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REVIEW AND SYNTHESIS

Functional responses and scaling in predator–prey interactions of marine fishes: contemporary issues and emerging concepts

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Abstract

Predator–prey interactions are a primary structuring force vital to the resilience of marine communities and sustainability of the world's oceans. Human influences on marine ecosystems mediate changes in species interactions. This generality is evinced by the cascading effects of overharvesting top predators on the structure and function of marine ecosystems. It follows that ecological forecasting, ecosystem management, and marine spatial planning require a better understanding of food web relationships. Characterising and scaling predator–prey interactions for use in tactical and strategic tools (i.e. multi-species management and ecosystem models) are paramount in this effort. Here, we explore what issues are involved and must be considered to advance the use of predator–prey theory in the context of marine fisheries science. We address pertinent contemporary ecological issues including (1) the approaches and complexities of evaluating predator responses in marine systems; (2) the 'scaling up' of predator–prey interactions to the population, community, and ecosystem level; (3) the role of predator–prey theory in contemporary fisheries and ecosystem modelling approaches; and (4) directions for the future. Our intent is to point out needed research directions that will improve our understanding of predator–prey interactions in the context of the sustainable marine fisheries and ecosystem management.

Keywords

Ecosystem models, individual-based models, marine fisheries, multi-species model, predator responses, predation, population regulation, scaling.

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INTRODUCTION

It has long been recognised that predator–prey interactions play an important role in the dynamics of marine fish populations (Sissenwine 1984). Predation represents a large source of fish mortality, often exceeding the mortality rates imposed on species targeted by commercial fisheries (Tyrrell *et al.* 2011). Predation, alone or in combination with competition, can also cause density-dependent mortality in marine fishes (Hixon & Jones 2005), and acts as a structuring force in marine food webs (Frank *et al.* 2005). Thus, reductions in predator densities may cause trophic cascades and ecosystem shifts into alternate states (Frank *et al.* 2005), potentially weakening ecosystem resilience (Folke *et al.* 2004). An improved understanding of how predator and prey populations are regulated should lead to the capacity to identify key trophic linkages and more effectively model marine fish population dynamics and food webs.

The emerging push for scientific advice to support ecosystem-based management (Link 2010) and for ecological forecasting in general (Clark *et al.* 2001) highlights the need to better understand predator–prey linkages in marine food webs. Over the past decade, substantial progress has been made in the advancement of multi-species modelling (Hollowed *et al.* 2000; Whipple *et al.* 2000; Plagányi 2007) and the development of food web and ecosystem models (Christensen & Walters 2004; Plagányi 2007 and references therein). These models

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have improved our ability to evaluate the potential influence of species interactions on population dynamics. However, we still face important challenges in modelling trophic interactions. Marine systems are highly variable in space and time, and marine fishes are largely opportunistic predators therefore traditional predator–prey models developed for specialist predators in terrestrial systems (e.g. Holling 1959) are difficult to apply to marine food webs. Nevertheless, functional responses (i.e. the relationship between prey density and per-predator prey consumption; Solomon 1949; Holling 1959) are the foundation of many models used in marine ecosystems. Given the complexities of these systems, some guidelines for how functional responses might be applied to better understand the impact of predator–prey interactions would be a novel contribution.

A central issue in theoretical, behavioural and fisheries ecology is the scale dependency of predator responses. Ecologists realise that patterns and processes of ecological phenomena can shift across scales (Wiens 1989; Levin 1992). For instance, consumption rates of predators and observed functional responses have been shown to vary with the size of experimental arenas (Bergström & Englund 2002, 2004). In marine systems, there is a need to characterise predator–prey interactions at population, community, and ecosystem levels, and particularly at the scales over which fisheries operate and are managed. However, what we measure at the laboratory and local scale is not easily translated to complex seascapes. Moreover, it is difficult to derive fine-scale predator responses from fisheries data, which are often aggregated across space and time, thereby obscuring key sources of variability. To apply predator–prey theory at scales relevant to marine fisheries ecology, we must 'scale up' local observations (individuals) to populations (stocks), as well as to the habitat context where interactions occur in nature. Solutions to the scaling issue are needed to improve our estimates of species interactions in fisheries and ecosystem models, and in turn, our management and conservation strategies for marine ecosystems (Levin 1992).

Predator–prey theory and concepts of scaling have been studied extensively for several decades. The intent of this article is not to review the expansive work on predator responses or the scale dependence of ecological processes, as this has already been done (e.g. Jeschke *et al.* 2002; Englund & Cooper 2003). A detailed review of contemporary fisheries and ecosystem models is also beyond the scope of this article. Instead, our goal is to discuss the needs and considerations for advancing the use of predator–prey theory in the context of marine fisheries science. We do so by first identifying the unique challenges of estimating predation rates of marine fish predators. We focus on predator response models because they are readily used in multi-species and ecosystem applications to describe predator–prey interactions. Next, we present the state of the art in how to scale-up local observations of predator–prey interactions to larger contexts. We then discuss the role of predator–prey theory in common modelling approaches used to explore and forecast dynamics of marine systems. We conclude with suggestions for innovative future lines of research that can improve our ability to understand and predict the dynamics of predator and prey populations.

PREDATORY INTERACTIONS AND IMPACTS

There are different approaches to estimate predation mortality and obtain quantitative representations of predator–prey interactions. Fundamentally, the first step is to use one of several methods to quantify predator feeding rates. Commonly used feeding rate estimation techniques include: stomach contents/evacuation rates, bioenergetics models, and visual observations (as in reef or lab studies) (see Ney 1990 and references therein). The feeding rate can then be used to parameterise predator responses in a suite of models to predict how predation rates may change as a function of extrinsic variables and to identify a predator's capacity to regulate prey populations.

Predator responses

Holling (1959) described various types of functional and numerical response (collectively known as the 'predator response') to better understand the components of predator–prey interactions. The functional response describes the relationship between per capita predator consumption and prey density (Solomon 1949), and is typically defined at scales much smaller than the target ecosystem. The three main types of functional response are linear (Type I), decelerating (Type II), and sigmoidal (Type III) relationships between individual predator feeding rate and prey density (Holling 1959). More complex and less well-known forms of the classical prey-dependent functional responses include predator-dependent and multi-species dependent responses. Predator-dependent responses (Abrams & Ginzburg 2000; Walters & Kitchell 2001; Essington & Hansson 2004) occur when the total consumption of prey is decoupled from predator abundance due to processes such as predator interference (DeAngelis 1975), prey refuge use (Abrams 1994), or spatial heterogeneity in predator and prey abundance (Keeling *et al.* 2000). Multi-species functional responses may include feeding by a single predator on multiple prey types (e.g. Rindorf & Gislason 2005). Synergistic effects of multiple predator species are becoming increasingly apparent (Hixon & Carr 1997), although how these effects should be represented in multi-predator functional response equations is not entirely clear.

Functional response models are often part of larger ecosystem models that predict how predator feeding rates change as a function of multiple variables in addition to prey density (e.g. predator body size, prey size and quality, predator and prey overlap). Ecosystem models, which are increasingly used to provide guidance on fisheries management questions, are sensitive to the assumptions surrounding functional responses. Thus, it is important that predator responses are understood as thoroughly as possible. The exact form of the functional response might not be critical if a model is being used strategically, if prey groups are not at an extreme biomass (high or low), or if similar conclusions are reached regardless of the form of the functional response. However, it is critical to use the correct form of the functional response when prey groups do reach extreme biomass levels and the form of the response changes model behaviour and performance. It is prudent to compare models using different forms of functional responses and to be cognizant that there may not be one 'best' functional response type across predators (Moustahfid *et al.* 2010), models and environments. Also, derived estimates of functional response parameters may be verified through alternative methods used to model predator foraging, such as probability-based approaches that are based on empirically derived predation components (encounter, attack and capture; O'Brien 1979).

The numerical response represents the change in predator numbers as a function of prey density (Holling 1959). This response has been partitioned into a *reproductive numerical response* (Hassell 1966), typically at larger spatial and temporal scales, and a behavioural *aggregative response* at small spatial and temporal scales (Hassell 1966; Murdoch &

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Stewart-Oaten 1989). In marine fishes, numerical responses of predators to prey populations are complicated by complex ontogenetic changes in diet and the possibility that population dynamics are dictated by events that occur during key life history stages. That is, the availability of specific prey types during critical, often early life history stages, can govern annual reproductive success. Thus, availability of prey to adult stages will be manifest by increased growth and fecundity, but this may not directly translate into enhanced reproduction in any given year. In contrast, there are several lines of evidence for behavioural, aggregative responses (White *et al.* 2010). For example, in a temperate system, an aggregative response in combination with a Type II functional response by a piscivorous kelp bass caused spatial density dependence in kelp perch (Anderson 2001). Also, it has been suggested that differences in the functional response of piscivorous fishes to pelagic prey (Type II) and demersal prey (Type III) may arise from aggregations of pelagic fishes that attract large numbers of predators (Moustahfid *et al.* 2010). Because of the smaller scales involved, aggregative responses are logistically much easier to demonstrate than reproductive responses (Hixon & Carr 1997; Anderson 2001).

