



## Ecosystem models for fisheries management: finding the sweet spot

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### Abstract

The advent of an ecosystem-based approach dramatically expanded the scope of fisheries management, creating a critical need for new kinds of data and quantitative approaches that could be integrated into the management system. Ecosystem models are needed to codify the relationships among drivers, pressures and resulting states, and to quantify the trade-offs between conflicting objectives. Incorporating ecosystem considerations requires moving from the single-species models used in stock assessments, to more complex models that include species interactions, environmental drivers and human consequences. With this increasing model complexity, model fit can improve, but parameter uncertainty increases. At intermediate levels of complexity, there is a 'sweet spot' at which the uncertainty in policy indicators is at a minimum. Finding the sweet spot in models requires compromises: for example, to include additional component species, the models of each species have in some cases been simplified from age-structured to logistic or bioenergetic models. In this paper, we illuminate the characteristics, capabilities and short-comings of the various modelling approaches being proposed for ecosystem-based fisheries management. We identify key ecosystem needs in fisheries management and indicate which types of models can meet these needs. Ecosystem models have been playing strategic roles by providing an ecosystem context for single-species management decisions. However, conventional stock assessments are being increasingly challenged by changing natural mortality rates and environmentally driven changes in productivity that are observed in many fish stocks. Thus, there is a need for more tactical ecosystem models that can respond dynamically to changing ecological and environmental conditions.

**Keywords** ecosystem-based management, fisheries, marine, model complexity, trade-off

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<b>Introduction</b>	<b>2</b>
<b>Fishery ecosystem models</b>	<b>3</b>
Characteristics of models: complexity and uncertainty	3
Considerations in choosing and developing models	4
<i>Maintaining population realism</i>	4
<i>Incorporating species interactions</i>	5
<i>Incorporating environmental drivers</i>	6
<i>Incorporating human dimensions</i>	7
<b>Use of ecosystem models in fisheries management</b>	<b>8</b>
What are the key ecosystem needs for models?	8
What types of models can meet these needs?	9
<i>Strategic ecosystem models to inform fisheries management</i>	9
<i>Tactical ecosystem models to specify harvest policy</i>	10
How can these models be used?	11
<i>Ecosystem reference points and indicators</i>	11
<i>Multispecies biological reference points</i>	12
<i>Visualization and communication</i>	13
<b>Existing applications to management</b>	<b>15</b>
Models with environmental drivers	15
Multispecies models	16
<b>Discussion</b>	<b>16</b>
Progress in following best practices in ecosystem modelling	17
Finding the sweet spot	18
Application of ecosystem models to fisheries management	18
Summary and conclusions	19
<b>Acknowledgements</b>	<b>20</b>
<b>References</b>	<b>20</b>

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## Introduction

With the increasing efforts towards ecosystem-based fisheries management (EBFM) and the looming prospect of substantial changes in marine ecosystems from climate change, a number of quantitative approaches to describing marine ecosystems for management purposes have emerged. Several countries, including Australia, have formally adopted an ecosystem-based approach to fisheries management (Essington and Punt 2011; Kruse *et al.* 2012). In the United States, the regional fisheries management councils are at various stages of developing ways to implement an ecosystem approach. In parallel, large-scale oceanographic research programmes such as GLOBEC (Barange *et al.* 2010) have been aimed at understanding how climate change and variability will translate into changes in the structure and dynamics of marine ecosystems and fish production. Although there have been preliminary efforts

to compare and evaluate early quantitative approaches (Hollowed *et al.* 2000; Cury *et al.* 2008; FAO 2008), there remains a need for comprehensive comparison, with an emphasis on contrasting and evaluating the various alternative approaches in the context of the specific fisheries management issues that need to be addressed.

Most quantitative approaches to ecosystem assessment involve models to organize and quantify our understanding of ecological processes and to project the likely consequences of regulations on populations and communities in the context of a changing ecosystem (Dickey-Collas *et al.* 2013). A variety of modelling approaches have been applied to this problem, motivated primarily by a quest for greater holism through the inclusion of species interactions, environmental variability and socio-economic effects (Botsford *et al.* 1997; Pickett *et al.* 2004.). However, there has been little scrutiny of how well these models can be expected to represent the dynamics of the added ecosystem

components. Similarly, there is a range of needs and uses for models in EBFM, and some models may serve certain purposes better than others.

The terms associated with ecosystem-based fisheries management (EBFM) have varied definitions (Pikitch *et al.* 2004; Sissenwine and Murawski 2004; Fogarty 2014). Here, we focus on steps towards EBFM that account for interactions among the key species present, and the influences of a variable environment on those species. We place less emphasis on the social and economic considerations that are also part of an ecosystem approach. Socio-economic considerations have long been part of conventional fisheries management, but they need to be considered more explicitly in EBFM, especially where there are multiple conflicting objectives (Kellner *et al.* 2011). The quantitative approaches we evaluate here are mainly different types of ecological models (i.e. logistic type, age/size-structured, food web, multi-species oceanographic simulations) and various proposed indicators of ecosystem state. Our focus is somewhat narrower than the full range of modelling considerations, as we do not attempt to provide a systematic review of ecosystem models (see FAO 2008). Rather, we focus on how well models will represent ecosystem dynamics to inform decision-makers in the pursuit of their specific ecosystem goals.

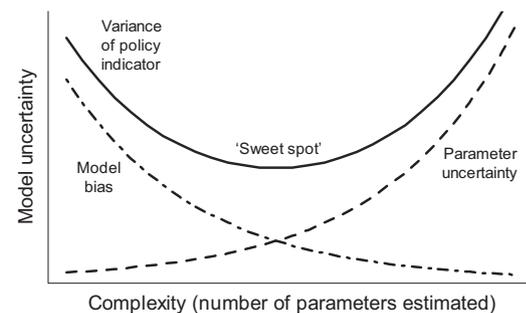
While an ecosystem perspective is conceptually desirable, ecosystems are complex and unpredictable, and there will likely be limited financial resources with which to formulate ecosystem models. Process-based data needed to configure ecosystem models and the long-term data required for model validation will also be limited in many situations (Livingston *et al.* 2011b). These constraints have led to the development of models that incorporate more ecosystem components, but do so with a simpler description of the population dynamics of each species, compared with the assessment models used in single-species management. One of our primary goals in this paper is to describe the consequences of such simplifications. We seek to inform scientists and decision-makers regarding the nature of results possible from various types of models. We start by reviewing the consequences of adding complexity and the data needs of ecosystem models being developed for fisheries management. Next, we identify the key ecological considerations that these models must address in fisheries management and the types of

models that could meet these needs. We evaluate the extent to which best practices for ecosystem modelling (FAO 2008) are being followed. Finally, we review the present use of ecosystem models in decision-making and discuss impediments that hinder the uptake of ecosystem considerations in fisheries management.

## Fishery ecosystem models

### Characteristics of models: complexity and uncertainty

The call to include ecosystem considerations requires models to move from simple to complex as they include additional factors, ecosystem components and variability in space or time (Fig. 1). To maintain a tractable model and to avoid exceeding data availability, one approach is to simplify the description of each component, as more components are added. But overly simple models may not be able to represent important aspects of ecosystem dynamics and can thus have large *model bias*. On the other hand, fully augmented models require increased understanding of species and environmental interactions to specify the dynamics in greater detail. The uncertainty in these models shifts from bias to *parameter uncertainty*, arising from the sheer number of paramete-



**Figure 1** A schematic view of the way in which model bias declines and parameter uncertainty increases with increasing model complexity. Model bias is related to model fit, as measured by the residual error variance. If the number of parameters is too large, a statistical model will ‘fit the noise’ and can give biased predictions. Parameter uncertainty is measured by the variance–covariance matrix of the parameter estimates. The variance of key policy indicators is the product of these two sources of error and therefore has a minimum at an intermediate level of complexity (adapted from Walters 1986).

ters and therefore the amount of data needed to estimate them. To reduce this uncertainty requires additional observations to estimate parameter values and to constrain model predictions. While the need for realism pushes model choice towards complexity, the need for empirically based parameters of the system limits complexity. Walters (1986) developed a mathematical treatment of this trade-off to show that the variance of key policy indicators (such as harvest rates or reference points) is the product of these two sources of error. In the end, the model used should be as simple as possible without neglecting any essential components or processes. For most specific purposes, a model of intermediate complexity is thus preferable (Plagányi *et al.* 2014).

