



OPINION PIECE

Bridging the gap: integrating models and observations for better ecosystem understanding

Morten D. Skogen^{1,*}, Johanna M. Aarflot¹, Luz María García-García², Rubao Ji³, Manuel Ruiz-Villarreal², Elin Almroth-Rosell⁴, Andrea Belgrano^{5,6}, Déborah Benkort⁷, Ute Daewel⁷, Moa Edman⁴, René Friedland⁸, Shuang Gao¹, Mariana Hill-Cruz⁹, Solfrid Sætre Hjøllo¹, Martin Huret¹⁰, Julie B. Kellner³, Sonja van Leeuwen¹¹, Ane Lopez de Gamiz-Zearra¹², Marie Maar¹³, Erik Askov Mousing¹, Myron A. Peck¹¹, Ane Pastor Rollan¹⁴, Sévrine F. Sailley¹⁵, Sofia Saraiva⁴, Cassie Speakman¹⁴, Tineke Troost¹⁶, Veli Çağlar Yumruktepe¹⁷

¹Ecosystemprocesses Group, Institute of Marine Research, Pb.1870, 5817 Bergen, Norway

Full author addresses are given in the Appendix

ABSTRACT: Our understanding of complex marine ecosystem dynamics is often hindered by significant uncertainties and issues of representativeness associated with models and observations. Both observations and models provide a limited view of real-world complexities depending on what is specifically measured or simulated. When used together, they provide the ability to gain a broader understanding of important ecological processes. How to properly integrate models and observations while utilizing the advantages of both approaches remains a challenge. In this paper, we draw attention to commonly overlooked limitations of both observations and models, and use examples to illustrate potential strategies to mitigate bias, properly interpret results, and help improve both models and observations. We emphasize that proper validation of all data sources (models and observations) is necessary in all marine ecosystem studies, with a careful assessment of the spatio-temporal scales that the data represent.

KEY WORDS: Marine ecosystems · Models · Observations · Representativity · Validation

1. INTRODUCTION

Marine ecosystems are complex, and large amounts of data are essential for a proper assessment of ecosystem state and functioning. Consequently, the availability and open access to data products and information are critical for guiding and informing decision-making processes and stakeholder-driven management interactions (Iwamoto et al. 2019). Marine data may come from observations or marine

mechanistic ecosystem models (MMEMs), which both have their own strengths and weaknesses.

One can argue that MMEMs are observations in a virtual space and, depending on the model structure, it is possible to generate data on variables and/or processes that are difficult or impossible to observe *in situ* with high temporal and spatial resolution. However, an MMEM is also a simplified representation of processes or a system and is often limited by insufficient process knowledge. Therefore, MMEMs only

*Corresponding author: morten.skogen@hi.no

offer an incomplete representation or parameterization of processes and components of a natural system (Oreskes et al. 1994). By contrast, observations are generally given with high precision but are limited by incomplete sampling in time and space (see Fig. 1). Empirical studies are also models, models that are based on the interpretation of the information available to the observer (Underwood et al. 2000, Bar-Yam 2016, Skogen et al. 2021). Due to the inherent incompleteness of observations in capturing natural phenomena, relying solely on observation will yield a restricted comprehension of a system's behaviour (Oreskes et al. 1994). Nevertheless, observations are still often judged as the gold standard and accepted as the 'truth' against which models are evaluated. As such, proper interpretation and the true value of MMEMs is often overlooked (Skogen et al. 2021).

Marine ecosystem data from both MMEMs and observations require that they are evaluated for both error and uncertainty. Proper model validation (Dee 1995) is, and has always been, a necessity before models can be used for real-world applications (e.g. Hufnagl & Peck 2011, Juza et al. 2016, Salon et al. 2019, Yumruktepe et al. 2022), and models are normally confirmed by agreement between observation and model outputs; although it is also argued that validation is about differences rather than similarities (Woods 2002). Confirmation is inherently partial (Oreskes et al. 1994), and it is rare to obtain adequate observations for proper verification of models (Woods 2002); thus, validation of MMEMs should be performed using all data relevant to the purpose of the model simulations in question. When observations are accepted as truth, a consequence is that MMEMs are mistrusted if their results do not match the observational evidence. However, if ϵ_o and ϵ_m represent the observation and model errors respectively, and $\delta = \epsilon_o - \epsilon_m$, their mismatch, then $\delta = 0$ (no mismatch), only implies that models and observations agree, not that the error is 0 (Lynch et al. 2009). The validity of observations is less frequently challenged (e.g. Kennedy 2014), and improper extrapolation of observational data is often done without careful consideration of scale-dependent uncertainties. The properties observed in natural systems are an integrated effect or outcome of all processes acting on a large variety of spatio-temporal scales. Since actual observations can only capture certain scales that can be difficult to identify, they are often interpreted to represent processes and patterns at a range of scales. Proper validation of all data sources, including observations, with a careful assessment of the spatio-temporal scales they represent, should therefore be a prerequisite in all marine ecosystem studies.

In meteorology, the term 'representativeness' has been defined as: '... the extent to which a set of measurements taken in a space-time domain reflects the actual conditions in the same or different space-time domain taken on a scale appropriate for a specific application' (Nappo et al. 1982, p. 761). Representation error, primarily caused by incomplete sampling, stands out as a crucial factor in assessing observation uncertainties (Schutgens et al. 2017). Unlike natural systems, observations are always derived from discontinuous spatio-temporal sampling. In repeated surveys, the control over observed variations in time versus space is seldom clear (Steiner et al. 2016), and representation error varies depending on whether spatial or temporal sampling dominates (Schutgens et al. 2017). The representation error thus depends on sampling technique, spatio-temporal resolution (Omori & Hamner 1982), and the natural variability of the system under study. Understanding representation error is crucial for accurately characterizing knowledge gained from observations. Similarly, MMEMs also have representation errors due to model resolution, and the incomplete representation of processes and components in the simulated system.

A widely held belief is that model limitations outweigh observational uncertainty ($\epsilon_m > \epsilon_o$), thus diminishing the perceived significance of observational reference limitations. In the present paper, this assumption will be challenged and discussed. Accepting the fact that observations also need to be assessed in terms of their uncertainties and representativeness, a discussion on limitations and how MMEMs can be used to improve observations is presented, followed by a similar discussion on the representation error within MMEMs and the use of observations to improve MMEMs. Data assimilation is not included in the latter, as data assimilation is based on the idea that models should be constrained to be consistent with observations rather than accepting the idea that they both are uncertain. The discussion is followed by some thoughts on what kind of observations are needed to improve and possibly validate MMEMs, and finally some examples are given of how MMEMs and observations can be used together to address questions that neither method is qualified to answer in isolation.

