ICES Journal of Marine Science Advance Access published December 17, 2015

ICES Journal of Marine Science

ICES International Council for the Exploration of the Sea
CIEM Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science; doi:10.1093/icesjms/fsv231

Uncertainties in projecting climate-change impacts in marine ecosystems

Mark R. Payne[1]*, Manuel Barange[2], William W. L. Cheung[3], Brian R. MacKenzie[1], Harold P. Batchelder[4], Xochitl Cormon[5], Tyler D. Eddy[6], Jose A. Fernandes[2], Anne B. Hollowed[7], Miranda C. Jones[3,8], Jason S. Link[9], Philipp Neubauer[10], Ivonne Ortiz[11], Ana M. Queirós[2], and José Ricardo Paula[12]

[1]*Centre for Ocean Life, National Institute of Aquatic Resources (DTU-Aqua), Technical University of Denmark, 2920 Charlottenlund, Denmark*
[2]*Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL13 DH, UK*
[3]*Changing Ocean Research Unit, Institute for the Oceans and Fisheries, The University of British Columbia, AERL, 2202 Main Mall, Vancouver, BC, Canada V6T 1Z4*
[4]*North Pacific Marine Science Organization (PICES), 9860 West Saanich Road, Sidney, BC, Canada V8L4B2*
[5]*IFREMER, Channel and North Sea Fisheries Research Unit, 150 Quai Gambetta, BP 699, 62321 Boulogne-sur-Mer, France*
[6]*Biology Department, Dalhousie University, 1355 Oxford Street, Halifax, Nova Scotia, Canada B3H 4J1*
[7]*National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA*
[8]*Department of Zoology, Cambridge University, Downing Street, Cambridge CB2 3EJ, UK*
[9]*National Oceanic and Atmospheric Administration, National Marine Fisheries Service, 166 Water St, Woods Hole, MA 02543, USA*
[10]*Dragonfly Data Science, PO Box 27535, Wellington 6141, New Zealand*
[11]*Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, WA 98195, USA*
[12]*MARE—Marine and Environmental Sciences Centre, Laboratório Marítimo da Guia—Faculdade de Ciências da Universidade de Lisboa, Av. Nossa Senhora do Cabo, 939, 2750-374 Cascais, Portugal*

**Corresponding author: tel: +45 3588 3455; e-mail: mpay@aqua.dtu.dk*

Payne, M. R., Barange, M., Cheung, W. W. L., MacKenzie, B. R., Batchelder, H. P., Cormon, X., Eddy, T. D., Fernandes, J. A., Hollowed, A. B., Jones, M. C., Link, Jason S., Neubauer, P., Ortiz, I., Queirós, A. M., and Paula, J. R. Uncertainties in projecting climate-change impacts in marine ecosystems. – ICES Journal of Marine Science, doi: 10.1093/icesjms/fsv231.

Received 6 July 2015; revised 9 November 2015; accepted 10 November 2015.

Projections of the impacts of climate change on marine ecosystems are a key prerequisite for the planning of adaptation strategies, yet they are inevitably associated with uncertainty. Identifying, quantifying, and communicating this uncertainty is key to both evaluating the risk associated with a projection and building confidence in its robustness. We review how uncertainties in such projections are handled in marine science. We employ an approach developed in climate modelling by breaking uncertainty down into (i) structural (model) uncertainty, (ii) initialization and internal variability uncertainty, (iii) parametric uncertainty, and (iv) scenario uncertainty. For each uncertainty type, we then examine the current state-of-the-art in assessing and quantifying its relative importance. We consider whether the marine scientific community has addressed these types of uncertainty sufficiently and highlight the opportunities and challenges associated with doing a better job. We find that even within a relatively small field such as marine science, there are substantial differences between subdisciplines in the degree of attention given to each type of uncertainty. We find that initialization uncertainty is rarely treated explicitly and reducing this type of uncertainty may deliver gains on the seasonal-to-decadal time-scale. We conclude that all parts of marine science could benefit from a greater exchange of ideas, particularly concerning such a universal problem such as the treatment of uncertainty. Finally, marine science should strive to reach the point where scenario uncertainty is the dominant uncertainty in our projections.

Keywords: climate change, initialization uncertainty, parametric uncertainty, projections, scenario uncertainty, structural uncertainty, uncertainty.

Introduction

Climate change is expected to have major consequences for marine ecosystems, including changes in biogeochemical cycles, trophic flows, species life histories, distributions, and seasonality (IPCC, 2014; Gattuso *et al.*, 2015). Such changes in turn impact how society depends on, and is influenced by, marine ecosystems and foodwebs. For example, there is a growing consensus that the roles of the oceans in the production of food for humans and as a sink for carbon dioxide will be altered due to climate change, and that such alterations will have socio-economic consequences (Barange *et al.*, 2014).

Climate-change projections are based on models that attempt to represent reality within the constraints of process understanding, observational data, and future conditions. However, such models may perform better at some spatial and temporal scales than others (or can only perform at one scale), even though there may be profound impacts on ecosystems and humans at other scales where model performance is less satisfactory. Moreover, the skill of a model often varies between variables; for example, global climate models typically predict surface temperatures better than precipitation. Consequently, the quality of model outputs depends on both the variable(s) being forecasted and the space-time-scale considered.

In an ecosystem or fisheries management context, however, what often matters most is not necessarily how the climate or ocean abiotic conditions will change, but how the biological components of an ecosystem might respond to environmental change. For example, if temperatures rise or ocean pH falls, how will these changes affect fishery yields and biodiversity, where in the global ocean will such changes be greatest, and when will these changes occur? To answer these types of questions, it is necessary to combine or integrate the oceanic component of climate models with models of species ecology, population dynamics, and entire foodwebs. As a result, uncertainty in physical climate models is carried forward into ecological models. Moreover, there are often multiple ways to model the same biological response (e.g. species distributions, reproductive success, predator–prey overlap, or the growth rates of individuals or a population); often, the use of different biological models with the same climate-ocean model output has led to different biological outcomes (Jones *et al.*, 2012; MacKenzie *et al.*, 2012; Meier *et al.*, 2012; Gårdmark *et al.*, 2013; Niiranen *et al.*, 2013). Consequently, efforts to adapt to and/or mitigate the effects of climate change on marine ecosystems must operate in a framework characterized by uncertainty from multiple sources.

The uncertainties associated with any type of projection can be broken down into subcomponents. In this work, we consider four main types of uncertainty: (i) structural (model) uncertainty, (ii) initialization and internal variability (IIV) uncertainty, (iii) parametric uncertainty, and (iv) scenario uncertainty. These are the most commonly recognized types used in climate science (e.g. Hawkins and Sutton, 2009); however, other model-uncertainty taxonomies also exist, including in a living marine resource context, e.g. stock-assessment scientists refer to measurement error, model-misspecification, and process error (Hilborn, 1987; Charles, 1998; Francis and Shotton, 1998; Regan *et al.*, 2002; Harwood and Stokes, 2003; Peterman, 2004; Hill *et al.*, 2007). However, these taxonomies generally converge on the forms of uncertainty identified above anyway and we choose to follow this scheme. We discuss the meaning of each of these terms in the corresponding sections below.

Some scientific fields have quantified the relative importance of each of these types of uncertainties and how they vary. A particularly powerful and motivating example of what can be done comes from meteorology where the total variability between climate projections is partitioned into components due to model, scenario, and initialization uncertainties (Hawkins and Sutton, 2009). At short time-scales, initialization uncertainty dominates, while at longer time-scales, scenario uncertainty is generally the most important (Figure 1). Marine science has not quantified its understanding of uncertainty in such a formal and quantitative manner, although the evaluation of model skill is clearly a rapidly developing area in the various disciplines of marine and climatological science (Lynch *et al.*, 2009; Stow *et al.*, 2009; Zhang *et al.*, 2010; Link *et al.*, 2015). However, it is also unclear how predictions from ecological models map onto this partitioning of uncertainty over time, and what role parametric uncertainty, for example, plays in this partitioning. Nevertheless, much can be learned from the example of other fields.

