

## Introduction

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Marine ecosystems represent a rich assemblage of co-evolved species that have complex, non-linear dynamics. This has made them difficult to manage and the recent record of exploitation of marine ecosystems suggests that the mechanisms currently in place for their management are inappropriate for sustained and intensive exploitation (Pauly *et al.* 2002). Fisheries science has developed sophisticated single- and multispecies approaches to modelling resource dynamics but these have shown mixed success when used to advise about the regulation of exploitation levels. However, it is commonly acknowledged that attempting to model whole or partial ecosystems also has limited utility because the demands this has for data and knowledge about the system far outweigh the financial, logistical and intellectual resources available (Yodzis 1998). Although some computer-intensive approaches are currently being attempted<sup>1</sup>, their ability to improve predictions of the dynamics of marine ecosystems appears to be quite limited.

This whole- or partial-systems approach to modelling marine ecosystems is driven by a belief in the connectivity of predator–prey processes within ecosystems and the conviction that, with appropriate parameterization, the behaviour of these systems can be predicted within bounds of confidence that are sufficiently narrow to convince us that the investment in the modelling effort has been useful. However, to date the cost–benefit analysis of these approaches has not been computed and the few simple systems in which the approach has been applied soon run into trouble. Whole-system approaches to modelling have been largely discredited because there is always insufficient information for adequate parameterization (Plaganyi

<sup>1</sup> The most recent version of an ecosystem-level model to be tested is known as GADGET.

& Butterworth 2004). The move towards the partial-system (or ‘minimum realistic’, e.g. Punt & Butterworth 1995) approach leads to a necessity to define a ‘horizon of relevance’, meaning that components of the ecosystem that lie beyond this horizon are deemed to be of sufficiently low relevance to the focus of management that they will not have an important influence on the outcome of the scenarios being modelled (Schweder (Chapter 21 in this volume)). However, these partial-system models are challenged by the problems of diffuse effects (Yodzis 2000) which mean that the horizon of relevance often lies well beyond our data resources (Plaganyi *et al.* 2001). The problems that dog the whole-system approach to modelling marine ecosystems therefore also dog the partial-system approach.

Like the ‘event horizon’ in cosmology, we contend that the horizon of relevance in ecosystem modelling is an insurmountable boundary that severely limits the extent to which we will ever be able to model rationally constrained management scenarios for biological resources in the oceans (and perhaps in all complex ecosystems). This is a fairly gloomy outlook but there may be some hope for the future. This hope comes from two directions: one involves the potential/possibility that ecosystem dynamics could be constrained to a narrow set of rules similar to those involved in, or associated with, the allometry of individual organisms (Garlaschelli *et al.* 2003); the other direction, which is the one that is explored in this book, is to reject the reductionist approaches to ecosystem modelling by establishing ecosystem boundaries and only examining ecosystem dynamics at these boundaries. This is like attempting to understand the crustal dynamics of the Earth by only looking at surface features. It may be possible to measure some of the critical outputs of the ecosystem in a way that provides an insight into the internal dynamics and that could lead to some broad predictions about the behaviour of the ecosystem, especially when correlated with known inputs. In biogeochemical terms the inputs and outputs of an ecosystem involve primary production and the products of respiration plus the sequestration of organic carbon, in this case as sediment on the seabed. However, in ecological terms, the outputs could be seen as the terminal links in food chains, sometimes also known as the top of the food chain. Moreover, it may also be possible to understand the outputs from the terminal links in the food chains without the necessity of understanding the intermediate linkages between them and the physical-forcing processes that are the inputs driving the food-chain dynamics. Many who like to model the internal dynamics of these systems will consider this to be a leap of faith but, where the intermediate dynamics have complex properties, there may be no choice.

In practical terms, this means using the species at the top of marine food chains as our indicators of ecosystem status and performance. We refer to these species as ‘top predators’ but this is synonymous with ‘upper-trophic-level predators’. For most purposes here we refer to top predators as pinnipeds (true seals, sea lions, fur seals and walrus), seabirds, cetaceans and some large predatory fish. In general, they are species beyond the level of secondary consumers. This approach has advantages and disadvantages as outlined below.

