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LETTER

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Predicting the impacts of anthropogenic disturbances on marine populations

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Abstract

Marine ecosystems are increasingly exposed to anthropogenic disturbances that cause animals to change behavior and move away from potential foraging grounds. Here we present a process-based modeling framework for assessing population consequences of such sub-lethal behavioral effects. It builds directly on how disturbances influence animal movements, foraging and energetics, and is therefore applicable to a wide range of species. To demonstrate the model we assess the impact of wind farm construction noise on the North Sea harbor porpoise population. Subsequently, we demonstrate how the model can be used to minimize population impacts of disturbances through spatial planning. Population models that build on the fundamental processes that determine animal fitness have a high predictive power in novel environments, making them ideal for marine management.

KEYWORDS

agent-based model, anthropogenic disturbances, cumulative effects, displacement, harbor porpoise, individual-based modeling, marine spatial planning, movement model, *Phocoena phocoena*

1 | INTRODUCTION

Human impacts on marine ecosystems are increasing globally (Halpern et al., 2015), and fisheries bycatch and anthropogenic noise in particular pose a growing threat to many species (Lewison, Crowder, Read, & Freeman, 2004; Slabbekoorn et al., 2010; Shannon et al., 2016). Whereas bycatch directly influences animal survival, noise from offshore activities is more likely to cause animals to change behavior, thereby reducing their foraging performance and fitness (Figure 1; DeRuiter et al., 2013; Francis & Barber, 2013; Pirotta, Brookes, Graham, & Thompson, 2014). Although such impacts on animal behavior are increasingly recognized, it is not yet well understood how different human activities jointly influence the persistence of wildlife populations. This continues to be a major question in ecological research and a serious obstacle for sustainable environmental management (Sutherland & Freckleton, 2012).

A key challenge in this research field has been to develop models that maintain their predictive power when applied in novel environments. This requires process-based models that build on the mechanisms that determine system behavior (Evans et al., 2013; Stillman, Railsback, Giske, Berger, & Grimm, 2015). Because impacts of anthropogenic disturbances are largely mediated by their effects on animal movement and foraging, these processes should be at the core

FIGURE 1 Examples of disturbances that influence marine populations. Both (a) pile-driving noise emitted during wind farm construction and (b) noise from seismic surveys may elicit behavioral responses in animals over vast areas. © Ballast Nedam and iStock

of models used for predicting cumulative impacts of disturbances on marine populations. One class of models that facilitates this process-based approach is agent-based models (ABMs). In ABMs, population dynamics and other system-level properties emerge from interactions among autonomous individuals (or "agents") that respond to the environment as animals do in nature (Grimm & Railsback, 2005; Grimm et al., 2005). ABMs are typically spatially explicit, which makes them ideal both for marine spatial planning aimed at minimizing population impacts of anthropogenic activities, and for environmental impact assessments.

Here we present a spatially explicit modeling framework for predicting impacts of anthropogenic disturbances on marine populations based on their influence on animal movement and fitness. We use the North Sea harbor porpoise (*Phocoena phocoena*) population as a case study, and demonstrate how the framework can be used to evaluate the impact of offshore wind farm construction noise. This type of noise is increasingly prevalent due to the high demand for green energy (Gibson, Wilman, & Laurance, 2017), and currently there are >900 offshore wind farms at various stages of development in Europe alone (https://www.4coffshore.com/windfarms/). Porpoises are strictly protected in European waters (EU, 1992), so assessing the impacts of construction noise is critical for regulators. We demonstrate how the framework can be used for spatial planning to partly mitigate population impacts of disturbances.