Starting from a non-structured, single-species model with no environmental or human influences, model complexity can develop in at least four different dimensions: (i) increased population structure in time, space, age or stage; (ii) increased environmental influences affecting larval dispersal, lower trophic levels, and the growth, fecundity and survival of upper trophic levels; (iii) increased number of species, with nonlinear trophic interactions among food-web components; and (iv) increased human interactions beyond harvest (e.g. fleet dynamics, economics and policy influences). Each ecosystem model that is used to inform management will have augmented complexity in one or more of these, with a full ecosystem model being one that includes additional complexity in all four dimensions. Along this gradient from simple to more complex, there is a 'sweet spot' that balances diminishing model bias with increasing parameter uncertainty (Fig. 1). We use the term 'sweet spot' as the level of complexity that will maximize the usefulness of ecosystem models to fishery management.

### Considerations in choosing and developing models

#### *Maintaining population realism*

One of the ways that ecosystem models could be simplified is to adopt a simpler form of the population component (e.g. go from an age-structured population model to a logistic model). Age-structured and logistic models have a long history of parallel use in fisheries since the 1950s (Schaefer 1954; Beverton and Holt 1957). The rationale underlying why population models can improve with increased structure is based on the funda-

mental definition of what makes an adequate state variable (Caswell 2001). In most fish populations, a logistic model would not be considered to represent an adequate state variable because the heterogeneity in age, size or space was not included; rather 'the population is to be regarded, in effect, as a continuous, homogeneous mass of living matter' (Beverton and Holt 1957, p. 330). These authors advocated inclusion of the age-dependence of survival, growth and fecundity, noting that the effect of a unit of biomass on population dynamics would depend on whether it was part of a reproductively mature individual. A similar sensitivity to aggregating population numbers over age classes was illustrated with a stage-structured model; combining every two ages led to a dramatic, unrealistic reduction in environmentally induced population variability (Botsford *et al.* 2011).

Many demographic parameters depend on size, life-history stage or age (Caswell 2001). Individuals have a maturity schedule, natural mortality typically decreases with size, and most fishing gears are size-selective. If growth rate does not vary with time, the behaviour of age-structured models is essentially the same as that of size-structured models, which is why most stock assessment models are age-structured. However, age-structured models require age-structured data to enable parameter estimation and model validation. Age determination is laborious and expensive and often is therefore limited to species of commercial importance.

Size-based models are good candidates for ecosystem models because length distributions are routinely measured for a larger suite of species. If size information is available, then the model can be size-structured, as long as the growth pattern (size vs. age) is known. Size-spectrum models, which base an individual's contribution to dynamics on size, have provided useful insights on how perturbations propagate through food webs (Kerr and Dickie 2001; Benoît and Rochet 2004). Within the size-spectrum, species mature at different sizes and grow to different asymptotic lengths. To be an adequate description of the state of an ecosystem, size-based models need to track individual species (Hall *et al.* 2006; Andersen and Pedersen 2010), not just the total abundance across species at each size. An advantage of size-based models is that they can be based on allometric relationships and can therefore be parameterized with a small number of parameters for each species (Pope *et al.* 2006).

A second consideration in structuring models is space. If individuals at each age have different vital rates at different locations, or if they are exposed to different fishing mortality rates [either in or out of a marine protected area (MPA), for example], then spatial structure must be taken into account. Although spatial structure had been considered in classic population dynamics models used in fisheries (Beverton and Holt 1957), inclusion of spatial detail became essential when MPAs became a popular management tool (Hastings and Botsford 1999; Botsford *et al.* 2001).

In addition to variability in fishing mortality rates over space, another reason for making models spatially explicit is the specific consideration of habitat. If there are differences in individual vital rates among habitats, then explicit representation of these habitats may improve the representation of state. Spatial resolution is also needed to assess the impacts of bottom fishing on benthic communities and to provide habitat information needed for spatial management. The U.S. Magnuson-Stevens Act requires essential fish habitat (EFH) to be defined for all federally managed species. In Australia, quantitative models are starting to be used to assess impacts on benthic species (Dichmont *et al.* 2008). An approach adopted in Australia, termed Ecological Risk Assessment for the Effects of Fishing, has been used to assess over 2000 species and more than 200 habitat types (e.g. see Hobday *et al.* 2011).

In summary, even at the single-species level, there is a broad range of population models based on different definitions of state. These range from models in which all individuals in a population are assumed to be identical to those in which individuals at different ages, sizes and locations have different vital rates, and ultimately to assuming each individual is unique. Individual-based models (IBMs) are based on the idea that variability among individuals (even with an age or size class) is important to population and community dynamics (DeAngelis and Mooij 2005). While the individual-based approach is popular in fish modelling, the high data demands have generally confined IBMs for use as theoretical and strategic tools, not in tactical fisheries management.

Thus far, we have focused on the number of variables and the amount of data (Fig. 1). As we now turn our attention from the population to the ecosystem level by considering multiple species, environmental variability and human interactions,

we will not be merely adding variables or objects modelled. Moving forward we need to also account for the mechanisms underlying the interactions among model components.

#### *Incorporating species interactions*

New models for EBFM will include descriptions of species interactions, to improve descriptions of the state dynamics and to account for the indirect effects of harvesting one species on other species. Viewed from a state variable point of view, addition of other component species is required to describe the state of the ecosystem and the component populations. This step presumes an understanding of the interactive relationships and the data on which to base that understanding.

There is a long history of studying the trophic interactions among species and representing them with mathematical models. The need for a mechanistic understanding has led to exploration of alternative bases for dynamics. One thread started with food webs, which began as mass-balance energy budgets (Steele 1974) and were later converted to dynamic systems of coupled differential equations (Walters *et al.* 1997). The second thread started with Lotka-Volterra predator-prey dynamics and was then extended to include more species with more realistic interaction terms (May *et al.* 1979). While these two threads are interwoven and have converged at dynamic multispecies models, the two strands can still be distinguished. The food-web thread has led to complex end-to-end models that are often used to simulate ecosystem dynamics, but lack structure for individual species. The predator-prey thread has led to age and size-structured multispecies models, such as Multispecies Virtual Population Analysis (MSVPA, Sparre 1991), but lack a holistic ecosystem view.

The dynamic behaviour of population models quickly becomes highly complex with the addition of multiple species linked with interaction terms with complex feedback loops. Even moving from one to two species complicates the analytical computation of system dynamics, stability properties, and the impacts of harvesting and choice of target reference points. Model analysis shifts from mathematical methods to numerical simulation. As a result, there remains little theoretical underpinning of these multispecies models. Overly complex models can be avoided by including only those species needed to address a specific management question. Plagányi *et al.* (2014) suggested a rule

of thumb that includes sufficient fishing sectors and predators to account for at least 90% of the mortality on each prey species.

Statistical multispecies age-structured models are extensions of MSVPA, which in turn was derived from Andersen and Ursin's (1977) full ecosystem model of the North Sea. Species are linked by natural mortality, which is a dynamic function of predator abundance and prey availability. Multi-species age-structured models require diet composition data by predator age, in addition to the catch-at-age and survey data typically used in age-structured stock assessments. One of the first statistical, multispecies, age-structured models was developed for the eastern Bering Sea (Jurado-Molina *et al.* 2005); this approach has also been employed in a number of other ecosystems, including the North Sea, Baltic Sea, Aleutian Islands, Gulf of Alaska and Georges Bank. Advantages of this multispecies model formulation are the similarity with existing age-structured stock assessments and the ability to quantify uncertainty with statistical model fitting (Curti *et al.* 2013).

#### *Incorporating environmental drivers*

Accounting for the effects of the environment in fisheries has a long history stretching back to early debates of whether unusual variability in a fishery was due to natural variability or the fact that the population had been fished (e.g. the cod stocks in Lofoten in the early 20th century, Rollesen 1954). Measures of environmental variability have been used to adjust productivity (Quinn and Deriso 1999), survival (Scheuerell and Williams 2005) and growth estimates (Wells *et al.* 2007, 2008b; Satterthwaite *et al.* 2012). For example, Schirripa *et al.* (2009) incorporated sea surface height in a spawner–recruit curve for sablefish (*Anoplopoma fimbria*, Anoplopomatidae). Similarly, upwelling values have been used to adjust expectations of coho salmon (*Oncorhynchus kisutch*, Salmonidae) production and survival (Logerwell *et al.* 2003; Scheuerell and Williams 2005).

The potential advantages of accounting for environmental variability are to better understand the drivers of population dynamics and to provide better predictions based on available or inexpensive observations of the state of the physical environment. The failure of a number of environmentally based predictors has led to some scepticism regarding their usefulness in stock assessments for fear that the models will fail to work over the long

term as environmental conditions shift (Walters and Collie 1988; Myers 1998). To reduce the likelihood of these events, we argue that the mechanisms that link environmental variables to biological responses be specified and quantified appropriately and used in that context for the prediction of population trends. The mechanistic connections between upper trophic-level fish and their environment can be complex, depending not only on the trophic level of the fish but also on the flexibility of its diet and habitat needs. Likewise, models designed for lower trophic-level fish can be complicated by bottom-up and top-down impacts. Wells *et al.* (2008a) proposed using path analysis, in combination with quantitative multivariate statistics, as a method for constructing reasonable connections and deriving mechanistic understanding of how an environmental factor, as well as predators and prey, directly or indirectly affects the fish population of interest.

