

KRILL PANEL ON WESTERN ANTARCTIC PENINSULA: WHAT WE KNOW NOW ON KRILL AND WHAT NEEDS TO BE KNOWN IN IMMEDIATE FUTURE

Robert Y. George*, So Kawaguchi+, Christian Reiss and Stephen Nicol ++**

*Prof. Robert Y. George (George Institute, North Carolina, USA), +Dr. So Kawaguchi (Antarctic Division, Australia), **Dr. Christian Reiss (NOAA, Southwestern Fisheries Center, La Jolla., Calif.,USA), ++Dr. Stephen Nicol (IMAS, University of Tasmania, Hobart, Australia,)

INTRODUCTION

This report summarizes what transpired during the ‘KRILL PANEL’ on June 13, 2017 at the 3rd International Krill symposium at St Andrews University in Scotland, UK There were four presentations, namely (1) What we know on krill physiology under high pressure and high pCO₂ conditions (Robert Y. George) (2) What is our understanding of krill distribution and also threats from Ocean Acidification, (So Kawaguchi) (3) Krill and its predators in Scotia Sea and Western Antarctic Peninsula (Christian Reiss). There was also a fourth presentation on our knowledge of krill off Eastern Antarctica (Stephen Nicol).

OUR PRESENT KNOWLEDGE ON KRILL PHYSIOLOGY UNDER HYPERBARIC CONDITIONS AND HIGH pCO₂ IN WATER COLUMN IN DEEPR DEPTHS?

ROBERT Y. GEORGE

In 1982, at the first International Krill symposium (George, 1984, editor), the focus was primarily on Antarctic krill *Euphausia superba* because Sir George Deacon and the symposium convenor Dr. Robert George felt the need to exclude krill predators (Penguins, baleen whales and seals) and also other Euphausiid species in the Southern Ocean and elsewhere in the world oceans. However, they included scientists who were experts on primary production and phytoplankton in the Southern Ocean. The first krill symposium in Wilmington, North Carolina, which focused on studies conducted during the international BIOMASS Program (El-Sayed, 1994), rekindled a genuine interest on Antarctic krill initiated by *Discovery* scientists. These early studies included studies on development of young stages of Antarctic krill by Fraser (1936), krill embryology by Bergmann (1945), Marr’s (1962) classical monograph on natural history of krill and Mackintosh’s (1972) report on krill distribution in relation to sea-ice extent and water- masses as described by Deacon (1982, 1984). The First International Krill Symposium included new information on krill swarms and life history adaptations of krill as well as new ways to age krill.

In this 3rd Krill International Symposium there was a focus more on warming, particularly in the Western Antarctic Peninsula (WAP) Region and this in essence is the primary theme of this KRILL PANEL associated with warming in recent decades (1940-2017), there is also the decrease in sea-ice-extent as shown in Fig. 1 below. George and Hayden (2017) gave clear evidence of reduction of ice-shelf starting in 1986 in Amundsen Sea. Fig 1 also indicated the fluctuation in krill density in Scotia Sea and Atlantic Sector of Southern Ocean since 1980.

