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A foodweb model to explore uncertainties in the South Georgia shelf pelagic ecosystem

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ABSTRACT

Foodweb models provide a useful framework for compiling data on biomass, production, consumption and feeding relationships. They are particularly useful for identifying gaps and inconsistencies in the data, and for exploring plausible scenarios of change. We compiled data on the pelagic foodweb of the South Georgia shelf, which is one of the most intensively studied areas in the Southern Ocean. The data suggest that current average annual copepod production is three times that of Antarctic krill and that flying seabirds and fish are, respectively, responsible for 25% and 21% of local krill consumption. The most striking inconsistency was that estimated consumption of fish was 5 times their estimated production. We developed a static mass balance model of the foodweb representing one of many possible solutions to the inconsistencies in the data. The model included sufficient fish biomass to balance the original consumption estimate, and consequently fish became the main krill consumers. Nonetheless, only 74% of local krill production was consumed by predators, suggesting that there are additional mortality sources that we did not explicitly model. We developed further models to explore scenarios incorporating plausible climate-driven reductions in krill biomass. In scenarios with unchanged predator diets, an 80% reduction in krill biomass resulted in a 73% reduction in vertebrate biomass. However, when predators with diverse diets were able to switch to feeding on alternative zooplankton prey, total vertebrate biomass was maintained at current levels. Scenarios in which 80% of krill biomass was replaced with copepod biomass required 28% more primary production because the estimated consumption rate of copepods is higher than that of krill. The additional copepod biomass did not alter the consequences for vertebrates. These scenarios illustrate the wide range of potential consequences of a shift from a krill to a copepod dominated system in a warming climate. They suggest that both maintenance and dramatic reduction of vertebrate production are plausible outcomes, although the former requires major changes in predator diets.

1. Introduction

Antarctic krill, *Euphausia superba*, plays a major role in the pelagic marine foodweb on the South Georgia shelf (Atkinson et al., 2001; Murphy et al., 2007a). It is an important prey item for many vertebrate predators including demersal and pelagic fish, mammals, and seabirds (Croxall et al., 1997; Main and Collins, 2011; Reid and Arnould, 1996; Shreeve et al. 2009). Krill are also one of the main metazoan grazers of phytoplankton and therefore a major regulator of production and nutrient flows (Atkinson and Whitehouse, 2001; Schmidt et al., 2011; Whitehouse et al., 2009, 2011). In addition to these direct trophic interactions, krill might have indirect competitive interactions with other grazers. Observations at South Georgia suggest that high copepod abundance coincides with relatively low krill abundance (Atkinson et al., 1999). When krill are scarce, some ordinarily krill-feeding predators switch to carnivorous macroplankton which, in turn, feed mainly on copepods (Croxall et al., 1999).

The abundance of krill in the South Georgia shelf system is highly variable. This variability can include years of famine, such as the summer of 2008/09 when krill was virtually absent from the diets of many predators and there were no fishery catches (BAS unpublished data). Such events are almost certainly linked to climate variability. South Georgia is near the northern limit of krill's distribution, and the variability in its local and regional abundance is correlated with climatic indices (Murphy et al., 2007b; Whitehouse et al., 2008). These relationships, combined with decreases in krill recruitment and abundance within the Scotia Sea (Atkinson et al., 2004; Siegel and Loeb, 1995; Trivelpiece et al., 2011), have led to predictions that plausible

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climate change could remove most of the krill from the South Georgia shelf, causing a prolonged extension of the conditions observed in 2008/09 (Mackey et al., 2012; Murphy et al., 2007b).

Dramatic changes in the abundance of an important organism will inevitably affect the structure of the wider foodweb. Such changes could also affect critical aspects of foodweb operation including its resilience to further change, and therefore its ability to support ecosystem services including production of commercially harvested species, carbon cycling, and the biodiversity that underpins wildlife tourism. It is therefore important to understand the potential consequences of climate induced change for the structure and operation of the ecosystem.

The marine ecosystem around South Georgia is one of the most studied in the Southern Ocean. It was frequently surveyed during the *Discovery Expeditions* between 1928 and 1935 because of its importance to the whaling industry, and it is currently the focal area for many of the British Antarctic Survey's marine ecological studies. It would be valuable to bring the abundant available data together to produce a quantitative description of the ecosystem. A useful first step in this direction is to describe the foodweb. The widely used Ecopath foodweb modelling framework (Christensen and Pauly, 1992; Christensen and Walters, 2004) provides a useful template for compiling relevant data on biomass, rate processes, and feeding relationships. This is particularly useful for identifying gaps and inconsistencies in the data. Ecopath can also be used to model the propagation of change (induced, for example, by harvesting and climate) through the foodweb to identify plausible consequences.

This study develops a quantitative description of the South Georgia shelf pelagic foodweb with the particular aim of identifying major inconsistencies in the data and evaluating the trophic roles of krill and copepods. It also uses foodweb models to explore how changes in krill abundance might affect both zooplankton and vertebrate predators, and how these impacts might be modulated by flexibility in predator diets.

