



Use of Our Future Seas: Relevance of Spatial and Temporal Scale for Physical and Biological Indicators

Neda Trifonova^{1*}, Beth Scott¹, Michela De Dominicis² and Judith Wolf²

¹ School of Biological Sciences, University of Aberdeen, Aberdeen, United Kingdom, ² National Oceanography Centre, Liverpool, United Kingdom

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*Correspondence:

Neda Trifonova
neda.trifonova@abdn.ac.uk

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There is about to be an abrupt step-change in the use of our coastal seas, specifically by the addition of large-scale offshore renewable energy developments to combat climate change. Many trade-offs will need to be weighed up for the future sustainable management of marine ecosystems between renewables and other uses (e.g., fisheries, marine protected areas). Therefore, we need a much greater understanding of how different marine habitats and ecosystems are likely to change with both natural and anthropogenic transformations. This work will present a review of predictive Bayesian approaches from ecosystem level, through to fine scale mechanistic understanding of foraging success by individual species, to identify consistent physical (e.g., bottom temperature) and biological (e.g., chlorophyll-*a*) indicators of habitat and ecosystem change over the last 30 years within the North Sea. These combined approaches illuminate the feasibility of integrating knowledge across scales to be able to address the spatio-temporal variability of biophysical indicators to ultimately strengthen predictions of population changes at ecosystem scales across broadly different habitat types. Such knowledge will provide an effective baseline for more strategic and integrated approaches to both monitoring studies and assessing anthropogenic impacts to be used within marine spatial planning considerations.

Keywords: marine ecosystem, marine spatial planning, climate change, fisheries, marine protected areas, seabirds and marine mammals, potential energy anomaly, net primary production

INTRODUCTION

There is clear evidence of climate change within shallow seas, which are being affected by rising temperatures, for example, the well-studied United Kingdom waters north of Scotland and the North Sea have suffered rapid warming with temperatures increasing by up to 0.24°C per decade (Tinker et al., 2020). Latest projections imply increased coastal-flood risk due to sea-level rise (Horsburgh et al., 2020), reduced oxygen (Mahaffey et al., 2020; Wakelin et al., 2020), and exacerbating impacts from ocean acidification (Humphreys et al., 2020). These physical changes are having an impact throughout the food web, with effects on abundance, distribution, and biodiversity, seen in plankton (Edwards et al., 2020), fish (Wright et al., 2020), seabirds (Mitchell et al., 2020), and mammals (Evans and Waggitt, 2020).

One of the more likely solutions to combat climate change is the introduction of large-scale offshore renewable energy (ORE) developments (wind, tidal and wave) of 100 s of gigawatts (GW) (IRENA, 2019). However, the introduction of new structures and the extraction of more energy

either from wind, wave or tides will have cumulative effects within the world's shallow seas and therefore will also influence whole ecosystems. The size of these developments may also end up using more than 30% of coastal sea space (**Figure 1**), and some of the consequences that will most likely follow include physical habitat change (De Dominicis et al., 2018), displacement of fisheries (Kafas et al., 2017) and possible creation of de facto marine protected areas (MPAs) (Raoux et al., 2019).

However, to be able to move toward a much better evidence base for marine spatial planning (MSP), there is the need to identify and quantify the impacts separately from both climate change and ORE developments. To do this, we first need to understand how marine habitats are likely to change across different spatial scales and over time and so too their associated ecosystem characteristics, specifically their structures and function. To address this, we need to define indicators of habitat and ecosystem change but first we need to assess what makes a good indicator of change in marine ecosystems. It is generally assumed that visible top predators, such as seabirds and mammals, are sirens of ecosystem change. However, often nothing other than annual productivity and/or foraging trip durations are measured (Wanless et al., 2009; Russell et al., 2014), and without measured linkages to other physical and/or biological indicators at an ecosystem scale, it is not clear what exactly are they indicating that is changing. As an example, a series of studies that has tried to understand the details in the ecosystem linkages that drive kittiwake annual breeding success (Eerkes-Medrano et al., 2017) has shown that there is a need to understand more detail about other trophic levels and in this case, not only the biomass but the phenology of zooplankton is essential to include to predict kittiwake breeding success. Therefore, the increase in knowledge about which indicators to use and what they are telling us about how the ecosystem is functioning is necessary to add to the use of top predators and will ultimately guide future studies across a range of spatial and temporal scales and will reduce uncertainties of direct and indirect effects on populations across a range of trophic levels. Full understanding, due to the complex nature of ecosystems is challenging, however, we need to have pragmatic approaches to deal with the rapid expansion of ORE that is happening now (IRENA, 2019).

In this review, we suggest making the direct use of physical (e.g., bottom temperature) and biological (e.g., net primary production) indicators, that will be impacted by both predicted climate change and large-scale ORE extraction (Boon et al., 2018; Sadykova et al., 2020; **Figure 2**). An indicator is a physical and/or biological ecosystem component, that could be seen described as an environmental predictor, a response, or a pressure but we choose to use the terminology "indicator" to describe ecosystem components that have been found to help predict ("indicate") habitat and/or ecosystem change over the last 30 years within the North Sea. The indicators are defined based on the literature reviewed for this study scoping the range of variables found to be significant drivers of variation, or direction of change, in either behaviors, distributions and/or population dynamics of the highly mobile top predator marine species from very fine spatial scales through to large ecosystem scales, thus delivering

an understanding of the indicators of habitat and ecosystem change in the North Sea over the last 30 years. We present evidence from a range of case studies from large ecosystem-level through to fine spatial scales which show that the defined physical and biological indicators are effective predictors of habitat and ecosystem change. The results presented are based on recent novel modeling approaches and outputs, with the aim to effectively integrate and combine knowledge across spatial scales (i.e., individuals to populations and meta-populations). We reviewed the outputs to ensure that those are the models that have the highest confidence and are the most consistently predictable indicators of ecosystem change to ultimately increase certainty of predictions of future population changes and ecosystem dynamics. We synthesize what we have learned from marine ecosystem modeling approaches with respect to understanding the impacts of climate change and large-scale ORE developments, with the aim to effectively use and communicate their combined outputs to increase confidence in model projections and obtain more holistic knowledge of complex ecological systems. Finally, we discuss the implications from our synthesis and propose possible directions for future research and approaches with the aim to better utilize knowledge from existing data sources, survey techniques and modeling formulations to help guide future multitrophic studies to be performed at the most meaningful ecological scales for the types of investigations being proposed.

BACKGROUND

The Importance of Spatial and Temporal Scale to Define Specific Indicators

The spatial and temporal scale of physical and biological indicators is a challenging issue with respect to understanding the multiplicity of mechanisms underlying observed patterns and variability changes (Wiens, 1989, 1990; Levin, 1992) and especially the trophic interactions of highly mobile marine animals (fish, seabirds, and marine mammals) within dynamic marine environments. Case studies from around the globe represent the complexity between scale and the need to define indicators to be able to support management and conservation: e.g., Bay of Fundy (Johnston et al., 2005; Johnston and Read, 2007), Florida Bay (Torres et al., 2008), Pacific coast (Zamon, 2001), south coast of Australia (Ropert-Coudert et al., 2009), southern oceans (Bost et al., 2009). Recognizing the spatial and temporal heterogeneity of physical and biological indicators to understand habitat suitability, species distribution and behavior has been discussed on a wider scale for different cetacean species (Chavez-Rosales et al., 2019), but also on a finer scale for fish in the California current (Sabal et al., 2020), elephant seals in the Pacific Ocean (Abrahms et al., 2018) and whales in the Mediterranean (Cotté et al., 2011). These examples illustrate the importance of scale-dependent interplay between the physical environment, individual fitness, predator-prey interactions, and the mechanisms that drive population dynamics at multiple scales.

The North Sea has been considered as a coastal biome (Longhurst, 2010), a large marine ecosystem

