitoring) or distinguish between different possible management actions (for adaptive monitoring). One issue is that it is often difficult to define what constitutes a biologically appropriate unit of assessment because many local populations are not genetically or demographically isolated. Another is that most marine mammal species are long lived and slow to reproduce, so any negative impact that causes reproductive failure or juvenile mortality, or any beneficial management action, will take a very long time to cause a significant population trend. However, the main issue is that population (or stock) size is a parameter that is notoriously difficult to measure precisely, particularly for marine mammals that often range over a large area and are invisible when underwater. Visual methods requiring human observers remain the most commonly used for marine mammals, particularly cetaceans—either shipboard or aerial line transect surveys or photographic capture–recapture (Buckland and York, 2009). For colonial pinnipeds, colony counts are sometimes used, with a correction factor (derived from animal-borne tags) for those at sea (Buckland and York, 2009); for some pinnipeds such as grey seals, pup production at breeding colonies is estimated and a population dynamics model is used to scale up to total population size (e.g., Thomas et al., 2005). For animals that are widely dispersed, it tends to be the spatial variation that causes low precision;

for rare or hard-to-see animals it is the low sample size; for colony counts it is estimating the scaling factor. The result is that the ability to detect all but the most drastic population trends is often limited. For example, Taylor et al. (2007) reviewed the precision of abundance estimates for 127 stocks under U.S. management and concluded that, overall, 70% were not precise enough to detect a precipitous decline of 50% over 15 years of monitoring. Jewell et al. (2012) examined the utility of combining results from multiple abundance surveys worldwide: for the best-fitting model, the smallest population decline detectable with high (>0.8) power was more than 50% for 5 out of the 11 taxonomic and geographic groupings used.

Despite this pessimistic message, more precise monitoring is possible for some stocks, particularly those that live in restricted areas relatively close to shore (e.g., southern resident killer whales) or all pass close to shore at some point in their life cycle (e.g., gray whales). New technology may also play a part in enabling more precise population estimation—for example, potentially replacing visual surveys with remote aerial vehicle surveys using high-definition cameras or video recorders (Buckland et al., 2012) or passive acoustic surveys from fixed or floating sensors, or remote underwater vehicles (Marques et al., 2013). Many of these techniques are still under active development; for passive acoustic methods a critical limitation is knowledge of the acoustic biology of the target species required to convert call density into animal density and abundance. New statistical methods that make better use of existing or emerging data streams also offer the potential for better precision—for example, the recent ability to extend capture–recapture analysis to utilize information about the location of the captures (Borchers, 2012; Royle et al., 2013; Pirota et al., 2015c). Taylor et al. (2007) discuss some other potential routes to increased precision. However, it is important to emphasize that, at the current time, estimation of population size remains a very imprecise science for almost all marine mammal stocks.

One possibility sometimes suggested for obtaining more precise estimates of population status is to measure indices of population size, such as uncalibrated acoustic detections and sightings from shore-watch schemes or from platforms of opportunity. However, straightforward interpretation of changes in the index as changes in population numbers requires that the relationship between the two is linear and has constant variance over the range of both indices, or that the shape of the relationship and variance is known (Williams et al., 2001, Section 12.7). In practice, the relationship is rarely linear (indeed it may not even be monotonic) or with constant variance. Nevertheless, carefully chosen indices may still be effective as early warning metrics, for example, if they are sensitive to changes in population size or disturbance for the species of interest and are relatively inexpensive to deploy at the population scale. Passive acoustic detections may be a good candidate in this regard, in that large amounts of data can be collected at moderate

expense (for vocal species); however, its efficacy has yet to be demonstrated.

In determining the cause of population declines, it is often insightful to focus on the components of the population likely to be affected first. This is discussed in the next section.

## MONITORING DEMOGRAPHIC PARAMETERS

Population dynamics are governed by four fundamental demographic parameters: survival, fecundity, immigration, and emigration. One or more of these must decline (or increase in the case of emigration) for population declines to occur. Hence, measuring these parameters may make for a more sensitive monitoring system than waiting for a detectable change in population size. However, it is typically infeasible to monitor all of these parameters with good precision, so one will typically need to prioritize. To do so, one needs to consider which of these parameters is expected to be most strongly affected by cumulative impacts of stressors, the influence changes in these parameters have on population size, and the feasibility of accurately measuring the parameter.

Many marine mammals are relatively long lived and reproduce infrequently but over multiple occasions. Under these circumstances, ecological theory leads us to predict that reproductive-age adult females should evolve strategies that enable them to delay breeding or abandon investment in young when conditions are harsh in order to prioritize their own survival and hence maximize their future reproductive output when conditions may be better. Therefore, there is an expectation that adult female survival will remain high and relatively constant in fluctuating environments, while fecundity and calf or pup survival should fluctuate with the conditions. A similar phenomenon occurs as populations approach carrying capacity and, based partly on empirical observations, Eberhardt (2002 and references therein) proposed the following sequence of changes as conditions worsen:

- increase in mortality rate of immatures
- increase in age of first reproduction
- reduction in reproductive rate of adult females
- increase in mortality rate of adults

The committee's opinion is that there is no strong theoretical reason to suggest that pup or calf mortality should always increase before fecundity-related parameters decrease; this may depend on the cost of pregnancy and gestation, and whether the species is adapted to uncertainty in the ability to provision young. For species where these costs are low, and that are adapted to uncertain provisioning conditions, adult females may tend to continue to produce pups or calves but then not be able to successfully rear them. Hence, from an early warning perspective, fecundity

(including age at first breeding) and calf or pup survival are all parameters to target.

To determine influence on population size, it is useful to consider the findings of matrix population modeling (Caswell, 2001), in particular from sensitivity analysis, which quantifies how much population growth will be affected by identically sized changes in each demographic parameter in the model. Exact results depend on the model, but in general, population growth is most sensitive to changes in adult survival, with changes of the same magnitude in fecundity and pup or calf survival having much less effect (Eberhardt, 2002).

Putting these last two threads together it is expected that birth rates and/or pup or calf survival are likely to be first affected by cumulative stressors, but that they will have the least effect on population growth rate. This provides a strong justification for monitoring these parameters as part of an early warning system, where they may show a strong signal of population stress before the population trajectory is strongly affected. However, it is important to recognize that natural population processes such as density dependence will also result in low birth rates and/or with pup or calf survival, and hence measurements need to be put into the context of natural population dynamics. Also, as stated earlier, these demographic parameters are expected to show the highest levels of natural variation, so picking out a declining trend among strong interannual variation may be difficult.

The last consideration is the feasibility of accurately monitoring the parameters. Many demographic parameters can be estimated from an intensive capture–recapture survey; typically for marine mammals this involves photographic identification, although genetic identification from biopsies or fecal samples (or even potentially blow samples) is possible. Each of these methods is labor intensive, and only feasible in situations where animals are accessible and a reasonable recapture rate is likely. In planning a study, the expected precision can readily be evaluated using a straightforward simulation approach (Devineau et al., 2006).

Age-specific mortality can also be derived from analysis of age structure of a population, assuming a stable age structure (as in when the population is growing exponentially, or has reached carrying capacity); this is the basis of life-table analysis. One example of this is Moore and Read (2008), who used the age structure of harbor porpoise deaths from all mortality sources and the age structure of deaths from fisheries bycatch to estimate the effect of bycatch on vital rates and the likelihood of population decline. The use of strandings is, however, problematic due to the length of time required to obtain a sufficient number of carcasses for age structure analysis, and the fact that it can only be used on inshore populations in areas where stranded carcasses are reported and can be investigated. For this reason it cannot be recommended as a general monitoring method.

Fecundity (or at least pregnancy) can also potentially be estimated from hormone analysis (e.g., Kellar et al., 2006;

Hunt et al., 2014) and from looking at pregnancy rates (and possibly pregnancy history) of stranded or sampled animals. However, high pregnancy rates alone may not mean good population status: if calf or pup survival is low then females do not need to devote energy to provisioning their young and hence may recover and breed again more quickly—thus elevating pregnancy rates. Hence pup or calf survival should also be measured.

Overall, although birth rates and pup or calf survival seem at first glance to be the best parameters to monitor for early warnings, it will be important to undertake some form of power or precision analysis to determine whether a signal of the expected magnitude can be detected given expected levels of interannual variation and measurement error.

Another generally applicable approach is to focus on indices of demography that can readily be measured in the field. One prominent example is the ratio of adults to juveniles in a sightings survey (or, relatedly, the proportion of mother–calf pairs in populations where this is an appropriate metric). Calves or pups are typically readily distinguishable from adults; it may also be possible to distinguish juveniles and record similar metrics on them. In conclusion, collection and analysis of stage-structured population data may provide a useful early warning of poor population status.

## MONITORING POPULATION HEALTH

Chapter 5 provided a definition of individual health, as well as reviewing some of the various indices used to assess individual health. However, it is important to distinguish between assessing the health of an individual versus assessing the health of a population, the latter being focused on the measurement of the distribution of health outcomes in a population or a subset of a population, *as well as* the determinants or factors that influence those outcomes (Ryser-Degiorgis, 2013). The term “health outcomes” is used rather than the more narrow term “health status” because the latter refers to health at a single point in time rather than over a period of months or even years that it may take for a disease to develop (and demographic consequences to become manifest) (Kindig and Stoddart, 2003). As a field of research, population health focuses on multiple potential contributing factors for health outcomes; it considers the complex interactions among factors, the biological mechanisms underlying a given health outcome, and the influence of different factors over time and throughout an organism’s life cycle (Kindig and Stoddart, 2003; Ryser-Degiorgis, 2013). In this respect, population health studies not only address the detection of changes in health outcomes, but also simultaneously address the potential causal factors.

The concept of population health involves different criteria from population status. The National Marine Fisheries Service (NMFS) assesses the status of a marine mammal population or “stock” by assessing its range, minimum population estimate, current population trends and productivity

rates, human-caused mortality, and other factors that may cause a decline or impede recovery (NMFS, 2004). Populations that are large and near carrying capacity will usually have a good population status but could have a lower level of population health. A population that is at or nearing carrying capacity may exhibit a high prevalence of disease (e.g., malnutrition or infectious disease), and the population’s size in relation to its expected carrying capacity should be considered as a potential driver when poor population health is observed. In this context, population health (i.e., the distribution of health outcomes in a population or a subset of a population) may produce a false-positive indication of population decline. While this chance of false positives for populations for which status is completely unknown decreases specificity, population health will in most cases provide greater sensitivity and is a more tractable approach as compared to monitoring population status, which requires precise estimation of population size and current productivity rate in relation to an expected productivity rate. Carrying capacity is generally not known and is difficult to estimate. However, the objective of monitoring as outlined in this chapter is early detection of population declines. If poor population health is observed, continued monitoring over time would allow the hypothesis of carrying capacity being the underlying driver to be confirmed or rejected.

Population health monitoring can take two primary forms: passive health surveillance (also referred to as scanning surveillance) and targeted health surveillance. Passive health surveillance focuses on in-depth investigation of disease incidence and for wild marine mammals is generally conducted using carcasses or tissues collected from stranded animals. In the United States, under the 1992 Amendments to the Marine Mammal Protection Act, the Marine Mammal Health and Stranding Response Program (MMHSRP) was formalized to coordinate efforts to investigate marine mammal strandings.<sup>1</sup> The intent of the program is to improve the knowledge of rates and causes of mortality and morbidity to gain a better understanding of population threats and stressors, and to detect emerging or unusual events. Since 1991, 62 marine mammal unusual mortality events (UMEs) have been recognized in the United States,<sup>2</sup> and in those where causes have been attributed (only 56%), these have included biological toxins, infections, human interactions, oil spills, and changes in oceanographic conditions (Gulland and Hall, 2007). An additional important component of the MMHSRP is biomonitoring, i.e., sampling, archiving, and analysis of tissues to allow for examination of geographic and temporal patterns in exposure to chemical contaminants, biological toxins, and/or pathogens (e.g., Fire et al., 2009; Twiner et al., 2012; Simeone et al., 2015). A real-time, nationally centralized system for reporting marine mammal health data has been proposed (Simeone et al., 2015) and would

<sup>1</sup> See <http://www.nmfs.noaa.gov/pr/health/MMHSRP.html>.

<sup>2</sup> See <http://www.nmfs.noaa.gov/pr/health/mmume/events.html>.

greatly facilitate the conduct of epidemiological analyses to more rapidly detect and identify contributing factors for UMEs, as well as to explore more subtle changes in population health over space and/or time in relation to one or more stressors. Standardization of databases for marine mammal health within and across nations could facilitate more global analyses. However, with the exception of nearshore species, the utility of passive surveillance for marine mammal populations will still be limited due to the extremely low probability of recovering carcasses (Williams et al., 2011; Barbieri et al., 2013; Carretta et al., 2015).

**Recommendation 7.2: A real-time, nationally centralized system for reporting marine mammal health data should be established.**

In contrast, *targeted health surveillance* is carried out proactively, focusing on live animals that in some cases are apparently healthy, and relying primarily on cross-sectional study designs that require only a single sampling occasion (Ryser-Degiorgis, 2013). Targeted health surveillance in the form of capture–release health assessment has been successfully conducted for a number of species along the U.S. coast (e.g., Wells et al., 2004; Aguirre et al., 2007; Greig et al., 2010). Physical examination, diagnostic ultrasound, and blood sampling for hematology, serum biochemistry, and hormone analysis can be conducted and synthesized to determine the prevalence of specific disease conditions (Schwacke et al., 2014a), and serology (to determine antibody prevalence) can help to evaluate prior pathogen exposure, or lack thereof, assisting in the development of management plans (M. Barbieri, personal communication). Portable auditory evoked potential systems also allow for hearing tests (Finneran and Houser, 2007) to be performed, which are particularly relevant for understanding hearing loss among various populations. Unfortunately, capture–release studies can only be conducted on relatively small, tractable marine mammal species, and to date have focused on the nearshore where individuals can be temporarily caught and restrained on land (e.g., seals and polar bears; Stirling et al., 1989; Polischuk et al., 2001) or in shallow waters (e.g., small delphinids, and manatees; Bonde et al., 2012). However, methods could and should be developed to extend such sampling to other coastal, continental shelf, and/or oceanic species, although an extension of these types of approaches to large cetaceans will be complicated by the logistical challenges of capturing and restraining them. Nevertheless, remote sampling techniques are rapidly advancing and can be applied to large cetaceans. Hunt et al. (2013) review currently available techniques for obtaining physiological information on large whales that include remote collection of respiratory (“blow”) samples, skin/blubber samples, and fecal samples. Perhaps most promising is the collection of blow, as techniques for analysis of metabolites, hormones, and pathogens have been demonstrated using cetacean respi-

ratory samples (Acevedo-Whitehouse et al., 2009; Hunt et al., 2013; Aksenov et al., 2014; Cumeras et al., 2014), and recent developments in human breath analysis indicate promise for eventually obtaining a broad array of physiologically relevant indicators of health (reviewed by Hunt et al., 2013). However, collection methods are still being refined and will require extensive validation as well as collection of baseline samples to understand the inherent variability for the suite of measures across species, life-history stages, and varying environmental conditions. Likewise, “-omics” approaches (primarily proteomics and transcriptomics) are being pursued using sampling matrices that can be remotely collected (blow, skin/blubber; reviewed by Hunt et al., 2013), but characterization of expression profiles is still in its infancy, and identifying patterns that provide meaningful information on health state is complicated by lack of information on cetacean genomes (Hunt et al., 2013), variation among life-history stages, genetic stock, and varying environmental conditions (e.g., Van Dolah et al., 2015), and the fact that some remotely collected samples (i.e., skin/blubber) simply may not be appropriate matrices for detecting expressional changes associated with many health conditions.

Targeted surveillance could also be supported through photographic studies. Photographic monitoring has been used to identify emerging zoonotic disease (Rotstein et al., 2009) and support epidemiological investigations of skin disease in both terrestrial (e.g., Oleaga et al., 2011) and marine mammals (e.g., Hart et al., 2012; Van Bressemer et al., 2015). Visual health assessment based on body and skin condition, and the presence of cyamids and rake marks, has been applied for right whales (*Eubaleana glacialis*), and an index of health based on these criteria has been developed that is predictive of survival and reproduction (Schick et al., 2013). In addition, Fearnbach et al. (2015) have applied photogrammetry to assess body condition based on proportional head width in endangered Southern Resident killer whales (*Orcinus orca*). Furthermore, recent development of techniques to obtain photographs using unmanned aircraft systems (Durban et al., 2015) will greatly facilitate photographic monitoring to measure body condition and/or assess parasites, skin disease, or other externally visible indicators of compromised health.

These novel health assessment methods are primarily designed to be applied to individuals, but because population health emerges from the health status of a population’s members, appropriate sampling at the individual level can lead to inferences about population status. In this vein, body condition, as measured by a visual health assessment or photogrammetry (see above paragraph), could represent a first-pass metric for overall population health. Sampling would need to include a sufficiently large number of animals to assess the health of groups critical to population growth, such as a large cross-sectional sample of adult females across a variety of life-history stages or of juveniles. A broad measure of health, such as body condition, would not necessarily



be sensitive to quick changes because fat reserves may not be affected until the late stage of a disease; however, because most pathways of declining health eventually affect body condition, it could capture the consequences of a variety of potential stressors.

One important caveat here, just as with measuring demographic parameters, is that care needs to be taken not to misinterpret poor health caused by natural demographic processes, such as reaching carrying capacity, with poor health that is of concern; in other words, measurements need to be put in the context of expectation given the population status.

## EARLY WARNING OF TIPPING POINTS

As described in Chapter 6, the existence of multiple stable states and tipping points in natural ecosystems is now beyond reasonable doubt. However, the real challenge for managers and scientists alike is the ability to anticipate and predict regime shifts, especially as the impacts of anthropogenic stressors and drivers on ecosystem function and processes appear to be increasing. The potential for predicting regime shifts in marine environments and their management depends on the characteristics of the regime shifts: their drivers, scale, and potential for management action.

Recent theoretical findings (Drake and Griffen, 2010; Dai et al., 2012; Dakos et al., 2015) suggest that ecosystems tend to recover more slowly from small perturbations if they are in the vicinity of tipping points. This phenomenon is referred to as “critical slowing down,” and its temporal and spatial indicators may under some conditions provide early warning signals of a system approaching a tipping point where it could easily pass through a critical transition into an alternate state (Dakos et al., 2015). However, applying these theoretical insights to the management of marine mammal populations is limited by a lack of critical ecological

data in many species: without these data it is challenging to characterize baseline variability in populations and resources well enough to detect changes that might indicate a potential tipping point. There is also the important consideration that many population parameters for marine mammals are measured with such low precision that detecting any signal among the noise may be nearly impossible.

Levin and Möllmann (2015) argue that “accounting for marine regime shifts in management clearly requires integrative, cross-sectoral ecosystem-based management (EBM) approaches.” EBM is widely used for ocean management worldwide and is well suited for dealing with regime shifts, as it considers the multiple interacting drivers and ecosystem linkages that generate ecosystem shifts. They make a case for the use of Integrated Ecosystem Assessment (IEA) (Levin et al., 2009), an EBM framework used by a number of management agencies in the United States.<sup>3</sup> IEAs are becoming more common, but they are still new enough in their development to allow the inclusion of regime shift concepts in an emerging EBM framework. IEAs could provide a transparent means of characterizing the status of ecosystem components, “prioritizing potential risks and evaluating alternative management strategies against a backdrop of actual environmental conditions.” To be useful, IEAs will need to identify ecosystem attributes and anthropogenic stressors; “develop and test indicators and reference levels that reflect key ecosystem attributes and the drivers; explore the susceptibility of an indicator to natural or human threats as well as the ability of the indicator to return to its previous state after being perturbed; evaluate the potential different management strategies to influence the status of key ecosystem components and the pressures that affect these ecosystem components”; and consider the precision with which the indicator can be measured, relative to the expected strength of the signal generated.

<sup>3</sup> See <http://www.noaa.gov/iea>.

## 8

## Approaches to Assess Cumulative Impacts

### INTRODUCTION

The previous chapters of this report have reviewed a variety of “approaches to assess cumulative effects of multiple stressors on marine mammal populations that, in turn, have direct and indirect effects on vital rates and population health” as stipulated in the statement of task (see Chapter 1). There are very few situations where one can link exposure to stressors directly to effects on marine mammal populations. Several approaches are discussed, beginning with those of limited use for marine mammals and then moving on to those with greater utility for this task.

### APPROACHES WITH LIMITED APPLICATION FOR EVALUATING CUMULATIVE EFFECTS IN MARINE MAMMALS

#### Factorial Experiments

The primary experimental method used to evaluate cumulative effects of stressors involves factorial experiments that manipulate two or more stressors in animals that can be held in controlled settings. As discussed in Chapter 4, many stressors are likely to interact, and their effects should only be assumed to be additive if there are sound biological (as opposed to purely statistical) reasons for this assumption. The committee’s review of meta-analyses of these experiments concluded that there are no obvious generalities that could help us to predict the effects of interactions between stressors on marine mammals in the wild. There are so many stressors affecting marine mammals and the ecosystems upon which they depend that the traditional approach of starting with impacts of individual stressors and then studying interactions when small sets of stressors are added together is not practical. Halpern et al. (2007) found that all of the

marine ecosystems they surveyed were threatened by at least nine stressors, leading to hundreds of potential interactions that would need to be studied. This is not practical for marine mammals.

#### Alternative Model Species

The difficulties of studying cumulative effects in protected, large, long-lived animals such as marine mammals has led some to argue for consideration of other easier-to-study taxa as surrogate model species (Caro and O’Doherty, 1999). However, as Chapter 3 discusses, terrestrial mammals may differ enough in responses to stressors that they may not be good model systems for marine mammals. For example, investigations in pinnipeds have shown that increased oxidative stress during fasting and diving is ameliorated by oxidant-induced hermetic responses that increase antioxidant capacity more than would be predicted using studies from terrestrial mammals (reviewed by Vázquez-Medina et al., 2012). There also are serious questions about extrapolating information about interactions between marine stressors from nonmammalian marine model species to apply to marine mammals. As homeotherms, the response of marine mammals to temperature is very different from that of animals whose temperature matches the ambient. As animals that breathe air, marine mammals are much less sensitive to water-borne compounds than animals that extract oxygen from water. In this report the committee urges caution when extrapolating from non-marine mammal species in assessing cumulative effects of stressors on marine mammals.

#### Laboratory Studies

There are significant logistical and ethical problems with experiments that intentionally expose marine mammals in the

laboratory to stressors such as pathogens. However, studies have been conducted on stressors such as sound, toxins, and temperature. Chapter 2 reviews studies on effects of sound on marine mammals. De Swart et al. (1996) and Ross et al. (1996b) fed harbor seals with herring from either relatively uncontaminated areas of the Atlantic Ocean or from the contaminated Baltic Sea. Baltic herring was immunotoxic to the seals, potentially reducing their resistance and increasing risk from infectious diseases. Yeates and Houser (2008) determined how low the temperature of air or water had to go before the metabolic rate of their bottlenose dolphin subjects became elevated. Water temperature had a stronger effect than air temperature, and little synergy was observed between the two. These studies of physiological responses to stressors illustrate that laboratory studies can demonstrate causal relationships between stressors and effects.

There may be further scope for laboratory research on effects of stressors on marine mammals, but there is a major advantage for research on wild animals. Marine mammals are exposed to such broad and poorly quantified arrays of stressors that it would be difficult to attempt to reproduce these combinations of stressors in the laboratory. By contrast, if one wants to study the effect of adding one stressor, such as sound, to a population influenced by many stressors, then one can select subjects from the wild population that are exposed to the current combination of stressors. Exposure to intrinsic stressors will vary with life history, and exposure to extrinsic stressors will vary in time and space. If the goal is to study animals whose allostatic load is high, this suggests selecting times when both intrinsic and extrinsic stressors lead to the energy demand exceeding supply (McEwan and Wingfield, 2003). This goal suggests an alternative to fully sampling the range of exposures in the wild. However, studies that involve adding one stressor to a wide sample of subjects in the wild actually do evaluate the cumulative effects of all the stressors to which the subjects are exposed. One cannot count on the same being true for studies of animals that are maintained in laboratory environments where animals are well fed and free from predation and many other stressors. These considerations suggest that wild marine mammals may be more appropriate subjects for studies of cumulative effects than captive animals.

### SAMPLING STRATEGIES THAT DEPEND ON RANGING PATTERNS

The opportunities and obstacles for making critical measurements depend on the ranging patterns of the species under study. There are four main patterns for marine mammals that are relevant for sampling strategies for assessing cumulative effects of stressors in marine mammals.

#### Accessible Resident Populations

Species with home ranges that are small and near shore can be studied in a cost-effective manner by biologists using small vessels to sight individuals that can be identified by markings. These kinds of studies have proven valuable for tracking birth, growth, and death of nearly every individual in a population (e.g., Brault and Caswell, 1993). The overall exposure of the population can be measured on a seasonal or annual basis for a range of stressors based on environmental sampling. Comprehensive health assessments also are able to measure the dosage of individuals for some stressors, along with data on responses to stressors. These studies have been conducted with several populations of bottlenose dolphins that live in coastal waters of the southeastern United States, providing demographic data that can be compared across sites. Comprehensive health assessments involving suites of biomedical sampling (Wells et al., 2004) have also taken place at several of these sites, providing critical data for evaluating the dosage and effects of stressors that impact only one or a few of the sites. For example, Schwacke et al. (2014b) compared results from dolphins oiled after the *Deep-water Horizon* event to those from a population in Sarasota Bay, Florida, far from the oiling, and Venn-Watson et al. (2015) compared oiled dolphins to those that had stranded in other areas. For populations with limited home ranges, these concurrent studies in several populations provide a powerful tool for studying effects of stressors whose exposure varies across the locations.

Some species associated with deep oceanic areas have small enough home ranges for observational methods to provide important longitudinal data in areas where deep water is close to shore. For example, some beaked whale species are thought to have limited home ranges near seamounts or undersea canyons. Claridge (2013) was able to obtain important life-history data from populations of Blainville's beaked whale (*Mesoplodon densirostris*) in Bahamian waters. Similar data have been obtained for pilot whales in the Strait of Gibraltar where a small population of pilot whales resides (Verborgh et al., 2009). These situations may give a biased view, however. For example, pilot whales in most other study sites range so widely that there are relatively low rates of resighting individuals in one location.

#### Species with Predictable Locations for Birth on Land

Pinnipeds that come ashore in between foraging trips at sea and that give birth on land offer special opportunities for study. Long-term studies of identified individuals in this case can more easily involve sampling, weighing, and tagging than studies for species where animals do not come ashore. The foraging trips may take days to months—durations that are well within the scope of established tag attachments. Some of these species are suitable for the analysis of body condition through measuring buoyancy during drift dives. New et al.

(2014) showed how data on weight and survival of mothers and pups could be coupled with tag data measuring how foraging affects body condition. These data can be incorporated into the kind of model developed in Chapter 5 to relate how variation in stressors leads to variation in reproduction and calf survival. The main obstacles to studying interactions between stressors in these species involve development of more studies of identified individuals, and development of ways to measure exposure and response to stressors. These species are among the most promising for development of studies using the model from Chapter 5.

### **Species That Are Accessible at Some Points Within Large Home Ranges or During Annual Migrations**

Some migratory species of cetacean congregate near shore for enough of their annual cycle to be studied by shore-based researchers. When accessible, these populations can be studied by observing individual animals that have distinctive marks. For species with several such sites, comparing sightings can allow movements to be tracked, but this is biased by the observation sites and is likely to lead to an incomplete view of the population range. For example, the population of right whales in the Northwest Atlantic is well studied from sightings during the summer foraging season, enough to estimate risk of extinction (Caswell et al., 1999). A subset of the population migrates to coastal waters off the southeastern United States, but little is known about where the other segment winters. Similarly, long-term observations of a small population of killer whales that are routinely sighted in Puget Sound, Washington, has provided solid evidence of a decline, enough to list the population as endangered (Ford, 2013). However, this population ranges as far as California during the winter, and little is known about their exposure or response to stressors during this part of the year. In these cases, focused tagging efforts may be needed to supplement local field studies. Obtaining measurements and attaching tags to these animals will be more challenging than working with animals that haul out on land. In addition many of these migrations occur on an annual basis, requiring longer tag attachment times than for most species that give birth on land, to cover the time at sea away from the nearshore site. Many species that have large home ranges or migrate annually have been tagged with satellite tags, but this is expensive, so the sample size is low. Few tags are available with longevity sufficient to cover an entire migration period, but the success rate and length of attachment duration are increasing as the technology evolves (Mate et al., 2007).

### **Open Ocean Species**

Species that are widely distributed in the open ocean are the most challenging for studies of cumulative effects. It is difficult to develop longitudinal studies that involve resighting individuals over such large areas, and it is more difficult

to sample or tag animals on the high seas than on land or in shallow coastal waters. Some solutions have been developed for these problems. Remote tagging and biopsy methods have been developed, but these are more limited than those available onshore or where one can handle the animals. Further development of sampling and tag attachments will be required to apply the approaches recommended in this report for open ocean species. Researchers studying the stress to pelagic dolphins of encirclement in tuna nets used the encirclement itself to enable handling, sampling, and tagging dolphins in a floating restraint system (Scott and Chivers, 2009), but this is unlikely to be possible for larger whales. Smith et al. (1999) report on a systematic and standardized effort to photo-identify and biopsy sample humpback whales throughout the North Atlantic. Similar scales of effort would likely be required for sampling exposure and response to stressors for populations of marine mammals that span ocean basin scales. The methods recommended in this report for studying cumulative effects will need considerable development to be applicable for these species.

Combining the difficulty of studying these four groups of marine mammals with the vulnerability of their populations suggests a broad set of priorities. The marine mammal species most at risk of extinction over the past few decades have not been the migratory large whale species, but rather populations of river dolphins, such as the baiji or Chinese river dolphin (*Lipotes vexillifer*) (Turvey et al., 2007). A range of anthropogenic stressors have been implicated in the decline and extinction of the baiji, with physical injury as a result of interactions with fishing gear being the most important. The limited home ranges of the resident species make them more vulnerable to localized concentrations of stressors. By contrast, the harder-to-study migratory and open ocean large whale species may be less vulnerable. Even though most of these species were exploited during the era of commercial whaling, some populations are large and/or recovering (Whitehead, 2002; Thomas et al., 2016), and the scale of their distribution and movements may render them less vulnerable to local exposure to stressors. This combination of difficulty of study and lower vulnerability may lower the priority for this group for studies of cumulative effects. However, some migratory baleen whale populations, such as the right whales of the western North Atlantic, are exposed to many stressors and have a small and declining population (Kraus and Rolland, 2007). Their coastal distribution puts them at higher risk and makes them easier to study, promoting their priority.

## **APPROACHES TO ASSESS COMPONENTS OF THE PCOMS FRAMEWORK**

Chapter 5 presented a framework for analyzing cumulative effects of stressors on marine mammals. Here we describe approaches to assess cumulative effects organized by the different components of this framework. This sec-

tion focuses on methods to estimate critical parameters in the context of studying relationships between exposure to stressors and (1) behavioral or physiological responses, (2) health, or (3) vital rates.

### Measuring Exposure to Stressors

Lioy and Rappaport (2011) identified two different ways by which biomedical researchers could estimate exposure to chemical stressors that influence human health: a geographical approach and a subject-oriented approach. The geographical approach focuses on different external sources of exposure to a contaminant, which must be summed up to estimate aggregate exposure. Identifying external sources can help prioritize ways to reduce exposure. However, it can involve massive effort and can miss internal sources of chemical stressors, which may be very important for health (Rappaport, 2011). A subject-oriented approach samples directly from the subjects to measure contaminants or their biomarkers. This subject-oriented approach suggests the utility of sampling blood or other tissues in order to estimate the dosage of stressors at the animal to evaluate their impact on health and vital rates (Rappaport, 2011). Placing the sampler on the subject frees the study from needing to track the changing location of the subject, and to associate exposure with time spent in each location. The pros and cons of geographical and subject-oriented approaches to measuring stressors in marine mammals are similar to those identified by Rappaport (2011) for humans.

#### *Spatial and Temporal Distribution of Stressors in the Environment*

The geographical approach to identify potential risks from the complex combination of stressors in the world's oceans requires mapping the distribution of the species of concern along with mapping stressors in space and time. An assumption of this geographical approach is that stressors must overlap with the species to exert a cumulative effect. For example, risk of physical injury from fishing or shipping can be estimated by the flux of categories of ships or the density of fishing gear that pose different threats of injury (e.g., fast versus slow ships, gillnets versus other nets). Similarly if predators, competitors, or anthropogenic sources need to be relatively nearby to be perceived as a threat, then data on the distribution of these stressors may provide a useful estimate of exposure. However, mapping noise from acoustic stressors cannot always be derived from information about the location of intense sources alone. Underwater sound can propagate so well that the same sound produced in the Indian Ocean can be detected off California and off Bermuda but at different levels (Munk et al., 1994). The best way to estimate exposure to one or several intense acoustic stressors is to combine acoustic propagation modeling with measurements of levels of sound produced at known ranges and of the

transmission loss in the environment. Acoustic propagation models can use source and transmission loss data to predict the sound field around these sources and to guide selection of recording sites to best ground-truth predictions. In cases where sources cannot be so readily identified or measured, ambient noise can be monitored directly. Increasing numbers of acoustic observing systems are coming online globally (Miksis-Olds and Nichols, 2016), providing useful data on integrated exposure to noise from all acoustic stressors.

Similarly, the risks from biological or nonbiological toxins cannot always be derived simply from mapping occurrence of sources of toxins or concentrations in the environment. The processes by which toxins are released, transported, and distributed from sources through environmental media and potentially through the food web to marine mammals are complex and will depend on a number of variables related to the toxin, the habitat, and the species of marine mammal. In some cases, it is possible to examine environmental samples from water, sediment, or prey to predict exposure for marine mammals, but, for toxins that can be detected directly in marine mammal tissues or fluids, direct collection and measurement in marine mammal samples is a preferred approach for characterizing dosage. As discussed in Chapter 3, persistent organic pollutants (POPs), many inorganic contaminants, and harmful algal bloom toxins have been routinely measured from a variety of remotely collected tissue samples. Metabolomic analyses of respiratory samples and proteomic and transcriptomic analysis of tissue samples hold promise for the development of biomarkers that indicate cumulative dosages of many toxins. Respiratory samples also hold promise for detection of markers indicative of pathogenic infections. Similar to toxins, exposure to pathogens can often be better characterized by direct sampling of the animal as the presence of a pathogen in the environment does not necessarily translate to an exposure risk. The actual exposure the animal experiences will depend on a variety of factors, including the presence of transmission vectors, or social structure and aggregation (e.g., colonial breeding) that affect contact rates with infected conspecifics. However, while direct measurement from actual tissues from marine mammals is a preferred approach to measure dosage for toxins, this approach requires extensive sampling effort and analyses that are often very costly. In this regard, it would be beneficial for researchers from multiple disciplines and agencies to collaborate and leverage efforts across projects to collect and analyze samples, building a baseline of data that allows examination of geographic trends for multiple stressors.

Prey limitation is a key factor influencing body condition and, as Chapter 6 emphasizes, is a critical part of the interaction web for marine mammals. Marine mammals are well adapted to use sensory cues from echolocation, vibrissae, and more standard mammalian senses to detect, select, and capture prey. Human methods using ship-based echosounders and nets to map prey are crude by comparison and cannot

yield a complete view of availability of preferred prey for marine mammals. However, Friedlaender et al. (2016) have shown that inclusion of prey density and distribution can explain variation in dive behavior of foraging blue whales in a way that greatly increases the power to detect responses to other stressors, such as anthropogenic sound. Further development of methods to measure prey fields may improve these estimates. However, there are considerable obstacles to measuring prey fields in a way that accurately estimates prey limitation for marine mammals. Well-funded long-term censuses of commercially important fish have not solved the challenge of mapping their distribution, even for informing the management of those commercial stocks. There are very few stock assessments of species that are important prey for marine mammals but not important for human fisheries. In addition, measuring prey fields may not provide a complete estimate for the stressor of prey limitation. For example, if prey change their behavior or localized distribution so they are less accessible, then a foraging marine mammal may experience prey limitation even when the prey are present in the area. Here also, the specifics of how, when, and where marine mammals forage may be needed to assess the level of stress from prey limitation. Exposure to prey limitation as a stressor may be estimated by such measures of prey availability, although such data are often limited and difficult to interpret for generalist predators. All of these considerations emphasize the importance of developing measures of foraging success of individual marine mammals over time.