Contemporary issues of predator responses relevant to marine fishes

Predator responses can be influenced by a number of environmental variables other than prey abundances, including the characteristics (e.g. size) of focal prey, the density and characteristics of alternative prey, predators and competitors, environmental factors that can influence predator physiology (e.g. temperature), and habitat architecture (e.g. seascape). Moreover, many key environmental variables are heterogeneous in space and time and can interact with each other (e.g. temperature influence on prey size). Below, we provide examples of several factors that complicate the application of functional response models over broader temporal and spatial scales.

Variability in predator preferences

While recognising that there are some highly specialised marine predators, the diverse diet of many species indicates that feeding is often opportunistic. Heterogeneity in predator selection for a particular prey species (either passive or active selection) through space and time can be influenced by the relative abundance of other prey (Murdoch 1969; Abrams & Matsuda 2005). Predator preference for a particular prey species typically increases with the abundance of that species relative to other available prey. This mechanism is known as positive prey switching (Chesson 1984) and generalist predators can exert a Type III functional response primarily due to this foraging behaviour (Murdoch *et al.* 1975). Positive prey switching has profound implications for predator and prey population stability (Murdoch 1969) and therefore is an important area of study. However, for marine predators it is not known whether diversity in feeding habits represents a switching response of predators (feeding disproportionately more than expected on a particular prey type that has high relative abundance) or simply diversity in prey encounter rates and little preference for any single prey type. Modelling a predator as a 'switching' versus 'encounter rate' predator can make a difference in predictions of predation. For example, if a climate model predicts a change in prey community or shift in prey distribution, then how a predator's diet would change, and thus our ability to predict their impact, would be highly influenced by whether the predator was modeled as a 'switching' or 'encounter rate' type. A switching predator is more likely to have regulatory effects than an encounter rate predator. Resolving these issues of high diet breadth will require technological and observational advances that permit the measurement of prey selection in response to local- and regional-scale prey fields.

Interactions among predators

Facilitation and interference among predators (intra- or interspecific) can be important in explaining temporal and spatial variability in predator responses. There are instances when multiple predator species can actually facilitate prey capture. Hixon & Carr (1997) showed that the synergistic action of resident and transient predators exhibiting different search behaviours led to more intense predation on coral-reef fish prey. Also, adult predators may alleviate the predation risk that smaller conspecifics encounter in 'foraging arenas' by consuming potential predators/competitors of juveniles (Walters & Kitchell 2001). This in turn improves the foraging success of younger life stages. Alternatively, predators can affect the functional response of conspecifics through interference (Abrams & Ginzburg 2000), which is one mechanism leading to predator-dependent functional responses (Essington & Hansson 2004). Given the same prey density, an increase in predator abundance will most likely reduce the per capita availability of prey and therefore reduce the per capita consumption rate (see Buckel & Stoner 2004 and references therein). At the ecosystem level, comparisons between prey-dependent and predator-dependent functional responses may shed light on the potential importance of predator interference and facilitation (Abrams & Ginzburg 2000; Essington & Hansson 2004).

Habitat architecture and local features

Spatial variability in landscape features, such as vegetation or bottom substrate, will affect the spatial variability of predator responses. For example, the presence of refugia can influence various attributes of the functional response (Anderson 2001). The mechanisms are not always clear, although increased physical structure appears to provide refuge for only low numbers of prey. Heterogeneity in 'seascape' features (e.g. fronts, eddies, thermal and biological structure) creates ephemeral refugia for prey and affects multiple aspects of predator and prey behaviours (e.g. predator and prey concentration at fronts, prey refugia in structure). This, in turn, can also influence the feeding response of predators on their prey. In marine environments, clear examples can be found for the effects of light and turbidity on the reaction distance and feeding intensity of the predator (Fiksen *et al.* 1998), the effect of turbulence on encounter rate and prey pursuit probability (Mackenzie *et al.* 1994), and the effect of water temperature on predator physiology, swimming speed and encounter rate with prey (e.g. Sanford 1999). As we discover additional sources of spatial and temporal heterogeneity in predator–prey interactions, the variability they produce accumulates over the small-scale observations to predict seascape-level dynamics.

Complications in sampling and estimation of predator–prey interaction

Although predator–prey theory and the role of the functional and aggregative responses in population regulation are well grounded, tests of these theories are mostly limited to laboratory experiments (but see Anderson 2001; Essington & Hansson 2004; Rindorf & Gislason 2005). Given the complexities of predator responses, the usefulness of laboratory experiments to mimic reality and parameterise large spatial scale population level models has been called into question (Abrams &

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Ginzburg 2000). However, field measurements can also be problematic because logistical and data limitations can lead to mismatches in what is required to describe functional responses compared to what is possible to measure. For example, measurements of prey densities and feeding rates are often derived from trawl and hydroacoustic surveys. These surveys may miss certain prey species due to differential catchability or availability to the sampling gears, and they may not sample over the same area as the predators (Rindorf *et al.* 2006). Also, predator stomach contents may reflect food consumption over a longer period relative to the short trawl hauls, and therefore prey densities observed in the trawls may not match what the predator encountered. The mismatches between field data and parameterisation of functional response models may be handled by addressing the issues of scale.

DEALING WITH THE PROBLEM OF SCALE

The consequences of heterogeneity for predator responses raise the issue of how best to 'scale-up' local observations to make ecosystem-level predictions. All ecological processes have a characteristic scale defined by the regions of space and time over which processes generate variability in the measurement of interest (Levin 1992; Urban 2005). Often, multiple processes that operate at different scales influence quantities of interest (e.g. densities of predators and prey). Such heterogeneity presents a significant challenge for understanding natural systems because our knowledge of ecological processes is typically derived from empirical studies that are substantially restricted in time and space. In this discussion, it is important to distinguish between the 'process scale', which includes the interactions of animals with their environment and other individuals, and the 'observational scale' which is the resolution (grain) and extent at which processes are sampled. Often it is suggested that the process scale should determine the observational scale (Levin 1992; White *et al.* 2010), but this is often impractical, especially if one desires to understand a process that has a fine resolution over a large spatial or temporal extent. The difference in scales at which predation events occur and fisheries are managed further complicates the situation. The large extent of marine ecosystems necessitates that managers consider results from tactical and strategic models that analyse and predict system responses to anthropogenic forcing (e.g. marine spatial planning and fishing) (Hollowed *et al.* 2011). These models may build upon observations made at much smaller scales (Levin 1990); therefore, it becomes important to scale up (or scale down) results from observations made over a different domain of space and time (Fig. 1). These issues lead to specific questions in the context of predator–prey interactions: (1) What are the key scales at which systems are regulated and structured?; (2) At what scale should we measure functional and aggregative responses?; (3) What processes produce heterogeneity in predator–prey systems, and how do processes at different scale interact to produce emergent properties?; and (4) What procedures allow us to translate from one scale to another?

Key aspects of the scaling problem for predator–prey interactions

Interpreting information from empirical studies can be facilitated by a careful consideration of both the extent and grain of the study (Wiens 1989). The extent and grain (or resolution) of the study will determine the openness of a system, and will therefore affect the relative importance of demographic rates underlying the ecological processes measured. For example, when the area of study is small, the perimeter:area ratio will be relatively high and abundance may be strongly influenced by movement (e.g. aggregative responses of predators). In contrast, when the area of study is larger, perimeter to area ratios decrease, and birth and death rates (reproductive response) may be primary determinants of abundance (e.g. Englund & Hamback 2007). Studies with greater extent tend to detect greater variability because the effects of both small- and large-scale processes will be included (Levin 1992; Urban 2005; Fig. 1). A similar phenomenon occurs when sampling over time, as low-frequency events tend to introduce variability in both abiotic and biotic variables ('1/*f*-noise'; Halley 1996; Denny *et al.* 2004). Accurately characterising variability in ecological systems is important because many ecological processes are nonlinear. Because of nonlinearities, the biological consequences of certain processes cannot be inferred from average environmental conditions – a phenomenon known as Jensen's inequality (Fig. 2; also see Ruel & Ayres 1999). Any attempt to average a nonlinear process over heterogeneities in space or time will produce a bias like that shown in the Fig. 2; this bias is termed the aggregation error.