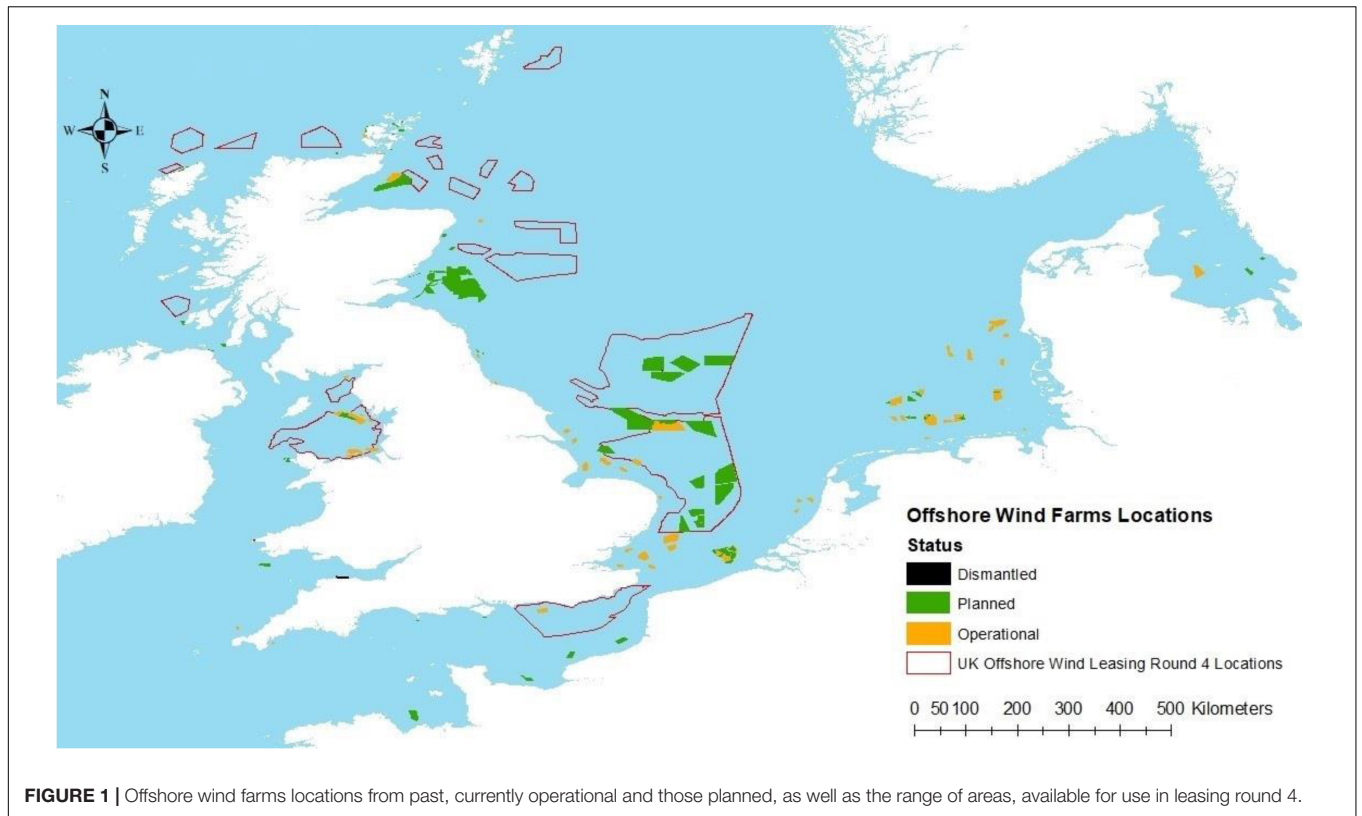


FIGURE 1 | Offshore wind farms locations from past, currently operational and those planned, as well as the range of areas, available for use in leasing round 4.

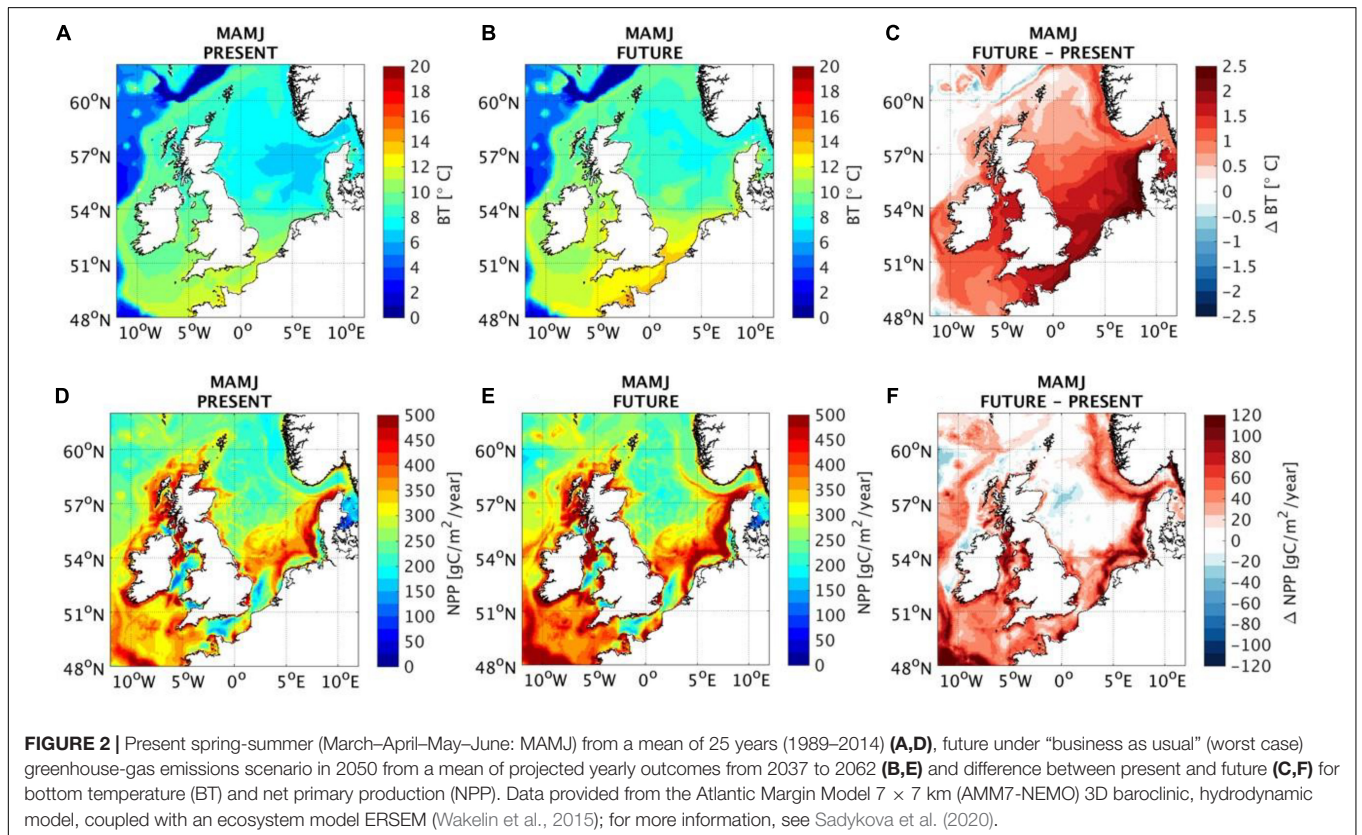
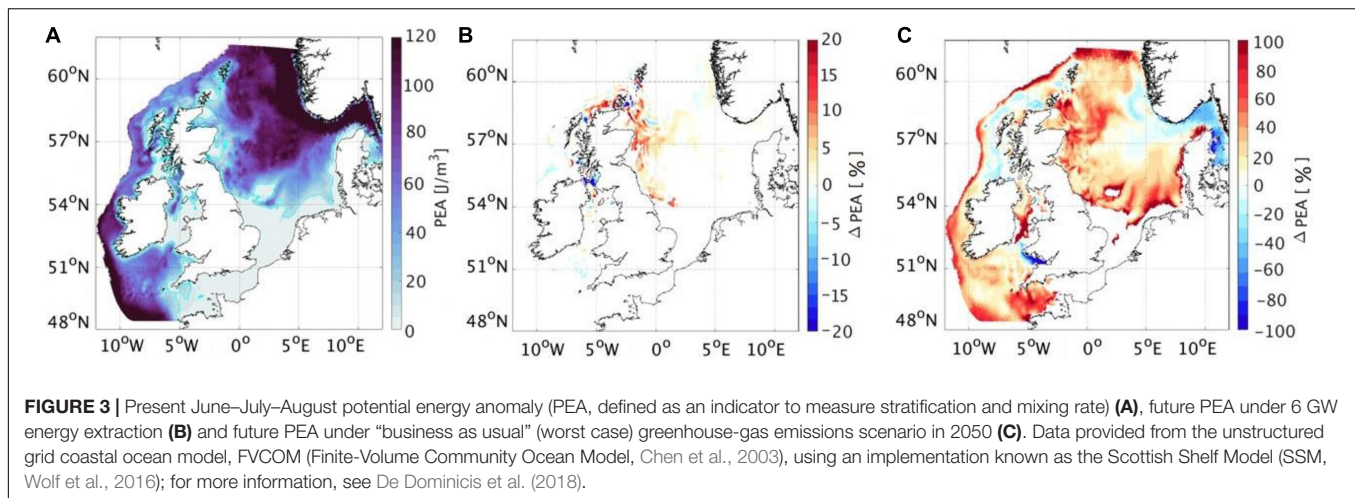


FIGURE 2 | Present spring-summer (March–April–May–June: MAMJ) from a mean of 25 years (1989–2014) (A,D), future under “business as usual” (worst case) greenhouse-gas emissions scenario in 2050 from a mean of projected yearly outcomes from 2037 to 2062 (B,E) and difference between present and future (C,F) for bottom temperature (BT) and net primary production (NPP). Data provided from the Atlantic Margin Model 7×7 km (AMM7-NEMO) 3D baroclinic, hydrodynamic model, coupled with an ecosystem model ERSEM (Wakelin et al., 2015); for more information, see Sadykova et al. (2020).