A more comprehensive understanding of the biophysical coupling that drives population dynamics will be facilitated by the increasing breadth of observations of ocean state becoming available from land, sea and satellite monitoring platforms. While long time series of modelled and observed ocean surface conditions have been available at a relatively gross spatial scale, remotely sensed data series now comprise over a decade of high-resolution spatially and temporally explicit surface conditions. Further, improved data management has made these data series readily accessible. Such improved data and increased availability have permitted the development of mechanistic models representing the relationships between the environment and the biological responses at the appropriate spatial and temporal scales (see Chassot *et al.* 2011 for a more exhaustive review). For example, the cumulative spawning habitat available for sardine (*Sardinops sagax*, Clupeidae) and anchovy (*Engraulis mordax*, Engraulidae) was evaluated across the California Current by relating shipboard collection with remote-data series of sea surface temperature (Reiss *et al.* 2008). Bi *et al.* (2008) used satellite-derived chlorophyll *a* data and water depth to characterize the habitat usage of juvenile chinook (*Oncorhynchus tshawytscha*, Salmonidae) and coho salmon off the U.S. west coast. Remote sensing is also quite useful for spatial management of fisheries resources and protected species. Hobday and Hartmann (2006) and Howell *et al.* (2008) used remote sensing for

the near-real time locations of potential habitat for species of concern. With this information available, fishery managers could make educated decisions about the risk of interactions with these protected species.

A second advance that will aid in the addition of environmental variables is development of improved circulation models. Advances in regional oceanographic model simulations (e.g. ROMS, Shchepetkin and McWilliams 2005) now allow for the retrospective analysis of horizontal and vertical oceanographic conditions at relatively high spatial and temporal resolution. These model-derived data now make it possible to examine the relationships between the biology and estimates of oceanographic conditions in three spatial dimensions over time. Huff *et al.* (2012) provide a recent example wherein the habitat of benthic green sturgeon is modelled from representations of flow, temperature and oxygen conditions in the bottom 5 m of the California Current. Similarly, Song *et al.* (2012) ground-truthed physical circulation results for describing potential spawning habitat of sardines. At the coarsest spatial and temporal scales, global climate models can project future environmental conditions in the context of global climate change. Improving these models and linking them with biological models is critical to understanding how best to plan mitigation in the future (Hobday and Lough 2011; Stock *et al.* 2011).

In summary, there is a growing understanding of how oceanographic processes affect the life-history stages of marine species and a growing ability to measure the oceanographic variables at the appropriate spatial scales. Models that incorporate these environmental linkages will have increased explanatory power and require much-increased computer power. Such modelling efforts must bear in mind that environmental effects tend to be non-additive (Planque *et al.* 2010) and that new approaches may be required to address this state dependence (Deyle *et al.* 2013).

#### *Incorporating human dimensions*

Humans are central to ecosystem-based fisheries management because they are part of the interacting system of organisms in an ecosystem and also because it is human activities that are ultimately being regulated. Quantifying the impacts of ecosystem changes and the consequences of fishery management actions on human user groups will lead to better-informed decision-making. Just as there is

a range of model complexity for natural resource dynamics, there are a variety of ways in which the interactions of humans with marine ecosystems are modelled, ranging from simple indicators to coupled end-to-end models (DeYoung *et al.* 2008; Plagányi *et al.* 2011a). There are fundamental differences between human and ecological systems, which makes it challenging to reconcile their different drivers operating at different scales (Sievanen *et al.* 2011). Links between human behaviour and management actions, and the associated uncertainty, need to be incorporated into models to avoid management decisions with unintended consequences such as effort displacement (Fulton *et al.* 2011b).

Qualitative and quantitative use of socio-economic information through the use of cost-benefit analysis (CBA), social impact analysis and indicators are some of the more prevalent forms of analysis to support decision-making (DeYoung *et al.* 2008). In addition to the more direct estimates of cost and benefits associated with changes in revenue to the affected fishery, analyses may also identify affected human communities that may be most linked to the fishery (Sepez *et al.* 2007), use input-output or computable general equilibrium models to quantify other industries or regions that may be affected (Seung and Waters 2010) or use non-market valuation techniques that employ surveys to quantify the public's values (e.g. protection of endangered species, Lew *et al.* 2010). Indicators for EBFM range from those related to annual decision-making of particular fisheries (Diedrich *et al.* 2010; Kim and Zhang 2011) to more aggregated indices for decision-support (Paterson *et al.* 2010; Seung and Zhang 2011). Some socio-economic indicators, such as those measuring fishery productivity, can be derived from modelling, which employs a wide variety of primarily econometric estimation techniques (Morrison Paul *et al.* 2010).

Dynamic models that incorporate human behaviour at a variety of levels are also used in EBFM. These may involve spatiotemporal examinations of fleet behaviour and be based on individual vessels (Smith and Wilen 2003; Venables *et al.* 2009). These fishing choice location models may be linked to a biological model of fish distribution and abundance (Smith and Wilen 2003) or location-specific production models (Morrison Paul *et al.* 2010). Fishing choice models can be useful in evaluating effort changes, economic impacts and

biological benefits of various spatial closures, and also for conducting management strategy evaluations (Dichmont *et al.* 2008).

Incorporating human considerations is still in its infancy, but a number of lessons have been learned to date. These include understanding the motives and behaviours underlying bycatch and discards (Pascoe 1997), how human behavioural responses can undermine management intent (Fulton *et al.* 2011b) and how ignoring sociopolitical and economic factors can aggravate illegal fishing and hence derail a fishery management system (Raemaekers *et al.* 2011). Including sociocultural considerations may help avoid unintended consequences and thus improve future potential policy outcomes (Plagányi *et al.* 2013). These insights should improve strategies for achieving the goals of EBFM with better predictive capabilities when using fleet dynamics models (Van Putten *et al.* 2012) and strategies for maximizing economic yield in multispecies fisheries (Dichmont *et al.* 2010).

A large focus of the efforts to join biological and economic models is with respect to quantifying impacts of climate change on marine ecosystems. As noted by Haynie and Pfeiffer (2012), it is essential to consider fishermens' behaviour in these models to improve understanding of the possible trajectories of impact, even though this may broaden the range of outcomes. A range of model complexity is being used for both the biophysical and human dynamics (Fulton 2011; Ianelli *et al.* 2011; Plagányi *et al.* 2011a,b).

### **Use of ecosystem models in fisheries management**

#### **What are the key ecosystem needs for models?**

The continuum of ecosystem models can be categorized as (i) conceptual models aimed at developing understanding of ecosystem processes; (ii) models for strategic management decisions; or (iii) models for short-term tactical management advice (FAO 2008). Whole ecosystem models are often used for pedagogical purposes, to impart and illustrate an understanding of ecosystem dynamics. Strategic advice concerns broad, policy-setting, context-level issues such as ecosystem services, system-wide productivity and biodiversity goals. Tactical advice involves the specification of harvest rates and quotas so as to meet the strategic objectives.

Fishery ecosystem models should be focused on specific objectives and attributes of interest to stakeholders or managers (Dickey-Collas *et al.* 2013). The key ecosystem dimensions of fisheries are well known, and in some cases, fishery managers have considered them in decision-making for some time (Sissenwine and Murawski 2004). They include (i) accounting for environmental variability and climate change; (ii) protecting fish habitat; (iii) trophic interactions among harvested species; and (iv) the ecological effects of mixed-stock fisheries, bycatch and discards. For all four types of ecosystem consideration, models tailored to the interacting components have been developed to project the likely consequences of management actions as evidenced in the northeast Pacific examples provided by Hollowed *et al.* (2011).

