Beyond big fish: The case for more detailed representations of top predators in marine ecosystem models

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ABSTRACT

Seabirds and marine mammals are generally not well represented in marine ecosystem models, despite the important roles that these groups play in determining ecosystem dynamics. This is an important gap in model development, particularly for end-to-end ecosystem models, which are becoming increasingly important tools for fisheries and ecosystem based management and assessment. Examination of large-scale and widely-applied pelagic end-to-end ecosystem models indicates that representations of predators are currently best developed for fish groups. The methods for modelling seabirds and marine mammals on the other hand, are less well developed. This is potentially due to the challenges involved in data collection and in representing the complex life histories of many of these species. To examine the effect that different representations of higher trophic level predators might have on ecosystem model predictions, we developed a set of simple nested qualitative network models and examined their responses to perturbations. Responses differed between models across a range of trophic levels under a simple scenario for environmental change, highlighting that how predators are modelled can have implications for ecosystem-level predictions. We conclude with a discussion around potential approaches for developing more detailed representations of predator groups, and suggest incorporating dynamic energy budget theory in individual-based models to represent higher trophic level predators with more complex life histories.

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Contents

1. Introduction

Changing dynamics of top predators may signal lasting change in bottom-up forcing of marine ecosystems (e.g. Constable et al., 2014 for Antarctic ecosystems, Boaden and Kingsford, 2015 for tropical reefs). This is because life time performance of individuals is an integration of short term variability in the system, and for top predators is reflected in longer term trends as a result of their comparatively longer lives (Hindell et al., 2003; Travers

Table 1
Key life history and reproductive traits of seabirds and marine mammals that are challenging to represent in models but can be captured using a DEB-IBM approach.

Top predator traits	Implications for model (representations)
Delayed and intermittent reproduction	• Depending on the species there might be a significant diapause in the breeding cycle. • Not all species or even individuals will breed every year. Breeding is generally dependent on individual energy reserves allocated to reproduction, or could be dependent on environmental parameters in a selected year.

Distinct breeding behaviour of colony breeders	Colony breeders need to come on land for mating and raising their offspring.
	
	• Marine Mammals such as seals
	  • Return to the water after impregnation
	  • Females need to increase their food intake during pregnancy
	  • Females need to come on land for birth and fast during weaning.
	• Seabirds such as penguins
	  • Come on land to lay eggs and fast while brooding.
	  • Seabirds may swap roles between male and female over guard and crèche stages of breeding.
	  • Increased intake of food needs to be accounted for, for both sexes during the guard and crèche stages.
	• Seabirds, as income breeders (see below) need to forage while providing for their chicks and thus have limited foraging ranges.

Distinct breeding behaviour of wholly pelagic predators	Wholly pelagic predators, such as whales, may not feed for a period of time while they are moving to, or in breeding grounds. This means that, in a model, energy budgets may need to be managed both inside and outside a given model domain.
Capital vs. income breeders (Houston et al., 2007)	Patterns of food intake during pregnancy (or egg production) and lactation/provisioning are most easily represented using a DEB-IBM approach. • Capital breeders store energy for feeding offspring • Income breeders forage and feed offspring concurrently.
Prey selection behaviours	Many predators have the ability to switch prey under certain circumstances (e.g. Bedford et al., 2015). This allows them to maximise their energy intake, while minimising their energy expenditure (Watanabe et al., 2014; Bestley et al., 2015). While prey-switching can be represented functionally (Holling, 1965), DEB-IBMs provide more flexibility to represent prey selection behaviours.
Site fidelity (Arthur et al., 2015)	Some species, such as seals, exhibit strong site fidelity – which means that these individuals return to the same foraging grounds each year. This needs to be given consideration in models where environmental changes are represented spatially as this will have an effect on the available prey field to these individuals.

et al., 2007; Thompson et al., 2012). The slower response to change means that they may exert significant pressures on their environment and the ecosystem; directly through top down predation (Smetacek and Nicol, 2005; Sala 2006; Heithaus et al., 2008; Estes et al., 2011; Boaden and Kingsford, 2015; Kiszka et al., 2015), and also through indirect effects (Trathan et al., 2007; Estes et al., 2011; Ruppert et al., 2013; Constable et al., 2014; Heupel et al., 2014). Such effects may include behavioural avoidance by prey (Creel and Christianson, 2008; Heithaus et al., 2008; Kiszka et al., 2015), and facilitation of the recycling of nutrients, thereby enhancing carbon cycling (Atwood et al., 2015; Ratnarajah et al., 2016). There is also some evidence that predators can stabilise foodwebs, making these foodwebs more resilient to stress (Sala, 2006).

Despite the vital roles played by higher trophic level predators, these species are often not well represented in ecosystem models. This is particularly the case for seabirds and marine mammals whose complex life histories (Table 1), and as a consequence allocation of energy from prey, are difficult to model. Factors to consider when modelling these species are the dislocation of breeding sites from main foraging areas, combined with investment of energy in latent reproductive capacity, as well as parental care. These factors can contribute to complex predator-prey relationships which may not be easily represented through simple mortality rates for lower trophic levels. This is important as such changes in energetics and behaviour of predators may play crucial roles in their demand for food, and their allocation and use of acquired energy. Complex representation of higher trophic level species are not needed in all models, particularly if addressing specific questions in well-defined scenarios (Starfield, 1997; Essington and Plagányi, 2014); indeed, simplified representations can lead to greater computational efficiency (see e.g. Fulton et al., 2003a; Essington and Plagányi, 2014; Punt et al., 2016). However, a process is needed to check whether conclusions are likely to be robust to the represen-

tation of these predators; in other words, when might complexity matter?

Here, we examine the importance of including detailed and realistic representations of seabirds and marine mammals in marine ecosystem models, with a focus on end-to-end ecosystem models. We use a broad literature survey of commonly used approaches for representing higher trophic level predators in ecosystem models (Fulton, 2010; Murphy et al., 2012; Young et al., 2015; see Section 2), highlighting examples of model frameworks which implement more detailed representations of top predators (Table 2; Fulton et al., 2004; Gray et al., 2006; Maury, 2010; Fiechter et al., 2016). We use a qualitative network model to demonstrate how a simplified representation of top predators may limit perspectives on ecosystem dynamics (Dambacher et al., 2002; Melbourne-Thomas et al., 2012; see Section 3). Taking into consideration the key life history and reproductive traits of seabirds and marine mammals that are challenging to represent in models (Table 1), we suggest using individual-based models (IBMs) that incorporate dynamic energy budget (DEB) theory (Kooijman, 2010, DEB-IBMs, Martin et al., 2012; see Section 4), as a suitable modelling tool (see also Constable, 2005 on energetic modelling approaches) for representing these traits in ecosystem models. Here, we use the term 'ecosystem model' when referring to general representations of ecological systems and the term 'end-to-end ecosystem model' for representations of the combined physical, chemical, biological and human systems (Fulton et al., 2003a; Fulton 2010; Rose et al., 2010; Shin et al., 2010; Murphy et al., 2012).

2. Representations of predators in marine ecosystem models

The approaches used for representing predator species in end-to-end ecosystem models vary widely; from closure terms for