2. HOW CAN MODELS BE USED TO IMPROVE OBSERVATIONS?

Availability and quality of observations differ in time and space as well as for different ecosystem com-

ponents. The sampling model of marine observations is challenged by discontinuous temporal scales and limited spatial view combined with high natural variability, and the sampling frequency will determine the possibility of identifying variability over time (Laane 2012, Pointin & Payne 2014). Complex procedures for operating an instrument allow for unintentional mistakes, and hardware needs frequent maintenance, calibration, and checking. Equipment might be lost or cannot be used under rough conditions, and long-term observational time series may experience changes in equipment, technology, staff, and implementation (e.g. Boyce et al. 2010, Gordó-Vilaseca et al. 2023). Monitoring surveys which cover predefined transects over the same time period between years are generally constrained by budgets and logistics (e.g. Zingone et al. 2015), and knowledge of the temporal versus spatial control of the observed variation is highly uncertain (Steiner et al. 2016). To assess confidence in observations, OSPAR (the Convention for the Protection of the Marine Environment of the North-East Atlantic) quantified different sources of uncertainty within the observational data available via its Common Procedure Eutrophication Assessment Tool (supplementary Fig. 3 in Appendix B in van Leeuwen et al. 2023). Evaluation of such monitoring efficiency requires data collection over multiple years before it may be performed, and thus is both time-consuming and expensive (Holmin et al. 2020). Consequently, changes to survey timing, methodology, or design are problematic since earlier efforts may be lost, and this argument is often used to avoid making necessary improvements (Jennings et al. 2009).

Marine observations are also challenged by uncertainty in the observation model. Very often, a scientific instrument is measuring a related quantity rather than the quantity of interest. In this sense, observations are just another type of model in which the quantity of interest is a result of either empirically or semi-analytically derived algorithms from another quantity (Fettweis et al. 2019, Rousso et al. 2022). Animal characteristics, behaviour, and individuality add complexity when observing natural populations. Plankton, for instance, rarely constitute continuous fields but rather patchy patterns with strong gradients in both space and time (e.g. Mackas et al. 1985, Maar et al. 2003, Martin 2003). Rapid growth and short generation times further challenge the interpretation of such observations, as measurements are presumably taken at different stages of development over the course of a single sampling program (J. M. Aarflot unpubl. data). The full advective history of plankton

or behavioural history of fish is difficult to assess only with point measurements, while observed abundance and trends depend on the assumption that catchability is known and constant in time (Kimura & Somerton 2006, Everett et al. 2017). This is further complicated by the fact that many species conduct vertical migrations on diel and seasonal cycles or perform long-distance horizontal migrations, which inevitably structures availability in a certain region or depth transect at a given point in time (Shanks & Brink 2005, Cowen & Sponaugle 2009, Varpe & Fiksen 2010, Dippner & Krause 2013, Holmin et al. 2020). Finally, most species respond to light, and may even display strong avoidance behaviour when exposed to artificial light mounted on sampling gear or on the research vessels themselves (Berge et al. 2020, Geoffroy et al. 2021).

In situ data may not be representative of the mean state of a system, as the bulk of the variability may be due to uneven and low coverage rather than inter-annual variability of the mean. For these reasons, *in situ* data sets should be used with caution in trend and inter-annual variability studies (de Mora et al. 2013). It is also challenging to assess the true state of a system, as the efficiency between observational platforms may differ, thereby giving a synthesized data set with potentially contradictory information (Dippner & Krause 2013, Yumruktepe et al. 2022). The best way to reduce the observational representation error is through repeated (synoptic) observations. Since *in situ* observations are inherently costly, the use of MMEMs is presumably the most cost-effective approach to analyze representativity and plan for future observations. Modelling has long been used as an active part of atmosphere observing system assessment and designs (Atlas 1997). Using a circulation model, Hatun et al. (2005) revealed the difficulty in unambiguously removing the seasonal cycle and describing decadal-scale temperature variations in the Faroe-Shetland Inflow Waters if hydrographical sections were surveyed less than 4 times a year. Coastal monitoring (e.g. as conditioned under the EU Water Framework Directive, WFD) tends to comprise a network of permanent sampling locations, generally lacking an evaluation of how well each location represents the conditions in the broader surrounding area. Here, models can be used to justify the extrapolation of measurements taken at one location to represent another location or a wider region (Edman et al. 2018). The assessment areas used in OSPAR's eutrophication assessment are based on both modelled results and observational knowledge (van Leeuwen et al. 2023). Schutgens et al. (2017) estimated the representation errors of observations for a

range of time and length scales by collocating high-resolution models with the observations to generate an objective truth. The study concluded that subsequent temporal averaging reduced the representation error but that the representation error remained larger than the typical measurement error, even after a substantial averaging (Schutgens et al. 2016a,b). Sandvik et al. (2016) compared a high-resolution model of the Norwegian Shelf with hydrographic observations obtained at a fixed coastal station off north-western Norway to compute the representation error of a single point measurement and the acceptable deviation between the modelled and observed temperatures.

Laane (2012) claims that the optimal monitoring network does not exist and that before a monitoring strategy can be applied, the natural variability of the indicator to be observed should be known. However, large efforts are today mobilized to design and evaluate ocean observing systems, and a summary of recent efforts of Observing System Evaluation is given in Fujii et al. (2019). In this context, MMEMs become important tools and can be utilized for characterizing the natural variability in a system and to optimize sampling time and frequency through Observing System Simulation Experiments. Hjøllø et al. (2021) used an MMEM to evaluate historic and present sampling schemes for zooplankton in the Norwegian Sea and demonstrated how different sampling patterns would lead to 2- to 4-fold differences in biomass estimates within a given year. Holmin et al. (2020) coupled an MMEM simulating the abundance and distribution of Norwegian spring spawning herring and northeast Atlantic mackerel to an observation model simulating survey data and investigated the sensitivity of monitoring surveys to shifts in time or spatial coverage to show how both survey timing and direction affected the stock estimate. McGillcuddy et al. (2001) showed that incomplete spatial sampling is the major contributing factor for a potential mismatch between observed and true copepod abundance, and Lin et al. (2010) used an MMEM to show that optimal sampling strategies for phytoplankton and zooplankton differ due to the differences in intrinsic biological processes. The challenge is not just where and when to sample but also how to do so within budget constraints. Hansen et al. (2021) used MMEMs to assess representativeness and suggested an optimal monitoring program with different options for frequency and coverage for a selection of indicators from the Barents Sea Management Plan.

What we observe is the sum of processes (possibly integrated over time) that are on different temporal

and spatial scales, and a point in time–space with respect to the processes will be different for the next observation at the same place. Biological samples depend on the integral of the environment over time and, therefore, an individual's current state is not only determined by its present conditions. MMEMs can be used to separate out different processes for cause–effect studies (e.g. Daewel et al. 2011), anthropogenic impact from natural variability (e.g. Skogen & Mathisen 2009), and to backtrack observations to obtain the full advective history of individuals (e.g. Christensen et al. 2007). MMEMs are generally formulated using patterns and processes learned from observed natural variations. In this context, MMEMs represent a framework for knowledge validation (Aarflot et al. 2022), whereby available information can be integrated and tested to disclose knowledge gaps and possible inconsistencies between independent studies and observational data sets. In this sense, MMEMs are an important first step for synthesizing different observational and experimental studies to explore possible ranges and ecological constraints of multiple trophic levels (Lindstrøm et al. 2017).