2 | METHODS

We constructed a model, termed DEPONS, to simulate individual animals' movements, energetics and survival in realistic landscapes. It builds on existing models of porpoise movement and energetics, where home ranges and population dynamics emerge from the animals' competition for food (Nabe-Nielsen, Tougaard, Teilmann, Lucke, & Forchhammer, 2013; Nabe-Nielsen, Sibly, Tougaard, Teilmann, & Sveegaard, 2014), but introduces a direct relationship between noise and the extent to which simulated animals are deterred. In the following we present a summary description of the model. The TRACE document (Schmolke, Thorbek, DeAngelis, & Grimm, 2010) in the online Supporting Information (SI) presents additional evidence that our model was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

2.1 | Modeling fine-scale movements and population dynamics

Animal movements are modeled using a combination of correlated random walk and spatial memory (Codling, Plank, & Benhamou, 2008; Fagan et al., 2013; Smouse et al., 2010), where the spatial memory enables animals to return to patches where they previously found food. This behavior gradually becomes prevailing when animals find little food using undirected movements. Jointly, these mechanisms enable animals to optimize their foraging behavior and produce movements that closely resemble those of satellite-tracked harbor porpoises (Nabe-Nielsen et al., 2013).

Population dynamics are linked to the individual animals' ability to maintain high energy levels. As animals move through the landscape, they use energy at a constant rate and obtain energy from food patches they pass through. Given the absence of direct data on spatial variation in prey availability, we follow the approach used in previous studies of wide ranging marine top predators and assume that patches with higher food availability occur in those parts of the landscape where observed population densities are high (Biuw et al., 2007; Robinson et al., 2012). Porpoise densities were modeled from survey data (see Gilles et al., 2016), with a relatively high degree of uncertainty, particularly in poorly sampled areas. Food gradually replenishes in patches that animals have visited. The animals' energy levels do not affect their chance of becoming pregnant, which is related to their age and time of the year, but low energy levels make them more likely to abandon lactating calves or die. Population dynamics therefore emerge from a balance between reproduction and mortality.

