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Meeting report

Comparative analysis of marine ecosystems: workshop on predator–prey interactions

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Climate and human influences on marine ecosystems are largely manifested by changes in predator–prey interactions. It follows that ecosystem-based management of the world's oceans requires a better understanding of food web relationships. An international workshop on predator–prey interactions in marine ecosystems was held at the Oregon State University, Corvallis, OR, USA on 16–18 March 2010. The meeting brought together scientists from diverse fields of expertise including theoretical ecology, animal behaviour, fish and seabird ecology, statistics, fisheries science and ecosystem modelling. The goals of the workshop were to critically examine the methods of scaling-up predator–prey interactions from local observations to systems, the role of shifting ecological processes with scale changes, and the complexity and organizational structure in trophic interactions.

Keywords: predator–prey; food webs; scaling; marine ecosystems

1. INTRODUCTION

Predator–prey interactions in marine ecosystems are of critical importance in the structuring of marine communities and determining the health of the world's oceans. The cascading effects of overharvesting top trophic level predators and of environmental regime shifts on community structure of marine ecosystems are well documented (Pauly *et al.* 1998; Frank *et al.* 2007). Uncertainties in characterizing predator–prey interactions and how to scale them for use in state-of-the-art tactical and strategic tools, such as multi-species management and ecosystem models, make it particularly difficult to manage fisheries. The methodology of scaling-up from the observation of local scale processes to the ecosystem dynamics level has been especially problematic, as well as understanding

how the importance of processes may shift with the observational scale.

The workshop was held on 16–18 March 2010 in Corvallis, OR, USA and was inspired by the 50th anniversary of the publication of C. S. Holling's seminal paper on predator–prey interactions (Holling 1959). The workshop was attended by 41 invited scientists from eight countries. Participants included a careful blend of youth and maturity, including graduate students (nine), postdoctoral fellows (four) and more senior scientists at various stages of their careers. The areas of expertise ranged from individual behaviours to ecosystem models, with research settings including laboratory and field studies from northern seas to tropical reefs. The workshop was funded by the National Oceanic and Atmospheric Administration/National Science Foundation's (NOAA/NSFs) Comparative Analysis of Marine Ecosystem Organization (CAMEO) programme.

The workshop was structured into five modules focusing on predator–prey interactions involving fishes, either as predators or as prey. There were two plenary lectures in each module, one specifically on fish predator–prey interactions and the other providing a perspective from another viewpoint. After each module, there was a plenary discussion, followed by smaller breakout sessions. Morning sessions also included 'lightning' or 'icebreaker' talks (less than or equal to 3 min) that were meant to introduce new ideas and facilitate interaction.

2. WORKSHOP MODULES

The workshop modules included predator–prey functional and numerical responses, scaling, models and networks, ecosystems, and new technology/concepts. The following key questions were posed: (i) do functional and numerical responses regulate population abundance? (ii) do mechanisms of population regulation change across scales? (iii) how to scale up predator–prey interactions from local observations to ecosystems? and (iv) how do we go from mechanistic models of species interactions to management actions?

(a) *Functional and numerical responses*

Functional responses are based on observations of individuals feeding at different prey densities, usually leading to type 2 (decelerating) and type 3 (sigmoid) models. The type 3 model is important because it leads to density-dependence in the prey population. The workshop started with a review by Jeff Buckel of predator–prey trophic interactions including functional and numerical (which is here defined as having aggregative and reproductive components) responses. The complexities of functional responses and influences of various factors have been well documented in experimental studies. Applying the concept to the field has been difficult, given issues with estimating feeding responses and prey availability, and considering the various aspects of predator and prey dependence, alternate prey and switching (Abrams & Ginzburg 2000). Bill Sydeman and Stephani Zador provided perspectives different from that of fishes, discussing the conspicuous diversities in the behaviour of seabirds in their predator–prey interactions. Seabird morphological characteristics affect predator–prey interactions and foraging behaviour. Diving seabirds

are poor fliers and have higher energy requirements relative to surface/subsurface foraging seabirds with light bodies and long wings. Central-place foraging constraints in combination with varying life-history strategies also influence seabird predator–prey interactions. For example, seabirds with restricted foraging ranges or specialist diet are more sensitive to variation in prey availability than generalists or species with large foraging ambits. Fishes may have similar diversities, but thus far our observational capabilities have been limited.

