

The importance of krill predation in the Southern Ocean

Philip N Trathan and Simeon L Hill

British Antarctic Survey, Madingley Road, Cambridge CB3 0ET

## **Abstract**

Antarctic krill is a major prey species for a diverse array of Southern Ocean predators. The amount of krill that predators consume, and how this changes over space and time, is a key issue in understanding both regional and circumpolar aspects of the Southern Ocean food-web. We assess current knowledge of consumption by the various predator groups, and the ecological processes through which krill and its predators influence each other. Knowledge has improved greatly over recent decades and has revealed a high level of complexity in the processes that govern krill consumption. We focus on the Antarctic Peninsula and Scotia Sea region where both krill and its consumers occur in significant concentrations and where an updated estimate of krill consumption by the main vertebrate groups is 55 million tonnes per year. Research has mainly focused on mammalian and avian predators of post-larval krill, particularly penguins. Potentially important consumer groups like fish, cephalopods and carnivorous zooplankton remain poorly understood, as does consumption of the early life stages of krill. As a consequence of these knowledge gaps and the variability that arises from complexity, a reliable seasonally, spatially or taxonomically resolved description of krill consumption remains elusive. One of the key motivations for attempting to estimate krill consumption is to understand how changes in krill availability impact predator populations. Such understanding is an important requirement for ecosystem based management of the Antarctic krill fishery. We therefore propose that integrated study areas in strategic fishing locations should be developed to directly assess the response of krill predators to changes in krill availability.

## **Keywords**

Krill consumption, top-down control, krill surplus hypothesis, ecosystem perturbation, ecosystem recovery.

## 1. Introduction

Antarctic krill, *Euphausia superba*, is a widespread and abundant species in the Southern Ocean and most of its life history stages are important prey for a wide range of organisms (Miller and Hampton 1989). These predators include species of commercial interest (fish and squid) and conservation concern (marine mammals and seabirds) as well as an array of zooplankton and benthic invertebrates. Krill also indirectly supports predators that feed on other krill consumers. Consistent with its key role in many predators' diets, krill apparently exerts bottom-up control on predator variables such as reproductive output and, ultimately, population size (Murphy 1995, Reid et al 2005; Atkinson et al 2014; Forcada and Trathan 2009). Conversely, the idea that predators exert top-down controls on the abundance and distribution of krill has been influential in the study of Southern Ocean ecology (Laws 1977, Mori and Butterworth 2006, Hill et al 2006). Because of its circumpolar distribution, krill connects many Southern Ocean food-webs, while highly migratory predators such as baleen whales and albatrosses extend the influence of these trophic interactions into other oceans. Thus, to fully comprehend the ecological importance of krill requires quantification of trophic interactions and energy flows involving all life history stages at a range of spatial and temporal scales.

Knowledge about krill consumption is key to many of the critical questions about Southern Ocean food-webs, including:

- i. How do these food-webs function both temporally and spatially, at the regional and circumpolar scale,
- ii. How do the population processes and reproductive output of predator species respond to natural variation in the availability of krill,

- iii. What is the natural mortality of krill and how does it affect krill population dynamics,
- iv. What are the implications of altered krill availability in food-webs which might result from rapid, regional changes in climate, and
- v. What are the implications of krill harvesting for Southern Ocean food-webs?

Despite its clear importance as a central process in Southern Ocean food-webs, there is considerable uncertainty about many aspects of krill consumption, which even extends to identifying which predators are the major consumers (Atkinson et al. 2012). The reasons for these uncertainties include sparse data on many predator species and significant inter-annual variability in krill population size, which is connected to bottom-up environmental variation (Atkinson et al 2004, Trathan et al. 2006, 2007, Murphy et al. 2007, Steinberg et al 2015), and which may interact with top-down predation controls operating over multi-decadal scales.

The study of interactions between krill and its predators is a major part of Southern Ocean ecology, which has produced a substantial literature and increased understanding of the many influences on krill consumption. One consequence of these insights is a growing appreciation of the complex role that krill plays in Southern Ocean food-webs. For example, recent studies have shown that krill feed on the benthos year round throughout Antarctica, with an estimated ~20% of the stock deeper than 200 m at any one time (Schmidt et al. 2011), although others (see chapter 2, Siegel and Watkins 2016) suggest that the percentage below 200 m may only be around 5%. Further, Clarke and Tyler (2008) have shown that krill habitat also extends to abyssal depths (including to 3000 m and even 3500 m). These observations revise our understanding of the depth distribution and ecology of Antarctic krill, suggesting

that krill connects food-webs not just horizontally, between regions, but vertically, between depth zones.

In this chapter we consider the consumption of krill by its many predators (Figure 1), and discuss aspects of predator-prey ecology that contribute to our understanding of consumption. We focus mainly on the Antarctic Peninsula and Scotia Sea region where there is a greater biomass of krill (Atkinson et al. 2009) and probably also of krill consumers; further, information from this region also extends back in time for a number of decades given the interest of early integrated ecological studies such as the *Discovery Investigations* (e.g. Marr 1962, Mackintosh 1974). We present information about consumption by various taxonomic groups, and highlight penguins as one of the most studied groups of krill predators, but emphasise that important gaps still exist even for this group. We recognise that there are regional differences in the diets of many predators, which have a strong dependency on krill where it is regionally abundant, but have other dominant prey elsewhere (e.g. Staniland et al. 2010). This is one of many complexities that mean that accurately describing the many trophic interactions, particularly those related to the early life stages of krill, remains challenging. We highlight a number of major uncertainties that remain to be addressed if we are to properly understand the role of krill in the Antarctic marine ecosystem. We also consider a major application of this understanding, in the ecosystem-based management of Antarctic krill fisheries, and suggest a way of gaining the necessary insight into the relevant predator-prey dynamics despite uncertainties in consumption estimates.

## **2. Historical perspective**

Estimates of krill consumption by marine predators date back at least to Marr (1962), who estimated the annual consumption of krill by large baleen whales during the mid 1930s. Later estimates by Everson (1977), built on calculations of krill consumption by seals (Laws 1977),

birds (Prevost 1981) and whales (e.g. Mackintosh 1974, Laws 1977), but recognised that there were no consumption estimates for other important krill-eating groups, including fish and squid. The importance of krill to predators in the Southern Ocean and the potential for commercial krill fishing to affect these predators became central to the establishment of the ecosystem-based management approach adopted by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Everson 2000).

Estimating consumption generally requires information about diet composition, feeding rate, and population size. Information on each of these elements has increased considerably since CCAMLR first met in 1982. For example, Croxall et al. (1985a) compiled the available information to estimate consumption of krill by seabirds in the Scotia Sea, and identified macaroni penguins *Eudyptes chrysolophus* breeding at South Georgia as a major krill consumer. Boyd (2002) arrived at a similar consumption estimate for macaroni penguins and provided insight into some of the uncertainties in the estimate. Further studies (Green et al. 2001, 2002) suggested that macaroni penguin metabolic rates are higher than those assumed by Boyd (2002) but that population sizes are now considerably smaller, as a result of a decline since the late 1970s (Trathan et al. 2012). However, consumption estimates remain uncertain because of a lack of information about pre-breeders and about winter diets of all demographic classes. Knowledge about krill consumption by macaroni penguins has therefore accumulated over time but the ecosystem has also changed within this same time interval, and uncertainties in consumption estimates therefore remain. This is despite the fact that macaroni penguins are relatively easy to observe compared to fully marine predator groups such as cephalopods, fish, whales and planktonic invertebrates, where the complexities are more difficult to overcome.