This article addresses the topic of uncertainties in the projection of marine climate-change impacts on ecosystems. We survey the state-of-the-art and, for each of the uncertainty types, ask "what is the current state of the art in assessing the relative importance of the uncertainty type in marine biological science"? We consider whether the marine scientific community has addressed these types of uncertainty sufficiently. In cases where more work is required, we highlight the opportunities and challenges associated with doing a better job. In a companion article in this volume (Cheung *et al.*, 2015), a framework is proposed that can be used to quantify the various forms of uncertainty in greater detail. Together, these articles enable the marine science community to be both more aware and more transparent about the limitations, robustness, and usefulness of their projections.

Structural uncertainty

Structural, or model, uncertainty can be characterized as the uncertainty associated with how the model is built up, i.e. how the model

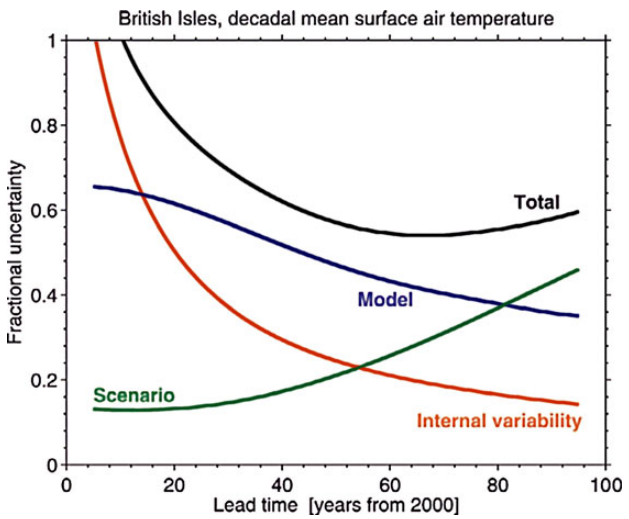

Figure 1. Contributions of various types of uncertainty to the total uncertainty in IPCC model ensemble projections of mean surface temperature over the British Isles. Relative (fractional) uncertainty of the total (black) and each individual component: model uncertainty (blue), scenario uncertainty (green), and internal variability (initialization uncertainty: orange). Note the change in the relative importance of the individual components. Reprinted from Hawkins and Sutton (2009). ©American Meteorological Society. Used with permission. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

translates inputs into outputs. Such uncertainty arises because we often do not completely understand all of the mechanisms or processes that occur in the real world. Consequently, there can be multiple working-hypotheses, each of which could be feasible. Data considerations (e.g. presence-only observations, incomplete coverage of the full range of variability), practical limitations (e.g. available computational power), and implementation decisions (e.g. choice of spatial/temporal resolution/aggregation, coding decisions) may also influence our ability to produce an appropriate model. Structural uncertainty arises as a direct consequence of these constraints, and the fact that they can be accommodated in multiple ways.

Modellers have often attempted to classify their models as a way of understanding the differences between their approaches. An early classification scheme (Levins, 1966) proposed the idea of three basic model traits: precision, realism and generality. Levins then called models that maximize realism and precision "*empirical*" models (e.g. species distribution models), models that maximize generality and realism "*mechanistic*" models (e.g. IPCC-class models), and models that are precise and general "*analytical*" models (e.g. Lotka–Volterra predator–prey models). While this scheme has been controversial, receiving both sharp criticism (Orzack and Sober, 1993; Orzack, 2005, 2012) and robust defence (Levins, 1993; Odenbaugh, 2003), it is still a useful framework within which to discuss model structure. Of particular interest here are the empirical models and the mechanistic models; analytical models are rarely used to make climate-change projections and will therefore not be considered further.

The most common examples of *empirical* models are species distribution models. These models typically involve explaining a set of observations of a species in terms of environmental correlates; the assumption is that the models are able to identify and represent the ecological niche of the species (Guisan and Zimmermann, 2000). A wide variety of models to link the observations and predictors are available and the consideration of alternative model structures, approaches, and/or predictors is becoming common (Planque *et al.*, 2011b; Jones *et al.*, 2012). The readiness of such comparisons is enabled, in part, by the relatively low investment required to perform species distribution modelling today: tools such as the BioMOD package in R (Thuiller *et al.*, 2009) allow an ensemble of model structures with standardized outputs to be rapidly fitted to a set of observations. Such model-comparison exercises clearly reveal the importance of model structure; for example, a comparison of three different models predicting the spatial distribution of mackerel, *Scomber scombrus* (Figure 2), showed agreement between the models in some areas (e.g. the North Sea), but also substantial disagreement in others (e.g. Iceland; Jones *et al.*, 2012). This disagreement between different models that have otherwise similar inputs is the essence of structural uncertainty.

The consideration of model structure in large *mechanistic* models (*sensu* Levins, 1966), such as circulation, biogeochemical, and ecosystem models, in contrast to *empirical* models, is less common. Such models can be high in complexity, requiring large research groups to run and maintain; developing multiple model structures is therefore often not practical. More generally, where comparisons of model structure exist, they tend to be made in separate papers focused on the comparison aspect (e.g. Spitz, 2003; Friedrichs *et al.*, 2007; Travers *et al.*, 2010; MacKenzie *et al.*, 2012; Gårdmark *et al.*, 2013), or via dedicated intercomparison projects, e.g. the Marine Ecosystem Model Intercomparison Project, MAREMIP (Hashioka *et al.*, 2013; Sailley *et al.*, 2013; Vogt *et al.*, 2013).

However, most model-structure comparison exercises are limited in their scope by the fact that performing intercomparisons is complex and time-consuming. Models are typically built for specific purposes and usually have different coverage of species, areas, and time frames. Comparing model structures that are fundamentally different (e.g. including both *empirical* and *mechanistic* models) and are built for different purposes can therefore be challenging. However, such approaches are seen in the physical sciences; for example, the IRI/CPC ENSO (*El Niño*/*La Niña*) forecasting system includes both "dynamic" (*mechanistic*) and "statistical" (*empirical*) models in its ensemble (Barnston *et al.*, 2012). Attempts are now being made in marine science to widen the scope of such intercomparison exercises [e.g. the recently developed Fisheries Impact Model Intercomparison Project (FISH-MIP) has solicited contributions from a wide range of modelling groups and model types (ISI-MIP, 2015)]. Applying this intercomparison approach more generally will help improve our understanding of the role of model structure.

A common feature of model-structure intercomparisons is that they are often reported as "model democracies" with a "one model-one vote" paradigm (Knutti, 2010), i.e. equal weights for all models. Such an approach is often employed as a pragmatic compromise to avoid the contentious question of which is the "best" model. However, this approach can only identify a range of possible outcomes: by failing to assign probabilities or weights to each model structure, it is not possible to say which of these outcomes is the most likely. For example, a model-comparison project on the future of cod (*Gadus morhua*) in the Baltic (Gårdmark *et al.*, 2013) gave a set of outcomes that included both extinction of the species and futures with unprecedented high levels. While there were also key commonalities found among the models, such as the importance of fishing pressure, not identifying the most likely of these outcomes limits the usefulness in a climate-change adaptation context. A basic challenge thus involves moving beyond "model democracies" towards finding methods to identify the "best" model or models from an ensemble of candidates, or stated alternatively, a suite of models that bounds a range of outcomes with quantified probabilities (Townsend *et al.*, 2014).

The question of the "best model structure" has been regularly treated in both the statistical and modelling literature. A variety of statistical methods exist to make such judgements (Johnson and Omland, 2004) and can be used to weight the members of an ensemble of models based on their historical predictive skill. The most common of these are the so-called "information criteria" metrics, such as the Akaike information criterion (AIC; Burnham and Anderson, 2002), which aim at finding a balance between the goodness-of-fit and the complexity of the model. Such approaches have recently made their way into marine science, and are being used regularly in, for example, stock-assessment (Millar *et al.*, 2014; Ianelli *et al.*, 2015). Cross-validation techniques have also been used extensively in the marine literature and are closely related. Alternatively, and largely independently, a large number of metrics and approaches have arisen in the modelling community to quantify the skill of models (see, for example, the review by Stow *et al.*, 2009) and are also starting to see uptake in marine science (Loots *et al.*, 2011; Planque *et al.*, 2011a; Cormon *et al.*, 2014; Link *et al.*, 2015).

However, it is also clear that there is no "right" answer to identifying the "best" model, and the choice should ultimately be driven by the question being asked (Dickey-Collas *et al.*, 2014). Nevertheless, the continued application of such techniques in marine science represents a valuable opportunity to improve the treatment of structural uncertainty in this field.