Both the shape and parameterization of functional responses are extremely important for the predictions made by ecosystem models. Experimental evidence may support type 2 or type 3 functional responses, but large variation in the data caused by stochasticity in the feeding process frequently makes it difficult to choose among alternative models. This problem is often aggravated by sparse observations at the low end of the prey densities where the differences between responses are clearest. Data on functional responses often indicate an inverse relationship between density and mortality (depensatory relationship), whereas analyses of mortality often indicate that predation risk should increase with density (compensatory relationship). This incongruity may be caused by aggregative responses. When type 3 functional response relationships are found, they usually regulate density only within a narrow range of prey densities, although different predators may forage for prey at different scales. The aggregative response should be a focus of further investigation. Predators use a variety of clues to find patchy prey. Among them are consistent habitat features such as fronts and eddies, and olfactory and visual cues. There was a general consensus that more understanding of predator search and social behaviour and prey responses to predators is desirable.

(b) *Scaling*

Scaling emerged as a critical question in ecology in the 1980s, yet other than the concept of ‘keeping scale in mind’, it seems progress has not matched its importance in marine trophic studies. How to match observation scale to process, how do processes change as scale changes and the role of spatial heterogeneity and domains of scale are difficult questions facing ecologists. Some of this complexity has been addressed as the problem of averaging local and nonlinear ecological processes over time and space. Functional responses constitute one of the best documented examples of such processes in natural systems. Göran Englund presented a state-of-art talk on the methods for scaling-up predator–prey interactions from local functional responses to system-level population dynamics. Because predator–prey responses typically depend on local densities and habitats, translating this functional response to larger systems requires that both variance and covariance in predator and prey distribution are accounted for. This can be achieved using the technique of moment approximation (Bergström *et al.* 2006). Will White presented empirical evidence for prey behaviour leading to such nonlinear scaling using examples from

coral reef fishes. Behavioural arms races between predators and prey can produce spatial heterogeneity in predator–prey interactions, including predators employing hierarchical or fractal prey search behaviours and prey avoiding high-risk locations. However, disentangling these behavioural mechanisms from confounded environmental factors remains an important challenge.

The applicability of nonlinear scaling theories to fisheries data and management generated much discussion. Because dynamics of whole populations can emerge as small-scale processes combined over larger scales, the scale of ‘process resolution’ may be different from actual sampling scales. For example, nonlinear scaling can predict whole population stability from local covariance in the distribution of predators and prey. In this case, assessing covariance might require sampling at scales that differ from those of underlying predator–prey responses. The applicability of qualitative predictions (e.g. stable equilibrium versus population cycles) to fisheries management was also questioned, given important data requirements to control for uncertainty and for dependence upon confounding environmental effects.

(c) *Models of predator–prey interactions*

Predator–prey dynamics are represented in different ways in various fisheries models whether they are heuristic, tactical or strategic models. A fair number of these models require information on the functional response of predators, while other cases need information on diet composition. Jason Link gave an overview of fisheries models ranging from single-species management to end-to-end ecosystem models, and the data requirements of each. An important distinction among models is their heuristic, tactical or strategic objective. Geir Huse presented the modelling case study of cod–capelin interactions in the Barents Sea. He showed how the cold polar front acted as a refuge from predators, and demonstrated the importance of movement rules in modelled outcomes.

The scale of predator–prey interactions in many management models is generally system-wide and centred on either annual or seasonal consumption rates. Spatial homogeneity is usually assumed, or at least spatial heterogeneity is represented the same way every year. Large ecosystem models might incorporate submodels that link processes happening on different scales simultaneously; that is, a hierarchical approach (Fauchald & Tveraa 2006). We anticipate that multi-species assessment models will become more important over time. Currently, there are conflicts with agencies and stakeholders over the differences with traditional single-species assessment models.