Nonetheless, the literature contains circumpolar krill consumption estimates for many predator groups including seals and whales (Laws 1977, Bengston 1984, Armstrong and Siegfried 1991, Ichii and Kato 1991, Mori and Butterworth 2006), seabirds (Everson 1977, Croxall et al. 1984, 1985a), cephalopods (Everson 1984) and fish (Lubimova and Shust 1980, Kock 1992, Hureau 1994). Various authors, including Everson (1977), Miller and Hampton (1989), Barrera-Oro (2002) and Mori and Butterworth (2006), have drawn on these sources to estimate total circumpolar krill consumption in the post-whaling era. These estimates are in the range of 90 to 387 million tonnes per year (Table 1), which overlaps with the range of krill gross post-larval production estimates (342 to 536 million tonnes per year) presented in Atkinson et al. (2009). For comparison, Hill et al. (2007) compiled estimates of krill consumption in the Scotia Sea region (FAO Subareas 48.1, 48.2 and 48.3), which we have here updated to include two key missing groups: flying seabirds (Croxall et al. 1985a) and pack ice seals (Forcada et al. 2012), and revised estimates for macaroni penguins and fur seals (Trathan et al. 2012). This suggests that krill consumption in the Scotia Sea region is at least 55 million tonnes per year.

These consumption estimates give an indication of the importance of krill to higher trophic levels, but they also highlight some of the uncertainties that affect our understanding of the Southern Ocean food-web. For example, there is a difference of almost 300 million tonnes year<sup>-1</sup> between the minimum and maximum circumpolar consumption estimates. This difference is greater than the uncertain estimate of late 20<sup>th</sup> century circumpolar krill biomass (~215 million tonnes: Atkinson et al. 2009, updated in Hill 2013). The available circumpolar estimates suggest that the dominant predator group could be any of crabeater seals, minke whales, cephalopods, or fish, whereas comparison with historical Scotia Sea estimates reveals an apparent underestimate of the importance of Antarctic fur seals at the circumpolar scale.

With the exception of estimates of consumption by mesopelagic fish, circumpolar consumption estimates are generally concerned with predation on post-larval krill, and so omit the significant consumption of eggs and larvae (see below). This omission reflects gaps in the available information, which also mean that the level of information varies between predator groups. Much research has continued to focus mainly on birds and seals and, even in these groups, the level of information varies widely between locations and taxa. For example, in 2007, CCAMLR, which is responsible for managing the krill fishery and its effects on dependent and related species, established a specialist sub-group to address the need for information about predator abundance as part of the requirement to estimate predator demand for krill (SC-CAMLR 2007). In 2008, the sub-group identified short and medium term aims which concerned only birds and seals, with an acknowledgement that future work should also include fish (SC-CCAMLR 2008). At present there is no equivalent strategic focus on cephalopods, other invertebrates, or even whales. This restricted focus reflects the limited resources available to the sub-group, and therefore the size of the challenge implied by the ambition to estimate predator demand for krill.

In the last decade, several authors have developed food-web models which provide holistic representations of consumption and production throughout the food-web (Cornejo-Donoso and Antezana 2008, Pinkerton et al. 2010, Hill et al. 2012, Ballerini et al. 2014, Gurney et al. 2014). Such models provide a useful synthesis of available information, which often includes new consumption estimates for predators which have not been studied directly. They are also useful for exploring uncertainties in consumption estimates (Hill et al. 2012). The current generation of models focus on relatively small geographical areas but it is technically possible to use this approach to produce synoptic estimates of krill consumption at the regional scale (e.g. for the Scotia Sea) or for the whole Southern Ocean. Such models, and the



plausible regional estimates of krill consumption they produce, have an important role to play in addressing the critical questions about Southern Ocean food-webs outlined above. However, the ability to constrain and validate such models is limited by the available data and knowledge. In data poor situations, models can be particularly valuable for identifying critical knowledge gaps, such as the assumptions which most strongly influence conclusions about krill consumption (Hill et al 2012, Hill and Matthews 2013, Southwell et al 2015).

### **3. Regional perspectives**

Atkinson et al. (2008) highlight that, in contrast to many other species of zooplankton, the distribution of krill is concentrated between 0°W and 90°W, with more than 70% of the krill stock found in the Atlantic sector. These high levels of abundance are also partly why the commercial krill fishery now only operates in these waters. The concentration of krill in the Atlantic sector also means that there are large numbers of krill predators in this region. Consequently, many studies of predator-prey dynamics have been undertaken in the Atlantic sector, particularly within the Scotia Sea. In addition to the long history of research, this part of the krill-based ecosystem is also the focus of current attempts by CCAMLR to produce krill consumption estimates for use in management of the krill fishery.

In addition to the Atlantic sector, studies of predator-prey interactions are conducted in various other Southern Ocean regions, with important foci in the Ross Sea and in East Antarctica. These complementary studies have provided important advances in understanding about predator-prey dynamics as well as identifying regional contrasts and similarities. For example, studies from East Antarctica by Deagle et al. (2007, 2008) have shown that DNA analysis of faecal material from macaroni penguins accords well with dietary studies based on other analysis techniques. Similarly, Jarman et al. (2013) used DNA analysis of faecal material from Adélie penguins *Pygoscelis adeliae* to show spatial and temporal changes in diet

from 12 populations and that prey diversity was greater than previously thought. Jarman et al. (2013) showed that krill, fish, copepods and amphipods were the most important prey, which accords with other studies based on hard part remains or stable isotope analysis. However, their DNA analysis also showed that a substantial proportion of Adélie penguin diet comprised gelatinous groups such as jellyfish and comb jellies, and a range of other prey not previously identified in the diet of these penguins.

#### **4. Problems in relating consumption to production and standing stock**

Croxall et al. (1985a) considered various ecological interactions between krill and its predators, highlighting some of the difficulties that exist when attempting to make comparisons between the amounts of krill consumed by seabirds and marine mammals and estimates of the standing stock of krill available in the water, or at least as estimated by acoustic or net-based surveys. They emphasised that important sources of error result from a number of factors. (i) The flux of krill, as water (and krill) is transported across a region. For example, they noted that the standing stock of krill in the Scotia Sea is likely to be replenished by upstream sources including from both the Weddell Sea and the Belingshausen Sea, making balancing ecological budgets extremely difficult. While this conundrum remains valid today, flux is not the only process contributing to the turnover of krill. Atkinson et al. (2009) estimated that the total circumpolar gross post-larval production was about 2.5 to 4 times circumpolar biomass. This might overestimate the production available to predators as it does not include the effects of mortality but it suggests that such production might exceed the standing stock. Thus, the actual quantity of krill available to predators might be a complex interaction between standing stock, production, and flux. (ii) The diel vertical migration of krill continually alters the distribution of the standing stock. Individual krill migrate through the water column, moving to the surface at night, and returning to deeper

depths through the day. This migration not only affects foraging seabirds and seals which are restricted in their dive depth range, but also affects any acoustic estimates of krill biomass which might be used when attempting to understand whether biomass is sufficient to meet consumption demand. This is because acoustic surveys generally cover a limited depth range, omitting the surface layer and deeper reaches of the water column. (iii) The patchy nature of krill aggregations also leads to difficulties in surveying all potential habitats with adequate survey effort when generating estimates of standing stock. With constraints on research budgets, this remains a constant challenge. For example, the last large scale krill survey in the Scotia Sea was 15 years ago in 2000 (Trathan et al. 2001, Hewitt et al. 2004). (iv) Finally, Croxall et al. (1985a) noted that estimates of standing stock are generally restricted in their temporal coverage whereas it is now apparent that krill density can vary considerably between seasons (e.g. Saunders et al. 2007). As predator consumption varies between seasons, extrapolation of temporally limited data for either predators or prey can compound uncertainties.