3. HOW CAN OBSERVATIONS BE USED TO IMPROVE MODELS?

Depending on the processes to be studied, models will almost always include a basic spatial and temporal resolution that is key to properly reproduce the actual scales of variability. The model resolution is constrained by the computational resources required (see Introduction of Chassignet & Xu 2021), although in recent years, the number of high-resolution models (e.g. Juza et al. 2016) that allow for a better representation of mesoscale and sub-mesoscale dynamics has increased (Hansen & Samuelsen 2009, Lévy et al. 2012, McKiver et al. 2015, Holt et al. 2017, Docquier et al. 2019). Improvements in the physics related to model resolution have been reported both at the global scale (Chassignet & Xu 2021) and the regional scale (Tonani et al. 2019). A proper representation of physics is crucial for marine ecological modelling applications due to the tight links between physics and biology, and in many cases, it is physics that explains the model misrepresentation (Doney et al. 2004, Skogen & Moll 2005, Najjar et al. 2007, Sinha et al. 2010, Popova et al. 2012). Some studies detail improvements in biogeochemical models related to increased model resolution (e.g. Jin et al. 2018), also achieved through model downscaling (Machu et al. 2015, Skogen et al. 2018). Thus, even with continuous

improvements in MMEMs to minimize uncertainties in parameterization and formulation of biological processes, there still remain uncertainties in model results from unresolved physics, model bathymetry, numerical methods, initial and boundary forcing quality, and meteorological and river forcings (see also Fox-Kemper et al. 2019).

MMEMs are simplifications of real-world systems and are by nature limited by knowledge gaps and insufficient understanding of ecosystems. In addition, even if biological primitive equations should exist (Woods 2002), it is not necessarily possible to formulate observed patterns mathematically by available parameters, either by those observed or those modelled. Parameters are mainly constant while ecosystem dynamics on the individual level should be time and space varying (Mattern et al. 2012). Insufficient ecosystem understanding and knowledge gaps also raise the question of whether the most important processes are included in an MMEM. MMEMs can be of different complexity (Fennel et al. 2022), and the choice often depends on the purpose of the study and the availability of other data (Radchuk et al. 2016). Simple MMEMs can be as good as complex ones for a specific question if site specificities are accounted for (Friedrichs et al. 2007), and complex models do not necessarily guarantee better results due to their uncertainties in the description of their additional ecological processes, the lack of accurate input data,

and the difficulties in the parameterization to represent the modelled processes and relationships (Anderson 2005, Kriest et al. 2010, Ward et al. 2013, Kwiatkowski et al. 2014, Xiao & Friedrichs 2014, Radchuk et al. 2016). Together, model structure, complexity, input data, and parameterization all contribute to errors and inaccuracies in the modelled predictions.

Building an MMEM is an iterative process in which an initial and often simplistic understanding of the system is gradually refined through successive repeated model validation and improved functional relationships (Fig. 1). To do this, MMEMs need targeted observations. This includes using observational process understanding to select mathematical equations that are representative, as well as observational information to aid with the selection of model parameters and initial and boundary conditions. Together with the limitations in the method of integration, these are also the main sources of model errors. Even simple biophysical models are complex and e.g. the description of growth, mortality, and other biological processes is made by means of mathematical equations which contain several parameters that, dependent on how they are chosen, can lead to completely different model evolution, including changes to the stability of the model. Information about the typical ranges of some of these parameters can be obtained from experiments and *in situ* observations, while

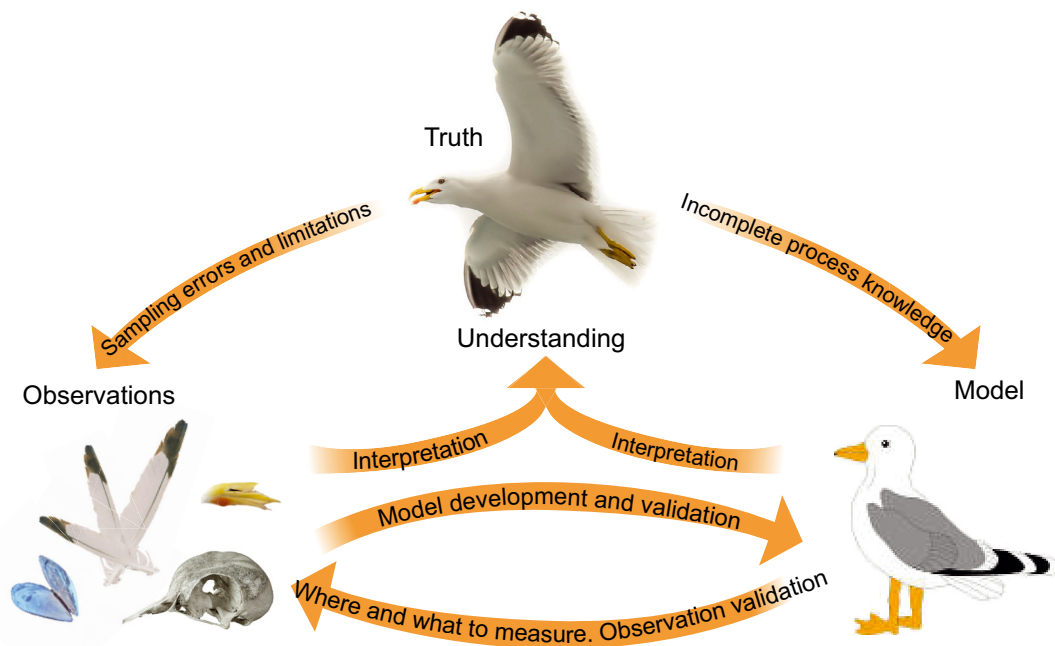


Fig. 1. Relationship between sparse high precision observations, simplified model representation, and combined use of models and observations to enhance overall ecosystem understanding

others that are difficult to measure can be estimated using data assimilation techniques (Gharamti et al. 2017). Parameters obtained from observations made in the lab are usually obtained under controlled environmental conditions and for a particular species but are often extrapolated to variable environmental conditions and groups of species in models for which these parameters might not be representative. Uncertainties associated with mathematical formulations and parameters are transferred to the model results and can be the largest contributor to the total uncertainty of the model outputs (e.g. Schartau et al. 2017, Mammun et al. 2022).