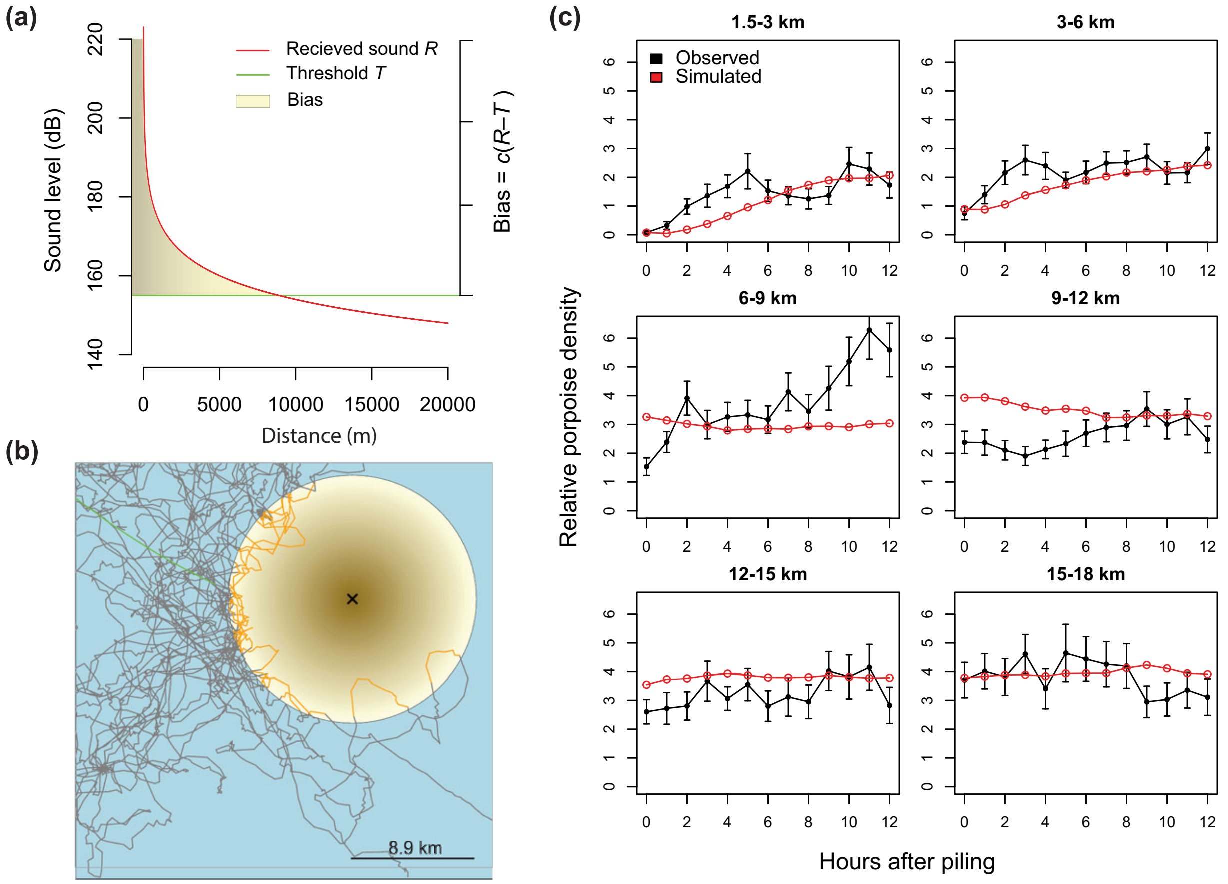

FIGURE 2 Modeling responses to noise. (a) Decrease in deterrence (bias away from noise) with distance to sound source and influence of deterrence coefficient *c* on bias. (b) Simulated movements near continuous pile-driving (black x); yellow circle shows area where animals are deterred. (c) Population recovery at different distances from nearest pile-driving. All simulations used sound source level = 234 dB (sound exposure level), as observed during construction of the Gemini wind farm, $T = 155$ dB and $c = 0.07$ (see SI for details)

2.2 | Modeling responses to noise

Simulated animals change behavior when noise increases above a threshold level *T*, which, in nature, would depend on the background noise level (Ellison, Southall, Clark, & Frankel, 2012). We assume that they respond by being biased away from the sound source and let the relationship between the bias and the part of the noise which exceeds *T* be determined by a deterrence coefficient *c* (Figure 2a). Far from the source, noise hardly biases the animals' movements, but close to the source it causes them to move almost directly away if $c \rangle\rangle 0$. The sound source level and *T* jointly determine the response distance, which is the maximum distance at which animals react to a given noise.

To ensure that animal energetics is influenced realistically by noise, *T* and *c* must be calibrated to make simulated animals respond to noise like real animals do. In the case of harbor porpoises, this movement response cannot be observed directly. Instead we monitored the population density during construction of Gemini, a Dutch offshore wind farm, by recording the echolocation sounds that porpoises use for navigating (see Williamson et al., 2016). Afterwards we created a virtual Gemini landscape where wind turbines were built in the same order, and generating the same amount of noise, as in the wind farm where porpoises had been monitored. This landscape was used for running scenarios to select the values of *T* and *c* that resulted in the most realistic local population recovery rates at different distances from the wind farm (Figure 2c). These values cause simulated porpoises to be deterred by pile-driving noise, and hence to be scared away from potential foraging grounds, in a realistic manner.

2.3 | Simulating large-scale movements

Animals occasionally switch between movement modes which enables them to make optimal use of resources in different parts of the landscape (Owen-Smith, Fryxell, & Merrill, 2010). To mimic such behavioral switching, we equipped simulated animals with a persistent memory of the net energy intake rate previously attained in different areas, which allows them to disperse towards the most profitable area when their energy stores decrease. After calibrating the animals' preferred dispersal distance, the model produced home