Standing stock estimates provide an indicator, but not a definitive measure of krill availability to predators. Caution is therefore necessary in comparing consumption to standing stock. Alternative comparisons to production are useful for assessing impacts over short time scales (e.g. Shreeve et al 2009). Model-based studies generally include an explicit representation of turnover (such as the production to biomass ratio in mass-balanced food-web models e.g. Hill et al. 2012), but the difficulties with estimating these parameters suggested by Croxall et al. (1985a) still apply.

## **5. Consumption of krill eggs and larvae**

Adult female krill are reproductively active during summer, showing a comparatively high investment in the ovary, which may reach up to 46% of the total wet weight of krill at some

locations in some years (Tarling et al. 2007). A semi-empirical model used by Tarling et al. (2007) predicted that 11% of females complete 1 spawning episode year<sup>-1</sup>, 60% complete 2, and 29% complete 3 or more. The number of spawning events may vary spatially and temporally, but on average, krill release many thousands of eggs each year. For example, at South Georgia the average female krill releases 12,343 eggs year<sup>-1</sup>. Tarling et al. (2007) show that where eggs are unable to complete the descent–ascent developmental cycle because bathymetry is too shallow (i.e. on-shelf) eggs will sink to the sea floor; eggs that sink to the seabed are then vulnerable to predation by the benthos. In deeper water (i.e. off-shelf), eggs may return to the surface either as a metanauplii or as the 1<sup>st</sup> calyptopis stage. Tarling et al. (2007) concluded that predation on larvae is a major cause of local recruitment failure. Observed concentrations of larvae can be very high; for example, in the eastern Bellinghousen Sea, Pakhomov et al. (2004) found mean concentrations of almost 9,000 larvae m<sup>-2</sup> and maximum concentrations in excess of 30,000 larvae m<sup>-2</sup>. At the Antarctic Peninsula, Brinton and Townsend (1984) found 45,000 larvae m<sup>-2</sup>. In contrast, Siegel et al. (2011) reported much higher larval numbers along the western Antarctic Peninsula, with average values of 65,000 m<sup>-2</sup> and with many stations having numbers in excess of 200,000 m<sup>-2</sup>. Even higher levels have been reported in the Scotia Sea where a maximum of 1.8 10<sup>6</sup> larvae m<sup>-2</sup> were recorded during 1981 (Siegel 2005). Such high larval numbers (see chapter 2, Siegel and Watkins 2016) indicate the considerable predation potential.

In the maritime Sub-Antarctic, for example at South Georgia, some of the principle predators of krill larvae are Myctophid fish (Pakhomov et al. 1996), the hyperiid amphipod *Themisto gaudichaudii* (Pakhomov and Perissinotto 1996) and chaetognaths (Øresland 1990). An individual Myctophid fish can consume approximately 30 larvae day<sup>-1</sup>, while an individual *Themisto gaudichaudii* might predate about 3 larvae day<sup>-1</sup> and an individual chaetognath may

eat around 0.5 larvae day<sup>-1</sup> (Tarling et al. 2007). When the relative abundance of these predators in the South Georgia region is considered, estimates indicate that they have the potential to consume approximately 500 larvae m<sup>-2</sup> day<sup>-1</sup>. A succession of such predators feeding on a patch of larvae would therefore diminish numbers quite rapidly (Tarling et al. 2007).

Predation on eggs and larvae almost certainly occurs elsewhere, including in Antarctic waters. Understanding exactly where and when eggs and larvae are produced is therefore important when considering potential predation levels. Hofmann and Hüsrevoğlu (2003) showed that, as successful completion of the descent–ascent cycle is determined by both bathymetry and water mass, there are likely to be significant regional differences in the production of larvae. Predation on eggs and larvae is thus likely to be intimately linked to krill biogeography.

The nutritional value of eggs and larvae lost to predation, either pelagically, or within the benthos is potentially enormous, but remains largely unquantified. The consumption is probably highly seasonal, as eggs and larvae are available mainly during late summer and autumn, though multiple spawning episodes will prolong this period. Estimates of development times, from egg to post larva, vary but are of the order of 40 to 120 days (Ikeda 1984, Ross and Quetin 1982, 1983, Brinton and Townsend 1984), meaning that species that predate krill eggs and larvae must either cease feeding or find alternate nutritive sources at other times of year.

## **6. Consumption of krill by fish and squid**

There are a number of species of fish that eat Antarctic krill, including species from two (largely) demersal families, the Nototheniidae and Channichthyidae (order Perciformes), as

well as species from the pelagic family Myctophidae. Life history information is scarce for many of these krill-eating fish, so considerable uncertainty remains about the importance of krill in their diets.

As a group, the Perciform fish occupy a number of different habitats (which are even more diverse if different life stages are also considered), therefore the diets of these fish are also highly variable. For some Perciform fish, krill may be only one of many different prey items; such species include *Notothenia rossii*, *Pseudochaenichthys georgianus* and *Chionodraco* spp. (Kock 1992). In contrast krill is probably the main prey item for others, including for *Champscephalus gunnari*, *Lepidnothen larseni*, *Chaenodraco wilsoni* and *Pleuragramma antarcticum* (Kock 1992). Fish are clearly the most important predators in many other marine food-webs (Scheffer et al. 2005). However, the balance of predators in the Southern Ocean has been affected by serial over-exploitation of seals, whales, and demersal fish. The many effects of this include an apparent reduction in demersal fish populations to levels far below those which were present in the 1960s (Myers and Worm 2003). Thus, it is possible that these species were a more important group of krill consumers before they were depleted.

Antarctic krill occur in the diets of many Myctophid fish species, including *Electrona carlsbergi*, *Electrona antarctica*, *Krefftichtys anderssoni*, *Gynoscopelus braueri*, *Gynoscopelus nicholsi* and *Gynoscopelus opisthopterus* (Pusch et al. 2004, Shreeve et al. 2009, Saunders et al. 2014). For *E. antarctica* and *Gynoscopelus* spp., they are probably the dominant prey species (Kock 1992). In addition to the Myctophids, other abundant mesopelagic fish, including *Notolepis coatsi*, *Notolepis annulata* and *Bathylagus antarcticus* predominantly feed on krill (Kock 1992).

Rates of daily food intake vary considerably during the ontogenetic development of different fish species and they also vary seasonally (Kock 1992). For example, Kock (1992) reports

that *N. rossii* shows reduced feeding in winter compared with summer, possibly by as much as a factor of 2 or 3. Feeding in some fish species also decreases or even stops prior to and during spawning; for example *N. rossii* and *C. gunnari* often have empty stomachs during this period, with as many as 90% of fish fasting.

Hill et al. (2007) suggest that estimates of krill consumption per unit biomass are an order of magnitude lower for fish than for penguins and seals. However, Hill et al. (2007) also suggest that Myctophid fish are possibly the main consumers of krill in the Southern Ocean, though estimates of Myctophid abundance need to be re-evaluated to reduce existing levels of uncertainty. Collins et al. (2012) suggested that Myctophid biomass in the Scotia Sea is around 4.5 million tonnes with zooplankton consumption around 25 million tonnes year<sup>-1</sup>, although they did not estimate the krill fraction of this consumption.