#### *Advantages*

- (1) By definition, top predators are downstream, in terms of energy flow, of changes within an ecosystem. This means that changes in ecosystem structure that also affect the energy flows through the system are likely to be reflected in changes at the top of food chains.
- (2) Top predators often exploit marine resources at similar spatial and temporal scales to those used by man, thus increasing the potential for competition. It is a truism of marine-ecosystem management that it is only possible to manage the activities of man; however, the data we collect about the marine ecosystem – data that come from these activities – are collected at similar spatial and temporal scales to those that are relevant to understanding how resource variability is likely to affect other predators that also forage at the same scales.
- (3) Many predators are accessible during important parts of their life histories mainly because they have terrestrial breeding seasons. This also constrains their foraging ranges because of their need to return regularly to the breeding site. Not only does this make it relatively easy to provide consistent indices of population sizes, it also allows estimation of regional productivity from the productivity of the predators themselves. This advantage applies only to seabirds and pinnipeds, and has the effect of narrowing the focus of interest in using top predators as measures of ecosystem outputs to these groups. This bias is reflected in many of the following chapters.
- (4) Most of the species used for measuring the outputs from ecosystems command a high level of public interest and studies of them are likely to attract support over the long time periods needed to measure these ecosystem outputs.

#### *Disadvantages*

- (1) Measuring the changes in top-predator populations or in the behaviour, performance or productivity of predators does not necessarily titrate the effects of different management interventions within ecosystems.

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- (2) Top-predator responses are not necessarily predictive so they are difficult to use in the context of classical fisheries science to set catch levels, although there may be some circumstances where they can help define the broad boundaries of catch limits (e.g. Boyd 2002).
- (3) Not all situations in which there is a need for management have an appropriate community of predators available for study. In fact, predators appropriate for use in the context of fisheries management are mainly confined to temperate and subpolar regions and even then they are likely to be of most relevance to coastal and shelf-seas management.
- (4) By their very nature, top predators may be several trophic links remote from the main drivers of change in ecosystems, especially if these drivers affect the distribution and abundance of primary production. This could lead to attenuation of signals from variation in inputs to the ecosystem, either through the effects of physical forcing or through the effects of management actions.
- (5) Responses of different predators to the same management or environmental drivers may differ, not only in terms of magnitude but even in some cases in the direction of response. In reality, many predator studies are of single species – or at best groups of similar predators – and this makes it difficult to assess consistency of responses. Ideally the emphasis should be on integrated multispecies approaches but securing funding for this is often problematic.

This book sets out to explore the hypothesis that top predators can be used in a whole-system approach to managing marine ecosystems. In some circumstances these predators may also provide information relevant to the management of specific resources. The emphasis on this hypothesis does not preclude other approaches or imply that measuring predator responses will always be informative. However, such an approach could potentially be part of the set of measures, insights and interpretations used within sophisticated management systems. Such an integrated approach is particularly useful where there is a need to balance the competing demands for adequate precaution in setting resource exploitation levels against the economic and social demands to increase these levels of exploitation still further. It takes the focus of attention away from the resource being managed and places it onto the ecosystem in a way that is comprehensible to most components of the decision-making hierarchy of the management structure and to the public.

The book represents a collection of case studies and reviews of top predators as indicators of marine-ecosystem dynamics. Many of these studies are

syntheses of other published work because the intention was to provide an overview of the subject that would stretch the boundaries of this field to a non-specialist audience in marine science and resource management. The results of some of these studies are already being incorporated explicitly into resource-management procedures. The studies are weighted towards the North Sea system because we considered that it was important to develop a reasonably complete description of the state of knowledge within one particular system. To provide contrast we have also included several chapters on the krill-based systems of the Southern Ocean. Consideration is also given to the northwest Atlantic, Arctic, North Pacific and the Barents Sea. However, we emphasize that our intention is not to provide a comprehensive survey of the topic as the use of predators to provide information for management is present in some form within all of the most productive fisheries management zones in the world. One particular example that we have not illustrated is that of the California Current, for which a substantial body of work is available (Sydeman *et al.* 2001).