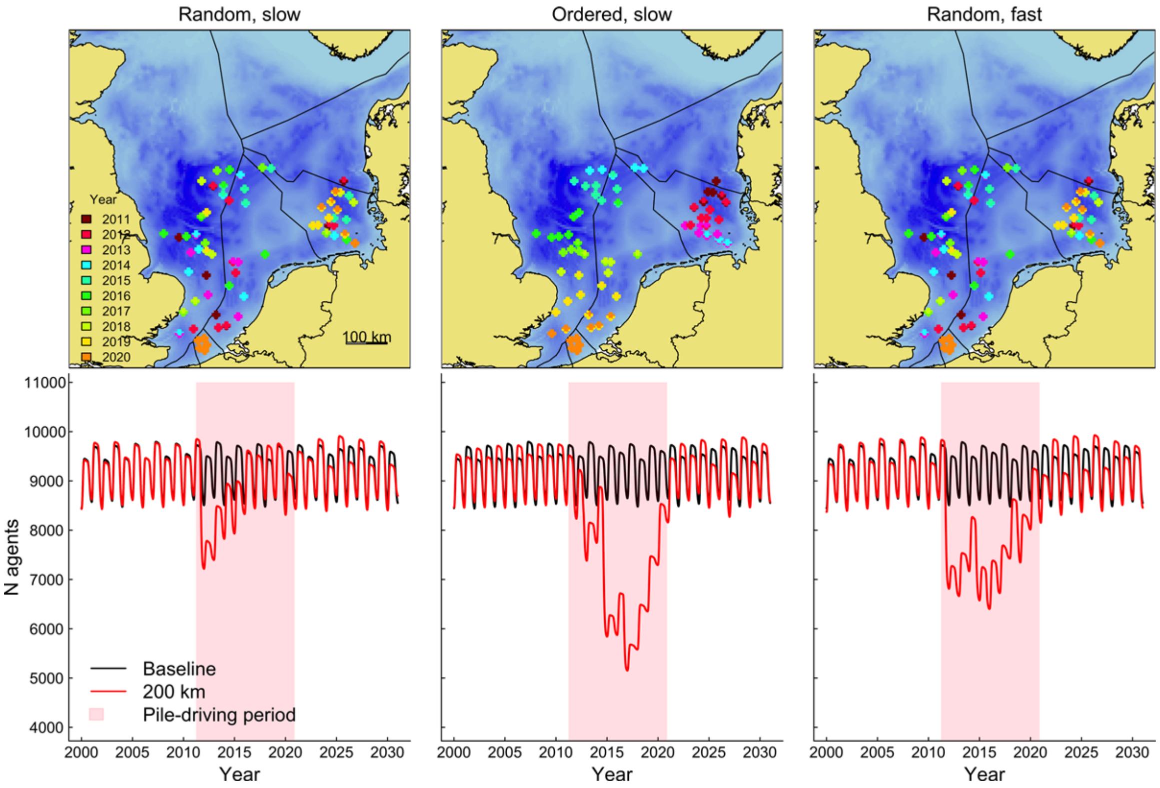

FIGURE 3 Population impacts of alternative wind farm construction schedules in scenarios with a response distances of 200 km. The number of simulated porpoises was counted in the entire North Sea landscape. Fast construction means using a short break between consecutive pilings. Colored dots indicate wind farms with 60 turbines each; dark blue indicates areas with high food levels. If we assume a response distance of 8.9 km, as for the Gemini wind farm, population dynamics are indistinguishable from the baseline scenario

ranges that resembled those observed for satellite-tracked porpoises in the North Sea (see Figure S10 in SI).

2.4 | Noise scenarios

To assess the impact of wind farm construction noise on the North Sea porpoise population we developed a range of scenarios. All scenarios except the noise-free baseline scenario included pile-driving noise from 3,900 turbines distributed on 65 wind farms (Figure 3). These were placed at random in 15–40 m water depth, with a number per country corresponding to the EU 2020 renewable energy target (EU, 2009). Scenarios included three different construction schedules: (1) wind farms built in random order; (2) wind farms built in eastern North Sea first, then in the west; (3) construction order as in the first scenario, but with a 1-day break between consecutive piling events instead of the 2-day break used in the other scenarios. Each schedule was used in combination with either a response distance of 8.9 km (realistic deterrence, based on calibrated values of T and c; Figure 2b) or a response distance of 200 km. This extreme distance was used to amplify the population's response to the choice of construction schedule to better demonstrate how impacts of disturbances can be reduced using spatial planning.

3 | RESULTS

Assuming that noise influenced porpoise movements as observed by the Gemini wind farm, the North Sea porpoise population was not affected by construction of 65 wind farms as required to meet the EU renewable energy target. Local population densities around the Gemini wind farm recovered 2–6 hours after piling, and similar recovery rates were obtained in the model after calibrating the individual animals' response to noise (Figure 2c). At the North Sea scale, population dynamics were indistinguishable from those in the noise-free baseline scenario when porpoises reacted to noise up to 8.9 km from the construction sites, as in Gemini (Figure 4). Wind farm construction noise only influenced population dynamics in the North Sea landscape when simulated animals were assumed to respond at distances exceeding 20–50 km from the wind farms (Figure 4). In these scenarios, the population effect of noise was more strongly related to the distance at which animals reacted to noise than to the deterrence coefficient c, or to the amount of time animals remained deterred after the noise stopped (residual disturbance; Merchant, Faulkner, & Martinez, 2017. See sensitivity analysis in SI).