A general property of multi-species models is that they deliver more conservative estimates than single-species counterparts, making it difficult to gain acceptance among stakeholders and managers. Another issue with predator–prey models that hampers their acceptance is the perception that the models are generally data hungry and the necessary data are sometimes lacking and expensive to obtain. In reality, an ecosystem-based approach will incur extra costs to

manage fisheries. There was a broad consensus that multi-species models, be they pure interaction, network or energy-balancing models, are a cornerstone of every ecosystem-based management approach. They are useful for strategic questions, such as the effects of overfishing non-target species or destruction of habitat, and other contextual and supportive information that cannot be derived by single-species models. Furthermore, different descriptions of the food web provided by different models can help identify key interactions. A main conclusion from the discussion was that a multi-model or ‘ensemble’ approach is necessary, as demonstrated in climate studies.

(d) *Ecosystems and fisheries management*

This module was an opportunity to present case studies of predator–prey interactions in different ecosystems and their link with fisheries management. Jim Kitchell talked about the strategic use of ecosystem models involving trade-offs between changes in management strategies and effects on the billfish/tuna/turtle complex of species. George Rose presented a perspective on managing predator–prey systems off the Newfoundland/Labrador coast in the wake of the collapse of the northern and other cod stocks. This system is currently managed using single-species approaches, although predator–prey relationships are considered. For example, the tight coupling between cod and capelin stocks is well recognized and there is concern about growing harp seal numbers (now 7 million). Rebuilding of cod stocks seems particularly dependent on predator–prey relationships, but also on fishing levels and ocean climate. Ken Frank discussed the predator–prey system of the Scotian Shelf of Canada demonstrating the need for community and ecosystem approaches for understanding why fisheries collapse or persist, and why collapsed fisheries recover more slowly than expected. The overfishing of cod had propagating effects through the food chain, and the slow recovery of cod has revealed a weakness in our understanding of the marine ecosystem. The removal of top predators may promote a ‘role reversal’, where the predator early life stages become the prey of lower trophic level species after their release from predation.

Management of human interactions in marine ecosystems is possible, but ecosystem engineering often has unpredictable and unintended consequences. Top-down management of marine ecosystems (such as selectively removing predators) is often socially unacceptable, whereas a bottom-up approach building on production estimates of lower trophic levels can be informative. A common experience is that fisheries models can answer the ‘what’ but not the ‘why’ questions. Ecosystem models are needed to develop management strategies that take into account the broader aspects of ecosystem structure and functioning including biodiversity, conservation, bycatch and trophic cascades.

(e) *New developments and methods*

Jim Kitchell described fish predator–prey interactions as ‘the art of the possible’, where in reality you do the best with what you have and know in a difficult

situation. With that in mind, we can considerably improve our knowledge and ecological toolbox. Kung–Sik Chan discussed new mathematical statistics approaches, using wavelet analysis, that may be useful for dealing with spatial heterogeneity and scaling effects in predator–prey functional responses. Kun Chen presented a cellular automata model that was developed to understand scaling effects of functional responses in the arrowtooth flounder–pollock interaction in the eastern Bering Sea. Tim Essington provided a review of data needs and theoretical development to foster improved understanding and prediction of predator–prey dynamics in marine ecosystems. Central to these needs is an improved understanding of how fixed and dynamic spatial structures that characterize marine ecosystems act to govern predation. There is a tremendous opportunity for model development that explicitly incorporates size structure and physiology in larger food web models. Most important was the development of methods to measure and predict interaction strengths in food webs. Finally, fishing and predation are both sources of fish mortality and should share a common conceptual framework in the future.

3. CONCLUDING REMARK

After the workshop, Göran Englund noted: ‘There is an interesting tension between theory, applied ecology and management.’ This tension results from different approaches related to heuristic, tactical and strategic objectives of scientists working at different scales. Continued dialogue among us will enhance both our understanding and management of organisms and ecosystems.

We thank the participants of the workshop for their contributions. A complete list of participants can be found on the web page <http://bioweb.coas.oregonstate.edu/~ciannellilab/cameo/> constructed by J. Rohde. We thank the CAMEO programme of NOAA/NSF for funding and COAS of Oregon State University for hosting the workshop.

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