A consistent underlying theme within the book is the need to view whole ecosystems as the products of an evolutionary process (Fowler & MacMahon 1982) which has been challenged in very recent times by a new, powerful, adaptable and highly selective predator in the form of man (Trites *et al.* (Chapter 2 in this volume)). The consequences of this and other natural forcing of ecosystem change – not only for the absolute abundance of species but also for their genetic structure, size structure and nutrient turnover – are likely to have caused irreversible changes in ecosystems, some of which may be evident in the changes within top-predator populations (Iverson *et al.* (Chapter 7) and Wolf *et al.* (Chapter 19) in this volume).

A challenge to observing this process using top predators appears to be the non-linearity of responses shown by predators to changes in food supply. Several authors have emphasized the importance of these non-linearities (see chapters by Croxall (Chapter 11), Furness (Chapter 14) and Constable (Chapter 22) in this volume). Empirical observation shows that as resource availability declines there can be little change in predator population productivity up to a critical point, after which declines can occur quickly. The reasons for these non-linearities probably relate to the ability of top predators to switch between different groups of prey (Asseburg *et al.* (Chapter 18 in this volume)) and in their use of rule-based approaches to foraging which are adaptive to changes in food distribution and abundance (Mori & Boyd 2004). These largely behavioural adjustments can enable individuals to maintain high feeding rates even at relatively low levels of food availability.

Many of the predators considered in the range of studies represented in this book appear to depend to a large extent upon a small range of prey species. These are usually represented by planktivorous omnivores, mainly small fish species but also crustaceans. In the case studies described here, sandeels (*Ammodytes* spp.) and krill (*Euphausia*) feature prominently; in other ecosystems these are replaced by species like sardines (e.g. *Sardinops sagax*), anchovies (e.g. *Engraulis ringens*) or capelin (e.g. *Mallotus villosus*) (e.g. Chavez *et al.* 2003). Many of these are keystone species in their ecosystems. While many predator species show a wide-ranging diet with complex multispecies functional responses (Asseburg *et al.* (Chapter 18 in this volume)), these results suggest that energy flow to top predators may be channelled mainly through a narrow range of species involving relatively high energy-transfer efficiencies.

Although the generality of this conclusion will need further study, its implications for using top predators to indicate change in ecosystems are wide-ranging. Firstly, top predators may be less remote, and therefore more responsive, than first thought to physical drivers, such as those giving rise to decadal ocean-climate oscillations in the Atlantic and Pacific Oceans, as well as in the Southern Ocean (Trathan *et al.* (Chapter 3 in this volume)). This is because there are fewer steps along the food chain than expected, thus reducing the potential for signal attenuation. Secondly, they may be potent indicators of general energy flow through marine ecosystems because they are dependent upon the omnivorous keystone species so that large-scale changes in the dynamics of energy flow are likely to affect the top predators. Thirdly, they are less likely to be direct competitors with man than first thought because they are likely to prey mainly at trophic levels below that normally targeted by fisheries (Greenstreet (Chapter 15 in this volume)). However, recent trends in fishing suggest that fisheries are beginning to have an impact on the same trophic levels as the top predators (Pauly *et al.* 1998).

To an extent, the principle is now accepted that top predators in marine ecosystems are responsive to changes in their environment and that these responses can be measured and used to inform management. Now, the focus is on attempting to understand the observed dynamics of top predators in terms of changes further down in the food chains.

The story of the North Atlantic fulmar (*Fulmarus glacialis*) illustrates this shift (Thompson (Chapter 10 in this volume)), as do the communities of predators foraging on krill from South Georgia in the Southern Ocean and on sandeels in the North Sea. The species present in these communities appear to forage at different spatial scales and capitalize on different prey

distributions in the water column (Camphuysen *et al.* (Chapter 6) and Scott *et al.* (Chapter 4) in this volume). A wide range of variables can be measured cheaply and consistently across these predators, including indicators of breeding success, population growth, and individual growth and survival. All these variables have the potential to be used individually or as groups to examine the dynamics of prey populations, even to the extent that they can be used in specific circumstances to sample the age or size structure of prey populations (Reid *et al.* (Chapter 17 in this volume)).