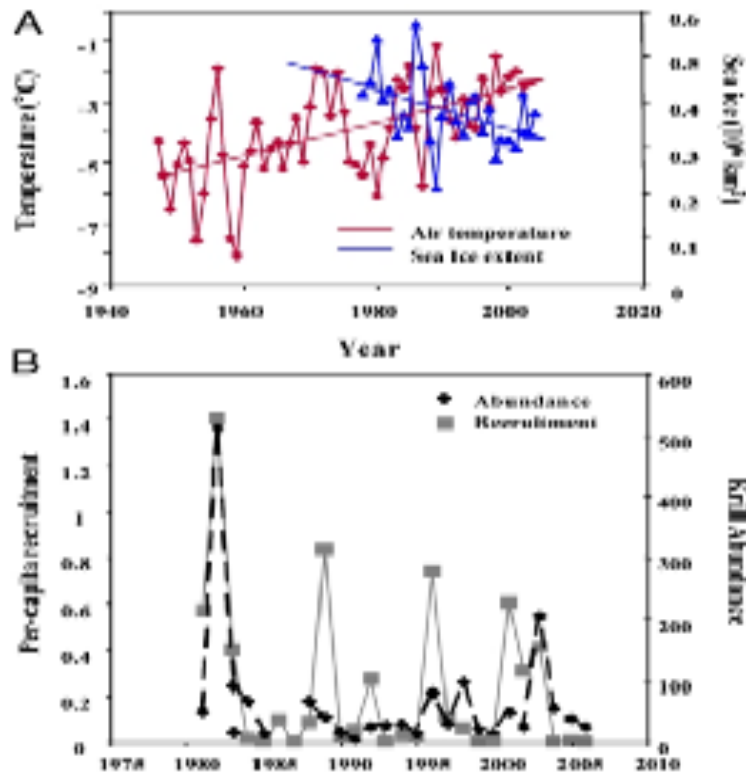


Fig. 1. A. Air temperature change (warming) illustrated in red and declining Sea Ice extent (in blue) from 1940 to present. B. Krill recruitment and krill abundance from 1975 to 2005.

Nicol (2006) addressed the krill distribution in a comprehensive way by summarizing how this important key-stone species in Southern Ocean interacts with different circumpolar currents around Antarctica and also with inter-annual variations in sea ice. This conceptual model on the life history of Antarctic krill acknowledges the fact that our knowledge on krill biology is still far from complete. The relationship between krill and its biotic environment (including predation from a vast array of vertebrate species such as penguins and marine mammals) and the abiotic environment (sea ice, water masses, currents and also changing carbonate chemistry in the light of climate change) is complex and long-term in nature.

Nicol (2006) concluded that krill life history is a reflection of evolved interactions between the species and the environment. His conceptual model of the spatial-temporal aspects of krill life history places particular emphasis on the different forces that act on both larval and adult stages of krill and on the interaction between krill behavior and ocean currents systems. These current systems were first as defined by Deacon (1982) and are now profoundly influenced by the ongoing climate-related changes such as decrease in sea ice extent. The effect of projected decreases in pH in the water column has also been discussed by Kawaguchi et al., (2011, 2013) and by George (2017). Krill production and reproductive success appears to be higher in high ice . However, in low ice years, there is diminished reproductive success, as depicted in the figure below.

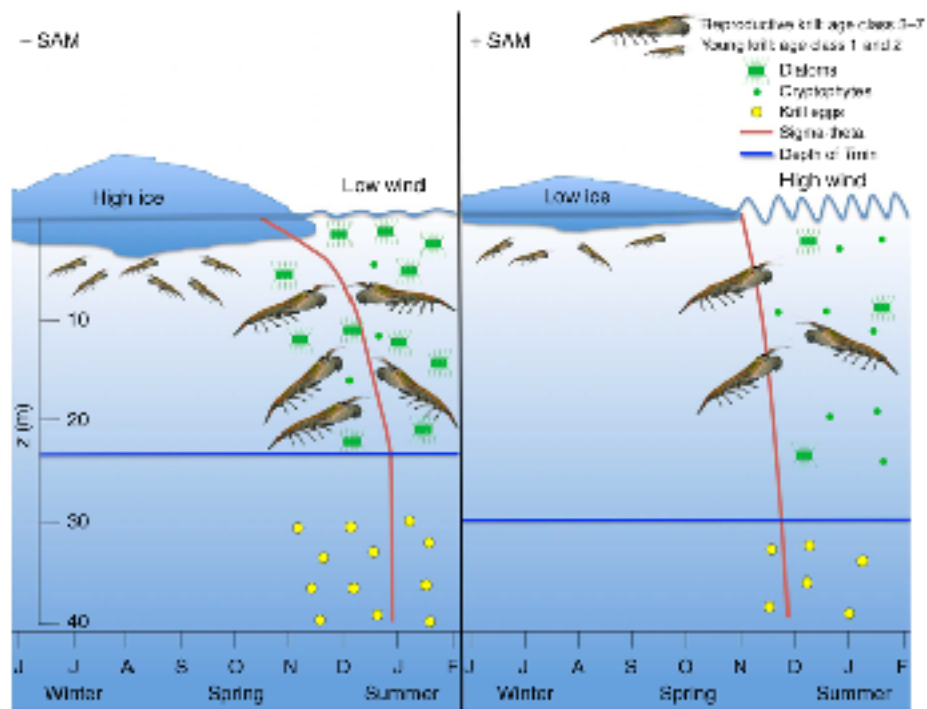


Fig. 2. Krill High Ice conditions vs Low Ice conditions (after Nicol, 2006)