Predation pressure is a stressor that can be an important driver, but measurement of predation risk is difficult for marine mammals. Two important predators of marine mammals are sharks, such as great white sharks (*Carcharodon carcharias*) and the killer whale (*Orcinus orca*) (Jefferson et al., 1991). When killer whales are hunting small marine mammals in coastal waters, kills can often be observed visually for an estimation of predation pressure (Baird and Dill, 1995). Baird and Dill (1996) were able to follow killer whales and observe predation events to estimate rates of predation from the predator's perspective. However, these observations are not the same as estimating the risk of predation from the point of view of marine mammals targeted by the predator. Springer et al. (2008) discussed reasons why killer whale predation on large whales may be underestimated by visual observation. Some preliminary work has demonstrated the ability of tags to detect predation events on tagged pinnipeds. Horning and Mellish (2014) analyzed data from 36 Steller sea lions tagged with life-history tags (Horning and Hill, 2005) and were able to conclude that 15 of these sea lions had been killed by a predator. This tagging work identified a new unsuspected shark predator of these sea lions, but this approach is not appropriate for all species, and its cost limits the sample size, making it unlikely to provide robust estimates of predation risk even for species where it can be used. When predation events cannot be studied directly, another method for estimating the risk of preda-

tion is to measure when predators interact with prey. Some investigators use scars from shark or killer whale attacks as indicators of predation pressure (Heithaus, 2001), but this is problematic as the scarred individuals are the ones that got away. Accurate estimation of predation pressure for marine mammals remains a significant challenge.

#### *Animal-Oriented Approaches to Measuring Extrinsic and Intrinsic Stressors*

Mapping of stressors allows one to estimate exposure at specific locations. However, many marine mammals range over wide areas. If their path is not known, stressor maps may not suffice to estimate exposure. And, as discussed above, broad geographical overlap is not enough to predict exposure for stressors that concentrate in a narrow part of the geographical area, in particular substrates such as sediment, or in prey that must be ingested. As Chapter 3 notes, in these circumstances, the preferred approach is often to sample tissue from a marine mammal to characterize its dosage of chemical stressors. Tissues can currently be sampled from animals that are held for health assessment, but capabilities for sampling critical tissues such as blood are limited for many marine mammal species. New methods will need to be developed for this subject-oriented approach to reach its full potential for marine mammals.

Passive and active personal dosimeters have become established as useful methods for measuring the dosage of stressors. Here the stressor is either absorbed into a passive matrix (O'Connell et al., 2014) or measured by an active device on the animal or human (Boziari et al., 2010). Dosimeter tags have been developed to measure the dosage of some stressors on marine mammals. Acoustic sensors have been placed on marine mammal tags to quantify the dosage of sound at the animal (Johnson and Tyack, 2003). Optical sensors have also been deployed on tags on marine mammals, both to form images of prey (Hooker et al., 2002) and to measure bioluminescence from potential prey (Vacqu e-Garcia et al., 2012). A variety of sensors have been used to detect attempts to capture prey (Pl t z et al., 2001; Miller et al., 2004a) or the ingestion of prey (Austin et al., 2006), which may provide direct measures of foraging rates.

#### *Managing Information on Stressors and Ecological Drivers*

The obstacles described above for measuring prey limitation and predation pressure highlight the difficulties of assessing single components of interaction webs. The movement toward Integrated Ecosystem Assessments may support broader studies of interaction webs that focus on all human and natural nodes (Samhoury et al., 2014) and that prioritize focal ecosystem components (Levin et al., 2014). However, it will require substantial investments from funders in order to

improve the estimates and accuracy of the various exposures to drivers and their effects.

As discussed in Chapter 7, long-term monitoring across broad spatial and temporal scales (including both passive and active surveillance) could help improve understanding of the geographic and temporal patterns of stressors as well as associated adverse effects, and also could help in detecting emerging health issues in marine mammals that are potentially indicative of a population at risk. In addition, understanding patterns of dosage and exposure for multiple stressors could help to inform future study designs to elucidate potential cumulative effects. This information will be most powerful if it is made widely available to scientists and managers through a centralized data management system that can interface with other databases that allows integration of marine mammal health data with ecosystem and oceanographic data.

Such a data management system, the Marine Mammal Health Monitoring and Analysis Platform (MM Health MAP), has been proposed and is in the early developmental stages (Simeone et al., 2015), being led by the U.S. National Marine Fisheries Service's (NMFS's) Marine Mammal Health and Stranding Response Program (MMHSRP) and the U.S. Marine Mammal Commission. The goal of the MM Health MAP is to support mandates under Title IV of the U.S. Marine Mammal Protection Act (MMPA) to gather data on marine mammal health trends and correlate these with biological, physical, and chemical variables.<sup>1</sup> However, the successful development and implementation of the MM Health MAP will depend on support not only from the NMFS but also from other federal managers, as well as cooperation and collaboration across the marine mammal research community. These efforts require willingness of, and financial support for, independent research groups to make data available. Other management and funding agencies should also encourage data management policies that lead to broader analyses and synthesis of information, including incorporation of data and model products into such databases. Similar levels of cooperation between the research community and public-sector agencies involved in tracking emerging diseases and specifically zoonotics have been observed (IOM and NRC, 2009). One such example is the PREDICT program within the U.S. Agency for International Development's Emerging Pandemic Threats Program. The PREDICT program is one of the world's most comprehensive zoonotic disease surveillance and capacity development programs; they have developed training for staff and low-cost detection tools for new viruses from targeted virus families in 32 laboratories in 20 developing nations. Such efforts, supported by modern data management practices and information sharing, have helped characterize human and ecological drivers of disease spillover from animals to people, and strengthened

models for predicting disease emergence in wildlife (Jonna Mazet, personal communication).

To ensure comparability of the marine mammal health and stressor exposure data across studies and over space and time, such a system would require standardized information and proper quality assurance plans for the various analytical results. One of the components of the MMHSRP, which was established under the 1992 amendments to the MMPA, has been to coordinate analytical quality assurance of data from chemical analyses of marine mammal tissues. The quality assurance program for analysis of POPs, fatty acids, and trace elements in marine mammal tissues has been implemented through the National Institute of Standards and Technology and includes interlaboratory comparison exercises, as well as the development of control materials and standard reference materials for marine mammal tissues. Similar quality assurance measures would need to be identified and, if not in existence, would need to be established for other types of health data (e.g., stress hormones) in order to ensure accuracy and interpretability of results across laboratories. Such efforts would broaden understanding of stressor exposure across regions, provide necessary information to managers to assist in evaluating potential stressor mitigation strategies, and inform researchers interested in hypothesis generation for future analytical studies.

**Finding 8.1:** Improving the estimates of the exposure to and dosage of stressors, and their effects, will require better data availability, standardization, and management. The merger of both stressor and ecological driver-related data through a centralized database would facilitate integration and analyses.

### Measuring Change in Behavior and Physiology

Most studies on the effects of sound on marine mammals focus on end points related to disturbance, such as behavioral changes. Where concern has focused on acute effects, such as strandings of beaked whales in response to sonar, it can be very useful to document levels of sound below which no short-term response occurs that poses a risk of stranding. Fernández et al. (2005, 2012) argue that exposure to sonar may also pose a risk of decompression sickness (DCS). Analyses of dive profiles using physiological models of gas dynamics during diving have been used to estimate the risk of physiological changes that could lead to DCS (Kvadsheim et al., 2012). Diving responses of beaked whales to actual sonar exercises have not been quantified, but they have been measured for experiments that used controlled exposures of sonar to tagged beaked and other whales. The behavioral responses to sonar observed in these experiments led to modeled end-dive  $N_2$  tensions thought not to pose a significant risk of DCS. However, sonar exercises involve more intense and prolonged exposure than occurred during these experiments, which were designed to minimize risk of

<sup>1</sup> See <http://www.nmfs.noaa.gov/pr/health/MMHSRP.html>.

injury. Therefore, while the exposure levels linked to these experiments do not pose a significant risk of DCS, the study cannot rule out that behavioral and physiological responses to actual sonar exercises could cause DCS. Testing for DCS in animals that strand coincident with sonar exercises may benefit from careful measurement of the distribution, volume, and gas composition of bubbles, as this may help discriminate between decompression and decomposition in stranded marine mammals (Bernaldo de Quiros et al., 2012).

For many other responses, there is a critical need to develop methods to evaluate the effects of chronic exposure. Analysis of health in terms of energy stores is a promising way to do this, as it can integrate with energetic models of survival and reproduction (e.g., New et al., 2013b). Further development of methods to estimate the energetic consequences of changes in foraging behavior and the physiology of metabolism will strengthen the promising approaches of Biuw et al. (2003) and New et al. (2014). For example, Wilson et al. (2006, 2008) advocate use of accelerometry to estimate metabolic rates of tagged subjects, and Fahlman et al. (2016) and Roos et al. (2016) describe improvements in methods that use respiration to estimate the metabolic rate of cetaceans.

Another important approach for measuring physiological changes resulting from exposure to stressors involves measuring glucocorticoid stress hormones. A few studies have measured changes in stress hormone levels of marine mammals exposed to sound (Romano et al., 2004; Rolland et al., 2012). Methods are being developed to sample stress hormones from a variety of tissues, such as blubber biopsy, feces, and blows. These methods are critical for practical sampling of animals in the wild, and data from these tissues need to be calibrated against data from blood, which is the standard.

### **The Functions Relating Exposure to Stressors to Behavioral or Physiological Responses**

Short-term tags are well suited to experiments studying responses to acute exposure to intense sounds, and these experiments can produce probabilistic dose–response functions (e.g., Figure 1a in Box 2.2). Once these responses are characterized, monitoring programs can be developed to evaluate responses to longer-term and larger-scale exposures (e.g., Moretti et al., 2014). However, few of these studies have estimated exposure to other stressors that might influence cumulative effects. To evaluate cumulative effects of other stressors in addition to noise, these studies would need to include measurements of exposure to other stressors and responses to them.

The levels of exposure for an individual marine mammal to stressors such as noise, prey limitation, perceived threats, and disease may vary considerably as the animal moves over time periods of minutes to days. The biological responses to a sound stimulus are likely to vary as a function of behavioral

states, such as traveling or foraging, and of physiological states, such as oxygen reserves or acute disease infection, that may vary on scales of seconds to days or more. These time scales require behavioral and physiological measurements along with estimates of stressor exposure that are local to the animal. These kinds of data on behavioral and physiological states have been used in experiments to evaluate the effect of behavioral context and the responses of marine mammals to acoustic stimuli (e.g., Goldbogen et al., 2013); this approach may offer some promise for studying cumulative effects involving other stressors.

There is also a data gap for studying effects of chronic exposure to sound. Short-term experiments can expose the same subjects several times to the same or different acoustic stimuli (Antunes et al., 2014; Miller et al., 2014). These experiments enable testing whether responses differ for the first exposure versus later ones, which is a first step in studying responses to repeated sounds. Some studies have taken advantage of unplanned events to study the impact of reductions in chronic noise on marine mammals. For example, Rolland et al. (2012) happened to be studying stress hormones in right whales before and after the terrorist attacks on the World Trade Center and Pentagon on September 11, 2001. Noise levels and the occurrence of ships passing near the whales were greatly reduced due to a pause in commercial shipping after these events; during this period of low noise and ship activity, the levels of stress hormones were lower than those recorded before September 11, 2001, or for the same period in other years. However, this opportunistic study lacks the controls required for a standard experimental design. New designs for experiments and opportunistic studies will be required to document the effects of planned changes in chronic noise and disturbance associated with ship passage induced by changes in shipping lanes or in shipping technology.

### **Use of Health Indices to Detect and Manage Species at Risk**

Chapter 5 developed the Population Consequences of Multiple Stressors (PCoMS) framework that uses health parameters to help integrate effects of multiple stressors over longer time periods than those captured by individual physiological or behavioral responses to acute stressor exposures. Measuring these health parameters can improve the ability to model the linkages between stressor dosage or exposure and long-term effects on populations. Changes in health integrate short-term changes in exposure to multiple stressors, providing a longer-term measure that can more readily be linked to changes in vital rates. Because changes in health can be measured more rapidly than changes in vital rates, health may help provide an early warning indicator for individual animals. If enough individuals in a population are sampled for health, as Chapter 7 discusses, this information



on population health may provide an early warning indicator for populations at risk.

### *Comprehensive Health Evaluation*

Comprehensive health assessments are of particular value because they provide information on multiple aspects of an animal's condition and are therefore more likely to detect a compromised health state. In addition, health assessments that utilize an array of indicators can help to identify specific causal factors for compromised health and can inform management decisions about which steps to take to reduce risks. Comprehensive health assessments have been developed for pinnipeds and some cetacean species, such as bottlenose dolphins (*Tursiops truncatus*). In pinnipeds, contaminant burdens measured in tissues, and pathogen exposures sampled from nasal and rectal swabs, can be included in physiology workups for tag deployments and recoveries that also include body condition, stress hormones, and immune markers (e.g., Goldstein et al., 2013; Peterson et al., 2015; Peck et al., 2016). For example, recent work using nasal swabs showed that tagged elephant seals were exposed to the H1N1 virus between instrument deployments and recoveries in 2010 (Goldstein et al., 2013). Comprehensive health assessments have also been conducted for coastal populations of bottlenose dolphins in several sites in the southeastern United States (Wells et al., 2004; Fair et al., 2006; Schwacke et al., 2010). In some cases, these studies have identified adverse health effects in association with stressor exposure. For example, a high prevalence of anemia, low thyroid hormone levels, and immune suppression were associated with polychlorinated biphenyl exposure in bottlenose dolphins inhabiting an estuary near a hazardous waste site in Brunswick, Georgia (Schwacke et al., 2012). Most of these studies rely on sampling of blood but may also include sampling of other tissues or body fluids, and ultrasound examination of organs. Baseline data from these kinds of assessments are critical for studying stressor dosage and responses to stressors.

Understanding the health status of a population aids in the identification of threats that can be effectively mitigated to support recovery, whether or not they have been major contributing factors for the population's decline. For example, health studies of highly endangered Hawaiian monk seals found that the species was immunologically naïve to morbillivirus, which posed a significant epidemic threat, and furthermore that the lack of genetic diversity could potentially limit the ability of the species to respond to other newly introduced diseases such as toxoplasmosis, West Nile virus, and influenza (NMFS, 2016b). In response, NMFS identified an action to "Detect and prevent catastrophic disease outbreak and disease-related mortality" as a priority in the 5-year action plan for recovery of this species that was on the brink of extinction. A disease outbreak preparedness plan, including the development of a morbillivirus vaccina-

tion program, has now been implemented as part of ongoing health research activities.

### *Assessing Health in Populations That Cannot Be Handled*

Current methods and technologies limit comprehensive health assessments to a few species that can be temporarily captured, restrained, and evaluated. This limitation has led to the development of less comprehensive health assessments for other species, often including two types of readily accessible indicators of health: body condition and stress hormones. As these measures can be obtained using visually observed indicators for body condition, or remote sampling for stress hormones, they can be collected for many marine mammal species.

#### *Body Condition*

As discussed in Chapter 5, body condition is an indicator of health and allostatic or homeostatic load that can be measured directly for species that can be handled. Methods are more limited for species that cannot be handled. These include visual observations of condition and use of tags to estimate changes in buoyancy of wild marine mammals. Pettis et al. (2004) estimated body condition by scoring the concavity of an area just behind the blowhole that accumulates fat and that is visible in some photographs taken to identify individual whales. C.A. Miller et al. (2012) used aerial photographs taken directly over a right whale to more precisely measure the body shape and quantify the condition of right whales. Unmanned aerial or underwater vehicles may offer more cost-effective ways to obtain such images optimized for measuring features of interest. The tagging method for estimating body condition involves measuring the vertical acceleration of diving animals during drifting periods of the dive. Drift dives, however, do not occur in all species. More detailed research on the forces acting on swimming marine mammals may allow estimation of the static buoyancy force and percentage of lipid in animals that are not passively drifting, but are gliding during ascent and descent phases of normal dives (Miller et al., 2004b; Watanabe et al., 2006; Aoki et al., 2011). This may broaden the number of species that can be studied using this method.

#### *Stress*

As discussed in Chapter 4, chronic activation of the hypothalamic-pituitary-adrenal axis may be an important mechanism by which cumulative effects of different stressors exert effects on health and vital rates. Glucocorticoid (GC) stress hormones have usually been measured from blood samples, but an array of other matrices for stress hormones, including blubber, feces and exhaled blow, and baleen and earplugs in baleen whales are also being studied for analysis of stress. These other matrices provide longer-term

measures of GC levels than blood and may be more useful for investigating long-term stress dosage and effects. Feces and exhaled blow can be collected noninvasively for some species, and blubber can be sampled by biopsy darting in almost all marine mammal species. The promise of these new matrices cannot be fulfilled without cross-sectional and/or longitudinal studies that help to establish distributions for expected values across different species, age classes, sexes, and reproductive states. Pregnancy changes corticosterone levels in blubber, so such samples also need to measure progesterone to control for this effect.

### *Remote Assessment of Health*

Pettis et al. (2004) conducted an early effort to develop a scale for assessing the health of individual right whales in the western North Atlantic. They took advantage of an extensive photo-identification catalog to score body condition, skin condition, presence of “rake marks,” and cyamids near the blowhole. This assessment scheme was limited to features that were visible from photographs used to identify individual whales. The development of indices that include information from biopsies, blow, and feces will enrich the power of health assessments that are limited to remote sampling.

Health studies that include assessment of body condition as well as collection of contaminant and health biomarkers have been identified as a priority action for the recovery of highly endangered Southern Resident killer whales (NMFS, 2016c). The goal of these health studies is to compare the health of Southern Residents with other killer whale populations to identify potential sources of decreased survival and/or reproduction. High concentrations of emerging contaminants, and specifically flame-retardant chemicals, have been reported in these apex predators (Rayne et al., 2004). Therefore, the health studies are particularly focused on identifying sources for the emerging contaminants and understanding potential associated health effects in order to guide water quality recommendations and reduce contaminant inputs into Southern Resident killer whale habitat.

**Finding 8.2:** Assessment of health is central to the PCoMS model proposed in this report. Comprehensive health assessments of a cross section of a marine mammal population can also help managers decide when the population is at risk and help them decide which management actions can most effectively support recovery.

### **Stressor Exposure: Health Response Function**

The PCoMS model presented in Chapter 5 has the capability to analyze the short-term links between a health effect and the combination of stressors to which an animal has been exposed. As a sample of wild animals moves through their habitat and/or experiences seasonal changes, they are likely

to be exposed to a wide distribution of the stressors that are present in their environment at that time. If the dosage or exposure to the stressors and the effects of each combination of stressors can be measured, then, as Chapter 6 notes, this approach offers the potential for a much larger sample of dose–response measurements than can be tested in experiments, perhaps improving the ability to identify which combinations of stressors have an observable effect on health.

The desired characteristics of the health variables introduced in Chapter 5 are that they can be measured in wild marine mammals, they integrate effects of repeated exposures to multiple stressors, they change over shorter time scales than vital rates, and yet they can influence the vital rates of each individual. The committee has argued that free-ranging marine mammals are influenced by so many stressors, each of whose effects may vary depending on life-history stage of the animal, and that the number of combinations of stressors is too large for experimental studies of how all combinations interact. The committee’s proposed PCoMS framework uses a small number of health variables to integrate the effects from multiple stressors and to improve current understanding of the mechanisms by which combinations of stressors affect vital rates.

Exposure to many of the stressors discussed here varies on an hourly to weekly basis, and even exposure to toxic compounds that have stable concentrations in one area will vary as marine mammals move from area to area. Marine mammals are long lived and give birth at most once per year. This means that studies linking exposure to stressors with reproductive success cannot sample effects more frequently than yearly. By contrast, some of the health variables proposed here have much finer time resolution—more appropriate for linking to stressor exposures. For example, Biuw et al. (2003) state that for estimating body condition from buoyancy in drift dives “biologically realistic changes in drift rate (are) expected to be detectable over a period of 5-6 days.”

If changes in health and exposure to stressors can be sampled over shorter time periods than vital rates, then longitudinal studies may be able to repeatedly measure stressor–health combinations many times within a breeding cycle. Longitudinal studies are particularly well suited for situations where tags can be attached for significant parts of the annual cycle and can sample the health variables of interest. Tags can currently sample body condition in the few species with drift dives but are not able directly to sample the other health variables discussed here. Development of long-term tags that can sample such variables could support this approach for studying cumulative effects. Initial scoping for development would be useful, but breakthroughs are not expected in the next 5-10 years. For these other variables and for species where it is not possible to use tags to measure body condition, it may be more productive to conduct cross-sectional studies where exposure to stressors and the health variables are measured in a large number of individuals within a population. Rather than measuring changes in health

as the pattern of exposure to stressors changes, this approach would sample each individual at a single time point, linking the stressor and health values observed at that time. This approach assumes that the values of stressors observed are close to those that led to the health value measured at the same time. The cross-sectional approach may be less able to detect adverse outcome pathways that involve sequential exposures to stressors over longer time periods.

These kinds of longitudinal and cross-sectional studies are relatively well established for coastal populations of marine mammals in which individuals are small enough to be handled and where relatively comprehensive health assessments have been established. Remote biopsy methods have been developed, but the data obtained by this method are more limited than those available from onshore populations or when one can handle the animals. However, there are precedents for large-scale efforts to sample large, highly mobile whale species. For example, Smith et al. (1999) report on a systematic and standardized effort to photo-identify and biopsy sample humpback whales throughout the North Atlantic. They report that “during 666 days at sea aboard 28 vessels, 4,207 tail fluke photographs and 2,326 skin biopsies were collected.” Their assessment was that “an oceanwide approach to population assessment of baleen whales is practicable.”

One of the goals of the statement of task for this committee is to identify how exposure to nonacoustic stressors may affect a marine mammal’s response to an acoustic stressor. In this context, evaluation of the health status of potential subjects for response studies may help to identify those individuals that may be particularly sensitive or vulnerable to an acoustic stressor. A basic element of the allostasis model is that animals already carrying a large allostatic load may be driven into allostatic overload by a relatively small additional exposure to a stressor. This would suggest that subjects already in adverse health status may be the most vulnerable to even small doses of another stressor. Note, however, that this does not mean that the subject will be the most sensitive in the sense of most likely to show a behavioral response at low exposure levels (Gill et al., 2001). For example, Beale and Monaghan (2004) have shown that birds under nutritional stress may be less likely to stop feeding and move away from a threat than birds of better body condition that may more easily be able to afford the lost foraging opportunities. This emphasizes the importance of measuring the response to stressor in terms of changes in health as well as observing behavioral reactions.

### Health Response: Vital Rates Function

The functional relationship between health and vital rates is an important link in the PCoMS model. Parameterizing this relationship will require measuring health and vital rates in the same individuals and populations. Several

different methods are used or have been proposed for studying vital rates.

#### *Mark–Recapture Methods*

As Chapter 7 notes, vital rates have been estimated for wild marine mammal populations where the same individuals can reliably be resighted. Many demographic parameters can be estimated from focused mark–recapture surveys of animals that can reliably be sighted nearly every year and for which it can be determined whether adult females have given birth. Birth rates and survival of the young are highlighted in Chapter 7 as early demographic indicators of problems; these are most easily studied in species that give birth on land where it can be observed or where young animals are easily distinguished. Several new methods may be appropriate for species where this is not possible, and these will be discussed next.

#### *Matrices That Store Information on Age-Specific Reproduction and Age at Death*

One common method for determining the age of mammals involves counting growth layers in tissues such as teeth, baleen, or wax laid down in the ear canal of baleen whales (called the ear plug). Growth layers in teeth have been used to determine the age of dolphins (Hohn et al., 1989), polar bears (Calvert and Ramsey, 1998), and pinnipeds (Scheffer, 1950). Not only can these tissues be used to age marine mammals, but recent work has shown that ear plugs and baleen can provide time records of reproductive and stress hormones as well as contaminants over the lifespan in the case of the ear plug (Trumble et al., 2013) and over several years in the case of baleen (Hunt et al., 2014). Baleen and earplugs are laid down in layers that differ during different parts of the annual cycle, such as feeding, migration, and breeding, making it possible to track each year of life of the animal. Both of these tissues are relevant only for baleen whales—more work on tissues such as teeth that lay down layers throughout the lifespan would help broaden this approach to other marine mammals. In many organisms that lay down these kinds of layers, characteristics of the layer may also indicate the nutritional state of the organism at the time of deposition (Fritts, 2012), potentially providing information on changes in condition.

#### *Life History Tags*

Problems with estimating age-specific mortality, and especially causes of mortality in open ocean species, led Horning and Hill (2005) to develop an electronic tag that is implanted internally, recording life-history data through the life of a marine mammal, and that releases and transmits data upon expulsion from the dead animal. Insertion of a tag into the peritoneal cavity requires surgery, but Horning et al. (2008) report that 4 California sea lions (*Zalophus*

*californianus*) and 15 juvenile Steller sea lions (*Eumetopias jubatus*) recovered well under veterinary care after the tag insertion. The sea lions were then released into the wild and tracked with satellite tags. The behavior of sea lions with implanted tags was monitored for up to half a year and was similar to that of sea lions tagged only with satellite tags. Distinct signatures of temperature and light identify when an animal has been killed by a predator (Horning and Mellish, 2014). Temperature data from 15 of the 36 sea lions tagged by Horning and Mellish (2014) indicated that they had been killed by predators. These sea lions were followed for a total of 111 years, so 15 deaths indicate a relatively high predation rate.

The costs and risks of surgical insertion of the life-history tag limit the sample sizes achievable for this kind of tagging, and it may not be appropriate for many marine mammal species. Surgical implantation raises ethical and animal welfare concerns that would require evidence of a clear benefit to these populations that would be sufficient to outweigh the welfare cost. However, this research showed that tags can be developed to record data from within an animal until it dies. This mode of tagging suggests a new approach for active personal dosimeters. The dosimeters described above are designed to measure the dosages of stressors to which an animal is exposed. The potential of a tag that can sample the internal milieu of a marine mammal throughout the lifespan would be greatly expanded if, as with earplugs, it could also sample life-history events, stressor dosage, and response to a variety of stressors. Passive personal dosimeters have been designed with materials optimized for absorbing and storing chemical compounds of interest (Paulik et al., 2016). Tags placed inside the body are best located to measure physiological parameters, such as hormones, and dosages of stressors, such as contaminant loads. For species that do not have tissues from which age-specific samples can be recovered, such as the earplug, there may be benefit in designing passive samplers that can sample compounds of interest at known times throughout the lifespan. Some compounds and other stressors, such as sound, can be detected actively by sensors on an electronic tag, but development of active sensing in lifetime tags will face considerable obstacles in terms of power requirements and space limitations.

### **Stressor Exposure: Vital Rates Function**

Modeling each component of the PCoMS model is very challenging, but it is necessary in most cases, because a direct link cannot be made between stressor exposure and vital rates. However, in cases where a direct link can be made, it may be possible to bypass all the intermediate modeling stages. Such studies have been attempted for several seabird species whose demography and movements have been well documented. Some studies have used the approach taken by Forcada et al. (2006) to compare annual variation in demographic parameters to natural variation in more than

one stressor on a year-by-year basis. For example, Rolland et al. (2009) used 26 years of demographic data from a study of black-browed albatross on Kerguelen Island to study the impact of fishing bycatch under various climate conditions. Levels of ocean warming expected for the next century were predicted to enhance the growth of this population, potentially compensating for controlled increases in fishing effort. This analysis was useful to inform management of fisheries in the presence of climate change. However, the authors did not explicitly model potential interactions between stressors.

Few studies on marine mammal populations have used methods similar to those just discussed for seabirds and summarized by Barbraud et al. (2012). However, the demographic parameters for populations of pinnipeds that breed on land could be studied using similar methods. Similar analyses should be possible for species such as resident coastal cetacean populations with long-term studies of identified individuals whose tissue can be sampled and whose vital rates are estimated (Bowen et al., 2010). Exposure to environmental stressors such as ocean temperature and interactions with fisheries can be characterized for marine mammals using spatiotemporal sampling of parameters such as effort statistics similar to those used in the seabird studies. For example, Caillat and Smout (2015) studied the potential effects of prey availability, grey seal numbers, and exposure to biotoxins on the fecundity and pup survival of harbor seals off the east coast of the United Kingdom. They found that a single (but different) dominant stressor explained the observed variations in each demographic rate. It may be possible to identify interactions between these stressors in other populations that have undergone more dramatic changes in abundance.

The potential for tissues such as baleen whale earplugs or manmade sampling devices to provide a lifetime record of age-specific fertility, age at death, and exposure to some stressors suggests the potential for a new approach to studying the relationship between exposure to stressors and vital rates in marine mammal populations. Given the low probability that long-term studies of vital rates and spatiotemporal mapping of exposure to stressors will provide sufficient data over long enough time intervals for marine mammal populations, we recommend research on natural matrices that may provide a lifetime record of stressors and effects. The development of tags to accomplish the same goal for species without such natural matrices faces significant obstacles but is worth scoping as a potential opportunity for the long term.

**Finding 8.3:** Natural and artificial matrices have potential as tools for documenting dosage of chemical stressors and changes in hormone levels over long enough time periods to test the relationship between stressor dosage and response in terms of health or vital rates. Natural matrices that are laid down in semiannual layers from birth to death are particularly promising.

### *Measuring the Lifetime Exposure of an Organism to Stressors*

Wild (2005) argued for the importance of tracking exposure of stressors throughout the lifespan. He developed the concept of an “exposome”—defined as the lifetime exposure of an organism to stressors from the prenatal period to death. It is clearly a great challenge to measure the exposome, but a series of papers have emphasized the importance of gathering exposure data on stressors, in both the internal and the external environments, throughout the lifetime (e.g., Lioy and Rappaport, 2011). Rappaport (2011) suggests an approach to measuring the exposome by repeated sampling of blood at critical times of life, with each sample analyzed for “important classes of toxic chemicals, notably, reactive electrophiles, metals, metabolic products, hormone-like substances, and persistent organic compounds.” He argues that as the extent of this sampling increases, economies of scale should create positive feedback for growth of exposome sampling. A similar sampling scheme for accessible marine mammal populations using cross-sectional studies supplemented by individuals sampled throughout their lifespan could help to define combinations of stressors that cause adverse cumulative effects. Longitudinal, spatially comprehensive collection of data on exposure to and effects of multiple stressors could be excessively costly. However, ongoing research studies being funded and/or conducted by multiple federal agencies (e.g., National Oceanic and Atmospheric Administration, U.S. Navy, Bureau of Ocean Energy Management, and the U.S. Geological Survey) and independent researchers could be leveraged and expanded to simultaneously collect samples and conduct analysis to assess exposure to and effects of multiple stressors. The value of a centralized database would be increased with additional information from active surveillance (see Chapter 7).

### **Health: Vital Rates Function**

Most of the health indices discussed in this report can be measured directly for species that can be handled for sampling. The committee has suggested several other approaches for tagging or sampling other matrices in the wild that can be used to assess health. Vital rates can also be estimated directly for species where individuals can regularly be resighted and where birth of the young can be detected reliably. For other species, the committee suggests some new approaches that also include tagging animals with artificial matrices or sampling natural matrices that lay down tissue in layers that can be used for aging and that can store hormones.

The best example of estimating the function relating health to vital rates comes from New et al. (2014), who took advantage of studies of elephant seals on beaches where lipid and lean mass could be measured from pregnant females as they left and returned from foraging trips. Their pups were weighed soon after birth and after weaning. These measure-

ments allowed New et al. (2014) to estimate the energy transferred from mother to pup, and to relate pup natal mass to survival. The relationships between the health variable of body condition, expressed as maternal lipid mass, to the pup’s weaning mass, and between the pup’s weaning mass and the vital rate of pup survival enabled the evaluation of the relationship between health and vital rates for this species.

The committee found no examples of similar studies relating health to vital rates in other marine mammals but does suggest some new approaches that may enable such studies. A major problem for these studies is the long time period required to measure vital rates. The discovery that baleen whale earplugs provide a lifetime record of reproductive hormones for each year of life may enable studies of the vital rate of reproduction, and the age at death can be measured from the earplug, providing age-specific mortality. The earplug has been shown to store the health variables of contaminants and stress hormones, and some tissues that are laid down in layers also provide indications of body condition. If large enough samples of earplugs can be recovered and analyzed for health and vital rates, this could enable a new way to evaluate the relationship between these critical parameters. This is the only shortcut found by the committee for retrospective studies of health and vital rates where one can use tissue from dead animals to study these relationships from birth to death. This possibility is promising enough to justify exploration of other matrices, such as teeth and baleen, that may provide similar timelines of health and vital rates.

## **RECOMMENDATIONS**

**Recommendation 8.1: Future research initiatives should support evaluation of the range of emerging technologies for sampling and assessing individual health in marine mammals, and identification of a suite of health indices that can be measured for diverse taxa and that best serves to predict future changes in vital rates.** Potentially relevant measures include hormones, immune function, body condition, oxidative damage, and indicators of organ status, as well as contaminant burden and parasite load. New technology for remotely obtaining respiratory, blood, and other tissue samples and for remote assessment (e.g., visual assessment of body condition) should also be pursued.

Establishing baseline values of these parameters and their associations in species will provide critical information for assessing individual and population health. Assessment of health is not only central to the PCoMS model proposed in this report, but comprehensive assessments of stressor exposure and health of a population of marine mammals can also help managers decide when the population is at risk, and help them decide which management actions can most effectively support recovery. Long-term studies of known individuals will be important in this regard. Cross-sectional

sampling and repeated sampling from the same individuals of blood or other tissues during critical life-history phases can help to document dosages and health effects of stressors.

**Recommendation 8.2: Agencies charged with monitoring and managing the effects of human activities on marine mammals should identify baselines and document exposures to stressors for high-priority populations.** High-priority populations should be selected to include those likely to experience extremes (both high and low) of stressor exposure in order to increase the probability of detecting relationships. This will require stable, long-term funding to maintain a record of exposures and responses that could inform future management decisions. Information on baselines and contextual variables is critically important to interpreting responses.

**Recommendation 8.3: Standards for measurement of stressors should be developed along with national or international databases on exposure of marine mammals to high-priority stressors and associated health measures that are accessible to the research community.**

**Recommendation 8.4: Techniques should be developed that will allow historical trajectories of stress responses to be constructed based on the chemical composition of the large number of baleen whale earplugs and baleen samples in museums or similar matrices in other species. Artificial matrices should be studied for their potential to absorb materials (hormones or chemical stressors) and thereby provide a record of exposures and responses to stressors.**

There are opportunities to explore the potential for natural or artificial matrices (that store chemical stressors and hormones over long enough time periods) to test the relationship between exposure to the stressors and response in terms of health or vital rates.

Such techniques with museum samples could provide critical information on the relationships between contaminants, stress, and reproductive intervals. Natural matrices that are laid down in semiannual layers from birth to death are particularly promising.



## References

- Aarts, G., M. MacKenzie, B. McConnell, M. Fedak, and J. Matthiopoulos. 2008. Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* 31:140-160.
- Acevedo-Whitehouse, K., and A.L.J. Duffus. 2009. Effects of environmental change on wildlife health. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:3429-3438. doi: 10.1098/rstb.2009.0128.
- Acevedo-Whitehouse, K., A. Rocha-Gosselin, and D. Gendron. 2009. A novel non-invasive tool for disease surveillance of free-ranging whales and its relevance to conservation programs. *Animal Conservation* 13(2):217-225.
- Aguilar, A., and A. Borrell. 1994. Abnormally high polychlorinated biphenyl levels in striped dolphins (*Stenella coeruleoalba*) affected by the 1990-92 Mediterranean epizootic. *Science of the Total Environment* 154:237-247.
- Aguirre, A.A., T.J. Keefe, J.S. Reif, L. Kashinsky, P.K. Yochem, J.T. Saliki, J.L. Stott, T. Goldstein, J.P. Dubey, R. Braun, and G. Antonelis. 2007. Infectious disease monitoring of the endangered Hawaiian monk seal. *Journal of Wildlife Diseases* 43(2):229-241.
- Aksenov, A.A., L. Yeates, A. Pasamontes, C. Siebe, Y. Zrodnikov, J. Simmons, M.M. McCartney, J.-P. Deplanque, R.S. Wells, and C.E. Davis. 2014. Metabolite content profiling of bottlenose dolphin exhaled breath. *Analytical Chemistry* 86:10616-10624.
- Alexander, N., Y. Kuepper, A. Schmitz, R. Osinsky, E. Kozyra, and J. Hennig. 2009. Gene-environment interactions predict cortisol responses after acute stress: Implications for the etiology of depression. *Psychoneuroendocrinology* 34(9):1294-1303.
- Anderson, M.J., and A.A. Thompson. 2004. Multivariate control charts for ecological and environmental monitoring. *Ecological Applications* 14:1921-1935.
- Andrew, R.K., B.M. Howe, and J.A. Mercer. 2011. Long-time trends in ship traffic noise for four sites off the North American West Coast. *Journal of the Acoustical Society of America* 129(2):642-651.
- Angliss, R.P., and K.L. Lodge. 2002. Alaska Marine Mammal Stock Assessments, 2002. U.S. Department of Commerce, *NOAA Technical Memorandum*. NM FSAFSC-133, 224 pp.
- Ankley, G.T., R.S. Bennett, R.J. Erickson, D.J. Hoff, M.W. Hornung, R.D. Johnson, D.R. Mount, J.W. Nichols, C.L. Russom, P.K. Schmieder, and J.A. Serrano. 2010. Adverse outcome pathways: A conceptual framework to support ecotoxicology research and risk assessment. *Environmental Toxicology and Chemistry* 29(3):730-741.
- Antunes, R., P.H. Kvaldsheim, F.P.A. Lam, P.L. Tyack, L. Thomas, P.J. Wensveen, and P.J.O. Miller. 2014. High thresholds for avoidance of sonar by free-ranging long-finned pilot whales (*Globicephala melas*). *Marine Pollution Bulletin* 83:165-180.
- Aoki, K., Y.Y. Watanabe, D.E. Crocker, P.W. Robinson, M. Biuw, D.P. Costa, N. Miyazaki, M. Fedak, and P. Miller. 2011. Northern elephant seals adjust gliding and stroking patterns with changes in buoyancy: Validation of at-sea metrics of body density. *Journal of Experimental Biology* 214(17):2973-2987.
- Arnomb, T., M.A. Fedak, I.L. Boyd, and B.J. McConnell. 1993. Variation in weaning mass of pups in relation to maternal mass, postweaning fast duration, and weaned pup behavior in southern elephant seals at South Georgia. *Canadian Journal of Zoology* 71:1772-1781.
- Asseburg, C., J. Harwood, J. Matthiopoulos, and S. Smout. 2006. The functional response of generalist predators, and their implications for the monitoring of marine ecosystems. Pp. 262-274 in *Top Predators in Marine Ecosystems: Their Role in Monitoring and Management*, I.L. Boyd, S. Wanless, and K. Camphuysen, eds. Cambridge: Cambridge University Press.
- Atkinson, S., D. Crocker, D. Houser, and K. Mashburn. 2015. Stress physiology in marine mammals: How well do they fit the terrestrial model? *Journal of Comparative Physiology B* 185(5):463-486.
- Austin, D., W.D. Bowen, J.I. McMillan, and D.J. Boness. 2006. Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. *Journal of Animal Ecology* 75(2):408-420.
- Ayres, K.L., R.K. Booth, J.A. Hempelmann, K.L. Koski, C.K. Emmons, R.W. Baird, K. Balcomb-Bartok, M.B. Hanson, M.J. Ford, and S.K. Wasser. 2012. Distinguishing the impacts of inadequate prey and vessel traffic on an endangered killer whale (*Orcinus orca*) population. *PLoS ONE* 7:e36842.
- Baggeroer, A., and W. Munk. 1992. The Heard Island feasibility test. *Physics Today* 45:22-30.
- Bailey, H., B. Senior, D. Simmons, J. Rusin, G. Picken, and P.M. Thompson. 2010. Assessing underwater noise levels during pile-driving at an offshore windfarm and its potential impact on marine mammals. *Marine Pollution Bulletin* 60:888-897.
- Bailey, H., K.L. Brookes, and P.M. Thompson. 2014. Assessing environmental impacts of offshore wind farms: Lessons learned and recommendations for the future. *Aquatic Biosystems* 10:8.