The quantitative state of an ecosystem can be integrated into fisheries management at a number of points, ranging from informing the management system of general results about key ecosystem components and long-term dynamics to specifying harvest guidelines. At the level of conceptual understanding, single-species models can simply be examined in the context of ecosystem status. At this level, a broad range of ecosystem models could be used together with empirical ecosystem indicators to provide a qualitative assessment of when to add more precaution to annual single-species management advice, as done in Alaska (Livingston *et al.* 2005, 2011a). At the strategic level, ecosystem models can be run in parallel with single-species assessments to check whether medium-term harvest policies will impact other ecosystem components or conversely whether key parameters of single-species models need adjusting in response to shifts in ecosystem structure. At this level, the single and multispecies dynamics may remain unlinked or there may be unidirectional links. For example, multispecies models can provide estimates of natural mortality for use in single-species models (Garrison *et al.* 2010). Conversely, projections of single-species models can be used to check for adverse effects on dependent predators. When concerned with environmental linkages, one-way linkages may suffice because environmental variability affects single-species dynamics, but single species do not affect environmental variability. In many cases, the trophic feedback is in two directions, which necessitates a fully coupled dynamic model. Tactical

models used to specify harvest guidelines will be models of intermediate complexity that incorporate the important ecosystem components with strong linkages (Plagányi *et al.* 2014).

### What types of models can meet these ecosystem needs?

#### *Strategic ecosystem models to inform fisheries management*

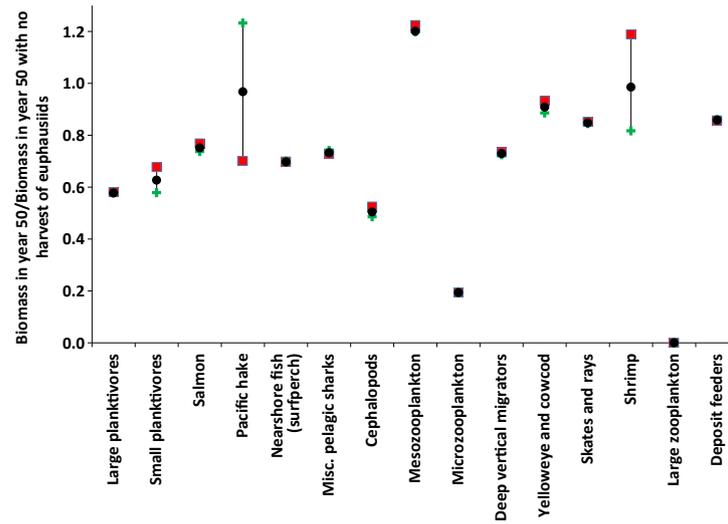
There is an interplay between tactical and strategic models, as tactics provide the means to strategic ends. The development of simpler tactical models has often led to questions about the importance of environmental considerations, which in turn motivated the development of strategic models to address these issues. By highlighting sensitive or key system components (e.g. the level of productivity) and identifying which management tools are most useful in the particular ecosystem of interest, the output of strategic models provides context for tactical management decisions. Once the output from a strategic (or even conceptual) model has indicated which tool to use, tactical models can be implemented to determine the specific level for that management tool.

Ecosystem models that are used in strategic roles include Ecosim and Ecospace (EwE, Walters *et al.* 1997), OSMOSE (Shin and Cury 2004) and Atlantis (Fulton 2004; Fulton *et al.* 2011a). Strategic models must be based on the best available data and, when possible, should capture and propagate the uncertainty in the input data (e.g. Ecosense routines, Aydin *et al.* 2007). Fitting complex ecosystem models to data remains a challenge. Parameters of these models typically are not fit statistically to data, although at least one example exists where this has been done using EwE (Gaihas *et al.* 2011). Sensitivity of model outputs to model form can and should be tested with 'bounded parameterizations' for key parameters (Fulton 2010); however, long computer run times usually preclude more complete exploration of the parameter space. Selection of bounded parameterizations requires careful decisions by the model developer and a preliminary understanding of the sensitivity of the model. Such bounded scenarios for strategic models have a direct analogue in single-species fisheries management, where the decision-table framework is often used to highlight key uncertainties ('states of nature') in biology and fisheries (Hilborn and Walters 1992). An example

of such a bounding scenario for a strategic ecosystem model is shown below (Fig. 2).

Forward projections of strategic ecosystem models that include human behaviour have been used to inform management related to multiple sectors such as energy, tourism and fishing (InVitro, Fulton *et al.* 2011b). Management systems such as southeast Australia's Alternative Management Strategies project (Fulton *et al.* 2014) and NOAA's Integrated Ecosystem Assessment (Levin *et al.* 2009) have applied strategic models to evaluate and rank the performance of broad fisheries management strategies such as closed areas, quotas and fishing gear requirements. Perhaps the most promising strategic role for complicated ecosystem models is as an operating model for Management Strategy Evaluation (Sainsbury 2000; Fogarty 2014), in which the performance of simulated monitoring, assessment and management decisions can be tested within complex ecosystem operating models.

A key question in providing management advice for some stocks or in some jurisdictions pertains to the economic optimization of multispecies harvests. One example is provided by a study of optimal fishing policies for parrotfish, snapper and grouper in the Caribbean. An important starting point for understanding the dynamics of this ecosystem is that parrotfish are essential as grazers in maintaining healthy reefs by preventing macroalgae from dominating the system (Mumby *et al.* 2007). Thus, there is an existence value for parrotfish, which can be assigned an economic value from the role of reefs in ecotourism, in addition to the value of reefs for biodiversity. There are also well-documented and modelled trophic interactions among grouper, snapper and parrotfish: the primary predator of both snapper and parrotfish is grouper, while the grouper has a broad diet (Kellner *et al.* 2010). A set of bioeconomic models for fishing in this system can be made by optimizing fishing effort over time and either looking at each species singly, or all three at once, and also either by including the existence value of parrotfish or not (Kellner *et al.* 2011). Notable among the modelling results are that there is little difference in optimal catch between the models of each species by itself vs. looking at all three species, but the inclusion of the existence value for the parrotfish makes a substantial change (reduction) in optimal fishing levels. This bioeconomic model demonstrates the economic



**Figure 2** Analyses using the Horne *et al.* (2010) California Current Atlantis model suggest that complete depletion of euphausiids (large zooplankton) would lead to substantial declines in many predators in the California Current. Using a bounded parameterization approach, this figure asks how robust this result is to uncertainty in abundance of a key predator, Pacific hake (*Merluccius productus*), quantified by Ralston *et al.* (2011). Results from the base scenario are represented by black circles, and results from scenarios with high and low Pacific hake biomass are represented by green crosses and red squares, respectively. Pacific hake abundance does little to vary the magnitude or direction of effects that euphausiid depletion has on other food-web components. When euphausiids are fully depleted, varying Pacific hake generally changes food-web effects by <5%.

value of choosing harvest rates that differ from the single-species optimum.

#### *Tactical ecosystem models to specify harvest policy*

Models of intermediate complexity for ecosystem assessment (MICE) are considered by many the way forward to provide tactical fisheries management advice based on rigorous models that include more than a single species (Plagányi *et al.* 2014). One of the key characteristics of models used for tactical fisheries decision-making is that the parameters are statistically estimated from time-series data collected for the ecosystem under consideration, and diagnostic tools are applied to evaluate model performance (e.g. residual analysis, variance estimation). It is common to include prior information (e.g. on growth and predation rates, assimilation efficiencies) and to include fits to diet data in the objective function to be optimized (Kinzey and Punt 2009; Van Kirk *et al.* 2010). When multiple data sources are available, each needs to be weighted based on the confidence associated with the data. In cases in which the data are somewhat contradictory, data weighting needs to be done carefully (Francis 2011), and the sensitivity

of the results to different data weighting schemes should be explored.

A critical characteristic of tactical EBFM models is that they adequately account for parameter uncertainty with Markov Chain Monte Carlo (MCMC) sampling, inversion of the Hessian matrix or likelihood profiles. If available data are insufficient to support precise parameter estimation, then an acceptable alternative would be to bound the range of uncertainty (Plagányi *et al.* 2014). Given the greater level of structural uncertainty associated with more complex ecosystem models (relative to single-species models), sensitivity to structural uncertainty needs to be demonstrated, for example, by testing alternative functional response formulations (Gaichas *et al.* 2012) or comparing the results from multiple (independent) models (Smith *et al.* 2011).

Evaluating alternative model structures is a key step in addressing uncertainty, which has been identified as one of the critical areas for advancing ecosystem modelling (Marasco *et al.* 2007). Hill *et al.* (2007) provided a useful list of best practices for dealing with structural uncertainty in ecosystem modelling: (i) developing models or parameterizations

that represent plausible limits on key sources of structural uncertainty; (ii) including models and parameterizations that fall between these plausible limits; (iii) considering whether to evaluate possible future scenarios that extend outside the range of historic data; (iv) weighting models or parameterizations by their plausibility (if possible); and (v) avoiding model averaging unless the distribution of results across all models or parameterizations is unimodal.