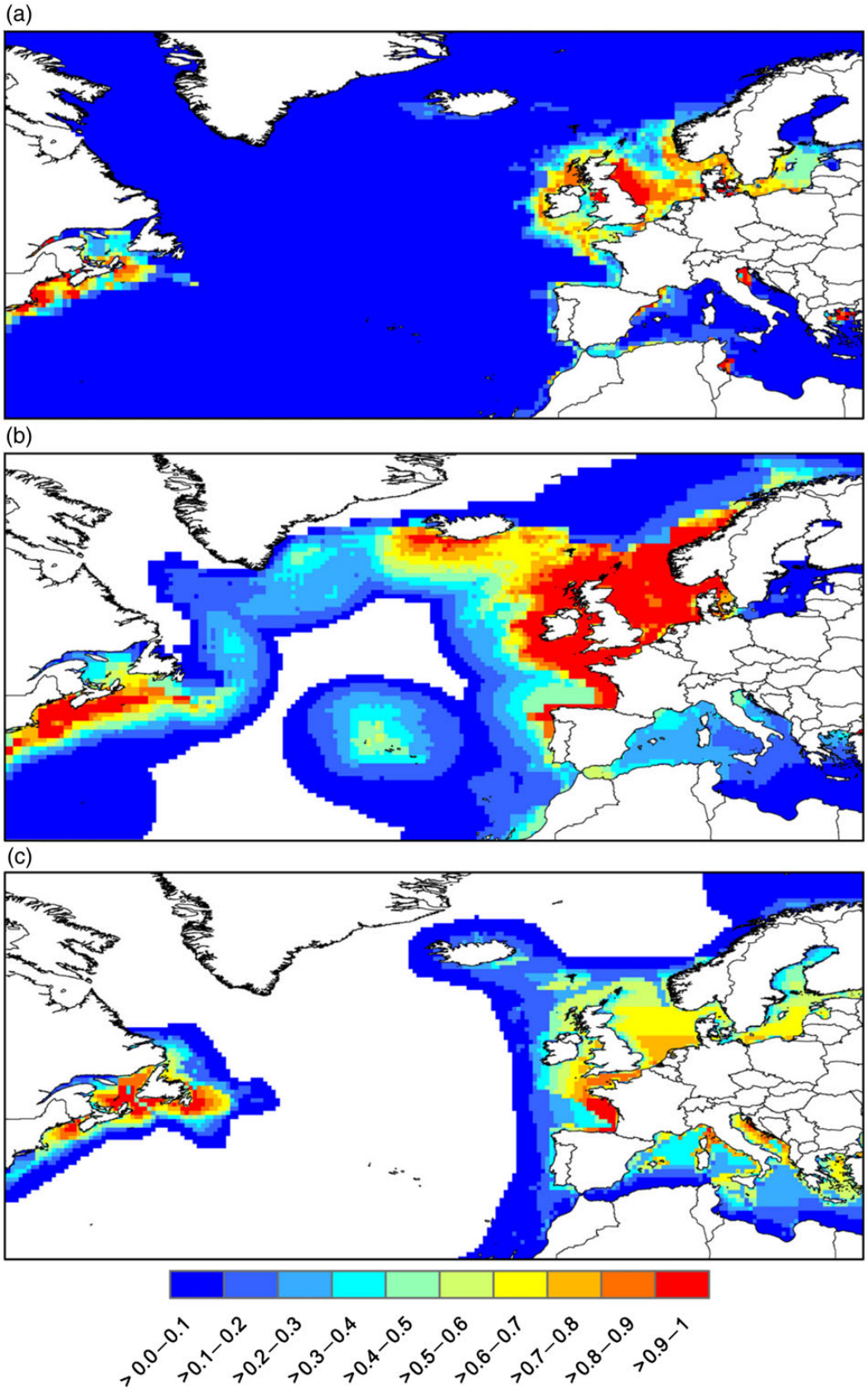

Figure 2. Predicted distributions of relative habitat suitability (0 – 1) for Atlantic mackerel, *S. scombrus*, using three different species distribution models parameterized using the same input data: (a) Maxent; (b) AquaMaps; (c) Sea Around Us Project model. Note the differences between model predictions around Iceland and the Azores. Reprinted from Jones *et al.* (2012) with permission from Elsevier. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Initialization and internal variability uncertainty

IIV uncertainty is two different aspects of what is essentially one feature of uncertainty. Initialization uncertainty is associated with the initial conditions of a model (i.e. the state of the system from which the model then integrates forward in time) and arises from our inability to fully and accurately observe or characterize the system at hand. Internal variability, on the other hand, is a characteristic of all complex models and results in feedbacks, nonlinearities, and periodicities that may, or may not, be realistic. The interaction between these two processes can give rise to chaotic behaviour, where small differences in starting points (states) are amplified and the resulting trajectories diverge, instead of converging. Uncertainty in the initialization can therefore be amplified by the internal variability inherent in a model.

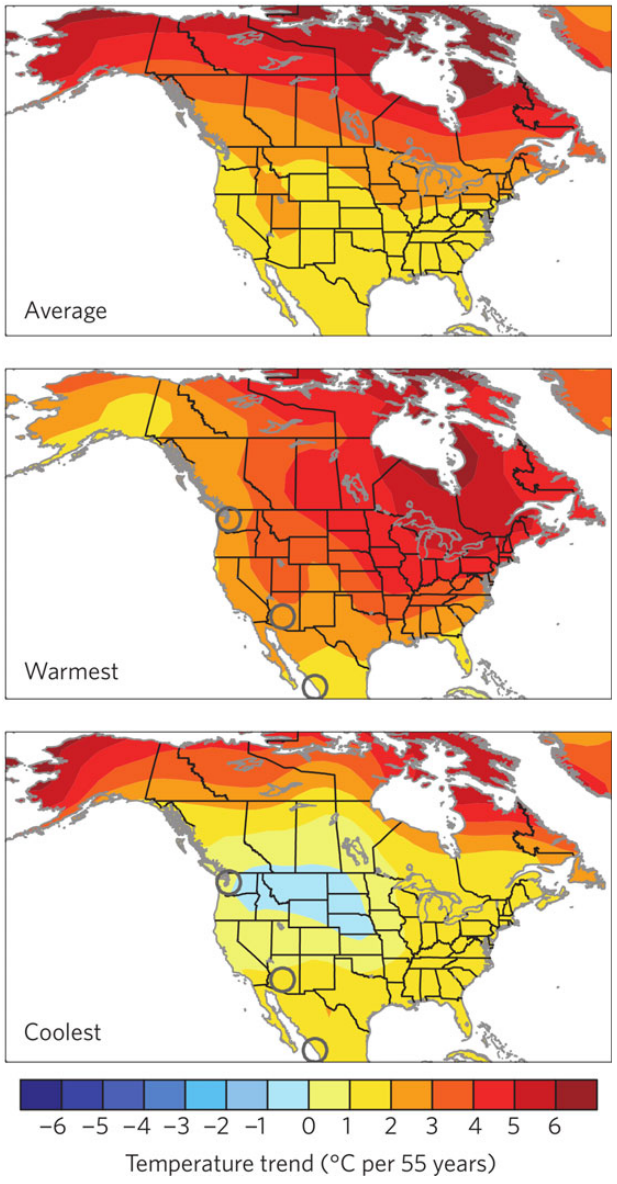

Figure 3. The impact of initialization and internal variability uncertainty on projections of surface air temperature across North America. A 40 member ensemble of projections was generated under a single climate-change scenario and model and with identical initial ocean, land, and sea ice model components but slightly different atmospheric initial conditions. Plots show the spatial distribution of winter (December–January–February) temperature trends during 2005–2060 for the average of all ensemble members (top panel), and the warmest (middle panel) and coolest (bottom panel) trends for the region as a whole. Note the substantial spatial differences in trends between the warmest and coolest ensemble members, and the difference in signs in the centre of North America. Reprinted by permission from Macmillan Publishers Ltd. Deser *et al.* (2012). Copyright 2012.