- Baird, R.W., and L.M. Dill. 1995. Occurrence and behaviour of transient killer whales: Seasonal and pod-specific variability, foraging behaviour, and prey handling. *Canadian Journal of Zoology* 73(7):1300-1311.
- Baird, R.W., and L.M. Dill. 1996. Ecological and social determinants of group size in transient killer whales. *Behavioral Ecology* 7(4):408-416.
- Baird, R.W., S.W. Martin, D.L. Webster, and B.L. Southall. 2014. *Assessment of Modeled Received Sound Pressure Levels and Movements of Satellite-Tagged Odontocetes Exposed to Mid-Frequency Active Sonar at the Pacific Missile Range Facility: February 2011 Through February 2013*. Prepared for U.S. Pacific Fleet, submitted to NAVFAC PAC by HDR Environmental, Operations and Construction, Inc.
- Ban, S.S., N.A.J. Graham, and S.R. Connolly. 2014. Evidence for multiple stressor interactions and effects on coral reefs. *Global Change Biology* 20:681-697.
- Banner, A., and M. Hyatt. 1973. Effects of noise on eggs and larvae of two estuarine fishes. *Transactions of the American Fisheries Society* 102(1):134-136.
- Barber, J.R., K.R. Crooks, and K.M. Fristrup. 2010. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution* 25:80-189.
- Barbieri, M.M., S. Raverty, M.B. Hanson, S. Venn-Watson, J.K.B. Ford, and J.K. Gaydos. 2013. Spatial and temporal analysis of killer whale (*Orcinus orca*) strandings in the North Pacific Ocean and the benefits of a coordinated stranding response protocol. *Marine Mammal Science* 29:E448-E462.
- Barbraud, C., V. Rolland, S. Jenouvrier, M. Nevoux, K. Delord, and H. Weimerskirch. 2012. Effects of climate change and fisheries bycatch on Southern Ocean seabirds: A review. *Marine Ecology Progress Series* 454:285-307.
- Basner, M., W. Babisch, A. Davis, M. Brink, C. Clark, S. Janssen, and S. Stansfeld. 2014. Auditory and non-auditory effects of noise on health. *The Lancet* 383:1325-1332.
- Bayne, E.M., L. Habib, and S. Boutin. 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. *Conservation Biology* 22:1186-1193.
- Beale, C.M., and P. Monaghan. 2004. Behavioural responses to human disturbance: A matter of choice. *Animal Behaviour* 68:1065-1069.
- Beaugrand, G. 2004. The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progress in Oceanography* 60(2):245-262.
- Bejarano, A., F. Gulland, T. Goldstein, J.S. Leger, M. Hunter, L. Schwacke, F. VanDolah, and T. Rowles. 2008a. Demographics and spatio-temporal signature of the biotoxin domoic acid in California sea lion (*Zalophus californianus*) stranding records. *Marine Mammal Science* 24:899-912.
- Bejarano, A.C., F.M. VanDolah, F.M. Gulland, T.K. Rowles, and L.H. Schwacke. 2008b. Production and toxicity of the marine biotoxin domoic acid and its effects on wildlife: A review. *Human and Ecological Risk Assessment* 14(3):544-567.
- Bejder, L., A. Samuels, H. Whitehead, and N. Gales. 2006. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Animal Behaviour* 72(5):1149-1158.
- Bejder, L., A. Samuels, H. Whitehead, H. Finn, and S. Allen. 2009. Impact assessment research: Use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series* 395:177-185.
- Benson, S.R., D.A. Croll, B.B. Marinovic, F.P. Chavez, and J.T. Harvey. 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997-98 and La Niña 1999. *Progress in Oceanography* 54(1):279-291.
- Bernaldo de Quiros, Y., O. González-Díaz, M. Arbelo, E. Sierra, S. Sacchini, and A. Fernández. 2012. Decompression vs. decomposition: Distribution, amount, and gas composition of bubbles in stranded marine mammals. *Frontiers in Physiology* 3:177.
- Bexton, S., D. Thompson, A. Brownlow, J. Barley, R. Milne, and C. Bidewell. 2012. Unusual mortality of pinnipeds in the United Kingdom associated with helical (corkscrew) injuries of anthropogenic origin. *Aquatic Mammals* 38:229-240.
- Bishop, A., P. Pomeroy, and S.D. Twiss. 2015. Breeding male grey seals exhibit similar activity budgets across varying exposures to human activity. *Marine Ecology Progress Series* 527:247-259.
- Biuw, M., B. McConnell, C.J.A. Bradshaw, H. Burton, and M.A. Fedak. 2003. Blubber and buoyancy: Monitoring the body condition of free-ranging seals using simple dive characteristics. *Journal of Experimental Biology* 206:3405-3423.
- Blickley, J.L., D. Blackwood, and G.L. Patricelli. 2012a. Experimental evidence for the effects of chronic anthropogenic noise on abundance of Greater Sage-Grouse at leks. *Conservation Biology* 26:461-471.
- Blickley, J.L., K.R. Word, A.H. Krakauer, J.L. Phillips, S.N. Sells, C.C. Taff, J.C. Wingfield, and G.L. Patricelli. 2012b. Experimental chronic noise is related to elevated fecal corticosteroid metabolites in lekking male Greater Sage-Grouse (*Centrocercus urophasianus*). *PLoS ONE* 7:e50462.
- Block, B.A., I.D. Jonsen, S.J. Jorgensen, A.J. Winship, S.A. Shaffer, S.J. Bograd, E.L. Hazen, D.G. Foley, G.A. Breed, A.-L. Harrison, J.E. Ganong, A. Swithenbank, M. Castleton, H. Dewar, B.E. Mate, G.L. Shillinger, K.M. Schaefer, S.R. Benson, M.J. Weise, R.W. Henry, and D.P. Costa. 2011. Tracking apex marine predator movements in a dynamic ocean. *Nature* 475(7354):86-90.
- Boas, M., U. Feldt-Rasmussen, N.E. Skakkebaek, and K.M. Main. 2006. Environmental chemicals and thyroid function. *European Journal of Endocrinology* 154:599-611.
- Bonde, R.K., A. Garrett, M. Belanger, N. Askin, L. Tan, and C. Wittnich. 2012. Biomedical health assessments of the Florida manatee in Crystal River—providing opportunities for training during the capture, handling, and processing of this unique aquatic mammal. *Journal of Marine Animals and Their Ecology* 5(2):17-28.
- Bonier, F., P.R. Martin, I.T. Moore, and J.C. Wingfield. 2009. Do baseline glucocorticoids predict fitness? *Trends in Ecology & Evolution* 24(11):634-642.
- Boonstra, R. 2005. Equipped for life: The adaptive role of the stress axis in male mammals. *Journal of Mammalogy* 86(2):236-247.
- Borchers, D.L. 2012. A non-technical overview of spatially explicit capture-recapture models. *Journal of Ornithology* 152:435-444.
- Bossart, G.D., T.A. Romano, M.M. Peden-Adams, A. Schaefer, S. McCulloch, J.D. Goldstein, C.D. Rice, J.T. Saliki, P.A. Fair, and J.S. Reif. 2011. Clinicopathologic findings in Atlantic bottlenose dolphins *Tursiops truncatus* with positive cetacean morbillivirus antibody titers. *Diseases of Aquatic Organisms* 97(2):103-112.
- Bottein, M.Y., L. Kashinsky, Z. Wang, C. Littnan, and J.S. Ramsdell. 2011. Identification of ciguatoxins in Hawaiian monk seals *Monachus schauinslandi* from the Northwestern and Main Hawaiian Islands. *Environmental Science & Technology* 45:5403-5409.
- Boucher, O., G. Muckle, and C.H. Bastien. 2009. Prenatal exposure to polychlorinated biphenyls: A neuropsychologic analysis. *Environmental Health Perspectives* 117:7-16.
- Bowen, W.D., J.D. Baker, D. Siniff, I.L. Boyd, R. Wells, J.K.B. Ford, S.D. Kraus, J.A. Estes, and I. Stirling. 2010. Long-term studies. Pp. 283-305 in *Marine Mammal Ecology and Conservation: A Handbook of Techniques*, I. Boyd, D. Bowen, and S. Iverson, eds. Oxford: Oxford University Press.
- Boyd, I.L. 2000. State-dependent fertility in pinnipeds: Contrasting capital and income breeders. *Functional Ecology* 14(5):623-630.
- Boziari, A., C. Koukorava, E. Carinou, C.J. Hourdakakis, and V. Kamenopoulou. 2010. The use of active personal dosimeters as a personal monitoring device: Comparison with TL dosimetry. *Radiation Protection Dosimetry* 144:173-176.
- Bräger, S., K. Brensing, R. Caddell, K.C. Detloff, S. Dolman, P. Evans, V. Frank, J. Haelters, R. Kless, K. Lucke, L. Nunny, G. Pavan, M. Simmonds, and H. Westerberg. 2009. Final Report of the ASCOBANS Intersessional Working Group on the Assessment of Acoustic Disturbance, August 11, 2009. Available at [http://www.ascobans.org/sites/default/files/basic\\_page\\_documents/AC17\\_4-08\\_ReportWGAcousticDisturbance.pdf](http://www.ascobans.org/sites/default/files/basic_page_documents/AC17_4-08_ReportWGAcousticDisturbance.pdf).

- Branch, T.A., K.M. Stafford, D.M. Palacios, C. Allison, J.L. Bannister, C.L.K. Burton, E. Cabrera, C.A. Carlson, B. Galletti Vernazzani, P.C. Gill, R. Huckle-Gaete, K.C.S. Jenner, M.-N.M. Jenner, K. Matsuoka, Y.A. Mikhalev, T. Miyashita, M.G. Morrice, S. Nishiwaki, V.J. Sturrock, D. Tormosov, R.C. Anderson, A.N. Baker, P.B. Best, P. Borsari, R.L. Brownell, Jr., S. Childerhouse, K.P. Findlay, T. Gerrodette, A.D. Ilangakoon, M. Joergensen, B. Kahn, D.K. Ljungblad, B. Maughan, R.D. McCauley, S. McKay, T.F. Norris, Oman Whale and Dolphin Research Group, R.M. Warneke, S. Rankin, F. Samaran, D. Thiele, and K. Van Waerebeek. 2007. Past and present distribution densities and movements of blue whales in the Southern Hemisphere and Northern Indian Ocean. *Mammal Review* 37:116-175.
- Branchi, I., F. Capone, E. Alleva, and L.G. Costa. 2003. Polybrominated diphenyl ethers: Neurobehavioral effects following developmental exposure. *Neurotoxicology* 24(3):449-462.
- Brandt, M.J., A. Diederichs, K. Betke, and G. Nehls. 2011. Responses of harbor porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea. *Marine Ecology Progress Series* 421:205-216.
- Brandt, M.J., C. Hoschle, A. Diederichs, K. Betke, R. Matuschek, and G. Nehls. 2013. Seal scarers as a tool to deter harbour porpoises from offshore construction sites. *Marine Ecology Progress Series* 475:291-302.
- Brandt-Lassen, R., S.P. Lund, and G.B. Jepsen. 2000. Rats exposed to toluene and noise may develop loss of auditory sensitivity due to synergistic interaction. *Noise Health* 3:33-44.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* 74:1444-1454.
- Brenner, I., J. Castellani, C. Gabaree, A. Young, J. Zamecnik, R. Shephard, and P. Shek. 1999. Immune changes in humans during cold exposure: Effects of prior heating and exercise. *Journal of Applied Physiology* 87(2):699-710.
- Brinton, E., V.J. Loeb, M.C. Macaulay, and E. Shulenberg. 1987. Variability of *Euphausia superba* populations near Elephant Island and the South Shetlands: 1981 vs. 1984. *Polar Biology* 7(6):345-362.
- Brock, P.M., A.J. Hall, S.J. Goodman, M. Cruz, and K. Acevedo-Whitehouse. 2013a. Immune activity, body condition and human-associated environmental impacts in a wild marine mammal. *PLoS ONE* 8(6):e67132.
- Brock, P.M., A.J. Hall, S.J. Goodman, M. Cruz, and K. Acevedo-Whitehouse. 2013b. Applying the tools of ecological immunology to conservation: A test case in the Galapagos sea lion. *Animal Conservation* 16(1):19-31.
- Brough, T.E., S. Henderson, M. Guerra, and S.M. Dawson. 2016. Factors influencing heterogeneity in female reproductive success in a critically endangered population of bottlenose dolphins. *Endangered Species Research* 29:255-270.
- Brumm, H., and S.A. Zollinger. 2011. The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour* 148:1173-1198.
- Buckland, S.T., and A.E. York. 2009. Abundance estimation. Pp. 1-5 in *Encyclopedia of Marine Mammals*, W.F. Perrin, B. Wursig and J.G.M. Thewissen, eds. San Diego, CA: Academic Press.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and L. Thomas. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford: Oxford University Press.
- Buckland, S.T., M.L. Burt, E. Rexstad, M. Mellor, A. Williams, and R. Woodward. 2012. Aerial surveys of seabirds: The advent of digital methods. *Journal of Applied Ecology* 49:960-967.
- Buckstaff, K.C. 2004. Effects of watercraft noise on the acoustic behavior of bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine Mammal Science* 20:709-725. doi: 10.1111/j.17487692.2004.tb01189.x.
- Bunkley, J.P., and J.R. Barber. 2015. Noise reduces foraging efficiency in pallid bats (*Antrozous pallidus*). *Ethology* 121:1116-1121.
- Burek, K.A., F. Gulland, and T.M. O'Hara. 2008. Effects of climate change on Arctic marine mammal health. *Ecological Applications* 18(sp2):S126-S134.
- Burgin, S., and N. Hardiman. 2015. Effects of non-consumptive wildlife-oriented tourism on marine species and prospects for their sustainable management. *Journal of Environmental Management* 151:210-220.
- Burns, W.C. 1997. The International Whaling Commission and future of cetaceans: Problems and prospects. *Colorado Journal of International Environmental Law and Policy* 8(1):31-88.
- Caillat, M., and S. Smout. 2015. *Harbour Seal Decline: Population Modeling*. Sea Mammal Research Unit, University of St. Andrews, Report to Scottish Government, no. CSD 4, St. Andrews, 29 pp. Available at [http://www.smru.standrews.ac.uk/documents/scotgov/CSD4\\_population\\_model\\_VF2.pdf](http://www.smru.standrews.ac.uk/documents/scotgov/CSD4_population_model_VF2.pdf).
- Calabrese, E.J. 2005. Paradigm lost, paradigm found: The re-emergence of hormesis as a fundamental dose response model in the toxicological sciences. *Environmental Pollution* 138(3):378-411.
- Calabrese, E.J., K.A. Bachmann, A.J. Bailer, P.M. Bolger, J. Borak, L. Cai, N. Cedergreen, M.G. Cherian, C.C. Chiueh, T.W. Clarkson, and R.R. Cook. 2007. Biological stress response terminology: Integrating the concepts of adaptive response and preconditioning stress within a hormetic dose-response framework. *Toxicology and Applied Pharmacology* 222(1):122-128.
- Calvert, W., and M.A. Ramsay. 1998. Evaluation of age determination of polar bears by counts of cementum growth layer groups. *Ursus* 449-453.
- Caro, T.M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. *Conservation Biology* 13(4):805-814.
- Carpenter, D.O. 2006. Polychlorinated biphenyls (PCBs): Routes of exposure and effects on human health. *Reviews on Environmental Health* 21(1):1-23.
- Carretta, J.V., K. Danil, S.J. Chivers, D.W. Weller, D.S. Janiger, M. Berman-Kowalewski, K.M. Hernandez, J.T. Harvey, R.C. Dunkin, D.R. Casper, S. Stoudt, M. Flannery, K. Wilkinson, J. Huggins, and D.M. Lambourn. 2015. Recovery rates of bottlenose dolphin (*Tursiops truncatus*) carcasses estimated from stranding and survival rate data. *Marine Mammal Science* 32:349-362.
- Cassoff, R.M., K.M. Moore, W.A. McLellan, S.G. Barco, D.S. Rotstein, and M.J. Moore. 2011. Lethal entanglement in baleen whales. *Diseases of Aquatic Organisms* 96:175-185.
- Castellote, M., C.W. Clark, and M.O. Lammers. 2012. Acoustic and behavioural changes by fin whales (*Balaenoptera physalus*) in response to shipping and airgun noise. *Biological Conservation* 147(1):115-122.
- Caswell, H. 2001. *Matrix Population Models*, 2nd Ed. Sunderland, MA: Sinauer Associates.
- Caswell, H., M. Fujiwara, and S. Brault. 1999. Declining survival probability threatens the North Atlantic right whale. *Proceedings of the National Academy of Sciences of the United States of America* 96(6):3308-3313.
- Celi, M., F. Filiciotto, M. Vazzana, V. Arizza, V. Maccarrone, M. Ceraulo, S. Mazzola, and G. Buscaino. 2015. Shipping noise affecting immune responses of European spiny lobster (*Palinurus elephas*). *Canadian Journal of Zoology* 93(2):113-121.
- Champagne, C., D. Crocker, M. Fowler, and D. Houser. 2012. Fasting physiology of the pinnipeds: The challenges of fasting while maintaining high energy expenditure and nutrient delivery for lactation. Pp. 309-336 in *Comparative Physiology of Fasting, Starvation, and Food Limitation*, M. D. McCue, ed. Berlin: Springer.
- Chan, A.A., Y.H. Chan, W.D. Stahlman, D. Garlick, C.D. Fast, D.T. Blumstein, and A.P. Blaisdell. 2010. Increased amplitude and duration of acoustic stimuli enhance distraction. *Animal Behaviour* 80:1075-1079.
- Christiansen, F., and D. Lusseau. 2015. Linking behavior to vital rates to measure the effects of non-lethal disturbance on wildlife. *Conservation Letters* 8(6):424-431.
- Christiansen, F., G.A. Vikingsson, M.H. Rasmussen, and D. Lusseau. 2014. Female body condition affects foetal growth in a capital breeding mysticete. *Functional Ecology* 28:579-588.
- Claridge, D.E. 2013. Population Ecology of Blainville's Beaked Whales (*Mesoplodon densirostris*). Doctoral dissertation, University of St. Andrews.

- Clark, C.W., W.T. Ellison, B.L. Southall, L.T. Hatch, S.M. Van Parijs, A. Frankel, and D. Ponirakis. 2009. Acoustic masking in marine ecosystems: Intuitions, analysis, and implications. *Marine Ecology: Progress Series* 395:201-222.
- Cohen, J. 1991. Was underwater "shot" harmful to the whales? *Science* 252(5008):912.
- Conn, P.B., and G.K. Silber. 2013. Vessel speed restrictions reduce risk of collision-related mortality for North Atlantic right whales. *Ecosphere* 4(4):43.
- Connon, R.E., J. Geist, and I. Werner. 2012. Effect-based tools for monitoring and predicting the ecotoxicological effects of chemicals in the aquatic environment. *Sensors* 12(9):12741-12771.
- Constantine, R. 2001. Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. *Marine Mammal Science* 17(4):689-702.
- Conversi, A., V. Dakos, A. Gårdmark, S. Ling, C. Folke, P.J. Mumby, C. Greene, M. Edwards, T. Blenckner, M. Casini, A. Pershing, and C. Möllmann. 2015. A holistic view of marine regime shifts. *Philosophical Transactions of the Royal Society B* 370:20130279. doi: 10.1098/rstb.2013.0279.
- Cook, P.F., C. Reichmuth, A.A. Rouse, L.A. Libby, S.E. Dennison, O.T. Carmichael, K.T. Kruse-Elliott, J. Bloom, B. Singh, V.A. Fravel, L. Barbosa, J.J. Stuppino, W.G. Van Bonn, F.M.D. Gulland, and C. Ranganath. 2015. Algal toxin impairs sea lion memory and hippocampal connectivity, with implications for strandings. *Science* 350(6267):1545-1547.
- Cooke, R.M. 1991. *Experts in Uncertainty: Opinion and Subjective Probability in Science*. New York: Oxford University Press.
- Cooke, S.J., S.S. Killen, J.D. Metcalfe, D.J. McKenzie, D. Mouillot, C. Jørgensen, and M.A. Peck. 2014. Conservation physiology across scales: Insights from the marine realm. *Conservation Physiology* 2(1):cou024.
- Cordes, L. 2011. Demography and Breeding Phenology of a Marine Top Predator. PhD thesis, University of Aberdeen.
- Costantini, D., A. Fanfani, and G. Dell'omo. 2008. Effects of corticosteroids on oxidative damage and circulating carotenoids in captive adult kestrels (*Falco tinnunculus*). *Journal of Comparative Physiology B* 178(7):829-835.
- Costantini, D., V. Marasco, and A.P. Møller. 2011. A meta-analysis of glucocorticoids as modulators of oxidative stress in vertebrates. *Journal of Comparative Physiology B* 181(4):447-456.
- Côté, I.M., E.S. Darling, and C.J. Brown. 2016. Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences* 283:2015-2592.
- Cote, J., S. Meylan, J. Clobert, and Y. Voituron. 2010. Carotenoid-based coloration, oxidative stress and corticosterone in common lizards. *Journal of Experimental Biology* 213(12):2116-2124.
- Cox, T.M., T.J. Ragen, A.J. Read, E. Vos, R.W. Baird, K. Balcomb, J. Barlow, J. Caldwell, T. Cranford, L. Crum, A. D'Amico, G. D'Spain, A. Fednandez, J. Finneran, R. Gentry, W. Gerth, F. Gulland, J. Hildebrand, D. Houser, T. Hullar, P.D. Jepson, D. Ketten, C.D. MacLeod, P. Miller, S. Moore, D.C. Mountain, D. Palka, P. Ponganis, S. Rommel, T. Rowles, B. Taylor, P. Tyack, D. Wartzok, R. Gisiner, J. Mead, and L. Benner. 2006. Understanding the impacts of anthropogenic sound on beaked whales. *Journal of Cetacean Research Management* 7:177-187.
- Crain, C.M., K. Kroeker, and B.S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11:1304-1315.
- Cranford, T.W., and P. Krysl. 2015. Fin whale sound reception mechanisms: Skull vibration enables low-frequency hearing. *PLoS ONE* 10:1-17.
- Creel, S., D. Christianson, S. Liley, and J.A. Winnie. 2007. Predation risk affects reproductive physiology and demography of elk. *Science* 315:960.
- Creel, S., J.A. Winnie, and D. Christianson. 2009. Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. *Proceedings of the National Academy of Sciences of the United States of America* 106:12388-12393.
- Crocker, D.E., B.J. Le Boeuf, and D.P. Costa. 1997. Drift diving in female northern elephant seals: Implications for food processing. *Canadian Journal of Zoology* 75:27-39.
- Crocker, D.E., D.P. Costa, B.J. Le Boeuf, P.M. Webb, and D.S. Houser. 2006. Impact of El Niño on the foraging behavior of female northern elephant seals. *Marine Ecology Progress Series* 309:1-10.
- Crofton, K.M., D.-L. Ding, R. Padich, M. Taylor, and D. Henderson. 2000. Hearing loss following exposure during development to polychlorinated biphenyls: A cochlear site of action. *Hearing Research* 144(1-2):196-204.
- Croll, D.A., C.W. Clark, A. Acevedo, B. Tershy, S. Flores, J. Gedamke, and J. Urban. 2002. Only male fin whales sing loud songs. *Nature* 417:809.
- Croll, D.A., B. Marinovic, S. Benson, F.P. Chavez, N. Black, R. Ternullo, and B.R. Tershy. 2005. From wind to whales: Trophic links in a coastal upwelling system. *Marine Ecology: Progress Series* 289:117-130.
- Croxall, J.P., T. Callaghan, R. Cervellati, and D.W.H. Walton. 1992. Southern Ocean environmental changes: Effects on seabird, seal and whale populations [and discussion]. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 338(1285):319-328.
- Cumeras, R.H.K., W. Cheung, F. Gulland, D. Goley, and C.E. Davis. 2014. Chemical analysis of whale breath volatiles: A case study for non-invasive field health diagnostics of marine mammals. *Metabolites* 4(3):790-806.
- Curé, C., R. Antunes, A.C. Alves, F. Visser, P.H. Kvadsheim, and P.J. Miller. 2013. Responses of male sperm whales (*Physeter macrocephalus*) to killer whale sounds: Implications for anti-predator strategies. *Scientific Reports* 3:1579.
- Dähne, M., A. Gilles, K. Lucke, V. Peschko, S. Adler, K. Krügel, J. Sundermeyer, and U. Siebert. 2013. Effects of pile-driving on harbour porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. *Environmental Research Letters* 8:025002.
- Dai, L., D. Vorselen, K.S. Korolev, and J. Gore. 2012. Generic indicators for loss of resilience before a tipping point leading to population collapse. *Science* 336(6085):1175-1177.
- Dakos, V., S.R. Carpenter, E.H. van Nes, and M. Scheffer. 2015. Resilience indicators: Prospects and limitations for early warnings of regime shifts. *Philosophical Transactions of the Royal Society B* 370:1659. doi: 10.1098/rstb.2013.0263.
- D'Amico, A.D., R. Gisiner, D.R. Ketten, J.A. Hammock, C. Johnson, P. Tyack, and J. Mead. 2009. Beaked whale strandings and naval exercises. *Aquatic Mammals* 35(4):452-472.
- Dantzer, B., Q.E. Fletcher, R. Boonstra, and M.J. Sheriff. 2014. Measures of physiological stress: A transparent or opaque window into the status, management and conservation of species? *Conservation Physiology* 2(1):cou023.
- Darling, E.S., and E.M. Côté. 2008. Quantifying the evidence for ecological synergies. *Ecology Letters* 11:1278-1286.
- Daszak, P., A.A. Cunningham, and A.D. Hyatt. 2000. Emerging infectious diseases of wildlife—threats to biodiversity and human health. *Science* 287(5452):443-449.
- Dawson, S.M., S. Northridge, D. Waples, and A.J. Read. 2013. To ping or not to ping: The use of active acoustic devices in mitigating interactions between small cetaceans and gillnet fisheries. *Endangered Species Research* 19:201-221.
- De Guise, S., D. Martineau, P. Beland, and M. Fournier. 1998. Effects of in vitro exposure of beluga whale leukocytes to selected organochlorines. *Journal of Toxicology and Environmental Health, Part A: Current Issues* 55:479-493.
- de Little, S.C., C.J.A. Bradshaw, C.R. McMahon, and M.A. Hindell. 2007. Complex interplay between intrinsic and extrinsic drivers of long-term survival trends in southern elephant seals. *BMC Ecology* 7:3. doi: 10.1186/1472-6785-7-3.
- De Swart, R.L., P.S. Ross, J.G. Vos, and A.D. Osterhaus. 1996. Impaired immunity in harbour seals (*Phoca vitulina*) exposed to bioaccumulated environmental contaminants: Review of a long-term feeding study. *Environmental Health Perspectives* 104(Suppl. 4):823-828.

## REFERENCES

- De Vries, R.D., S. McQuaid, G. Van Amerongen, S. Yüksel, R.J. Verburgh, A.D. Osterhaus, W.P. Duprex, and R.L. De Swart. 2012. Measles immune suppression: Lessons from the macaque model. *PLoS Pathogens* 8(8):e1002885.
- DeMaster, D.P., A.W. Trites, P. Clapham, S. Mizrock, P. Wade, R.J. Small, and J. Ver Hoef. 2006. The sequential megafauna collapse hypothesis: Testing with existing data. *Progress in Oceanography* 68:329-342.
- DeRijk, R.H., E.M. Sternberg, and E.R. De Kloet. 1997. Glucocorticoid receptor function in health and disease. *Current Opinion in Endocrinology, Diabetes and Obesity* 4(3):185-193.
- DeRuiter, S.L., B.L. Southall, J. Calambokidis, W.M.X. Zimmer, D. Sadykova, E.A. Falcone, A.S. Friedlaender, J.E. Joseph, D. Moretti, G.S. Schorr, L. Thomas, and P.L. Tyack. 2013. First direct measurements of behavioral responses by Cuvier's beaked whales to mid-frequency active sonar. *Biology Letters* 9. doi: 10.1098/rsbl.2013.0223.
- Devineau, O., R. Choquet, and J.-D. Lebreton. 2006. Planning capture-recapture studies: Straightforward precision, bias and power calculations. *Wildlife Society Bulletin* 34:1028-1035.
- Di Poi, C., S. Atkinson, A. Hoover-Miller, and G. Blundell. 2015. Maternal buffering of stress response in free-ranging Pacific harbor seal pups in Alaska. *Marine Mammal Science* 31:1098-1117.
- Diamanti-Kandarakis, E., J.P. Bourguignon, L.C. Giudice, R. Hauser, G.S. Prins, A.M. Soto, R.T. Zoeller, and A.C. Gore. 2009. Endocrine-disrupting chemicals: An Endocrine Society scientific statement. *Endocrine Reviews* 30:293-342.
- Diaz, R.J., and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321(5891):926-929.
- Dickens, M.J., and L.M. Romero. 2013. A consensus endocrine profile for chronically stressed wild animals does not exist. *General and Comparative Endocrinology* 191:177-189.
- Dickens, M.J., D.J. Delehanty, and L.M. Romero. 2009. Stress and translocation: Alterations in the stress physiology of translocated birds. *Proceedings of the Royal Society B: Biological Sciences* 276:1664. doi: 10.1098/rspb.2008.1778.
- Dietz, R., F. Riget, and P. Johansen. 1996. Lead, cadmium, mercury and selenium in Greenland marine animals. *Science of the Total Environment* 186(1):67-93.
- Dietz, R., P.M. Outridge, and K.A. Hobson. 2009. Anthropogenic contributions to mercury levels in present-day Arctic animals—A review. *Science of the Total Environment* 407(24):6120-613.
- Dietz, R., C. Sonne, N. Basu, B. Braune, T. O'Hara, R.J. Letcher, T. Scheuhammer, M. Andersen, C. Andreasen, D. Andriashek, and G. Asmund. 2013. What are the toxicological effects of mercury in Arctic biota? *Science of the Total Environment* 443:775-790.
- Doak, D.F., J.A. Estes, B.S. Halpern, U. Jacob, D.R. Lindberg, J. Lovvorn, D.H. Monson, M.T. Tinker, T.M. Williams, J.T. Wootton, I. Carroll, M. Emmerson, F. Micheli, and M. Novak. 2008. Understanding and predicting ecological dynamics: Are major surprises inevitable? *Ecology* 89(4):952-961.
- Donaldson, R., H. Finn, and M. Calver. 2010. Illegal feeding increases risk of boat-strike and entanglement in bottlenose dolphins in Perth, Western Australia. *Pacific Conservation Biology* 16(3):157-161.
- Doney, S.C., M. Ruckelshaus, J.E. Duffy, J.P. Barry, F. Chan, C.A. English, H.M. Galindo, J.M. Grebmeier, A.B. Hollowed, N. Knowlton, and J. Polovina. 2012. Climate change impacts on marine ecosystems. *Marine Science* 4:11-37.
- Doniol-Valcroze, T., D. Berteaux, P. Larouche, and R. Sears. 2007. Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. *Marine Ecology: Progress Series* 335:207-216.
- Donovan, C.R., C. Harris, J. Harwood, and L. Milazzo. 2013. A simulation-based method for quantifying and mitigating the effects of anthropogenic sound on marine mammals. *Proceedings of Meetings on Acoustics* 17:070043.
- Doroff, A.M., J.A. Estes, M.T. Tinker, D.M. Burn, and T.J. Evans. 2003. Sea otter population declines in the Aleutian archipelago. *Journal of Mammalogy* 84(1):55-64.
- Dowling, D.K. and L.W. Simmons. 2009. Reactive oxygen species as universal constraints in life-history evolution. *Proceedings of the Royal Society B: Biological Sciences* 276(1663):1737-1745.
- Downs, C.J., and N.A. Dochtermann. 2014. Testing hypotheses in ecoinmunology using mixed models: Disentangling hierarchical correlations. *Integrative and Comparative Biology* 54(3):407-418.
- Drake, J.M., and B.D. Griffen. 2010. Early warning signals of extinction in deteriorating environments. *Nature* 467(7314):456-459.
- Dunne, J.A., R.J. Williams, and N.D. Martinez. 2002. Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America* 99:12917-12922.
- Durban, J., H. Fearnbach, L. Barret-Lennard, W. Perryman, and D. LeRoi. 2015. Photogrammetry of killer whales using a small hexacopter launched at sea. *21st Biennial Conference on the Biology of Marine Mammals*. San Francisco, CA, December 2015.
- Durbin, E., G. Teegarden, R. Campbell, A. Cembella, M.F. Baumgartner, and B.R. Mate. 2002. North Atlantic right whales, *Eubalaena glacialis*, exposed to paralytic shellfish poisoning (PSP) toxins via a zooplankton vector, *Calanus finmarchicus*. *Harmful Algae* 1:243-251.
- Eales, J.G. 1988. The influence of nutritional state on thyroid function in various vertebrates. *American Zoologist* 28:351-362.
- Eberhardt, L.L. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology* 83:2841-2854.
- Eberle, K.C., T.E. Waters, E.D. Jensen, S.K. Venn-Watson, and R.E. Sacco. 2013. Development and application of specific cytokine assays in tissue samples from a bottlenose dolphin with hyperinsulinemia. *Frontiers in Endocrinology* 4:134.
- Ellison, W.T., B.L. Southall, C.W. Clark, and A.S. Frankel. 2011. A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. *Conservation Biology* 26:21-28.
- Engås, A., S. Løkkeborg, E. Ona, and A.V. Soldal. 1996. Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). *Canadian Journal of Fisheries and Aquatic Sciences* 53(10):2238-2249.
- Engelhard, G.H., A.N.J. Baarspul, M. Broekman, J.C.S. Creuwels, and P.J.H. Reijnders. 2002. Human disturbance, nursing behaviour, and lactational pup growth in a declining southern elephant seal (*Mirounga leonina*) population. *Canadian Journal of Zoology* 80(11):876-1886.
- EPA (U.S. Environmental Protection Agency). 2000. *Supplementary Guidance for Conducting Risk Assessment of Chemical Mixtures*. EPA/630/R-00/002, August 2000.
- EPA. 2002. *Guidance on Cumulative Risk Assessment of Pesticide Chemicals That Have a Common Mechanism of Toxicity*. Office of Pesticide Programs, January 14, 2002.
- EPA. 2007. *Concepts, Methods and Data Sources for Cumulative Health Risk Assessment of Multiple Chemicals, Exposures and Effects: A Resource Document*. EPA/600/R-06/013F. National Center for Environmental Assessment, Office of Research and Development, U.S. Environmental Protection Agency, Cincinnati, OH. [http://ofmpub.epa.gov/eims/eimscmm.getfile?p\\_download\\_id=474337](http://ofmpub.epa.gov/eims/eimscmm.getfile?p_download_id=474337).
- Erbe, C. 2013. International regulation of underwater noise. *Acoustics Australia* 41:12-19.
- Ercal, N., H. Gurer-Orhan, and N. Aykin-Burns. 2001. Toxic metals and oxidative stress part I: Mechanisms involved in metal-induced oxidative damage. *Current Topics in Medicinal Chemistry* 1(6):529-539.
- Eriksson, P., E. Jakobsson, and A. Fredriksson. 2001. Brominated flame retardants: A novel class of developmental neurotoxicants in our environment? *Environmental Health Perspectives* 109(9):903-908.
- Estes, J.A., M. Tinker, T.M. Williams, and D.F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282(5388):473-476.