Best practice involves acknowledging the paramount importance of interaction terms among species and between species and environmental factors (FAO 2008). A first step towards integrating environmental drivers has been to incorporate a single or limited number of key covariates mapped to the life-history trait of interest (e.g. recruitment, maturation) at the appropriate spatial and temporal scale (Maunder and Watters 2003). A probable mechanistic link should exist between an environmental covariate and the biological response. Otherwise, the chosen covariate may simply be responding to a third unexamined variable; an undetected change in that variable will lead to a degradation of the model. For example, wind characteristics aligned with coastal geography create conditions conducive to improved krill production in the California Current (Santora *et al.* 2011). The timing of the upwelling season and development of krill is matched to the average timing of emigration by salmon to the sea, which is a critical period for defining recruitment strength (Beamish and Mahnken 2001). With this mechanistic link, models can be extended to forecast salmon recruitment from upwelling characteristics and krill dynamics (Wells *et al.* 2012). Given that many of the relationships between biology and environment are nonlinear, there is a need to monitor the relationships and adjust the models as necessary.

Three primary considerations relate to the covariation between a biological trait and the environmental variable: timing, spatial scale and inherent structure of the system. If the phenology of the system changes, such that there is a secular trend in the timing of the covariates of interest, the defined mechanisms may change (Bograd *et al.* 2009). Similarly, changes in the spatial distribution of the environmental characteristics (Friedland *et al.* 1998; Song *et al.* 2012) or in the distribution of the fish (Nye *et al.* 2009) will lead to a spatial mismatch.

A logical first step in using ecosystem models in tactical decision-making has been to build on existing approaches. Hence, a handful of multispecies models, which are essentially extensions of single-species approaches, are being used to inform management. Multispecies model results are most sensitive to the consumption rate per predator, predator functional responses (the prey–predator interaction terms) and feeding selectivities or suitabilities (Tsou and Collie 2001; Fulton *et al.* 2003). The potential sensitivity to alternative interaction representations demonstrates why it is essential that model robustness to formulations be examined (Kinzey and Punt 2009). Models need to be closely scrutinized to understand the extent to which underlying model assumptions and input parameters predetermine the results obtained (Plagányi and Butterworth 2004).

Tactical ecosystem models are increasingly producing outputs that could be used for decision-making. Several such models have been developed to quantify predator–prey interactions in the Antarctic (Mori and Butterworth 2006) and to assess the impact on dependent predator populations of different spatial distributions of krill (Plagányi and Butterworth 2012; Watters *et al.* 2013). Despite many models seemingly finding the sweet spot, few if any have yet been fully integrated into the decision-making process. Rather, their role to date has been primarily in providing accessory information as context, bounding possible outcomes or providing estimates of the predation mortality rate for explicitly modelled prey species (Gjøsaeter *et al.* 2002; Garrison *et al.* 2010), without necessarily using the multispecies model itself to determine appropriate levels of fishing mortality.

### How can these models be used?

#### *Ecosystem reference points and indicators*

Ecosystem reference points or targets allow us to judge the status or trend of an ecosystem relative to a management objective. Reference points are most often based on observable indicators that allow us to concretely evaluate whether a broader goal of ecosystem-based management has been achieved (Link 2005). The use of ecosystem models in this case is to understand the shape of the relationship between a pressure (e.g. fishing or pollution) and an indicator (e.g. fish abundance or human health effects), to quantify the trade-offs between conflicting objectives. Ecosystem models

have been used to identify 'tipping points', beyond which harvesting would shift the ecosystem to a different state, for instance in the Gulf of Alaska (Gaichas *et al.* 2012). However, non-modelling approaches can also be used to identify ecosystem reference points, such as focusing on historical baselines and time-series trends, identifying social norms (Livingston *et al.* 2005; Samhuri *et al.* 2011) or making comparisons to other areas or regions (Samhuri *et al.* 2012).

For Puget Sound, on the west coast of the United States, a science and management process (the Puget Sound Partnership) mandated by the state of Washington has identified ecosystem indicators and reference levels (Samhuri *et al.* 2011). Ecosystem models have been used as one of several tools to screen and identify potential ecological indicators and used to test for the possible correlation between ecosystem attributes and potential indicators. Additionally, population models of protected species have been used to identify reference levels for these 'vital sign' species, such as chinook salmon and bald eagles (Kershner *et al.* 2011). These vital sign species and associated reference points are understood by the public to represent general ecosystem condition, rather than the status of only that single species. In a similar way, shellfish have been monitored throughout the United States for over 20 years as proxies for environmental contamination (Kimbrough *et al.* 2008), with reference points based on functional relationships between contaminant doses and human health effects.

Link (2005) proposed 14 ecosystem indicators, warning thresholds and limit reference points. Although some of these reference points and thresholds were based on 'rules of thumb' or empirical observations from the northwest Atlantic, others were informed by ecosystem and multispecies models (Gislason and Rice 1998). Indicators included those derived from body size (e.g. slope of the size-spectrum), biomass of different species (e.g. biomass of all piscivores), diversity (e.g. species richness), trophic dynamics (interactions per species), network properties of the food web (e.g. number of cycles) and indicator species (e.g. volume of gelatinous zooplankton). Although these reference points have not directly influenced management actions, many of these indicators are included in documents that provide managers an ecosystem context for fishery decisions (Ecosystem Assessment Program 2009). A similar approach is

used to inform fishery managers off Alaska (Livingston *et al.* 2005). In Australia, Fulton *et al.* (2005) used an Atlantis model to test a set of ecosystem indicators similar to those proposed by Link (2005) and identified indicators that were strongly correlated to attributes (e.g. diversity or food-web structure) across a range of ecological and fishing scenarios.

#### *Multispecies biological reference points*

Biological reference points (BRPs) for single fish stocks are based on the concept of maximum sustainable yield (MSY), maintaining a specified percentage of unfished biomass or other precautionary levels (Quinn and Deriso 1999). The single-species approach has been extended to production models fit to data aggregated across species in the community (Brown *et al.* 1976; Muter and Megrey 2006). These models imply compensation in aggregate fish production and supported the limit on total catch that formerly existed in New England and the two million ton limit on total harvest in the Bering Sea. However, where multiple fleets catch multiple interacting species, disaggregated multispecies models are needed.

Using systems of coupled differential equations, May *et al.* (1979) demonstrated that, for a predator-prey system, the joint sustainable yield is not equivalent to the sum of the individual MSYs computed based on single-species harvest principles. Instead, the sustainable harvest of one species is conditional on the abundance and hence harvest rate of other species, which gives rise to trade-offs in the sustainable harvest of predators and prey. Computation of a global optimum, even for only two species, is complicated further by considerations of the ecological role, economic value and practicalities of different industries targeting different species (May *et al.* 1979). This landmark study was motivated by the depletion of baleen whales in the Southern Ocean. At that time, there was a perception of a large harvestable surplus of Antarctic krill and concern that a krill harvest could jeopardize the recovery of whale populations. Since that time, two main approaches have developed for setting multispecies reference levels: precautionary and dynamic.

The precautionary approach is based on the broad objective of maintaining the relationships between harvested and dependent species (Sainsbury 2000). The Commission for the Conservation

of Antarctic Marine Living Resources (CCAMLR) adopted 75% of pristine spawner biomass as a precautionary reference point (Plagányi and Butterworth 2012). Predator–prey models for the krill population were not used because they were judged to be too uncertain. The operating model included uncertainty in recruitment, growth and mortality, and in the krill abundance estimates.

Renewed concerns about the status and important ecosystem role of forage species have prompted expert groups to recommend precautionary harvest policies to ensure that biomass of forage species does not fall below 75% of unexploited biomass (Smith *et al.* 2011). In these studies, models of several ecosystems have been used to identify generic thresholds for the safe harvest of forage species, which can then be applied to data-limited ecosystems. A precautionary approach is especially appropriate when there are concerns about protected, endangered or threatened species. A weakness of this approach is that the proposed harvest guidelines depend on assumptions of the ecosystem models and estimates derived from them. For example, the pristine biomass of small pelagic fish species is notoriously difficult to estimate because of their ‘spasmodic’ variability (Caddy and Gulland 1983). Technical considerations aside, in addition to their existence value, predator and prey species have different values to different sectors.

The dynamic approach stems from the realization that biological reference points are conditional on the abundance of interacting species and prevailing environmental conditions (Collie and Gislason 2001). For example,  $F_{MSY}$  of herring (*Clupea harengus*, Clupeidae) and sprat (*Sprattus sprattus*, Clupeidae) in the Baltic Sea depends on the prevailing level of cod (*Gadus morhua*, Gadidae) predation. Where these linkages are sufficiently well understood and the interactions have been quantified, BRPs can be modified to account for trophic interactions and dependencies (Tyrrell *et al.* 2011). Although it is important to recognize that they can change over time, establishing BRPs for harvest guidelines requires consensus among participants in the management system; when BRPs change, this consensus can be lost or questioned (e.g. when setting rebuilding targets).