Due to the uncertainties associated with MMEMs, a proper evaluation of model outputs is necessary (Rykiel 1996), and observations are normally used to validate models. However, observations only allow for a partial assessment of models because they are normally instantaneous values, limited in space and time, of those state variables that it is possible to observe (Oreskes et al. 1994) and should themselves be validated in terms of representativity and bias (see above) before they are used to assess model performance. In the case of high-resolution models, the difficulties in the validation increase because these structures are not accurately monitored by present observations (Mourre et al. 2018, Jacobs et al. 2021). Moreover, when these high-resolution models are evaluated against observations, the traditional point-wise statistics might result in a worse performance compared to coarser resolution models (see, for instance, Tonani et al. 2019) due to the 'double penalty' effect (e.g. Brassington 2017). Considering some of the traditional methods of evaluating model performance (see a compilation in Mourre et al. 2018), like the mean square error, mean bias error, or mean absolute deviation, Moore & Rowland (1990) showed that the observational error could be the main source of discrepancy between models and observations, and proposed a diagnostic tool for determining whether random observational errors are significant. In addition, the way in which the comparison between model results and observations is carried out is important, and Piñeiro et al. (2008) demonstrated that scatterplots and subsequent regression analysis of observations and models were dependent on the choice of x and y variables. These facts call for alternative evaluation methods (Ebert 2008, Mourre et al. 2018), with this being an area of active research.

Observations of nutrients, and biological data on species composition, biomass, and distribution of plankton and fish are used in the development of MMEMs, but sometimes such information cannot be

used directly by these models (Everett et al. 2017). Models depend on observed conversion factors between e.g. wet and dry weights and carbon-to-nitrogen ratios, and vertically resolved models are compared with observed depth-integrated biomass with unknown catchability. MMEMs are not the main concern for most monitoring programs; thus, what models need and what is available from observations does not necessarily overlap. Moreover, many observational campaigns only focus on updates of existing time series with an unknown representativity and bias, while the need for MMEMs often is on improved ecosystem understanding and parameterisation through more dedicated studies of different processes. *In situ* observations are also dominated by estimates of status (like biomass), while rates (such as production) are rare. For model validation, there is also a need for independent data sets that have not been used for parameterisation, while updates of observational time series are not necessarily that critical as historical data can be used by a robust model.

Observations are most helpful for the development of MMEMs when they are measured in different areas and depths and at different times and thus capture a variety of conditions over space and time. A full list with precise details on what kind of observations are needed will depend on the complexity of the model and the system it represents, even if some attempts have been made for specific applications (e.g. Steiner et al. 2016, Smith et al. 2019).

4. COMBINED USE OF MODELS AND OBSERVATIONS TO ENHANCE OVERALL ECOSYSTEM UNDERSTANDING

Both MMEMs and observations are continuously being improved in terms of quality, resolution, and precision, and combined use has become more common. One of the most frequent ways to combine the 2 approaches is for designing and improving sampling programs, and there are numerous examples of this. In the GLOBEC Germany program (2002–2007, exploring the trophodynamic structure and function of the Baltic and North Sea), spatio-temporal estimates of copepod abundance from a lower trophic level model were used to justify taking multiple net hauls at some stations to better understand the natural variability associated with net sampling methods. Ellis et al. (2022) used biophysical modelling combined with estimated environmental DNA (eDNA) decay to determine the temporal and spatial detection limits of eDNA from 2 marine pests in Australia. Based on the

study, a recommendation on how sampling should be conducted in the area was also made. Curchitser et al. (2015) reviewed how a high-resolution circulation model coupled to an individual-based model and combined with observational data could be used to link environmental variables to ecosystem and population responses, and Benkort et al. (2020) used this approach to identify seasonal circuits of areas favourable for krill production in the Gulf of St. Lawrence and assess how these were coherent with the areas where krill had been sampled during field campaigns. Kubeneck et al. (2021) investigated vivianite formations in the Baltic Sea and used results from numerical model simulations (Almroth-Rosell et al. 2016, Edman et al. 2018) to locate appropriate sediment areas with high burial rates of organic phosphorus and to design the field cruises.

There are several caveats which concern the validity of environmental assessments purely based on observations. One is related to the representativity of the monitoring programs and another is related to the definition of a reference state with corresponding thresholds against which, for instance, water quality can be evaluated. Through the combined use of *in situ* data and MMEMs, there is a great potential to improve such assessments. To determine the 'Good Environmental Status' of the western Baltic Sea, Schernewski et al. (2015) first applied a model to estimate the present and the pre-eutrophic state. Then, using observations from the regular monitoring undertaken within the EU Marine Strategy Framework Directive and WFD, the present state was transferred to the historic situation applying the relative change from the simulations. García-García & Ruiz-Villarreal (2023) used a biogeochemical model and satellite chlorophyll data to fill temporal and spatial sampling gaps from the Palacus survey covering the shelf from Porto (Portugal) to the Southern Bay of Biscay. With this combined data set, they demonstrated the importance of the interplay between the upwelling–downwelling pulses–relaxations and the river plume dynamics to understand the interannual variability in primary production around the sampling time for the *in situ* observations. In preparation for the fourth application of the 'Common Procedure', included in the OSPAR QSR2023, an ensemble of ecosystem models was used to define the pre-eutrophic state of European marine waters (Lenhart et al. 2022, van Leeuwen et al. 2023). These simulated results, based on model results weighted with observational fit, were then used to derive thresholds for eutrophication indicators within assessment areas, and eutrophication status was then derived from the

comparison of the thresholds to *in situ* observations. Here, the use of a model ensemble ensured a (uniform) high spatial and temporal coverage for threshold derivation compared to patchy observational evidence.

It is hard to separate out different processes for cause–effect studies based on observations alone, but MMEMs provide an opportunity to fill in data gaps, test hypotheses, perform 'what-if' scenarios, and investigate relationships between observed and modelled data series. By combining field observations of oyster size and food concentration with outputs from a hydrodynamic model, Saraiva et al. (2020) were able to explain differences in observed growth rates at different sites and consequently reach more realistic conclusions about the ecosystem dynamics. In an analysis of 87 studies that have combined biophysical models and observed population genetic data, Jahnke & Jonsson (2022) indicated that using a combination of both methods can help to identify underlying processes that are difficult to assess otherwise. There is high uncertainty in the biomass of mesopelagic fish, with global estimates ranging more than one order of magnitude. Hill-Cruz et al. (2023) used an ecosystem model calibrated against observed biomass to provide mortality estimates for adult and juvenile mesopelagic fish for the Eastern Tropical South Pacific Ocean, thus providing an explicit representation of predation and starvation that direct measurements cannot account for.

For a better understanding of stock distribution or connectivity between different stocks, a combination of biophysical models and population genetic data enables investigations of drivers of connectivity, implications of barriers to dispersal, and potential impacts of climate. Using microsatellite DNA analyses of coastal and offshore cod in the North Sea–Skagerrak area in combination with a Lagrangian particle tracking model of cod eggs and larvae, Knutsen et al. (2004) evaluated the potential for larval transport from the North Sea into coastal populations, and Knutsen et al. (2012) used a similar setup to investigate the connectivity between different stocks of roundnose grenadier *Coryphaenoides rupestris* in the North Atlantic. The complementary strengths of a genetic parentage data set and biophysical models were proven by Bode et al. (2019), who produced an accurate picture of larval dispersal patterns at regional scales, while Gogina et al. (2020) combined a large set of observations for benthic crustacean species in the Baltic Sea with environmental data from 2 biogeochemical models to construct a species distribution model. The model was then used to estimate

the relative importance of driving variables for the change in species distribution for future scenarios.