- Estes, J.A., D.F. Doak, A.M. Springer, and T.M. Williams. 2009a. Causes and consequences of marine mammal population declines in southwest Alaska: A food-web perspective. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 364(May):1647-1658.
- Estes, J.A., D.F. Doak, A.M. Springer, T.M. Williams, and G.B. van Vliet. 2009b. Trend data do support the sequential nature of pinniped and sea otter declines in the North Pacific, but does it really matter? *Marine Mammal Science* 25:748-754.
- Estes, J.A., J.S. Brashares, and M.E. Power. 2013a. Predicting and detecting reciprocity between indirect ecological interactions and evolution. *The American Naturalist* 181(Suppl.):S76-S99.
- Estes, J.A., R.S. Steneck, and D.R. Lindberg. 2013b. Exploring the consequences of species interactions through the assembly and disassembly of food webs: A Pacific/Atlantic comparison. *Bulletin of Marine Science* 89:11-29.
- European Union. 2008. Directive 2008/56/EC of European Parliament and of The Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). *Official Journal of the European Union, L: Legislation* 164:19-40.
- Evans, D.L., and G.R. England. 2001. *Joint Interim Report Bahamas Marine Mammal Stranding Event of 14-16 March 2000*. Washington, DC: U.S. Department of Commerce and U.S. Navy. Available at [http://www.nmfs.noaa.gov/pr/pdfs/health/stranding\\_bahamas2000.pdf](http://www.nmfs.noaa.gov/pr/pdfs/health/stranding_bahamas2000.pdf).
- Fahlman, A., S.K. Hooker, A. Olszowka, B.L. Bostrom, and D.R. Jones. 2009. Estimating the effect of lung collapse and pulmonary shunt on gas exchange during breath-hold diving: The Scholander and Kooyman legacy. *Respiratory Physiology & Neurobiology* 165(1):28-39.
- Fahlman, A., P.L. Tyack, P.J. Miller, and P.H. Kvadsheim. 2014. How man-made interference might cause gas bubble emboli in deep diving whales. *Frontiers in Physiology* 5:13.
- Fahlman, A., J. van der Hoop, M.J. Moore, G. Levine, J. Rocho-Levine, and M. Brodsky. 2016. Estimating energetics in cetaceans from respiratory frequency: Why we need to understand physiology. *Biology Open* 5(4):436-442. doi: 10.1242/bio.017251.
- Fair, P.A., T.C. Hulsey, R.A. Varela, and J.D. Goldstein. 2006. Hematology, serum chemistry, and cytology findings from apparently healthy Atlantic bottlenose dolphins (*Tursiops truncatus*) inhabiting the estuarine waters of Charleston, South Carolina. *Aquatic Mammals* 32(2):182.
- Falcone, E.A., G.S. Schorr, A.B. Douglas, J. Calambokidis, E. Henderson M.F. McKenna, J. Hildebrand, and D. Moretti. 2009. Sighting characteristics and photo-identification of Cuvier's beaked whales (*Ziphius cavirostris*) near San Clemente Island, California: A key area for beaked whales and the military? *Marine Biology* 156:2631-2640.
- Falke, K.J., R.D. Hill, J. Qvist, R.C. Schneider, M. Guppy, G.C. Liggins, P.W. Hochachka, R.E. Elliott, and W.M. Zapol. 1985. Seal lungs collapse during free diving: Evidence from arterial nitrogen tensions. *Science* 229(4713):556-558. doi: 10.1126/science.4023700.
- Farina, M., J.B. Rocha, and M. Aschner. 2011. Mechanisms of methylmercury induced neurotoxicity: evidence from experimental studies. *Life Sciences* 89(15-16):553-563. doi: 10.1016/j.lfs.2011.05.019. Epub 2011 Jun 13.
- Fearnbach, H., J. Durban, D. Ellifrit, K. Balcomb, and L. Barre. 2015. Aerial photogrammetry reveals declining body condition and impaired reproduction in endangered Southern Resident killer whales. *21st Biennial Conference on the Biology of Marine Mammals, San Francisco, CA, December 2015*.
- Feller, W. 1968. *Introduction to Probability Theory and Its Application*. New York: John Wiley & Sons.
- Ferguson, S.H., I. Stirling, and P. McLoughlin. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Marine Mammal Science* 21(1):121-135.
- Fernández, A., J.F. Edwards, F. Rodriguez, A.E. De Los Monteros, P. Herraez, P. Castro, J.R. Jaber, V. Martín, and M. Arbelo. 2005. Gas and fat embolic syndrome involving a mass stranding of beaked whales (family Ziphiidae) exposed to anthropogenic sonar signals. *Veterinary Pathology* 42(4):446-457.
- Fernández, A., E. Sierra, V. Martín, M. Méndez, S. Sacchini, Y. Bernaldo de Quiros, M. Andrada, M. Rivero, O. Quesada, M. Tejedor, and M. Arbelo. 2012. Last "atypical" beaked whales mass stranding in the Canary Islands (July, 2004). *Journal of Marine Science: Research and Development* 2:107.
- Finneran, J.J. 2016. Auditory weighting functions and TTS/PTS exposure functions for marine mammals exposed to underwater noise. Pp. 38-110 in National Marine Fisheries Service. Technical Guidance for Assessing the Effects of Anthropogenic Sound on Marine Mammal Hearing: Underwater Acoustic Thresholds for Onset of Permanent and Temporary Threshold Shifts. U.S. Department of Commerce, NOAA. *NOAA Technical Memorandum*. NMFS-OPR-55.
- Finneran, J.J., and D.S. Houser. 2007. Bottlenose dolphin (*Tursiops truncatus*) steady-state evoked responses to multiple simultaneous sinusoidal amplitude modulated tones. *Journal of the Acoustical Society of America* 121:1775-1782.
- Finneran, J.J., and A.K. Jenkins. 2012. *Criteria and Thresholds for U.S. Navy Acoustic and Explosive Effects Analysis*. Technical Report. Available at <http://www.dtic.mil/dtic/tr/fulltext/u2/a561707.pdf>.
- Finneran, J.J., and C.E. Schlundt. 2004. *Effects of Intense Pure Tones on the Behavior of Trained Odontocetes*. Technical Report 1913. SPAWAR Systems Center, San Diego, CA. Available at <https://ntrl.ntis.gov/NTRL/dashboard/searchResults/titleDetail/ADA424426.xhtml>.
- Fire, S.E., Z. Wang, T.A. Leighfield, S.L. Morton, W.E. McFee, W.A. McLellan, R.W. Litaker, P.A. Tester, A.A. Hohn, G. Lovewell, C. Harms, D.S. Rotstein, S.G. Barco, A. Costidis, B. Sheppard, G.D. Bossart, M. Stolen, W.N. Durden, and F.M. Van Dolah. 2009. Domoic acid exposure in pygmy and dwarf sperm whales (*Kogia spp.*) from southeastern and mid-Atlantic U.S. waters. *Harmful Algae* 8(5):658.
- Fisher, R.A. 1937. *The Design of Experiments*, 9th Ed. London: Macmillan.
- Fleshler, M. 1965. Adequate acoustic stimulus for startle reaction in the cat. *Journal of Comparative Physiological Psychology* 60:200-207.
- Fletcher, H. 1940. Auditory patterns. *Reviews of Modern Physics* 12:47-65.
- Flewelling, L.J., J.P. Naar, J.P. Abbott, D.G. Baden, N.B. Barros, G.D. Bossart, M.Y.D. Bottein, D.G. Hammond, E.M. Haubold, C.A. Heil, M.S. Henry, H.M. Jacocks, T.A. Leighfield, R.H. Pierce, T.D. Pitchford, S.A. Rommel, P.S. Scott, K.A. Steidinger, E.W. Truby, F.M. Van Dolah, and J.H. Landsberg. 2005. Red tides and marine mammal mortalities. *Nature* 435:755-756.
- Folt, C.L., C.Y. Chen, M.V. Moore, and J. Burnaford. 1999. Synergism and antagonism among multiple stressors. *Limnology and Oceanography* 44(3):865-877.
- Forcada, J., P.N. Trathan, K. Reid, E.J. Murphy, and J.P. Croxall. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology* 12(3):411-423.
- Ford, J.K.B., G.M. Ellis, P.F. Olesiuk, and K.C. Balcomb. 2010. Linking killer whale survival and prey abundance: Food limitation in the oceans' apex predator? *Biology Letters* 6:139-142.
- Ford, M.J. 2013. *Status Review Update of Southern Resident Killer Whales*. Conservation Biology Division Northwest Fisheries Science Center, National Marine Fisheries Service.
- Forney, K.A. 2000. Environmental models of cetacean abundance: Reducing uncertainty in population trends. *Conservation Biology* 14:1271-1286.
- Fowles, J.R., A. Fairbrother, M. Fix, S. Schiller, and N. Kerkvliet. 1993. Glucocorticoid effects on natural and humoral immunity in mallards. *Developmental & Comparative Immunology* 17(2):165-177.
- Francis, C.D. 2015. Vocal traits and diet explain avian sensitivities to anthropogenic noise. *Global Change Biology* 21:1809-1820.
- Francis, C.D., and J.R. Barber. 2013. A framework for understanding noise impacts on wildlife: An urgent conservation priority. *Frontiers in Ecology and the Environment* 11:305-313.

- Francis, C.D., C.P. Ortega, and A. Cruz. 2009. Noise pollution changes avian communities and species interactions. *Current Biology* 19:1415-1419.
- Francis, C.D., C.P. Ortega, R.I. Kennedy, and P.J. Nylander. 2012a. Are nest predators absent from noisy areas or unable to locate nests? *Ornithological Monographs* 74:101-110.
- Francis, C.D., N.J. Kleist, C.P. Ortega, and A. Cruz. 2012b. Noise pollution alters ecological services: Enhanced pollination and disrupted seed dispersal. *Proceedings of the Royal Society B: Biological Sciences* 279:2727-2735.
- Francis, R.C., and S.R. Hare. 1994. Decadal-scale regime shifts in the large marine ecosystems of the north-east Pacific: A case for historical science. *Fisheries Oceanography* 3(4):279-291.
- Frankel, A.S., W.T. Ellison, and J. Buchanan. 2002. Application of the Acoustic Integration Model (AIM) to predict and minimize environmental impacts. *Oceans '02 MTS/IEEE* 3:1438-1443.
- Frantzis, A. 1998. Does acoustic testing strand whales? *Nature* 392(6671):29.
- French, S.S., M. González-Suárez, J.K. Young, S. Durham, and L.R. Gerber. 2011. Human disturbance influences reproductive success and growth rate in California sea lions (*Zalophus californianus*). *PLoS ONE* 6(3):e17686.
- Frid, A., and L.M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6(1):11.
- Friedlaender, A.S., E.L. Hazen, J.A. Goldbogen, A.K. Stimpert, J. Calambokidis, and B.L. Southall. 2016. Prey-mediated behavioral responses of feeding blue whales in controlled sound exposure experiments. *Ecological Applications* 26(4):1075-1085.
- Frisén, M. 2009. Optimal sequential surveillance for finance, public health and other areas. *Sequential Analysis: Design Methods and Applications* 28:310-337.
- Fritts, H.C. 2012. *Tree Rings and Climate*. New York: Elsevier.
- Fromm, D.M. 2009. Reconstruction of acoustic exposure on orcas in Haro Strait. *NRL Review* 2009:127-129.
- Fuente, A., and B. McPherson. 2006. Organic solvents and hearing loss: The challenge for audiology. *International Journal of Audiology* 45:367-381.
- Fujiwara, M., and H. Caswell. 2001. Demography of the endangered North Atlantic right whale. *Nature* 414(6863):537-541.
- Gardner, S.C. and S. Chávez-Rosales. 2000. Changes in the relative abundance and distribution of gray whales (*Eschrichtius robustus*) in Magdalena Bay, Mexico during an El Niño event. *Marine Mammal Science* 16(4):728-738.
- Gascon, M., E. Morales, J. Sunyer, and M. Vrijheid. 2013. Effects of persistent organic pollutants on the developing respiratory and immune systems: A systematic review. *Environmental International* 52:51-56.
- Geiger, A.C., and C.J. Jeffries. 1987. Evaluation of seal harassment techniques to protect gill netted salmon. *Acoustical Deterrents in Marine Mammal Conflicts with Fisheries* 37-55. Workshop held February 17-18, 1986, Newport, Oregon.
- Gennings, C., W.H. Carter, R.A. Carchman, L.K. Teuschler, J.F. Simmons, and E.W. Carney. 2005. A unifying concept for assessing toxicological interactions: Changes in slope. *Toxicological Sciences* 88(2):287-297.
- George, J.C., M.L. Druckenmiller, K.L. Laidre, R. Suydam, and B. Person. 2015. Bowhead whale body condition and links to summer sea ice and upwelling in the Beaufort Sea. *Progress in Oceanography* 136:250-262.
- Gerodette, T. and W.G. Gilmartin. 1990. Demographic consequences of changed pupping and hauling sites of the Hawaiian monk seal. *Conservation Biology* 4(4):423-430.
- Gibbons, A. 1990. What's the sound of one ocean warming? *Science* 248(4951):33-34.
- Gill, J.A., K. Norris, and W.J. Sutherland. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation* 97:265-268.
- Gillespie, A. 2010. Noise pollution, the oceans, and the limits of international law. *Yearbook of International Environmental Law* 21:114-139.
- Gisiner, R., S. Harper, E. Livingston, and J. Simmen. 2006. Effects of Sound on the Marine Environment (ESME): An underwater noise risk model. *IEEE Journal of Oceanic Engineering* 138(4):1067-1081.
- Gobush, K.S., R.K. Booth, and S.K. Wasser. 2014. Validation and application of noninvasive glucocorticoid and thyroid hormone measures in free-ranging Hawaiian monk seals. *General and Comparative Endocrinology* 195:174-182.
- Goetz, K.T., D.J. Rugh, A.J. Read, and R.C. Hobbs. 2007. Habitat use in a marine ecosystem: Beluga whales *Delphinapterus leucas* in Cook Inlet, Alaska. *Marine Ecology Progress Series* 330:247-256.
- Goldbogen, J.A., B.L. Southall, S.L. DeRuiter, J. Calambokidis, A.S. Friedlaender, E.L. Hazen, E.A. Falcone, G.S. Schorr, A. Douglas, D.J. Moretti, C. Kyburg, M.F. McKenna, and P.L. Tyack. 2013. Blue whales respond to simulated mid-frequency military sonar. *Proceedings of the Royal Society B: Biological Sciences* 280(1765):20130657.
- Goldstein, T., J.A. Mazet, T.S. Zabka, G. Langlois, K.M. Colegrove, M. Silver, S. Bargu, F. Van Dolah, T. Leighfield, P.A. Conrad, J. Barakos, D.C. Williams, S. Dennison, M. Haulena, and F.M. Gulland. 2008. Novel symptomatology and changing epidemiology of domoic acid toxicosis in California sea lions (*Zalophus californianus*): An increasing risk to marine mammal health. *Proceedings of the Royal Society B: Biological Sciences* 275:267-276.
- Goldstein, T., T.S. Zabka, R.L. DeLong, E.A. Wheeler, G. Ylitalo, S. Bargu, M. Silver, T. Leighfield, F. Van Dolah, G. Langlois, I. Sidor, J.L. Dunn, and F.M. Gulland. 2009. The role of domoic acid in abortion and premature parturition of California sea lions (*Zalophus californianus*) on San Miguel Island, California. *Journal of Wildlife Diseases* 45:91-108.
- Goldstein, T., I. Mena, S.J. Anthony, R. Medina, P.W. Robinson, D.J. Greig, D.P. Costa, W.I. Lipkin, A. Garcia-Sastre, and W.M. Boyce. 2013. Pandemic H1N1 influenza isolated from free-ranging northern elephant seals in 2010 off the central California coast. *PLoS ONE* 8(5):e62259.
- Gordine, S.A., Fedak, M., and L. Boehme. 2015. Fishing for drifts: detecting buoyancy changes of a top marine predator using a step-wise filtering method. *Journal of Experimental Biology* 218:3816-3824.
- Gotelli, N.J. 2008. *A Primer of Ecology*, 4th Ed. Sunderland, MA: Sinauer Associates.
- Götz, T., and V.M. Janik. 2011. Repeated elicitation of the acoustic startle reflex leads to sensitisation in subsequent avoidance behaviour and induces fear conditioning. *BMC Neuroscience* 12:30.
- Götz, T., and V.M. Janik. 2013. Acoustic deterrent devices to prevent pinniped depredation: Efficiency, conservation concerns and possible solutions. *Marine Ecology: Progress Series* 492:285-302.
- Graham, A.L., D.M. Shuker, L.C. Pollitt, S.K. Auld, A.J. Wilson, and T.J. Little. 2011. Fitness consequences of immune responses: Strengthening the empirical framework for ecoimmunology. *Functional Ecology* 25(1):5-17.
- Green, D.M. 1985. Temporal factors in psychoacoustics. Pp. 122-140 in *Time Resolution in Auditory Systems*. Berlin: Springer.
- Greene, C.H., and A.J. Pershing. 2004. Climate and the conservation biology of North Atlantic right whales: The right whale at the wrong time? *Frontiers in Ecology and the Environment* 2:29-34.
- Greenland, S. 2007. Interactions in epidemiology: Relevance, identification, and estimation. *Epidemiology* 20:14-17.
- Greig, D.J., F.M. Gulland, C.A. Rios, and A.J. Hall. 2010. Hematology and serum chemistry in stranded and wild-caught harbor seals in central California: Reference intervals, predictors of survival, and parameters affecting blood variables. *Journal of Wildlife Diseases* 46(4):1172-1184.
- Grimes, C.B. 2001. Fishery production and the Mississippi River discharge. *Fisheries* 26(8):17-26.
- Gross, K., G. Pasinelli, and H.P. Kunc. 2010. Behavioral plasticity allows short-term adjustment to a novel environment. *American Naturalist* 176(4):456-464.
- Groves, P.M., and R.F. Thompson. 1970. Habituation: A dual-process theory. *Psychological Review* 77(5):419-450.

- Gulland, F.M.D., and A.J. Hall. 2007. Is marine mammal health deteriorating? Trends in the global reporting of marine mammal disease. *EcoHealth* 4:135-150.
- Gulland, F.M.D., M. Haulena, D. Fauquier, G. Langlois, M.E. Lander, T. Zabka, and R. Duerr. 2002. Domoic acid toxicity in Californian sea lions (*Zalophus californianus*): Clinical signs, treatment and survival. *Veterinary Record* 150:475-480.
- Gulland, F.M.D., A.J. Hall, D.J. Greig, E.R. Frame, K.M. Colegrove, R.K. Booth, S.K. Wasser, and J.C. Scott-Moncrieff. 2012. Evaluation of circulating eosinophil count and adrenal gland function in California sea lions naturally exposed to domoic acid. *Journal of the American Veterinary Medical Association* 241:943-949.
- Guzmán-Verri, C., R. González-Barrientos, G. Hernández-Mora, J.-A. Morales, E. Baquero-Calvo, E. Chavez-Olarte, and E. Moreno. 2012. *Brucella ceti* and brucellosis in cetaceans. *Frontiers in Cellular and Infection Microbiology* 2:1-22. doi: 10.3389/fcimb.2012.00003.
- Habib, L., E.M. Bayne, and S. Boutin. 2007. Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *Journal of Applied Ecology* 44(1):176-184.
- Halfwerk, W., L.J.M. Holleman, C.M. Lessells, and H. Slabbekoorn. 2011. Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology* 48:210-219.
- Hall, A., C. Duck, P. Hammond, G. Hastie, E. Jones, B. McConnell, C. Morris, J. Onoufriou, P. Pomeroy, D. Thompson, D. Russell, S. Smout, L. Wilson, and P. Thompson. 2015. Harbour Seal Decline Workshop II. Sea Mammal Research Unit, University of St. Andrews, Report to Scottish Government, no CSD6, St. Andrews, 12 pp. Available at [http://www.smru.st-andrews.ac.uk/documents/scotgov/CSD6\\_harbour\\_seal\\_workshop\\_II\\_VF1.pdf](http://www.smru.st-andrews.ac.uk/documents/scotgov/CSD6_harbour_seal_workshop_II_VF1.pdf).
- Hall, A.J., and E. Frame. 2010. Evidence of domoic acid exposure in harbour seals from Scotland: A potential factor in the decline in abundance? *Harmful Algae* 9:489-493.
- Hall, A.J., R.J. Law, D.E. Wells, J. Harwood, H.M. Ross, S. Kennedy, C.R. Allchin, L.A. Campbell, and P.P. Pomeroy. 1992. Organochlorine levels in common seals (*Phoca vitulina*) which were victims and survivors of the 1988 Phocine Distemper Epizootic. *Science of the Total Environment* 115:145-162.
- Hall, A.J., K. Hugunin, R. Deaville, R.J. Law, C.R. Allchin, and P.D. Jepson. 2006. The risk of infection from polychlorinated biphenyl exposure in the harbor porpoise (*Phocoena phocoena*): A case-control approach. *Environmental Health Perspectives* 114(5):704-711.
- Hall, A.J., G.O. Thomas, and B.J. McConnell. 2009. Exposure to persistent organic pollutants and first-year survival probability in gray seal pups. *Environmental Science and Technology* 43:6364-6369.
- Halpern, B.S., K.A. Selkoe, F. Micheli, and C.V. Kappel. 2007. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Conservation Biology* 21:1301-1315.
- Halpern, B.S., S. Walbridge, K.A. Selkoe, C.V. Kappel, F. Micheli, C. D'Agrosa, J.F. Bruno, K.S. Casey, C. Ebert, H.E. Fox, R. Fujita, D. Heinemann, H.S. Lenihan, E.M.P. Madin, M.T. Perry, E.R. Selig, M. Spalding, R. Steneck, and R. Watson. 2008. A global map of human impact on marine ecosystems. *Science* 319:948-952.
- Hammond, J.A., A.J. Hall, and E.A. Dyrinda. 2005. Comparison of polychlorinated biphenyl (PCB) induced effects on innate immune functions in harbour and grey seals. *Aquatic Toxicology* 74(2):126-138.
- Hammond, P.S., P. Berggren, H. Benke, D.L. Borchers, A. Collet, M.P. Heide-Jørgensen, S. Heimlich, A.R. Hiby, M.F. Leopold, and N. Øien. 2002. Abundance of harbour porpoises and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology* 39:361-376.
- Hanson, N.N., D. Thompson, C.D. Duck, S. Moss, and M. Lonergan. 2013. Pup mortality in a rapidly declining harbour seal (*Phoca vitulina*) population. *PLoS ONE* 8(11):e80727.
- Hanson, N.N., D. Thompson, C.D. Duck, J. Baxter, and M.E. Lonergan. 2015. Harbour seal (*Phoca vitulina*) abundance within the Firth of Tay and Eden Estuary, Scotland: Recent trends and extrapolation to extinction. *Aquatic Conservation: Marine and Freshwater Ecosystems*. doi: 10.1002/aqc.2609.
- Hare, S.R., and N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47(2):103-145.
- Harris, C.M., and L. Thomas. 2015. *Status and Future of Research on the Behavioral Responses of Marine Mammals to U.S. Navy Sonar*. CREEM Technical Report 2015-3, University of St. Andrews. Available at <http://hdl.handle.net/10023/7741>.
- Harris, C.M., D. Sadykova, S.L. DeRuiter, P.L. Tyack, P.J.O. Miller, P.H. Kvadshem, F.P.A. Lam, and L. Thomas. 2015. Dose response severity functions for acoustic disturbance in cetaceans using recurrent event survival analysis. *Ecosphere* 6(11):236.
- Hart, L.B., D.S. Rotstein, R.S. Wells, J. Allen, A. Barleycorn, B.C. Balmer, S.M. Lane, T. Speakman, E.S. Zolman, M. Stolen, W. McFee, T. Goldstein, T.K. Rowles, and L. Schwacke. 2012. Skin lesions on common bottlenose dolphins (*Tursiops truncatus*) from three sites in the Northwest Atlantic, USA. *PLoS ONE* 7(3):e33081.
- Harvell, C.D., C.E. Mitchell, J.R. Ward, S. Altizer, A.P. Dobson, R.S. Ostfeld, and M.D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296(5576):2158-2162.
- Harvey, B.P., D. Gwynn-Jones, and P.J. Moore. 2013. Meta-analysis reveals complex marine biological responses to the interactive effects of ocean acidification and warming. *Ecology and Evolution* 3(4):1016-1030.
- Harvey, P.W. 2016. Adrenocortical endocrine disruption. *Journal of Steroid Biochemistry and Molecular Biology* 155:199-206.
- Harwood, J. 1992. Assessing the competitive effects of marine mammal predation on commercial fisheries. *South African Journal of Marine Science* 12(1):689-693.
- Harwood, J. 2001. Marine mammals and their environment in the twenty-first century. *Journal of Mammalogy* 82(3):630-640.
- Harwood, L.A., T.G. Smith, and H. Melling. 2000. Variation in reproduction and body condition of the ringed seal (*Phoca hispida*) in western Prince Albert Sound, NT, Canada, as assessed through a harvest-based sampling program. *Arctic* 53(4):422-431.
- Hatch, L.T., C.W. Clark, S.M. Van Parijs, A.S. Frankel, and D.W. Ponirakis. 2012. Quantifying loss of acoustic communication space for right whales in and around a U.S. National Marine Sanctuary. *Conservation Biology* 26:983-994.
- Heithaus, M.R. 2001. Shark attacks on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: Attack rate, bite scar frequencies, and attack seasonality. *Marine Mammal Science* 17(3):526-539.
- Hildebrand, J.A. 2009. Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series* 395:5-20.
- Hobbs, R.C., D.J. Rugh, and D.P. DeMaster. 2000. Abundance of belugas, *Delphinapterus leucas*, in Cook Inlet, Alaska. 1994-2000. *Marine Fisheries Review* 62:37-45.
- Hohn, A.A., M.D. Scott, R.S. Wells, J.C. Sweeney, and A.B. Irvine. 1989. Growth layers in teeth from known-age, free-ranging bottlenose dolphins. *Marine Mammal Science* 5(4):315-342.
- Holt, M.M., D.P. Noren, V. Veirs, C.K. Emmons, and S. Veirs. 2009. Speaking up: Killer whales (*Orcinus orca*) increase their call amplitude in response to vessel noise. *Journal of the Acoustical Society of America* 125:EL27.
- Holt, M.M., D.P. Noren, R.C. Dunkin, and T.M. Williams. 2015. Vocal performance affects metabolic rate in dolphins: Implications for animals communicating in noisy environments. *Journal of Experimental Biology* 218:1647-1654.
- Hooker, S.K., I.L. Boyd, M. Jessopp, O. Cox, J. Blackwell, P.L. Boveng, and J.L. Bengtson. 2002. Monitoring the prey-field of marine predators: Combining digital imaging with datalogging tags. *Marine Mammal Science* 18(3):680-697.

- Hooker, S.K., A. Fahlman, M.J. Moore, N. Aguilar de Soto, Y. Bernaldo de Quirós, A.O. Brubakk, D.P. Costa, A.M. Costidis, S. Dennison, K.J. Falke, A. Fernandez, M. Ferrigno, J.R. Fitz-Clarke, M.M. Garner, D.S. Houser, P.D. Jepson, D.R. Ketten, P.H. Kvasdheim, P.T. Madsen, N.W. Pollock, D.S. Rotstein, T.K. Rowles, S.E. Simmons, W. Van Bonn, P.K. Weathersby, M.J. Weise, T.M. Williams, and P.L. Tyack. 2012. Deadly diving? Physiological and behavioural management of decompression stress in diving mammals. *Proceedings of the Royal Society B: Biological Sciences* 279(1731):1041-1050.
- Horning, M. and R.D. Hill. 2005. Designing an archival satellite transmitter for life-long deployments on oceanic vertebrates: The life history transmitter. *IEEE Journal of Oceanic Engineering* 30(4):807-817.
- Horning, M., and J.A.E. Mellish. 2014. In cold blood: Evidence of Pacific sleeper shark (*Somniosus pacificus*) predation on Steller sea lions (*Eumetopias jubatus*) in the Gulf of Alaska. Available at <http://hdl.handle.net/1957/54605>.
- Horning, M., M. Haulena, P.A. Tuomi, and J.A.E. Mellish. 2008. Intraperitoneal implantation of life-long telemetry transmitters in otariids. *BMC Veterinary Research* 4:51.
- Houde, M., P.F. Hoekstra, K.R. Solomon, and D.C. Muir. 2005. Organohalogen contaminants in delphinoid cetaceans. *Reviews of Environmental Contamination and Toxicology* 184:1-57.
- Houde, M., G. Pacepavicius, C. Darling, P.A. Fair, M. Alae, G.D. Bossart, K.R. Solomon, R.J. Letcher, A. Bergman, G. Marsh, and D.C. Muir. 2009. Polybrominated diphenyl ethers and their hydroxylated analogs in plasma of bottlenose dolphins (*Tursiops truncatus*) from the United States east coast. *Environmental Toxicology and Chemistry* 28(10):2061-2068.
- Houser, D.S., D.A. Helweg, and P.W.B. Moore. 2001. A bandpass filter-bank model of auditory sensitivity in the humpback whale. *Aquatic Mammals* 27:82-91.
- Houser, D.S., S.W. Martin, and J.J. Finneran. 2013a. Behavioral responses of California sea lions to mid-frequency (3250-3450 Hz) sonar signals. *Marine Environmental Research* 92:268-278.
- Houser, D.S., S.W. Martin, and J.J. Finneran. 2013b. Exposure amplitude and repetition affect bottlenose dolphin behavioral responses to simulated mid-frequency sonar signals. *Journal of Experimental Marine Biology and Ecology* 443:123-133.
- Hua, F., K.E. Sieving, R.J. Fletcher, and C.A. Wright. 2014. Increased perception of predation risk to adults and offspring alters avian reproductive strategy and performance. *Behavioral Ecology* 25:509-519.
- Huang, S.-L., L.-S. Chou, N.-T. Shih, and I.-H Ni. 2011. Implication of life history strategies for prenatal investment in cetaceans. *Marine Mammal Science* 27:182-194. doi: 10.1111/j.1748-7692.2010.00392.x.
- Huber, M., J.A. Knottnerus, L. Green, H. van der Horst, A.R. Jadad, D. Kromhout, B. Leonard, K. Lorig, M.I. Loureiro, J.W. van der Meer, P. Schnabel, R. Smith, C. van Weel, and H. Smid. 2011. How should we define health? *British Medical Journal* 343(7817):235-237.
- Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265(5178):1547-1551.
- Hunsicker, M.E., C.V. Kappel, K.A. Selkoe, B.S. Halpern, C. Scarborough, L. Mease, and A. Amrhein. 2016. Characterizing driver-response relationships in marine pelagic ecosystems for improved ocean management. *Ecological Applications* 26(3):651-663.
- Hunt, K.E., M.J. Moore, R.M. Rolland, N.M. Kellar, A.J. Hall, J. Kershaw, S.A. Raverty, C.E. Davis, L.C. Yeates, D.A. Fauquier, T.K. Rowles, and S.D. Kraus. 2013. Overcoming the challenges of studying conservation physiology in large whales: A review of available methods. *Conservation Physiology* 1:1-24.
- Hunt, K.E., R. Stimmelmayer, C. George, C. Hanns, R. Suydam, H. Brower, and R.M. Rolland. 2014. Baleen hormones: A novel tool for retrospective assessment of stress and reproduction in bowhead whales (*Balaena mysticetus*). *Conservation Physiology* 2(1):cou030.
- Hyrenbach, K.D., K.A. Forney, and P.K. Dayton. 2000. Marine protected areas and ocean basin management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 10:437-458.
- Inoue, Y., T. Itou, T. Sakai, and T. Oike. 1999. Cloning and sequencing of a bottle-nosed dolphin (*Tursiops truncatus*) interleukin-4-encoding cDNA. *Journal of Veterinary Medical Science* 61(6):693-696.
- IOM (Institute of Medicine) and NRC (National Research Council). 2009. *Sustaining Global Surveillance and Response to Emerging Zoonotic Diseases*. Washington, DC: The National Academies Press.
- Isaksson, C., B.C. Sheldon, and T. Uller. 2011. The challenges of integrating oxidative stress into life-history biology. *BioScience* 61(3):194-202.
- Isojunno, S., C. Curé, P.H. Kvasdheim, F.-P.A. Lam, P.L. Tyack, P.J. Wensveen, and P.J.O. Miller. 2016. Sperm whales reduce foraging effort during exposure to 1–2 kHz sonar and killer whale sounds. *Ecological Applications* 26(1):77-93.
- Jackson, M.C., C.J. Loewen, R.D. Vinebrooke, and C.T. Chimimba. 2016. Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology* 22(1):180-189.
- Jacobson, J.L. and S.W. Jacobson. 1996. Intellectual impairment in children exposed to polychlorinated biphenyls in utero. *New England Journal of Medicine* 335:783-789.
- Jadad, A.R., and L. O'Grady. 2008. How should health be defined? *British Medical Journal* 337(7683):1363-1364.
- Jefferson, T.A., and B.E. Curry. 1996. Acoustic methods of reducing or eliminating marine mammal interactions with fisheries: Do they work? *Ocean & Coastal Management* 31(1):41-70.
- Jefferson, T.A., P.J. Stacey, and R.W. Baird. 1991. A review of killer whale interactions with other marine mammals: Predation to co-existence. *Mammal Review* 21(4):151-180.
- Jensen, S.-K., J.-P. Lacaze, G. Hermann, J. Kershaw, A. Brownlow, A. Turner, and A.J. Hall. 2015. Detection and effects of harmful algal toxins in Scottish harbour seals and potential links to population decline. *Toxicol* 97:1-14.
- Jenssen, B.M. 2006. Endocrine-disrupting chemicals and climate change: A worst-case combination for arctic marine mammals and seabirds? *Environmental Health Perspectives* 114(Suppl. 1):76-80.
- Jepson, P.D., M. Arbelo, R. Deaville, I.A.P. Patterson, P. Castro, J.R. Baker, E. Degollada, H.M. Ross, P. Herraes, A.M. Pocknell, F. Rodriguez, F.E. Howiell, A. Espinosa, R.J. Reid, J.R. Jaber, V. Martin, A.A. Cunningham, and A. Fernández. 2003. Gas-bubble lesions in stranded animals: Was sonar responsible for a spate of whale deaths after an Atlantic military exercise? *Nature* 425(6958):575-576.
- Jepson, P.D., P.M. Bennett, R. Deaville, C.R. Allchin, J.R. Baker, and R.J. Law. 2005. Relationships between polychlorinated biphenyls and health status in harbor porpoises (*Phocoena phocoena*) stranded in the United Kingdom. *Environmental Toxicology and Chemistry* 24(1):238-248.
- Jewell, R., L. Thomas, C.M. Harris, K. Kaschner, R. Wiff, P.S. Hammond, and N.J. Quick. 2012. Global analysis of cetacean line-transect surveys: Detecting trends in cetacean density. *Marine Ecology Progress Series* 453:227-240.
- Jiang, M., M.W. Brown, J.T. Turner, R.D. Kenney, C.A. Mayo, Z. Zhang, and M. Zhou. 2007. Springtime transport and retention of *Calanus finmarchicus* in Massachusetts and Cape Cod Bays, USA, and implications for right whale foraging. *Marine Ecology Progress Series* 349:183-197.
- Johnson, A.C., P. Nylén, E. Borg, and G. Hoglund. 1990. Sequence of exposure to noise and toluene can determine loss of auditory sensitivity in the rat. *Acta Otolaryngologica* 109:34-40.
- Johnson, C.K., M.T. Tinker, J.A. Estes, P.A. Conrad, M. Staedler, M.A. Miller, D.A. Jessup, and J.A.K. Mazet. 2009. Prey choice and habitat use drive sea otter pathogen exposure in a resource-limited coastal system. *Proceedings of the National Academy of Sciences of the United States of America* 106(7):2242-2247.
- Johnson, M., and P.L. Tyack. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering* 28:3-12.
- Kajiwara, N., S. Kamikawa, K. Ramu, D. Ueno, T.K. Yamada, A. Subramanian, P.K. Lam, T.A. Jefferson, M. Prudente, K.H. Chung, and S. Tanabe. 2006. Geographical distribution of polybrominated diphenyl ethers (PBDEs) and organochlorines in small cetaceans from Asian waters. *Chemosphere* 64:287-295.