Uncertainty due to initialization and internal variability is well recognized in climate models and is the focus of significant research. In some cases, particularly in attribution studies, the variability in model outputs can be separated into those due to internal dynamics of the model and those that are due to external forcing (Thompson *et al.*, 2015). However, such analyses are computationally intensive and are therefore relatively limited. Other approaches have examined the sensitivity of model outputs to small perturbations in initial conditions; in one example based on an ensemble of 40 members with otherwise identical setups, small variations in the atmospheric initial state were able to change the sign of the projected temperature trend over parts of North America (Deser *et al.*, 2012; Figure 3). The recognition of the importance of internal variability and initialization uncertainty means that most climate model outputs today typically include several realizations starting from slightly different initial conditions.

The role of IIV processes is recognized and addressed in some parts of biological science. Chaos and the importance of initial conditions are well treated in the theoretical ecological literature. For example, the Lotka–Volterra system of models (Wangersky, 1978), a basic population dynamics model with feedbacks between predator and prey growth rates, is a common textbook example that shows strong sensitivity to initial conditions. Fisheries management is dominated by initialization uncertainties; stock-assessment estimates are more precise in the past than they are in the most recent year and catch option forecasts therefore often incorporate this uncertainty explicitly (e.g. ICES, 2012). The importance of IIV in limiting the predictability of plankton models has also been demonstrated (Baird, 2010). However, despite these examples, we are not aware of any cases where initialization and internal variability uncertainty has been treated explicitly in the context of climate-change projections of marine biological systems.

There exists, therefore, a need to address this uncertainty in more detail. For *empirical* models, such as correlative species distribution models, it seems likely that the internal variability and initialization uncertainty present in the physical models will propagate directly through into uncertainty in the biological outcomes. On the other hand, *mechanistic* models, such as large end-to-end models (e.g. ATLANTIS; Fulton *et al.*, 2011) and ecosystem models (e.g. NPZD plankton models), can be expected to exhibit a high degree of internal dynamics of their own (Rose *et al.*, 2010). How these dynamics interact with internal variability in the physical forcing will depend on the specifics of the situation; scenarios where dynamics can be both dampened out (e.g. long-lived species) and amplified (e.g. short-lived species) can be imagined, and can already be seen in simple models (e.g. Lotka–Volterra systems). However, we can expect that the resulting variance of the biological outputs will be at least comparable to, and probably greater than, the sum of the input variances due to internal variability.

Based on results from other fields, we can also expect that the importance of IIV uncertainty will vary depending on the time-scale of the question at hand. Hawkins and Sutton (2009) (Figure 1) showed

that at short time-scales, uncertainty in the initial conditions dominates, but its importance diminishes and eventually disappears over time. This phenomenon is critical in seasonal-to-decadal forecasting, and substantial improvements in the skill of such forecasts have been made as a direct result of improvements in initialization (Smith *et al.*, 2007; Matei *et al.*, 2012a, b): it therefore seems reasonable to expect that it will also be of importance in the emerging field of seasonal-to-decadal forecasting of marine ecosystems. Similarly, IIV is of less importance if the question at hand relates to a broad time-scale (e.g. decadal averages) or spatial region (e.g. continental averages), where the internal variability can be averaged-out. However, if the question is narrowly focused on a specific time or spatial point, then the variability between different realizations of the same model can be important.

Parametric uncertainty

Parametric uncertainty is the uncertainty associated with the parameters used in a model. Many processes can give rise to uncertainty in parameters, including imperfect measurements (e.g. uncertainty about the true parameter value in the statistical population); inadequate coverage of the range of natural variability; or natural variability of biological parameters (e.g. within-population variability in prey preference or growth rates; Figure 4). Furthermore, abstractions made in the model itself may lead to parameters that do not have direct biological interpretations, and are thus difficult or impossible to measure directly; they are inherently uncertain, e.g. the vulnerability

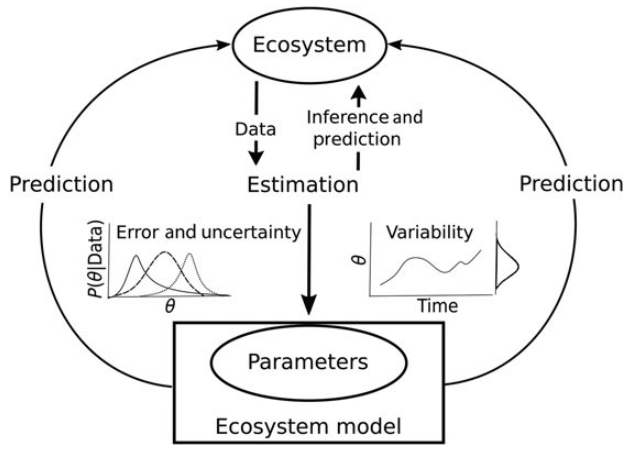

Figure 4. Parametric uncertainty in ecosystem models used to predict climate-change effects on ecosystems. Parameters of ecosystem models are commonly estimated from data using statistical methods or elicited from expert input. Parameter uncertainty can be decomposed into estimation error and uncertainty, resulting from finite and possibly biased data as well as the application of a specific set of estimation methods, and natural variability, which includes time-varying parameters (e.g. variable reproductive success). Ecosystem models that are specifically embedded within statistical frameworks (e.g. MICE models) can be used to quantify both types of uncertainty and employ a single model for estimation and forecasts (middle prediction arrow). Simulation models usually decouple parameter estimation/elicitation and forecasting, and, depending on the source of parameter uncertainty considered, different methods may be used to assess the impact of that uncertainty on forecasts of future ecosystem states (e.g. repeated simulations with random sets of parameters to account for estimation error/uncertainty, stochastic differential equations to simulate natural variability).

parameter in Ecopath (Christensen and Walters, 2004; Ahrens *et al.*, 2012), or the steepness parameter in stock assessments (Mace and Doonan, 1988; Myers *et al.*, 1999).

For well-bounded models, such as population dynamic models with relatively abundant observational data, statistical frameworks such as maximum likelihood and Bayesian methods are commonly used to estimate model parameters and their uncertainty (Maunder and Punt, 2013). Within these frameworks, a single model can be used to estimate parameters and produce predictions (Figure 4). Similarly, ecosystem model parameters such as trophic interactions and species life history parameters can often be obtained within these rigorous statistical frameworks, which allow estimation of natural variability and uncertainty in parameter estimates (Thorson and Minto, 2014; Neubauer and Jensen, 2015). However, even in models of such low complexity, it is often difficult to robustly determine which parameters may be affected by climate change, or to establish the mechanisms that govern this influence, e.g. a review of published environmental effects on recruitment in fish stocks revealed that few of these relationships held up under re-examination (Myers, 1998).

Where mechanistic relationships between model parameters and climate change are well established, these can be incorporated into integrated population-dynamics models. In the Baltic Sea, for example, the stock–recruitment relationship for sprat (*Sprattus sprattus*) is thought to be temperature-dependent, and would thus be affected by changing temperatures under climate change (MacKenzie *et al.*, 2012). When applied within a population-dynamics model of sprat, the recruitment is driven by temperature scenarios in detailed regional hydrographic models. However, substantial uncertainty in future sprat populations arises from unknown changes in cod (*G. morhua*) predation on sprat; since the model does not produce forecasts of cod biomass or explicitly model cod predation, the effect of different natural mortality rates had to be investigated via sensitivity analysis instead (MacKenzie *et al.*, 2012). In a similar example, Smith *et al.* (2015) bounded the range of parameter combinations used for estimating marine mammal consumption as a partial function of temperature to rule out which parameter sets would be infeasible. Thus, even in models that can be fit using statistical methods, it is often necessary to resort to more *ad hoc* sensitivity analyses for model components that cannot be explicitly fit to data.

Statistical quantification of parametric uncertainty can also be used for ecosystem models. However, such models are usually limited to data-rich subsets of whole ecosystems; such models are sometimes called "Models of Intermediate Complexity for Ecosystem assessments" (MICE; Plagányi *et al.*, 2014). As with single-species models, a mixture of statistical fitting and sensitivity analysis can be applied when using these models for climate-change forecasts. For more complex trophodynamic or ecosystem models, where observational data are limited to certain components of the system and parts of their natural variability (e.g. abundance and catches of selected fish and invertebrates, data from a single season), it is difficult to use formal statistical methods to estimate parameters and their uncertainties. In these cases, sensitivity analysis is to date the only option to explore the robustness of the model outputs to uncertainties associated with specific input parameter values: however, new methods, such as functionality filters, are also emerging (Fulton, 2010).