The potential importance of Antarctic krill in the diets of squid has been suggested (e.g. Miller and Hampton 1989), but is not well established (Collins and Rodhouse 2006). Serological methods have shown the presence of krill in the diet of *Psychroteuthis glacialis*, *Mastigoteuthis psychrophila*, *Moroteuthis knipovitchi*, *Moroteuthis robsoni*, *Slosarczykovia circumantarctica* and *Martialia hyadesi* (Kear 1992), though there are generally too few dietary data to determine whether krill is an important prey item for other squid species (Collins and Rodhouse 2006). Krill are certainly not a major prey item for Sub-Antarctic species such as *Martialia hyadesi* or *Moroteuthis ingens*, the only squid species for which there have been detailed dietary studies (Collins and Rodhouse 2006). That said, krill have been found to be an important dietary component for those squid species taken as by-catch in the Japanese krill fishery (Nemoto et al. 1985, 1988). These squid were all small and it is possible that krill might only be important during certain early developmental phases. Filippova and Yukhov (1979) suggest that squid that live near the ocean surface probably

feed almost exclusively on crustaceans (krill, hyperiid amphipods and mysids), while larger species that inhabit the mesopelagic and bathypelagic zones probably feed on crustaceans during early life.

Thus, the importance of krill consumption by squid remains difficult to quantify; many pelagic squid species are relatively short lived but exhibit very rapid growth rates. Given that krill occur in the diets of some species, and are probably important for many more during different developmental periods, consumption of krill by squid certainly should not be ignored (Miller and Hampton 1989).

## **7. Consumption of krill by seabirds**

One of the most comprehensive regional assessments of Antarctic krill consumption by seabirds is that of Croxall et al. (1985a). The focus of this work was the Scotia Sea which potentially includes 26-28% of the circumpolar krill stock (Atkinson et al. 2008). The Scotia Sea is a highly productive area that is important for a broad guild of seabirds that feed on krill. Thus, though the work of Croxall et al. (1985a) is now some 3 decades old, their assessment remains one of the key pieces of work on krill consumption, especially during summer. These authors show that krill is the most important dietary item for most seabirds in the Scotia Sea, comprising some 82% of their diet; by comparison, copepods, squid, fish and amphipods comprise only 8%, 4%, 3% and 2% respectively. Croxall et al. (1985a) report that 21 species of seabirds predate krill in this region, with the major consumers being macaroni penguins, chinstrap penguins *Pygoscelis antarctica*, and Antarctic prions *Pachyptila desolata* which together account for over 50% of all krill consumed by seabirds.

Techniques to better estimate the population sizes of some krill predators, particularly surface breeding species such as penguins, are now becoming available with the advent of high



resolution satellite imagery (e.g. Fretwell and Trathan 2009, Fretwell et al. 2012). These methods still need to be refined, but these new approaches look promising (e.g. Schwaller et al. 2013, LaRue et al. 2014) and will hopefully provide in the future better population estimates and hence better krill consumption estimates.

In 1985 Croxall and co-workers noted that there were important gaps in our understanding of food-web connections related to krill. These gaps still largely remain today in 2015. Croxall et al. (1985a) highlighted the need for better estimates of many predator population sizes, including for macaroni and chinstrap penguins, and small petrel species. Only macaroni penguin population estimates have been revised in the intervening period (Trathan et al. 2012), although this revision does not include estimates of pre-breeders which may comprise a sizable proportion of the population. Other factors which are still important to re-evaluate include better data on dietary composition and the energy available from krill, especially in winter, and better information about bio-energetics and the energy cost of certain activities. Gorman et al. (2014) have shown that such issues are complex, highlighting previously unknown trophic pathways and the need to consider gender and sex-specific foraging niches, particularly in relation to environmental variability and potential changes in future habitat.

CCAMLR has established an ecosystem monitoring programme focusing on krill-eating seals and seabirds, especially penguins, to better understand whether changes in the ecosystem might be brought about by fishery impacts.

## **8. Consumption of krill by marine mammals**

Croxall et al. (1985a) also provide estimates of krill consumption by a number of marine mammals. As with seabirds, krill consumption estimates for most mammalian species depend upon reliable estimates of their population size, yet these still remain uncertain. For example,

revised population estimates exist for crabeater seal *Lobodon carcinophagus* close to the Antarctic Peninsula (Forcada et al. 2012) and Antarctic fur seal *Arctocephalus gazella* at South Georgia (Boyd 1993, Boyd 2002); however, populations of these major krill consumers are known to be changing (e.g. Forcada and Hofmann 2014).

Recently, it has been inferred that elephant seals *Mirounga leonina* feed upon krill (Walters et al. 2014) which constitutes an abundant, easily accessible source of prey in water masses used by sub-yearling seals. Walters et al. (2014) used isotopic assessment and concurrent tracking of seals to successfully identify ontogenetic shifts in broad-scale foraging habitat use and diet in these animals. Although elephant seal population sizes in the Scotia Sea are reasonably well known (Boyd et al. 1996), the consumption of krill by juvenile elephant seals has not previously been considered.

The importance of krill in the diets of various species of baleen whale has long been recognised, and krill consumption by cetaceans has been studied over many years, including by the *Discovery Investigations* (e.g. Mackintosh 1974). Blue whale *Balaenoptera musculus*, fin whale *Balaenoptera physalus*, sei whale *Balaenoptera borealis*, minke whale *Balaenoptera bonaerensis*, humpback whale *Megaptera novaengliae* and right whale *Eubalaena australis*, all consume krill, though they all also predate other species including other crustaceans and sometimes fish. In some areas, particularly the Ross Sea, crystal krill *Euphausia crystallorophias* may become a dominant prey item. The baleen whales which feed in the Southern Ocean breed at lower latitudes. Each species arrives in the Southern Ocean at slightly different times of year and preferentially feeds in different habitats (Lockyer 1981a). For example minke whales are species of the pack ice (Friedlaender et al. 2014), while blue whales are species of the ice edge, fin whales are species of more open water and humpback whales are more coastal (Ropert-Coudert et al. 2014).

Reilly et al. (2004) reviewed techniques used to estimate krill consumption by baleen whales together with estimates of whale abundance. They concluded that consumption estimates are still very much less than they would be if baleen whale populations were to recover to pre-exploitation levels.

Baleen whales historically consumed substantial amounts of krill, not just in coastal areas such as at South Georgia, but across the entire Southern Ocean. The relationship between whale catch distribution and various physical properties of the Southern Ocean has been noted before (e.g. de la Mare et al. 1997, 2009, Ackley et al. 2003). This distribution also mirrors the circumpolar distribution of krill (Atkinson et al. 2004; 2008), reflecting the broadest scale over which krill predators operate.

## **9. The krill surplus hypothesis**

Understanding variability in patterns of distribution, abundance of species and structure of communities, together with the consequences for species diversity has been a central motivation for ecologists for many decades (Hutchinson 1959); notwithstanding, ecological knowledge about some of the processes that generate these patterns remains elusive. Perturbations to natural systems cause change, and observing these changes as they occur over various timescales can provide insight into the underlying processes. To quote Richard Feynman (Feynman et al. 1963), “We do not know what the rules of the game are; all we are allowed to do is to watch the playing. Of course, if we watch long enough, we may eventually catch on to a few of the rules”.

Some systems are particularly difficult to understand and ecological patterns only emerge after decades of observation. The Southern Ocean is one ecosystem where understanding has been slow to emerge (Hill et al. 2006). This is not simply because the Southern Ocean is

remote and logistically difficult to access; it is also because it is more complex than commonly held and has been perturbed over decades of commercial exploitation. However, in one sense, the perturbation caused by the removal of seals and whales through decades of unregulated exploitation can be viewed as a major *experiment* which can provide an opportunity for us to gain insight into ecological processes. Two contrasting ideas about the effects of this perturbation are that the removal of the great whales led to a possible “krill surplus” (Laws 1977, Ballance et al. 2006) or that it led to a possible reduction in krill (Nicol et al. 2010), (see below).