- Kakuschke, A., and A. Prange. 2007. The influence of metal pollution on the immune system a potential stressor for marine mammals in the North Sea. *International Journal of Comparative Psychology* 20:179-193.
- Karl, D.M., R. Letelier, D. Hebel, L. Tupas, J. Dore, J. Christian, and C. Winn. 1995. Ecosystem changes in the North Pacific subtropical gyre attributed to the 1991–92 El Niño. *Nature* 373:230-234.
- Kastak, D., J. Mulsow, A. Ghoul, and C. Reichmuth. 2008. Noise-induced permanent threshold shift in a harbor seal. *Journal of the Acoustical Society of America* 123:2986.
- Kastelein, R.A., N. Steen, C. de Jong, P.J. Wensveen, and W.C. Verboom. 2011. Effect of broadband-noise masking on the behavioral response of a harbor porpoise (*Phocoena phocoena*) to 1-s duration 6–7 kHz sonar up-sweeps. *Journal of the Acoustical Society of America* 129:2307-2315.
- Kastelein, R.A., N. Steen, R. Gransier, P.J. Wensveen, and C.A.F. de Jong. 2012. Threshold received sound pressure levels of single 1–2 kHz and 6–7 kHz up-sweeps and down-sweeps causing startle responses in a harbor porpoise (*Phocoena phocoena*). *Journal of the Acoustical Society of America* 131:2325-2333.
- Kastelein, R.A., R. Gransier, M. van den Hoogen, and L. Hoek. 2013. Brief behavioral response threshold levels of a harbor porpoise (*Phocoena phocoena*) to five helicopter dipping sonar signals (1.33 to 1.43 kHz). *Aquatic Mammals* 39:162-173.
- Keenan, R.E. 2000. An introduction to GRAB eigenrays and CASS reverberation and signal excess. Pp. 1065-1070 in *Oceans 2000 MTS/IEEE Conference & Exhibition, Volume 2*. New York: IEEE.
- Kellar, N.M., M.L. Trego, C.I. Marks, and A.E. Dizon. 2006. Determining pregnancy from blubber in three species of delphinids. *Marine Mammal Science* 22:1-16.
- Kenet, T., R.C. Froemke, C.E. Schreiner, I.N. Pessah, and M.M. Merzenich. 2007. Perinatal exposure to a noncoplanar polychlorinated biphenyl alters tonotopy, receptive fields, and plasticity in rat primary auditory cortex. *Proceedings of the National Academy of Sciences of the United States of America* 104(18):7646-7651.
- Ketten, D.R., J. Lien, and S. Todd. 1993. Blast injury in humpback whale ears: Evidence and implication. *Journal of the Acoustical Society of America* 94:1849-1850.
- Khudyakov, J.I., C.D. Champagne, L. Preeyanon, R.M. Ortiz, and D.E. Crocker. 2015. Muscle transcriptome response to ACTH administration in a free-ranging marine mammal. *Physiological Genomics* 47(8):318-330.
- Kight, C.R., M.S. Saha, and J.P. Swaddle. 2012. Anthropogenic noise is associated with reductions in the productivity of breeding eastern bluebirds (*Sialia sialis*). *Ecological Applications* 22:1989-1996.
- Killen, S.S., S. Marras, N.B. Metcalfe, D.J. McKenzie, and P. Domenici. 2013. Environmental stressors alter relationships between physiology and behaviour. *Trends in Ecology and Evolution* 28:623-680.
- Kindig, D., and G. Stoddart. 2003. What is population health? *American Journal of Public Health* 93(3):380-383.
- King, D.P., M.D. Schrenzel, M.L. McKnight, T.H. Reidarson, K.D. Hanni, J.L. Stott, and D.A. Ferrick. 1996. Molecular cloning and sequencing of interleukin 6 cDNA fragments from the harbor seal (*Phoca vitulina*), killer whale (*Orcinus orca*), and Southern sea otter (*Enhydra lutris nereis*). *Immunogenetics* 43(4):190-195.
- King, D.P., J.L. Sanders, C.T. Nomura, R.A. Stoddard, C.L. Ortiz, and S.W. Evans. 1998. Ontogeny of humoral immunity in northern elephant seal (*Mirounga angustirostris*) neonates. *Comparative Biochemistry and Physiology B* 121:363-368.
- King, S.L., R.S. Schick, C. Donovan, C.G. Booth, M. Burgman, L. Thomas, and J. Harwood. 2015. An interim framework for assessing the population consequences of disturbance. *Methods in Ecology and Evolution* 6:1150-1158.
- Kitaysky, A., J. Piatt, and J. Wingfield. 2007. Stress hormones link food availability and population processes in seabirds. *Marine Ecology Progress Series* 352:245-258.
- Klein, S.C., and M.E. Peterson. 2010. Canine hypoadrenocorticism: Part 1. *Canine Veterinary Journal* 51:63-69.
- Knowlton, A.R., P.K. Hamilton, M.K. Marx, H.M. Pettis, and S.D. Kraus. 2012. Monitoring North Atlantic right whale *Eubalaena glacialis* entanglement rates: A 30 year retrospective. *Marine Ecology: Progress Series* 466:293-302.
- Knowlton, N. 2004. Multiple “stable” states and the conservation of marine ecosystems. *Progress in Oceanography* 60(2):387-396.
- Kooyman, G.L. 1985. Physiology without restraint in diving mammals. *Marine Mammal Science* 1(2):166-178.
- Kooyman, G.L., and P.J. Ponganis. 1998. The physiological basis of diving to depth: Birds and mammals. *Annual Review of Physiology* 60(1):19-32.
- Kovacs, K.M., and C. Lydersen. 2008. Climate change impacts on seals and whales in the North Atlantic Arctic and adjacent shelf seas. *Science Progress* 91(2):117-150.
- Kovacs, K.M., C. Lydersen, J.E. Overland, and S.E. Moore. 2011. Impacts of changing sea-ice conditions on Arctic marine mammals. *Marine Biodiversity* 41(1):181-194.
- Kraus, S.D., and R. Rolland. 2007. *The Urban Whale: North Atlantic Right Whales at the Crossroads*. Cambridge, MA: Harvard University Press.
- Kraus, S.D., M.W. Brown, H. Caswell, C.W. Clark, M. Fujiwara, P.K. Hamilton, R.D. Kenney, A.R. Knowlton, S. Landry, C.A. Mayo, W.A. McLellan, M.J. Moore, D.P. Nowacek, D.A. Pabst, A.J. Read, and R.M. Rolland. 2005. North Atlantic right whales in crisis. *Science* 309:561-562.
- Kucklick, J., L. Schwacke, R. Wells, A. Hohn, A. Guichard, J. Yordy, L. Hansen, E. Zolman, R. Wilson, J. Litz, D. Nowacek, T. Rowles, R. Pugh, B. Balmer, C. Sinclair, and P. Rosel. 2011. Bottlenose dolphins as indicators of persistent organic pollutants in the western North Atlantic Ocean and northern Gulf of Mexico. *Environmental Science & Technology* 45:4270-4277.
- Kuehl, D.W., R. Haebler, and C. Potter. 1991. Chemical residues in dolphins from the United States Atlantic Coast including Atlantic bottlenose obtained during the 1987/88 mass mortality. *Chemosphere* 22:1071-1084.
- Kuitunen, M., E. Rossi, and A. Stenroos. 1998. Do highways influence density of land birds? *Environmental Management* 22:297-302.
- Kujawa, S.G., and M.C. Liberman. 2006. Acceleration of age-related hearing loss by early noise exposure: Evidence of a misspent youth. *Journal of Neuroscience* 26(7):2115-2123.
- Kvadsheim, P.H., P.J.O. Miller, P.L. Tyack, L.D. Sivle, F.P.A. Lam, and A. Fahlman. 2012. Estimated tissue and blood N<sub>2</sub> levels and risk of in vivo bubble formation in deep-, intermediate- and shallow diving toothed whales during exposure to naval sonar. *Frontiers in Aquatic Physiology* 3(125):1-14.
- Lafferty, K.D., J.W. Porter, and S.E. Ford. 2004. Are diseases increasing in the ocean? *Annual Review of Ecology, Evolution, and Systematics* 35:31-54.
- Lagardère, J.P. 1982. Effects of noise on growth and reproduction of *Crangon crangon* in rearing tanks. *Marine Biology* 71(2):177-185.
- Laidre, K.L., H. Stern, K.M. Kovacs, L. Lowry, S.E. Moore, E.V. Regehr, S.H. Ferguson, Ø.Wiig, P. Boveng, R.P. Angliss, E.W. Born, D. Litovka, L. Quakenbush, C. Lydersen, D. Vongraven, and F. Ugarte. 2015. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology* 29:724-737.
- Laist, D.W., A.R. Knowlton, J.G. Mead, A.S. Collet, and M. Podesta. 2001. Collisions between ships and whales. *Marine Mammal Science* 17:35-75.
- Lane, S.M., C.R. Smith, J. Mitchell, B.C. Balmer, K.P. Barry, T. McDonald, C.S. Mori, P.E. Rosel, T.K. Rowles, T.R. Speakman, and F.I. Townsend. 2015. Reproductive outcome and survival of common bottlenose dolphins sampled in Barataria Bay, Louisiana, USA, following the Deepwater Horizon oil spill. *Proceedings of the Royal Society B: Biological Sciences* 282(1818):20151944.
- Lataye, R., and P. Campo. 1997. Combined effects of a simultaneous exposure to noise and toluene on hearing function. *Neurotoxicology Teratology* 19:373-382.

## REFERENCES

- Lataye, R., P. Campo, and G. Loquet. 2000. Combined effects of noise and styrene exposure on hearing function in the rat. *Hearing Research* 139:86-96.
- Le Boeuf, B.J., and D.E. Crocker. 2005. Ocean climate and seal condition. *BMC Biology* 3(1):1.
- Leeper, R., J. Cooke, P. Trathan, K. Reid, V. Rowntree, and R. Payne. 2006. Global climate drives southern right whale (*Eubalaena australis*) population dynamics. *Biology Letters* 2(2):289-292.
- Lercher, P., G.W. Evans, and M. Meis. 2003. Ambient noise and cognitive processes among primary schoolchildren. *Environment and Behavior* 35:725-735.
- Levin, M., S. De Guise, and P.S. Ross. 2005. Association between lymphocyte proliferation and polychlorinated biphenyls in free-ranging harbor seal (*Phoca vitulina*) pups from British Columbia, Canada. *Environmental Toxicology and Chemistry* 24(5):1247-1252.
- Levin, P.S., and C. Möllmann. 2015. Marine ecosystem regime shifts: Challenges and opportunities for ecosystem-based management. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 370(1659): 20130275.
- Levin, P.S., M.J. Fogarty, S.A. Murawski, and D. Fluharty. 2009. Integrated ecosystem assessments: Developing the scientific basis for ecosystem-based management of the ocean. *PLoS ONE Biology* 7(1):e1000014.
- Levin, P.S., C.R. Kelble, R.L. Shuford, C. Ainsworth, R. Dunsmore, M.J. Fogarty, K. Holsman, E.A. Howell, M.E. Monaco, S.A. Oakes, and F. Werner. 2014. Guidance for implementation of integrated ecosystem assessments: A US perspective. *ICES Journal of Marine Science* 71(5):1198-1204.
- Lewisohn, R.L., L.B. Crowder, B.P. Wallace, J.E. Moore, T. Cox, R. Zydulis, S. McDonald, A. DiMatteo, D.C. Dunn, C.Y. Kot, and R. Bjorkland. 2014. Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. *Proceedings of the National Academy of Sciences of the United States of America* 111(14):5271-5276.
- Lewontin, R.C. 1969. The meaning of stability. Pp. 13-24 in *Diversity and Stability in Ecological Systems*, G.W. Woodwell and H.H. Smith, eds. Upton, NY: Brookhaven National Laboratory.
- Lie, E., H.J. Larsen, S. Larsen, G.M. Johansen, A.E. Derocher, N.J. Lunn, R.J. Norstrom, Ø. Wiig, and J.U. Skaare. 2004. Does high organochlorine (OC) exposure impair the resistance to infection in polar bears (*Ursus maritimus*)? Part I: Effect of OCs on the humoral immunity. *Journal of Toxicology and Environmental Health A* 67(7):555-582.
- Lie, E., H.J. Larsen, S. Larsen, G.M. Johansen, A.E. Derocher, N.J. Lunn, R.J. Norstrom, Ø. Wiig, and J.U. Skaare. 2005. Does high organochlorine (OC) exposure impair the resistance to infection in polar bears (*Ursus maritimus*)? Part II: Possible effect of OCs on mitogen- and antigen-induced lymphocyte proliferation. *Journal of Toxicology and Environmental Health A* 68(6):457-484.
- Lilienthal, H., P. Heikkinen, P.L. Andersson, L.T.M. van der Ven, and M. Viluksela. 2011. Auditory effects of developmental exposure to purity-controlled polychlorinated biphenyls (PCB52 and PCB180) in rats. *Toxicological Sciences* 122(1):100-111.
- Lindenmayer, D.B., and G.E. Likens. 2009. Adaptive monitoring: A new paradigm for long-term research and monitoring. *Trends in Ecology & Evolution* 24:482-486.
- Lioy, P.J., and S.M. Rappaport. 2011. Exposure science and the exposome: An opportunity for coherence in the environmental health sciences. *Environmental Health Perspectives* 119(11):A466-A467.
- Lochmiller, R.L., and C. Deerenberg. 2000. Trade-offs in evolutionary immunology: Just what is the cost of immunity? *Oikos* 88(1):87-98.
- Logan, D.C. 2009. Known knowns, known unknowns, unknown unknowns and the propagation of scientific enquiry. *Journal of Experimental Botany* 60(3):712-714.
- Løkkeborg, S., E. Ona, A. Vold, and A. Salthaug. 2012. Sounds from seismic air guns: Gear- and species-specific effects on catch rates and fish distribution. *Canadian Journal of Fisheries and Aquatic Science* 69(8):1278-1291.
- Loneragan, M., C.D. Duck, D. Thompson, B.L. Mackey, L. Cunningham, and I.L. Boyd. 2007. Using sparse survey data to investigate the declining abundance of British harbour seals. *Journal of Zoology* 271:261-269.
- Lucke, K., U. Siebert, P.A. Lepper, and M. A. Blanchet. 2009. Temporary shift in masked hearing thresholds in a harbor porpoise (*Phocoena phocoena*) after exposure to seismic airgun stimuli. *Journal of the Acoustical Society of America* 125:4060-4070.
- Luebke, R.W., C. Parks, and M.I. Luster. 2004. Suppression of immune function and susceptibility to infections in humans: Association of immune function with clinical disease. *Journal of Immunotoxicology* 1(1):15-24.
- Lundquist, D., M. Sironi, B. Würsig, V. Rowntree, J. Martino, and L. Lundquist. 2013. Response of southern right whales to simulated swim-with-whale tourism at Península Valdés, Argentina. *Marine Mammal Science* 29(2):E24-E45.
- Lusseau, D., and L. Bejder. 2007. The long-term consequences of short-term responses to disturbance experiences from whalewatching impact assessment. *International Journal of Comparative Psychology* 20:228-236.
- Lusseau, D., E. Slooten, and R.J.C. Currey. 2006. Unsustainable dolphin-watching tourism in Fiordland, New Zealand. *Tourism in Marine Environments* 3:173-178.
- Lusseau, D., L. New, C. Donovan, B. Cheney, G. Hastie, and J. Harwood. 2012. *The Development of a Framework to Understand and Predict the Population Consequences of Disturbances for the Moray Firth Bottlenose Dolphin Population*. Scottish Natural Heritage Commissioned Report No. 468. Available at [http://www.snh.org.uk/pdfs/publications/commissioned\\_reports/468.pdf](http://www.snh.org.uk/pdfs/publications/commissioned_reports/468.pdf).
- Madsen, P.T., B. Møhl, B.K. Nielsen, and M. Wahlberg. 2002. Male sperm whale behaviour during exposures to distant seismic survey pulses. *Aquatic Mammals* 28(3):231-240.
- Madsen, P.T., M. Wahlberg, J. Tougaard, K. Lucke, and P. Tyack. 2006. Wind turbine underwater noise and marine mammals: Implications of current knowledge and data needs. *Marine Ecology: Progress Series* 309:279-295.
- Mäkitie, A.A., U. Pirvola, I. Pyykkö, H. Sakakibara, V. Riihimäki, and J. Ylikoski. 2003. The ototoxic interaction of styrene and noise. *Hearing Research* 179(1-2):9-20.
- Malme, C.I., P.R. Miles, C.W. Clark, P. Tyack, and J.E. Bird. 1983. *Investigations of the Potential Effects of Underwater Noise from Petroleum Industry Activities on Migrating Gray Whale Behavior*. Report No. 5366. Prepared by: Bolt Beranek and Newman Inc. for Minerals Management Service Alaska OCS Office. NTIS PB86-174174. <https://ntrl.ntis.gov/NTRL>.
- Malme, C.I., P.R. Miles, C.W. Clark, P. Tyack, and J.E. Bird. 1984. *Investigations of the Potential Effects of Underwater Noise from Petroleum Industry Activities on Migrating Gray Whale Behavior*. Phase II: January 1984 Migration. Report No. 5586. Prepared by Bolt Beranek and Newman Inc. for Minerals Management Service Alaska OCS Office. NTIS PB86-218377. <https://ntrl.ntis.gov/NTRL>.
- Mancia, A., M.L. Lundqvist, T.A. Romano, M.M. Peden-Adams, P.A. Fair, M.S. Kindy, B.C. Ellis, S. Gattoni-Celli, D.J. McKillen, H.F. Trent, Y.A. Chen, J.S. Almeida, P.S. Gross, R.W. Chapman, and G.W. Warr. 2007. A dolphin peripheral blood leukocyte cDNA microarray for studies of immune function and stress reactions. *Developmental & Comparative Immunology* 31(5):520-529.
- Mann, D. A., Z. Lu, M.C. Hastings, and A.N. Popper. 1998. Detection of ultrasonic tones and simulated dolphin echolocation clicks by a teleost fish, the American shad (*Alosa sapidissima*). *Journal of the Acoustical Society of America* 104(1):562-568.
- Marques, T.A., L. Thomas, S.W. Martin, D.K. Mellinger, J.A. Ward, D.J. Moretti, D. Harris, and P.L. Tyack. 2013. Estimating animal population density using passive acoustics. *Biological Reviews* 88(2):287-309.
- Martin, L.B., E. Andreassi, W. Watson, and C. Coon. 2011. Stress and animal health: Physiological mechanisms and ecological consequences. *Nature Education Knowledge* 3(6):11.

- Martin, T., M. Burgman, F. Fidler, P. Kuhnert, S. Low-Choy, M. McBride, and K. Mengersen. 2012. Eliciting expert knowledge in conservation science. *Conservation Biology* 26:29-38.
- Martineau, D. 2007. Potential synergism between stress and contaminants in free-ranging cetaceans. *International Journal of Comparative Psychology* 20:194-216.
- Mason, J.T., C.J.W. McClure, and J.R. Barber. 2016. Anthropogenic noise impairs owl hunting behavior. *Biological Conservation* 199: 29-32.
- Mate, B., R. Mesecar, and B. Lagerquist. 2007. The evolution of satellite-monitored radio tags for large whales: One laboratory's experience. *Deep Sea Research, Part II: Topical Studies in Oceanography* 54(3): 224-247.
- Matthiopoulos, J., S.C. Smout, A. Winship, D. Thompson, I.L. Boyd, and J. Harwood. 2008. Getting beneath the surface of marine mammal-fisheries competition. *Mammal Review* 38(2-3):167-188.
- Matthiopoulos, J., L. Cordes, B. Mackey, D. Thompson, C. Duck, S. Smout, M. Caillat, and P. Thompson. 2014. State-space modeling reveals proximate causes of harbour seal population declines. *Oecologia* 174:151-162.
- Maxwell, S.M., E.L. Hazen, S.J. Bograd, B.S. Halpern, G.A. Breed, B. Nickel, N.M. Teutschel, L.B. Crowder, S. Benson, P.H. Dutton, H. Bailey, M.A. Kappes, C.E. Kuhn, M.J. Weise, B. Mate, S.A. Shaffer, J.L. Hassrick, R.W. Henry, L. Irvine, B.I. McDonald, P.W. Robinson, and D.P. Costa. 2013. Cumulative human impacts on marine predators. *Nature Communications* 4:2688.
- May, R.M. 1972. Will a large complex system be stable? *Nature* 238:413-414.
- May, R.M. 1976. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 260:471-477.
- Mazet, J. K., I.A. Gardner, D.A. Jessup, L.J. Lowenstine, and W.M. Boyce. 2000. Evaluation of changes in hematologic and clinical biochemical values after exposure to petroleum products in mink (*Mustela vison*) as a model for assessment of sea otters (*Enhydra lutris*). *American Journal of Veterinary Research* 61:1197-1203.
- McCarthy, E. 2007. *International Regulation of Underwater Sound: Establishing Rules and Standards to Address Ocean Noise Pollution*. New York: Springer.
- McCarthy, E., D. Moretti, L. Thomas, N. DiMarzio, R. Morrissey, S. Jarvis, J. Ward, A. Izzi, and A. Dilley. 2011. Changes in spatial and temporal distribution and vocal behavior of Blainville's beaked whales (*Mesoplodon densirostris*) during multiship exercises with mid-frequency sonar. *Marine Mammal Science* 27:E206-E226.
- McCauley, R.D., J. Fewtrell, A.J. Duncan, C. Jenner, M.N. Jenner, J.D. Penrose, R.I.T. Prince, A. Adhitya, J. Murdoch, and K. McCabe. 2000. Marine seismic surveys—a study of environmental implications. *APPEA Journal* 40:692-708.
- McCauley, R.D., J. Fewtrell, and A.N. Popper. 2003. High intensity anthropogenic sound damages fish ears. *Journal of the Acoustical Society of America* 113:638. doi: 10.1121/1.1527962.
- McClure, C.J., H.E. Ware, J. Carlisle, G. Kaltenecker, and J.R. Barber. 2013. An experimental investigation into the effects of traffic noise on distributions of birds: Avoiding the phantom road. *Proceedings of the Royal Society B: Biological Sciences* 280(1773):20132290.
- McDonald, B.I., and P.J. Ponganis. 2012. Lung collapse in the diving sea lion: Hold the nitrogen and save the oxygen. *Biology Letters*. doi: 10.1098/rsbl.2012.0743.
- McEwen, B.S. 1998. Stress, adaptation, and disease—allotaxis and allostasis load. Pp. 33-44 in *Neuroimmunomodulation*, W. Aerpauli and N.H. Specter, eds. New York: New York Academy of Sciences.
- McEwen, B.S., and J.C. Wingfield. 2003. The concept of allostasis in biology and biomedicine. *Hormones and Behavior* 43:2-15.
- McMahon, C.R., H.R. Burton, and M.N. Bester. 2000. Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science* 12:149-153.
- McMahon, C.R., H.R. Burton, and M.N. Bester. 2003. A demographic comparison of two elephant seal populations. *Journal of Animal Ecology* 72:61-74.
- Meegan, J., J.L. Dunn, S.K. Venn-Watson, C.R. Smith, I. Sidor, E.D. Jensen, W.G. Van Bonn, R. Pugh, T. Ficht, L.G. Adams, and K. Nielsen. 2012. Serologic response in bottlenose dolphins (*Tursiops truncatus*) infected with *Brucella* sp. using a dolphin-specific indirect ELISA. *Diseases of Aquatic Organisms* 102:73-85.
- Meir, J.U., C.D. Champagne, D.P. Costa, C.L. Williams, and P.J. Ponganis. 2009. Extreme hypoxic tolerance and blood oxygen depletion in diving elephant seals. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology* 297(4):R927-R939.
- Mellinger, D.K., and C.W. Clark. 2003. Blue whale (*Balaenoptera musculus*) sounds from the North Atlantic. *Journal of the Acoustical Society of America* 114:1108-1119.
- Mennitt, D., K.M. Fristrup, K. Sherrill, and L. Nelson. 2013. Mapping sound pressure levels on continental scales using a geospatial sound model. *Proceedings of Inter-Noise*. Innsbruck, Austria, September 15-18, 2013. 11 pp.
- Metcalfe, N.B., and C. Alonso-Alvarez. 2010. Oxidative stress as a life-history constraint: The role of reactive oxygen species in shaping phenotypes from conception to death. *Functional Ecology* 24(5):984-996.
- Meyer-Gutbrod, E.L., C.H. Greene, P.J. Sullivan, and A.J. Pershing. 2015. Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population. *Marine Ecology: Progress Series* 535:243-258.
- Miksis-Olds, J.L., and S.M. Nichols. 2016. Is low frequency ocean sound increasing globally? *Journal of the Acoustical Society of America* 139(1):501-511.
- Miller, C.A., P.B. Best, W.L. Perryman, M.F. Baumgartner, and M.J. Moore. 2012b. Body shape changes associated with reproductive status, nutritive condition and growth in right whales *Eubalaena glacialis* and *E. australis*. *Marine Ecology: Progress Series* 459:135-136.
- Miller, P.J.O., N. Biassoni, A. Samuels, and P.L. Tyack. 2000. Whale songs lengthen in response to sonar. *Nature* 405:903.
- Miller, P.J.O., M.P. Johnson, and P.L. Tyack. 2004a. Sperm whale behaviour indicates the use of echolocation click buzzes "creaks" in prey capture. *Proceedings of the Royal Society B: Biological Sciences* 271(1554):2239-2247.
- Miller, P.J.O., M.P. Johnson, P.L. Tyack, and E.A. Terray. 2004b. Swimming gaits, passive drag, and buoyancy of diving sperm whales *Physeter macrocephalus*. *Journal of Experimental Biology* 207:1953-1967.
- Miller, P.J.O., M.P. Johnson, P.T. Madsen, N. Biassoni, M.E. Quero, and P.L. Tyack. 2009. Using at-sea experiments to study the effects of air-guns on the foraging behavior of sperm whales in the Gulf of Mexico. *Deep-Sea Research* 56:1168-1181.
- Miller, P.J.O., R. Antunes, A. C. Alves, P. Wensveen, P. Kvadsheim, L. Kleivane, N. Nordlund, F.-P. Lam, S. van IJsselmuide, F. Visser, and P. Tyack. 2011. *The 35 Experiments: Studying the Behavioural Effects of Naval Sonar on Killer Whales (Orcinus orca), Sperm Whales (Physeter macrocephalus), and Long-Finned Pilot Whales (Globicephala melas) in Norwegian Waters*. Scottish Oceans Institute Technical Report SOI-2011-001.
- Miller, P.J.O., P.H. Kvadsheim, F.P.A. Lam, P.J. Wensveen, R. Antunes, A.C. Alves, F. Visser, L. Kleivane, P.L. Tyack, and L. Doksæter. 2012a. The severity of behavioral changes observed during experimental exposures of killer (*Orcinus orca*), long-finned pilot (*Globicephala melas*), and sperm (*Physeter macrocephalus*) whales to naval sonar. *Aquatic Mammals* 38(4):362-401.
- Miller, P.J.O., R.N. Antunes, P.J. Wensveen, F.I.P. Samarra, A.C. Alves, P.L. Tyack, P.H. Kvadsheim, L. Kleivane, F.-P.A. Lam, M.A. Ainslie, and L. Thomas. 2014. Dose-response relationships for the onset of avoidance of sonar by free-ranging killer whales. *Journal of the Acoustical Society of America* 135:975-993.
- Mohr, F.C., B. Lasley, and S. Bursian. 2008. Chronic oral exposure to bunker C fuel oil causes adrenal insufficiency in ranch mink (*Mustela vison*). *Archives of Environmental Contamination and Toxicology* 54:337-347.

- Mohr, F.C., B. Lasley, and S. Bursian. 2010. Fuel oil-induced adrenal hypertrophy in ranch mink (*Mustela vison*): Effects of sex, fuel oil weathering, and response to adrenocorticotrophic hormone. *Journal of Wildlife Diseases* 46(1):103-110.
- Möllmann, C., R. Diekmann, B. Müller-Karulis, G. Kornilovs, M. Plikshs, and P. Axe. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: A discontinuous regime shift in the Central Baltic Sea. *Global Change Biology* 15:1377-1393.
- Monaghan, P., N.B. Metcalfe, and R. Torres. 2009. Oxidative stress as a mediator of life history trade-offs: Mechanisms, measurements and interpretation. *Ecology Letters* 12(1):75-92.
- Montgomery, D.C. 1997. *Design and Analysis of Experiments*. New York: Wiley.
- Mooney, T.A., M. Yamato, and B.K. Branstetter. 2012. Hearing in cetaceans: From natural history to experimental biology. *Advances in Marine Biology* 63:197-246.
- Moore, J.E., and J.P. Barlow. 2013. Declining abundance of beaked whales (family Ziphiidae) in the California current large marine ecosystem. *PLoS ONE* 8(1):e52770. doi: 10.1371/journal.pone.0052770.
- Moore, J.E., and A.J. Read. 2008. A Bayesian uncertainty analysis of cetacean demography and bycatch mortality using age-at-death data. *Ecological Applications* 18(8):1914-1931.
- Moore, M.J., and G.A. Early. 2004. Cumulative sperm whale bone damage and the bends. *Science* 306(5705):2215.
- Moore, M.J., and J.M. van der Hoop. 2012. The painful side of trap and fixed net fisheries: Chronic entanglement of large whales. *Journal of Marine Biology* 2012:230653.
- Moore, S.C., and H.P. Huntington. 2008. Arctic marine mammals and climate change: Impacts and resilience. *Ecological Applications* 18(2 Suppl):s157-165.
- Moore, S.E., K.E.W. Shelden, L.K. Litzky, B.A. Mahoney, and D.J. Rugh. 2000. Beluga, *Delphinapterus leucas*, habitat associations in Cook Inlet, Alaska. *Marine Fisheries Review* 62(3):60-80.
- Morens, D.M., G.K. Folkers, and A.S. Fauci. 2004. The challenge of emerging and re-emerging infectious diseases. *Nature* 430(6996):242-249.
- Moretti, D., L. Thomas, T. Marques, J. Harwood, A. Dilley, B. Neales, J. Shaffer, E. McCarthy, L. New, S. Jarvis, and R. Morrissey. 2014. A risk function for behavioral disruption of Blainville's beaked whales (*Mesoplodon densirostris*) from mid-frequency active sonar. *PLoS ONE* 9:e85064.
- Mori, C., B. Morsey, M. Levin, P.R. Nambiar, and S. De Guise. 2006. Immunomodulatory effects of in vitro exposure to organochlorines on T-cell proliferation in marine mammals and mice. *Journal of Toxicology and Environmental Health A*. 69:283-302.
- Morris, W.F., and D.F. Doak. 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sunderland, MA: Sinauer Associates.
- Morton, A.B., and H.K. Symonds. 2002. Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia, Canada. *ICES Journal of Marine Science* 59(1):71-80.
- Mullin, K.D., K. Barry, C. Sinclair, J. Litz, K. Maze-Foley, E. Fougères, B. Mass-Guthrie, R. Ewing, A. Gorgone, J. Adams, and M. Tumlin. 2015. *Common Bottlenose Dolphins (Tursiops truncatus) in Lake Pontchartrain, Louisiana: 2007 to Mid-2014*. NOAA Technical Memorandum NMFS-SEFSC 673 43.
- Munk, W.H., R.C. Spindel, A. Baggeroer, and T.G. Birdsall. 1994. The Heard Island feasibility test. *Journal of the Acoustical Society of America* 96(4):2330-2342.
- Nabe-Nielsen, J., R.M. Sibby, J. Tougaard, J. Teilmann, and S. Sveegaard. 2014. Effects of noise and by-catch on a Danish harbour porpoise population. *Ecological Modelling* 272:242-251.
- Narayan, E.J., J.F. Cockrem, and J.M. Hero. 2013. Sight of a predator induces a corticosterone stress response and generates fear in an amphibian. *PLoS ONE* 8:e73564.
- New, L.F., J. Harwood, L. Thomas, C. Donovan, J.S. Clark, G. Hastie, P.M. Thompson, B. Cheney, L. Scott-Hayward, and D. Lusseau. 2013a. Modeling the biological significance of behavioural change in coastal bottlenose dolphins in response to disturbance. *Functional Ecology* 27:314-322.
- New, L.F., D.J. Moretti, S.K. Hooker, D.P. Costa, and S.E. Simmons. 2013b. Using energetic models to investigate the survival and reproduction of beaked whales (family Ziphiidae). *PLoS ONE* 8:e68725.
- New, L.F., J.S. Clark, D.P. Costa, E. Fleishman, M.A. Hindell, T. Klanjšček, D. Lusseau, S. Kraus, C.R. McMahon, P.W. Robinson, R.S. Schick, L.K. Schwartz, S.E. Simmons, L. Thomas, P. Tyack, and J. Harwood. 2014. Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. *Marine Ecology Progress Series* 496:99-108.
- New, L.F., A.J. Hall, R. Harcourt, G. Kaufman, E.C.M. Parsons, H.C. Pearson, A.M. Cosentino, and R.S. Schick. 2015. The modeling and assessment of whale-watching impacts. *Ocean and Coastal Management* 115:10-16.
- Newman, A.E.M., L.Y. Zanette, M. Clinchy, N. Goodenough, and K.K. Soma. 2013. Stress in the wild: Chronic predator pressure and acute restraint affect plasma DHEA and corticosterone levels in a songbird. *Stress* 16:363-367.
- Newman, K.B., S.T. Buckland, S.T. Lindley, L. Thomas, and C. Fernandez. 2006. Hidden process models for animal population dynamics. *Ecological Applications* 16(1):74-86.
- Newsome, D., A. Milewski, N. Phillips, and R. Annear. 2002. Effects of horse riding on national parks and other natural ecosystems in Australia: Implications for management. *Journal of Ecotourism* 1(1):52-74.
- Nichols, J.D., and B.K. Williams. 2006. Monitoring for conservation. *Trends in Ecology and Evolution* 21:668-673.
- Nichols, J.W., M. Breen, R.J. Denver, J.J. DiStefano, J.S. Edwards, R.A. Hoke, D.C. Volz, and X. Zhang. 2011. Predicting chemical impacts on vertebrate endocrine systems. *Environmental Toxicology and Chemistry* 30(1):39-51.
- NMFS (National Marine Fisheries Service). 2004. *A Requirements Plan for Improving the Understanding of the Status of U.S. Protected Marine Species: Report of the NOAA Fisheries National Task Force for Improving Marine Mammal and Turtle Stock Assessments*. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-F/SPO-63 112. Available at [http://www.nmfs.noaa.gov/pr/pdfs/sars/improvement\\_plan.pdf](http://www.nmfs.noaa.gov/pr/pdfs/sars/improvement_plan.pdf).
- NMFS. 2008. Recovery Plan for the Steller Sea Lion (*Eumetopias jubatus*). Revision. Silver Spring, MD: National Marine Fisheries Service. 325 pages.
- NMFS. 2015. Draft Recovery Plan for the Cook Inlet Beluga Whale (*Delphinapterus leucas*). National Marine Fisheries Service, Alaska Regional Office, Protected Resources Division, Juneau, AK.
- NMFS. 2016a. *Technical Guidance for Assessing the Effects of Anthropogenic Sound on Marine Mammal Hearing: Underwater Acoustic Thresholds for Onset of Permanent and Temporary Threshold Shifts*. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-OPR-55, 178 pp.
- NMFS. 2016b. Species in the Spotlight. Priority Actions: 2016-2020. Hawaiian Monk Seal (*Neomonachus schauinslandi*). NOAA Fisheries, Silver Spring, MD. Available at [http://www.nmfs.noaa.gov/stories/2016/02/docs/hawaiian\\_monk\\_seal\\_spotlight\\_species\\_5\\_year\\_action\\_plan\\_final\\_web.pdf](http://www.nmfs.noaa.gov/stories/2016/02/docs/hawaiian_monk_seal_spotlight_species_5_year_action_plan_final_web.pdf).
- NMFS. 2016c. Species in the Spotlight. Priority Actions: 2016-2020. Southern Resident Killer Whale DPS (*Orcinus ocrea*). NOAA Fisheries, Silver Spring, MD. Available at [http://www.nmfs.noaa.gov/stories/2016/02/docs/southern\\_resident\\_killer\\_whale\\_spotlight\\_species\\_5\\_year\\_action\\_plan\\_final\\_web.pdf](http://www.nmfs.noaa.gov/stories/2016/02/docs/southern_resident_killer_whale_spotlight_species_5_year_action_plan_final_web.pdf).
- Nordstad, T., M. Børge, J.O. Bustnes, C. Bech, O. Chastel, A. Goutte, K. Sagerup, C. Trouvé, D. Herzke, and G.W. Gabrielsen. 2012. Relationships between POPs and baseline corticosterone levels in black-legged kittiwakes (*Rissa tridactyla*) across their breeding cycle. *Environmental Pollution* 164:219-226.