Sensitivity analysis provides a common alternative where statistical approaches cannot be employed. Such analyses involve varying input parameters to examine the consequences of uncertainty or

error in model inputs, to assess the effects of temporal variability in specified parameters, or both. While both types of sensitivities often involve Monte Carlo procedures to randomly select parameters (i.e. at the start of the simulation for parameter uncertainty, and throughout the simulation for natural variability), the two types of sensitivity analyses can give very different answers about the uncertainty of predictions (Kremer, 1983). If conducted in a well-designed model "experiment", such sensitivity analyses can nevertheless be insightful and useful.

Sensitivity analyses are, for complex ecosystem models, often paired with expert judgement to assess output sensitivities to parameter uncertainty. Cheung and Sumaila (2008), for instance, used two approaches to test the sensitivity of parameters in an Ecopath with Ecosim model of the Northern South China Sea (NSCS). First, a sensitivity analysis approach was used, during which input parameters were varied by up to 50%. In the second approach, values of the input parameters of the NSCS models were randomly selected from statistical distributions predefined in the "pedigree" (Christensen *et al.*, 2005), a routine to allow expert assignment of reliability of each input parameter. Based on all values resulting in mass-balanced models, confidence limits for input parameters of the 1970s and 2000s NSCS models could be estimated (Cheung and Sumaila, 2008).

Sensitivity analyses and expert judgement can thus illustrate potential ranges of modelled output responses and identify the most sensitive parameters; however, they cannot formally determine which of the outputs are most likely. Although statistical methods currently used in single species and MICE models are probably not suited to more formal estimation in whole ecosystem models, emerging statistical methods such as approximate Bayesian computation (Toni *et al.*, 2009) and Bayesian history matching (Andrianakis *et al.*, 2015) are promising methods that can combine concepts akin to sensitivity analyses with formal statistical linking to data. In summary, the selection of approaches to estimate parameter uncertainty should be determined by the types of model, availability of observational data, our understanding of the processes modelled, and the modelling objective.

Scenario uncertainty

Improving forecasts of future ecosystem states is the primary goal of climate-change-focused research. However, it can be argued that no matter how much understanding of ecosystem complexity we achieve, ecological predictions will continue to be dominated by significant uncertainties. Even if we had models without structural, initialization or parametric uncertainty, the way society will respond to outcomes will generate feedback loops that will interact with predictions. In these circumstances, the scientific community has to rely on scenarios to consider complexity and irreducible uncertainty.

The use of scenarios originated in military planning, and was extended in the 1960s into strategic planning in businesses where decision makers wanted to analyse, in a systematic way, the implications of strategic decisions with long-term consequences (Moss *et al.*, 2010). Scenarios, which can use a combination of model outputs, expert analysis, and contrasting subjective alternatives, aim at the development of alternative, plausible trajectories of ecosystems, where the uncertainties are part of the scenario planning. This open acknowledgement of uncertainties is in contrast to forecasts that narrowly limit them to a single potential outcome that is assumed to be predictable (Schindler and Hilborn, 2015). It would be easy to argue that any policy response developed under the former will make us better prepared to face the challenges of climate change.

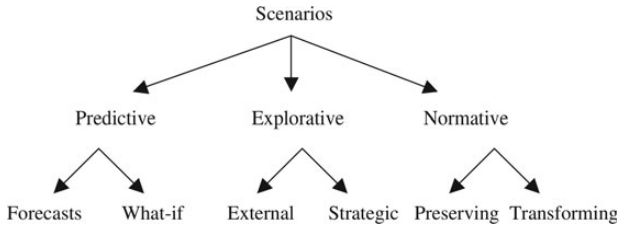

Figure 5. Scenario typology with three categories and six types. Reprinted from Börjeson *et al.* (2006) with permission from Elsevier.

The term "scenario" is used in many contexts and with different meanings, but they are all descriptions of possible futures that reflect different perspectives on the past, the present, and/or the future. Börjeson *et al.* (2006) offered a useful classification to understand scenarios, based on the principal questions we believe a user may want to pose about the future (Figure 5). If we are interested in knowing *what will happen,* then we are in search of *predictive* scenarios. These are either based on best-case scenarios (Forecasts) or on the likelihood of specific conditions to occur (if x then y, known as What-if). They are useful to planners and investors, who need to deal with foreseeable challenges and take advantage of foreseeable opportunities. Predictive scenarios are based on a statistical extrapolation of trends, such as patterns of biodiversity loss based on recent trends, or some form of deterministic model of reality.

Explorative scenarios, on the other hand, respond to the question *what can happen*? Their objective is to explore situations or developments that are regarded as possible, usually from a variety of perspectives and are usually easily understood and appreciated. Explorative scenarios can focus only on factors beyond the control of the relevant actors (External) or describe how the consequences of a decision can vary depending on which future development unfolds (Strategic). The IPCC SRES Scenarios (IPCC, 2000) were fundamentally exploratory, because they reflected future climates that might occur based on a range of external and internal decisions without specific probabilistic value.

Finally, *normative* scenarios respond to *how can a specific target be reached*? Their focus of interest is on certain future situations or objectives and how these could be realized, either to protect present states or to transform unwelcome states. Normative scenarios can be useful by inspiring policy or management action by providing a reflection of the future that would meet societal goals. They can also limit options by becoming an argument for taking the actions required. There is no "objective" mechanism or process to co-opt others into the normative vision, and one person's very serious normative scenario is another's silly fantasy. This lack of objectivity means that normative scenario outcomes, and the logic supporting their choices, must be communicated clearly.

A number of techniques are used to develop the different scenario types described above, ranging from workshops, expert panels, or surveys for generating and collecting ideas, and a set of modelling and time-series analysis to integrate these ideas into scenario results. In practice, most scenario analyses combine elements of predictive, exploratory, or normative principles. Using them wisely provides a strong basis for dealing with uncertainty without resolving it.

However, there are examples where scenarios are not only used to visualize the future but also to manage the intrinsic uncertainties that dominate in social–ecological systems. A particularly favoured

example in the context of marine fisheries is the management strategy evaluation (MSE) framework, which was developed to assess the consequences of a range of different living marine resource management strategies (De la Mare, 1986; Butterworth and Punt, 1999; Smith, 1999; Punt *et al.*, 2014). The strength of the MSE approach is that rather than using a single model to find an optimal solution, multiple candidate models, different formulations of one model, or various assumptions, forecasts, and management options are considered. MSE involves using an "operating model" to represent the "true" underlying dynamics of the fishery resource and to generate simulated future data; an "estimation model" which is then used to assess the state of the stock, species, or response group of interest relative to agreed target and limit reference points based on the simulated data; and one or more decision rules to determine what management actions should happen. The success of the MSE approach depends on the extent to which the true range of uncertainties can be identified and represented in the operating models, such as process, observation, estimation, model, and/or implementation error (Kell *et al.*, 2007). Under the MSE approach, each step of the adaptive-management approach is modelled and the consequences of alternative scenarios for each of the above uncertainties are evaluated in search of solutions that perform acceptably. Therefore, the use of "scenarios" is slightly different here, because it is not focused specifically on visualizing future options but on evaluating the contributions of all other sources of uncertainty in a scenario framework.

Discussion and conclusions

The perception of uncertainty in climate-change research is clearly evolving, including in the marine fisheries and ecological research communities. Until recently, uncertainty has been treated, if at all, in an aggregated way with little recognition or understanding of the factors that contribute to its magnitude, or has focused on only one or two aspects of uncertainty. In the fisheries research community, this focus could be on, for example, uncertainty in catches (due to misreporting); biological processes (e.g. natural mortality rates) that affect stock productivity or risk of overestimating fishing pressure, among others. However in the past 10–15 years, and with the increasing collaboration among scientists from different disciplines (particularly from climate and meteorological communities but also empiricists and modellers), a more general recognition that uncertainty is multifaceted and can be decomposed into several elements, as described above, is developing. Identifying these distinct facets helps to better address them and thus better handle uncertainty.