George (2017) deals with the hypothesis that by the end of 21st century ocean acidification stress, coupled with thermal increase due to climate-related warming as predicted by IPCC (Inter-Governmental Panel on Climate Change), may act in concert induce critical physiologically stress to Antarctic krill particularly in the Western Antarctic Peninsular (WAP) region. This trend may adversely impact normal krill egg development with decrease in pH in deeper water column, associated with increasing pCO₂ conditions. George (1984) also discovered that krill egg development is accelerated temperature from minus 0.5 to 2 C and therefore, hatching occurs at lesser depths (400 to 600 m) where pH is lower. Kawaguchi et al (2011, 2013) have also cautioned, based on their laboratory experimental studies, that in simulated high pCO₂ conditions krill organogenesis was impaired and that by 2300 krill may disappear from

Southern Ocean if the current, business as usual trend of enhanced carbon dioxide emissions continue.

Our knowledge of krill egg development as the eggs and embryos descend down the water column to depths as deep as 1000 meters is very scarce except for the experimental laboratory studies on krill egg development by George and Stromberg (1985). The recent discovery of adult krill at abyssal depths by Clarke and Tyler (2008) and Brierley (2008), raises the question whether we need to develop laboratory high pressure aquaria to conduct experiments on physiological adaptations in Antarctic krill.

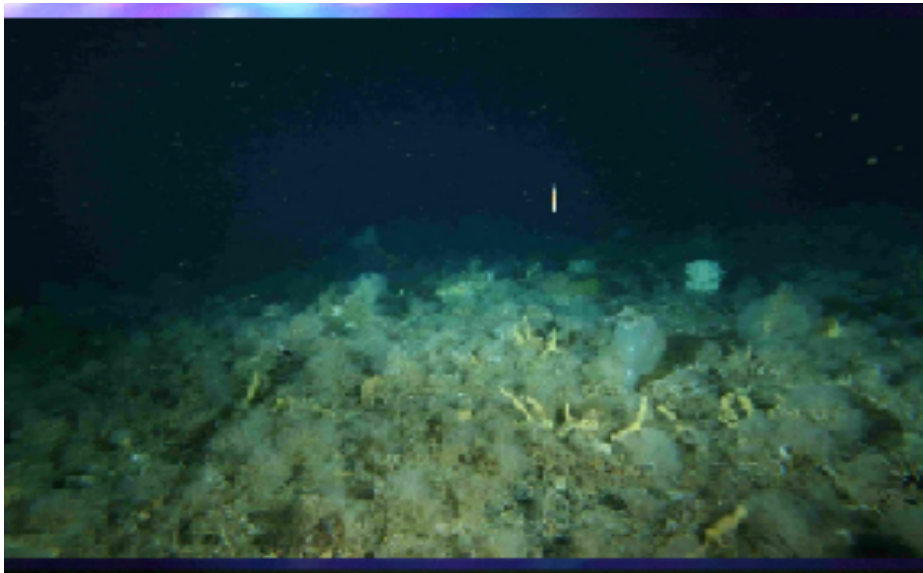


Fig. 3. Krill at abyssal depths m (Brierley, 2008)