Early commercial exploitation of Antarctic fur seals removed a considerable amount of krill-dependent biomass from the Southern Ocean, possibly many tens of thousands of tonnes (Mori and Butterworth 2006). Although these figures are vague, it is certain that the removal of so many seals meant that impacts on krill, their main prey species, would have been substantial (Emslie and Patterson 2007). Later, as commercial interests in the Southern Ocean shifted, the initial biomass of whales, estimated to have been 45.6 million tonnes, was reduced to just 8.2 million tonnes (Laws 1977), again with major impacts upon their main prey, krill. Further impacts on krill will also have resulted from the commercial fisheries which removed hundreds of thousands of tonnes of krill dependant finfish (Kock 1992). Commercial harvesting for finfish in the 1960s is known to have profoundly altered fish communities in the Sub-Antarctic, many of which fed upon krill (Kock 1992).

The subsequent annual release of prey resulting from just the removal of whales alone was thought to be enormous; approximately 147.0 million tonnes of krill, 7.1 million tonnes of squid and 3.3 million tonnes of fish (Laws 1977). It was recognised that such substantial changes in the marine ecosystem would have resulted in a major ecosystem response across a variety of trophic levels (Sladen 1964, Laws 1977, Ainley et al. 2007). The additional release

of krill arising from the removal of seals and fish, and its consequences for other predator populations, has not been adequately assessed, nor have the implications of the fact that some of these fish were alternative prey for other krill predators. Any such assessment would probably now be confounded by the serial nature of commercial removals, which would have facilitated different ecosystem responses, including in some of these harvested components.

Sladen (1964) first recognised that increases in populations of both chinstrap penguins and Adélie penguins in the Scotia Sea were likely to be a direct result of the declines in the baleen whale stocks. Documented increases in other species, including gentoo penguins *Pygoscelis papua*, and recovering Antarctic fur seal populations (Payne 1977), were also thought to be due to the much more abundant food supplies.

The Southern Ocean marine system has therefore shown clear signs of ecosystem change in the past century, following the massive perturbation caused by the removal of fur seals and the great whales. However, how such changes will act out into the future and how long the ecosystem will take to recover is still unknown (e.g. Murphy 1995).

## **10. Recovery of the seal and whale stocks**

Other changes in the Antarctic marine ecosystem may complicate the recovery of seal and whale populations. Mostly importantly, Antarctic krill is now thought to have undergone more than a two-fold decrease in abundance, at least in the Scotia Sea, between the early 1970s and late 1980s (Atkinson et al. 2004, 2008, 2014). Abundance estimates for the 1990s and 2000s indicate significant inter-annual variability but no trend (Atkinson et al. 2004, 2008, 2014). Atkinson et al. (2004) based their abundance estimates on samples taken from research nets. More recently, Fielding et al. (2014) have shown that density estimates based on acoustic surveys indicate that, at least at South Georgia, no further decline has been

detectable since the mid 1990s. However, any change in krill abundance is highly likely to have had a major impact upon those avian and mammalian consumers, such as penguins, seals and baleen whales that depend upon krill (Croxall et al. 1984). Other changes in the zooplankton community have also been reported, but these may be more subtle. Thus, studies (Ward et al. 2008) showed that in some regions zooplankton abundance values were very much lower in the early part of the 20<sup>th</sup> century than in recent years; however, their analyses did not reveal any systematic differences in species composition across years. The changes in zooplankton communities are not fully understood; however, changes in sea ice (Parkinson 2002, 2004) and water temperature (Whitehouse et al. 2008) have been implicated (Atkinson et al. 2004).

Populations of Antarctic fur seals, harvested almost to extinction in the 18<sup>th</sup> and 19<sup>th</sup> centuries, have nearly now recovered (Barlow et al. 2002). Indeed, populations at South Georgia, the main breeding centre for the species, have increased from a few tens of individuals in the 1950s to over 1.5 million by the early 1990s (Boyd 1993). Boyd (1993) reports that the population growth rate decreased from the exceptionally high level of 16.8% over the period 1955 to 1971 (Payne 1977) to 9.8% in the period 1977 to 1990. This is further supported by recent work that suggests that density dependent effects may be becoming important (Reid and Forcada 2005); data from long-term monitoring sites on Bird Island (see Forcada et al. 2005, Forcada and Hoffman 2014) indicate that the number of pups born annually at this site has actually decreased over the period 1984/85 to 2003/04.

Thus, fur seal population numbers may be approaching their upper limit in parts of their range at South Georgia. Consumption of krill by fur seals, based on existing energetic analyses (Boyd 2002), suggests that if populations were as high as 4 million animals (BAS

unpublished data), then krill consumption would probably be approaching 6.80 million tonnes year<sup>-1</sup>.

Although exploitation of whales in the Southern Ocean ceased with the moratorium on commercial whaling in 1986, comprehensive data are not yet available to describe the recovery of stocks which forage in Antarctic waters. Nevertheless, it is possible to deduce some of the likely changes in whale numbers using knowledge of the changes in their breeding population size based on counts in their calving areas. Two stocks that are known to be increasing are the humpback and southern right whales that calve in the coastal waters off Brazil and Argentina respectively (Zerbini et al. 2004, Leaper et al. 2006). These stocks feed around South Georgia during the summer months and both are thought to feed on krill when in the Scotia Sea (Tormosov et al. 1998, Reilly et al. 2004).

Thus, populations of marine mammals (seals and whales) are showing clear signs of recovery from historical exploitation, and as such, the hypothesised “krill surplus” (Laws 1977) might be expected to decrease. This will have important consequences for populations of other krill-dependant predators, such as penguins, that may have expanded as a consequence of increased food availability following the exploitation of seals and whales.

## **11. Guilds of krill predators**

Antarctic krill aggregate in a variety of forms, including loose, diffuse layers and dense, tightly packed swarms (Miller and Hampton 1989; see chapter 8, Tarling and Fielding 2016). As such there is a broad guild of species that prey upon krill and which, depending upon krill aggregation state, potentially benefit from increased feeding opportunities in ways that are not always easy to model or predict. Thus, the relative success of different predator species in

a given situation is likely to depend on the interaction between the form of the aggregation and species-specific foraging strategies.

Minke whales apparently specialize in swallow feeding under ice flows (Friedlaender et al. 2014), which may be made easier by their head shape and jaw structure (Lockyer 1981a, b). Other baleen whales that feed by swallowing are the blue, fin and humpback whales. In contrast, right whales are classed as skimmers (Lockyer 1981a, b). Swallow feeders rely upon concentrated plankton swarms, whilst skimmers swim with open mouths sifting the plankton from the water.

Other krill-eating species also have preferred foraging strategies, with different predators either surface seizing or plunge diving to find krill. The feeding strategies of pursuit divers, such as seals and penguins, have been studied extensively, respectively showing analogies with swallowing and skimming whales. For example, fur seals are known to feed in bouts (Boyd 1996) taking multiple krill during each dive within a bout. Most diving behaviour occurs at night, and most dives are shallow (Croxall et al. 1985b, Boyd and Croxall 1992). Mouth opening events occur mainly during the bottom phase of a dive (Iwata et al. 2012). Boyd (1996) has shown that the time taken for a fur seal to locate a new patch after leaving an old one is an indication of the distance between patches and that the intervals between bouts changes between years. These changes suggest that the structure and/or the spatial distribution of krill swarms varies between years and that fur seals must adapt their foraging behaviour accordingly. In contrast, penguins feed mainly during the day when they dive repeatedly with foraging dives relatively constant over the course of the foraging trip (e.g. Croxall et al. 1993). Penguins feed during periods when they undulate, or change depth rapidly, also generally during the bottom phase of a dive (Takahashi et al. 2004). During the course of these undulations the number of underwater beak-opening events increases, suggesting that the relative feeding intensity of each dive can be represented by depth-profile data. Underwater beak-opening patterns of krill-feeding penguin species are comparable with similar data from fish- and squid-feeding penguins (Takahashi et al. 2004).