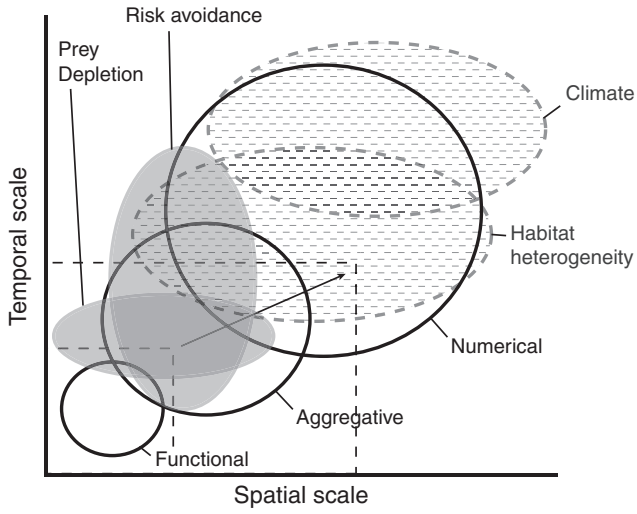

Figure 1 Schematic illustration of characteristic spatial and temporal scales of different processes that affect the density dynamics of predators and prey. Open black circles indicate predator functional responses, filled grey circles indicate prey responses to predator actions, and dashed circles indicate abiotic forces. Dashed boxes indicate scales of observation and/or management. Observations made at a particular scale will integrate variability created by processes falling within that box (i.e., processes occurring at small scales can contribute to variability observed at much larger scales). To 'scale up' from small-scale observations (small dashed box) to larger scale predictions (large dashed box), a scale transition must account for variance introduced by processes at the intervening scales.

The grain of a study has important implications for how to properly scale information. Observations will integrate variability from multiple processes operating below the grain, and scaling up information from the grain to the extent of the study will require information at both levels (Rastetter *et al.* 1992). For example, functional responses may be estimated by sampling predators and prey within trawls and comparing the mean number of prey consumed per predator as a function of mean prey density. However, such observations are summarising both the functional response (a property of individual predators) and any other processes that affect the distribution of individual predator's access to prey (e.g. aggregation and/or competition among predators). Scaling up the patterns of prey consumption within trawls to larger populations requires information on how

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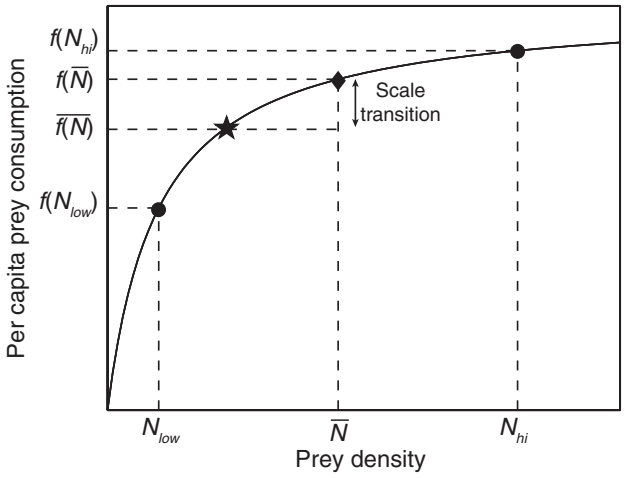

Figure 2 An illustration of Jensen's inequality. Solid line represents a functional response, $f(N)$, describing number of prey consumed per predator as a function of prey density. Because of the nonlinear relationship, the average result of fN, $\overline{f(N)}$, does not equal the result of the function at average prey densities, $f(\overline{N})$. Predicting prey consumption based on mean prey densities therefore gives a biased estimate of the mean number of prey consumed per predator: the aggregation error. Importantly, this bias will tend to increase with increased variability in prey density. If the distance between N_{hi} and N_{low} were greater, $f(\overline{N})$ would increase and $\overline{f(N)}$ would decrease.

predators and prey are distributed within the extent of the populations. A challenge for scaling empirical observations will therefore be to identify heterogeneity in processes that occur above or below the grain of study and account for them when transitioning observations across different domains of space and time.

A variety of strategies exist for minimising the aggregation error when scaling up. Several statistical approximations utilise information on the spatial variation at scales greater than the grain of the functional response (see Scale transition theory for nonlinear processes in heterogeneous systems). However, before applying any quantitative scaling method, it is worthwhile to consider the processes generating heterogeneity in the system so that the resulting spatial variation can be accounted for by sampling and modelling methods. For example, if habitat heterogeneity is responsible for spatial variance in attack success, then the granularity of the habitat structure may constrain predator foraging behaviour and define the spatial scale at which predators respond to prey (see White *et al.* 2010). In that situation, a large-scale approximation may require sampling (and scaling) at different resolutions within a single landscape according to the local habitat granularity. Alternatively, an individual based model (IBM) could respond directly to variation in habitat granularity (Bianchi *et al.* 2009). Heterogeneity may also arise from behavioural interactions. The typical null model of spatial predator–prey interaction is the ideal free distribution, although most natural systems violate one or more of the assumptions of perfect information, unconstrained movement, and sessile prey. In particular, mobile predators and prey may be involved in a spatial attraction-avoidance game, so the steady-state distribution of animals will depend on the relative movement rates of the species and spatial heterogeneity in habitat productivity (Sih 2005). The outcome of such games, as indicated in the previous section, may also depend on habitat structure if prey are more vulnerable in certain locations than in others. With mobile prey, it appears that models assuming that predators distribute themselves according to the prey resource or to locations of higher prey vulnerability are more successful than those assuming predators respond to local prey density (Flaxman & Lou 2009; Laundre 2010). This is also a case in which IBMs prove useful (Okuyama 2009).

Scale transition theory for nonlinear processes in heterogeneous systems

Despite a few examples in which small-scale observations accurately predict large-scale processes (reviewed by White *et al.* 2010), process scaling will produce aggregation errors in most cases. There are several approaches for correcting such errors. Conceptually, the simplest scaling approach is partitioning (Rastetter *et al.* 1992): partition the larger scale habitat into smaller units, run the model in each unit, and sum the output over all units (e.g. Bergström *et al.* 2006). This

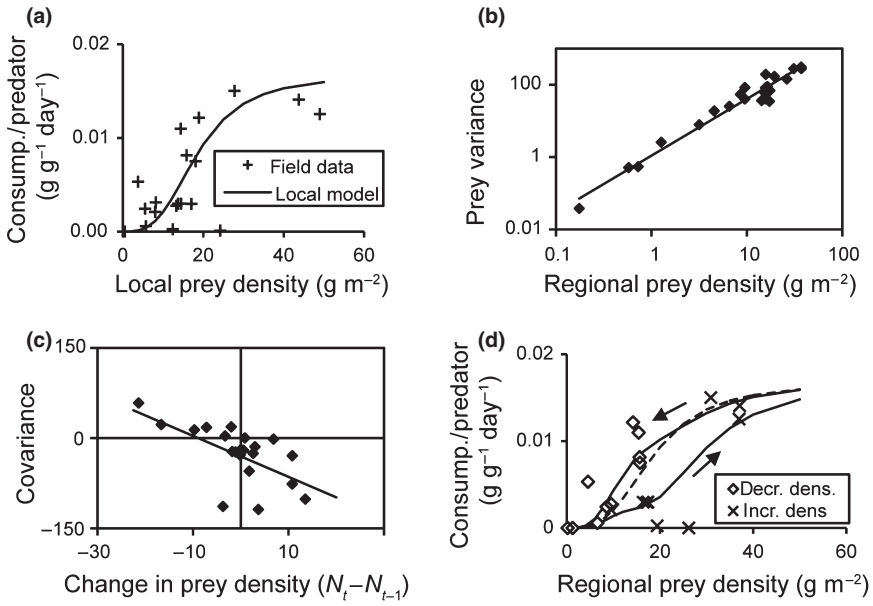

Figure 3 (a) Functional response of *Saduria* preying on *Monoporeia* fitted to field data collected at the local scale. (b) Relationship between regional mean prey density and the spatial variance in prey density (σ^2_N). (c) Relationship between the annual change in prey density and the spatial covariance of predator and prey density ($\sigma_{N,P}$). (d) Scale-transition-derived functional responses (solid curves) for periods of increasing (crosses, upward arrow) and decreasing (diamonds, downward arrow) prey abundance. For comparison the local-scale functional response (without the scale transition) is also shown (dashed line). Adapted from Englund & Leonardsson (2008).