Wind farm construction schedules and the length of the breaks between individual piling events influenced the

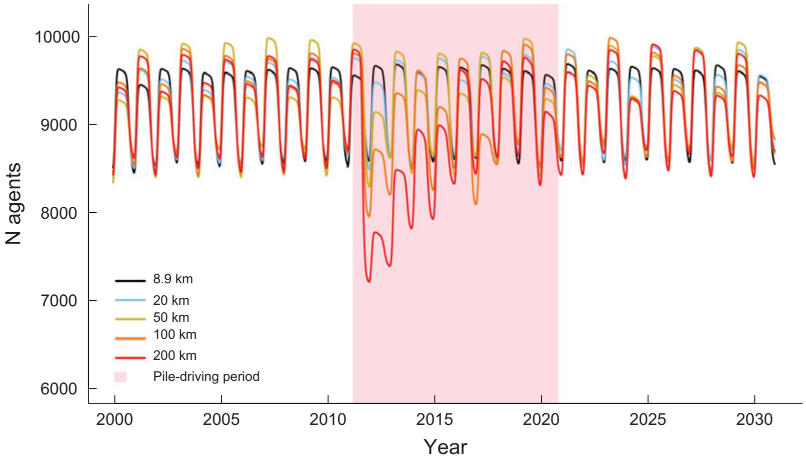

FIGURE 4 Population impacts of wind farm construction based on the “Random, slow” scenario when assuming different response distances. Response distances of 20, 50, 100, and 200 km are obtained by reducing *T* to 148, 140, 134, and 128 dB, respectively, retaining a sound source level of 234 dB (sound exposure level). Each line shows the mean value for eight simulations. The red line is identical to the one in Figure 3

population effects of noise. When the best foraging grounds in the western North Sea were continuously exposed to noise for several years, as in the “ordered” scenario (Figure 3), the effect of noise was larger and more persistent than when wind farms were constructed in random order. Similarly, when wind farm construction involved near continuous pile driving, as in the “fast” scenario, the population effects were larger than when local densities had more time to recover between consecutive pilings. This demonstrates how the modeling framework can be used for spatial planning to help mitigate population effects of disturbances.

4 | DISCUSSION

We present a mechanistically realistic framework for assessing population effects of anthropogenic disturbances in marine environments. We used harbor porpoise and offshore wind farm construction noise as an example. However, the processes that lie at the core of the framework, with autonomous individuals that strive to forage optimally, but become energetically stressed when deterred by noise, are general and not restricted to particular environmental conditions or species. Models that build on such general relationships are likely to maintain their predictive power under changing environmental conditions (Grimm & Berger 2016; Stillman et al., 2015), which makes them valuable to support environmental management. This contrasts with models that are based on statistical relationships among parameters (Evans et al., 2013), such as a direct relationship between population growth and noise, because statistical relationships may implicitly rely on factors that change under novel conditions. The modeling framework presented here is one of the first to link population effects of disturbances directly to the impacts that these have on animal movements and energetics (but see Costa et al., 2016), and we hope it will inspire a new direction for marine management.

Mechanistic models also have the advantage that they can be used for pinpointing processes that a species is particularly sensitive to, and therefore require further research. Dynamics of the harbor porpoise population were, for example, most sensitive to the distance at which animals responded to pile driving noise, and it is therefore important to collect data from more wind farm construction sites to test whether the response distance we found for Gemini is representative. In our study, population effects only became discernible when the response distance exceeded 20–50 km. This finding is, however, sensitive to how fast food replenishes after being eaten, and the impact of noise is smaller if food replenishes faster (Figure S18 in SI). In our study the food replenishment rate was estimated based on satellite tracking data, with a large degree of uncertainty (see Section 4.4 in SI). Population dynamics were also sensitive to other parameters related to energetics. Future research should therefore focus on gathering more data on animal energetics and the dynamics of their food, and particularly on investigating at which distance they respond to noise.