5. CONCLUDING REMARKS

As neither models nor observations are 'truth', models should not automatically be mistrusted if their results do not match observational evidence. Both sources of data have their own strengths and weaknesses and neither is inherently better than the other. Models can help us understand the underlying mechanisms of a system, how processes might be interacting, simulate the effects of changes, and make predictions that can be tested by observations. Models can provide insights that are not easily obtainable from observations, but models are also limited by their inherent assumptions, insufficient ecosystem understanding, and whether the most important processes are included. Observations provide direct and empirical evidence of real-world processes and can be used to refine models. Despite the rapidly increasing rise in observations, models will always have a place in helping us disentangle the underlying drivers of observed patterns. Observations can only measure the state of the system, while models, of some sort, are required to estimate fluxes and connections between state variables. Models are indispensable for characterizing behaviour without the need for observations under every conceivable condition and empirical testing of models further enriches the value of these observations. Models can help fill in gaps that we have not been able to observe because of technical or monetary constraints or that we cannot observe because they are in the future or an under-sampled past. As such, models can be a very helpful tool for evaluating uncertainty and assessing risks in individual, organizational, and social policy decisions (Hyder et al. 2015, Bar-Yam 2016).

Both models and observations are pieces of information, and in science all available data sets should be used. A better understanding of representation error is essential to characterizing the truth when integrating models and observations. Therefore, proper validation of all data is a prerequisite in marine ecosystem studies, and ideally, all data sets should pass the ecological and/or ocean general circulation model Turing test (Woods 2002, Haine et al. 2021), with Haine et al. (2021, p. E1487) saying that '...a subject-matter expert cannot tell [models and observations] apart'. Statistical models are useful to identify linkages as a base for knowledge in the construction of MMEMs, but we often tend to accept simple con-

ceptual and statistical models more readily than we accept sophisticated marine ecosystem models, even if observations accompanied with statistics only represent a theory in which the role of certain factors as the only causes of specific outcomes is assumed rather than tested (Bar-Yam 2016). Future progress will require that we trust insights gained from MMEMs, as models used for knowledge validation represent our best tool to balance a system or to find inconsistencies between observations and process understanding. Using models and observations together can generate synergies and allow for better support of science and thereby an increased knowledge and understanding of marine ecosystems (Skogen et al. 2021).

Acknowledgements. This work was initiated during meetings in the ICES-WGIPEM (ICES Working Group on Integrated, Physical–biological and Ecosystem Modeling). We thank all participants for encouraging discussions.

LITERATURE CITED

- ✦ Aarflot JM, Hjøllø SS, Strand E, Skogen MD (2022) Transportation and predation control structures the distribution of a key calanoid in the Nordic Seas. *Prog Oceanogr* 202:102761
- ✦ Almroth-Rosell E, Edman M, Eilola K, Meier H, Sahlberg J (2016) Modelling nutrient retention in the coastal zone of an eutrophic sea. *Biogeosciences* 13:5753–5769
- ✦ Anderson TR (2005) Plankton functional type modelling: Running before we can walk? *J Plankton Res* 27: 1073–1081
- Atlas R (1997) Atmospheric observations and experiments to assess their usefulness in data assimilation. *J Meteorol Soc Jpn* 75:111–130
- ✦ Bar-Yam Y (2016) The limits of phenomenology: from behaviorism to drug testing and engineering design. *Complexity* 21:181–189
- ✦ Benkort D, Lavoie D, Plourde S, Dufresne C, Maps F (2020) Arctic and Nordic krill circuits of production revealed by the interactions between their physiology, swimming behaviour and circulation. *Prog Oceanogr* 182: 102270
- ✦ Berge J, Geoffroy M, Daase M, Cottier F and others (2020) Artificial light during the polar night disrupts Arctic fish and zooplankton behaviour down to 200 m depth. *Commun Biol* 3:102
- ✦ Bode M, Leis JM, Mason LB, Williamson DH, Harrison HB, Choukroun S, Jones GP (2019) Successful validation of a larval dispersal model using genetic parentage data. *PLOS Biol* 17:e3000380
- ✦ Boyce DG, Lewis MR, Worm B (2010) Global phytoplankton decline over the past century. *Nature* 466:591–596
- ✦ Brassington GB (2017) Forecast errors, goodness, and verification in ocean forecasting. *J Mar Res* 75:403–433
- ✦ Chassignet EP, Xu X (2021) On the importance of high-resolution in large-scale ocean models. *Adv Atmos Sci* 38: 1621–1634
- ✦ Christensen A, Daewel U, Jensen H, Mosegaard H, St John