The relationship between a particular krill-eating species and variation in the availability of krill is influenced by many factors including (i) the factors that determine prey availability such as density, aggregation and location, (ii) how the species selects and interacts with its prey, including in the presence and absence of other krill-eating predators. (iii) how the species' demography and reproductive output interact with its diet; and, (iv) the species', demographic processes, including their rates of maturation and onset of sexual maturity (e.g. Lockyer 1972, 1974, Laws 1977).

While knowledge of these issues is increasing for some species Atkinson et al. (2012) note that inferences about krill populations derived from predator performance and diet can be prone to bias, nonlinearity and noise. A major source of bias is the fact that predators are not random samplers of the wider krill population. Factors such as the vertical and horizontal distribution of krill in relation to the foraging range and diving depth of predators, the density of swarms and the presence of competitors or natural enemies of the predators may all influence this (Croxall et al. 1985b, 1988, Reid et al. 1996, Trathan et al. 2012). Predators also select krill according to size, sex, etc. (Hill et al. 1996). Such interactions (including multiple predator interactions) are important to consider in ecosystem models (Hill et al. 2006).

A major nonlinearity arises from the predator's functional response, i.e. the way consumption rate changes with prey availability (Holling 1959). Various authors (e.g. Boyd and Murray 2001, Reid et al. 2005, Cury et al. 2011) present evidence for asymptotic functional responses in some krill predators. However, Waluda et al. (2012) suggest that the functional response for macaroni penguins is sigmoidal. This type of response is associated with abrupt switching from one prey type to another, which raises the additional complication that the functional response is modified by the availability of alternative prey (Hill et al. 2005).

## **12. Seasonality and temporal considerations**

The consumption of krill, whether by other zooplankton, fish, squid, seabirds or marine mammals, varies seasonally. Each predator has a natural cycle that governs its life-history processes; this not only includes its ontogenetic development from juvenile to adult, but also any recurrent cycle as it reproduces. At any different life stage an individual predator may feed upon different parts of the krill stock and have varying degrees of dependence upon krill.

Long-lived vertebrates potentially exemplify the complexity of these cycles. For example, sub-yearling elephant seals may feed upon krill, but once they mature, they feed upon other prey. Other predators, such as seals or whales may feed upon krill while they are in the Antarctic, but not whilst they are outside the Antarctic.

Any or all of a predator's weight gain, body condition, propensity to breed, or reproductive output may vary in response to prey availability. Such variation in life-history parameters might not be immediately apparent, but may be lagged by days, weeks or months. Where reproductive output is affected, changes in population might not be apparent until cohorts recruit months or years into the future. Thus, understanding how predator-prey interactions impact predator populations can be extremely complex.

## **13. Feed-backs from predators to krill**

Predators have the potential to alter not only the density, but also the structure of their prey field; for example, humpback whales feeding on krill may use streams of bubbles, so called bubble-netting, to cause krill to aggregate (e.g. Jurasz and Jurasz 1979). Diving predators may cause swarms to move deeper in the water column, possibly outside the reach of other species of diving predator, whilst demersal fish may cause krill to move off the seabed to mid water depths. Such predator-prey interactions have been suggested over many years.

A different sort of interaction between whales and krill has also been postulated more recently (e.g. Smetacek 2008, Nicol et al. 2010). Iron is generally thought to be the limiting micronutrient for phytoplankton in the Southern Ocean, which when released and remineralised following grazing by krill and other herbivores, cycles back through the marine system. An alternate major mechanism for recycling iron could also have been defecation by baleen whales after they have consumed krill. Nicol et al. (2010) show that whale faecal iron concentration is approximately ten million times that of Antarctic seawater, suggesting that whales could be an important source of the micronutrient. Nicol et al. (2010) also calculate that the krill population currently contains approximately 24% of the total iron in the surface waters of the Southern Ocean, thus acting as a long-term reservoir of iron. Pre-exploitation populations of whales must also have stored larger quantities of iron and recycled more iron in surface waters, enhancing overall ocean productivity through a positive feedback loop. Nicol et al. (2010) therefore speculate that allowing the baleen whales to recover could actually increase Southern Ocean productivity through making enhanced iron levels in surface waters available to phytoplankton.

Coupled with the ongoing debate about the relative impacts on krill of historical harvesting versus climate change (Trathan and Reid 2009, Trathan et al. 2012), uncertainty about whether krill predators actually enhance the abundance of their prey suggests a wide range of possible scenarios for how the Southern Ocean ecosystems might develop in the future. This highlights the uncertainty in any attempt to project the future state of the system and emphasises the challenges in managing activities that might influence this state.

#### **14. Why do we need to know about krill consumption? – a re-evaluation**

At the start of this chapter we highlighted a number of reasons why so much emphasis has been placed on determining the levels of krill consumed by its various predators. Ultimately

all of these reasons are about understanding ecosystem change, and managing human activities (particularly fishing) that potentially drive such change. Important progress has been made on quantifying some aspects of the general krill consumption problem (e.g. macaroni penguin population estimates, macaroni penguin winter distribution, etc.), but many aspects still remain unresolved (e.g. squid population estimates, Myctophid fish population estimates). Progress towards a comprehensive understanding of krill consumption and how this fits into Southern Ocean food-webs has therefore been relatively modest since Everson (1977) first addressed the issue.

The motivating questions outlined above all remain vitally important, particularly as we try to project how the Southern Ocean ecosystem might respond to ongoing climate change or react to increased levels of commercial krill harvesting. Such issues might become increasingly important as human populations continue to increase and governments seek to sustainably develop any remaining under-exploited sources of marine protein (such as krill). Therefore, we need realistic ways to characterise how krill is connected to its predators in the marine food-web.

CCAMLR established its ecosystem monitoring programme (CEMP) in the mid-1980s, with the aspiration of using the programme in managing the commercial fishery for Antarctic krill (CCAMLR 1985). CEMP monitors land-based krill predators and aims to understand whether changes in the ecosystem might be brought about by fishery impacts. At present, the CEMP has almost 30 years of monitoring data but is not well integrated into management. These data, analysed in conjunction with krill indices, have provided insights into the relationships between krill and its avian and mammalian predators which demonstrate, *inter alia*, that (i) significant natural variability in the physical marine ecosystem, which alters ecological relationships involving krill (Trathan et al. 2003, Murphy et al. 2007), also affects krill

predators such that some show very low levels of reproductive output in years of low krill availability (Reid et al. 2005, Trathan et al. 2006), whilst others might switch to alternative prey and still produce offspring (Waluda et al. 2012); and (ii) climate change may be having impacts on both on krill (Atkinson et al. 2004) and its predators (Forcada and Hofmann 2014). These issues provide important context for any proposed management system that relies on CEMP data.

There are additional challenges which remain to be addressed, including that (i) CEMP sites are few and far between, especially compared to the wide geographic distribution of the krill fishery (e.g. Murphy et al. 1997); (ii) the functional responses of the monitored species to differing levels of krill abundance are not well understood (e.g. Boyd and Murray 2001, Barlow et al. 2002); and (iii) the monitored species are unlikely to be the major consumers of krill and the relationships between these species and the state of the wider group of krill predators is not well understood.