- Northridge, S.P. 1984. *World Review of Interactions Between Marine Mammals and Fisheries*. Rome: Food and Agricultural Organization of the United Nations.
- Nowacek, D.P., M.P. Johnson, and P.L. Tyack. 2004. North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. *Proceedings of the Royal Society B: Biological Sciences* 271:227-231.
- Nowacek, D.P., L.H. Thorne, D.W. Johnston, and P.L. Tyack. 2007. Responses of cetaceans to anthropogenic noise. *Mammal Review* 37:81-115. doi: 10.1111/j.1365-2907.2007.00104.x.
- Nowacek, S.M., R.S. Wells, and A.R. Solow. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science* 17(4):673-688.
- NRC (National Research Council). 1994. *Low-Frequency Sound and Marine Mammals: Current Knowledge and Research Needs*. Washington, DC: National Academy Press.
- NRC. 2000. *Marine Mammals and Low-Frequency Sound: Progress Since 1994*. Washington, DC: National Academy Press.
- NRC. 2003a. *Ocean Noise and Marine Mammals*. Washington, DC: The National Academies Press.
- NRC. 2003b. *Decline of the Steller Sea Lion in Alaskan Waters: Untangling Food Webs and Fishing Nets*. Washington, DC: The National Academies Press.
- NRC. 2005. *Marine Mammal Populations and Ocean Noise: Determining When Noise Causes Biologically Significant Effects*. Washington, DC: The National Academies Press.
- NURC (NATO Undersea Research Centre). 2006. *NATO Undersea Research Centre Human Diver and Marine Mammal Risk Mitigation Rules and Procedures*. NURC-SP-2006-008.
- Oakley, G.G., U.-S. Devanaboyina, L.W. Robertson, and R.C. Gupta. 1996. Oxidative DNA damage induced by activation of polychlorinated biphenyls (PCBs): Implications for PCB-induced oxidative stress in breast cancer. *Chemical Research in Toxicology* 9(8):1285-1292.
- Ockendon, N., D.J. Baker, J.A. Carr, E.C. White, R.E. Almond, T. Amano, E. Bertram, R.B. Bradbury, C. Bradley, S.H. Butchart, and N. Doswald. 2014. Mechanisms underpinning climatic impacts on natural populations: Altered species interactions are more important than direct effects. *Global Change Biology* 20(7):2221-2229.
- O'Connell, S.G., L.D. Kincl, and K.A. Anderson. 2014. Silicone wristbands as personal passive samplers. *Environmental Science & Technology* 48(6):3327-3335.
- Oleaga, A., R. Casais, A. Balseiro, A. Espi, L. Llana, A. Hartasanchez, and C. Gortazar. 2011. New techniques for an old disease: Sarcoptic mange in the Iberian wolf. *Veterinary Parasitology* 181:255-266.
- Olesiuk, P.F., L.M. Nicol, M.J. Sowden, and J.B. Ford. 2002. Effects of the sound generated by an acoustic harassment device on the relative abundance and distribution of harbor porpoises (*Phocoena phocoena*) in Retreat Passage, British Columbia. *Marine Mammal Science* 18(4):843-862.
- Ortega, C.P. 2012. Effects of noise pollution on birds: A brief review of our knowledge. *Ornithological Monographs* 74:6-22.
- Oskam I, E. Ropstad, E. Lie, A. Derocher, Ø. Wiig, E. Dahl, S. Larsen, and J.U. Skaare. 2004. Organochlorines affect the steroid hormone cortisol in free-ranging polar bears (*Ursus maritimus*) at Svalbard, Norway. *Journal of Toxicology and Environmental Health A* 67:959-977.
- OSPAR. 2009. *Overview of the Impacts of Anthropogenic Underwater Sound in the Marine Environment*. OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic. Available at [www.ospar.org](http://www.ospar.org). 133 pp.
- Parks, S.E., C.W. Clark, and P.L. Tyack. 2007a. Short- and long-term changes in right whale calling behavior: The potential effects of noise on acoustic communication. *Journal of the Acoustical Society of America* 122:3725-3731.
- Parks, S.E., D.R. Ketten, J.T. O'Malley, and J. Arruda. 2007b. Anatomical predictions of hearing in the North Atlantic right whale. *Anatomical Record* 290:734-744.
- Parks, S.E., M. Johnson, D. Nowacek, and P.L. Tyack. 2010. Individual right whales call louder in increased environmental noise. *Biology Letters* 7:33-35.
- Parks, S.E., J.D. Warren, K. Stamiezkin, C.A. Mayo, and D. Wiley. 2012. Dangerous dining: Surface foraging of North Atlantic right whales increases risk of vessel collisions. *Biology Letters* 8:57-60.
- Patrick, L. 2009. Thyroid disruption: Mechanism and clinical implications in human health. *Alternative Medicine Review* 14:326-346.
- Paulik, L.B., B.W. Smith, A.J. Bergmann, G.J. Sower, N.D. Forsberg, J.G. Teeguarden, and K.A. Anderson. 2016. Passive samplers accurately predict PAH levels in resident crayfish. *Science of the Total Environment* 544:782-791.
- Payne, R., and D. Webb. 1971. Orientation by means of long range acoustic signalling in baleen whales. *Annals of the New York Academy of Sciences* 188:110-141.
- Peck, H.E., D.P. Costa, and D.E. Crocker. 2016. Body reserves influence allocation to immune responses in capital breeding female northern elephant seals. *Functional Ecology* 30:389-397.
- Peetchey, O.L., M. Pontarp, T.M. Massie, S. Kéfi, A. Ozgul, M. Weilenmann, G.M. Palamara, F. Altermatt, B. Matthews, J.M. Levine, D.Z. Childs, B.J. McGill, M.E. Schaepman, B. Schmid, P. Spaak, A.P. Beckerman, F. Pennekamp, and I.S. Pearse. 2015. The Ecological Forecast Horizon, and examples of its uses and determinants. *Ecology Letters* 18:597-611.
- Perrin, W.F., and J.E. Powers. 1980. Role of a nematode in natural mortality of spotted dolphins. *Journal of Wildlife Management* 44:960-963.
- Peterson, S.H., M.G. Peterson, C. Debier, A. Covaci, A.C. Dirtu, G. Malarrannan, D.E. Crocker, L. Schwarz, and D.P. Costa. 2015. Deep-ocean foraging northern elephant seals bioaccumulate persistent organic pollutants. *Science of the Total Environment* 533:144-155.
- Pettis, H.M., R.M. Rolland, P.K. Hamilton, S. Brault, A.R. Knowlton, and S.D. Kraus. 2004. Visual health assessment of North Atlantic right whales (*Eubalaena glacialis*) using photographs. *Canadian Journal of Zoology* 82:8-19.
- Piggott, J.J., C.R. Townsend, and C.D. Matthaei. 2015. Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution* 5:1538-1547.
- Pimm, S.L. 1979. The structure of food webs. *Theoretical Population Biology* 16:144-158.
- Pirotta, E., N.D. Merchant, P.M. Thompson, T.R. Barton, and D. Lusseau. 2015a. Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity. *Biological Conservation* 181:82-89.
- Pirotta, E., J. Harwood, P.M. Thompson, L. New, B. Cheney, M. Arso, P.S. Hammond, C. Donovan, and D. Lusseau. 2015b. Predicting the effects of human developments on individual dolphins to understand potential long-term consequences. *Proceedings of the Royal Society B: Biological Sciences* 282:20152109.
- Pirotta, E., P.M. Thompson, B. Cheney, C.R. Donovan, and D. Lusseau. 2015c. Estimating spatial, temporal and individual variability in dolphin cumulative exposure to boat traffic using spatially explicit capture-recapture methods. *Animal Conservation* 18:20-31.
- Plötz, J., H. Bornemann, R. Knust, A. Schröder, and M. Bester. 2001. Foraging behaviour of Weddell seals, and its ecological implications. *Polar Biology* 24:901-909.
- Polischuk, S.C., K.A. Hobson, and M.A. Ramsay. 2001. Use of stable-carbon and -nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. *Canadian Journal of Zoology* 79(3):499-511.
- Proulx, S.R., D.E.L. Promislow, and P.C. Phillips. 2005. Network thinking in ecology and evolution. *Trends in Ecology and Evolution* 20:345-353.
- Przeslawski, R., M. Byrne, and C. Mellin. 2015. A review and meta-analysis of the effects of multiple abiotic stressors on marine embryos and larvae. *Global Change Biology* 21(6):2122-2140.
- Punt, A.E., and D.S. Butterworth. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modeling the biological interaction between Cape fur seals *Arctocephalus pusillus pusillus* and the Cape hakes *Merluccius capensis* and *M. paradoxus*. *South African Journal of Marine Science* 16:255-285.

- Quick, N.J., S.J. Middlemas, and J.D. Armstrong. 2004. A survey of anti-predator controls at marine salmon farms in Scotland. *Aquaculture* 230:69-180.
- Quinn, J.L., M.J. Whittingham, S.J. Butler, and W. Cresswell. 2006. Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. *Journal of Avian Biology* 37:601-608. doi: 10.1111/j.2006.0908-8857.03781.x.
- Rabalais, N.N., R.E. Turner, Q. Dortch, D. Justic, V. J. Bierman, Jr., and W.J. Wiseman, Jr. 2002. Review. Nutrient-enhanced productivity in the northern Gulf of Mexico: Past, present and future. *Hydrobiologia* 475/476:39-63.
- Råberg, L., M. Grahn, D. Hasselquist, and E. Svensson. 1998. On the adaptive significance of stress-induced immunosuppression. *Proceedings of the Royal Society of London B: Biological Sciences* 265(1406):1637-1641.
- Rappaport, S.M. 2011. Implications of the exposome for exposure science. *Journal of Exposure Science and Environmental Epidemiology* 21(1):5-9.
- Ray, G.C., and F.M. Potter, Jr. 2011. The making of the Marine Mammal Protection Act of 1972. *Aquatic Mammals* 37:520-552.
- Rayne, S., M.G. Ikononou, P.S. Ross, G.M. Ellis, and L.G. Barrett-Lennard. 2004. PBDEs, PBBs, and PCNs in three communities of free-ranging killer whales (*Orcinus orca*) from the northeastern Pacific Ocean. *Environmental Science & Technology* 38(16):4293-4299.
- Read, A.J., P. Drinker, and S. Northridge. 2006. Bycatch of marine mammals in US and global fisheries. *Conservation Biology* 20(1):163-169.
- Redfern, J.V., M.C. Ferguson, E.A. Becker, K.D. Hyrenbach, C. Good, J. Barlow, K. Kaschner, M.F. Baumgartner, K.A. Forney, L.T. Ballance, P. Fauchald, P. Halpin, T. Hamazaki, A.J. Pershing, S.S. Qian, A. Read, S.B. Reilly, L. Torres, and F. Werner. 2006. Techniques for cetacean-habitat modeling. *Marine Ecology: Progress Series* 310:271-295.
- Reeves, R.R., R.J. Hofman, G.K. Silber, and D. Wilkinson. 1996. *Acoustic Deterrence of Harmful Marine Mammal-Fishery Interactions*. Proceedings of a workshop held in Seattle, Washington, March 20-22, 1996. NOAA Technical Memorandum NMFS NMFS-OPR-10. 70 pp.
- Regnault, M., and J.P. Lagardère. 1983. Effects of ambient noise on the metabolic level of *Crangon crangon* (Decapoda, Natantia). *Marine Ecology Progress Series* 11:71-78.
- Reif, J.S., M.M. Kliks, A.A. Aguirre, and D.L. Borjesson. 2006. Gastrointestinal helminths in the Hawaiian monk seal (*Monachus schauinslandi*): Associations with body size, hematology, and serum chemistry. *Aquatic Mammals* 32:157-167.
- Reijnders, P.J.H. 1986. Reproductive failure in common seals feeding on fish from polluted coastal waters. *Nature* 324:456-457.
- Reijnders, P.J.H. 2003. Reproductive and developmental effects of environmental organochlorines on marine mammals. Pp. 55-66 in *Toxicology of Marine Mammals*. London: Taylor & Francis.
- Reijnen, R., R. Foppen, C. Terbraak, and J. Thissen. 1995. The effects of car traffic on breeding bird populations in woodland. 3. Reduction of density in relation to the proximity of main roads. *Journal of Applied Ecology* 32:187-202.
- Reyero, M., E. Cacho, A. Martinez, J. Vazquez, A. Marina, S. Fraga, and J.M. Franco. 1999. Evidence of saxitoxin derivatives as causative agents in the 1997 mass mortality of monk seals in the Cape Blanc Peninsula. *Natural Toxins* 7:311-315.
- Richardson, W.J., B. Würsig, and C.R. Greene, Jr. 1986. Reactions of bowhead whales, *Balaena mysticetus*, to seismic exploration in the Canadian Beaufort Sea. *Journal of the Acoustical Society of America* 79(4):1117-1128.
- Ricklefs, R.E., and M. Wikelski. 2002. The physiology/life-history nexus. *Trends in Ecology & Evolution* 17(10):462-468.
- Rider, C.V., M.L. Dourson, R.C. Hertzberg, M.M. Mumtaz, P.S. Price, and J.E. Simmons. 2012. Incorporating nonchemical stressors into cumulative risk assessments. *Toxicological Sciences* 127(1):10-17.
- Rigét, F., B. Braune, A. Bignert, S. Wilson, J. Aars, E. Born, M. Dam, R. Dietz, M. Evans, T. Evans, and M. Gamberg. 2011. Temporal trends of Hg in Arctic biota, an update. *Science of the Total Environment* 409(18):3520-3526.
- Roberts, J.J., B.D. Best, L. Mannocci, E. Fujioka, P.N. Halpin, D.L. Palka, L.P. Garrison, K.D. Mullin, T.V.N. Cole, C.B. Khan, W.A. McLellan, D.A. Pabst, and G.G. Lockhart. 2016. Habitat-based cetacean density models for the U.S. Atlantic and Gulf of Mexico. *Scientific Reports* 6:22615.
- Robinson, P.W., D.P. Costa, D.E. Crocker, J.P. Gallo-Reynoso, C.D. Champagne, M.A. Fowler, C. Goetsch, K.T. Goetz, J.L. Hassrick, L.A. Hückstädt, and C.E. Kuhn. 2012. Foraging behavior and success of a mesopelagic predator in the northeast Pacific Ocean: Insights from a data-rich species, the northern elephant seal. *PLoS ONE* 7:e36728.
- Rocha, R.C., P.J. Clapham, and Y.V. Ivashchenko. 2014. Emptying the oceans: A summary of industrial whaling catches in the 20th century. *Marine Fisheries Review* 76(4):37-48.
- Rolland, R.M., S.E. Parks, K.E. Hunt, M. Castellote, P.J. Corkeron, D.P. Nowacek, S.K. Wasser, and S.D. Kraus. 2012. Evidence that ship noise increases stress in right whales. *Proceedings of the Royal Society B: Biological Sciences*. 279(1737):2363-2368.
- Rolland, R.M., R.S. Schick, H.M. Pettis, A.R. Knowlton, P.K. Hamilton, J.S. Clark, and S.D. Kraus. 2016. Health of North Atlantic right whales (*Eubalaena glacialis*) over three decades: From individual health to demographic and population trends. *Marine Ecology: Progress Series* 542:265-282.
- Rolland, V., M. Neveux, C. Barbraud, and H. Weimerskirch. 2009. Respective impact of climate and fisheries on the growth of an albatross population. *Ecological Applications* 19:1336-1346.
- Rollins-Smith, L.A., and P.J. Blair. 1993. The effects of corticosteroid hormones and thyroid hormones on lymphocyte viability and proliferation during development and metamorphosis of *Xenopus laevis*. *Differentiation* 54(3):155-160.
- Romano, T.A., M.J. Keogh, C. Kelly, P. Feng, L. Berk, C.E. Schlundt, D.A. Carder, and J.J. Finneran. 2004. Anthropogenic sound and marine mammal health: Measures of the nervous and immune systems before and after intense sound exposure. *Canadian Journal of Fisheries and Aquatic Sciences* 61(7):1124-1134.
- Romero, L.M., M.J. Dickens, and N.E. Cyr. 2009. The reactive scope model—a new model integrating homeostasis, allostasis, and stress. *Hormones and Behavior* 55(3):375-389.
- Roos, M.M.H., G.M. Wu, and P.J.O. Miller. 2016. The significance of respiration timing in the energetics estimates of free-ranging killer whales (*Orcinus orca*). *Journal of Experimental Biology* 219(13):2066-2077.
- Rosen, D.A., and S. Kumagai. 2008. Hormone changes indicate that winter is a critical period for food shortages in Steller sea lions. *Journal of Comparative Physiology B* 178:573-583.
- Ross, P., R. De Swart, P. Reijnders, H.V. Loveren, J. Vos, and A. Osterhaus. 1995. Contaminant-related suppression of delayed-type hypersensitivity and antibody responses in harbor seals fed herring from the Baltic Sea. *Environmental Health Perspectives* 103:162-167.
- Ross, P., R. De Swart, R. Addison, H. Van Loveren, J. Vos, and A. Osterhaus. 1996a. Contaminant-induced immunotoxicity in harbour seals: Wildlife at risk? *Toxicology* 112(2):157-169.
- Ross, P., R. De Swart, H. Timmerman, P. Reijnders, J. Vos, H. V. Loveren, and A. Osterhaus. 1996b. Suppression of natural killer cell activity in harbour seals (*Phoca vitulina*) fed Baltic Sea herring. *Aquatic Toxicology* 34:71-84.
- Ross, P.S., G.M. Ellis, M.G. Ikononou, L.G. Barrett-Lennard, and R.F. Addison. 2000. High PCB concentrations in free-ranging Pacific killer whales, *Orcinus orca*: Effects of age, sex and dietary preference. *Marine Pollution Bulletin* 40:504-515.
- Rotander, A., B. van Bavel, A. Polder, F. Rigét, G.A. Auðunsson, G.W. Gabrielsen, G. Víkingsson, D. Bloch, and M. Dam. 2012. Polybrominated diphenyl ethers (PBDEs) in marine mammals from Arctic and North Atlantic regions, 1986-2009. *Environment International* 40:102-109.

- Rotstein, D.S., L.G. Burdett, W. McLellan, L. Schwacke, T. Rowles, K.A. Terio, S. Schultz, and A. Pabst. 2009. Lobomycosis in offshore bottlenose dolphins (*Tursiops truncatus*), North Carolina. *Emerging Infectious Diseases* 15(4):588-590.
- Royle, J.A., R.B. Chandler, R. Shollmann, and B. Gardner. 2013. *Spatial Capture Recapture*. New York: Elsevier.
- Rudd, M.A. 2014. Scientists' perspectives on global ocean research priorities. *Frontiers in Marine Science* 1:36. doi: 10.3389/fmars.2014.00036.
- Rugh, D.J., K.E.W. Shelden, and R.C. Hobbs. 2010. Range contraction in a beluga whale population. *Endangered Species Research* 12:69-75.
- Runge, M.C., S.J. Converse, and J.E. Lyons. 2011. Which uncertainty? Using expert elicitation and expected value of information to design an adaptive program. *Biological Conservation* 144(4):1214-1223. doi: 10.1016/j.biocon.2010.12.020.
- Runge, M.C., C.A. Langtimm, J. Martin, and C.J. Fonnesebeck. 2015. *Status and Threats Analysis for the Florida Manatee (Trichechus manatus latirostris)*, 2012. U.S. Geological Survey Open-File Report 2015-1083. doi: 10.3133/ofr20151083.
- Ryser-Degiorgis, M.-P. 2013. Wildlife health investigations: Needs, challenges and recommendations. *BMC Veterinary Research* 9:223.
- Samhuri, J.F., A.J. Haupt, P.S. Levin, J.S. Link, and R. Shuford. 2014. Lessons learned from developing integrated ecosystem assessments to inform marine ecosystem-based management in the USA. *ICES Journal of Marine Science* 71:1205-1215.
- Sapolsky, R.M., L.M. Romero, and A.U. Munck. 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions 1. *Endocrine Reviews* 21(1):55-89.
- Scales, K.L., P.I. Miller, L.A. Hawkes, S.N. Ingram, D.W. Sims, and S.C. Votier. 2014. On the front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology* 51(6):1575-1583.
- Schaub, A., J. Ostwald, and B. M. Siemers. 2008. Foraging bats avoid noise. *Journal of Experimental Biology* 211:3174-3180.
- Scheffer, M. 2009. *Critical Transitions in Nature and Society*. Princeton, NJ: Princeton University Press.
- Scheffer, M., S. Carpenter, J.A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591-596.
- Scheffer, M., J. Bascompte, W.A. Brock, V. Brovkin, S.R. Carpenter, V. Dakos, H. Held, E.H. van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. *Nature* 461:53-59.
- Scheffer, V.B. 1950. Growth layers on the teeth of Pinnipedia as an indication of age. *Science* 112(2907):309-311.
- Schick, R.S., L.F. New, L. Thomas, D.P. Costa, M.A. Hindell, C.R. McMahon, P.W. Robinson, S.E. Simmons, M. Thums, J. Harwood, and J.S. Clark. 2013. Estimating resource acquisition and at-sea body condition of a marine predator. *Journal of Animal Ecology* 82(6):1300-1315.
- Scholin, C.A., F. Gulland, G.J. Doucette, S. Benson, M. Busman, F.P. Chavez, J. Cordaro, R. DeLong, A. De Vogelaere, J. Harvey, M. Haulena, K. Lefebvre, T. Lipscomb, S. Loscutoff, L.J. Lowenstine, R. Marin, P.E. Miller, W.A. McLellan, P.D.R. Moeller, C.L. Powell, T. Rowles, P. Silvagni, M. Silver, T. Spraker, V. Trainer, and F.M. Van Dolah. 2000. Mortality of sea lions along the central California coast linked to a toxic diatom bloom. *Nature* 403:80-84.
- Schultner, J., B. Moe, O. Chastel, S. Tartu, C. Bech, and A.S. Kitaysky. 2014. Corticosterone mediates carry-over effects between breeding and migration in the kittiwake *Rissa tridactyla*. *Marine Ecology Progress Series* 496:125-133.
- Schwacke, L.H., E.O. Voit, L.J. Hansen, R.S. Wells, G.B. Mitchum, A.A. Hohn, and P.A. Fair. 2002. Probabilistic risk assessment of reproductive effects of polychlorinated biphenyls on bottlenose dolphins (*Tursiops truncatus*) from the Southeast United States coast. *Environmental Toxicology and Chemistry* 21:2752-2764. doi: 10.1002/etc.5620211232.
- Schwacke, L.H., M.J. Twiner, S. De Guise, B.C. Balmer, R.S. Wells, F.I. Townsend, D.C. Rotstein, R.A. Varela, L.J. Hansen, E.S. Zolman, T.R. Spradlin, M. Levin, H. Leibrecht, Z.H. Wang, and T.K. Rowles. 2010. Eosinophilia and biotoxin exposure in bottlenose dolphins (*Tursiops truncatus*) from a coastal area impacted by repeated mortality events. *Environmental Research* 110:548-555.
- Schwacke, L.H., E.S. Zolman, B.C. Balmer, S. De Guise, R.C. George, J. Hogue, A.A. Hohn, J.R. Kucklick, S. Lamb, M. Levin, J.A. Litz, W.E. McFee, N.J. Place, F.I. Townsend, R.S. Wells, and T.K. Rowles. 2012. Anaemia, hypothyroidism and immune suppression associated with polychlorinated biphenyl exposure in bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society B: Biological Sciences* 279:48-57.
- Schwacke, L.H., C.R. Smith, F.I. Townsend, R.S. Wells, L.B. Hart, B.C. Balmer, T.K. Collier, S. De Guise, M.M. Fry, L.J. Guillette, Jr., S.V. Lamb, S.M. Lane, W.E. McFee, N.J. Place, M.C. Tumlin, G.M. Ylitalo, E.S. Zolman, and T.K. Rowles. 2014a. Health of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana, following the *Deepwater Horizon* oil spill. *Environmental Science and Technology* 48:93-103.
- Schwacke, L.H., C.R. Smith, F.I. Townsend, R.S. Wells, L.B. Hart, B.C. Balmer, T.K. Collier, S. De Guise, M.M. Fry, L.J. Guillette, Jr., S.V. Lamb, S.M. Lane, W.E. McFee, N.J. Place, M.C. Tumlin, G.M. Ylitalo, E.S. Zolman, and T.K. Rowles. 2014b. Response to comment on health of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana following the *Deepwater Horizon* oil spill. *Environmental Science & Technology* 48:4209-4211.
- Schwartz, J.A., B.M. Aldridge, J.L. Stott, and F.C. Mohr. 2004. Immunophenotypic and functional effects of bunker C fuel oil on the immune system of American mink (*Mustela vison*). *Veterinary Immunology and Immunopathology* 101:179-190.
- Schwarz, K.B. 1996. Oxidative stress during viral infection: A review. *Free Radical Biology and Medicine* 21(5):641-649.
- Scott, M.D., and S.J. Chivers. 2009. Movements and diving behavior of pelagic spotted dolphins. *Marine Mammal Science* 25(1):137-160.
- Seixas, T.G., H.D.A. Kehrig, M. Costa, G. Fillmann, A.P.M. Di Benedetto, E.R. Secchi, C.M. Souza, O. Malm, and I. Moreira. 2008. Total mercury, organic mercury and selenium in liver and kidney of a South American coastal dolphin. *Environmental Pollution* 154(1):98-106.
- Selkoe, K.A., T. Blenckner, M.R. Caldwell, L.B. Crowder, A.L. Erickson, T.E. Essington, J.A. Estes, R.M. Fujita, B.S. Halpern, M.E. Hunsicker, C.V. Kappel, R.P. Kelly, J.N. Kittinger, P.S. Levin, J.M. Lynha, M.E. Mach, R.G. Martone, L.A. Mease, A.K. Salomon, J.F. Samhuri, C.S. Scabborough, A.C. Stier, A.C. Stier, C. White, and J. Zedler. 2015. Principles for managing marine ecosystems prone to tipping points. *Ecosystem Health and Sustainability* 1(5):17.
- Senzaki, M., Y. Yamaura, C.D. Francis, and F. Nakamura. 2016. Traffic noise reduces foraging efficiency in wild owls. *Scientific Reports* 6:30602.
- Sepulveda, M., and D. Oliva. 2005. Interactions between South American sea lions *Otaria flavescens* (Shaw) and salmon farms in southern Chile. *Aquaculture Research* 36:1062-1068.
- Shannon, G., L.M. Angeloni, G. Wittemyer, K.M. Fristrup, and K.R. Crooks. 2014. Road traffic noise modifies behaviour of a keystone species. *Animal Behaviour* 94:135-141.
- Shannon, G., M.F. McKenna, L.M. Angeloni, K.R. Crooks, K.M. Fristrup, E. Brown, K.A. Warner, M.D. Nelson, C. White, and J. Briggs. 2015. A synthesis of two decades of research documenting the effects of noise on wildlife. *Biological Reviews* 91(4):982-1005. doi: 10.1111/brv.12207.
- Shannon, G., K.R. Crooks, G. Wittemyer, K.M. Fristrup, and L.M. Angeloni. 2016. Road noise causes earlier predator detection and flight response in a free-ranging mammal. *Behavioral Ecology*. doi: 10.1093/beheco/arw058.
- Shelden, K.E.W., D.J. Rugh, B.A. Mahoney, and M.E. Dahlheim. 2003. Killer whale predation on belugas in Cook Inlet, Alaska: Implications for a depleted population. *Marine Mammal Science* 19(3):529-544.

- Shelden, K.E.W., C.L. Sims, L. Vate Brattström, K.T. Goetz, and R.C. Hobbs. 2015. *Aerial Surveys of Beluga Whales (Delphinapterus leucas) in Cook Inlet, Alaska, June 2014*. AFSC Processed Report 2015-03. NOAA Alaska Fisheries Science Center, National Marine Fisheries Service, Seattle, WA.
- Sheldon, B.C., and S. Verhulst. 1996. Ecological immunology: Costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology & Evolution* 11(8):317-321.
- Shephard, R.J., and P.N. Shek. 1998. Cold exposure and immune function. *Canadian Journal of Physiological Pharmacology* 76:828-836.
- Shero, M.R., R.T. Krotz, D.P. Costa, J.P. Avery, and J.M. Burns. 2015. How do overwinter changes in body condition and hormone profiles influence Weddell seal reproductive success? *Functional Ecology* 29:1278-1291.
- Siemers, B.M., and A. Schaub. 2011. Hunting at the highway: Traffic noise reduces foraging efficiency in acoustic predators. *Proceedings of the Royal Society B: Biological Sciences* 278:1646-1652.
- Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution* 13:350-355.
- Simeone, C.A., F.M. Gulland, T. Norris, and T.K. Rowles. 2015. A systematic review of changes in marine mammal health in North America, 1972-2012: The need for a novel integrated approach. *PLoS ONE* 10:e0142105.
- Sivle, L.D., P.H. Kvadsheim, A. Fahlman, F.P.A. Lam, P.L. Tyack, and P.J.O. Miller. 2012. Changes in dive behavior during naval sonar exposure in killer whales, long-finned pilot whales, and sperm whales. *Frontiers in Physiology* 3(400):1-11.
- Small, R.J., P.L. Boveng, G.V. Byrd, and D.E. Withrow. 2008. Harbor seal population decline in the Aleutian Archipelago. *Marine Mammal Science* 24(4):845-863.
- Smith, C.R., T.K. Rowles, L.B. Hart, F.I. Townsend, R.S. Wells, E.S. Zolman, B.C. Balmer, B. Quigley, M. Ivančić, W. McKercher, M.C. Tumlin, K.D. Mullin, J.D. Adams, Q. Wu, W. McFee, T.K. Collier, and L.H. Schwacke. 2017. Slow recovery of Barataria Bay dolphin health following the Deepwater Horizon oil spill (2013-2014), with evidence of persistent lung disease and impaired stress response. *Endangered Species Research* 33:127-147. doi: 10.3354/esr00778
- Smith, T.D., J. Allen, P.J. Clapham, P.S. Hammond, S. Katona, F. Larsen, J. Lien, D. Mattila, P.J. Palsbøll, J. Sigurjónsson, and P.T. Stevick. 1999. An ocean-basin-wide mark-recapture study of the North Atlantic humpback whale (*Megaptera novaeangliae*). *Marine Mammal Science* 15(1):1-32.
- Smout, S., A. Rindorf, P.S. Hammond, J. Harwood, and J. Matthiopoulos. 2014. Modelling prey consumption and switching by UK grey seals. *ICES Journal of Marine Science: Journal du Conseil* 71:81-89.
- Sormo, E.G., I. Jussi, M. Jussi, M. Braathen, J.U. Skaare, and B.M. Jenssen. 2005. Thyroid hormone status in gray seal (*Halichoerus grypus*) pups from the Baltic Sea and the Atlantic Ocean in relation to organochlorine pollutants. *Environmental Toxicology and Chemistry* 24:610-616.
- Soto, S., A. Alba, L. Ganges, E. Vidal, J.A. Raga, F. Alegre, B. González, P. Medina, I. Zorrilla, J. Martínez, and A. Marco. 2011. Post-epizootic chronic dolphin morbillivirus infection in Mediterranean striped dolphins *Stenella coeruleoalba*. *Diseases of Aquatic Organisms* 96(3):187-194.
- Southall, B.L., A.E. Bowles, W.T. Ellison, J.J. Finneran, R.L. Gentry, C.R. Greene, Jr., D. Kastak, D.R. Ketten, J.H. Miller, P.E. Nachtigall, W.J. Richardson, J.A. Thomas, and P.L. Tyack. 2007. Marine mammal noise exposure criteria: Initial scientific recommendations. *Aquatic Mammals* 33:411-521.
- Spoon, T.R., and T.A. Romano. 2012. Neuroimmunological response of beluga whales (*Delphinapterus leucas*) to translocation and a novel social environment. *Brain, Behavior, and Immunity* 26:22-131.
- Springer, A.M., J.A. Estes, G.B. van Vliet, T.M. Williams, D.F. Doak, E.M. Danner, K.A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences of the United States of America* 100(21):12223-12228.
- Springer, A.M., J.A. Estes, G.B. Van Vliet, T.M. Williams, D.F. Doak, E.M. Danner, and B. Pfister. 2008. Mammal-eating killer whales, industrial whaling, and the sequential megafaunal collapse in the North Pacific Ocean: A reply to critics of Springer et al. 2003. *Marine Mammal Science* 24(April):414-442.
- Stamaton, K.A., D.B. Croft, and P.D. Shaughnessy. 2009. Behavioral responses of humpback whales (*Megaptera novaeangliae*) to whale-watching vessels on the southeastern coast of Australia. *Marine Mammal Science* 26(1):98-122. doi: 10.1111/j.1748-7692.2009.00320.x.
- Steele, J.H. 2004. Regime shifts in the ocean: Reconciling observations and theory. *Progress in Oceanography* 60(2):135-141.
- Steiger, J.W. 1994. The Consultation Provision of Section 7(a)(2) of the Endangered Species Act and its application to delegable federal programs. *Ecology Law Quarterly* 21:2. doi: 10.15779/Z382K05.
- Steneck, R.S., M.H. Graham, B.J. Bourque, D. Corbett, J.M. Erlandson, J.A. Estes, and M.J. Tegner. 2002. Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation* 29(4):436-459.
- Stephen, C. 2014. Toward a modernized definition of wildlife health. *Journal of Wildlife Diseases* 50(3):427-430.
- Stephens, P.A., W.J. Sutherland, and R.P. Freckleton. 1999. What is the Allee effect? *Oikos* 87:185-190.
- Sternberg, E.M., G.P. Chrousos, R.L. Wilder, and P.W. Gold. 1992. The stress response and the regulation of inflammatory disease. *Annals of Internal Medicine* 117(10):854-866.
- Stewart, K.R., R.L. Lewison, D.C. Dunn, R.H. Bjorkland, S. Kelez, P.N. Halpin, and L.B. Crowder. 2010. Characterizing fishing effort and spatial extent of coastal fisheries. *PLoS ONE* 5(12):e14451.
- Stewart, P.W., J. Reihman, E. Lonky, T.J. Darvill, and J. Pagano. 2003. Cognitive development in preschool children prenatally exposed to PCBs and MeHg. *Neurotoxicology and Teratology* 25:11-22.
- Stewart, P.W., E. Lonky, J. Reihman, J. Pagano, B.B. Gump, and T. Darvill. 2008. The relationship between prenatal PCB exposure and intelligence (IQ) in 9-year-old children. *Environmental Health Perspectives* 116:1416-1422.
- Stier, K.S., B. Almasi, J. Gasparini, R. Pialut, A. Roulin, and L. Jenni. 2009. Effects of corticosterone on innate and humoral immune functions and oxidative stress in barn owl nestlings. *Journal of Experimental Biology* 212(13):2085-2091.
- Stirling, I., and C.L. Parkinson. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* 59(3):261-275.
- Stirling, I., C. Spencer, and D. Andriashek. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol® in the Canadian Arctic. *Journal of Wildlife Diseases* 25(2):159-168.
- Stirling, I., N.J. Lunn, and J. Iacozza. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52(3):294-306.
- Stirling, I., N.J. Lunn, J. Iacozza, C. Elliott, and M. Obbard. 2004. Polar bear distribution and abundance on the southwestern Hudson Bay coast during open water season, in relation to population trends and annual ice patterns. *Arctic* 57(1):15-26.
- Stohs, S.J. 1990. Oxidative stress induced by 2,3,7,8-tetrachlorodibenzo-p-dioxin (TCDD). *Free Radical Biology and Medicine* 9(1):79-90.
- Sugihara, G., R. May, H. Ye, C.H. Hsieh, E. Deyle, M. Fogarty, and S. Munch. 2012. Detecting causality in complex ecosystems. *Science* 338(6106):496-500.
- Sutherland, J.P. 1974. Multiple stable points in natural communities. *American Naturalist* 108(964):859-873.
- Sutherland, W.J. 2006. Predicting the ecological consequences of environmental change: A review of the methods. *Journal of Applied Ecology* 43:599-616.
- Sutherland, W.J., and M.A. Burgman. 2015. Use experts wisely. *Nature (London)* 526:317-318.