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approach is often infeasible because of the sheer number of partitions required by the fine scales at which predator functional responses operate. Alternatively, the calibration approach (Rastetter *et al.* 1992) involves fitting the small-scale function directly to large-scale data. An example is when a functional response model is fitted to prey densities and stomach contents observed in trawl surveys (Rindorf & Gislason 2005). The resulting parameter estimates are likely different from the rates observed at a scale relevant for predator behaviour, but it could be used to model consumption as function of large-scale average prey density. An important strength of this method is that it allows all sources of aggregation errors to be corrected without increasing the complexity of the model. A disadvantage is that the estimated parameter values do not correctly represent the small-scale process. In general, the degree of bias involved in scaling up (or down) will depend on the degree of nonlinearity in the functional response and the magnitude of spatial variation in prey abundance. White (2011) used a coral reef fish example to illustrate how one can model variation in those two factors analytically and compare the results to field data to determine the degree to which large-scale dynamics are affected by the scale transition.

A useful approach to the scaling problem is the moment approximation or scale transition (Bergström *et al.* 2006). This approach has been successfully applied to a range of predator–prey systems (Melbourne & Chesson 2006; Englund & Leonardsson 2008). This technique is based on a Taylor series expansion whereby the small-scale function is approximated around the mean and the resulting polynomial is then averaged over all observed variable values (Rastetter *et al.* 1992; Melbourne & Chesson 2006). The resulting equation contains expressions for statistical moments around the mean, such as variance, skewness, and kurtosis. In ecological applications it is common to ignore terms higher than second order (i.e. including only mean, variance and covariance), which is a reasonable assumption when distributions are close to normal or the nonlinear function is close to quadratic (Bergström *et al.* 2006). This assumption works well for the Type II predator functional response because all derivatives with respect to prey density are close to zero for high prey densities where the Type II model deviates most strongly from a quadratic function (Bergström *et al.* 2006). To our knowledge, Bergström *et al.* (2006) provide the only marine example of the scaling up a predator functional response (of a predatory isopod feeding on amphipods in the Baltic Sea) using the moment approximation approach (see Box 1). Note that a key to their success was the existence of a long-term data set with sampling at both fine grain (10 s of m) and coarse grain (10 s of km). These grain sizes are small in the context of marine fisheries, which are managed at the coastline or ecosystem scale to encompass the range of the population of interest. To apply the moment approximation approach more broadly, relatively fine scale sampling must be conducted first to determine whether typical trawl or acoustic survey techniques are able to sample at a scale similar to the granularity of the study system. If they are too coarse, it will be necessary to supplement them with finer-scale sampling to parameterise the moment approximation.

Box 1 Application of the scale transition technique

One of the first applications of scale transition theory to a marine predator–prey system has been developed for the isopod *Saduria entomon*, which preys primarily upon the amphipod *Monoporeia affinis* in the benthos of the northern Baltic Sea (Bergström *et al.* 2006; Englund & Leonardsson 2008). A multi-decadal monitoring programme has sampled densities of both species at 11 stations within a 300 km^2 area. To describe predator–prey dynamics at this 'regional' spatial scale, Englund & Leonardsson (2008) scaled up estimates of the predator's functional response. The functional response reflects the prey density experienced by a predator at the scale of a single 0.1 m^2 benthic sample (the 'local' scale).
The scale transition equation is

$$G(\bar{N})\bar{P} \approx f(\bar{N})\bar{P} + f''(\bar{N})\bar{P}\sigma_N^2/2 + f'(\bar{N})\sigma_{N,P} \quad (1)$$

where $G(\bar{N})$ is the effective functional response (number of prey eaten per predator) at the regional scale, $f(\bar{N})$ is the functional response at the local scale (estimated in the field from stomach contents and gut evacuation rates, Fig. 3a), σ_N^2 is the spatial variance in prey density at the regional scale, and $\sigma_{N,P}$ is the spatial covariance between prey and predator densities at the regional scale. Overbars indicate spatial means at the regional scale.

The variance and covariance terms in the above equation approximate the influence of variability on the nonlinear functional response (Ruel & Ayres 1999; Melbourne & Chesson 2006). These terms were estimated from empirical data (Fig. 3b,c). Prey variance (σ_N^2) was found to be an increasing function of mean prey density (Fig. 3b), while predator–prey covariance ($\sigma_{N,P}$) was a function of predator density and also depended on whether the prey population was increasing or decreasing (Fig. 3c; predator–prey dynamics are cyclic in this tightly coupled system).

The empirical estimates of $f(\bar{N})$, σ_N^2, and $\sigma_{N,P}$ were combined to predict $G(\bar{N})$, yielding a much better fit to regional-scale data for period of increasing or decreasing prey density than the fit obtained by simply 'plugging in' the local-scale functional response (Fig. 3d; Englund & Leonardsson 2008).

ROLE OF PREDATOR–PREY INTERACTIONS IN FISHERIES AND ECOSYSTEM MODELS

There is increasing acceptance that ecosystem-based approaches to fisheries management (Link 2010) and fisheries science (Francis *et al.* 2007) are needed to sustain the productivity of fish stocks and to maintain the integrity of ecosystems in the face of harvesting and other factors. We view the growing development of multi-species and ecosystem models as providing a valuable contribution to understanding marine predator–prey dynamics. These models span a range of complexity and scales from minimal realistic models focused on two or more species that can be parameterised and fit to time series data (e.g. Kinzey & Punt 2009), to the detailed IBMs (Shin & Cury 2004) and end-to-end ecosystem models (Fulton 2010; Table 1). With respect to scale, these two approaches represent an important dichotomy: the former attempts to resolve the fine-scale processes from the emergent trends in population dynamics of predators and prey, while the latter attempts to predict population dynamics by specifying the rules of the fine-scale dynamics. While each model has its particular strength and limitations – particularly with regard to the ability to forecast future dynamics and to understand the role of local scale predation effects – we suggest that the greatest advancements will derive from the parallel development of models on both sides of this continuum, thereby marshalling the strengths of each direct

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Table 1 Structure, uses, frameworks and illustrative examples of major ecological models used in fisheries and ecosystem modelling today; ranging from minimal realistic models to whole system models

Major ecological model types	Extended SS assessment	Multi-species	Aggregate biomass	Food web	Network	Bio-geochemical	Biophysical	End-to-end
Model structures								
Static snapshots				x	x			x
Backcasted to fit time series	x	x	x	x		x	x	x
Projection as outputs, with forecasting	x	x	x	~	~	x	x	x
Dynamic model engines variable	x	x				~		
Dynamic model engines fixed					x	~		
Requires estimates of size selectivity	x	x		~	~		~	x
Requires estimates of type selectivity	x	x		~	~		~	x
Requires estimates of 'suitability'		x		x				
Requires estimates of diet composition	x	x		x	x			x
Dynamic diet	x	x					~	x
Fixed diet				x	x		~	~
Requires estimates of consumption	x	x	x	x	x	x	x	x
Requires estimates of functional response	~	~	~	x	?			x
Produces estimates of diet composition	x	x		x	x			x
Produces estimates of consumption	x	x	x	x	x		x	x
Produces projections of prey population	x	x	~	x	x			x
Produces projections of predator population	x	x	x	x	x		x	x
Produces projections of prey removals	x	x	x	x	~		~	x
Produces estimates of M2	x	x	x	x				x
Produces estimates of Z	x	x	x	x				x
Produces estimates of BRPs	x	x	x					x
Produces projections of BRPs	x	x	x					x
Estimates uncertainty	x	x	x	~			~	?
Uses								
Tactical management	x	x	x					
Strategic management				~	x	~	x	x
Trade-offs among taxa or fleets		x	~	x	x		x	x
Predation on targeted species	x	x		x	x		x	x
Predator footprints	x	x	x	x	x	x		x
Modelling frameworks[1]		MSM, MSVPA, MSFOR, MSPROD, IBM, Bioenergetic-allometric trophodynamic models		Ecopath		NEMURO, NPZD	Larval IBMs, DisMELS	Atlantis, EwE, OSMOSE-ROMS, InVitro NEMURO.Fish, SEAPODYM
Illustrative examples/applications[2]	Hollowed *et al.* 2000; Moustahfid *et al.* 2009	Garrison *et al.* 2010; Jurado-Molina & Livingston 2002, Koen-Alonso & Yodzis 2005	Mueter & Megrey 2006;	Aydin *et al.* 2007;	Gaichas & Francis 2008;	Kishi *et al.* 2007 & others in same issue	Kristiansen *et al.* 2009;	Fulton 2010;

[1]These models by no means represent an exhaustive list, but provide examples of contemporary modelling frameworks. Model Acronyms: MSM, Multi-species Statistical Models; MSVPA, Multi-species Virtual Population Analysis; MSFOR, Multi-species Forecasting; MSPROD, Multi-species Production Models; IBM, Individual-Based Model; NEMURO, North Pacific Ecosystem Model for Understanding Regional Oceanography; NPZD, Nutrient Plankton Zooplankton Detritus, DisMELS, Dispersal Model for Early Life Stages; OSMOSE, Object-oriented Simulator of Marine ecOSystem Exploitation; ROMS, Regional Ocean Modeling System; EwE, Ecopath with Ecosim and Ecospace; SEAPODYM, Spatial Ecosystem and Populations Dynamics Model.