To some extent, CEMP offers a practical framework for assessing the ecosystem effects of krill fishing through monitoring accessible predators. However the utility of such information could be significantly improved by studying more directly how predator populations respond to local changes in krill.

This approach would require regular estimates of krill availability (distribution and abundance) and of the abundance of representative predators. The local scale might be more tractable than quantifying the seasonal demands of the whole guild of krill predators at a regional or circumpolar scale. However such local study areas would need to be understood in the regional context, particularly in terms of krill flux and seasonal variations in predator foraging range and diet. Such an approach might also usefully include reference areas (Figure

2) where the confounding impacts of climate change and harvesting might be more easily disentangled.

An integrated study area (Figure 2) should take into account both the regional and local oceanographic flow and flux of krill at varying scales (e.g. Murphy et al. 1998; Pinõnes et al 2011; 2013; Dinniman and Klink 2004) when identifying the location of reference areas, which should then be located upstream of any harvesting impacts. This is vital if the confounding impacts of fishing and climate change are to be resolved. Harvesting in reference areas would need to be prohibited, or stringently regulated. Harvesting in fished areas should be subject to a catch limit based on acoustic surveys to estimate regional krill biomass and assess whether depletion could be detected in the fished area over the course of the fishing season. This might necessitate a regional acoustic survey each year, followed by a series of local surveys in the area of fishing.

Many krill-eating species, particularly zooplankton, squid and fish are much more difficult to monitor than land-based predators. Therefore, like CEMP, an integrated study might usefully focus on a restricted set of ecosystem indicator species. These might include land-based predators such as penguins, and pelagic predators such as baleen whales. These species should be monitored across the region, including in both fished areas and reference areas. The problem remains that indicator species might have complex relationships with the state of the wider group of krill predators. This can be addressed to some extent by including contrasting species, but insights into the wider state of the ecosystem gained, for example, through monitoring predator diets, would be an important objective.

Modelling work has shown there is little evidence that krill predators maintain similar ecological niches across years (Friedlaender et al. 2011). Different species have unique physiological constraints and foraging behaviours which may have a stronger influence on

ecological niche than proximity to prey for some species (penguins and pack-ice seals). In contrast, fully marine predators (cetaceans), occupy ecological niches closer to prey. Nonetheless, Friedlaender et al. (2011) also suggest that the amount of overlap between modelled niches is relatively small, even for species with similar energetic requirements. Thus, in a rapidly changing environment, the relationships between monitored predators, their prey, and the wider ecosystem are likely to change as well. Detailed information about the local ecosystem context might therefore be essential in interpreting data from indicator species.

Integrated study areas are not a new concept and have been advocated by CCAMLR in the past. Indeed, integrated studies currently exist e.g. the Palmer LTER (Ducklow et al. 2007), the US AMLR grid (Trivelpiece et al. 2011) and the South Georgia Core Box (Murphy et al. 2007; Trathan et al. 2014). These studies are generally focussed on ecological understanding. Our proposal is to implement a similar scientifically robust framework in priority areas for fisheries management; any such efforts would almost certainly require scientific contributions from a number of research groups as well as from the krill-fishing industry.

The response of predators to prey availability has been a key ecological issue for many decades. In seeking to understand how krill predators respond to krill, integrated studies have the potential to greatly improve our understanding. For example, the Palmer LTER has revealed some of the ecological complexity found within predator-prey interactions. There, recent work has demonstrated that the foraging patterns of penguins, including foraging distance, relate to tidal phase (Bernard and Steinberg 2013). Moreover, Chapman et al. (2010) have shown that penguin chicks that fledge and survive to recruit into the breeding population are generally heavier at fledging than those that do not survive to breed. Spatial differences in prey nutritive value, as well as temporal differences, have also been shown to

have important implications for predators. Ruck et al. (2014) showed that across all sexes and maturity stages, krill in the southern part of the Palmer study region had higher total lipid content than that in the north. This regional variability in prey quality could affect the ability of apex predators to meet their energetic demands. These examples demonstrate the complexity of predator-prey interactions involving krill; other integrated study areas have revealed similar levels of complexity. Without such sustained long-term ecological research many such predator-prey complexities would be difficult to elucidate.

## **15. Conclusion**

Antarctic krill is rightly characterised as a central component of Southern Ocean food-webs and a key food source for a diverse array of predators in a wide range of marine habitats. It is true that simple three-step food chains (phytoplankton – krill – predators) are an important feature of these food-webs. However, this simplistic representation belies the complexity which decades of study into predation on krill have revealed. The size of krill changes by two orders of magnitude as it grows from egg to adult. It is found throughout the water column from surface layers to abyssal depths and at most latitudes south of the Polar Front. It has a highly heterogeneous distribution at a variety of spatial scales, from dense swarms at the 10 m scale to the concentration of circumpolar biomass in a few productive regions such as the Scotia Sea. These distribution patterns are constantly changing as a result of krill behaviour, flux and the influence of predators. The predators themselves are rarely obligate krill feeders, and so their diets vary ontogenetically, regionally and seasonally with the availability of krill and alternative prey. They employ a wide range of foraging strategies and travel different distances to feed, from the trans-ocean migrations of baleen whales to the relative immobility of some benthic organisms. Superimposed on this trophic complexity are the effects of environmental variability and change, which can cause major spatial and temporal shifts in



productivity and habitat quality, affecting the population dynamics of predators and prey alike. Moreover, the historical overexploitation of seals, whales and demersal fish has perturbed these dynamics, which continue to change as a result.

With this level of complexity, and the vastly different levels of information available on different krill predators, it is hardly surprising that although understanding of the trophic role of krill continues to grow, attempts to assess krill consumption at the circumpolar or regional scale yield crude and incomplete estimates. The key motivation behind such estimates is to understand how the food-web operates and how it responds to variability in the availability of krill. Climate change and krill fishing are potential drivers of this variability which require monitoring and, in the case of fishing, managing. Integrated study areas, designed to control the spatial patterns of fishing and monitor both the krill stock and krill predators offer a potentially more tractable means of understanding the food-web response to changes in the availability of krill.