- M, Schrum C (2007) Hydrodynamic backtracking of fish larvae by individual-based modelling. *Mar Ecol Prog Ser* 347:221–232
- ✦ Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Annu Rev Mar Sci* 1:443–466
- ✦ Curchitser EN, Rose KA, Ito Si, Peck MA, Kishi MJ (2015) Combining modeling and observations to better understand marine ecosystem dynamics. *Prog Oceanogr* 138:327–330
- ✦ Daewel U, Schrum C, Temming A (2011) Towards a more complete understanding of the life cycle of brown shrimp (*Crangon crangon*): modelling passive larvae and juvenile transport in combination with physically forced vertical juvenile migration. *Fish Oceanogr* 20:479–496
- ✦ de Mora L, Butenschon M, Allen J (2013) How should sparse marine *in situ* measurements be compared to a continuous model: an example. *Geosci Model Dev* 6:533–548
- Dee DP (1995) A pragmatic approach to model validation. In: Lynch D, Davies A (eds) *Quantitative skill assessment for coastal ocean models*. American Geophysical Union, Washington, DC, p 1–14
- ✦ Dippner J, Krause M (2013) Continuous plankton recorder underestimates zooplankton abundance. *J Mar Syst* 111–112:263–268
- ✦ Docquier D, Grist J, Roberts C, Roberts MJ and others (2019) Impact of model resolution on Arctic sea-ice and North Atlantic Ocean heat transport. *Clim Dyn* 53:4989–5017
- Doney SC, Lindsay K, Caldeira K, Campin JM and others (2004) Evaluating global ocean carbon models: the importance of realistic physics. *Global Biogeochem Cycles* 18:GB3017
- ✦ Ebert EE (2008) Fuzzy verification of high-resolution gridded forecasts: a review and proposed framework. *Meteorol Appl* 15:51–64
- ✦ Edman M, Eilola K, Almroth-Rosell E, Meier HM, Wählström I, Arneborg L (2018) Nutrient retention in the Swedish coastal zone. *Front Mar Sci* 5:415
- ✦ Ellis MR, Clark ZSR, Trembl EA, Brown MS and others (2022) Detecting marine pests using environmental DNA and biophysical models. *Sci Total Environ* 816:151666
- Everett JD, Baird ME, Buchanan P, Bulman C and others (2017) Modeling what we sample and sampling what we model: challenges for zooplankton model assessment. *Front Mar Sci* 4:77
- ✦ Fennel K, Mattern JP, Doney SC, Bopp L, Moore AM, Wang B, Yu L (2022) Ocean biogeochemical modelling. *Nat Rev Methods Primers* 2:76
- ✦ Fettweis M, Riethmüller R, Verney R, Becker M and others (2019) Uncertainties associated with *in situ* high-frequency long-term observations of suspended particulate matter concentration using optical and acoustic sensors. *Prog Oceanogr* 178:102162
- Fox-Kemper B, Adcroft A, Böning CW, Chassignet EP and others (2019) Challenges and prospects in ocean circulation models. *Front Mar Sci* 6:65
- ✦ Friedrichs MAM, Dusenberry JA, Anderson LA, Armstrong RA and others (2007) Assessment of skill and portability in regional marine biogeochemical models: role of multiple planktonic groups. *J Geophys Res Oceans* 112:C08001
- ✦ Fujii Y, Rémy E, Zuo H, Oke P and others (2019) Observing system evaluation based on ocean data assimilation and prediction systems: on-going challenges and a future vision for designing and supporting ocean observational networks. *Front Mar Sci* 6:417
- ✦ García-García LM, Ruiz-Villarreal M (2023) Variability of plankton production during the spring bloom in NW Iberia. *Mar Ecol Prog Ser* 708:45–78
- ✦ Geoffroy M, Langbehn T, Priou P, Varpe Ø and others (2021) Pelagic organisms avoid white, blue, and red artificial light from scientific instruments. *Sci Rep* 11:14941
- ✦ Gharamti ME, Tjiputra J, Bethke I, Samuelsen A, Skjelvan I, Bentsen M, Bertino L (2017) Ensemble data assimilation for ocean biogeochemical state and parameter estimation at different sites. *Ocean Model* 112:65–89
- ✦ Gogina M, Zettler ML, Wählström I, Andersson H, Radtke H, Kuznetsov I, MacKenzie BR (2020) A combination of species distribution and ocean-biogeochemical models suggests that climate change overrides eutrophication as the driver of future distributions of a key benthic crustacean in the estuarine ecosystem of the Baltic Sea. *ICES J Mar Sci* 77:2089–2105
- ✦ Gordó-Vilaseca C, Stephenson F, Coll M, Lavin C, Costello MJ (2023) Three decades of increasing fish biodiversity across the northeast Atlantic and the Arctic Ocean. *Proc Natl Acad Sci USA* 120:e2120869120
- ✦ Haine TWN, Gelderloos R, Jimenez-Urias MA, Siddiqui AH and others (2021) Is computational oceanography coming of age? *Bull Am Meteorol Soc* 102:E1481–E1493
- ✦ Hansen C, Samuelsen A (2009) Influence of horizontal model grid resolution on the simulated primary production in an embedded primary production model in the Norwegian Sea. *J Mar Syst* 75:236–244
- ✦ Hansen C, van der Meer GI, Loeng H, Skogen MD (2021) Assessing the state of the Barents Sea using indicators: How, when, and where? *ICES J Mar Sci* 78:2983–2998
- Hatun H, Sandø AB, Drange H, Bentsen M (2005) Seasonal to decadal temperature variations in the Faroe-Shetland inflow waters. In: Drange H, Dokken T, Furevik T, Gerdes R, Berger W (eds) *The Nordic Seas: an integrated perspective*. American Geophysical Union, Washington, DC, p 239–250
- ✦ Hill-Cruz M, Kriest I, Getzlaff J (2023) Diving deeper: mesopelagic fish biomass estimates comparison using two different models. *Front Mar Sci* 10:1121569
- ✦ Hjøllø SS, Hansen C, Skogen MD (2021) Assessing the importance of zooplankton sampling patterns with an ecosystem model. *Mar Ecol Prog Ser* 680:163–176
- ✦ Holmin AJ, Mousing EA, Hjøllø SS, Skogen MD, Huse G, Handegard NO (2020) Evaluating acoustic-trawl survey strategies using an end-to-end ecosystem model. *ICES J Mar Sci* 77:2590–2599
- ✦ Holt J, Hyder P, Ashworth M, Harle J and others (2017) Prospects for improving the representation of coastal and shelf seas in global ocean models. *Geosci Model Dev* 10:499–523
- ✦ Hufnagl M, Peck MA (2011) Physiological individual-based modelling of larval Atlantic herring (*Clupea harengus*) foraging and growth: insights on climate-driven life-history scheduling. *ICES J Mar Sci* 68:1170–1188
- ✦ Hyder K, Rossberg AG, Allen JI, Austen MC and others (2015) Making modelling count—increasing the contribution of shelf-seas community and ecosystem models to policy development and management. *Mar Policy* 61:291–302
- ✦ Iwamoto M, Dorton J, Newton J, Yerta M and others (2019) Meeting regional, coastal and ocean user needs with