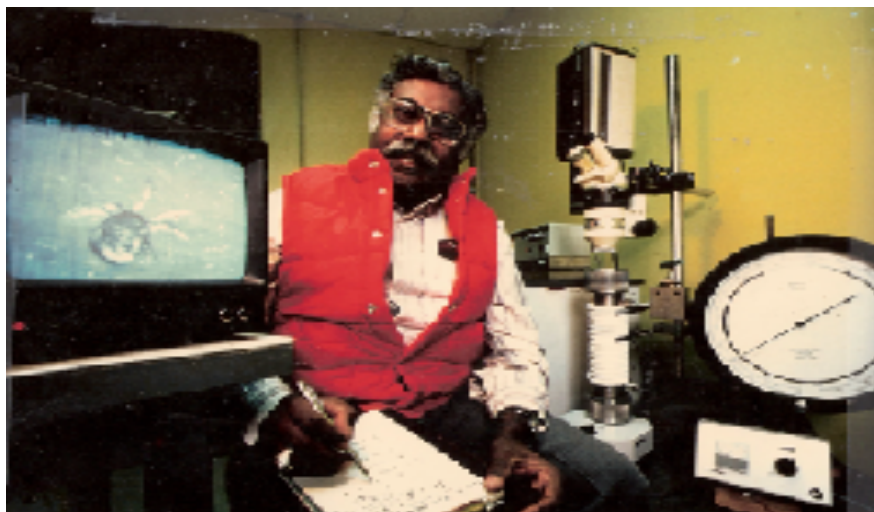


Fig. 4. Experimental apparatus to study krill egg development from fertilized eggs through cleavage, blastulation, gastrulation, organogenesis and hatching of nauplii (George and Stromberg, 1985).

Fevolden (1984) predicted a potential and possibly an exponential increase in fisheries around Antarctica, beyond Atlantic sector into the Pacific and Indian ocean sectors of the Southern Ocean and therefore, recommended to move a better understanding of population structure of *E. superba* both on temporal and spatial scales. His idea revolved around the existence of genetically differentiated krill stocks with distinct metabolic enzyme polymorphism and niche descriptors.

Fevolden and George (1984) in the austral summer of 1983 examined krill population structure in 15 krill schools or swarms in the WAP region. Only 4 out of the 15 krill schools contained gravid females. Subadults and juveniles were confined to inside of Palmer Archipelago and hence they proposed the hypothesis that the krill juveniles originated from Weddell Sea. Reproductive females were lacking near South Shetland Islands. In essence, there is now a genuine need to promote further krill research to ascertain the site of origin of krill in Scotia Sea, WAP, Amundsen Sea and Ross Sea by genetic markers, including enzyme polymorphism. In this context it is relevant to consider what Jarman (2017) recommended at the 3rd International Krill symposium in St. Andrews University. He advocated the need for “Krill-Omoics”, meaning a well- characterized “ Krill ‘Genome’, implying application of modern molecular technologies of DNA sequencing and analysis of a range of biomolecules from epigenomes, proteins and messenger RNA. There is a genuine appeal now on scientific basis to develop a “Krill Genome” that is bound to be order of magnitude more complex than “Human Genome” because of the physiological, biochemical (lipids) and metabolic plasticity of this unique crustacean species that is so abundant in the pelagic ecosystems of the Southern Ocean.

Our Current Understanding of krill in the Southern Ocean: How ocean acidification influence krill physiology and survival?

So Kawaguchi

It has been suggested that the numerical abundance of Antarctic krill declined between 1970 and 2000, and this has been attributed to the decline in sea ice cover in the South Atlantic (Atkinson et al. 2004). Antarctic krill abundance has also been correlated with climatic cycles of (ENSO). However, krill species concentrations and abundance relationships in recent years are remarkably similar to those reported for the Antarctic Peninsula during the 1928–1935 Discovery Investigations (Loeb and Santora 2015).

Although krill is one of the best studied crustaceans, there remain great uncertainties around its population dynamics. The Southern Ocean ecosystem is under threat from climate change and ocean acidification. The interplay between krill, ecosystem, and environmental change and ocean acidification is still beyond our understanding.

Although there are still only small number of published studies on ocean acidification impacts on krill, we are now starting to accumulate some information through experimental studies.

These studies, together with information from other krill species and general knowledge on physiology of crustaceans, we are now able to make some inferences on the impact of ocean acidification on the krill-based ecosystem.