[2]Hollowed *et al.* (2000), Whipple *et al.* (2000), Plagányi 2007; Tyrrell *et al.* (2011), Fulton (2010), Hollowed *et al.* (2011) provide detailed review and extensive list of references to primary developers and users.

SS, single-species; M2, predation mortality; Z, total mortality (fishing and natural mortality); BRP, Biological Reference Points. The ~ denotes 'maybe', i.e. may or may not be included in model structure.

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comparison and evaluation of model predictions and estimated quantities.

Despite the obvious need for multi-species and ecosystem models for management and conservation of marine resources, most assessments models that are currently used in management applications address single-species sustainable yields without directly addressing predator–prey interactions. These traditional models may not capture time trends in predation mediated mortality and thereby can lead to overly optimistic biomass and yield projections. The general reluctance of fishery managers to implement multi-species modelling approaches as the primary method of assessing marine resources is largely attributed to the uncertainty of species interactions. Multi-species and ecosystem models require more information than standard single-species methods, and the ecological traits of many species, particularly non-target species, are poorly understood (e.g. diet composition, population size, spatial distribution, reproductive rates, metabolic rates, etc.). Consequently, increased data requirements for building credible multi-species models are prohibitive in some situations (Plagányi 2007).

The minimal realistic models that include predation mortality and provide tactical management advice have been most successful in the management arena to date (e.g. Moustahfid *et al.* 2009; Tyrrell *et al.* 2011). Examples include extended single-species models and multi-species approaches, such as production, statistical, virtual population analysis, and forecasting models (Table 1). These models are valuable for directly addressing questions related to trade-offs in yield between predators and prey where both are economically important. They also hold promise as tools for assessing trade-offs among different management strategies (Sainsbury *et al.* 2000; see Hollowed *et al.* 2011) and providing information to fisheries managers within a multi-species context. For example, Jurado-Molina & Livingson (2002) used MSVPA and MSFOR models to examine the influence of human and climate forcing on species interactions in an attempt to provide useful information to improve fisheries management. The more flexible versions of minimal realistic models include a variety of functional-response types, and statistical criteria are applied to select the best-fit functional responses or evaluate multiple possibilities within models (Moustahfid *et al.* 2010). Also, these modelling approaches are not limited to single-predator and single-prey functional-response models (and combinations thereof). For example, within multi-species virtual population analysis models, predation mortality is estimated using a functional relationship between per capita feeding rates on all prey types and total prey density. Selectivity parameters are then used to allocate the 'total prey biomass consumed' to different prey types (e.g. Garrison *et al.* 2010). The scaling issues discussed above are still relevant to the functional-response measurements in these models and also to the way that selectivity and other parameters are determined from field data.

Aggregate biomass, food web, and network models address predator–prey interactions without including a functional response, because they are snapshots of food webs at a particular point in time (Table 1). These strategic/heuristic models are used to assess the status of resources as major groups/clusters (e.g. Mueter & Megrey 2006), and to evaluate species interactions, energy flows, and the network structure of the system surrounding fishery stocks (e.g. Aydin *et al.* 2007). They are valuable for identifying critical ecological interactions of target and non-target species for fishery scientists and managers (Gaichas & Francis 2008), or for identifying stocks with higher predation mortality than fishing mortality, which might benefit from multi-species approaches (Gaichas *et al.* 2010). These models do not provide tactical advice, but they still inform management about critical processes supporting sustainability and potential trade-offs among fisheries. Other ecosystem models that typically do not include functional responses are biogeochemical and biophysical models (or dynamic system models; Table 1). These models are used independently for strategic planning, i.e. forecasting and spatial planning, and are included as submodels in whole system modelling frameworks. The biogeochemical models are useful for evaluating fish within the context of broader material/environmental fluxes in a system and are especially valuable for modelling chemical accumulation in marine food webs. The biophysical models are mostly coupled with IBMs and address questions regarding the influence of physical/environmental conditions on low trophic level resources, recruitment processes and stock dynamics. An important challenge of biophysical models is that they require known or estimated responses of fish to environmental conditions, but these responses are often uncertain or are solely based on correlative relationships between fish stocks and the environment.

Individual based models incorporating predator and prey behavioural rules have become an increasingly popular tool to model trophic interactions (Grimm & Railsback 2005 and references therein; Table 1). Behaviour related to movement and inherent physical capabilities (e.g. reactive distance, swimming speed, visual range, capture success) can be used to derive theoretical numerical and functional responses, set boundaries for distribution of predators and prey, and understand spatial and temporal prey refugia. Within multi-species to whole-ecosystem modelling frameworks, IBMs can be used to simulate the behaviour of a foraging predator at a fine scale within a heterogeneous model landscape of the desired extent, and then results of many such simulations can be aggregated to obtain the emergent large-scale pattern (Fauchald 1999; Pascual & Levin 1999). However, model complexity, data needs, and computational costs of IBM modelling approaches greatly increase when the spatial structure of the habitat is specified and multiple species are included. Thus, IBMs are used to better understand a subset of predator and prey interactions (Rose *et al.* 1999) and to make comparisons with results from field data and ecosystem models, and are not typically used in larger food web models. Also, IBMs do not easily fit in with the data-driven parameter estimation framework used in fisheries stock assessments, whereas other multi-species ecosystem models (e.g. MSVPA or Ecopath with Ecosim) have this capacity. The future use of IBMs could be as a generating model for management strategy evaluation (Sainsbury *et al.* 2000); they are already beginning to be used in this role (McDonald *et al.* 2008).

Whole system or end-to-end models explicitly incorporate functional responses and similar predation processes (e.g. Atlantis, EwE, OSMOSE-ROMS, InVitro, Table 1). These models represent the dynamic, two-way coupling of all ecosystem components and the anthropogenic and natural drivers of the system (Fulton 2010). They have the most potential for testing management scenarios in complex systems that include fished stocks, predator–prey interactions, and other interactions. For example, they are useful for addressing questions such as: (1) what is the total sustainable yield/production from a given ecosystem and how might that vary under different management and climate scenarios? and (2) how stable is the fish community under different management and climate scenarios? However, these models are not yet commonly used in management applications because of their large data demands and issues of model size, uncertainty and application (non-stationarity) (Fulton 2010).

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At the core, whole system models require an understanding of predator–prey relationships and they warrant careful consideration of the functional response term. The form of the functional response used in both multi-species and ecosystem models can have a substantial impact on model behaviour and performance (Fulton *et al.* 2003; Koen-Alonso & Yodzis 2005). It seems prudent to be particularly mindful of groups with high turnover rates that are most responsive to changing ecosystem conditions, as they have been shown to be the most sensitive to model formulations (Fulton *et al.* 2003). Also, predator responses to forage species that are of increasing economic importance, including marine invertebrates such as squid and krill, deserve particular attention so that potential deleterious effects of their removal from marine food webs can be better identified. Furthermore, an improved understanding of the functional responses of invertebrate predators (e.g. squid, crustaceans) to prey densities is needed to elucidate their influence on community structure and their capacity to regulate prey populations.

FUTURE DIRECTIONS

There are key opportunities and emerging ideas to advance our ability to understand and model predator–prey dynamics in marine ecosystems. For example, field-based estimates of predator responses could substantially improve our understanding of species interactions and elucidate the most appropriate form of the functional response model to represent feeding behaviour. Most of our progress in addressing questions related to functional and aggregative responses of marine fishes in the field has come from nearshore reefs (e.g. Anderson 2001) and much can be learned from these systems. However, findings based on reef fishes may have limited application to pelagic predator–prey interactions, where both predators and prey are highly mobile in three dimensions, making the scaling issue potentially more complicated.