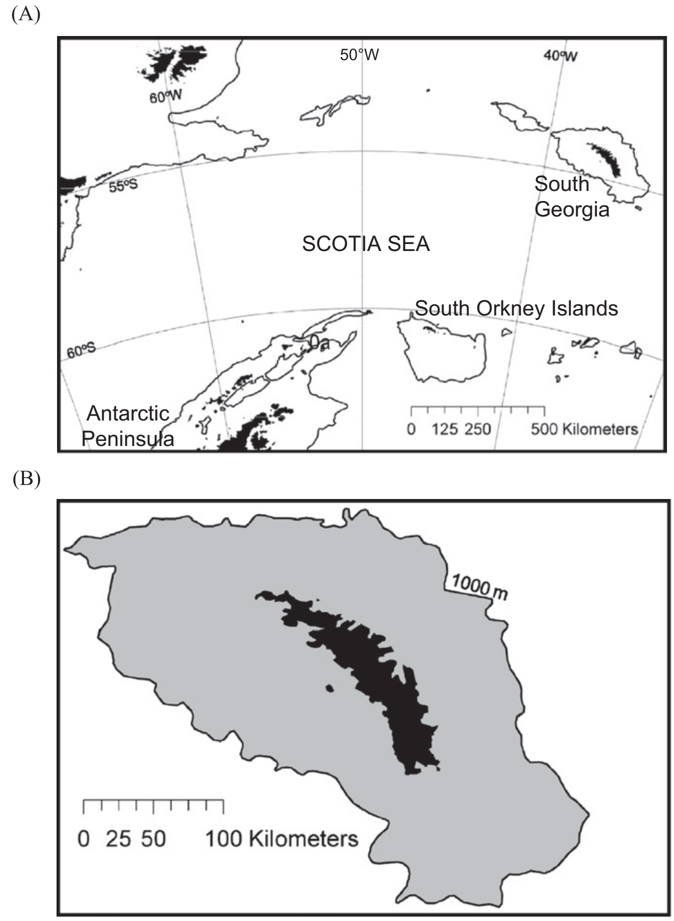

Fig. 1. The modelled area (South Georgia shelf to the 1000 m isobath) in the regional (A) and (B) local context.

2. Methods

2.1. Database

We developed a foodweb model to investigate how changes to the zooplankton might impact the abundant vertebrate predators concentrated around South Georgia. These predators and their prey interact with other larger ecosystems (including the Scotia Sea to the South and the Antarctic Circumpolar Current system) at a variety of scales (Murphy et al., 2007a). The South Georgia shelf pelagic system is a pragmatic scale to develop a foodweb model to address these questions, partly because many of the available data are more applicable to this system than to larger scales and partly because this system encloses both the breeding colonies of seabirds and seals on the South Georgia archipelago and the entire habitat of the shelf's demersal fish. The choice of scale and focus is reflected in the model structure including: the choice of functional groups, which are resolved to species level for many vertebrates but are more aggregated for invertebrates and basal groups; the approach to modelling interactions with neighbouring ecosystems, which is explained in detail below; and the inclusion of an aggregated general "*benthos*", which represents a boundary for the more explicitly modelled pelagic system.

We compiled available information on the pelagic foodweb of the South Georgia shelf to construct an Ecopath dataset. For the purposes of this study, the boundaries of this ecosystem are the shoreline of South Georgia and the 1000 m bathymetric contour, encompassing an area of 45,530 km^2 (Fig. 1). The dataset nominally represents the average state of the foodweb during the past decade.

Ecopath is a widely used framework for constructing internally consistent marine foodweb models (Christensen and Walters, 2004). It describes foodwebs in terms of the biomass, consumption, production rates and diets of species or life stages aggregated into functional groups on the basis of trophic similarity. These parameters are described in a consistent metric, which was wet mass km^{-2} in this case. Ecopath is used to produce mass-balance models that obey the logical constraint that the consumption of any trophic group cannot exceed production by that group over some appropriate time period, which was 1 yr in this case. Production can, however, exceed consumption and this difference is described in the "ecotrophic efficiency" (EE) parameter which we discuss later.

Following a review of the available information and consultation with the experts listed in the Supplementary Information (SI), we structured the model around 30 functional groups (Table 3). The vertebrates were grouped on the basis of taxonomy and similarity of adult diets, and invertebrates were aggregated on the combined basis of data availability and functional similarity. The names of these functional groups are given in italics throughout the text.

Compiling this information was a detailed process drawing on a range of sources (primary and grey literature, unpublished datasets, expert opinion, and proxies from other species and areas) and sometimes requiring subjective interpretation. Our summary of the available data is defensible but there is considerable uncertainty in this (and any pelagic foodweb dataset), which has not been possible to fully characterise. This could mean that there are alternative, equally defensible, values for many of our