Impacts of ocean acidification on krill biology

Antarctic krill use the entire ocean depth for their habitat throughout their early life-history stages. They lay sinking eggs at the surface layer, and the embryos develop as they sink, and after about 6 days they hatch out at 700-1000m. The current atmospheric and surface ocean CO₂ level is about 400 ppm but the CO₂ level at depth is generally higher, reaching over 550 $\mu\text{atm pCO}_2$ between 200-300m (Figure 1). Further, ocean carbon circulation models projects levels as high as 1400 $\mu\text{atm pCO}_2$ within the egg sinking range at the end of the century in some areas in the Southern Ocean (Kawaguchi et al. 2011). Experimental studies show that Antarctic krill’s egg hatch rates decline rapidly at CO₂ levels of 1250 μatm and above, with almost no hatching at 2000 $\mu\text{atm pCO}_2$. There is a huge geographical heterogeneity in the decrease in the predicted hatch rates compared to present day’s hatch rates. Some areas are predicted to exhibit a

60-70% decrease by the year 2100, and more than a 90% decrease throughout the Southern Ocean under IPCC business as usual scenario (Kawaguchi et al. 2013).

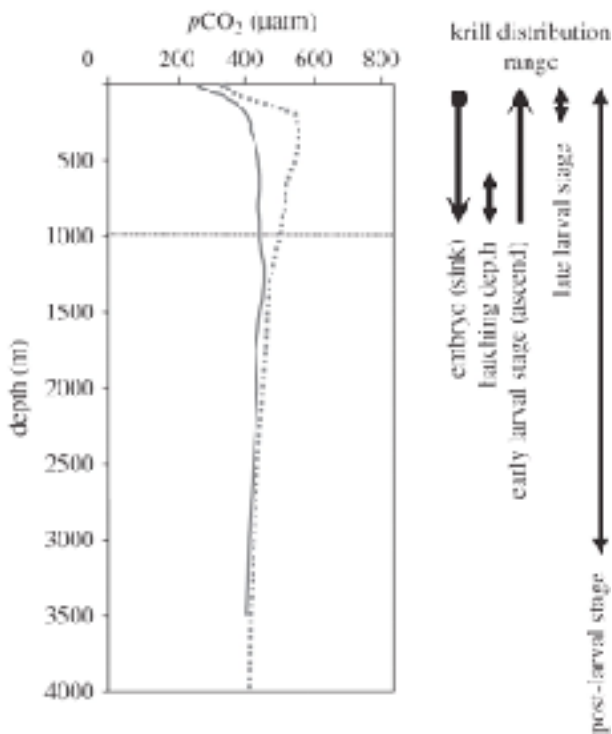


Figure 1. Vertical distribution range of krill and pCO₂ vertical profile at Scotia Sea (59–30S, 47–30W; thick line) and Weddell Sea (64–30S, 34–30W; dotted line), the known main krill habitats around the Antarctic. (Figure reproduced from Figure 1 of Kawaguchi et al. 2011 with permission)

Antarctic krill adults respond to elevated CO₂ by increasing ingestion rates, nutrient release rates, and metabolic activity, reflecting enhanced energetic requirements at levels of CO₂ only slightly beyond the current CO₂ level observed in the krill habitat (Saba et al. 2012). Early life stages of the Pacific krill species, *Euphausia pacifica*, show developmental delays and significantly decreased survival in the laboratory under pH conditions to which they are currently exposed in the field (McLaskey et al_2016). However, adult *E. pacifica* showed no effects on growth and mortality through mid-term experiments at the upper pCO₂ level currently experienced by *E.*

pacifica during their diel migrations (Cooper et al_2017). Sub-adult northern Atlantic krill

species *Nyctiphanes couchii* did not show an increased mortality rate at CO₂ levels as high as 1200 µatm which is upper end of the CO₂ level within their current habitat, but showed increased mortality at 1700 µatm pCO₂ (Sperfeld et al. 2014).