Considering the BRPs of multiple interacting species leads to the concept of multispecies maximum sustainable yield. Worm *et al.* (2009) used a size-based model to illustrate the trade-off between

total yield, biomass and number of collapsed species in a community. In this example, all species were subject to the same fishing pressure with selectivity an increasing function of size. But the same total yield could be caught by different combinations of fishing effort of fleets catching different species. Maximizing the total biomass of landings favours high-volume fisheries, often on forage species. Economic optimization tends to result in extreme solutions, depending on the relative value of predator and prey species (May *et al.* 1979), unless the optimization is constrained by biological reference points. Either the prey species are not harvested to provide food for the more valuable predators, or the predators are sacrificed for their more valuable prey.

Instead of maximizing the total yield, we can think of multispecies sustainable yield as a region in the parameter space defined by the fishing mortality rates of interacting species, within which the biomass of each species stays above its precautionary level. Conventional theory can provide guidance as to the parameter space in which a community of species remains sustainable under different fishing intensities, but additional socio-economic considerations are necessary to inform choices of appropriate targets. Using the results of an MSVPA for the Baltic Sea, Gislason (1999) identified combinations of pelagic and demersal fishing effort within which cod, herring and sprat would all be maintained above their respective precautionary biomass levels.

#### *Visualization and communication*

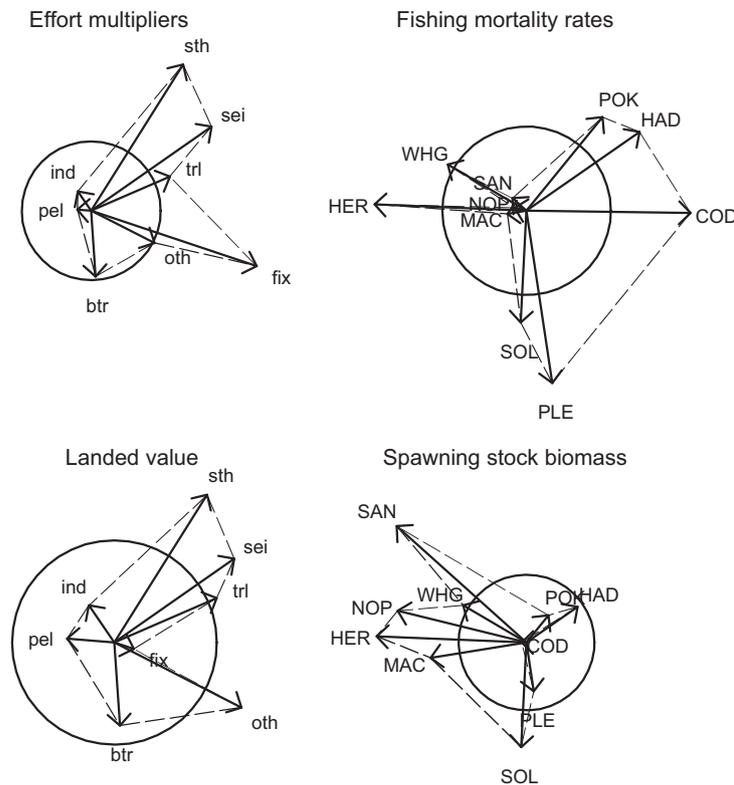
Ecosystem models that are scientifically sound, targeted at appropriate research questions, and built around appropriate management reference points (i.e. near the ‘sweet spot’) will still fail if they are not communicated adequately to decision-makers. Even in scientific papers it is difficult to provide all the details of ecosystem models. The challenge is to communicate the rationale and assumptions underlying the model, not just the complex results. Without adequate communication, visualization of output, and subsequent model review and discussion, such models are at risk of remaining academic exercises.

An example of ecosystem model communication in the U.S. management arena is the incorporation of food-web models into ecosystem considerations chapters for stock assessments such as the Bering Sea walleye pollock stock assessment. In the

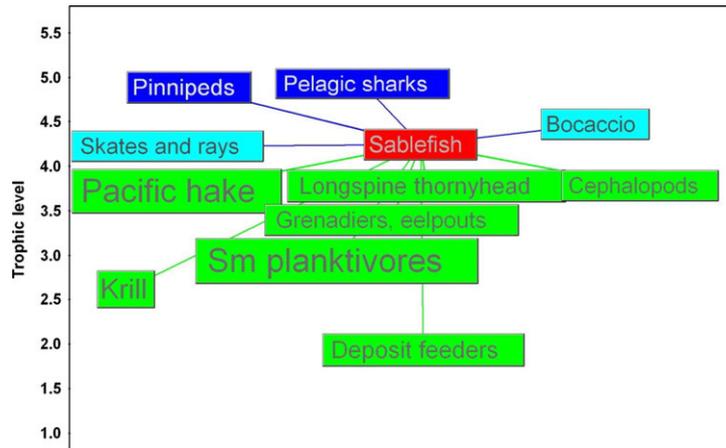
California Current, an Integrated Ecosystem Assessment (IEA; Levin *et al.* 2013) has been one venue to provide ecosystem context to fishery managers. The IEA is a science framework to synthesize and analyse natural and socio-economic information, and present this information in the context of the goals identified by managers and stakeholders. This framework has provided opportunities to present output from a range of ecosystem models and analyses, tailored to focus on key species. For instance, in a briefing report to the Pacific Fishery Management Council, Levin and Wells (2011) distilled outputs from a suite of ecosystem approaches to focus on two primary fishery target species (Pacific hake, *Merluccius productus*, Merlucciidae and sablefish) and two rockfish (*Sebastes*) species of conservation concern. This narrow focus is appropriate given the incremental nature of the shift to ecosystem-based fishery man-

agement and the need for clients of ecosystem models – usually fishery managers – to identify scientific and management needs that will shape development of both tactical and strategic models.

AMOEBAs plots have been used to display changes in fishing mortality, landed value and spawning stock biomass resulting from changes in fishing effort in a multispecies, multifleet fishery (Fig. 3). Ordination was used to give the shape of the AMOEBAs functional meaning by relating fish species to the fleets that catch them. The underlying model incorporates both fishing fleet and predator-prey interactions (Collie *et al.* 2003). The vector angles show which species are caught by which fleets; the vector lengths indicate the magnitude of each variable scaled by a reference level given by the circle with unit radius. In this North Sea example, effort levels for multispecies MSY were obtained by simultaneously maximizing the



**Figure 3** AMOEBA plots for the North Sea with effort levels to maximize the landed value of each fleet. In each AMOEBA, the circle represents the reference level, and the arrows are the levels predicted with the multispecies model. Effort and landings were plotted relative to the status quo. Fishing mortality and spawning stock biomass were plotted relative to their precautionary levels. Broken lines enclose each AMOEBA. The fleet abbreviations are as follows: btr – beam trawl, fix – fixed gear, ind – industrial trawl, pel – pelagic, sth – saithe trawl, sei – seine net, trl – trawl, oth – other gears. The species abbreviations are as follows: COD – cod, HAD – haddock, WHG – whiting, POK – saithe, MAC – mackerel, HER – herring, NOP – Norway pout, SAN – sandeel, PLE – plaice, SOL – sole.



**Figure 4** Primary food web of sablefish. Major predators are pinnipeds and pelagic sharks (dark blue in the electronic version of this document). Skates and rays and bocaccio are both prey and predators of sablefish (for instance, juvenile sablefish may be eaten by bocaccio adults, but adult sablefish may eat juvenile bocaccio). All other species are major prey items of sablefish (prey coloured green in the electronic version of this document). Position in the y-direction is approximately related to trophic level. Size of the box is related to biomass of the group. Links between boxes represent links in the food web; most diet information depicted here involves adult predators. The diagram excludes minor prey items and predators that inflict small proportions of predation mortality on the focal group. Food-web visualization software (ECOVIZ 2.3.6) was provided by the author, K. Aydin, NOAA, Alaska Fisheries Science Center, Seattle, WA, USA.

landed value of each fleet. Relative to status-quo effort levels, MSY would involve increasing effort in the fixed, seine, trawl and saithe fisheries while decreasing effort in the industrial and pelagic fisheries (Fig. 3). This result occurs primarily because the former group of fleets targets 'roundfish', which are far more valuable than the 'industrial' species targeted by the industrial and pelagic fleets. Furthermore, herring and sandeel (*Ammodytes dubius*, Ammodytidae) are important prey species for the roundfish. With more forage fish available, there would be less predation among the roundfish, thus increasing their yield.