Our survey of marine science has shown that the treatment of uncertainty varies greatly with the type of uncertainty and the discipline; for example, scenario and structural uncertainties are widely recognized and commonly approached in the species distribution literature, while parametric uncertainty is more commonly handled in the ecosystem literature and IIV uncertainty appears to be rarely treated. The different approaches and degree of understanding we encountered was surprising, given the relatively small size of marine science. However, each of these disciplines has its own questions and challenges and given the tendency for scientific fields to be isolated from each other, such differences are perhaps not so surprising on second thought. It is nevertheless clear that all fields in marine science could benefit from greater exchange of ideas, particularly concerning a common problem such as the treatment of uncertainty.

Nevertheless, some parts of marine science clearly have a much better developed approach to uncertainty than others. For example, the MSE community in particular has been grappling with the many facets of uncertainty for nearly three decades and in some regards is more developed than in the climate sciences. The advanced state can most likely be attributed to the close linkage between fisheries science and the ongoing need to routinely and regularly make high-stakes management decisions in the face of uncertainty (Dankel *et al.*, 2012). Adapting the tools and approaches of this field to questions about future change may be a potentially productive focus area for future research.

Here, we have discussed the various types of uncertainty independently of each other. While this is both a traditional and convenient manner of approaching these issues, it is important to remember that uncertainties in the real world do not combine linearly or additively. Non-linearities and feedbacks are common in marine ecosystem models and can both amplify and reduce uncertainties. Partitioning uncertainty into its components is a convenient way to address and understand the various contributions to uncertainty, and is useful to focus future development. However, the question of how these uncertainty components propagate through the modelling system and potentially reinforce or cancel each other ultimately depends on the specifics of the individual system, and therefore needs to be addressed for each individual instance.

Marine ecosystem models are usually modular in nature, and typically consist of a biological component coupled to physical and biogeochemical components. The coupling of these modules is not a straightforward task, and can pose challenging scientific and practical questions; for example, should the grazing pressure in an individual-based fish-larval model feed back into the dynamics of lower trophic levels (e.g. Daewel *et al.*, 2011) or is one-way coupling sufficient (e.g. Christensen *et al.*, 2013)? Similarly, inputs of physical parameters need to be matched to the temporal and spatial scales on which biological models (e.g. species distribution models) operate; the choice of downscaling method (to convert global-scale climate model predictions to regional-scale predictions) can be as important as the choice of climate model itself. It is tempting to consider this additional complexity as an additional type of uncertainty, ("coupling uncertainty") unique to ecological models. However, similar coupling problems also occur in the physical sciences, e.g. general circulation models typically couple oceanographic, atmospheric, and often biogeochemical models that were developed separately. Such uncertainty can best be considered as another aspect of structural uncertainty, and can be handled by considering the various permutations of physical and biological models and their coupling (e.g. MacKenzie *et al.*, 2012; Niiranen *et al.*, 2013).

Assessments of the accuracy and precision of any model projection typically involve comparisons against observational data. However, data, by definition, are always historical in nature, and therefore we ultimately can only judge the past performance of the model. Good *historical* performance, however, is no guarantee of good *future* performance (Barnsley, 2007). Climate-change projections almost always involve extrapolation of some form and processes and interactions that become important in the future [e.g. adaptation of organisms to ocean acidification (Sunday *et al.*, 2014)] may not be parameterised appropriately or omitted from models altogether. These "*unknown unknowns*" are the ultimate limitation on the skill of our model projections. Although past model performance sometimes is the only guide to future reliability, we suggest that model projections be accompanied with a thorough

and formal assessment of known uncertainties. These will however represent a lower-bound on the true uncertainty, whose magnitude is difficult (and perhaps impossible) to quantify.

Beyond data availability issues, uncertainty associated with limited process understanding is somewhat implicit in any model structure. Experimental research frequently focuses on short-term, individual-level impacts in isolation. However, climate change will impact distinct aspects of species ecology, such as metabolic rates and complex predator–prey interactions, in different directions; such changes cannot be predicted by investigating individual-level impacts in isolation, or by considering climate stressors separately. Poor model skill can be indicative of such limitations, and can be used to help identify future direction for observational research. A close collaboration between experimentalists and modellers is therefore essential to ensuring progress in this field (Queirós *et al.*, 2015).

Clarity about the different types of uncertainty and their relative importance is also important for focusing research where the greatest gains can be made. While some uncertainty types can potentially be reduced, others cannot (at least in the foreseeable future), e.g. the actual CO_2 emission pathway that comes to be realized is largely beyond the control of marine scientists and little can be done to reduce this type of uncertainty. In contrast, other types of uncertainty can potentially be reduced via developing better knowledge of key processes that generate the highest uncertainty. If, for example, the largest source of uncertainty is due to structural uncertainty, then it might be relevant to conduct new (field, lab, modelling) studies to identify and quantify the sources of uncertainty and develop new model formulations. MacKenzie *et al.* (2012) used this approach to highlight uncertainty in stock–recruitment processes as dominating uncertainty in projections of the physical environment. Similarly, at short time-scales where initialization uncertainty is the most important source of uncertainty, improvements in the initialization of oceanographic models have led to great advances in decadal forecasting (Matei *et al.*, 2012b). Understanding the relative importance of each uncertainty type can therefore highlight where the greatest improvements can be made.

Finally, these considerations define a clear goal for research on the impacts of climate change on marine ecosystems. We propose that the research community should strive to improve projection models to the point where the largest uncertainty is due to scenario uncertainty, while other uncertainties are comparatively minor. Scenario uncertainty will remain large as it is the space where researchers and users explore plausible outcomes on the basis on irreducible elements (e.g. policy changes, economic development aspirations, etc.). The relative magnitude of this scenario uncertainty is therefore a useful yardstick for our field's progress and one that allows us to realistically and reliably judge the robustness of our projections.

Acknowledgements

This manuscript stems from the "Workshop on addressing uncertainty in projecting climate-change impacts in marine ecosystems" held as part of the "Third International Symposium on Effects of Climate Change on the World's Oceans" in Santos, Brazil, 21–27 March 2015. The authors would like to recognize and thank all those that participated in the workshop for the lively discussions and insightful comments that formed the foundation of this work. Furthermore, Martin Dorn and Charles Stock provided valuable input during the initial development of the manuscript, while Nancy Shackell and two other anonymous reviewers are thanked for their constructive comments during the review phase. The research leading to these results has received funding from the European Union 7th Framework Programme (FP7 2007-2013) under grant agreement number 308299 (NACLIM) and 265847 (ECO2). WLC acknowledges funding support from The Natural Sciences and Engineering Research Council of Canada and the Nippon Foundation-UBC Nereus Program. TDE and XC acknowledge travel support from ICES that allowed them to attend the workshop. JRP is supported by a PhD Scholarship from the Portuguese Foundation for Science and Technology (FCT) SFRH/BD/111153/2015 and acknowledges travel support from UNESCO/IO. PN was supported by Marsden Fund Fast-Start 14-DFG-001, administered by the Royal Society of New Zealand. AMQ acknowledges support from Marine Ecosystems Research Programme (jointly funded by the UK Natural Environment Research Council and the UK Department for Environment, Food and Rural Affairs, contract agreement NE/L003279/1). The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of their respective agencies.

References

Ahrens, R. N. M., Walters, C. J., and Christensen, V. 2012. Foraging arena theory. Fish and Fisheries, 13: 41–59.

Andrianakis, I., Vernon, I. R., McCreesh, N., McKinley, T. J., Oakley, J. E., Nsubuga, R. N., Goldstein, M., *et al.* 2015. Bayesian history matching of complex infectious disease models using emulation: a tutorial and a case study on HIV in Uganda. PLoS Computational Biology, 11: e1003968.

Baird, M. E. 2010. Limits to prediction in a size-resolved pelagic ecosystem model. Journal of Plankton Research, 32: 1131–1146.

Barange, M., Merino, G., Blanchard, J. L., Scholtens, J., Harle, J., Allison, E. H., Allen, J. I., *et al.* 2014. Impacts of climate change on marine ecosystem production in societies dependent on fisheries. Nature Climate Change, 4: 211–216.

Barnsley, M. J. 2007. Environmental Modeling: a Practical Introduction. CRC Press, Boca Raton, FL. 432 pp.

Barnston, A. G., Tippett, M. K., L'Heureux, M. L., Li, S., and DeWitt, D. G. 2012. Skill of real-time seasonal ENSO model predictions during 2002–11: is our capability increasing? Bulletin of the American Meteorological Society, 93: 631–651.