(Sherman et al., 2009) and a specific ecoregion (Spalding et al., 2007), but several studies demonstrate the need for detailed physical and biological understanding at a finer scale (Embling et al., 2012; Jones et al., 2014; Scales et al., 2017; Cox et al., 2018; Sadykova et al., 2020). The high hydrodynamic variability of some central North Sea areas, due to the large variability in duration of mixed and stratified conditions, described by van Leeuwen et al. (2016), suggests the hypothesis that such areas might be characterized by a more heterogeneous spatial pattern on a finer scale.

Physical and biological processes exhibit high spatial variability in the oceans (Tweddle et al., 2018). For example, there are large differences over small spatial distances in vertical gradients in light levels (Falkowski and Raven, 2013), horizontal and vertical gradients in temperature and salinity (Boyer et al., 2013), turbulent mixing (Simpson and Sharples, 2012), nutrient concentrations (Hydes et al., 2001; Boyer et al., 2013; Tweddle et al., 2013), phytoplankton concentrations and primary productivity (Behrenfeld et al., 2006), as well as predator-prey species distributions (Scott et al., 2010; Kaltenberg and Benoit-Bird, 2013). Many of these processes also vary temporally in their occurrence and as such, the distributions of highly mobile marine top predators across oceanographically dynamic areas may vary over both large (seasonal) and short (bi-weekly) temporal scales, due to seasonal stratification and the bi-weekly formation of tidal-mixing fronts (Johnston et al., 2005; Scales et al., 2014; IJsseldijk et al., 2015; Cox et al., 2016). Therefore, temporal changes in highly mobile top predator distributional patterns are likely to reflect those of their preferred prey, which may, in turn, be bottom-up driven by dynamic oceanographic processes (Cox et al., 2018). Such spatio-temporal variability has implications for the ecosystem structure and function and ecosystem responses to disturbances, all of which are likely to be scale dependent (Fauchald et al., 2011; Trifonova et al., 2015, 2021; Preciado et al., 2019; Heim et al., 2021).

Stratification of the water column is a key control for coastal shelf seas, as it is the main determinant in the spatial distribution of habitat types (Sharples et al., 2020). The timing and strength of stratification, which is mainly determined by annual season

weather patterns, tidal forcing, and depth (Simpson and Sharples, 2012), is a main mechanistic driver for primary and secondary production, can influence the distribution of marine animals (Scott et al., 2010; Carroll et al., 2015; Cox et al., 2018) and cause implications to the breeding success of seabirds (Durant et al., 2006; Scott et al., 2006; Borstad et al., 2011). A warming climate is likely to alter the timing and length of summer stratification (Holt et al., 2010), which is a key physical control for the formation and level of production of the spring plankton bloom (Sharples et al., 2020). Change in the timing of blooms can lead to a temporal mismatch between fish larvae and their plankton prey, with implications for recruitment (Wright et al., 2020), fisheries production and other marine life (Edwards et al., 2020), highlighting the complex relationship between the change in physical habitat, following climate warming and predator-prey interactions. Worryingly, it has been found that both climate change and very large-scale tidal ORE developments can act in the same direction in terms of increasing stratification and consequently impact primary production. However, in the one direct comparison study that has been done, the effect of climate change is an order of magnitude higher than tidal effects by as early as 2050 and the tidal extraction effects are extremely location specific (De Dominicis et al., 2018; **Figure 3**).

Definitions of Scale and Types of Offshore Renewable Energy Extraction

In this section, we provide reason for and define the range of spatial scales (**Figure 4**) used in this study along with the background information on the major ecosystem level changes over the last 30 years in the North Sea. The largest scale is the entire shallow shelf sea area (in this specific example, defined as covering the North Sea and the United Kingdom continental shelf between 48° and 62° North and 10° West and 12° East; **Figure 4A**). The whole shallow shelf sea scale is relevant for numerous issues in the management and conservation of mobile marine species such as migratory fish species, seabirds, and marine mammals (Hammond et al., 2013; Cook et al., 2014b; Rutterford et al., 2015; Sadykova et al., 2017). The next

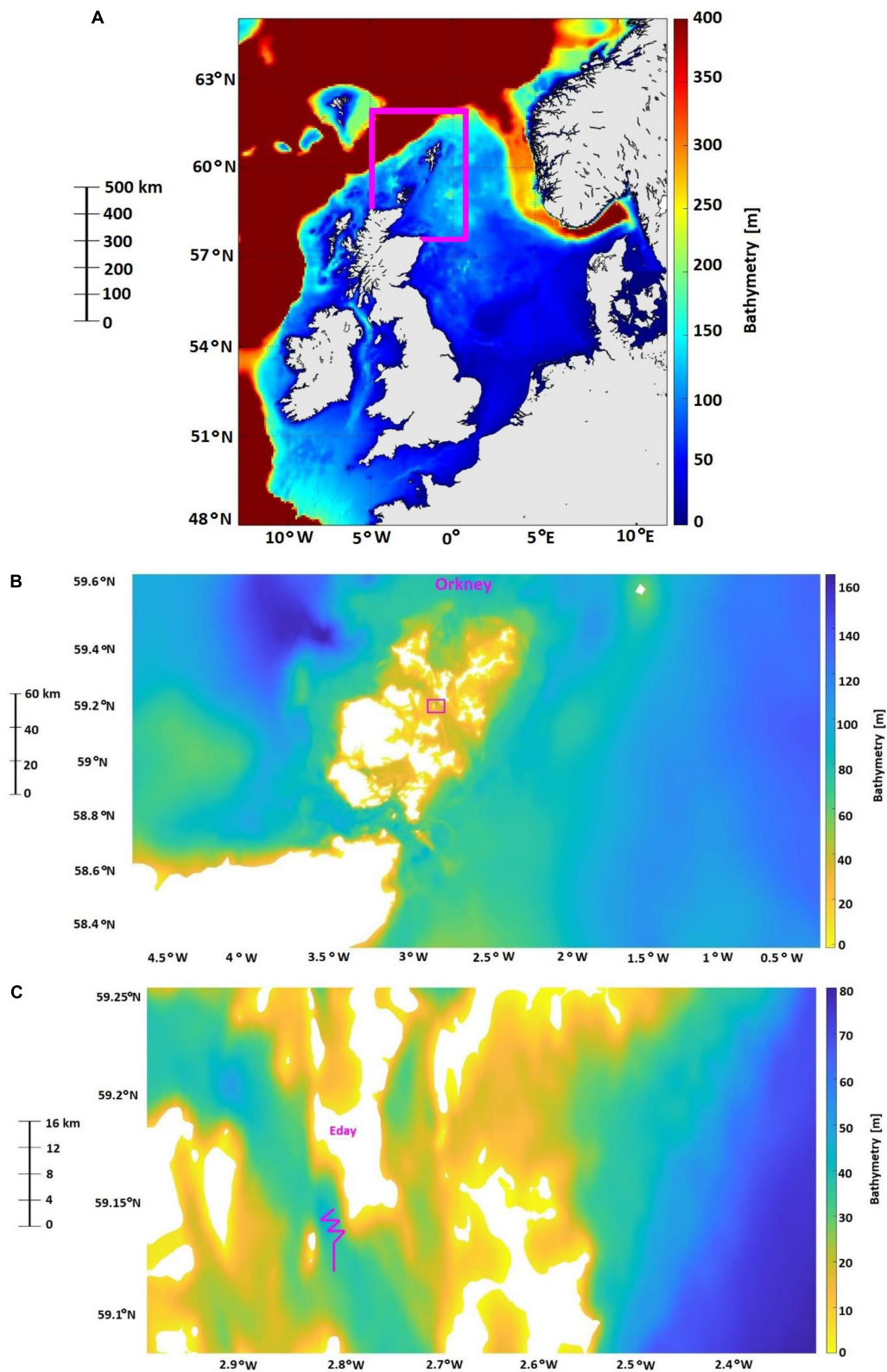


FIGURE 4 | The North Sea and the United Kingdom continental shelf and the spatial boundaries of Shetland and Orkney region (highlighted in purple) to represent the shallow shelf sea and regional scales **(A)**, respectively, as defined in this work, the archipelago of Orkney as a representation of the local scale **(B)** and the island of Eday and an example of vessel-based transects, based on Waggitt et al. (2016b), as a representation of the fine scale **(C)**.

scale down is the regional spatial scale and it can encompass populations and/or meta-populations of mobile species and each region consists of contrasting habitat types, which are more or less suitable for different ORE industries, based on depth and exposer/or not to wider oceanic influences. In the North Sea, these are four regions [each sized approximately 3500 km²; see Trifonova et al. (2021) and **Figure 4A**, that shows the Shetland and Orkney region] and range from the western Scottish waters, that are mainly influenced by western Atlantic Ocean conditions and targeted for wave energy developments (Davies et al., 2012); the Shetland and Orkney region with shelf edge habitats and some of the best tidal resources in the world (Davies et al., 2012); the northern North Sea that represents an expanse of deep (>60 m) areas, suitable for floating wind (Sectoral Marine Plan for Offshore Wind Energy, 2020) and shallow southern North Sea areas with depths < 50 m, suitable for static offshore wind (Offshore Renewable Energy Strategy European Commission, 2020).