Ongoing technological advances can provide us with the opportunity to validate experimental observations of pelagic fishes foraging behaviour *in situ* (e.g. baited cameras, animal-mounted cameras). Satellite tracking is becoming more common with large marine predators and has been used to record high-resolution behavioural data (Gleiss *et al.* 2009). Electronic markers (e.g. pop-up satellite tags) have also been proposed as an important tool for ecosystem-based fisheries management. These markers have the potential to reveal complex behavioural interactions between fish and their environments, thus enabling a better understanding of biological processes and better quantitative assessments of wild populations (Fromentin *et al.* 2009). Data that can provide insight into *in situ* foraging behaviour (e.g. telemetry, remote sensing) can help us determine how behaviour affects the inferences (e.g. average abundance, stomach samples, spatial distribution) made about fish populations and predator–prey interactions. For instance, modellers often have no way of knowing how predators and prey move in relation to environmental conditions and often assume a random distribution with predator/prey encounters dependent on factors such as swimming speeds and visual range. Telemetry data could provide environmental preference models for predator and prey which would allow for improved predictions of predator and prey habitat use and thus their degree of overlap in space and time.

New technologies provide opportunities to precisely link predator densities and feeding levels to prey density under field conditions. Spatial and temporal variability in prey availability can produce 'hot spots' and 'hot moments' of intense predation (e.g. Mello & Rose 2005) and the causes and consequences of these productive periods and regions are unknown. One recent advance is the use of satellite tracking to distinguish foraging hot spots of fish from their long-distance movement (Sims *et al.* 2009). In cases where predators have distinctive foraging behaviours, active-acoustics may be able to empirically describe the foraging response to local variation in prey abundance (Benoit-Bird & Au 2003). The use of this technology as a means to gain a better understanding of the importance of facilitation or interference within or between predator species should be explored. Alternatively, implantable tags that measure physiological parameters such as body temperature (Kitagawa *et al.* 2004), stomach pH (Papastamatiou *et al.* 2007), or activity patterns (Whitney *et al.* 2007) can provide detailed information on individual foraging rates. The interpretations of studies based on these technologies require independent assessment of prey fields, while similarly resolved and co-occurring information on prey distribution is often unavailable. Thus, these advances still remain a step away from directly measuring the foraging response to prey variation in support of robust predictions about population and community dynamics. However, there is recent evidence that predators may move in response to prey resources or landscape features other than prey density (Flaxman & Lou 2009; Laundre 2010), so the additional physical and physiological information provided by implantable tags could provide useful information despite not resolving the prey field. Ultimately, a better understanding is needed of what gives rise to gross patterns of covariation of predator and prey distribution (high, low overlap), how stable or dynamic those patterns are, and the implications for governing strength of bottom-up and top-down regulation. In general, the new technologies have a small sample size and a large cost, but the data are novel and often more robust relative to traditional sampling and indirect methods. However, these technologies should not be viewed as replacements of traditional sampling since the two data types are not interchangeable.

Essential to our understanding of marine fish population dynamics is how environmental conditions dictate the nature and intensity of predator–prey interactions. Changes in temperature conditions can affect species' phenology, resulting in shifts in marine fish distributions and the spatial and temporal scales at which predator–prey interactions occur. Temperature can also influence the behavioural components of the functional response such as handling and searching of the predator, the escape ability of prey, and individual growth rate and metabolism. Furthermore, increasing temperatures, increasing atmospheric CO_2 concentrations, and coastal eutrophication lead to decreased pH and dissolved oxygen concentrations. The impacts of environmental variables on predator responses need to be evaluated through predator–prey and food web modelling approaches (e.g. Logan & Wolesensky 2007) and included in model forecasting. Some environmental effects are beginning to be taken into account within a multi-species stock assessment context (e.g. Teschner *et al.* 2010) and in process-based whole ecosystem models (e.g. Atlantis, INVITRO, BEST-BSIERP modelling efforts). These efforts are valuable for improving our understanding of environmental influences on species interactions and our ability to predict how marine fish population dynamics may change under alternate climate scenarios.

Advances in statistical methodologies have the potential to address some of the issues relevant to spatial and temporal heterogeneity in species interactions. The variables affecting functional and numerical responses act in a non-additive fashion, which poses a serious

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challenge because predator responses are typically nonlinear, and it is difficult to quantify non-additivity in a nonlinear framework. However, there are a number of promising developments in the analysis of spatially variable and temporally non-stationary systems in a nonlinear framework. The variable coefficient generalised additive models (GAM; Wood 2006) have been used to model spatially variable species environment relationships (e.g. Bacheler *et al.* 2009) and density-dependent habitat selection (Bartolino *et al.* 2011). This modelling framework has great potential for evaluating how environmental conditions can modify the overlap between predator and prey. In cases of nonstationarity, the variable coefficient GAM can accommodate changing relationships over contrasting environmental phases via the inclusion of threshold formulation (e.g. Ciannelli *et al.* 2004). Wavelet analysis is also an emerging tool for finding the 'appropriate' scale or resolution at which to study marine predator–prey predator–prey systems. This versatile mathematical method can be used to analyse various features of a function on different scales (Nason 2008). The wavelet approach generally requires regularly spaced data, which are available in marine fisheries systems from fisheries trawl and hydroacoustic surveys. Furthermore, certain scaling issues in a fisheries setting may be addressed through simulation studies using cellular automata approaches. Cellular automata methods are process simulation methods that can be used to evaluate if and how spatially varying functional responses impact the estimation of these characteristics from data collected at various scales.

An important element of ecosystem-based management (Link 2010) is the need for an improved capacity to predict the indirect ecological effects that follow from targeted removal of species that act as key predators or prey within food webs (Francis *et al.* 2007). In ecological terms, this is equivalent to predicting interaction strengths. These have proven to be exceptionally difficult to measure except when long time series data are available (Ives *et al.* 2003) that span periods when dominant biophysical forcing functions have not shifted. These conditions are typically not met for marine ecosystems; the ecological landscape can be fundamentally altered by decadal-scale changes in climate that shifts communities into new states (Hunt *et al.* 2002), as well as seasonal, if not daily, shifts in oceanographic phenomena. One promising avenue is the development of heuristic rules of thumb that describe the ecological contexts under which strong or weak interactions are most likely. For example, an overall pattern gleaned from the work of Frank *et al.* (2006) suggests that top-down control may be more prevalent in low productive northern latitudes while bottom-up forcing may prevail in highly productive southern latitudes.

CONCLUSION

The number and complexity of tools available to model marine ecosystems and to identify critical predator–prey interactions for fishery management are growing rapidly. Although they are not yet widely accepted in management applications, they do afford an unprecedented understanding of the importance of predator–prey interactions in the marine ecosystem organisation. Most such models require estimates of trophic interaction strengths and predator functional responses, and we have reviewed some complications that should be accounted for when modelling those processes. Notably, our understanding of functional responses has moved beyond simple Type I, II, and III curves to include multiple prey types, spatial heterogeneity and multi-predator interactions. Some problems related to the scale mismatches that occur when estimating functional responses and predation rates can be handled using scale transition theory, although that approach has only been used in a few cases and does require extensive, scale-appropriate sampling. Other emerging techniques and novel sampling technologies may improve our ability to accommodate the non-additivity of nonlinear predator functional responses. However, the sheer number and diversity of habitats that marine fishes inhabit make a one-size-fits-all theory of predation unlikely to be applicable, at least without proper consideration of the idiosyncrasies that various marine ecosystems introduce to the predation process. Nonetheless, the exploration of appropriate functional forms and scalability should not delay the use of marine ecosystem models when robust outcomes are evident. This is especially true given the increasing evidence that demographic density dependence in at least demersal marine fishes is often caused by predation (review by Hixon & Jones 2005).

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AUTHORSHIP

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REFERENCES

Abrams, P.A. (1994). Should prey overestimate the risk of predation. *Am. Nat.*, 144, 317–328.

Abrams, P.A. & Ginzburg, L.R. (2000). The nature of predation: prey dependent, ratio dependent or neither? *Trends Ecol. Evol.*, 15, 337–341.

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Abrams, P.A. & Matsuda, H. (2005). The effect of adaptive change in the prey on the dynamics of an exploited predator population. *Can. J. Fish. Aquat. Sci.*, 62, 758–766.

Anderson, T.W. (2001). Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology*, 82, 245–257.