The methods used to measure most variables in many species of seabirds and seals are well established and this has resulted in sets of data collected using consistent methodologies over several decades (e.g. Croxall (Chapter 11 in this volume)). These types of datasets are beginning to provide the foundation for approaches to combining indices from top predators that integrate across those predator species that operate at similar spatial and temporal scales among species (see Croxall (Chapter 11) and Constable (Chapter 22) in this volume). We are on the verge of developing sophisticated approaches to target management advice based on predator performance, approaches that can predict how the physical dynamics of the oceans may affect foraging success in these top predators (Scott *et al.* (Chapter 4) and Trathan *et al.* (Chapter 3) in this volume).

An important element in developing a predictive approach to the response of predators to the dynamics of their food supply is provided by modelling predator behaviour from first principles (Ollason *et al.* (Chapter 20 in this volume)). Apart from the few occasions when it is possible to relate predator responses directly to prey dynamics, models fitted to predator behaviour may be the only way of understanding the form of the functions that relate predator responses to prey dynamics. It seems to us that it is vital to know as much as possible about the non-linear form of these functions through a combination of modelling and targeted experimental studies. The different approaches to modelling are illustrated by the predictive models of Ollason *et al.* (Chapter 20 in this volume) and the *post hoc* statistical fitting to data of Wolf *et al.* (Chapter 19 in this volume). The approach taken by Enstipp *et al.* (Chapter 13 in this volume), which models the energy budgets of predators, also provides an analysis that points to the range of environmental productivity required to sustain predators.

Current systems used in the management of marine bioresources are adapting slowly to the need to include information from predators. Two contrasting approaches are illustrated by Constable (Chapter 22) and Tasker (Chapter 24 in this volume). In general, traditional fisheries management approaches cannot be easily adapted to include information from predators

but Constable points us in a direction that could lead to appropriate integration; in addition, the scenario models described by Schweder (Chapter 21 in this volume) for the Barents Sea are beginning to develop a framework for integrating top-predator information into fisheries management procedures. Although there are moves to include these approaches within some fisheries management procedures, especially in the Southern Ocean, it seems likely that the systems involving most northern-hemisphere fisheries, where biology is tensioned more strongly against social and economic issues, will take much longer to fall into line. Here, as Tasker points out, a less sophisticated and more pragmatic system of thresholds and targets for predator populations is appropriate and more likely to gain acceptance. It has been in the context of the North Sea that fisheries management targets have been adjusted based upon the breeding performance of the black-legged kittiwake (*Rissa tridactyla*). This approach may represent the kind of operational decision rule that is required in the future for integrating the traditional single-species approach to management of a fish population with information for top predators that are also dependent on that resource.

Finally, the creation of marine protected areas based upon the distribution of marine predators is a management procedure that has a wider-ranging effect upon ecosystem sustainability than might be possible with procedures targeted at the exploited components of an ecosystem (Hooker (Chapter 23 in this volume)). This is underpinned by the principle that maintaining healthy top-predator populations is closely linked with maintaining a healthy ecosystem.

The current research effort is providing a range of management techniques that are underpinned by a whole-system approach to bioresource management. This book represents a synthesis that reflects the state of the research field and is intended to provide managers, and those with interests in marine-resource management, with the materials necessary to understand what has been achieved to date. However, it is important to emphasize that the approach to marine-bioresource management advocated here is not an easy option and to be successful it will require targeted research in several key areas:

- (1) Coordinated data collection and management schemes like that developed for the Southern Ocean by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Agnew 1997, Constable (Chapter 22 in this volume)). That there is no coordinated system of data collection and management for pinnipeds within Europe is a reflection of the fractured nature of



marine-ecosystem research in the region, with competing national interests and funding structures driving the science agenda.

- (2) Greater intellectual input to the methods of integrating predator data into management structures is required, although a prerequisite of this is the provision of opportunity for integration through the development of appropriately open-minded management regimes.
- (3) Continuation and, where possible, enhancement of detailed process studies involving marine predators and their response to changes in food availability and, in some cases, investigation of the physical drivers of these changes.
- (4) Identification of the critical foraging and breeding habitat of marine predators as a prerequisite to identifying regions that can be protected not only for the conservation of the predators themselves but also the ecological relationships that help to sustain them.

We hope that this book will illustrate that we are part of the way to achieving these objectives.

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