The size of the local spatial scale (in the range of 100s km; **Figure 4B**) is defined based on the characteristics at the base of marine food chains: phytoplankton and primary productivity (Holt et al., 2012; Tweddle et al., 2018). This approach allows knowledge about the base of ecosystems to be used to assist assessment of environmental status within MSP (including MPAs) and within sectoral licensing to support ecosystem-based sustainable management (Tweddle et al., 2018). In addition, recognizing the importance of inter-annual variability in the timing of spring stratification and plankton blooms is a key component to the understanding of the mechanisms behind variations in marine animal populations on a local scale (Sharples et al., 2006). The fine spatial scale (<1 km; **Figure 4C**) is defined to provide a more mechanistic understanding of which habitat variables are more important to an individual of a given species and most importantly, to achieve an understanding of preferred foraging habitats, including preferences for local hydrodynamic conditions, which can then be conveyed at an ecosystem level (Sharples et al., 2013; Waggitt et al., 2016a; Williamson et al., 2019).

PHYSICAL AND BIOLOGICAL INDICATORS FOR MULTIPLE SPATIAL AND TEMPORAL SCALES

Physical Indicators: Stratification

One of several possible physical indicators to measure stratification is the potential energy anomaly (PEA, J/m³). PEA represents the amount of work required to bring about complete vertical mixing per unit of volume (Simpson and Bowers, 1981) and indicates the level of stratification and mixing rate (De Boer et al., 2008; De Dominicis et al., 2018). Recent modeling outcomes reveal that PEA plays a significant role in predicting the abundance changes of both lower (e.g., sandeel larvae) and higher trophic level (e.g., harbor porpoise, black-legged kittiwake) marine species on a regional spatial scale (Carroll et al., 2015; Trifonova et al., 2021) and to a lesser

extent, in determining habitat preferences on a North Sea scale (Sadykova et al., 2017; Wakefield et al., 2017). PEA can reflect more subtle spatial and temporal changes within a habitat type (van Leeuwen et al., 2016) and season (Simpson and Bowers, 1981), thus further highlighting the importance of spatial and seasonal distribution of physical processes as good indicators up through the entire trophic chain and any changes that are affecting ecosystem functioning.

On a local spatial scale, work by Sharples et al. (2013), has shown how seabed topography, in particular, during the period of established stratification, can have a significant effect on the levels of primary production, which were correlated with fish behavior, foraging seabirds and fisheries response and activity. On a fine spatial scale, stratification was also a key indicator and specifically when looking at the impacts of offshore wind farm structures (for example, by reducing vertical ocean mixing: Afsharian and Taylor, 2019 or reducing wind speeds and resultant wind stresses at the sea surface: Miles et al., 2020) that will have consequences for primary production (Carpenter et al., 2016; Schultze et al., 2020). Few studies have included analyses of the wind farm and/or tidal turbine impacts on primary production, and their results differ among regions due to their unequal topographic and oceanographic conditions. However, the studies showed that physical processes controlling rates of mixing and stratification are of key importance to understanding changes in the level of primary production on a relatively fine to local scale (van der Molen et al., 2014, 2016; Schultze et al., 2020) and ecosystem-wide spatial scales (Ludewig, 2015). Thus, using the PEA indicator to capture changes in stratification is important as changes in primary production may lead to further impacts on ecosystem services, such as fisheries, but also mobile marine predator populations.

Physical Indicators: Bottom Temperature and Sea Surface Temperature

Temperature is a major driver of marine ecosystems and one of the key factors affecting the physiology and ecology of all marine organisms (Simpson et al., 2011; Edwards et al., 2020; Evans and Waggitt, 2020). On a North Sea spatial scale, bottom temperature (BT, °C) was found to be important only for some top predator species in Sadykova et al. (2017). However, it has been shown that warming BTs can induce changes in the distribution, abundance, and richness of fish species in the North Sea, including the west of Scotland region (Dulvy et al., 2008; Ter Hofstede et al., 2010), Celtic Sea (Mérillet et al., 2020) and other large shelf marine ecosystems (Hunt et al., 2008; Sagarese et al., 2014). Similarly, BT was found to be a better physical indicator of abundance and/or biomass change on a regional spatial scale, compared to the sea surface temperature (SST, °C), except in the southern North Sea where the water column is generally fully mixed (Trifonova et al., 2021). Daily to seasonal SST values have higher variability, as SST is more rapidly affected by atmospheric variation, whereas changes in BT reflect longer-term, integrated trends in warming/cooling. Therefore, it is likely that changes in SST reflect a wider range of the daily/seasonal extremes, whilst the BT reflects steady changes over longer periods of time. Thus,

it is not surprising that SST has been used as one of the most important physical parameters influencing marine ecosystems linked to ecosystem changes in the North Sea due to climate variability in the North Atlantic Oscillation (Simpson et al., 2011; Pitois et al., 2012; Lynam et al., 2017; Edwards et al., 2020; Evans and Waggitt, 2020).

On a local to fine spatial scales, there has been a lot of work to relate SST with breeding success of kittiwakes (Frederiksen et al., 2005, 2007; Scott et al., 2006; Cook et al., 2014a), with most recent studies suggesting that temperature affects the abundance and timing of sandeels and their prey, which in turn has complex implications for kittiwakes, which are surface-feeders specializing on sandeels (Eerkes-Medrano et al., 2017; Wanless et al., 2018; Régnier et al., 2019). The relationships between SST and breeding success have been documented for other seabirds as well, including northern fulmar, Arctic tern, Atlantic puffin, and European shag (Durant et al., 2006; Borstad et al., 2011; Burthe et al., 2014; Cook et al., 2014a; Howells et al., 2017). However, this mechanism of “trophic mismatch,” where warming SSTs may affect seabirds through temporal mismatch between prey availability and energy demands during breeding is still unclear and poses challenges, due to the interacting effects from other factors (e.g., weather events, ORE developments) (Mitchell et al., 2020).

Physical Indicators: Horizontal Currents Speed

Local and regional hydrodynamic characteristics and processes can influence primary productivity and occupancy patterns of mobile animals by increasing food availability and abundance (Skov and Prins, 2001; Johnston et al., 2005; Ballance et al., 2006; Markones, 2007; Embling et al., 2012; Thompson, 2013; Scales et al., 2014; Cox et al., 2016; Sadykova et al., 2017; Scherelis et al., 2020; Trifonova et al., 2021). Specifically, depth-averaged (entire water column) horizontal currents speed (Hspeed, m/s) was found to be a key variable determining the abundance of mobile top predators, as stronger currents can promote foraging opportunities (Pierpoint, 2008; Embling et al., 2010; Gilles et al., 2011; IJsseldijk et al., 2015; Lambert et al., 2017; Diaz-López and Methion, 2018), specifically within tidal stream environments (Waggitt et al., 2016a,b, 2018b; Bouveroux et al., 2020), which has important implications with respect to mitigating population-level impacts from tidal stream energy extraction. Hydrodynamic characteristics have been hypothesized to aggregate, disaggregate, and disorient prey, affecting prey availability and foraging efficiency (Scott et al., 2014; Benjamins et al., 2015; Waggitt et al., 2016a), leading to effects on the energetics of individuals with possible effects on population-level across trophic levels (Zamon, 2003; Fraser et al., 2018; Williamson et al., 2019). Such findings are important for top predators, specifically when changes in fish behavior and distribution have been found to be more important than changes in abundance (Hastie et al., 2016; Waggitt et al., 2016b). Recent findings on very fine spatial scales (<500 m) demonstrate that man-made structures (e.g., decommissioned tidal turbine) and physical features (e.g., eddies and boils) generate wake features that attract top predators, which has implications for the distribution of species and identification

of foraging hotspots (Embling et al., 2012; Waggitt et al., 2016a,b; Benjamins et al., 2017; Lieber et al., 2019). Therefore, quantifying spatio-temporal variation in animal site usage in relation to hydrodynamic features may help to identify which and when areas may be used (Bertrand et al., 2014; Jones et al., 2014; Waggitt and Scott, 2014; Benjamins et al., 2015; Hastie et al., 2016; Waggitt et al., 2017).

Biological Indicators: Net Primary Production, Maximum Chlorophyll-*a*, and Phytoplankton Patchiness

Net primary production (NPP, mg C/m²; depth averaged NPP, that is the total carbon uptake by phytoplankton minus the phytoplankton respiration in a day) is a key driver of species dynamics from zooplankton through to top predators. Thus, it is through energy transfer along the food web, that NPP provides bottom-up control on fisheries production, identified within the North Sea and across other large marine ecosystems around the globe (Chassot et al., 2007; Conti and Scardi, 2010; Blanchard et al., 2012; Barange et al., 2014; Bentley et al., 2019; Hervann et al., 2020). Specifically, across different regional spatial scales within the North Sea, the magnitude of NPP and its high temporal variability focused attention on NPP as a good indicator of changes felt throughout the trophic chain. The effect of NPP has enormous implications for fisheries production, given future climate and fisheries management changes (Capuzzo et al., 2018; Trifonova et al., 2021). NPP plays a significant role in determining habitat preferences and facilitating foraging for both fish prey and top predator species, highlighting that prey and predators are selecting aspects of the habitat type very differently and that might be a reflection of prey species avoiding areas with predators (Sadykova et al., 2017, 2020; Cox et al., 2018). This further supports the Longhurst Provinces approach (Vichi et al., 2011), that defining the predictability of primary production throughout the trophic chain should be taken into consideration in terms of future spatial management of anthropogenic aspects that can change mixing (Tweddle et al., 2018).