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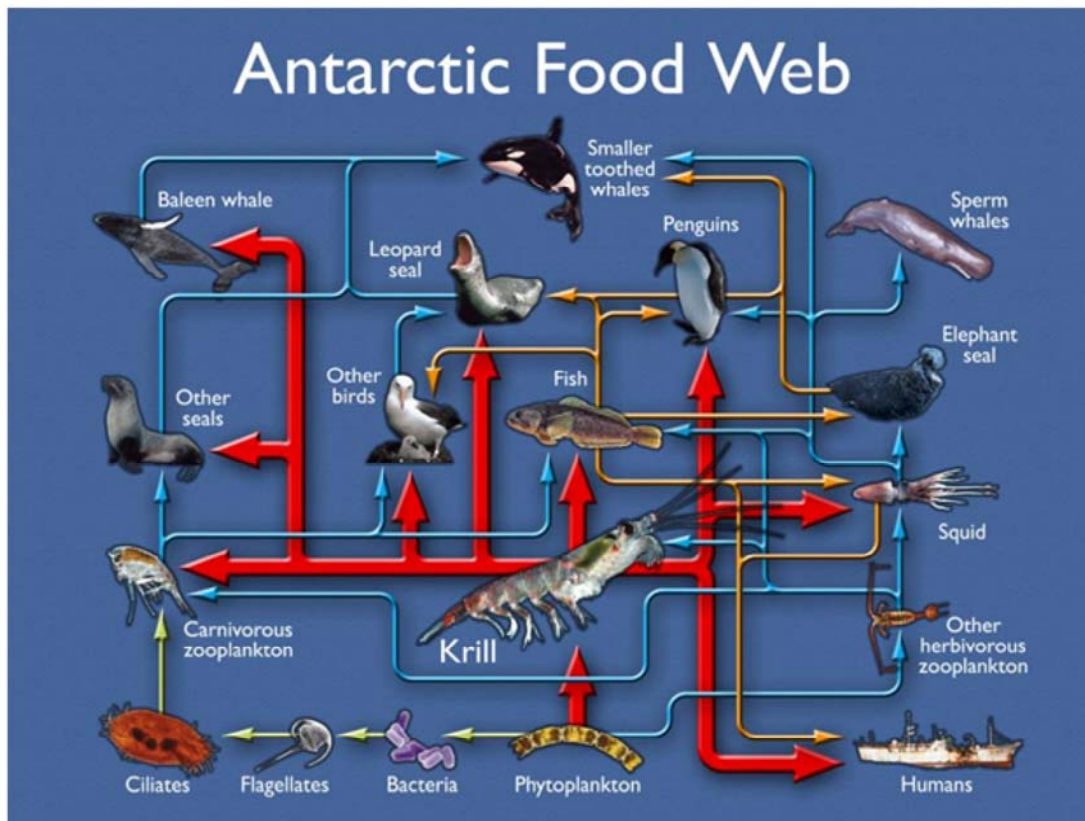
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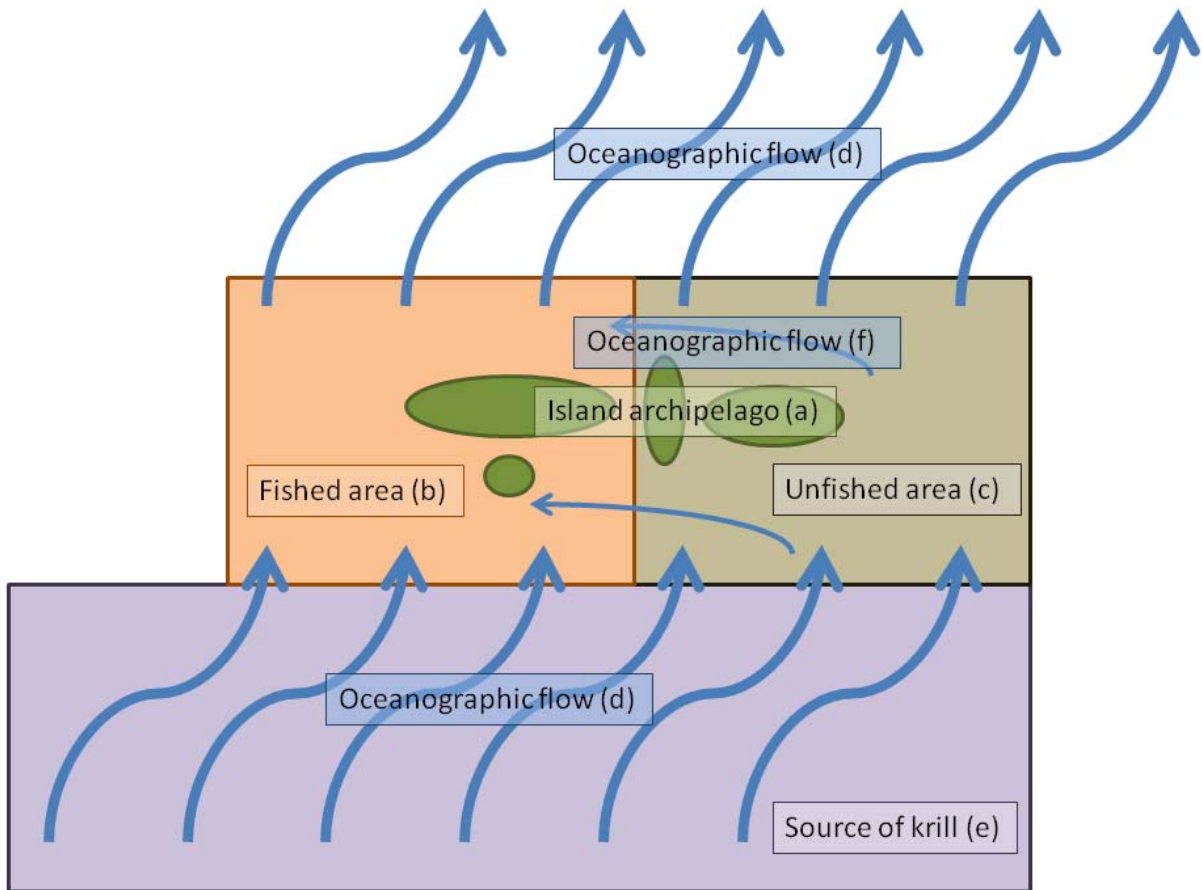
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## Tables and Figures



**Figure 1.** The major predators of Antarctic krill (source: [www.discoveringantarctica.org.uk](http://www.discoveringantarctica.org.uk)). Individual predators in the figure are representative of a broad range of individual species; e.g. Penguins might variously include Adélie, chinstrap, gentoo, emperor and macaroni.



**Figure 2.** Potential experimental design of an integrated study region including a reference area; (a) archipelago of islands; (b) area where fishing for krill is allowed; (c) reference area where no krill fishing is allowed; (d) regional oceanographic flow; (e) regional source of krill; (f) local oceanographic flow. See text for explanation.





**Table 1.** Available estimates of Antarctic krill consumption by various predator groups at the circumpolar and Scotia Sea scales. Values in italics are not full circumpolar estimates (see notes). Shaded rows show selected subgroups of the group above.

Predator group	Circumpolar					Circumpolar		<sup>(m)</sup> Scotia Sea	
						Min	Max		
Whales	<sup>(a)</sup> 34	<sup>(b)</sup> 43	<sup>(c)</sup> 85	<sup>(d)</sup> 3-120			3	120	2
<i>Minke</i>	8	20	75		<sup>(e)</sup> 36	<sup>(f)</sup> 140			
Seals	<sup>(a)</sup> 129	<sup>(b)</sup> 64		<sup>(d)</sup> 24-73			24	129	8
<i>Crabeater</i>	128	63							1
<i>Antarctic fur</i>	0	0							7
<i>Leopard</i>	1	1							0
Seabirds	<sup>(g)</sup> 15-20						15	20	8
<i>Penguins</i>									5
Fish	<sup>(h)</sup> 18-20	<sup>(i)</sup> 21-36	<sup>(j)</sup> 40-50	<sup>(k)</sup> 28-61			18	61	37
<i>Mesopelagic</i>		20-35		5-32					25
Cephalopods	<sup>(l)</sup> 30-56						30	56	
<b>Total</b>							<b>90</b>	<b>387</b>	<b>55</b>

Notes:

a. Bengston (1984).

b. Laws (1977).

c. Everson (2000).

d. Mori and Butterworth (2006).

e. Armstrong and Siegfried (1991).

f. Ichii and Kato (1991).

g. Everson (1977).

h. Lubimova and Shust (1980).

i. Kock (2002). The demersal fish component of the consumption estimate is for the Scotia Arc only.

j. Hureau (1994).

k. Kock et al. (2012). The Mesopelagic fish component of the consumption estimate is for the Atlantic sector only.

l. Everson (1984).

m. Hill et al. (2007). We have updated the consumption estimate to include new information about pack ice seals (Forcada et al. 2012), Antarctic fur seals (Trathan et al. 2012) and macaroni penguins (Trathan et al. 2012) and to include flying seabirds (Croxall et al. 1985).