Our results show how ABMs can be used in spatial planning to reduce population effects of disturbances. Wind farm construction affected the population most strongly when important foraging grounds were continuously exposed to noise for several years (the “Ordered, slow” scenario, assuming response distances of 200 km; Figure 3). This continuous noise exposure caused most animals to move out of the profitable foraging areas, which resulted in substantial population declines. By the time wind farm construction had terminated in the profitable areas, few surviving animals remembered them, so instead animals dispersed at random from the areas where construction now commenced. This caused the population to decline further. The importance of allowing sufficient time for local populations to recover was also visible in scenarios using a fast piling schedule. Such effects of wind farm construction schedule could not have been detected if impacts had been calculated by combining population density maps and noise pressure maps (e.g., Maxwell et al., 2013; Merchant et al., 2017), as this method ignores the animals' ability to avoid noise by temporarily moving away, which is what causes the population impacts to be relatively small in the "Random slow" scenario. The complex, yet realistic, effects of varying the timing and spatial distribution of disturbances demonstrated here can only be adequately investigated using movement-based mechanistic frameworks.

The DEPONS model resembles other models of marine species in that a number of simplifying assumptions have been introduced to maintain model tractability and due to uncertainty in the available data (see Pirotta et al., 2018). One of the key assumptions in our study is that population density is a good proxy for food availability. Although this assumption is likely to hold true for harbor porpoises, as they rely on a continuously high food intake (Kastelein, Helder-Hoek, & Jennings, 2018; Wisniewska et al., 2016), lack of suitable fish survey data and uncertainty over the factors affecting prey availability prevent empirical testing of this assumption. The study also assumes that the satellite-tracked porpoises used for parameterizing movement are representative for North Sea animals, as animal home range sizes influence their access to resources. Further, it assumes that the animals' reaction to noise is accurately captured by variations in their echolocation activity. For porpoises, changes in echolocation activity are mirrored in aerial survey data (Dähne et al., 2013; Williamson et al., 2016), but the validity of the assumption should be reconsidered when using the model for other species.

Our model builds on general relationships between population regulation and resource availability (Goss-Custard et al., 2006; Sinclair, 2003), which makes it applicable to a wide range of species, provided that movement data are available. This includes several species of birds, cetaceans, and possibly fish, which are groups that have been reported to be displaced by noise (Gibson et al., 2017; Shannon et al., 2016). It differs from previous models developed for assessing impacts of anthropogenic disturbances in marine environments (Langton, Davies, & Scott, 2014; Topping & Petersen 2011; Warwick-Evans, Atkinson, Walkington, & Green, 2018) in explicitly considering the links between disturbances/noise, animal movement, fitness and population dynamics. The generality of the processes included in the model should, in principle, allow realistic population dynamics to emerge, but lack of independent data currently precludes corroboration of model predictions. Therefore the support for our model being realistic enough for its intended purpose relies on the rationale of pattern-oriented modeling (POM; Grimm & Railsback, 2012, Grimm et al., 2005). In POM, patterns observed in reality at different scales and levels of organization are used to reject unrealistic models and/or parameter values. The more patterns a model reproduces simultaneously, the more likely it validly represents reality. In our case, we made the model reproduce three different patterns (Section 6 in SI), suggesting a quite high level of structural realism, notwithstanding the uncertainties mentioned above.

Arguably the most useful feature of spatially explicit, process-based models is that they can capture the cumulative impacts of different kinds of anthropogenic disturbances, including noise, bycatch, and commercial use of potential food resources, and take account of when and where the disturbances occur. This, combined with their capacity to directly incorporate the mechanisms that regulate wildlife populations, is critical for predicting dynamics of populations in human influenced environments (Zurell et al., 2015). Population persistence–or not–depends on the responses of individual animals to all these pressures, so process-based models will be increasingly important in protecting vulnerable wildlife populations as human impacts on marine environments continue to increase.

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REFERENCES

Biuw, M., Boehme, L., Guinet, C., Hindell, M., Costa, D., Charrassin, J.-B., … Fedak, M. A. (2007). Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 13705–13710.