Similarly, maximum chlorophyll-*a* at any depth (Chl-*a*, mg C/m³; the highest biomass of chlorophyll found at any vertical location in the water column but generally found at the base of the pycnocline; Ross and Sharples, 2007; Scott et al., 2010; Cullen, 2015), has also been identified as a good indicator of changes felt throughout the food web and specifically, its potential role to the structure and dynamics of marine ecosystems, including the North Sea (Trifonova et al., 2021), but also other shelf seas e.g., Celtic Sea (Mérillet et al., 2020) and other large marine ecosystems (Ware and Thomson, 2005; Frank et al., 2006; Friedland et al., 2012; Kidé et al., 2015). The Chl-*a* can be influenced by a greater variety of weather and physical variables, enhancing the importance of specific processes of bottom-up control of the planktonic food web (Molinero et al., 2013). This suggests that locations of Chl-*a* are very ecologically important (Scott et al., 2010; Scales et al., 2014), as they can represent new and/or aggregated primary production, but they may not have high values of biomass and hence, do not show up as areas of high, depth integrated NPP (Hickman et al., 2012). There is evidence that increased Chl-*a* can be used as an indicator of areas of

importance to top predators (Suryan et al., 2012; Sabarros et al., 2014; Bennisson and Jessopp, 2015; Grecian et al., 2016; Nowak et al., 2020), potentially indicating that the dynamics of top predators can be predicted using a combination of temperature and first level trophic indicators (Lynam et al., 2017; Trifonova et al., 2021). In particular, on a local to fine scale, foraging behavior of Manx shearwater and guillemots has been associated with areas of high concentrations of Chl-*a* off the west coast of Ireland (Kane et al., 2020) and off the east coast of Scotland, respectively (Cox et al., 2013). However, the processes behind this association are yet to be fully explained (Grémillet et al., 2008; Sharples et al., 2013).

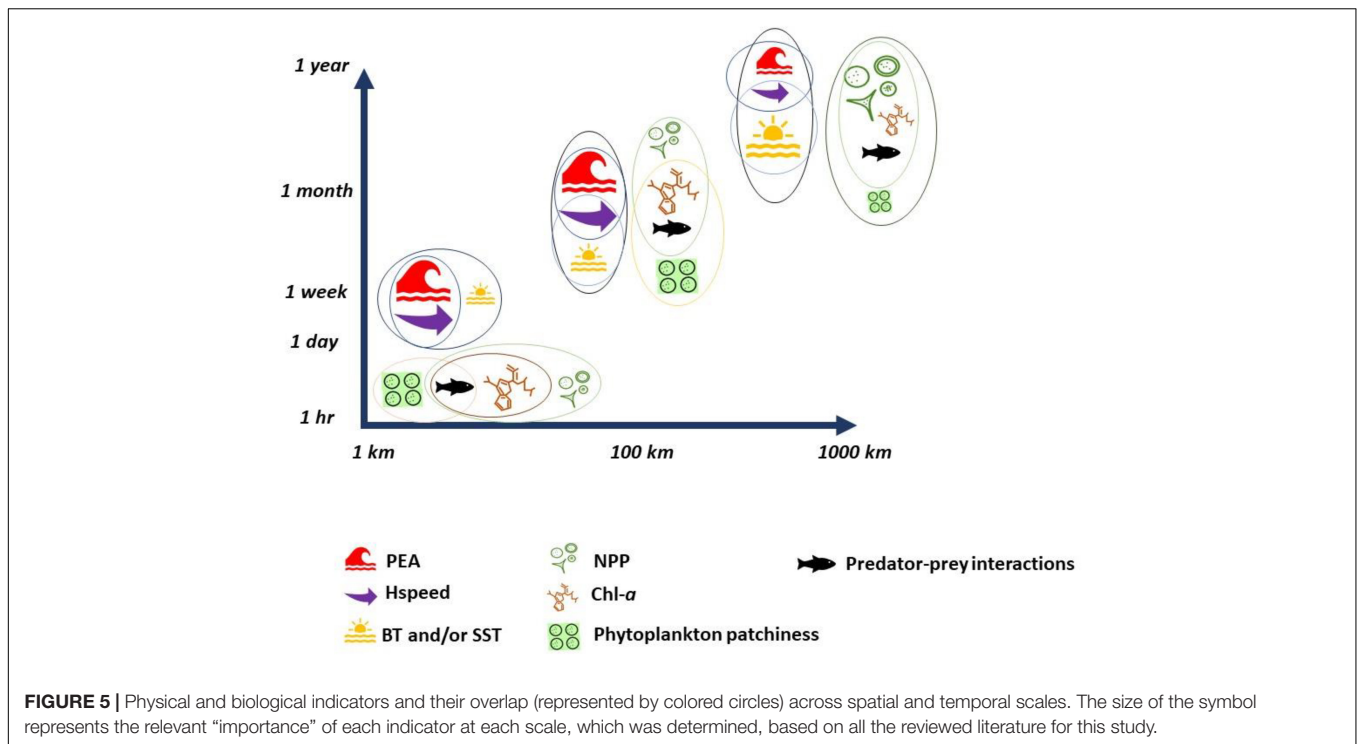
The marine environment is subject to spatial and temporal phytoplankton “patchiness,” driven by physical processes across spatial scales, e.g., upwelling along the continental shelf break or tidal mixing fronts (MacIsaac et al., 1985; Videau, 1987; Joint et al., 2001; Sharples et al., 2013). Patchiness in phytoplankton is extremely important as it affects predators’ ability to find food, therefore spatial and temporal changes in locations and/or quantity of patchiness will impact the entire trophic web (Scott et al., 2010; Benoit-Bird and McManus, 2012). Periodic phytoplankton and subsurface blooms leading to accumulated new “patchy” production, greater than usually assumed in some regions (e.g., Dogger Bank) might explain the high fish production in the North Sea, compared to other temperate seas (Richardson et al., 2000; Weston et al., 2005). Such high production areas have been reported along the shelf edge in the north-eastern North Sea, coincidental with high species richness and fishing activity, which could have implications for the ecosystem structure (Bendtsen and Richardson, 2020). In addition, the timing (phenology) of the phytoplankton blooms has been highlighted important for the function of food webs on a global scale, specifically affecting energy flow pathways in ecosystems and the productivity of different species (Friedland et al., 2018).

Biological Indicators: Predator–Prey Interactions

Studying predator–prey interactions should bring extra knowledge about consequences for the dynamics of marine ecosystems in a bio/physical environment that is changing rapidly. In marine ecosystems, top predator populations are influenced by environmental factors that affect their prey abundance and distribution at multiple spatial scales and are often used as indicators (Bertrand et al., 2008; Wolf et al., 2009; Boyd et al., 2017; Carroll et al., 2017; **Figure 5**). Sadykova et al. (2020) showed the complex relationship between the change in physical habitat, following climate warming and predator–prey interactions (including competition for prey between gray and harbor seals), with the more severe population declines predicted in harbor seals (SCOS, 2019; Evans and Waggitt, 2020). The spatio-temporal overlap between cod and its predators increased with increasing temperature, indicating that food web processes might reduce the recovery potential of cod during warm periods (Kempf et al., 2010). Seasonal changes in migration patterns, stock sizes and locations of prey, due to climate warming,

has had an influential role in controlling the movements of killer whales off northern Scotland (Samarra and Foote, 2015) and the large north to south distribution shift of the harbor porpoise within the southern North Sea (Camphuysen, 2004; Camphuysen and Peet, 2006; Evans and Waggitt, 2020) and might also be partly responsible for the increase in sightings of humpback whales in the north-western North sea (Evans and Bjørge, 2013). At the same time, prey may be abundant but not accessible due to removal by fisheries, which has often resulted in population-level effects (Cury et al., 2011; Bertrand et al., 2012; Barbraud et al., 2018), ecosystem shifts and consequent reversal of predator–prey roles, where adult prey attack vulnerable young predators (Frank et al., 2005; Heithaus et al., 2008; Fauchald, 2010; Estes et al., 2011). For example, the North Sea cod recruitment has been negatively related to the spawning-stock biomass of herring, as they are found to prey on cod eggs and larvae (Fauchald, 2010), and also exacerbated by climate-induced declines in the plankton production, which is a major food source for cod larvae (Beaugrand et al., 2003; Edwards et al., 2020). The identified impact of predators (e.g., cod, saithe, and gray seals) on juvenile cod and whiting advocated the use of ecosystem modeling alongside single stock assessments to better inform fisheries management in the west of Scotland region (Baudron et al., 2019).