Aydin, K., Gaichas, S., Ortiz, I., Kinzey, D. & Friday, N. (2007). A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. NOAA Technical Memorandum NMFS-AFSC-178.

Bacheler, N.M., Bailey, K.M., Ciannelli, L., Bartolino, V. & Chan, K.S. (2009). Density-dependent, landscape, and climate effects on spawning distribution of walleye pollock *Theragra chalcogramma*. *Mar. Ecol. Prog. Ser.*, 391, 1–12.

Bartolino, V., Ciannelli, L., Bacheler, N.M. & Chan, K.S. (2011). Ontogeny and sex disentangle density-dependent and density-independent spatiotemporal dynamics of a marine fish population. *Ecology*, 92, 189–200.

Benoit-Bird, K.J. & Au, W.W.L. (2003). Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behav. Ecol. Sociobiol.*, 53, 364–373.

Bergström, U. & Englund, G. (2002). Estimating predation rates in experimental systems: scale-dependent effects of aggregative behaviour. *Oikos*, 97, 251–259.

Bergström, U. & Englund, G. (2004). Spatial scale, heterogeneity and functional responses. *J. Anim. Ecol.*, 73, 487–493.

Bergström, U., Englund, G. & Leonardsson, K. (2006). Plugging space into predator-prey models: an empirical approach. *Am. Nat.*, 167, 246–259.

Bianchi, F.J.J.A., Schellhorn, N.A. & van der Werf, W. (2009). Foraging behaviour of predators in hetergeneous landscapes: the role of perceptual ability and diet breadth. *Oikos*, 118, 1363–1372.

Buckel, J.A. & Stoner, A.W. (2004). Negative effects of increasing group size on foraging in two estuarine piscivores. *J. Exp. Mar. Biol. Ecol.*, 307, 183–196.

Chesson, P.L. (1984). Variable predators and switching behavior. *Theor. Popul. Biol.*, 26, 1–26.

Christensen, V. & Walters, C.J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model*, 172, 109–139.

Ciannelli, L., Chan, K.S., Bailey, K.M. & Stenseth, N.C. (2004). Nonadditive effects of the environment on the survival of a large marine fish population. *Ecology*, 85, 3418–3427.

Clark, J.S., Carpenter, S.R., Barber, M., Collins, S., Dobson, A., Foley, J.A. *et al.* (2001). Ecological forecasts: an emerging imperative. *Science*, 293, 657–660.

DeAngelis, D.L. (1975). Stability and connectance in food web models. *Ecology*, 56, 238–243.

Denny, M.W., Helmuth, B., Leonard, G.H., Harley, C.D.G., Hunt, L.J.H. & Nelson, E.K. (2004). Quantifying scale in ecology: lessons from a wave-swept shore. *Ecol. Monogr.*, 74, 513–532.

Englund, G. & Cooper, S.D. (2003). Scale effects and extrapolation in ecological experiments. *Adv. Ecol. Res.*, 33, 161–213.

Englund, G. & Hamback, P.A. (2007). Scale dependence of immigration rates: models, metrics and data. *J. Anim. Ecol.*, 76, 30–35.

Englund, G. & Leonardsson, K. (2008). Scaling up the functional response for spatially heterogeneous systems. *Ecol. Lett.*, 11, 440–449.

Essington, T.E. & Hansson, S. (2004). Predator-dependent functional responses and interaction strengths in a natural food web. *Can. J. Fish. Aquat. Sci.*, 61, 2215–2226.

Fauchald, P. (1999). Foraging in a hierarchical patch system. *Am. Nat.*, 153, 603–613.

Fiksen, Ø., Utne, A.C.W., Aksnes, D.L., Eiane, K., Helvik, J.V. & Sundby, S. (1998). Modelling the influence of light, turbulence and ontogeny on ingestion rates in larval cod and herring. *Fish. Oceanogr.*, 7, 355–363.

Flaxman, S.M. & Lou, Y. (2009). Tracking prey or tracking the prey's resource? Mechanisms of movement and optimal habitat selection by predators. *J. Theor. Biol.*, 256, 187–200.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. *et al.* (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.*, 35, 557–581.

Francis, R.C., Hixon, M.A., Clarke, M.E., Murawski, S.A. & Ralston, S. (2007). Fisheries management - ten commandments for ecosystem-based fisheries scientists. *Fisheries*, 32, 217–233.

Frank, K.T., Petrie, B., Choi, J.S. & Leggett, W.C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308, 1621–1623.

Frank, K.T., Pertrie, B., Shackell, N.L. & Choi, J.S. (2006). Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecol. Lett.*, 9, 1096–1105.

Fromentin, J.M., Ernande, B., Fablet, R. & de Pontual, H. (2009). Importance and future of individual markers for the ecosystem approach to fisheries. *Aquat. Living Resour.*, 22, 395–408.

Fulton, E.A. (2010). Approaches to end-to-end ecosystem models. *J. Mar. Syst.*, 81, 171–183.

Fulton, E.A., Smith, A.D.M. & Johnson, C.R. (2003). Mortality and predation in ecosystem models: is it important how these are expressed? *Ecol. Model*, 169, 157–178.

Gaichas, S.K. & Francis, R.C. (2008). Network models for ecosystem-based fishery analysis: a review of concepts and application to the Gulf of Alaska marine food web. *Can. J. Fish. Aquat. Sci.*, 65, 1965–1982.

Gaichas, S.K., Aydin, K.Y. & Francis, R.C. (2010). Using food web model results to inform stock assessment estimates of mortality and production for ecosystem-based fisheries management. *Can. J. Fish. Aquat. Sci.*, 67, 1490–1506.

Garrison, L.P., Link, J.S., Kilduff, D.P., Cieri, M.D., Maffley, B., Vaughan, D.S. *et al.* (2010). An expansion of the MSVPA approach for quantifying predator-prey interactions in exploited fish communities. *ICES J. Mar. Sci.*, 67, 856–870.

Gleiss, A.C., Norman, B., Liebsch, N., Francis, C. & Wilson, R.P. (2009). A new prospect for tagging large free-swimming sharks with motion-sensitive data-loggers. *Fish. Res.*, 97, 11–16.

Grimm, V. & Railsback, S.F. (2005). *Individual-Based Modeling and Ecology*. Princeton University Press, Princeton.

Halley, J.M. (1996). Ecology, evolution and 1/f-noise. *Trends Ecol. Evol.*, 11, 33–37.

Hassell, M. (1966). Evaluation of parasite or predator responses. *J. Anim. Ecol.*, 35, 65–75.

Hixon, M.A. & Carr, M.H. (1997). Synergistic predation, density dependence, and population regulation in marine fish. *Science*, 277, 946–949.

Hixon, M.A. & Jones, G.P. (2005). Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology*, 86, 2847–2859.

Holling, C.S. (1959). *The Components of Predation as Revealed by a Study of Small Mammal Predation of the European Pine Sawfly. Canadian Entomologist*, 91, 293–320.

Hollowed, A.B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P. *et al.* (2000). Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES J. Mar. Sci.*, 57, 707–719.

Hollowed, A. B., Aydin, K.Y., Essington, T.E., Ianelli, J.N., Megrey, B.A., Punt, A.E. *et al.* (2011). Experience with quantitative ecosystem assessment tools in the northeast Pacific. *Fish Fish.*, 12, 189–208.

Hunt, G.L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R.D., Napp, J.M. *et al.* (2002). Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Res. PT II*, 49, 5821–5853.

Ives, A.R., Dennis, B., Cottingham, K.L. & Carpenter, S.R. (2003). Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.*, 73, 301–330.

Jeschke, J.M., Kopp, M. & Tollrian, R. (2002). Predator functional responses: discriminating between handling and digesting prey. *Ecol. Monogr.*, 72, 95–112.

Jurado-Molina, J. & Livingson, P.A. (2002). Climate-forcing effects on trophically linked groundfish populations: implications for fisheries management. *Can. J. Fish. Aquat. Sci.*, 59, 1941–1951.

Keeling, M.J., Wilson, H.B. & Pacala, S.W. (2000). Reinterpreting space, time lags, and functional responses in ecological models. *Science*, 290, 1758–1761.

Kinzey, D. & Punt, A.E. (2009). Multispecies and single-species models of fish population dynamics: comparing parameter estimates. *Nat. Res. Model.*, 22, 67–104.

Kishi, M.J., Kashiwai, M., Ware, D.M., Megrey, B.A., Eslinger, D.L., Werner, F.E. *et al.* (2007). NEMURO - a lower trophic level model for the North Pacific marine ecosystem. *Ecol. Model*, 202, 12–25.