Börjeson, L., Höjer, M., Dreborg, K.-H., Ekvall, T., and Finnveden, G. 2006. Scenario types and techniques: Towards a user's guide Futures, 38: 723–739.

Burnham, K. P., and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY. 488 pp.

Butterworth, D. S., and Punt, A. E. 1999. Experiences in the evaluation and implementation of management procedures. ICES Journal of Marine Science, 56: 985–998.

Charles, A. T. 1998. Living with uncertainty in fisheries: analytical methods, management priorities and the Canadian groundfishery experience. Fisheries Research, 37: 37–50.

Cheung, W. W. L., Frölicher, T. L., Asch, R. G., Jones, M. C., Pinsky, M. L., Reygondeau, K. B., Rodgers, K. B., Rykaczewski, R. R., *et al.* 2015. Building confidence in projections of the responses of living marine resources to climate change. ICES Journal of Marine Science, doi:10.1093/icesjms/fsv250.

Cheung, W. W. L., and Sumaila, U. R. 2008. Trade-offs between conservation and socio-economic objectives in managing a tropical marine ecosystem. Ecological Economics, 66: 193–210.

Christensen, A., Butenschön, M., Gürkan, Z., and Allen, I. J. 2013. Towards an integrated forecasting system for fisheries on habitat-bound stocks. Ocean Science, 9: 261–279.

Christensen, V., and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172: 109–139.

Christensen, V., Walters, C. J., and Pauly, D. 2005. Ecopath with Ecosim: a User's Guide. Vancouver, Canada. 154 pp.

Cormon, X., Loots, C., Vaz, S., Vermard, Y., and Marchal, P. 2014. Spatial interactions between saithe (*Pollachius virens*) and hake (*Merluccius merluccius*) in the North Sea. ICES Journal of Marine Science, 71: 1342–1355.

Daewel, U., Peck, M. A., and Schrum, C. 2011. Life history strategy and impacts of environmental variability on early life stages of two marine fishes in the North Sea: an individual-based modelling approach. Canadian Journal of Fisheries and Aquatic Sciences, 68: 426–443.

Dankel, D. J., Aps, R., Padda, G., Röckmann, C., Van Der Sluijs, J. P., Wilson, D. C., and Degnbol, P. 2012. Advice under uncertainty in the marine system. ICES Journal of Marine Science, 69: 3–7.

De la Mare, W. K. 1986. Simulation studies on management procedures. Reports of the International Whaling Commission, 36: 429–450.

Deser, C., Knutti, R., Solomon, S., and Phillips, A. S. 2012. Communication of the role of natural variability in future North American climate. Nature Climate Change, 2: 775–779.

Dickey-Collas, M., Payne, M. R., Trenkel, V. M., and Nash, R. D. M. 2014. Hazard warning: model misuse ahead. ICES Journal of Marine Science, 71: 2300–2306.

Francis, R. I. C. C., and Shotton, R. 1998. "Risk" in fisheries management: a review. Oceanographic Literature Review, 7: 1228.

Friedrichs, M. A. M., Dusenberry, J. A., Anderson, L. A., Armstrong, R. A., Chai, F., Christian, J. R., Doney, S. C., *et al.* 2007. Assessment of skill and portability in regional marine biogeochemical models: role of multiple planktonic groups. Journal of Geophysical Research, 112: C08001.

Fulton, E. A. 2010. Approaches to end-to-end ecosystem models. Journal of Marine Systems, 81: 171–183.

Fulton, E. A., Link, J. S., Kaplan, I. C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., *et al.* 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries, 12: 171–188.

Gårdmark, A., Lindegren, M., Neuenfeldt, S., Blenckner, T., Heikinheimo, O., Müller-Karulis, B., Niiranen, S., *et al.* 2013. Biological ensemble modelling to evaluate potential futures of living marine resources. Ecological Applications, 23: 742–754.

Gattuso, J-P., Magnan, A., Bille, R., Cheung, W. W. L., Howes, E. L., Joos, F., Allemand, D., *et al.* 2015. Contrasting futures for ocean and society from different anthropogenic CO_2 emissions scenarios. Science, 349: aac4722.

Guisan, A., and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. Ecological Modelling, 135: 147–186.

Harwood, J., and Stokes, K. 2003. Coping with uncertainty in ecological advice: lessons from fisheries. Trends in Ecology and Evolution, 18: 617–622.

Hashioka, T., Vogt, M., Yamanaka, Y., Le Quéré, C., Buitenhuis, E. T., Aita, M. N., Alvain, S., *et al.* 2013. Phytoplankton competition during the spring bloom in four plankton functional type models. Biogeosciences, 10: 6833–6850.

Hawkins, E., and Sutton, R. 2009. The potential to narrow uncertainty in regional climate predictions. Bulletin of the American Meteorological Society, 90: 1095–1107.

Hilborn, R. 1987. Living with uncertainty in resource management. North American Journal of Fisheries Management, 7: 1–5.

Hill, S. L., Watters, G. M., Punt, A. E., McAllister, M. K., Le Quéré, C., and Turner, J. 2007. Model uncertainty in the ecosystem approach to fisheries. Fish and Fisheries, 8: 315–336.

Ianelli, J., Holsman, K. K., Punt, A. E., and Aydin, K. 2015. Multi-model inference for incorporating trophic and climate uncertainty into stock assessments. Deep Sea Research Part II: Topical Studies in Oceanography, doi:10.1016/j.dsr2.2015.04.002.

ICES. 2012. Report of the Benchmark Workshop on Pelagic Stocks (WKPELA 2012), 13–17 February 2012, Copenhagen, Denmark. ICES CM 2012/ACOM: 47. ICES CM 2012/ACOM: 06. 317 pp.

IPCC. 2000. Summary for Policymakers: Emissions Scenarios. A Special Report of Working Group III of the Intergovernmental Panel on Climate, Change. 20 pp.

IPCC. 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 1132 pp.

ISI-MIP. 2015. The Inter-Sectoral Impact Model Integration and Intercomparison Project. ISI-MIP2.1. Simulation protocol. Version 1.8. (Published 19 August 2015). 124 pp.

Johnson, J., and Omland, K. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution, 19: 101–108.

Jones, M. C., Dye, S. R., Pinnegar, J. K., Warren, R., and Cheung, W. W. L. 2012. Modelling commercial fish distributions: prediction and assessment using different approaches. Ecological Modelling, 225: 133–145.

Kell, L. T., Mosqueira, I., Grosjean, P., Fromentin, J-M., Garcia, D., Hillary, R., Jardim, E., *et al.* 2007. FLR: an open-source framework for the evaluation and development of management strategies. ICES Journal of Marine Science, 64: 640–646.

Knutti, R. 2010. The end of model democracy? Climatic Change, 102: 395–404.

Kremer, J. N. 1983. Ecological implications of parameter uncertainty in stochastic simulation. Ecological Modelling, 18: 187–207.

Levins, R. 1966. The strategy of model building in population biology. American Scientist, 54: 421–431.

Levins, R. 1993. A response to Orzack and Sober: formal analysis and the fluidity of science. The Quarterly Review of Biology, 68: 547.

Link, J., Mason, D., Lederhouse, T., Gaichas, S., Hartley, T., Ianelli, J., Methot, R., *et al.* 2015. Report from the Joint OAR-NMFS Modeling Uncertainty Workshop. NOAA Technical Memorandum NMFS-F/SPO-153. 31 pp.

Loots, C., Vaz, S., Planque, B., and Koubbi, P. 2011. Understanding what controls the spawning distribution of North Sea whiting (*Merlangius merlangus*) using a multi-model approach. Fisheries Oceanography, 20: 18–31.

Lynch, D. R., McGillicuddy, D. J., and Werner, F. E. 2009. Skill assessment for coupled biological/physical models of marine systems. Journal of Marine Systems, 76: 1–3.

Mace, P. M., and Doonan, I. J. 1988. A generalised bioeconomic simulation model for fish population dynamics. MAFFish, NZ Ministry of Agriculture and Fisheries.

MacKenzie, B. R., Meier, H. E. M., Lindegren, M., Neuenfeldt, S., Eero, M., Blenckner, T., Tomczak, M. T., *et al.* 2012. Impact of climate change on fish population dynamics in the Baltic sea: a dynamical downscaling investigation. Ambio, 41: 626–636.