Codling, E. A., Plank, M. J., & Benhamou, S. (2008). Random walk models in biology. *Journal of the Royal Society Interface*, *5*, 813–834.

Costa, D. P., Schwarz, L., Robinson, P., Schick, R. S., Morris, P. A., Condit, R., … Kilpatrick, A. M. (2016). *A bioenergetics approach to understanding the population consequences of disturbance: Elephant seals as a model system. Eff. Noise Aquat. Life II, Advances in Experimental Medicine and Biology*. New York: Springer.

Dähne, M., Gilles, A., Lucke, K., Peschko, V., Adler, S., Krügel, K., … Siebert, U. (2013). Effects of pile-driving on harbour porpoises

(*Phocoena phocoena*) the first offshore wind farm in Germany. *Environmental Research Letters*, *8*, 25002.

DeRuiter, S. L., Southall, B. L., Calambokidis, J., Zimmer, W. M. X., Sadykova, D., Falcone, E. A., … Tyack, P. L. (2013). First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. *Biology Letters*, *9*, 20130223.

Ellison, W. T., Southall, B. L., Clark, C. W., & Frankel, A. S. (2012). A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. *Conservation Biology*, *26*, 21–28.

EU. (1992). *Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora*.

EU. (2009). *Directive 2009/28/EC of the European Parliament and of the Council of 23 April 2009 on the promotion of the use of energy from renewable sources and amending and subsequently repealing Directives 2001/77/EC and 2003/30/EC (Text with EEA relevance)*.

Evans, M. R., Bithell, M., Cornell, S. J., Dall, S. R. X., Díaz, S., Emmott, S., … Benton, T. G. (2013). Predictive systems ecology. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131452,.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., … Mueller, T. (2013). Spatial memory and animal movement. *Ecology Letters*, *16*, 1316–1329.

Francis, C. D., & Barber, J. R. (2013). A framework for understanding noise impacts on wildlife: An urgent conservation priority. *Frontiers in Ecology and the Environment*, *11*, 305–313.

Gibson, L., Wilman, E. N., & Laurance, W. F. (2017). How green is "green" energy? *Trends in Ecology & Evolution*, *17*, 922–935.

Gilles, A., Viquerat, S., Becker, E. A., Forney, K. A., Geelhoed, S. C. V., Haelters, J., … Aarts, G. (2016). Seasonal habitat-based density models for a marine top predator, the harbor porpoise, in a dynamic environment. *Ecosphere*, *7*, e01367.

Goss-Custard, J. D., Burton, N. H. K., Clark, N. A., Ferns, P. N., McGrorty, S., Reading, C. J., … Worrall, D. H. (2006). Test of a behavior-based individual-based model: Response of shorebird mortality to habitat loss. *Ecological Applications*, *16*, 2215–2222.

Grimm, V., & Berger, U. (2016). Structural realism, emergence, and predictions in next-generation ecological modelling: Synthesis from a special issue. *Ecological Modelling*, *326*, 177–187.

Grimm, V., & Railsback, S. F. (2005). *Individual-based modeling and ecology*. Princeton University Press, Princeton, New Jersey, USA.

Grimm, V., & Railsback, S. F. (2012). Pattern-oriented modelling: A "multi-scope" for predictive systems ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 298–310.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., … DeAngelis, D. L. (2005). Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science*, *310*, 987–991.

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., … Walbridge, S. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications*, *6*, 7615.

Kastelein, R. A., Helder-Hoek, L., & Jennings, N. (2018). Seasonal changes in food consumption, respiration rate, and body condition of a male harbor porpoise (*Phocoena phocoena*). *Aquatic Mammals*, *44*, 76–91.

Langton, R., Davies, I. M., & Scott, B. E. (2014). A simulation model coupling the behaviour and energetics of a breeding central place forager to assess the impact of environmental changes. *Ecological Modelling*, *273*, 31–43.

Lewison, R. L., Crowder, L. B., Read, A. J., & Freeman, S. A. (2004). Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology & Evolution*, *19*, 598–604.