- Svensson, E., L. Råberg, C. Koch, and D. Hasselquist. 1998. Energetic stress, immunosuppression and the costs of an antibody response. *Functional Ecology* 12(6):912-919.
- Swaddle, J.P., C.D. Francis, J.R. Barber, C.B. Cooper, C.M. Kyba, D.M. Dominoni, G. Shannon, E. Aschehoug, S.E. Goodwin, A.Y. Kawahara, D. Luther, K. Spoelstra, M. Voss, and T. Longcore. 2015. A framework to assess evolutionary responses to anthropogenic light and sound. *Trends in Ecology & Evolution* 30(9):550-560.
- Symons, J., E. Pirotta, and D. Lusseau. 2014. Sex differences in risk perception in deep-diving bottlenose dolphins leads to decreased foraging efficiency when exposed to human disturbance. *Journal of Applied Ecology* 51:1584-1592.
- Tabuchi, M., N. Veldhoen, N. Dangerfield, S. Jeffries, C.C. Helbing, and P.S. Ross. 2006. PCB-related alteration of thyroid hormones and thyroid hormone receptor gene expression in free-ranging harbor seals (*Phoca vitulina*). *Environmental Health Perspectives* 114:1024-1031.
- Tartu, S., F. Angelier, J. Bustnes, B. Moe, S. Hanssen, D. Herzke, G.W. Gabrielsen, N. Verboven, J. Jerreault, P. Labadie, H. Budzinski, J.C. Wingfield, and O. Chastel. 2015. Polychlorinated biphenyl exposure and corticosterone levels in seven polar seabird species. *Environmental Pollution* 197:173-180.
- Tasker, M.L., M. Amundin, M. Andre, A.D. Hawkins, W. Lang, T. Merck, A. Scholik-Schlomer, J. Teilman, F. Thomsen, S. Werner, and M. Zakharia. 2010. *Marine Strategy Framework Directive: Task Group 11 Report: Underwater Noise and Other Forms of Energy*. JRC Scientific and Technical Report No. EUR 24341 EN-2010, European Commission and International Council for the Exploration of the Sea, Luxembourg.
- Taylor, B.L., and D.P. Demaster. 1993. Implications of non-linear density dependence. *Marine Mammal Science* 9(4):360-371.
- Taylor, B.L., P.R. Wade, D.P. De Master, and J. Barlow. 2000. Incorporating uncertainty into management models for marine mammals. *Conservation Biology* 14:1243-1252.
- Taylor, B.L., M. Martinez, T. Gerrodette, J. Barlow, and Y.N. Hrovat. 2007. Lessons from monitoring trends in abundance of marine mammals. *Marine Mammal Science* 23:157-175.
- Tennessen, J.B., S.E. Parks, and T. Langkilde. 2014. Traffic noise causes physiological stress and impairs breeding migration behaviour in frogs. *Conservation Physiology* 2:cou032.
- Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M. Ferreira de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A.T. Peterson, O.L. Phillips, and S.E. Williams. 2004. Extinction risk from climate change. *Nature* 427:145-148. doi: 10.1038/nature02121.
- Thomas, L., S.T. Buckland, K.B. Newman, and J. Harwood. 2005. A unified framework for modeling wildlife population dynamics. *Australian and New Zealand Journal of Statistics* 47:19-34.
- Thomas, P.O., R.R. Reeves, and R.L. Brownell. 2016. Status of the world's baleen whales. *Marine Mammal Science* 32(2):682-734.
- Thompson, D., J. Onoufriou, A. Brownlow, and A. Bishop. 2015. Preliminary Report on Predation by Adult Grey Seals on Grey Seal Pups as a Possible Explanation for Corkscrew Injury Patterns Seen in the Unexplained Seal Deaths: Addendum. Sea Mammal Research Unit, University of St. Andrews, Report to Scottish Government. Available at [http://www.smru.st-andrews.ac.uk/documents/scotgov/USD1and%206\\_addendum\\_report\\_VF2.pdf](http://www.smru.st-andrews.ac.uk/documents/scotgov/USD1and%206_addendum_report_VF2.pdf).
- Thompson, P.M., B. Mackey, T.R. Barton, C. Duck, and J.R.A. Butler. 2007. Assessing the potential impact of salmon fisheries management on the conservation status of harbour seals (*Phoca vitulina*) in north-east Scotland. *Animal Conservation* 10:48-56.
- Thompson, P.M., D. Lusseau, T. Barton, D. Simmons, J. Rusin, and H. Bailey. 2010. Assessing the responses of coastal cetaceans to the construction of offshore wind turbines. *Marine Pollution Bulletin* 60:1200-1208.
- Thompson, P.M., K.L. Brookes, I.M. Graham, T.R. Barton, K. Needham, G. Bradbury, and N.D. Merchant. 2013a. Short-term disturbance by a commercial two-dimensional seismic survey does not lead to long-term displacement of harbour porpoises. *Proceedings of the Royal Society of London B: Biological Sciences* 280:20132001.
- Thompson, P.M., G.D. Hastie, J. Nedwell, R. Barham, K.L. Brookes, L.S. Cordes, H. Bailey, and N. Mclean. 2013b. Framework for assessing impacts of pile-driving noise from offshore wind farm construction on a harbour seal population. *Environmental Impact Assessment Review* 43:73-85.
- Tinker, M.T., G. Bentall, and J.A. Estes. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proceedings of the National Academy of Sciences of the United States of America* 105:560-565.
- Tougaard, J., J. Carstensen, and J. Teilmann. 2009. Pile driving zone of responsiveness extends beyond 20 km for harbor porpoises (*Phocoena phocoena* (L.)). *Journal of the Acoustical Society of America* 126:11-14.
- Trickey, J.S., B.K. Branstetter, and J.J. Finneran. 2010. Auditory masking of a 10 kHz tone with environmental, comodulated, and Gaussian noise in bottlenose dolphins (*Tursiops truncatus*). *Journal of the Acoustical Society of America* 128:3799-3804.
- Trillmich, F., K.A. Ono, D.P. Costa, R.L. DeLong, S.D. Feldkamp, J.M. Francis, R.L. Gentry, C.B. Heath, B.J. Le Boeuf, P. Majluf, and A.E. York. 1991. The effects of El Niño on pinniped populations in the eastern Pacific. Pp. 247-270 in *Pinnipeds and El Niño*. Berlin: Springer.
- Trites, A.W., V.B. Deecke, E.J. Gregr, J.K.B. Ford, and P.F. Olesiuk. 2007. Killer whales, whaling, and sequential megafaunal collapse in the North Pacific: A comparative analysis of the dynamics of marine mammals in Alaska and British Columbia following commercial whaling. *Marine Mammal Science* 23(4):751-765.
- Trumble, S.J., E.M. Robinson, M. Berman-Kowalewski, C.W. Potter, and S. Usenko. 2013. Blue whale earplug reveals lifetime contaminant exposure and hormone profiles. *Proceedings of the National Academy of Sciences of the United States of America* 110(42):16922-16926.
- Tubelli, A.A., A. Zosuls, D.R. Ketten, M. Yamato, and D.C. Mountain. 2012. A prediction of the minke whale (*Balaenoptera acutorostrata*) middle-ear transfer function. *Journal of the Acoustical Society of America* 132:3263-3272.
- Turvey, S.T., R.L. Pitman, B.L. Taylor, J. Barlow, T. Akamatsu, L.A. Barrett, X. Zhao, R.R. Reeves, B.S. Stewart, K. Wang, and Z. Wei. 2007. First human-caused extinction of a cetacean species? *Biology Letters* 3(5):537-540.
- Twiner, M.J., S. Fire, L. Schwacke, L. Davidson, Z.H. Wang, S. Morton, S. Roth, B. Balmer, T.K. Rowles, and R.S. Wells. 2011. Concurrent exposure of bottlenose dolphins (*Tursiops truncatus*) to multiple algal toxins in Sarasota Bay, Florida, USA. *PLoS ONE* 6(3):e17394.
- Twiner, M.J., L.J. Flewelling, S.E. Fire, S.R. Bowen-Stevens, J.K. Gaydos, C.K. Johnson, J.H. Landsberg, T.A. Leighfield, B. Mase-Guthrie, L. Schwacke, F.M. Van Dolah, Z. Wang, and T.K. Rowles. 2012. Comparative analysis of three brevetoxin-associated bottlenose dolphin (*Tursiops truncatus*) mortality events in the Florida Panhandle region (USA). *PLoS ONE* 7:e42974.
- Tyack, P.L., and C.W. Clark. 1998. *Quick-Look Report: Playback of Low-Frequency Sound to Gray Whales Migrating Past the Central California Coast*. Woods Hole, MA: Woods Hole Oceanographic Institution.
- Tyack, P.L., and V.J. Janik. 2013. Effects of noise on acoustic signal production. Pp. 251-271 in *Animal Communication and Noise*, H. Brumm, ed. Berlin: Springer.
- Tyack, P.L., W.M.X. Zimmer, D. Moretti, B.L. Southall, D.E. Claridge, J.W. Durban, C.W. Clark, A. D'Amico, N. DiMarzio, S. Jarvis, E. McCarthy, R. Morrissey, J. Ward, and I.L. Boyd. 2011. Beaked whales respond to simulated and actual navy sonar. *PLoS ONE* 6(3):e17009.

- Uchida, K., M. Murakami, Y. Horii, N. Murakami, R. Yamaguchi, and S. Tateyama. 1999. Non-purulent meningoencephalomyelitis of a Pacific striped dolphin (*Lagenorhynchus obliquidens*). The first evidence of morbillivirus infection in a dolphin at the Pacific Ocean around Japan. *Journal of Veterinary Medical Science* 61(2):159-162.
- Ulbrich, B., and R. Stahlmann. 2004. Developmental toxicity of polychlorinated biphenyls (PCBs): A systematic review of experimental data. *Archives of Toxicology* 78:252-268.
- U.S. Department of the Navy. 2013. Hawaiian-Southern California Training and Testing Activities. Final Environmental Impact Statement/Overseas Environmental Impact Statement. Available at <http://hstteis.com/Completedin2013/DocumentsandReferences/HSTTDocuments/FinalEISOEIS.aspx>.
- USFWS (U.S. Fish and Wildlife Service). 2013. Southwest Alaska Distinct Population Segment of the Northern Sea Otter (*Enhydra lutris kenyoni*) Recovery Plan. Available at <https://www.fws.gov/alaska/fisheries/mmm/seaotters/pdf/Recovery%20Plan%20SW%20AK%20DPS%20Sea%20Otter%20Aug13.pdf>.
- Vacqué-García, J., F. Royer, A.-C. Dragon, M. Viviant, F. Bailleul, and C. Guinet. 2012. Foraging in the darkness of the Southern Ocean: Influence of bioluminescence on a deep diving predator. *PLoS ONE* 7(8):e43565.
- Valavanidis, A., T. Vlahogianni, M. Dassenakis, and M. Scoullos. 2006. Molecular biomarkers of oxidative stress in aquatic organisms in relation to toxic environmental pollutants. *Ecotoxicology and Environmental Safety* 64(2):178-189.
- Van Bresse, M.-F.E., J.A. Raga, G. Di Guardo, P.D. Jepson, P.J. Duignan, U. Siebert, T. Barrett, M.C. de Oliveira Santos, I.B. Moreno, S. Siciliano, and A. Aguilar. 2009. Emerging infectious diseases in cetaceans worldwide and the possible role of environmental stressors. *Diseases of Aquatic Organisms* 86(2):143-157.
- Van Bresse, M.-F.E., P.J. Duignan, A. Banyard, M. Barbieri, K.M. Colegrove, S. De Guise, G. Di Guardo, A. Dobson, M. Domingo, D. Fauquier, and A. Fernandez. 2014. Cetacean morbillivirus: Current knowledge and future directions. *Viruses* 6(12):5145-5181.
- Van Bresse, M.-F.E., L. Flach, J.C. Reyes, M. Echegaray, M. Santos, F. Viddi, F. Félix, L. Lodi, and K. Van Waerebeek. 2015. Epidemiological characteristics of skin disorders in cetaceans from South American waters. *Latin American Journal of Aquatic Mammals* 10(1):20-32.
- Van den Berg, M., L.S. Birnbaum, M. Denison, M. De Vito, W. Farland, M. Feeley, H. Fiedler, H. Hakansson, A. Hanberg, L. Haws, and M. Rose. 2006. The 2005 World Health Organization reevaluation of human and mammalian toxic equivalency factors for dioxins and dioxin-like compounds. *Toxicological Sciences* 93(2):223-241.
- Van der Graaf, A.J., M.A. Ainslie, M. André, K. Brensing, J. Dalen, R.P.A. Dekeling, S. Robinson, M.L. Tasker, F. Thomsen, and S. Werner. 2012. European Marine Strategy Framework Directive—Good Environmental Status (MSFD GES): Report of the Technical Subgroup on Underwater Noise and Other Forms of Energy. Available at [http://ec.europa.eu/environment/marine/pdf/MSFD\\_reportTSG\\_Noise.pdf](http://ec.europa.eu/environment/marine/pdf/MSFD_reportTSG_Noise.pdf).
- Van der Zande, A.N., W.J. ter Keurs, and W.J. Weijden. 1980. The impact of roads on the densities of four bird species in an open field habitat—evidence of a long-distance effect. *Biological Conservation* 18:299-321.
- Van Dolah, F.M. 2005. Effects of harmful algal blooms. Pp. 85-99 in *Marine Mammal Research, Conservation Beyond Crisis*, J. Reynolds, W. Perrin, R. Reeves, S. Montgomery, and T. Ragen, eds. Baltimore, MD: The Johns Hopkins University Press.
- Van Dolah, F.M., M.G. Neely, L.E. McGeorge, B.C. Balmer, G.M. Ylitalo, E.S. Zolman, T. Speakman, C. Sinclair, N.M. Kellar, P.E. Rosel, K.D. Mullin, and L.H. Schwacke. 2015. Seasonal variation in the skin transcriptome of common bottlenose dolphins (*Tursiops truncatus*) from the Northern Gulf of Mexico. *PLoS ONE* 10(6):e0130934.
- Van Loveren, H., P.S. Ross, A.D. Osterhaus, and J.G. Vos. 2000. Contaminant-induced immunosuppression and mass mortalities among harbor seals. *Toxicology Letters* 112-113:319-324.
- Van Neer, A., L.F. Jensen, and U. Siebert. 2014. Grey seal (*Halichoerus grypus*) predation on harbour seals (*Phoca vitulina*) on the island of Helgoland, Germany. *Journal of Sea Research* 97:1-4.
- Vanderlaan, A.S.M., and C.T. Taggart. 2007. Vessel collisions with whales: The probability of lethal injury based on vessel speed. *Marine Mammal Science* 23:144-156.
- VanWormer, E., P.A. Conrad, M.A. Miller, A.C. Melli, T.E. Carpenter, and J.A.K. Mazet. 2013. *Toxoplasma gondii*, source to sea: Higher contribution of domestic felids to terrestrial parasite loading despite lower infection prevalence. *EcoHealth* 10(3):277-289.
- VanWormer, E., M.A. Miller, P.A. Conrad, M.E. Grigg, D. Rejmanek, T.E. Carpenter, and J.A.K. Mazet. 2014. Using molecular epidemiology to track *Toxoplasma gondii* from terrestrial carnivores to marine hosts: Implications for public health and conservation. *PLoS Neglected Tropical Diseases* 8(5):e2852.
- Vázquez-Medina, J.P., T. Zenteno-Savín, R. Elsnér, and R.M. Ortiz. 2012. Coping with physiological oxidative stress: A review of antioxidant strategies in seals. *Journal of Comparative Physiology B* 182:741-750.
- Vecchione, A., M.M. Peden-Adams, T.A. Romano, and P.A. Fair. 2008. Recent cytokine findings and implications toward health assessment of the bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals* 34(1):93-101.
- Vélez-Espino, A., J.K.B. Ford, H.A. Araujo, G. Ellis, C.K. Parken, and R. Sharma. 2015. Relative importance of chinook salmon abundance on resident killer whale population growth and viability. *Aquatic Conservation: Marine and Freshwater Ecosystems* 25(6):756-780.
- Venn-Watson, S., C.R. Smith, E.D. Jensen, and T. Rowles. 2013. Assessing the potential health impacts of the 2003 and 2007 firestorms on bottlenose dolphins (*Tursiops truncatus*) in San Diego Bay. *Inhalation Toxicology* 25:481-491.
- Venn-Watson, S., K.M. Colegrove, J. Litz, M. Kinsel, K. Terio, J. Saliki, S. Fire, R. Carmichael, C. Chevis, W. Hatchett, J. Pitchford, M. Tumlin, C. Field, S. Smith, R. Ewing, D. Fauquier, G. Lovell, H. Whitehead, D. Rotstein, W. McFee, E. Fougères, and T. Rowles. 2015. Adrenal gland and lung lesions in Gulf of Mexico common bottlenose dolphins (*Tursiops truncatus*) found dead following the Deepwater Horizon oil spill. *PLoS ONE* 10:e0126538.
- Verborgh, P., R. De Stephanis, S. Pérez, Y. Jaget, C. Barbraud, and C. Guinet. 2009. Survival rate, abundance, and residency of long-finned pilot whales in the Strait of Gibraltar. *Marine Mammal Science* 25(3):523-536.
- Vert-pre, K.A., R.O. Amoroso, O.P. Jensen, and R. Hilborn. 2013. Frequency and intensity of productivity regime shifts in marine fish stocks. *Proceedings of the National Academy of Sciences of the United States of America* 110(5):1779-1784.
- Villegas-Amtmann, S., L.K. Schwarz, J.L. Sumich, and D.P. Costa. 2015. A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. *Ecosphere* 6(10):183.
- Wade, P.R., V.N. Burkanov, M.E. Dahlheim, N.A. Friday, L.W. Fritz, T.R. Loughlin, S.A. Mizroch, M.M. Muto, and D.W. Rice. 2007. Killer whales and marine mammal trends in the North Pacific—A re-examination of evidence for sequential megafauna collapse and the prey-switching hypothesis. *Marine Mammal Science* 23(4):766-802.
- Wade, P.R., J.M. Ver Hoef, and D.P. Demaster. 2009. Mammal-eating killer whales and their prey—trend data for pinnipeds and sea otters in the North Pacific Ocean do not support the sequential megafaunal collapse hypothesis. *Marine Mammal Science* 25:737-747.
- Wagemann, R., S. Innes, and P.R. Richard. 1996. Overview and regional and temporal differences of heavy metals in Arctic whales and ringed seals in the Canadian Arctic. *Science of the Total Environment* 186(1-2):41-46. doi: 10.1016/0048-9697(96)05085-1.
- Wale, M.A., S.D. Simpson, and A.N. Radford. 2013. Noise negatively affects foraging and antipredator behaviour in shore crabs. *Animal Behaviour* 86:111-118.
- Walters, C.J. 1986. *Adaptive Management of Renewable Resources*. New York: MacMillan.

- Ward, E.J., E.E. Holmes, and K.C. Balcomb. 2009. Quantifying the effects of prey abundance on killer whale reproduction. *Journal of Applied Ecology* 46:632-640.
- Ward, W.D., E.M. Cushing, and E.M. Burns. 1976. Effective quiet and moderate TTS: Implications for noise exposure standards. *Journal of the Acoustical Society of America* 59(1):160-165.
- Ware, H.E., C.J. McClure, J.D. Carlisle, and J.R. Barber. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. *Proceedings of the National Academy of Sciences of the United States of America* 112:12105-12109.
- Watanabe, Y., E.A. Baranov, K. Sato, Y. Naito, and N. Miyazaki. 2006. Body density affects stroke patterns in Baikal seals. *Journal of Experimental Biology* 209:3269-3280.
- Watkins, W.A., P. Tyack, K.E. Moore and J.E. Bird. 1987. The 20-Hz signals of finback whales (*Balaenoptera physalus*). *Journal of the Acoustical Society of America* 82:1901-1912.
- Weih, P., P. Grandjean, F. Debes, and R. White. 1996. Health implications for Faroe Islanders of heavy metals and PCBs from pilot whales. *Science of the Total Environment* 186(1):141-148.
- Weinrich, M., and C. Corbelli. 2009. Does whale watching in Southern New England impact humpback whale (*Megaptera novaeangliae*) calf production or calf survival? *Biological Conservation* 142:2931-2940.
- Wells, R.S., H.L. Rhinehart, L.J. Hansen, J.C. Sweeney, F.I. Townsend, R. Stone, D.R. Casper, M.D. Scott, A.A. Hohn, and T.K. Rowles. 2004. Bottlenose dolphins as marine ecosystem sentinels: Developing a health monitoring system. *EcoHealth* 1(3):246-254.
- Wells, R.S., J.B. Allen, S. Hofmann, K. Bassos-Hull, D.A. Fauquier, N.B. Barros, R.E. DeLynn, G. Sutton, V. Socha, and M. Scott. 2008. Consequences of injuries on survival and reproduction of common bottlenose dolphins (*Tursiops truncatus*) along the west coast of Florida. *Marine Mammal Science* 24(4):774-794.
- Westgate, M.J., G.E. Likens, and D.B. Lindenmayer. 2013. Adaptive management of biological systems: A review. *Biological Conservation* 158:129-139.
- Whitehead, H. 2002. Estimates of the current global population size and historical trajectory for sperm whales. *Marine Ecology Progress Series* 242:295-304.
- Whitehead, H., and I.D. Jonsen. 2013. Inferring animal densities from tracking data using Markov chains. *PLoS ONE* 8:e60901.
- Wild, C.P. 2005. Complementing the genome with an "exposome": The outstanding challenge of environmental exposure measurement in molecular epidemiology. *Cancer Epidemiology, Biomarkers & Prevention* 14(8):1847-1850.
- Wiley, D.N., M.A. Thompson, R.M. Pace, and J. Levenson. 2011. Modeling speed restrictions to mitigate lethal collisions between ships and whales in the Stellwagen Bank National Marine Sanctuary, USA. *Biological Conservation* 144:2377-2381.
- Williams, B.K. 2011a. Adaptive management of natural resources: Framework and issues. *Journal of Environmental Management* 92:1346-1353.
- Williams, B.K. 2011b. Passive and active adaptive management: Approaches and an example. *Journal of Environmental Management* 92(5):1371-1378.
- Williams, B.K., J.D. Nichols, and M.J. Conroy. 2001. *Analysis and Management of Animal Populations*. San Diego, CA: Academic Press.
- Williams, R., S. Gero, L. Bejder, J. Calambokidis, S.D. Kraus, D. Lusseau, A.J. Read, and J. Robbins. 2011. Underestimating the damage: Interpreting cetacean carcass recoveries in the context of the Deepwater Horizon/BP incident. *Conservation Letters* 4:228-233.
- Williams, R., G.A. Vikingsson, A. Gislason, C. Lockyer, L. New, L. Thomas, and P.S. Hammond. 2013. Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four decades of varying environmental conditions. *ICES Journal of Marine Science* 70(6):273-1280.
- Williams, R., E. Ashe, L. Bright, M. Jasny, and L. Nowlan. 2014. Viewpoint: Marine mammals and ocean noise: Future directions and information needs with respect to science, policy and law in Canada. *Marine Pollution Bulletin* 86:29-38.
- Williams, R., C. Erbe, E. Ashe, and C.W. Clark. 2015. Quiet(er) marine protected areas. *Marine Pollution Bulletin* 100:154-161.
- Wilson, B., H. Arnold, G. Bearzi, C.M. Fortuna, R. Gaspar, S. Ingram, C. Liret, S. Probanic, A.J. Read, V. Ridoux, K. Schneider, K.W. Urian, R.S. Wells, C. Wood, P.M. Thompson, and P.S. Hammond. 1999. Epidermal diseases in bottlenose dolphins: Impacts of natural and anthropogenic factors. *Proceedings of the Royal Society B: Biological Sciences* 266:1077-1083.
- Wilson, M., H.B. Shack, P.T. Madsen, A. Surlykke, and M. Wahlberg. 2011. Directional escape behavior in allis shad (*Alosa alosa*) exposed to ultrasonic clicks mimicking an approaching toothed whale. *Journal of Experimental Biology* 214:22-29. doi: 10.1242/jeb.043323.
- Wilson, R.P., C.R. White, F. Quintana, L.G. Halsey, N. Liebsch, G.R. Martin, and P.J. Butler. 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology* 75(5):1081-1090.
- Wilson, R.P., E.L.C. Shepard, and N. Liebsch. 2008. Prying into the intimate details of animal lives: Use of a daily diary on animals. *Endangered Species Research* 4:123-137.
- Wiseman, S.B., Y. Wan, H. Chang, X. Zhang, M. Hecker, P.D. Jones, and J.P. Giesy. 2011. Polybrominated diphenyl ethers and their hydroxylated/methoxylated analogs: Environmental sources, metabolic relationships, and relative toxicities. *Marine Pollution Bulletin* 63(2011):179-188.
- Wobeser, G.A. 1981. *Diseases of Wild Waterfowl*. New York: Plenum Press.
- Wolkers, H., C. Lydersen, and K.M. Kovacs. 2004. Accumulation and lactational transfer of PCBs and pesticides in harbor seals (*Phoca vitulina*) from Svalbard, Norway. *Science of the Total Environment* 319:137-146.
- Wright, A.J., and L.A. Kyhn. 2015. Practical management of cumulative anthropogenic impacts with working marine examples. *Conservation Biology* 29:333-340.
- Yang, W.C., V.F. Pang, C.R. Jeng, L.S. Chou, and L.L. Chueh. 2006. Morbilliviral infection in a pygmy sperm whale (*Kogia breviceps*) from Taiwanese waters. *Veterinary Microbiology* 116(1):69-76.
- Yeates, L.C., and D.S. Houser. 2008. Thermal tolerance in bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Biology* 211(20): 3249-3257.
- Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69:508-515.
- Yordy, J.E., R.S. Wells, B.C. Balmer, L.H. Schwacke, T.K. Rowles, and J.R. Kucklick. 2010. Life history as a source of variation for persistent organic pollutant (POP) patterns in a community of common bottlenose dolphins (*Tursiops truncatus*) resident to Sarasota Bay, FL. *Science of the Total Environment* 408:2163-2172.
- Zanette, L., A. White, M. Allen, and M. Clinchy. Perceived predation risk reduces the number of offspring songbirds produce per year. 2011. *Science* 334:1398-1401.
- Zoeller, R.T., A.L.S. Dowling, C.T.A. Herzig, E.A. Iannoccone, K.J. Gauger, and R. Bansal. 2002. Thyroid hormone, brain development, and the environment. *Environmental Health Perspectives* 110(Suppl. 3):355-361.

# Appendix A

## Workshop Agenda

Workshop for the Committee on the Assessment of the Cumulative Effects of  
Anthropogenic Stressors on Marine Mammals

Arnold and Mabel Beckman Center of the National Academies of Sciences, Engineering, and Medicine  
100 Academy Dr, Irvine, CA 92617 • (949) 721-2200  
October 1-2, 2015

### OPEN SESSION AGENDA

#### Thursday, October 1

8:00 a.m. *Breakfast for committee members and speakers*

8:30 a.m. **Welcome and Introductions, *Peter Tyack***

9:00 a.m. **Cumulative Effects – Approaches from Global Health and Ecotoxicology**

*Moderator: Lori Schwacke*

- Jonna Mazet, University of California, Davis

10:15 a.m. *Break*

10:30 a.m. **Indirect Effects on Marine Mammals from Predators, Prey, and Competition**

*Moderator: Clint Francis*

- Tim Essington, University of Washington
- Jesse Barber, Boise State University

12:30 p.m. *Lunch for all attendees*

1:30 p.m. **Application of Biosensors to Marine Mammals**

*Moderator: Dan Crocker*

- Shekhar Bhansali, Florida International University
- Kim Anderson, Oregon State University

3:30 p.m. *Break*

3:45- **Plenary Discussion of Day 1 Topics**

5:45 p.m.

**Friday, October 2**

8:00 a.m. *Breakfast for committee members and speakers*

**8:30 a.m. Recap of Day 1 and Introductions, *Peter Tyack***

**9:00 a.m. Cumulative Effects – Review of Ecological Studies**

*Moderator: Jim Estes*

- Carrie Kappel, University of California, Santa Barbara
- Sara Maxwell, Old Dominion University

**11:00 a.m. Long-Term Monitoring and Adaptive Management**

*Moderator: John Harwood*

- Steve Beissinger, University of California, Berkeley
- Mitch Eaton, U.S. Geological Survey

1:00 p.m. *Lunch for all attendees*

**2:00 p.m. Plenary Discussion of Day 2 Topics**

3:30 p.m. *Adjourn Workshop*

# Appendix B

## Relevant Laws and Regulations

### RELEVANT U.S. LEGISLATION

In the United States, there are many statutes and regulations that are important to the well-being of marine mammals and their habitats. This appendix highlights three primary statutes that provide the general legal framework for addressing impacts to marine mammals. They are the National Environmental Policy Act (NEPA), the Endangered Species Act (ESA), and the Marine Mammal Protection Act (MMPA). The way, and extent to which, these statutes address cumulative impacts or effects varies. In addition, this appendix identifies and briefly discusses four other federal statutes that require or authorize spatial planning and conservation and management measures important to marine mammals and the protection of their habitats. These are the Ports and Waterways Safety Act, the National Marine Sanctuaries Act, the Outer Continental Shelf Lands Act, and the Magnuson-Stevens Fishery Conservation and Management Act. International laws are also discussed briefly. This appendix is not intended to be a comprehensive discussion of all laws and regulations that impact marine mammals, but rather to provide further policy context for the consideration that agencies must give to cumulative impacts of stressors and other noise on marine mammals.

#### National Environmental Policy Act (NEPA)

Congress enacted NEPA in December 1969, and President Nixon then signed the statute into law on January 1, 1970.<sup>1</sup> The stated purpose of NEPA was “[t]o declare a national policy which will encourage productive and enjoy-

able harmony between man and his environment; to promote efforts which will prevent or eliminate damage to the environment and biosphere and stimulate the health and welfare of man; to enrich the understanding of the ecological systems and natural resources important to the Nation; and to establish a Council on Environmental Quality.”<sup>2</sup> “NEPA itself does not mandate particular results” in order to accomplish these ends.<sup>3</sup> Rather, NEPA imposes only procedural requirements on federal agencies with a particular focus on requiring agencies to undertake analyses of the environmental impact of their proposals and actions.<sup>4</sup> The Council on Environmental Quality (CEQ) was established in the Executive Office of the President and is the primary agency responsible for ensuring that other federal agencies meet the requirements set forth by NEPA. The CEQ regulations promulgated under this act require consideration of cumulative impacts<sup>5</sup> and define cumulative impact as noted above.<sup>6</sup>

At the heart of NEPA is a requirement that federal agencies “include in every recommendation or report on proposals for legislation and other major Federal actions significantly affecting the quality of the human environment, a detailed statement by the responsible official on—(i) the environmental impact of the proposed action, (ii) any adverse environmental effects which cannot be avoided should the proposal be implemented, (iii) alternatives to the proposed action, (iv) the relationship between local short-term uses of man’s environment and the maintenance and enhancement of long-term productivity, and (v) any irreversible and irretrievable commitments of resources which would be involved

<sup>1</sup> (Pub. L. 91-190, 42 U.S.C. 4321-4347, January 1, 1970, as amended by Pub. L. 94-52, July 3, 1975, Pub. L. 94-83, August 9, 1975, and Pub. L. 97-258, § 4(b), Sept. 13, 1982).

<sup>2</sup> 42 U.S.C. § 4321.

<sup>3</sup> *Robertson v. Methow Valley Citizens Council*, 490 U.S. 332, 350, 109 S.Ct. 1835, 104 L.Ed.2d 351 (1989).

<sup>4</sup> See *id.*, at 349-350, 109 S.Ct. 1835.

<sup>5</sup> 40 C.F.R. § 1508.25.

<sup>6</sup> 40 C.F.R. § 1508.7.

in the proposed action should it be implemented.”<sup>7</sup> CEQ regulations clarify that “major Federal actions” may include “projects and programs entirely or partially financed, assisted, conducted, regulated, or approved by Federal agencies; new or revised agency rules, regulations, plans, policies, or procedures; and legislative proposals.” Significance, according to the regulations, is determined based on the context and intensity of the action, and the regulations require the agency to consider “[w]hether the action is related to other actions with individually insignificant but cumulatively significant impacts.”<sup>8</sup> “Significance exists if it is reasonable to anticipate a cumulatively significant impact on the environment. Significance cannot be voided by terming an action temporary or by breaking it down into small component parts.”<sup>9</sup>

The detailed statement called for in 42 U.S.C. § 4332(2)(C) is termed an Environmental Impact Statement (EIS). The CEQ regulations allow an agency to prepare a more limited document, an Environmental Assessment (EA), if the agency’s proposed action neither is categorically excluded from the requirement to produce an EIS nor would clearly require the production of an EIS.<sup>10</sup> The EA is to be a “concise public document” that “[b]riefly provide[s] sufficient evidence and analysis for determining whether to prepare an [EIS].”<sup>11</sup> If, pursuant to the EA, an agency determines that an EIS is not required under applicable CEQ regulations, it must issue a “finding of no significant impact,” which briefly presents the reasons why the proposed agency action will not have a significant impact on the human environment.<sup>12</sup> EISs and EAs developed in accordance with NEPA and the corresponding CEQ regulations are required to consider direct, indirect, and cumulative impacts.<sup>13</sup> It is worth noting that, according to CEQ regulations, NEPA does not require an EA or EIS for those actions that are categorically excluded, meaning that the responsible agency has determined that the action falls within a category of actions that do “not individually or cumulatively have a significant effect on the quality of the environment.”<sup>14</sup>

Courts have further considered how well federal agencies implement NEPA and how cumulative impacts should be addressed in environmental documents developed in accordance with NEPA. The Supreme Court has stated that, in light of agencies’ broad discretion, the role of the courts with regard to NEPA is to ensure that the agencies take a “hard look” at the environmental consequences of their proposed

major actions and alternatives.<sup>15</sup> Multiple circuit courts have weighed in on what constitutes a “hard look.”<sup>16</sup>

The Ninth Circuit has held that the analysis of cumulative impacts must “be more than perfunctory; it must provide a useful analysis of the cumulative impacts of past, present and future projects.”<sup>17</sup> Courts have also signaled that the analysis must involve more than “generalized, conclusory assertions from agency experts.”<sup>18</sup> Instead, the Ninth Circuit requires that agencies provide supporting data in a manner that can be understood by members of the public.<sup>19</sup>

Litigants have also used the NEPA “hard look” mandate to clarify federal agencies’ legal duties to consider the habitat impacts of federally licensed extractive activities. For example, in *American Oceans Campaign v. Daley*, 183 F. Supp.2d 1 (D.D.C. 2000) the court found that the environmental assessments for current fishery management plans lacked sufficient analysis of alternative habitat protection measures. Similar rulings have resulted from NEPA litigation over oil and gas development on the continental shelf or the construction of oil and liquefied natural gas terminals. In this litigation, courts may be asked whether the federal agency had a responsibility to find or fund additional research on reasonably foreseeable environmental impacts of its preferred alternative. Courts often find that the duty depends on severity of the potential impacts or the ready availability of simulation studies or models.<sup>20</sup> When scientific experts express conflicting views regarding the scope and significance of potential impacts, the courts have interpreted NEPA as affording the agency with discretion to rely on the reasonable opinions of its own qualified experts.<sup>21</sup>

Access to courts for judicial opinions such as these is most available for species listed as either endangered or threatened because the ESA has a citizen suit provision. For non-ESA-protected species, agency decisions based on insufficient or conflicting scientific evidence may be challenged as a violation of the Administrative Procedures Act.

<sup>15</sup> *Kleppe, Secretary of the Interior, et al. v. Sierra Club et al.* citing *NRDC v. Morton*.

<sup>16</sup> *Britt v. U.S. Army Corps of Eng’rs*, 769 F.2d 84, 90 (2d Cir. 1985); *Northwest Indian Cemetery Protective Ass’n v. Peterson*, 764 F.2d 581, 588 (9th Cir. 1985), rev’d on other grounds, 485 U.S. 439 (1988); *Maryland Wildlife Fed’n v. Dole*, 747 F.2d 229 (4th Cir. 1984) (reasonable alternatives must be considered but not every alternative conceivable to the mind of man).

<sup>17</sup> *Oregon Natural Resources Council Fund v. Brong* citing *Klamath-Siskiyou Wildlands Center v. BLM* (2004) citing *Ocean Advocates* 361 F.3d 1108 (2003) quoting *Kern*, 284 F.3d at 1075 (quoting *Muckleshoot Indian Tribe v. United States Forest Serv.*, 177 F.3d 800, 810 (9th Cir. 1999) for the “useful analysis...”).

*Klamath-Siskiyou* also quotes *Neighbors of Cuddy Mountain v. United States Forest Serv.*, 137 F.3d 1372, 1379-80 (9th Cir. 1998).

<sup>18</sup> *Or. Natural Res. Council Fund v. Goodman*, 505 F.3d 884, 893 (9th Cir. 2007).

<sup>19</sup> *Or. Natural Res. Council Fund v. Goodman*, 505 F.3d 884, 893 (9th Cir. 2007).

<sup>20</sup> *Roosevelt Campobello International Park Comm’n v. US EPA*, 684 F.2d 1041 (1st Cir. 1982).

<sup>21</sup> *NRDC v. Evans*, 232 F.Supp.2d 1003 (N.D. Cal. 2002).

<sup>7</sup> 42 U.S.C. § 4332(2)(C).

<sup>8</sup> 40 C.F.R. § 1508.27.

<sup>9</sup> 40 C.F.R. § 1508.27(b)(7).

<sup>10</sup> 40 C.F.R. §§ 1501.4(a)-(b).

<sup>11</sup> 40 C.F.R. § 1508.9(a).

<sup>12</sup> 40 C.F.R. §§ 1501.4(e), 1508.13.

<sup>13</sup> “Effects” and “impacts” are considered synonymous according to the CEQ regulations.

<sup>14</sup> 40 C.F.R. § 1508.4.