Link *et al.* (2010) discussed the need for efforts to improve visualization tools and recommended further collaboration with cognitive psychologists and computer visualization experts. In the California Current and Alaska, several recent efforts to present ecosystem model output in relevant and useful ways include Ecoviz diagrams (Fig. 4) and colour-coded ocean condition indices. In practice, these visualizations often convey status and trends from model projections, few communicate major uncertainties (e.g. see Watters *et al.* 2013). New graphical interfaces have been developed that allow the full distributions of parameters estimates and policy outcomes to be visualized (Booshehrian *et al.* 2012).

## Existing applications to management

### Models with environmental drivers

Characterized by its boom-and-bust dynamics, the Pacific sardine is one of few species that has been managed with an explicit consideration of the environment in tactical decision-making. A generalized additive model (GAM) was first used to quantify the dependence of sardine recruitment on spawning stock biomass (SSB) and the 3-year running mean of sea surface temperature (SST, Jacobson and MacCall 1995). This relationship formed the basis of a temperature-dependent harvest rule that was implemented by the Pacific Fishery Management Council (PFMC 1998). Above a cut-off of 150 000 tons, the allowable catch was a quadratic function of SST, ranging from 5% of available biomass under cool conditions to 15% for warm SST. A reanalysis of this relationship with 17 more years of recruitment data used a temperature-dependent Ricker model and SST measured from quadrants of the Pacific Ocean corresponding to the sardine habitat, rather than SST measured at Scripps Pier (McClatchie *et al.* 2010). This analysis suggested that the relationship between sardine recruitment and SST was no longer significant; the temperature-dependent harvest rule was abandoned in 2012.

A more recent analysis using the same model formulation as Jacobson and MacCall (1995) with data from 1981 to 2010 found that both SSB and SST were significant terms in the GAM (Lindgren and Checkley 2013). *In situ* temperatures from the CalCOFI survey were better predictors of sardine recruitment than Scripps Pier SST. Apart from the anomalous 1983 El Niño year, the fitted relationships were similar to a temperature-dependent Ricker model. Weaknesses of these statistical model approaches are that they assume stationary relationships, ignore the time-series nature of the data and do not readily accommodate potential interactions between the effects of SST and SSB on recruitment. State-space models provide an alternate approach that allows the relationship between recruitment and SST to depend on the level of SSB. State-space models are appropriate for populations like the California sardine that exhibit non-linear dynamics (Deyle *et al.* 2013). Convergent cross-mapping was used to show that a model incorporating SST was best able to predict recruitment 1 year in advance.

There are several lessons to take away from this example. The choice of model structure and the specification of input variables both affected the inference about the strength of the recruitment–environment relationship. Methods should be used that account for the autocorrelation inherent in oceanic and coupled biological variables. Statistical models should be cross-validated by testing their ability to predict values not included in the original fit. Even so, there remains a possibility that recruitment–environment relationships will change over time, particularly with altered climatic conditions that have not been observed before. Coupled environment–fisheries models therefore need to be periodically updated. Finally, environmental harvest-control rules need rigorous simulation testing over a broad range of environmental conditions and plausible model structures.

### Multispecies models

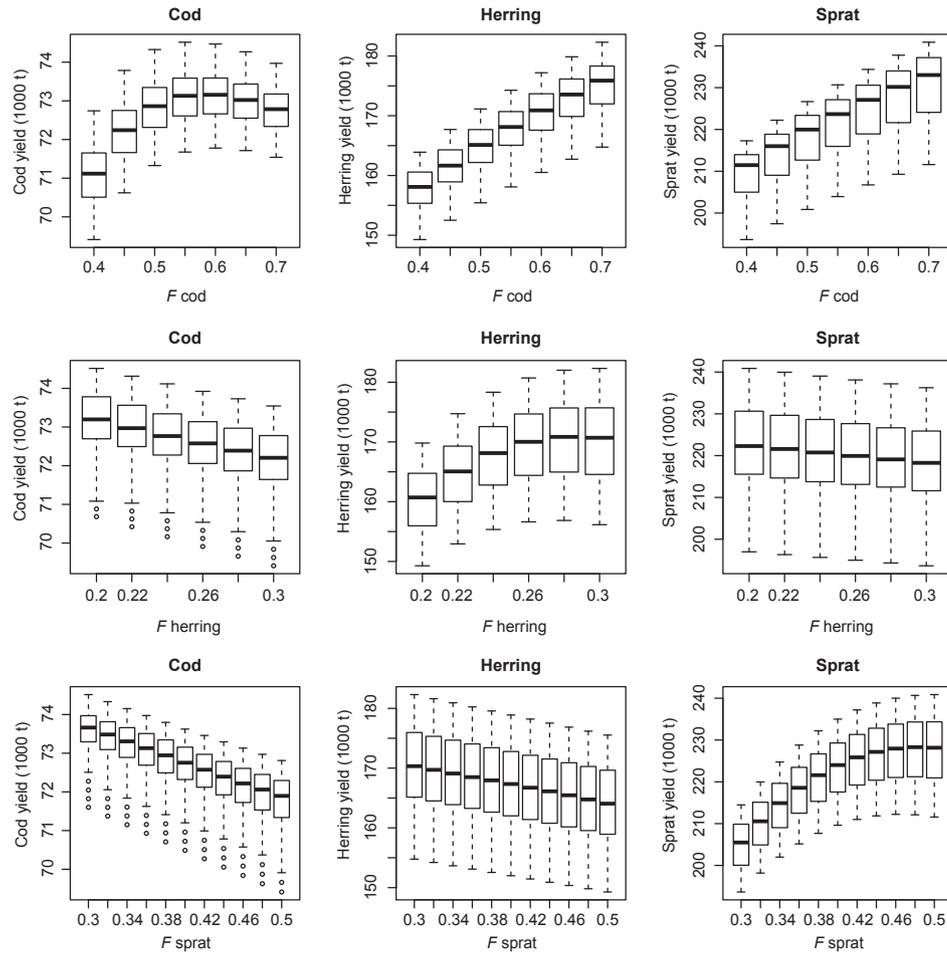
A recent simple example from the U.S. west coast illustrates how ecosystem models at the ends of the complexity spectrum – very simple and quite complex – can be used to provide strategic ecosystem advice. In the context of the California Current IEA (Levin and Wells 2011), Pacific Fishery Management Council committees were briefed on the ecosystem considerations relevant to four har-

vested species: sablefish, Pacific hake, bocaccio and canary rockfish (*Sebastes paucispinis* and *S. pinnegger*, Sebastidae). Relatively simple qualitative modelling (Dambacher *et al.* 2009) and a fairly complex Atlantis model (Horne *et al.* 2010) were both used to identify key predators and prey for these four species. A consensus list of predators and prey was visualized with the Ecoviz approach developed by NOAA's Alaska Fishery Science Center (Fig. 4). Such conceptual understanding is a first step by which ecosystem models can inform future management actions.

The Baltic Sea fish community is relatively simple, comprising cod, herring and sprat, which limits the number of interactions that need to be quantified. Multispecies models – first MSVPA and now the statistical multispecies model SMS – have been used to provide estimates of predation mortality by cod, which are then used in the single-species assessments of herring and sprat (Lewy and Vinther 2004). The SMS model has been used to project the joint biomass and catch levels in relation to the fishing mortality rates of the three species (Fig. 5). With SMS, cod yields would be maximized at higher fishing mortality rates than with the corresponding single-species model. The yields of herring and sprat depend strongly on the rate of fishing mortality, and hence abundance, of cod. The Baltic SMS model is providing insight on multispecies target and limit biomass considerations when considering trade-offs between predators, prey and cannibalism. The 2013 benchmark workshop on Baltic Sea multispecies assessments (WKBALT) ran the single-species and multispecies models in parallel and used the results to frame multispecies advice (ICES 2013). The Baltic Sea provides an example of fisheries management evolving over several decades from single-species to a multispecies perspective.

### Discussion

Having accepted the basic tenets of ecosystem-based management (EBFM), governments and their fishery management agencies around the globe are facing the challenge of how best to implement them. Here, we have drawn attention to a predominant aspect of that challenge, the question of how the levels of uncertainty in new models being proposed can be evaluated and how that information can be used to integrate results from these models into the management process.



**Figure 5** Box plots of scenario results of yield at equilibrium from an SMS model (Lewy and Vinther 2004) of the Baltic Sea for combinations of fishing mortality ( $F$ ) on the three species. Simulations were conducted with stochastic recruitment. Figure courtesy of Morten Vinther, DTU.

The increase in holism that motivates the move towards EBFM can reduce uncertainty in management predictions if the appropriate data are available, but eventually the increase in the number of parameters will begin to increase uncertainty.