- tailored data products: a stakeholder-driven process. *Front Mar Sci* 6:290
- ✦ Jacobs G, D'Addezio JM, Ngodock H, Souopgui I (2021) Observation and model resolution implications to ocean prediction. *Ocean Model* 159:101760
- ✦ Jahnke M, Jonsson PR (2022) Biophysical models of dispersal contribute to seascape genetic analyses. *Philos Trans R Soc B* 377:20210024
- Jennings S, Kaiser M, Reynolds JD (2009) *Marine fisheries ecology*. John Wiley & Sons, Hoboken, NJ
- ✦ Jin M, Deal C, Maslowski W, Matrai P and others (2018) Effects of model resolution and ocean mixing on forced ice-ocean physical and biogeochemical simulations using global and regional system models. *J Geophys Res Oceans* 123:358–377
- Juza M, Mourre B, Renault L, Gómara S and others (2016) SOCIB operational ocean forecasting system and multi-platform validation in the Western Mediterranean Sea. *J Oper Oceanogr* 9:s155–s166
- ✦ Kennedy JJ (2014) A review of uncertainty in *in situ* measurements and data sets of sea surface temperature. *Rev Geophys* 52:1–32
- ✦ Kimura D, Somerton D (2006) Review of statistical aspects of survey sampling for marine fisheries. *Rev Fish Sci* 14: 245–283
- ✦ Knutsen H, André C, Jorde PE, Skogen MD, Thuroczy E, Stenseth NC (2004) Transport of North Sea cod larvae into the Skagerrak coastal populations. *Proc R Soc B* 271: 1337–1344
- ✦ Knutsen H, Jorde PE, Bergstad OA, Skogen M (2012) Population genetic structure in a deepwater fish *Coryphaenoides rupestris*: patterns and processes. *Mar Ecol Prog Ser* 460:233–246
- ✦ Kriest I, Khatiwala S, Oschlies A (2010) Towards an assessment of simple global marine biogeochemical models of different complexity. *Prog Oceanogr* 86:337–360
- ✦ Kubeneck L, Lenstra W, Malkin S, Conley D, Slomp C (2021) Phosphorus burial in vivianite-type minerals in methane-rich coastal sediments. *Mar Chem* 231:103948
- ✦ Kwiatkowski L, Yool A, Allen JI, Anderson TR and others (2014) iMarNet: an ocean biogeochemistry model intercomparison project within a common physical ocean modelling framework. *Biogeosciences* 11:7291–7304
- Laane RWPM (2012) Innovative monitoring of the water quality in the Dutch coastal part of the North Sea: background document. Tech Rep 1204469-000, Deltares, Delft
- Lenhart H, Blauw A, Desmit X, Fernand L and others (2022) ICG-EMO report on model comparison for historical scenarios as basis to derive new threshold values, Tech Rep 895/2022. OSPAR, London
- ✦ Lévy M, Iovino D, Resplandy L, Klein P and others (2012) Large-scale impacts of submesoscale dynamics on phytoplankton: local and remote effects. *Ocean Model* 43-44: 77–93
- ✦ Lin P, Ji R, Davis CS, McGillicuddy DJ Jr (2010) Optimizing plankton survey strategies using observing system simulation experiments. *J Mar Syst* 82:187–194
- ✦ Lindstrøm U, Planque B, Subbey S (2017) Multiple patterns of food web dynamics revealed by a minimal non-deterministic model. *Ecosystems* 20:163–182
- ✦ Lynch D, McGillicuddy D Jr, Werner F (2009) Skill assessment for coupled biological/physical models of marine systems. *J Mar Syst* 76:1–3
- ✦ Maar M, Nielsen TG, Stips A, Visser A (2003) Microscale distribution of zooplankton in relation to turbulent diffusion. *Limnol Oceanogr* 48:1312–1325
- ✦ Machu E, Goubanova K, Le Vu B, Gutknecht E, Garçon V (2015) Downscaling biogeochemistry in the Benguela eastern boundary current. *Ocean Model* 90:57–71
- Mackas DL, Denman KL, Abbott MR (1985) Plankton patchiness: biology in the physical vernacular. *Bull Mar Sci* 37: 652–674
- Mamnun N, Völker C, Vrekoussis M, Nerger L (2022) Uncertainties in ocean biogeochemical simulations: application of ensemble data assimilation to a one-dimensional model. *Front Mar Sci* 9:984236
- ✦ Martin A (2003) Phytoplankton patchiness: the role of lateral stirring and mixing. *Prog Oceanogr* 57:125–174
- ✦ Mattern JP, Fennel K, Dowd M (2012) Estimating time-dependent parameters for a biological ocean model using an emulator approach. *J Mar Syst* 96–97:32–47
- ✦ McGillicuddy D Jr, Lynch D, Wiebe P, Runge J, Durbin E, Gentleman W, Davis C (2001) Evaluating the synopticity of the US GLOBEC Georges Bank broad-scale sampling pattern with observational system simulation experiments. *Deep Sea Res II* 48:483–499
- ✦ McKiver W, Vichi M, Lovato T, Storto A, Masina S (2015) Impact of increased grid resolution on global marine biogeochemistry. *J Mar Syst* 147:153–168
- ✦ Moore RD, Rowland JD (1990) Evaluation of model performance when the observed data are subject to error. *Phys Geogr* 11:379–392
- Mourre B, Aguiar E, Juza M, Hernandez-Lasheras J and others (2018) Assessment of high-resolution regional ocean prediction systems using multi-platform observations: illustrations in the western Mediterranean Sea. In: Chassignet EP, Pascual A, Tintore J, Verron J (eds) *New frontiers in operational oceanography*. GODAE Ocean View, p 663–694
- Najjar RG, Jin X, Louanchi F, Aumont O and others (2007) Impact of circulation on export production, dissolved organic matter, and dissolved oxygen in the ocean: results from Phase II of the ocean carbon cycle model intercomparison project (OCMIP-2). *Global Biogeochem Cycles* 21:GB3007
- ✦ Nappo CJ, Caneill JY, Furman RW, Gifford FA and others (1982) The workshop on the representativeness of meteorological observations, June 1981, Boulder, Colo. *Bull Am Meteorol Soc* 63:761–764
- ✦ Omori M, Hamner W (1982) Patchy distribution of zooplankton: behavior, population assessment and sampling problems. *J Mar Biol* 72:193–200
- ✦ Oreskes N, Shrader-Frechette K, Belitz K (1994) Verification, validation, and confirmation of numerical models in the Earth sciences. *Science* 263:641–646
- ✦ Piñeiro G, Perelman S, Guerschman JP, Paruelo JM (2008) How to evaluate models: Observed vs. predicted or predicted vs. observed? *Ecol Modell* 216:316–322
- ✦ Pointin F, Payne MR (2014) A resolution to the blue whiting (*Micromesistius poutassou*) population paradox? *PLOS ONE* 9:e106237
- Popova EE, Yool A, Coward AC, Dupont F and others (2012) What controls primary production in the Arctic Ocean? Results from an intercomparison of five general circulation models with biogeochemistry. *J Geophys Res Oceans* 117:C00D12
- ✦ Radchuk V, Oppel S, Groeneveld J, Grimm V, Schtickzelle N (2016) Simple or complex: relative impact of data availability and model purpose on the choice of model