It is evident that changes in the population dynamics of higher trophic levels are likely to reflect those of their preferred prey, which may, in turn, be bottom-up driven by dynamic biophysical oceanographic processes across spatial and temporal scales (Shealer, 2002; Bertrand et al., 2014; Boyd et al., 2015; Woodson and Litvin, 2015; McInnes et al., 2017; Cox et al., 2018; **Figure 5**). For example, on a local scale, by accounting for the influence of tidal state and stratification on foraging habitat, seabird–fish interactions were identified, highlighting that critical marine habitats occur at limited spatial locations but also within specific temporal intervals (Cox et al., 2013; Calle et al., 2018). The extent to which spatial and tidal temporal oceanographic features are important to seabirds is dependent on the use of such features by their prey (Daunt et al., 2006; Stevick et al., 2008; Heim et al., 2019). On a fine spatial scale, prey behavior and availability and/or predictability in tidal stream environments may be more important in attracting predators than absolute prey abundance (Zamon, 2002; Grémillet et al., 2008; Skov and Thomsen, 2008; Benoit-Bird et al., 2013; Wilson et al., 2013; Benjamins et al., 2016) and that memory of profitable areas can also play an important role in deterministic selection of foraging habitat (Nabe-Nielsen et al., 2013; Regular et al., 2013). This might explain why the relationship between foraging seabirds and harbor porpoise with current speeds sometimes differs between studies (Booth et al., 2013; Jones et al., 2014; Scott et al., 2014; Benjamins et al., 2015; Benjamins et al., 2017) and highlights the importance of including prey when looking at the behavior and distribution of top predators. For example, prey transitional behavior moving between habitats, due to mixed and stratified water, has been found important for top predators, suggesting that predators may select foraging habitats by trading-off several measurements of prey availability (Waggitt et al., 2018a,b).



WHAT HAVE WE LEARNED FROM MARINE ECOSYSTEM MODELING APPROACHES FOR CLIMATE CHANGE AND OFFSHORE RENEWABLE ENERGY DEVELOPMENTS?

Introduction of the Different Modeling Approaches

Significant progress has been made in developing ecosystem models that use traditional statistical approaches to understand the relationships between a number of variables (Lynam et al., 2017), including “end-to-end” dynamic ecosystem models to predict impacts of environmental change on the structure and function of marine food webs and the services they provide (Marine Ecosystems Research Programme¹; Spence et al., 2018). The model developed in Lynam et al. (2017) is a particularly good example as it uses a non-deterministic approach that incorporated different trophic levels from over 40 years on a North Sea spatial scale. The model linked top-down and bottom-up effects simulating complex long-term changes under a combination of stressor scenarios for the North Sea marine system, providing useful outcomes to support the ecosystem approach to management. Size-based ecosystem modeling is also emerging as a powerful way to assess ecosystem-level impacts of natural and anthropogenic changes from individual-level processes (Barange et al., 2014; Blanchard et al., 2017). In particular, a size-based food web model coupled with a physical-biogeochemical model was used to investigate the impacts

of climate change on fish biomass and primary production (Blanchard et al., 2012).

Ecopath with Ecosim (EwE) models (Polovina, 1984; Christensen and Walters, 2000) are also useful to capture the impacts, on a relatively local spatial scale, assessing wind farm “before” and “after” effects and one was developed for the Bay of Seine ecosystem (Raoux et al., 2017). This was the first holistic approach to examine the offshore wind farm impacts on ecosystems functioning using trophic web modeling tools. The approach successfully determined how the local food web structure and function may change 30 years after the installation of the offshore wind farm, examining changes from the “reef effect” on apex predators and highlighting the “wasp-waist” controlled food webs (Raoux et al., 2017).

Species-specific individual-based models (IBMs) have been developed to quantify impacts from ORE developments (DEPONS, Nabe-Nielsen et al., 2018; SeabORD, Searle et al., 2014), however, they require highly detailed spatial information and are currently under improvement. Models, such as AgentSeal, are the first step in providing solid understanding of animals’ physiology, movement, and behavior, that can be integrated into IBMs to understand cumulative effects of stressors (Chudzinska et al., 2021). At the population-level, a promising avenue for future research includes the use of IBMs with telemetry data to better understand population dynamics and predict population-level distribution, following changes to species environment (McClintock et al., 2013; Carroll et al., 2020).

An EwE approach was also applied to model ecosystem effects of fishing and climate warming in the North Sea, highlighting the interactions between predator-prey and climate

¹https://www.marine-ecosystems.org.uk/Research_outcomes/Modelling

change, which will have significant implications for fisheries management (Lynam and Mackinson, 2015). The EwE approach was also developed on a much finer spatial scale for the west coast of Scotland to assess the combined impacts of fishing and rising temperature on selected species. Modeling outcomes revealed that gray seals, cod, herring, and haddock were facing severe declines, whilst some species (e.g., whiting) were not affected, highlighting the importance of including rising temperatures in the ecosystem approach to achieve sustainable fisheries management (Serpetti et al., 2017). While the EwE model cannot, in its present state, be used for short-term decisions due to too many uncertainties relating to the numerous processes it encompasses, the approach might be useful in terms of informing managers on likely future long-term trends in biomass and catches under various “what if” scenarios, such that this approach is currently being used to investigate small-scale impacts of multi-purpose platforms (Serpetti et al., 2017).

Bayesian network models have also been applied to investigate the consequences of fisheries catch, temperature and primary productivity scenarios on different fish and zooplankton species, outlining the importance of trophic interactions and the spatial relationship between neighboring areas (Trifonova et al., 2017). The success of using a hidden variable to identify indicator species of key importance to the ecosystem dynamics that has also been helpful in illuminating the possible mechanisms behind functional ecosystem changes has been shown for the North Sea (Trifonova et al., 2015) but also for other systems, e.g., Barents Sea (Uusitalo et al., 2018) and Gulf of Mexico (Trifonova et al., 2019). Bayesian hierarchical hurdle and zero-inflated joint models with integrated nested Laplace approximation (INLA) have been used to model the common spatial habitat between predators and prey and more recently, to predict the “ecological costs” in population terms, following the projected effects of climate change (Sadykova et al., 2020).

New Modeling Formulations, How to Effectively Combine Outputs From Different Approaches, Do Not Create New Models but Use Different Approaches Effectively Together

New modeling formulations might be needed to be able to assess multiple stressors, account for behavior of species, demographic data, as well as predator-prey interactions occurring at different spatial and temporal scales. Machine-learning and bioinformatics techniques can be greatly utilized to aid such work due to their “crossover potential” in predictive ecology (Tucker and Duplisea, 2012), including animal behavior and movement (Mattei et al., 2018; Pirodda et al., 2018). Coupling existing models (e.g., physical, biological, economic) is another avenue that has proven successful (Planque et al., 2011; Robinson et al., 2011; Kempf et al., 2013; Peck et al., 2018). Mechanistic food-web model and Bayesian hierarchical species distribution model have been used complementary to take a more holistic approach to estimating species distributions (Coll et al., 2019). Another alternative could be nested sub-models, based on principles

from graph and network theory that can be used to overcome scale issues more easily by linking up to existing ecosystem or species-based models. For example, by using bipartite network principles to create species-habitat networks, the scale of the ecological information was matched to the scale of the landscape management intervention to assist landscape management and multispecies conservation (Marini et al., 2019).