Under this law, courts will defer to agencies' expert judgments in interpreting and applying key statutory terms and standards, such as "harassment" or "unmitigable adverse impact." Judicial review is deferential to agency expertise but will entail an examination of information that was presented to the agency prior to its decision. Under this deferential standard of review, the agency's decision will be upheld unless the record shows the agency considered factors, including political pressures, other than those which Congress directed it to consider.<sup>22</sup>

### Endangered Species Act (ESA)

The Endangered Species Act (ESA) was passed by the U.S. Congress and signed into law in 1973.<sup>23</sup> The ESA calls for the listing and protection of endangered and threatened species, and the designation of critical habitat for endangered species. According to the ESA, an endangered species is a species that "is in danger of extinction throughout all or a significant portion of its range."<sup>24</sup> The ESA defines threatened species as those species that are "likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range."<sup>25</sup>

The U.S. Fish and Wildlife Service (FWS) is the lead agency for implementing the ESA for most species. However, most threatened or endangered anadromous fish and marine species are managed by the National Marine Fisheries Service (NMFS) with the exception of walrus, polar bear, sea otters, and sirenians, which are managed by FWS under both the ESA and the MMPA. For listing of shared species, for example, sea turtles, or for policies applicable to all species, the two agencies often issue joint listings or joint guidance, for example, on designation of critical habitat or on inter-agency consultation.

The ESA protects endangered species from both private and public actions. Section 9 of the ESA states that no one, public or private, may "take" any endangered species.<sup>26</sup> The ESA broadly defines "take" to mean "harass, harm, pursue, hunt, shoot, wound, kill, trap, capture or collect."<sup>27</sup> Section 7 of the ESA also directs federal agencies to carry out programs for the conservation of threatened and endangered species. It further requires federal agencies to ensure that their actions (i.e., all actions authorized, funded, or carried out by the agency) are not likely to jeopardize the existence of a listed species or adversely modify the critical habitat of a listed species. As part of these assurances, Section 7 also

requires agencies to consult with FWS or NMFS (Steiger, 1994) regarding any activities that may affect listed species.<sup>28</sup> "Procedurally, before initiating any action in an area that contains threatened or endangered species, federal agencies must consult with the FWS (for land based species and selected marine mammals) or NMFS (for all other marine species) to determine the likely effects of any proposed action on species and their critical habitat."<sup>29</sup>

Although the text of the ESA does not directly address cumulative impacts or effects, the implementing agencies (FWS and NMFS) and the courts have interpreted Section 7 as to require consideration of cumulative effects during the consultation process. The regulations promulgated under the ESA define "cumulative effects" as "those effects of future State or private activities, not involving Federal activities, that are reasonably certain to occur within the action area of the Federal action subject to consultation."<sup>30</sup> Guidance produced by the FWS and NMFS regarding Section 7 consultations specifically states that this more narrow definition should not be conflated with the broader definition of "cumulative impacts" used in NEPA and pertains only to ESA Section 7 analyses.<sup>31</sup> The Ninth Circuit in *Conservation Congress v. USFS* has reiterated this point also.

After listing, two other processes under Section 4 of the ESA are important. These are the requirement to prepare and update recovery plans for listed species and the obligation to designate critical habitat. The latter requirement is central to ensuring that under Section 7 federal agencies do not take or approve actions that adversely modify critical habitat or its key components. Failure to do so can be a basis for litigation, which may result in an injunction until further analysis is done. Recent developments suggest the critical habitat provisions are increasingly important in protecting the marine acoustic environment and in incorporating the latest scientific findings and impact assessment methods. In 2015, NMFS made a legal determination that newly available scientific information warranted proceeding with a petition to revise the critical habitat designation for the Southern Resident killer whale (*Orcinus orca*) Distinct Population Segment. The revision would expand the designation to include essential foraging and wintering areas along the

<sup>22</sup> *Earth Island Institute v. Hogarth*, 494 F.3d 757 (9th Cir. 2007).

<sup>23</sup> This law repealed the earlier legislation aimed at protecting "selected species" and habitats, including the Endangered Species Preservation Act of 1966 and the Endangered Species Conservation Act of 1969. The ESA has since been amended in 1978, 1979, and 1982.

<sup>24</sup> 16 U.S.C. § 1532 (6).

<sup>25</sup> 16 U.S.C. § 1532 (20).

<sup>26</sup> 16 U.S.C. § 1538 (a)(1).

<sup>27</sup> 16 U.S.C. § 1532 (19).

<sup>28</sup> 16 U.S.C. § 1536 (a). The agency first determines whether their proposed action "may affect" a listed species or its habitat. If the agency determines it may, then formal consultation with either FWS or NOAA Fisheries is automatically required. If the agency determines that the action is not likely to affect a listed species or its habitat and the consulting agency agrees with this assessment, then further formal consultation is not necessary. If, however, the consulting agency does not agree with the assessment, then a formal consultation is required. *Conservation Congress v. USFS*, 720 F.3d 1048 (9th Cir. 2013).

<sup>29</sup> *Conservation Congress v. USFS*, 720 F.3d 1048 (9th Cir. 2013) citing *Natural Res. Defense Council v. Houston*, 146 F.3d 1118, 1125 (9th Cir. 1998) and *Forest Guardians v. Johanns*, 450 F.3d 455, 457 n.1.

<sup>30</sup> 50 C.F.R. § 1508.7.

<sup>31</sup> See [https://www.fws.gov/ENDANGERED/esa-library/pdf/esa\\_section7\\_handbook.pdf](https://www.fws.gov/ENDANGERED/esa-library/pdf/esa_section7_handbook.pdf).



West Coast and adopt as a “primary constituent element” of that habitat protective underwater noise levels.<sup>32</sup> In the 2008 recovery plan for the Southern Resident killer whale, the National Oceanic and Atmospheric Administration (NOAA) did not include sound levels as a primary constituent element (PCE),<sup>33</sup> likely because of limitations of available information (Williams et al., 2014).

### Marine Mammal Protection Act (MMPA)

The MMPA was passed and signed into law in 1972 at a time when environmental issues resonated particularly strongly with the public. By 1971, 42 marine mammal protection and conservation bills had been filed in Congress (Ray and Potter, 2011). The death of hundreds of thousands of pelagic dolphins annually in the tuna fishing industry, where purse seine nets were set on dolphin schools that were associated with tuna below; the apparent impotence of the International Whaling Commission to prevent the continued decline of great whale stocks; and the harvesting of pup and juvenile harp and northern fur seals by clubbing were primary drivers of the public demand for congressional action. The MMPA charted new territory in environmental legislation by focusing on the ecosystem and requiring that marine mammals be maintained at the optimal sustainable population at which they are significant functioning elements of their ecosystem. With few exceptions, the MMPA prohibited the taking or importing any marine mammal or marine mammal product<sup>34</sup> where a “take” was defined as “harass, hunt, capture, or kill, or attempt to harass, hunt, capture, or kill.”<sup>35</sup> The rights of Alaskan Natives to take marine mammals for subsistence purposes, however, were preserved under the MMPA.<sup>36</sup>

The Act is enforced in the 200-mile Exclusive Economic Zone of the United States, and any person, vessel, or other conveyance subject to the jurisdiction of the United States is also prohibited from taking any marine mammal on the high seas.<sup>37</sup> Exemptions to these prohibitions may be made in specific cases in which the Secretary of the Interior or Commerce (depending on whether the species in question falls under FWS or NMFS jurisdiction) authorizes a permit for such activity. Permits may be acquired for scientific research; enhancing the survival or aiding in the recovery of a marine mammal stock or species; commercial and educational photography; first-time import for public display; capture of wild animal for public display; and incidental, i.e.,

nondirected, take.<sup>38</sup> An incidental take permit may be issued provided that the taking would (1) be of small numbers, (2) have no more than a “negligible impact” on those marine mammal species or stocks, and (3) not have an “unmitigable adverse impact” on the availability of the species or stock for subsistence uses.<sup>39</sup> Fisheries are allowed incidental take outside the normal permit process subject to take reduction plans that seek to reduce mortality and serious injury rates to a rate approaching zero.

Takes by harassment account for almost all takes for which permits are issued. The MMPA has defined two levels of harassment with a somewhat different definition when the harassment is caused by a “military readiness activity” or “a scientific research activity conducted by or on behalf of the Federal Government.” Level A harassment occurs when the action “has the potential to injure a marine mammal or marine mammal stock in the wild”<sup>40</sup> or for military readiness “any act that injures or has the significant potential to injure a marine mammal or marine mammal stock in the wild.”<sup>41</sup> Level B harassment occurs when the action “has the potential to disturb a marine mammal or marine mammal stock in the wild by causing disruption of behavioral patterns, including, but not limited to, migration, breathing, nursing, breeding, feeding, or sheltering.”<sup>42</sup> Or for military readiness “any act that disturbs or is likely to disturb a marine mammal or marine mammal stock in the wild by causing disruption of natural behavioral patterns, including, but not limited to, migration, surfacing, nursing, breeding, feeding, or sheltering, to a point where such behavioral patterns are abandoned or significantly altered.”<sup>43</sup>

In developing regulations to implement the MMPA in so far as acoustic harassment is concerned, NMFS has determined that injury equates to a permanent threshold shift (PTS), which is a loss of hearing within a particular frequency range that is not reversible. A temporary threshold shift (TTS) is one in which hearing sensitivity within a particular frequency range is reduced for a period of minutes to hours but recovers to its prior level of sensitivity. NMFS recently published acoustic thresholds for the onset of TTS and PTS (NMFS, 2016a) based on the best current available science. These guidelines have separate PTS thresholds for impulsive and nonimpulsive sounds for five categories of marine mammals: low-, mid-, and high-frequency cetaceans, phocids, and otariids.<sup>44</sup> For each marine mammal category

<sup>32</sup> NOAA, 80 Fed. Reg. 9682-87 (Feb. 24, 2015).

<sup>33</sup> Primary constituent element (PCE): A physical or biological feature essential for conservation upon which a critical habitat is based. See <http://www.fws.gov/nc-es/fish/glossary.pdf>.

<sup>34</sup> 16 U.S.C. § 1372.

<sup>35</sup> 16 U.S.C. § 1362. See also 50 C.F.R. § 216.3.

<sup>36</sup> 16 U.S.C. § 1371(b).

<sup>37</sup> 16 U.S.C. § 1372.

<sup>38</sup> 16 U.S.C. § 1374.

<sup>39</sup> 50 C.F.R. § 216.102; see also <http://www.nmfs.noaa.gov/pr/permits/incidental>.

<sup>40</sup> 16 U.S.C. § 1362 Sec. 3(18)(A)(i).

<sup>41</sup> 16 U.S.C. § 1362 Sec. 3(18)(B)(i).

<sup>42</sup> 16 U.S.C. § 1362 Sec. 3(18)(A)(ii).

<sup>43</sup> 16 U.S.C. § 1362 Sec. 3(18)(B)(i).

<sup>44</sup> Low-frequency cetaceans are all the baleen whales. High-frequency cetaceans are all porpoises, river dolphins, pygmy and dwarf sperm whales, all dolphins in the genus *Cephalorhynchus*, and two species of *Lanenorhynchus*, *L. australis* and *L. cruciger*. Mid-frequency cetaceans are all the odontocetes not in the high-frequency group.

two thresholds are given for impulsive sounds: one for peak sound pressure level ( $SPL_{pk}$ ) and one for cumulative sound exposure level ( $SEL_{cum}$ ) accumulated over 24 hours; and one threshold for nonimpulsive sounds: the cumulative sound exposure level ( $SEL_{cum}$ ) accumulated over 24 hours. The  $SPL_{pk}$  ranges from 202 dB re 1  $\mu$ Pa for high-frequency cetaceans to 232 dB re 1  $\mu$ Pa for otariid pinnipeds in water. The  $SEL$  values for impulsive sounds range from 155 dB re 1  $\mu$ Pa<sup>2</sup>-s for high-frequency cetaceans to 203 dB re 1  $\mu$ Pa<sup>2</sup>-s for otariids, and the threshold values for nonimpulsive sounds range from 173 dB re 1  $\mu$ Pa<sup>2</sup>-s for high-frequency cetaceans to 219 dB re 1  $\mu$ Pa<sup>2</sup>-s for otariids.

NMFS has not proposed any update to their Level B behavioral harassment criteria. They remain  $SPL_{RMS}$  of 160 dB for impulsive sounds and 120 dB for nonpulse sounds.<sup>45</sup> Currently NMFS classifies a variety of sonar signals as impulsive for Level B criteria, although the recently released Technical Guidance (NMFS, 2016a) classifies them as non-impulsive for Level A criteria. The Navy has adopted more conservative criteria for behavioral response thresholds for beaked whales (140 dB re 1  $\mu$ Pa) and for harbor porpoises (120 dB re 1  $\mu$ Pa) exposed to sonar (Finneran and Jenkins, 2012).

### Other Important U.S. Laws

The U.S. Coast Guard has responsibility to implement the Ports and Waterways Safety Act as well as to enforce all other marine environmental laws. As the international shipping community continues to address the issue of shipping noise, this law will be the basis for implementing any resulting international standards or regulations for environmentally sensitive “Areas to Be Avoided” approved by the International Maritime Organization (IMO). The Papahānaumokuākea Marine National Monument in Hawaii is an example of marine mammal habitat subject to such shipping regulations. Standards for ship noise are under consideration by a correspondence working group of the IMO’s Marine Environmental Protection Committee in which both the Coast Guard and NOAA participate. In addition, the Coast Guard conducts ship routing and port access studies under the Ports Act; the law proved to be an important authority in reducing deadly ship strikes of endangered North Atlantic right whales through real-time, whale location reporting and reduced speed limits.

The National Marine Sanctuaries Act can also be used to designate as marine protected areas those marine mammal habitats that are currently quiet, with a minimal amount of anthropogenic noise, preserving this protective status quo as a precautionary measure (Williams et al., 2015) and to offset acoustic degradation that cannot be avoided or mitigated. If a marine sanctuary is established and its management plan

identifies the in-water sound levels as sanctuary resources, federal agencies will review proposed federal activities, leases, or licenses for their potential impact on these resources. This process would protect all marine mammals that use the marine sanctuary but would be especially valuable for a species that is neither “depleted” under the MMPA nor listed under the ESA and therefore not protected by the “negligible impact” and “adversely modify” habitat provisions of those laws.

Other relevant legislation regulating the introduction of pollution stressors into the ocean are the Rivers and Harbors Act (RHA) and Clean Water Act (CWA). The RHA regulates activity affecting navigation in U.S. waters. Section 13 of the RHA, commonly named The Refuse Act, 33 U.S.C. § 407 (1976), prohibits discharge of “any refuse matter of any kind or description” into navigable waters. In a similar vein Section 404 of the CWA regulates the discharge of dredged or fill material resulting from water resource projects, infrastructure development, and mining projects in U.S. waters. Applying for a permit to discharge requires showing that steps have been taken to avoid impacts on aquatic resources.<sup>46</sup>

Marine resource development laws such as the Outer Continental Shelf Lands Act (OCSLA), as amended, and the Magnuson-Stevens Fishery Conservation and Management Act, as amended, have important environmental planning and permitting processes that are subject to judicial review under the Administrative Procedures Act or NEPA or both. The OCSLA process could be used to identify and exclude from leasing for offshore renewable energy development (e.g., wind farms) those tracts that are acoustically significant marine mammal habitat. In addition, anthropogenic noise can scatter prey and interact with fisheries extractions to reduce the quality of marine mammal habitat, especially in foraging areas near rookeries. NEPA analyses of fishery operations and catch levels provide an opportunity to review these potential impacts. Again, this could prove especially important for marine mammal life stages that are vulnerable to prey disruption but are not yet listed as MMPA-“depleted” or in danger of extinction and do not trigger Section 7 inter-agency consultation.

### INTERNATIONAL SOUND REGULATIONS

Several national and international regulatory bodies have adopted regulations or guidelines for the effects of underwater sound on marine life, including marine mammals. These share the same scientific underpinning as U.S. regulations but may emphasize different effects, different taxa, and different spatial and temporal scales.

McCarthy (2007) pointed out that low-frequency sound travels so far in the ocean that some sound sources create noise that must be treated as a transboundary pollutant.

<sup>45</sup> See [http://www.westcoast.fisheries.noaa.gov/protected\\_species/marine\\_mammals/threshold\\_guidance.html](http://www.westcoast.fisheries.noaa.gov/protected_species/marine_mammals/threshold_guidance.html).

<sup>46</sup> See [https://www.epa.gov/sites/production/files/2015-03/documents/404\\_reg\\_authority\\_fact\\_sheet.pdf](https://www.epa.gov/sites/production/files/2015-03/documents/404_reg_authority_fact_sheet.pdf).

Gillespie (2010) and McCarthy (2007) identify the United Nations Convention on the Law of the Sea (UNCLOS) as the appropriate international body to regulate ocean noise. UNCLOS article 1(4) says “‘pollution of the marine environment’ means the introduction by man, directly or indirectly, of substances or energy into the marine environment, including estuaries, which results or is likely to result in such deleterious effects as harm to living resources and marine life.” This definition includes acoustic energy along with other forms of energy if it harms marine life.

The International Maritime Organization is tasked with regulating pollution by vessels under the International Convention for the Prevention of Pollution by Ships (MARPOL Convention). In 2013, the Marine Environment Protection Committee of the IMO issued voluntary guidelines for the reduction of underwater noise from commercial shipping (MEPC 66/17).

The International Convention on Migratory Species (CMS, also known as the Bonn Convention) was signed by 117 countries (known as Parties to the Convention) under the auspices of the United Nations Environment Programme (UNEP). In 2008 the Parties to the CMS adopted resolution 9.19 on Adverse Anthropogenic Marine/Ocean Noise Impacts on Cetaceans and Other Biota, which urges the Parties to the Convention “to control the impact of emission of man-made noise pollution in habitat of vulnerable species and in areas where marine mammals or other endangered species may be concentrated.” Several regional agreements that operate under the auspices of the Bonn convention of UNEP have also established guidelines on ocean noise for their regions. The ACCOBAMS (Agreement on the Conservation of Cetaceans in the Black Sea Mediterranean Sea and Contiguous Atlantic Area) agreement has passed a resolution on “Guidelines to address the impact of anthropogenic noise on cetaceans in the ACCOBAMS area” and the ASCOBANS (Agreement on the Conservation of Small Cetaceans in the Baltic, North East Atlantic, Irish and North Seas) has issued a report on the assessment of acoustic disturbance (Bräger et al., 2009) and passed resolutions on effects of anthropogenic noise on marine mammals. The Convention for the Protection of the Marine Environment of the North-East Atlantic (the OSPAR Convention) involves the European Union (EU) and 15 European nations in support of conservation of the northeastern Atlantic. In 2009 the OSPAR Commission reviewed the effects of underwater sound on marine life, calling for more research on this problem. There are thus many international agreements, especially within Europe, that have addressed the impacts of anthropogenic noise on marine life, including the cumulative effects of noise plus other stressors, but none of these have established regulations to control these impacts.

Explicit guidelines or regulations have been developed by international or national authorities for three intense sources of underwater sound: pile driving, seismic survey, and naval sonar. Erbe (2013) describes how some countries

may prohibit seismic surveys in habitats and seasons when marine mammals are concentrated. Some countries stipulate that seismic surveys use the minimum practicable power or that construction of foundations of offshore wind turbines use methods other than pile driving in some settings. Where pile driving is used, some countries require the use of mitigation measures such as bubble curtains to reduce the sound that propagates from pile driving. Other mitigation measures required by some nations for pile driving, seismic survey, and naval sonar include visual and/or acoustic monitoring to make sure that protected animals do not enter a shutdown zone, 30 minutes of monitoring before starting transmissions to reduce the risk that animals are in the shutdown zone, and a ramp-up procedure that starts at low acoustic power and slowly increases to the full power over tens of minutes to allow animals to move away from aversive or harmful sound levels. The North Atlantic Treaty Organization (NATO) Undersea Research Centre (NURC; now called the Center for Maritime Research and Exploration) has for 50 years provided technical and scientific guidance to NATO nations on anti-submarine warfare, including the use of naval sonar. Frantzis (1998) documented an atypical mass stranding of beaked whales in the Mediterranean that coincided with a sonar trial by NURC in 1996. This evidence of adverse impact led NURC to conduct research on the effects of sonar on cetaceans and to develop Marine Mammal Risk Mitigation Rules and Procedures (NURC, 2006) for their own sonar trials that include similar mitigation measures to those listed above. However, each nation maintains its own procedures for operating naval sonar, including risk mitigation.

The EU has developed a very different strategy for protecting the marine environment and maintaining Good Environmental Status. In 2008, the EU adopted a Marine Strategy Framework Directive (MSFD) to protect the marine environment across the EU. The goal of the MSFD is to achieve Good Environmental Status (GES) by 2020 (European Union, 2008). The goals of the MSFD were to be incorporated into national legislation by July 15, 2010. Good Environmental Status represents a resilient ecosystem in which biodiversity is preserved and human effects, including pollution and noise, do not exceed that which is compatible with a functioning marine ecosystem. The Directive identifies 11 qualitative descriptors that assist member states in identifying what a GES ecosystem should look like. Qualitative Descriptor 11 deals with energy and noise. Technical Subgroups prepared implementation guidelines in 2010 and 2012. The 2010 guidelines (Tasker et al., 2010) identified three underwater noise indicators:

1. The proportion of days within a calendar year, over areas of 15°N × 15°E/W in which anthropogenic sound sources exceed either of two levels, 183 dB re 1μPa<sup>2</sup>-s (i.e., measured as SEL) or 224 dB re 1μPa peak (i.e., measured as peak sound pressure

level) when extrapolated to 1 meter, measured over the frequency band 10 Hz to 10 kHz.

2. The total number of vessels that are equipped with sonar systems generating sonar pulses below 200 kHz should decrease by at least  $x\%$  per year starting in [2012]. (The  $x\%$  was to be set by Member States.)
3. The ambient noise level measured by a statistical representative sets of observation stations in Regional Seas where noise within the 1/3 octave bands 63 and 125 Hz (center frequency) should not exceed the baseline values of year [2012] or 100 dB (re 1  $\mu$ Pa RMS; average noise level in these octave bands over 1 year).

The 2012 guidelines (Van der Graaf et al., 2012) defined an impulsive sound as “a sound for which the effective time duration of individual sound pulses is less than ten seconds and whose repetition time exceeds four times this effective time duration.” However, they abandoned the criteria established in 2010 for impulsive sounds and simply noted that “At the moment it is difficult to provide a more specific description of GES beyond the text of the Directive, due to insufficient knowledge on the cumulative impacts of impul-

sive sound on the marine environment.” In terms of ambient noise, they concluded “At the moment it is impossible to define those elevations of ambient noise from anthropogenic sources that would cause the marine environment to not be at GES. This is mainly due to a lack of knowledge on the impacts of elevated ambient noise on the marine environment. The TSG cannot therefore advise on a level of ambient noise that could be set as a target for this indicator.”

Many of the national regulations and guidelines to protect marine mammals from the effects of underwater sound emphasize short time scales (tens of minutes) and small spatial scales (hundreds of meters) around intense sound sources. However, the EU MSFD takes a much broader (regional sea) and longer (yearly) view of indicators for cumulative effects of noise to maintain good environmental status. This broader scale may be more appropriate for addressing cumulative effects of noise over time, but this approach is vulnerable to gaps in current scientific ability to predict cumulative effects of different combinations of stressors. There is currently little scientific basis for the indicators of GES for noise, but these kinds of large-scale indicators may prove to be important methods for monitoring stressors in a way that can be linked to effects.



# Appendix C

## Committee and Staff Biographies

### COMMITTEE

**Dr. Peter L. Tyack** (*Chair*) is a professor of marine mammal biology at the University of St. Andrews in Scotland and a senior scientist emeritus at the Woods Hole Oceanographic Institution. His research interests include social behavior and vocalizations of cetaceans, including vocal learning and mimicry in their natural communication systems and their responses to human noise. Dr. Tyack served on the National Academies of Sciences, Engineering, and Medicine's Ocean Studies Board from 2008 to 2013 and was a member of three previous National Research Council studies on marine mammals and sound, including the Committee on Describing Biologically Significant Marine Mammal Behavior, the Committee to Review Results of the Acoustic Thermometry of the Ocean Climate's Marine Mammal Research Program, and the Committee on Low-Frequency Sound and Marine Mammals. He has also served on the Office of Naval Research's Population Consequences of Disturbance Working Group. Dr. Tyack received his Ph.D. in animal behavior from Rockefeller University.

**Dr. Helen Bailey** is a research assistant professor at the Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science. She has published more than 30 journal articles specializing in marine mammals and sea turtles. She has studied habitat use of whales and dolphins, underwater sound levels and environmental impacts of offshore wind turbines on marine mammals, and migration pathways and hot spots of marine predators at the National Oceanic and Atmospheric Administration as part of the Census of Marine Life's Tagging of Pacific Predators project. She joined the University of Maryland in 2010, where her research focuses on studying patterns of habitat use and behavior of marine species and its application to manage-

ment and conservation. Dr. Bailey received her Ph.D. in biological sciences at the University of Aberdeen.

**Dr. Daniel E. Crocker** is a professor of biology at Sonoma State University. His research has focused on both the physiology and behavior of marine mammals. He has published widely on the metabolism, endocrinology, and toxicology of pinnipeds as well as their reproductive and foraging ecology. His current research is focused on the endocrine stress responses of marine mammals and how they vary with foraging success, fasting, and life-history stage. He is examining the interaction of stress responses with the reproductive and immune systems to better understand how stress has demographic impacts. The ultimate goal of this research is to better understand how marine mammals respond to climate variability and anthropogenic stressors. Dr. Crocker received a Ph.D. in biology from the University of California, Santa Cruz.

**Dr. James E. Estes** is a professor of ecology and marine biology at the University of California, Santa Cruz. He is an internationally known expert on marine mammals and a specialist in the critical role of apex predators in the marine environment. He has conducted field research in Alaska, California, Canada, Mexico, New Zealand, and Russia and has published more than 150 scientific articles, several books, and monographs, and has served on the editorial boards for a variety of professional societies. He is a Pew Fellow in marine conservation, a fellow of the California Academy of Sciences, and a member of the National Academy of Sciences. He received the Western Society of Naturalist's Lifetime Achievement Award in 2011 and the American Society of Mammalogists' C. Hart Merriam Award in 2012. Dr. Estes received his Ph.D. in biology/statistics from the University of Arizona.

**Dr. Clinton D. Francis** is an assistant professor in the Department of Biological Sciences at California Polytechnic State University. His research spans evolutionary ecology, community ecology, and global change biology, with a focus on avian behavior and ecology. Most of his research seeks to understand how organisms and ecological communities respond to novel environmental conditions created by human activities with an emphasis on how organisms and ecological systems respond directly and indirectly to changes in the acoustical environment. Current work includes (1) revealing links between anthropogenic forces, chronic stress, and fitness; (2) using manipulative field experiments to quantify the costs of anthropogenic noise on reproductive success; and (3) understanding how soundscapes mediate interactions between human and ecological systems. Dr. Francis received his Ph.D. in ecology and evolutionary biology at the University of Colorado.

**Dr. John Harwood** is a professor of biology at the University of St. Andrews. He is a former director of the Sea Mammal Research Unit, which advises the U.K. and Scottish governments on the conservation of seals and whales. He was also the director of the Centre for Research into Ecological and Environmental Modeling from 2004 to 2009. Currently, his main interest is in developing methods for assessing and mitigating the effects of anthropogenic disturbance on marine ecosystems. Additional research involves exploring the effects of individual variation and spatial structure on the population dynamics, genetics, and epidemiology of vertebrates, particularly marine mammals. He is currently co-chair of the Office of Naval Research's Population Consequences of Disturbance Working Group. Dr. Harwood received his Ph.D. in zoology from the University of Western Ontario.

**Dr. Lori H. Schwacke** is a biostatistician for the National Oceanic and Atmospheric Administration's National Centers for Coastal Ocean Science and Chief of the Oceans and Human Health Branch. Recognizing the parallels of studying disease in human populations and in populations of marine protected species, her research focuses on the application of statistical models developed for human medicine to assess the risk of stressors such as environmental contaminants, infectious disease, and natural toxins on marine mammals. Most recently, she has been integrally involved in the assessment of injuries to nearshore dolphin populations in the Gulf of Mexico following the *Deepwater Horizon* oil spill. Dr. Schwacke received her Ph.D. in biostatistics, epidemiology, and systems science from the Medical University of South Carolina.

**Dr. Len Thomas** is an ecological statistician at the University of St. Andrews. He is the director of the Centre for Research into Ecological and Environmental Modeling and a reader in the School of Mathematics and Statistics. He is also

part of the U.K. National Centre for Statistical Ecology and the Scottish Oceans Institute. His main research areas focus on the development of methods and software for estimating the size, density, and distribution of wild animal and plant populations, and the use of computer-intensive methods to fit and compare stochastic models of wildlife population dynamics and animal movement. Of relevance to this committee, he has led research projects developing methods for quantifying marine mammal density, distribution, and trends (particularly from passive acoustic data), analyzing cetacean behavioral response studies, and quantifying the population consequences of anthropogenic disturbance. He has also served on the BP-sponsored Working Group on Assessment of Cumulative Effects of Anthropogenic Underwater Sound, as well as the Office of Naval Research's Population Consequences of Disturbance Working Group. Dr. Thomas received his Ph.D. in forestry from the University of British Columbia.

**Dr. Douglas Wartzok** is a professor of biology at Florida International University, and the former provost, executive vice-president, and chief operating officer. His research on marine mammals has taken him from the Arctic Ocean to Antarctica to study seals, whales, and walrus. His research focuses on behavioral and physiological ecology of marine mammals; sensory systems involved in under-ice navigation by seals; and psychophysiological studies of captive marine mammals. For the past decade he has been involved in the issue of the effects of naval antisubmarine warfare sonar on marine mammals, in particular beaked whales. He recently served as chairman of the Committee of Scientific Advisors for the U.S. Marine Mammal Commission and is a former editor of *Marine Mammal Science*. He is a current member of the Ocean Studies Board, served on the National Research Council Committee on Assessing Ambient Noise in the Ocean with Regard to Potential Impacts on Marine Mammals, and chaired the Committee on Determining Biological Significance of Marine Mammal Responses to Ocean Noise. Dr. Wartzok received his Ph.D. in biophysics (neurophysiology) from Johns Hopkins University.

## STAFF

**Dr. Kim Waddell** is a senior program officer with the Gulf Research Program, after serving 3 years as a study director with the Ocean Studies Board at the National Academies of Sciences, Engineering, and Medicine in Washington, DC. His recently completed reports include *An Ecosystem Services Approach to Assessing the Impacts of the Deepwater Horizon Oil Spill in the Gulf of Mexico* and *Evaluating the Effectiveness of Fish Stock Rebuilding Plans in the United States*. Dr. Waddell rejoined the National Academies in 2011 after a 6-year hiatus during which he was a research associate professor at the University of the Virgin Islands and Texas

A&M University working to build marine and environmental research capacity in the Caribbean region. He received his Ph.D. in biological sciences from the University of South Carolina and his B.A. in environmental studies from the University of California, Santa Cruz.

**Stacey Karras** is an associate program officer with the Ocean Studies Board. She joined the National Academies of Sciences, Engineering, and Medicine in 2012 as a fellow and served as a research associate for the Ocean Studies Board between 2013 and 2015, when she took on her current role. She received her B.A. in marine affairs and policy with

concentrations in biology and political science from the University of Miami in 2007. The following year she received an M.A. in marine affairs and policy from the University of Miami's Rosenstiel School of Marine and Atmospheric Science. In 2012, she earned her J.D. from the University of Virginia School of Law.

**Payton Kulina** joined the Ocean Studies Board in June 2013 as a senior program assistant. He graduated from Dickinson College in 2010 receiving a B.A. in policy management. He is currently pursuing an M.S. degree in finance through the Kogod School of Business at American University. Prior to this position, Mr. Kulina worked as a coordinator with BP Alternative Energy, also in Washington, DC.





# Appendix D

## Glossary

**Accommodation** – A response of a biological system to an environmental stressor that restores the system to its normal or baseline condition or establishes a new set point.

**Acute Effect** – The severe, often lethal, effect of a stressor on an individual that occurs rapidly and is of short duration (see also Chronic Effect).

**Acute Exposure** – Exposure to a stressor that occurs for a single, discrete period of time (see also Chronic Exposure and Intermittent Exposure).

**Adaptive Management** – A systematic approach for improving resource management by learning from management outcomes.

**Additive Stressor Effect** – The combined effect of two or more stressors is considered additive when the shape of the dose–response function of either stressor does not change in the presence of the other stressor (see also Antagonistic Stressor Interaction, Interactions Among Stressors, Stressor, and Synergistic Stressor Interactions).

**Adverse Outcome Pathways** – A structured representation of biological events leading to adverse effects that is often considered in risk assessments.

**Aggregate Exposure** – The combined exposure to one stressor from multiple sources or pathways integrated over a defined relevant period: a day, season, year, or lifetime.

**Allostatic Load** – An organism’s cumulative physiological degradation resulting from exposure to stressors, as well as from heightened activity of physiological systems or changes in metabolism.

**Antagonistic Stressor Interaction** – The interaction of two or more stressors is considered antagonistic if the resulting effects are less than the sum of the effects of the individual stressors (see also Additive Stressor Effect, Stressor, and Synergistic Stressor Interactions).

**Bias** – The difference between a true population parameter and the expected value of the estimate of that parameter (see also Precision).

**Chronic Effect** – A stressor effect that does not immediately result in death or reproductive failure, but persists or is irreversible, and may influence long-term survival or reproductive success.

**Chronic Exposure** – Ongoing or continuously occurring exposure to a stressor (see also Acute Exposure and Intermittent Exposure).

**Cumulative Risk** – The combined risk from exposures to multiple stressors integrated over a defined relevant period: a day, season, year, or lifetime.

**Direct Effects** – When considering the influences and interactions among species, and between species and their abiotic environment, direct effects are the proximate impacts that one species or factor has on another species or factor without the effect occurring via an intervening species or factor. In the interaction webs in Chapter 6, these direct effects are depicted as single arrows pointing from one node to another node (see also Indirect Effects and Interaction Web).

**Dose** – The magnitude or amount of a stressor that is directly experienced or ingested, inhaled, or absorbed by an animal, ideally measured by a dosimeter on the animal.

**Dose–p(response) Function** – The relationship between the dose or dosage of a particular stressor and the probability of a particular response.

**Dose–Response Relationship** – The relationship between the amount of exposure (dose) to a stressor and the resulting changes in behavior, physiology, or health (response).

**Driver** – A biotic or abiotic feature of the environment that affects populations directly and/or indirectly by changing exposure to a single (or multiple) extrinsic stressor.

**Ecological Driver** – A biotic or abiotic feature of the environment that affects multiple components of an ecosystem directly and/or indirectly by changing exposure to a suite of extrinsic stressors. Ecological drivers may operate on multiple species at varying trophic levels, and may affect multiple ecosystems.

**Exposure** – Contact with or experience of a stressor, ideally measured in the environment near the animal.

**Extrinsic Stressor** – A factor in an animal’s external environment that creates stress in the animal (see also Intrinsic Stressor and Stressor).

**Health** – The ability of an organism to adapt and self-manage.

**Hearing Threshold** – The lowest intensity of a sound at a particular frequency that an organism is able to hear. These thresholds are defined as a function of frequency.

**Hearing Threshold Shift** – An increase in an organism’s hearing threshold (decrease in sensitivity), often caused by a high-intensity sound. This shift can be either temporary (temporary threshold shift, TTS) or permanent (permanent threshold shift, PTS).

**Homeostasis** – The tendency of the physiological systems of an organism to maintain internal stability in response to stimulus that might disturb its normal condition or function.

**Indirect Effects** – Interactions between species or between species and the abiotic environment that occur through one or more intervening species or abiotic factor.

**Interaction Web** – A means of considering the relationships and interactions among species, and between species and their abiotic environment as defined by Dunne et al. (2002). An interaction web is premised on the idea that the distribution and abundance of species in an ecosystem are determined by the interactions among and between species and abiotic environmental elements (see also Direct Effects and Indirect Effects).

**Interactions Among Stressors** – Interactions occur when the presence of one stressor changes the shape of the dose–response function of the other stressor (see also Additive Stressor Effect).

**Intermittent Exposure** – Exposure to a stressor that occurs intermittently, repeatedly, or in cycles (see also Acute Exposure and Chronic Exposure).

**Intrinsic Stressor** – An internal factor or stimulus that results in a significant change to an animal’s homeostatic set point. Short-term internal stresses that evoke physiological responses occurring daily to maintain an organism near its homeostatic set points *are not* considered stressors, but natural aspects of an individual’s life cycle (e.g., lactation, migration, molting, and fasting) that result in significant changes to homeostasis are considered stressors (see also Extrinsic Stressor and Stressor).

**Masking** – Acoustic interference that impedes an organism’s ability to detect biologically important signals.

**Noise** – Sounds that are unwanted by or are not useful for a receiver.

**Oxidative Stress** – Stress to an organism caused by a disturbance in the balance of prooxidants and antioxidants.

**Population Health** – The distribution of health outcomes in a population or a subset of a population, *as well as* the determinants or factors that influence those outcomes.

**Precision** – A statistical measure of the repeatability of a sample or an estimate, given by the inverse of the variance (see also Bias).

**Recovery** – Restoration of normal function after withdrawal of a stressor.

**Stressor** – Any causal factor or stimulus, occurring in either the animal’s internal or external environment, that challenges homeostasis of the animal.

**Synergistic Stressor Interactions** – The interaction of two or more stressors is considered synergistic if the resulting effects are more than that of the sum of the effects of the individual stressors (see also Additive Stressor Effect, Antagonistic Stressor Interaction, and Stressor).