Matei, D., Baehr, J., Jungclaus, J. H., Haak, H., Müller, W. A., and Marotzke, J. 2012a. Multiyear prediction of monthly mean Atlantic Meridional Overturning Circulation at 26.5°N. Science (New York, NY), 335: 76–79.

Matei, D., Pohlmann, H., Jungclaus, J., Müller, W., Haak, H., and Marotzke, J. 2012b. Two tales of initializing decadal climate prediction experiments with the ECHAM5/MPI-OM Model. Journal of Climate, 25: 8502–8523.

Maunder, M. N., and Punt, A. E. 2013. A review of integrated analysis in fisheries stock assessment. Fisheries Research, 142: 61–74.

Meier, H. E. M., Andersson, H. C., Arheimer, B., Blenckner, T., Chubarenko, B., Donnelly, C., Eilola, K., *et al.* 2012. Comparing reconstructed past variations and future projections of the Baltic Sea ecosystem—first results from multi-model ensemble simulations. Environmental Research Letters, 7: 034005.

Millar, C. P., Jardim, E., Scott, F., Osio, G. C., Mosqueira, I., and Alzorriz, N. 2014. Model averaging to streamline the stock assessment process. ICES Journal of Marine Science, 72: 93–98.

Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., van Vuuren, D. P., Carter, T. R., *et al.* 2010. The next generation of

scenarios for climate change research and assessment. Nature, 463: 747–756.

Myers, R. A. 1998. When do environment–recruitment correlations work? Reviews in Fish Biology and Fisheries, 8: 285–305.

Myers, R. A., Bowen, K., and Barrowman, N. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences, 56: 2404–2419.

Neubauer, P., and Jensen, O. P. 2015. Bayesian estimation of predator diet composition from fatty acids and stable isotopes. PeerJ, 3: e920.

Niiranen, S., Yletyinen, J., Tomczak, M. T., Blenckner, T., Hjerne, O., MacKenzie, B. R., Müller-Karulis, B., *et al.* 2013. Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. Global Change Biology, 19: 3327–3342.

Odenbaugh, J. 2003. Complex systems, trade-offs, and theoretical population biology: Richard Levin's "strategy of model building in population biology" revisited. Philosophy of Science, 70: 1496–1507.

Orzack, S. H. 2005. Discussion: what, if anything, is "the strategy of model building in population biology?" A comment on Levins (1966) and Odenbaugh (2003). Philosophy of Science, 72: 479–485.

Orzack, S. H. 2012. The philosophy of modelling or does the philosophy of biology have any use? Philosophical transactions of the Royal Society, Series B: Biological Sciences, 367: 170–180.

Orzack, S. H., and Sober, E. 1993. A critical assessment of Levins's the strategy of model building in population biology (1966). The Quarterly Review of Biology, 68: 533–546.

Peterman, R. M. 2004. Possible solutions to some challenges facing fisheries scientists and managers. ICES Journal of Marine Science, 61: 1331–1343.

Plagányi, É. E., Punt, A. E., Hillary, R., Morello, E. B., Thébaud, O., Hutton, T., Pillans, R. D., *et al.* 2014. Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. Fish and Fisheries, 15: 1–22.

Planque, B., Bellier, E., and Loots, C. 2011a. Uncertainties in projecting spatial distributions of marine populations. ICES Journal of Marine Science, 68: 1045–1050.

Planque, B., Loots, C., Petitgas, P., Lindstrøm, U., and Vaz, S. 2011b. Understanding what controls the spatial distribution of fish populations using a multi-model approach. Fisheries Oceanography, 20: 1–17.

Punt, A. E., Butterworth, D. S., de Moor, C. L., De Oliveira, J. A. A., and Haddon, M. 2014. Management strategy evaluation: best practices. Fish and Fisheries, doi:10.1111/faf.12104.

Queirós, A. M., Fernandes, J. A., Faulwetter, S., Nunes, J., Rastrick, S. P. S., Mieszkowska, N., Artioli, Y., *et al.* 2015. Scaling up experimental ocean acidification and warming research: from individuals to the ecosystem. Global Change Biology, 21: 130–143.

Regan, H. M., Colyvan, M., and Burgman, M. A. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. Ecological Applications, 12: 618–628.

Rose, K. A., Allen, J. I., Artioli, Y., Barange, M., Blackford, J., Carlotti, F., Cropp, R., *et al.* 2010. End-to-end models for the analysis of marine ecosystems: challenges, issues, and next steps. Marine and Coastal Fisheries, 2: 115–130.

Sailley, S. F., Vogt, M., Doney, S. C., Aita, M. N., Bopp, L., Buitenhuis, E. T., Hashioka, T., *et al.* 2013. Comparing food web structures and dynamics across a suite of global marine ecosystem models. Ecological Modelling, 261–262: 43–57.

Schindler, D. E., and Hilborn, R. 2015. Sustainability. Prediction, precaution, and policy under global change. Science, 347: 953–954.

Smith, A. 1999. Implementing effective fisheries-management systems—management strategy evaluation and the Australian partnership approach. ICES Journal of Marine Science, 56: 967–979.

Smith, D. M., Cusack, S., Colman, A. W., Folland, C. K., Harris, G. R., and Murphy, J. M. 2007. Improved surface temperature prediction for the coming decade from a global climate model. Science, 317: 796–799.

Smith, L. A., Link, J. S., Cadrin, S. X., and Palka, D. L. 2015. Consumption by marine mammals on the Northeast U.S. continental shelf. Ecological Applications, 25: 373–389.

Spitz, Y. H. 2003. Ecosystem response to upwelling off the Oregon coast: behavior of three nitrogen-based models. Journal of Geophysical Research, 108: 3062.

Stow, C. A., Jolliff, J., McGillicuddy, D. J., Doney, S. C., Allen, J. I., Friedrichs, M. A. M., Rose, K. A., *et al.* 2009. Skill assessment for coupled biological/physical models of marine systems. Journal of Marine Systems, 76: 4–15.

Sunday, J. M., Calosi, P., Dupont, S., Munday, P. L., Stillman, J. H., and Reusch, T. B. H. 2014. Evolution in an acidifying ocean. Trends in Ecology and Evolution, 29: 117–125.

Thompson, D. W. J., Barnes, E. A., Deser, C., Foust, W. E., and Phillips, A. S. 2015. Quantifying the role of internal climate variability in future climate trends. Journal of Climate, 28: 6443–6456.

Thorson, J. T., and Minto, C. 2014. Mixed effects: a unifying framework for statistical modelling in fisheries biology. ICES Journal of Marine Science, 72: 1245–1256.

Thuiller, W., Lafourcade, B., Engler, R., and Araújo, M. B. 2009. BIOMOD—a platform for ensemble forecasting of species distributions. Ecography, 32: 369–373.

Toni, T., Welch, D., Strelkowa, N., Ipsen, A., and Stumpf, M. P. 2009. Approximate Bayesian computation scheme for parameter inference and model selection in dynamical systems. Journal of the Royal Society Interface, 6: 187–202.

Townsend, H. M., Harvey, C., Aydin, K. Y., Gamble, R., Grüss, A., Levin, P. S., Link, J. S., *et al.* 2014. Report of the 3rd National Ecosystem Modeling Workshop (NEMoW 3): Mingling Models for Marine Resource Management—Multiple Model Inference. NOAA Technical Memorandum NMFS-F/SPO-149. 93 pp.

Travers, M., Watermeyer, K., Shannon, L. J., and Shin, Y. J. 2010. Changes in food web structure under scenarios of overfishing in the southern Benguela: comparison of the Ecosim and OSMOSE modelling approaches. Journal of Marine Systems, 79: 101–111.

Vogt, M., Hashioka, T., Payne, M. R., Buitenhuis, E. T., Le Quéré, C., Alvain, S., Aita, M. N., *et al.* 2013. The distribution, dominance patterns and ecological niches of plankton functional types in Dynamic Green Ocean Models and satellite estimates. Biogeosciences Discussions, 10: 17193–17247.

Wangersky, P. J. 1978. Lotka–Volterra population models. Annual Review of Ecology and Systematics, 9: 189–218.

Zhang, A., Hess, K., and Aikman, F., III 2010. User-based skill assessment techniques for operational hydrodynamic forecast systems. Journal of Operational Oceanography, 3: 11–24.

Handling editor: Manuel Hidalgo