Available information suggests that all the krill species examined so far generally start to display negative effects of CO₂ levels at the upper limit of their current habitat conditions, or at least habitat CO₂ levels that are expected by 2100 under the IPCC business as usual scenario. Physiological effects may start to kick in well below the CO₂ level that cause acute effects. This may result in increased energetic costs which may compromise their reproduction capacity and behaviour. We often think of change in abundance as the major metric to gauge environmental impacts. However, even more subtle changes in their physiology and behaviour could have major implications to the trophic linkages of the Southern Ocean. Krill is a social organism and their lifestyle is characterised by their schooling and swarming behaviour (Hamner and Hamner 2000), which makes krill an effective and attractive prey for the higher predators such as whales, seals and penguins which makes this species special in the ecosystem.

Climate change, ocean acidification and krill fishery

Change in sea ice dynamics due to environmental change has allowed krill fishery to access more southern fishing grounds for a longer period (Kawaguchi et al. 2009). Krill recruitment is also observed to be linked to change in sea ice pattern (Siegel and Loeb 1995). What will the interplay between changes and ocean acidification look like?

We often discuss about the importance of krill in the Southern Ocean. There is no doubts that krill is the centre-piece of the SO ecosystem, and concerns about the impact of climate change and Ocean acidification on the ecosystem has repeatedly been expressed. How should the fishery be managed under these changing environment, and what are the important role that fishery can play under this environment?

The CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) Scheme of International Scientific Observation is one of the most important sources of scientific information designed to gather and validate scientific information essential for assessing the population status of selected species and the impact of fishing on such populations, as well as those of related and dependent species (Kawaguchi and Nicol 2007).

Scientific surveys using research vessels are designed in a standardized way to collect information and data on krill and to answer particular scientific questions. There is no doubt that such surveys will be the primary source driving further understanding of krill biology but the krill fishery is also an excellent platform to contribute to a greater understanding of krill. This is becoming increasingly important especially under the current circumstances as access to ship time for research surveys becomes more difficult. The krill fishery continues to operate on krill swarms for days and weeks, and this provides an excellent platform for collecting data on

biological parameters, as well as the best means to observe and monitor swarm behaviour (Kawaguchi and Nicol 2007).

There is a large number of krill vessels (up to 20 at one time) operating throughout the fishing grounds, with an extensive coverage in time and space. The frequency of sampling operations and the size of nets overwhelms that of research vessels (Kawaguchi and Nicol 2007). There is a growing interest among the krill fishing vessels to voluntarily

undertake acoustic surveys (SC-CAMLR 2016). This will become a powerful mean for monitoring krill biomass in the changing Southern Ocean environment if this can be undertaken in a designed and coordinated manner in the future.

Krill fishery management in changing Southern Ocean environment

Taking into account of impacts of ongoing climate change and ocean acidification in krill fishery management is challenging. This is because the time scale of the effects of climate change and ocean acidification is of the order of a few decades to centuries at the global scale compared to the time scale of annual turnaround for the fishery management decisions and actions at regional scales. Climate change may not necessarily affect the ecosystem in a linear manner, and it is also almost impossible to predict the state and structure of the ecosystem with the confidence that is meaningful for the year- to-year fishery management decisions and actions at regional scales. It is critical that the management is undertaken in a precautionary manner taking into account the uncertainties of the ecosystem impacts due to climate change and ocean acidification for the foreseeable future. CCAMLR must continue to update and adjust its management using the best available science and monitoring data on krill biomass and ecosystem.

KRILL FISHERY AND KRILL PREDATORS IN WAP REGION CHRISTIAN REISS

Large and pervasive changes are occurring in the physical and biological components of the Antarctic Peninsula ecosystem (Montes Hugo et al. 2009;). These changes include bottom up processes owing to climate change that can impact the system production and potential top-down effects owing to changing predator populations and human activity (). This diversity of drivers and impacts means that future monitoring will need to leverage observational platforms to provide broader spatial and temporal coverage in areas where multiple interactions are likely to occur and in periods of time outside the traditional summer sampling and monitoring periods.