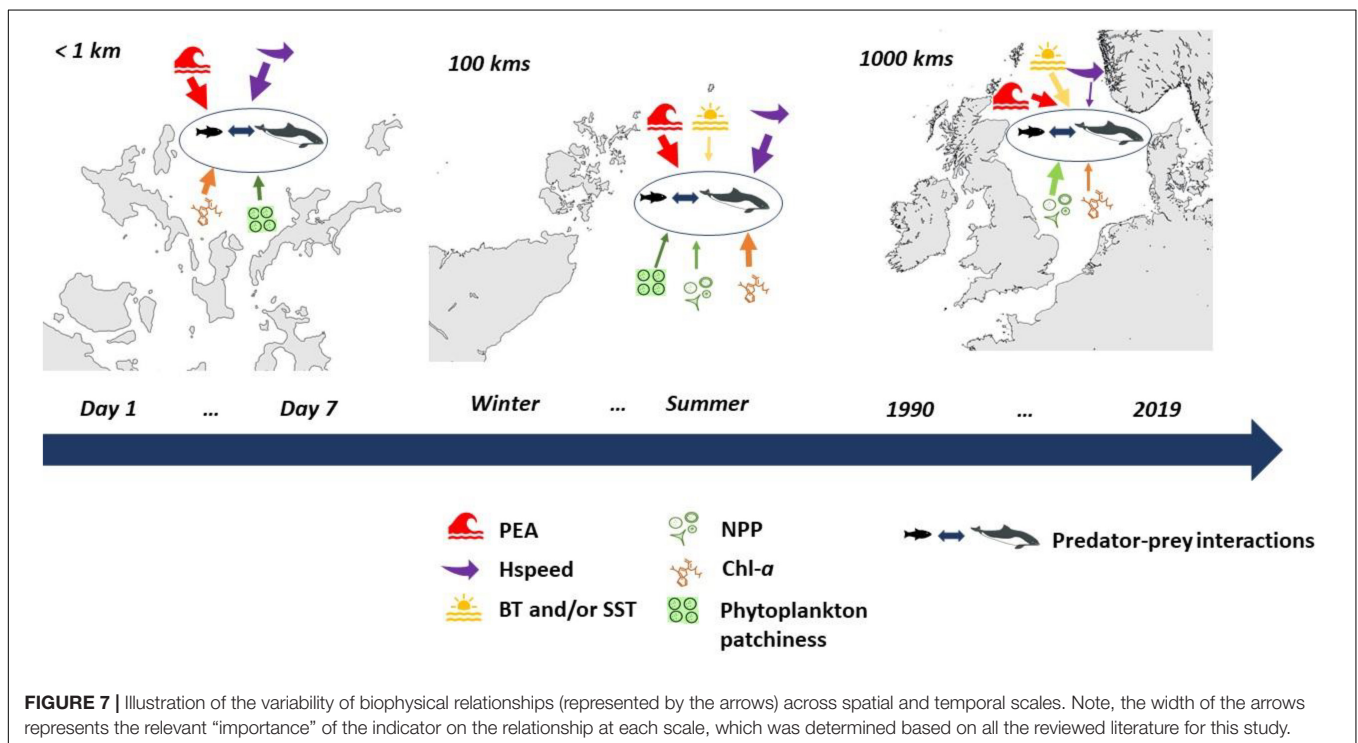
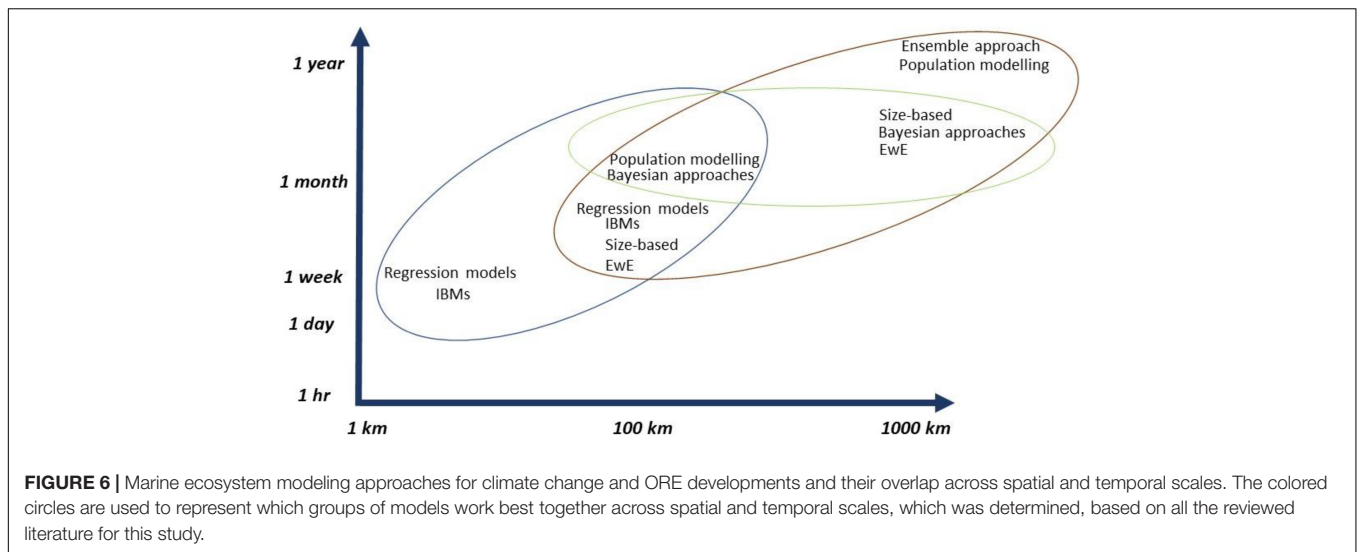
A useful future approach would be to use the interaction web as an emulator for a more complex model (Lynam et al., 2017) and consider an ensemble modeling approach (Gårdmark et al., 2013; Spence et al., 2018). Rather than trying to choose the “best” model, or taking some weighted average, it is important to exploit the strengths of each of the types of models, whilst learning from the differences between them, as it was shown in an ensemble model that was developed based on the relationships between a collection of mechanistic models (e.g., EwE), allowing for uncertainty to be included when making predictions under different scenarios (Spence et al., 2018; **Figure 6**). The approach was conducted to evaluate the impact of fishing on demersal fish species; however, the framework is not exclusive to ecosystem simulators in fisheries and is potentially applicable over a wide scope of complex ecological systems.

HOW TO IMPROVE ON INTEGRATION ACROSS SPATIAL AND TEMPORAL SCALES

Greater integration of both physical and biological indicators will potentially allow identification of the important biophysical interactions within different habitats that will allow evaluation of how ecosystems might change in the future. The optimal approach is to utilize knowledge across a range of spatial and temporal scales to be able to reduce uncertainties of direct and indirect effects on individuals and subsequently populations and ultimately, to provide sensible strategic advice for future sustainable spatial management. Most importantly, studies need to be performed at appropriate ecological scales, considering the spatial and temporal physical and biological variability, and recognizing the pragmatic importance of asking the “right question” at the “right scale” (Mannocci et al., 2017; Scales et al., 2017).

How to Improve Connection Between Scales (Better Use of Data, Fine Scale Studies Versus Large-Scale, Generalization Across Regions and Scales)

Focusing on explanatory physical and/or biological indicators, which can be quickly quantified across spatial and temporal scales, can be a pragmatic approach to generalize relationships (e.g., predator-prey and/or biophysical interactions) across marine systems but from different geographic regions, where data is limited (Tucker and Duplisea, 2012). In this way, local and regional studies from data rich areas (e.g., Moray Firth in northeast Scotland, ScotMER and MREF MASTS Workshop



October 5, 2019²; coastal monitoring sites³) should be explored in more detail to provide a robust understanding of the biophysical interactions across trophic levels and any changes that are affecting the ecosystem dynamics. By relying on the efficient and robust use of data from such well-studied areas, biophysical relationships can be confirmed and predicted for other habitats to generalize the relative influence from climate and other factors to support population-level studies across larger scales. Therefore,

²https://tethys.pnnl.gov/sites/default/files/publications/working-across-sector-groups_scotmer-masts-workshop_2019_final.pdf

³<http://marine.gov.scot/information/coastal-monitoring-site-stonehaven>

finer, local scale and site-specific surveys and monitoring only need to be conducted on few key demonstrator habitats focusing on interactions with few key species to build a baseline for the understanding of the North Sea (Bailey et al., 2014).

Data obtained from few key demonstrator sites can be integrated with site-specific data at proposed ORE development sites to provide a more robust understanding of population-level consequences and potentially identify alternative more suitable potential sites (Bailey et al., 2014). Hydrodynamic models are routinely used to assess energy resources and environmental impacts on hydrodynamics, which in combination with site-specific data, would allow useful information to be collected

relatively cheaply and easily. The challenge for modeling studies is to validate the models sufficiently for present-day conditions, so that we can have confidence in the results under assumptions about the response to deployment of ORE devices, which cannot yet be validated from observations (Wolf et al., 2021). If effort and resources were to be focused on selected species and seasons, post-installation monitoring and mitigation might be more clearly and easily managed. In this way, knowledge can be used to optimize site development and purpose, balancing benefits and trade-offs between the rapidly growing ORE industry and conservation.

Individual-based studies and short-term interactions can serve as a baseline to assess how particular pressures interact with broader scale variation in environmental conditions (Votier et al., 2005) or over time (Veran et al., 2007) to support a more general understanding of the long-term population consequences. Such baseline studies will also contribute to determine the spatial scales at which to further investigate more detailed prey and predator behaviors within sites of interest. For example, demographic and fecundity data can be used to assess the longer-term impact of any behavioral responses, following natural or anthropogenic changes (Boyd et al., 2015, 2017; Carroll et al., 2017; Barbraud et al., 2018). Then, quantification of fine scale usage can be utilized within population level models through generalized functional response methods and/or influences on energetic changes to understand how these individual effects translate into population-level changes at a wider spatial scale and ecosystem level (Matthiopoulos et al., 2015; **Figure 6**).

Different Sources of Data, Different Survey Techniques

With a greater mechanistic understanding of how and why fish and top predators use fine scale dynamic marine habitats (i.e., high-energy tidal sites, Hastie et al., 2018; use of wind turbine structures, Whyte et al., 2020) for foraging, predictable changes from the installation of ORE developments can be used to estimate cumulative effects at a population level and guide strategic approach to the monitoring and management of such devices (Williamson et al., 2017, 2019). However, very few studies are performed on a fine spatial scale and concurrent measurements of physical and biological data are lacking. Achieving this will require adopting novel methodological techniques (e.g., acoustics, underwater photography, cameras, gliders, telemetry) to improve our understanding of habitat use by marine animals to be able to link biophysical processes at a population level (Cotter and Polagye, 2020; Polagye et al., 2020; Whitt et al., 2020). However, given the cost and capacity related to data collection, existing sources of information should be optimized and their relevance to new data evaluated.