Here, we have focussed on how the structure of models creates the need for additional data, rather than the data collection. Generally the needed data have begun to accumulate as management agencies focus on the broader range of issues. Information on ecosystem functions has also accumulated from focused large-scale oceanographic research programmes such as GLOBEC, which have increased our understanding of marine ecosystem dynamics (Fogarty *et al.* 2013). This understanding has been incorporated in a spectrum of ecosystem models that range in their scope and complexity. Improved ecosystem understanding

would lead to improved fisheries management if the complex and uncertain science could be translated into improved decision-making. We list reasons why the results of ecosystem models have had limited use to date and suggest ways in which their use in fisheries management could be facilitated.

#### Progress in following best practices for ecosystem modelling

We find genuine progress in attempts to follow best practice in ecosystem modelling, as stated in the FAO (2008) technical guidelines for responsible fisheries. The development of models such as MICE, SMS and GADGET are examples of increasing efforts to account for parameter uncertainty, model structural uncertainty and implementation uncertainty. Structural uncertainty is being

acknowledged by checking whether structurally different models predict qualitatively similar results. Uncertainty in functional responses (the prey–predator interaction term) has been addressed in several studies (Kinzey and Punt 2009; Gaichas *et al.* 2012) but is ignored in the majority of ecosystem model examples. There is growing use of ecosystem models as part of management strategy evaluation to assess how well alternative candidate harvest rules achieve the objectives sought by management authorities (Fogarty 2014).

While more could be done regarding the independent review of models, there have been several large programmes and research projects to compare outputs of different model forms. Progress has been made on some fronts, but the number of ecosystem models that have been constructed globally outweighs considerably the effort that has been put into critical evaluation and review of these approaches. There are almost no critical reviews of how well the model predictions performed retrospectively, analogous to what is done for single-species models, but recognizing also the challenges of collecting data for multispecies assemblages. Possibly not enough has been done to address the FAO (2008) recommendation that process error, arising from natural variation in model parameters, needs to be included in projections when that variation contributes substantially to uncertainty in model outcomes.

### Finding the sweet spot

What practical criteria can modellers and managers use to determine whether their models are too simple or too complex? Models intended for tactical use should be statistically fit to data with measures of uncertainty that are propagated from the model parameters to the variables on which decisions are made (e.g. exploitable biomass, fishing mortality). Model uncertainty (e.g. different states of nature) should be considered in addition to the precision of the preferred model. In models with multiple species, environmental drivers or human responses, the mechanisms linking the interacting components should be identified and supported with process-oriented studies where available.

In the context of Fig. 1, a model is too simple when a dynamic component has been omitted or assumed constant over time (e.g. natural mortality, spatial distribution), creating bias in the policy

indicator. A model is too complex when its parameters cannot be estimated or are severely confounded with each other (e.g.  $|\text{correlation coefficients}| > 0.8$ ). Models need to adapt to the management question and are constrained by the data available to develop and evaluate them, such that finding the sweet spot depends on the context. It may not be possible to statistically fit models to data for data-limited stocks or areas. In these situations, qualitative models can indicate the direction of management action instead of a precise road map with reference levels.

A dialogue between modellers and managers is required for ecosystem models to gain traction in the management system. Model variables must be commensurate with the quantities used to make decisions, such as exploitable biomass, allowing for the selectivity of fishing gears. Conversely, the management system may need to adapt to an ecosystem approach, for example, by adjusting management boundaries, definitions of stock complexes or biological reference points. As new policy indicators are identified, model complexity may need to be adjusted to realign the sweet spot.

### Application of ecosystem models to fisheries management

Integrated ecosystem assessments represent one approach for furthering the use of ecosystem models in strategic management contexts. Still, most such approaches suffer from a weak relationship between model structure and suitability for addressing questions of strategy or tactics. The strength of climate change signals has brought fishery and environmental scientists closer together. Fundamental changes in ecosystem structure and function (regime shifts; DeYoung *et al.* 2008) reveal inadequacies in classic fisheries models and create new challenges of detecting ecosystem shifts and accounting for changing productivity.

There is still a gap between theoretical ecological research and its application to fisheries management. Complexity is introduced, not just by the number of state variables, but also by the nature of interactions among these variables. Complex models can be solved numerically without fully understanding their dynamical properties. We recognize the need for greater theoretical underpinning of multispecies models, but not much has been done since the seminal work of May *et al.* (1979).

Several misconceptions about ecosystem modeling may hinder its application to fisheries management, but there are also true impediments. Management agencies respond primarily to the legal mandates that govern their operation. Without a mandate, ecosystem considerations are likely to receive lower priority than other issues. In some regions, action on fishery ecosystem plans has been postponed by more pressing issues like rebuilding overfished stocks. Management agencies receive much more scrutiny of the decisions they make ('sins of commission') than issues they ignore ('sins of omission'), which leads to a natural tendency to consider only the essential elements.

Ecosystem models are considered by many to be too complex for tactical management use (Fogarty 2014). Data needs increase with increasing complexity, and the types of data required shift as a model is used for strategic vs. tactical management. Many feel that fisheries management is complicated enough without adding another layer of complexity. Further, our understanding of key environmental linkages and species interactions may be adequate for general understanding and strategic evaluation of the long-term effects of management actions, but still may be too uncertain for tactical decision-making. A case in point is the temperature-dependent harvest rule for Pacific sardine. Management agencies may be reluctant to implement ecosystem-based harvest strategies until there is a higher level of confidence in the underlying relationships. Rigorous and context-specific model testing is necessary for the high degree of model credibility that is required in order for tactical decisions to be defensible.

Finally, there is a hesitation to use ecosystem models for fisheries management decisions because of the lack of detailed understanding of the models by those charged to perform the assessments and those who make the decisions. As stock assessments become more sophisticated, assessment scientists tend to focus more on the technical aspects of parameter estimation and less on the underlying ecological processes (Dickey-Collas *et al.* 2013). There is concern that incorporation of environmental considerations will invariably lead to more precautionary reference points and reduced fishing opportunities. There is also a more general fear of unknown outcomes, for example, that the outcomes of multispecies management advice could differ from the status quo in ways that seem risky or alter the allocation of species

quotas. As understanding of ecosystem models grows, these general perceptions need to be tested with specific applications and the outcomes effectively communicated.

### Summary and conclusions

The recent push towards ecosystem-based fisheries management has motivated considerable development, implementation and testing of ecosystem models. We presented in this paper the required characteristics of ecosystem models and issues that need to be addressed, especially the challenge of increasing complexity. Depending on management needs, moving from single-species management to an ecosystem basis means that the complexity of models can develop in four main ways: by adding population structure, environmental influences, trophic interactions and human interactions. Increased availability and resolution of environmental data has permitted the development of mechanistic models representing the relationship between the environmental and the biological responses at appropriate spatial and temporal scales. An ecosystem approach requires more complete economic accounting because it makes the trade-offs among competing resource uses more explicit. Along the complexity continuum, there is a sweet spot at intermediate complexity that balances model bias with parameter uncertainty.

Finding the sweet spot depends on effort, cost and data to construct the models as well as the key scientific questions asked or management policies being considered. Ecosystem models can be used for strategic or tactical purposes, with the output of strategic models providing context for tactical management decisions. Complex ecosystem models can also be used as operating models in management strategy evaluations. Models of intermediate complexity, which incorporate the important ecosystem components with strong links, will ultimately be most useful to specify harvest guidelines. Among other considerations, they need to be statistically fit to data and account for structural uncertainty (e.g. predator functional responses). Precautionary and dynamic approaches exist for determining multispecies biological reference points. In an ecosystem context, the concept of *maximum* sustainable yield can be replaced with *multispecies* sustainable yield – the region of harvest rates within which all species are maintained at sustainable levels. Methods exist to visualize the

consequences of different combinations of harvest rates within this sustainable region.

Ecosystem models are increasingly being used to inform management by providing system-level context, and in some cases, for strategic management analyses. However, the use of ecosystem models in tactical decision-making in fisheries management has been slow to develop because the uncertainties in model outputs do not allow sufficient confidence for specific management decisions and because getting new methods fully incorporated into the regulatory structure of marine fisheries management is difficult. There are increasing numbers of examples where single-species methods have been expanded to include the effects of other species (mortality rates) and environment influences on recruitment. Age-structured, multispecies models are presently being used to provide tactical advice in the Baltic Sea, Barents Sea and elsewhere. But there is a large gap from these enhancements of single-species analyses to a full ecosystem-based evaluation. Facilitating the adoption of ecosystem models in fisheries management requires critical evaluations of different model forms and independent reviews of these approaches. Finding the sweet spot of minimal uncertainty will accelerate the use of ecosystem models for strategic analyses and generate momentum for their greater use in tactical decision-making.

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