- types for population viability analyses. *Ecol Modell* 323:87–95
- ✦ Rousso BZ, Bertone E, Stewart R, Aguiar A, Chuang A, Hamilton DP, Burford MA (2022) Chlorophyll and phycocyanin *in situ* fluorescence in mixed cyanobacterial species assemblages: effects of morphology, cell size and growth phase. *Water Res* 212:118127
- ✦ Rykiel EJ Jr (1996) Testing ecological models: the meaning of validation. *Ecol Modell* 90:229–244
- ✦ Salon S, Cossarini G, Bolzon G, Feudale L and others (2019) Novel metrics based on biogeochemical Argo data to improve the model uncertainty evaluation of the CMEMS Mediterranean marine ecosystem forecasts. *Ocean Sci* 15: 997–1022
- ✦ Sandvik A, Skagseth Ø, Skogen MD (2016) Model validation: issues regarding comparison of point measurements and high-resolution modeling results. *Ocean Model* 106:68–73
- ✦ Saraiva S, Freitas V, Ozório R, Rato A, Joaquim S, Matias D, Neves R (2020) Mechanistic approach for oyster growth prediction under contrasting culturing conditions. *Aquaculture* 522:735105
- ✦ Schartau M, Wallhead P, Hemmings J, Löptien U and others (2017) Reviews and syntheses: parameter identification in marine planktonic ecosystem modelling. *Biogeosciences* 14:1647–1701
- ✦ Schernewski G, Friedland R, Carstens M, Hirt U and others (2015) Implementation of European marine policy: new water quality targets for German Baltic waters. *Mar Policy* 51:305–321
- ✦ Schutgens N, Partridge DG, Stier P (2016a) The importance of temporal collocation for the evaluation of aerosol models with observations. *Atmos Chem Phys* 16: 1065–1079
- ✦ Schutgens NA, Gryspeerdt E, Weigum N, Tsyro S, Goto D, Schulz M, Stier P (2016b) Will a perfect model agree with perfect observations? The impact of spatial sampling. *Atmos Chem Phys* 16:6335–6353
- ✦ Schutgens N, Tsyro S, Gryspeerdt E, Goto D, Weigum N, Schulz M, Stier P (2017) On the spatio-temporal representativeness of observations. *Atmos Chem Phys* 17: 9761–9780
- ✦ Shanks AL, Brink L (2005) Upwelling, downwelling, and cross-shelf transport of bivalve larvae: test of a hypothesis. *Mar Ecol Prog Ser* 302:1–12
- ✦ Sinha B, Buitenhuis ET, Quéré CL, Anderson TR (2010) Comparison of the emergent behavior of a complex ecosystem model in two ocean general circulation models. *Prog Oceanogr* 84:204–224
- ✦ Skogen MD, Mathisen LR (2009) Long term effects of reduced nutrient inputs to the North Sea. *Estuar Coast Shelf Sci* 82:433–442
- ✦ Skogen MD, Moll A (2005) Importance of ocean circulation in ecological modeling: an example from the North Sea. *J Mar Syst* 57:289–300
- ✦ Skogen MD, Hjøllø SS, Sandø AB, Tjiputra J (2018) Future ecosystem changes in the Northeast Atlantic: a comparison between a global and a regional model system. *ICES J Mar Sci* 75:2355–2369
- ✦ Skogen MD, Ji R, Akimova A, Daewel U and others (2021) Disclosing the truth: Are models better than observations? *Mar Ecol Prog Ser* 680:7–13
- ✦ Smith GC, Allard R, Babin M, Bertino L and others (2019) Polar ocean observations: a critical gap in the observing system and its effect on environmental predictions from hours to a season. *Front Mar Sci* 6:429
- Steiner N, Deal C, Lannuzel D, Lavoie D and others (2016) What sea-ice biogeochemical modellers need from observers. *Elementa* 4:000084
- ✦ Tonani M, Sykes P, King RR, McConnell N and others (2019) The impact of a new high-resolution ocean model on the Met Office North-West European Shelf forecasting system. *Ocean Sci* 15:1133–1158
- ✦ Underwood AJ, Chapman MG, Connell SD (2000) Observations in ecology: you can't make progress on processes without understanding the patterns. *J Exp Mar Biol Ecol* 250:97–115
- van Leeuwen SM, Lenhart HJ, Prins TC, Blauw A and others (2023) Deriving pre-eutrophic conditions from an ensemble model approach for the north-west European seas. *Front Mar Sci* 10:1129951
- ✦ Varpe Ø, Fiksen Ø (2010) Seasonal plankton-fish interactions: light regime, prey phenology, and herring foraging. *Ecology* 91:311–318
- ✦ Ward BA, Schartau M, Oschlies A, Martin AP, Follows MJ, Anderson TR (2013) When is a biogeochemical model too complex? Objective model reduction and selection for North Atlantic time-series sites. *Prog Oceanogr* 116: 49–65
- Woods J (2002) Primitive equation modelling of plankton ecosystems. In: Pinaridi N, Woods J (eds) *Ocean forecasting: conceptual basis and applications*. Springer, Berlin, p 377–428
- ✦ Xiao Y, Friedrichs MAM (2014) Using biogeochemical data assimilation to assess the relative skill of multiple ecosystem models in the Mid-Atlantic Bight: effects of increasing the complexity of the planktonic food web. *Biogeosciences* 11:3015–3030
- ✦ Yumruktepe VÇ, Samuelsen A, Daewel U (2022) ECOSMO II (CHL): a marine biogeochemical model for the North Atlantic and the Arctic. *Geosci Model Dev* 15:3901–3921
- ✦ Zingone A, Harrison PJ, Kraberg A, Lehtinen S and others (2015) Increasing the quality, comparability, and accessibility of phytoplankton species composition time-series data. *Estuar Coast Shelf Sci* 162:151–160

Appendix. Full author addresses

Morten D. Skogen^{1,*}, Johanna M. Aarflot¹, Luz María García-García², Rubao Ji³,
 Manuel Ruiz-Villarreal², Elin Almroth-Rosell⁴, Andrea Belgrano^{5,6},
 Déborah Benkort⁷, Ute Daewel⁷, Moa Edman⁴, René Friedland⁸, Shuang Gao¹,
 Mariana Hill-Cruz⁹, Solfrid Sætre Hjøllø¹, Martin Huret¹⁰, Julie B. Kellner³,
 Sonja van Leeuwen¹¹, Ane Lopez de Gamiz-Zearra¹², Marie Maar¹³,
 Erik Askov Mousing¹, Myron A. Peck¹¹, Ane Pastor Rollan¹⁴, Sévrine F. Sailley¹⁵,
 Sofia Saraiva⁴, Cassie Speakman¹⁴, Tineke Troost¹⁶, Veli Çağlar Yumruktepe¹⁷

¹Ecosystemprocesses Group, Institute of Marine Research, Pb.1870, 5817 Bergen, Norway

²Instituto Español de Oceanografía (IEO, CSIC), Centro Oceanográfico de A Coruña, 15001 A Coruña, Spain

³Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

⁴Swedish Meteorological and Hydrological Institute, 601 76 Norrköping, Sweden

⁵Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Marine Research, Turistgatan 5, 453 30 Lysekil, Sweden

⁶Swedish Institute for the Marine Environment (SIME), University of Gothenburg, Box 260, 405 30 Gothenburg, Sweden

⁷Helmholtz-Zentrum Hereon, Institute of Coastal Systems–Analysis and Modelling, Max-Planck-Str. 1, 21502 Geesthacht, Germany

⁸Leibniz-Institute for Baltic Sea Research Warnemünde, Seestrasse 15, 18119 Rostock, Germany

⁹GEOMAR Helmholtz Centre for Ocean Research Kiel, Düsternbrooker Weg 20, 24105, Kiel, Germany

¹⁰DECOD (Ecosystem Dynamics and Sustainability), IFREMER, INRAE, Institut Agro, Brest, Pointe Du Diable, 29280 Plouzané, France

¹¹Coastal Systems Department, Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg (Texel), the Netherlands

¹²AZTI, Marine Research Division, Basque Research and Technology Alliance (BRTA), Txatxarramendi Ugarte a z/g, 48395, Sukarrieta, Spain

¹³Department of Ecoscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark

¹⁴School of Life & Environmental Sciences, Deakin University, Burwood, Victoria 3125, Australia

¹⁵Plymouth Marine Laboratory, Prospect Place, Plymouth, PL1 3DH, UK

¹⁶Deltares, PO Box 177, 2600 MH Delft, the Netherlands

¹⁷Nansen Environmental and Remote Sensing Center, Jahnebakken 3, 5007, Bergen, Norway

*Editorial responsibility: Elliott Hazen,
 Pacific Grove, California, USA
 Reviewed by: 3 anonymous referees*

Submitted: August 14, 2023

Accepted: May 8, 2024

Proofs received from author(s): June 10, 2024