Existing data (e.g., Copernicus⁴; INSITE⁵; MEDIN⁶; Seabird and mammal population data, Waggitt et al., 2020; Oil and gas environment interactive⁷) should be integrated more and used

to populate multiple approaches (from IBMs to population-level approaches) across spatio-temporal scales. Similarly, datasets such as ScotMap (Kafas et al., 2014) should be utilized more to investigate forage fish distribution across scales due to their central place in the North Sea marine system, linking bottom-up and top-down processes.

Remote sensing data (e.g., SeaWiFS⁸) offer a much extended spatial and temporal coverage but presenting some limitations related to image resolution and targets (Patil et al., 2002). Still, analyses of such data can be used in combination with field observations and expertise knowledge as an effective tool to assist the understanding of complex interactive biophysical effects within the environment and minimize uncertainty with future climate change to aid the evidence-based decision-making process (Patil et al., 2002; Moufaddal, 2005). In addition, physical and biological variables from remote sensors could be used as proxies to better understand foraging behavior and habitat preferences of animals across scales and how these vary with weather conditions and climate change (Medina-Lopez et al., 2021). Data from GPS and accelerometers of top predators can be used to investigate fine scale foraging locations and consequently determine prey behavior and distribution across trophic levels and scales that can advance the understanding of marine ecosystem dynamics (Ohman et al., 2013; Suberg et al., 2014).

New hydrodynamic modeling products, like the Scottish Shelf Waters Reanalysis Service⁹ are becoming available. The outstanding feature of the Service is the use of an unstructured mesh, which allows the reproduction of Scottish shelf waters dynamics that have a diverse character, from deep, almost enclosed coastal lochs on the west coast, with many islands, to the outer shelf. It fills the gap of large-scale modeling that does not have sufficient spatial resolution to resolve ORE sites. The multi-year run enables the analysis of inter-annual natural changes of the system to be compared with ORE impacts.

MOVING FORWARD

Many of the physical and biological indicators, presented in this work, show similar levels of importance from fine through to larger spatial scales, highlighting indicators such as stratification with mechanisms via bottom-up control driving the marine ecosystem dynamics in the North Sea. This study illuminates the feasibility of generalizing knowledge from such a well-studied region and the potential to translate it across other large marine ecosystems to be able to address the importance of indicators and to ultimately strengthen predictions of population changes at ecosystem scales in other shallow shelf seas. It is with the added baseline knowledge from this study, on what ecosystem components are more consistently found as the physical and biological indicators of habitat and ecosystem change and what they are telling us about how the ecosystem is functioning, that much more informed choices for MSP decisions should be made. The knowledge presented in this study can be used for future

⁴<https://www.copernicus.eu/en/access-data>

⁵<https://www.insitenorthsea.org/data/>

⁶<https://portal.medin.org.uk/portal/start.php>

⁷<https://storymaps.arcgis.com/stories/4b6d3b5867b14bb7aec6f6557a5fb82>

⁸<https://oceancolor.gsfc.nasa.gov/SeaWiFS/>

⁹<https://sites.google.com/view/ssw-rs/home>

guidance on the most sensible unit of measure (mean, median, or percentile) for both physical and biological indicators, given the specific spatial and temporal scales. Although, the mean is the mostly used unit across studies, examples illustrate that in some cases, other units have a more meaningful interpretation, for example maximum values of currents speed (Trifonova et al., 2021), maximum Chl-*a* (Scott et al., 2010). This work has also shown that the strength of the biophysical relationships may vary due to both strong climate and anthropogenic pressures such as fisheries, which is most important when interpreting and extrapolating relationships between animals and environmental variables (Mannocci et al., 2017; Scales et al., 2017). Thus, considering the variability of biophysical relationships at multiple spatial and temporal scales throughout different trophic levels is key to providing more accurate predictions of breeding success and survival of contrasting seabird, mammal and fish populations and ecosystem level changes these differences are driving (Figure 7).

Therefore, it is important that fine scale site-specific surveys and multidisciplinary research with simultaneous collections of oceanographic data, prey and predator characteristics are performed on key demonstrator sites and then, quantified across spatial scales to support a more general understanding of the important biophysical relationships to populations and regional wide ecosystem scale. We suggest that more general patterns of relationships should be aimed at, whilst effort should be emphasized on the integral “habitat” use and specifically, determine what aspects of the habitat are relevant to marine animals to be able to address a wider range of ecological questions. For example, by quantifying the effects of habitat preference and spatial usage, the effects of species interactions (e.g., competition, predation) on populations can be better understood. By investigating locations, where predator and prey or competing species overlap, we can better monitor and mitigate the potential natural and anthropogenic consequences on the marine environment (Williamson et al., 2021). This will allow for future-proofing of the locations of MPAs and improve decisions, such as where ORE developments should be placed.

A step-change is occurring in the use of our shallow seas, specifically by the addition of large-scale ORE developments, in part driven by the United Kingdom government aspiration to achieve Net Zero by 2050 and the Green Industrial Revolution. To ensure the compatibility of ORE developments with other marine management sectors, we need to evaluate cumulative effects through cumulative impact assessments (Cavallo et al., 2017; Willstead et al., 2018). However, cumulative assessments currently fail to include the linkages between different trophic levels, and the interactions between pressures, such as changes in the physical environment from the introduction of structures and extraction of GWs of energy up through the entire marine ecosystem. The cumulative environmental effects of ORE developments remain highly uncertain and require a multidisciplinary approach to provide more holistic and structured assessments (Willstead et al., 2017). Using ecosystem models at ecologically meaningful scales to understand how ecosystems respond to multiple stressors will support the cumulative assessment process (Piroddi et al.,

2015). To address that and to incorporate both direct and indirect effects on the ecosystem, ecosystem models need to be linked with a hydrodynamic-biogeochemical-sediments modeling system (Schuchert et al., 2018; Wolf et al., 2021). The study by van der Molen et al. (2016) is the only study that has integrated hydrodynamic-sediments-biogeochemistry effects. They found that a very large array of 8 GW located in the Pentland Firth (United Kingdom) can lead to changes in ecosystem variables of up to 10% at more than 100 km away from the array.

Ideally, holistic modeling approaches should be integrated at ecologically meaningful spatial and temporal scales in response to natural variability and /or anthropogenic pressures. Ecological and socio-economic effects need to be combined in one modeling framework to enable assessment of trade-offs between different uses of coastal seas. In fact, a common “currency” to communicate modeling outputs could be developed that works across different disciplines and stakeholder groups. Most ecosystem models use some aspect of biological biomass or numbers of animals, or ratios of size of predator to prey as the currency in the model. However, many industries and regulators use the level of risk as the central currency in decision making. A coming together of currencies could be used to communicate modeling outputs with different groups for a more coherent and comprehensive understanding of environmental perturbations following ORE developments and climate change. This way, a common “currency” could be the NPP or the amount of energy per kg (the energy flow or availability of energy, derived from key trophic interactions).

Natural capital is a method that has been adopted to achieve the use of financial currency across modeling frameworks. The natural capital approach provides a more holistic perspective of socio-ecological systems than traditional environmental impact assessment (Hooper et al., 2017). It is a useful tool to support impact assessment on the goods and services people receive from nature (Arkema et al., 2015; Guerry et al., 2015). Such a framework will also provide the likely outcomes from alternative management and climate scenarios, allowing the user to make judgments and decisions about the ecological and socio-economic benefits and trade-offs within spatial scales, among sectors, and between users. Such information will ideally support the communication with other sectors, both the conservation and financial sectors, and guide policy decisions and planning.

Lastly, a focus should be placed on the development of interactive visualization tools (such as InVEST¹⁰; MSP Simulation Platform¹¹; Virtual Ecosystem Scenario Viewer¹²) that assist in conveying complex outputs from state-of-the-art modeling tools, discussed already in the text. Modeling outputs should be brought together and better integrated for better communication and interactions with stakeholders to be able to represent and understand current and future trade-offs, following natural and/or anthropogenic changes across spatial

¹⁰<https://naturalcapitalproject.stanford.edu/software/invest>

¹¹<https://www.msppchallenge.info/>

¹²<https://www.fisheries.noaa.gov/resource/tool-app/virtual-ecosystem-scenario-viewer-ves-v>

scales for whole ecosystem levels. Therefore, different expertise can have a quantitative indication of the range of possible scenarios consistent with the data to give strategic advice on potential ecosystem response. In this way, we can proceed more rapidly than before by utilizing knowledge and using existing extensive data sources, predictive modeling approaches and visualization tools that will ultimately lead to more strategic and integrated approaches to both monitoring studies and assessing anthropogenic impacts to enable evaluation of trade-offs and benefits to provide the most sustainable future spatial use of our seas at whole ecosystem scales.

AUTHOR CONTRIBUTIONS

NT designed the study, performed the research, and wrote the manuscript. BS designed the study, wrote, reviewed, and edited the manuscript. MD, and JW wrote, reviewed, and edited the

manuscript. All authors contributed to the article and approved the submitted version.

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