Maxwell, S. M., Hazen, E. L., Bograd, S. J., Halpern, B. S., Breed, G. A., Nickel, B., … Costa, D. P. (2013). Cumulative human impacts on marine predators. *Nature Communications*, *4*, 2688.

Merchant, N. D., Faulkner, R. C., & Martinez, R. (2017). Marine noise budgets in practice. *Conservation Letters*, *44*

Nabe-Nielsen, J., Sibly, R. M., Tougaard, J., Teilmann, J., & Sveegaard, S. (2014). Effects of noise and by-catch on a Danish harbour porpoise population. *Ecological Modelling*, *272*, 242–251.

Nabe-Nielsen, J., Tougaard, J., Teilmann, J., Lucke, K., & Forchhammer, M. C. (2013). How a simple adaptive foraging strategy can lead to emergent home ranges and increased food intake. *Oikos*, *122*, 1307–1316.

Owen-Smith, N., Fryxell, J. M., & Merrill, E. H. (2010). Foraging theory upscaled: The behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B*, *365*, 2267–2278.

Pirotta, E., Brookes, K. L., Graham, I. M., & Thompson, P. M. (2014). Variation in harbour porpoise activity in response to seismic survey noise. *Biology Letters*, *10*, 20131090.

Pirotta, E., Mangel, M., Costa, D. P., Mate, B., Goldbogen, J. A., Palacios, D. M., … New, L. (2018). A dynamic state model of migratory behavior and physiology to assess the consequences of environmental variation and anthropogenic disturbance on marine vertebrates. *The American Naturalist*, *191*, E40–E56.

Robinson, P. W., Costa, D. P., Crocker, D. E., Gallo-Reynoso, J. P., Champagne, C. D., Fowler, M. A., … Yoda, K. (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.

Schmolke, A., Thorbek, P., DeAngelis, D. L., & Grimm, V. (2010). Ecological models supporting environmental decision making: A strategy for the future. *Trends in Ecology & Evolution*, *25*, 479–486.

Shannon, G., McKenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E., … Wittemyer, G. (2016). A synthesis of two decades of research documenting the effects of noise on wildlife. *Biological Reviews*, *91*, 982–1005.

Sinclair, A. R. E. (2003). Mammal population regulation, keystone processes and ecosystem dynamics. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *358*, 1729–1740.

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., & Popper, A. N. (2010). A noisy spring: The impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution*, *25*, 419–427.

Smouse, P. E., Focardi, S., Moorcroft, P. R., Kie, J. G., Forester, J. D., & Morales, J. M. (2010). Stochastic modelling of animal movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2201–2211.

Stillman, R. A., Railsback, S. F., Giske, J., Berger, U., & Grimm, V. (2015). Making predictions in a changing world: The benefits of individual-based ecology. *Bioscience*, *65*, 140–150.

Sutherland, W. J., & Freckleton, R. P. (2012). Making predictive ecology more relevant to policy makers and practitioners. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 322–330.

Topping, C., & Petersen, I. K. (2011). *Report on a Red-throated Diver agent-based model to assess the cumulative impact from offshore wind farms* (pp. 44). Aarhus C, Denmark: Aarhus University, DCE–Danish Centre for Environment and Energy.

Warwick-Evans, V., Atkinson, P. W., Walkington, I., & Green, J. A. (2018). Predicting the impacts of wind farms on seabirds: An individual-based model. *Journal of Applied Ecology*, *55*, 503–515.

Williamson, L. D., Brookes, K. L., Scott, B. E., Graham, I. M., Bradbury, G., Hammond, P. S., & Thompson, P. M. (2016). Echolocation detections and digital video surveys provide reliable estimates of the relative density of harbour porpoises. *Methods in Ecology and Evolution*, *7*, 762–769.

Wisniewska, D. M., Johnson, M., Teilmann, J., Rojano-Doñate, L., Shearer, J., Sveegaard, S., … Madsen, P. T. (2016). Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Current Biology*, *26*, 1441–1446.

Zurell, D., Eggers, U., Kaatz, M., Rotics, S., Sapir, N., Wikelski, M., … Jeltsch, F. (2015). Individual-based modelling of resource competition to predict density-dependent population dynamics: A case study with white storks. *Oikos*, *124*, 319–330.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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