Kitagawa, T., Kimura, S., Nakata, H. & Yamada, H. (2004). Diving behavior of immature, feeding Pacific bluefin tuna (*Thunnus thynnus orientalis*) in relation to season and area: the East China Sea and the Kuroshio-Oyashio transition region. *Fish. Oceanogr.*, 13, 161–180.

Koen-Alonso, M. & Yodzis, P. (2005). Multi-species modeling of some components of northern and central, Patagonia, Argentina. *Can. J. Fish. Aquat. Sci.*, 62, 1490–1512.

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Kristiansen, T., Vikebø, F., Sundby, S., Huse, G. & Fiksen, Ø. (2009). Modeling growth of larval cod (*Gadus morhua*) in large-scale seasonal and latitudinal environmental gradients. *Deep-Sea Res. II*, 56, 2001–2011.

Laundre, J.W. (2010). Behavioral response races, predator-prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. *Ecology*, 91, 2995–3007.

Levin, S.A. (1990). *Physical and Biological Scales, and Modelling of Predator-Prey Interactions in Large Marine Ecosystems*. AAAS Press, Washington, D.C.

Levin, S.A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73, 1943–1967.

Link, J.S. (2010). *Ecosystem-Based Fisheries Management: Confronting Trade-Offs*. Cambridge University Press, Cambridge, UK.

Logan, J.D. & Wolesensky, W. (2007). An index to measure the effects of temperature change on trophic interactions. *J. Theor. Biol.*, 246, 366–376.

Mackenzie, B.R., Miller, T.J., Cyr, S. & Leggett, W.C. (1994). Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnol. Oceanogr.*, 39, 1790–1799.

McDonald, A.D, Little, L.R., Gray, R., Fulton, E., Sainsbury, K.J. & Lyne, V.D. (2008). An agent-based modelling approach to evaluation of multiple-use management strategies for coastal marine ecosystems. *Math. Comput. Simulat.*, 78, 401–411.

Melbourne, B.A. & Chesson, P. (2006). The scale transition: scaling up population dynamics with field data. *Ecology*, 87, 1478–1488.

Mello, L.G.S. & Rose, G.A. (2005). Seasonal growth of Atlantic cod: effects of temperature, feeding and reproduction. *J. Fish Biol.*, 67, 149–170.

Moustahfid, H., Link, J.S., Overholtz, W.J. & Tyrrell, M.C. (2009). The advantage of explicitly incorporating predation mortality into age-structured stock assessment models: an application for Atlantic mackerel. *ICES J. Mar. Sci.*, 66, 445–454.

Moustahfid, H., Tyrrell, M.C., Link, J.S., Nye, J.A., Smith, B.E. & Gamble, R.J. (2010). Functional feeding responses of piscivorous fishes from the northeast US continental shelf. *Oecologia*, 163, 1059–1067.

Mueter, F.J. & Megrey, B.A. (2006). Using multi-species surplus production models to estimate ecosystem-level maximum sustainable yields. *Fish. Res.*, 81, 189–201.

Murdoch, W.W. (1969). Switching in general predators: experiments on predator specificity and the stability of prey populations. *Ecol. Monogr.*, 39, 335–354.

Murdoch, W.W. & Stewart-Oaten, A. (1989). Aggregation by parasitoids and predators - effects on equilibrium and stability. *Am. Nat.*, 134, 288–310.

Murdoch, W.W., Avery, S. & Smyth, M.E.B. (1975). Switching in predatory fish. *Ecology*, 56, 1094–1105.

Nason, G. (2008). *Wavelet Methods in Statistics with R*. Springer-Verlag, New York.

Ney, J.J. (1990). Trophic economics in fisheries - assessment of demand-supply relationships between predators and prey. *Rev. Aquat. Sci.*, 2, 55–81.

O'Brien, W.J. (1979). The predator-prey interaction of planktivorous fish and zooplankton. *Am. Sci.*, 67, 572–581.

Okuyama, T. (2009). Local interactions between predators and prey call into question commonly used functional responses. *Ecol. Mod.*, 220, 1182–1188.

Papastamatiou, Y.P., Meyer, C.G. & Holland, K.N. (2007). A new acoustic pH transmitter for studying the feeding habits of free-ranging sharks. *Aquat. Living Resour.*, 20, 287–290.

Pascual, M. & Levin, S.A. (1999). From individuals to population densities: searching for the intermediate scale of nontrivial determinism. *Ecology*, 80, 2225–2236.

Plagányi, E.E. (2007). Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper No. 477 FAO, Rome.

Rastetter, E.B., King, A.W., Cosby, B.J., Hornberger, G.M., O'Neill, R.V. & Hobbie, J.E. (1992). Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. *Ecol. Appl.*, 2, 55–70.

Rindorf, A. & Gislason, H. (2005). Functional and aggregative response of North Sea whiting. *J. Exp. Mar. Biol. Ecol.*, 324, 1–19.

Rindorf, A., Gislason, H. & Lewy, P. (2006). Prey switching of cod and whiting in the North Sea. *Mar. Ecol. Prog. Ser.*, 325, 243–253.

Rose, K.A., Rutherford, E.S., McDermot, D.S., Forney, J.L. & Mills, E.L. (1999). Individual-based model of yellow perch and walleye populations in Oneida Lake. *Ecol. Monogr.*, 69, 127–154.

Ruel, J.J. & Ayres, M.P. (1999). Jensen's inequality predicts effects of environmental variation. *Trends Ecol. Evol.*, 14, 361–366.

Sainsbury, K.J., Punt, A.E. & Smith, A.D. (2000). Design of operational management strategies for achieving fishery ecosystem objectives. *ICES J. Mar. Sci.*, 57, 731–741.

Sanford, E. (1999). Regulation of keystone predation by small changes in ocean temperature. *Science*, 283, 2095–2097.

Shin, Y.-J. & Cury, P. (2004). Using a individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Can. J. Fish. Aquat. Sci.*, 61, 414–431.

Sih, A. (2005). Predator-prey space use as an emergent outcome of a behavioral response race. In: *Ecology of Predator-Prey Interactions* (eds Barbosa, P. & Castellanos, I). Oxford University Press, New York, pp. 240–255.

Sims, D.W., Queiroz, N., Doyle, T.K., Houghton, J.D.R. & Hays, G.C. (2009). Satellite tracking of the World's largest bony fish, the ocean sunfish (*Mola mola* L.) in the North East Atlantic. *J. Exp. Mar. Biol. Ecol.*, 370, 127–133.

Sissenwine, M.P. (1984). *Why do Fish Populations Vary?* Exploitation of Marine Communities, Berlin.

Solomon, M.E. (1949). The natural control of animal populations. *J. Anim. Ecol.*, 18, 1–35.

Teschner, E.C., Kraus, G., Neuenfeldt, S., Voss, R., Hinrichsen, H.-H. & Köster, F.W. (2010). Impact of hypoxia on consumption of baltic cod in a multispecies stock assessment context. *J. Appl. Ichthyol.*, 26, 836–842.

Tyrrell, M.C., Link, J.S. & Moustahfid, H. (2011). The importance of including predation in fish population models: implications for biological reference points. *Fish. Res.*, 108, 1–8.

Urban, D.L. (2005). Modeling ecological processes across scales. *Ecology*, 86, 1996–2006.

Walters, C.J. & Kitchell, J.F. (2001). Cultivation/depensation effects on juvenile survival and recruitment. *Can. J. Fish. Aquat. Sci.*, 58, 39–50.

Whipple, S.J., Link, J.S., Garrison, L.P. & Fogarty, M.J. (2000). Models of predation and fishing mortality in aquatic ecosystems. *Fish Fish.*, 1, 22–40.

White, J.W. (2011). Can inverse density dependence at small spatial scales produce dynamic instability in animal populations? *Theor. Ecol.*, 4, 357–370.

White, J.W., Samhouri, J.F., Stier, A.C., Wormald, C.L., Hamilton, S.L. & Sandin, S.A. (2010). Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale. *Ecology*, 91, 1949–1961.

Whitney, N.M., Papastamatiou, Y.P., Holland, K.N. & Lowe, C.G. (2007). Use of an acceleration data logger to measure diel activity patterns in captive whitetip reef sharks, *Triaenodon obesus*. *Aquat. Living Resour.*, 20, 299–305.

Wiens, J.A. (1989). Spatial scaling in ecology. *Funct. Ecol.*, 3, 385–397.

Wood, S. (2006). *Generalized Additive Models: An Introduction with R*. Chapman & Hall, London.

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