Recent studies have described changes in phytoplankton productivity, zooplankton community, and fish distribution associated with climate change along the peninsula (Figure 1). Increasing open water in the western Antarctic peninsula has impacted the timing and magnitude of the spring bloom, while warming waters have increased the available habitat for salps that have increased many fold in the WAP compared to their established areas in the northern Antarctic peninsula. For ice-dependent fish species (e.g. *Pleuragramma antarctica*) that live in neritic, ice-

dominated areas and whose eggs are dependent on sea ice processes for retention and protection, sea ice declines along the peninsula have impacted their distribution and may be impacting their reproductive success (Vacchi et al. 2012; Ross et al. 2014). For species like Antarctic krill, changing patterns of ice have also altered the distribution of late season sea ice that could be critically important to recruitment success (Stammerjohn et al. 2008).

Traditional surveys of biological resources in the Antarctic Peninsula have been focused on establishing linkages between and among ecosystem components mostly by sampling for a brief time during summer or sampling more intensively over time from a single location (eg. science bases or camps) in areas where scientific resources, but all natural resources are concentrated. These temporally or spatially restricted studies have recently been augmented by the deployment of oceanographic and ecological moorings to collect detailed data in a few additional locations with high intensity and the use of autonomous vehicles to collect spatially relevant data in some areas (Bernard et al. 2014).

Monitoring programs are necessarily focused on collecting data in a repetitive manner in order to examine changes in the properties of interest (Agnew 1997). For example, the CCAMLR Environmental Monitoring Program (CEMP) routinely monitors the status and trends of a number of bird and mammal species during the summer reproductive period. The goal of that program is to understand the population dynamics in relation to changing environmental conditions, changing availability of krill, and the potential impacts of the krill fishery on them. In the Antarctic Peninsula region these monitoring efforts have historically been linked with in time with oceanographic and acoustic surveys of krill to provide a context for understanding the indices developed through the CEMP. As the fishery has expanded over the last two decades (Figure 2a) and has greatly concentrated its effort in a smaller area (Nicol et al. 2012) concerns have been raised about the potential for local effects (local depletion of resources) to impact predator populations more directly.

At the same time areas that have historically been unavailable to the fishery owing to seasonal sea ice development have become accessible during periods outside the summer period. This has, in some areas, partially explained shifts in the timing and duration of the fishery and impacts on predators outside the monitored period (Figure 2b). Recent compilations of tagging data from ARGOS, light-based geolocation, and GPS instruments placed on birds and mammals during summer and overwinter deployments have shown the spatial extent of habitat use during different reproductive phase and during presumed over winter dispersal (Hinke et al. 2017). An outcome of these tagging studies has been the demonstration of significant overlap between krill, their predators and the fishery, at a variety of spatio-temporal scales. Hinke et al. (2017) showed that these interactions were visible when penguins and seals were tagged at just a small fraction of rookeries along the Antarctic Peninsula (Fig 3). This overlap occurred both during and after the reproductive seasons of the predators and continued as these animals dispersed during winter. These observations clearly indicate that future monitoring must cover a much broader range of the annual time scale and both broader spatial scales (wherever the interactions may occur) across the peninsula and fine spatio-temporal scales (hours to days and meters to hundreds of

meters) that can answer questions regarding predator prey interactions at the individual scale to unravel the local effect of fishing, and climate change, especially the effects of sea ice decline.

This overlap has led to questions regarding the potential for the fishery to deplete krill biomass or disturb krill aggregations in local areas and thus have negative impacts on krill-dependent predators. This overlap also motivates changes to the manner in which data on krill are collected and on which we base management advice. There is a need to address basic scientific questions about local depletion or accumulation, active aggregation, and advection of krill (collectively termed “flux”), and a need to measure the local circulation. Resolving questions about krill flux through fishing areas and developing management strategies that can enable CCAMLR to meet its conservation and management objectives at a local scale seems to require data to be collected at the appropriate scales. Thus the challenge to answering these and other scale dependent questions is to design a monitoring program that couples the spatial scale of current ship-based survey designs and at the same time is able to resolve the finest scales to understand the interactions with krill, their predators and the fishery.

Properly addressing these questions regarding the predator prey fishery interactions in the Southern Ocean will require a much different approach than the historical sampling that has traditionally been the focus of research by management focused programs like the U.S. AMLR Program. This program has been focused on developing an annual time series of krill biomass and demography across a large 125 000 km² sampling area (Reiss et al. 2008). These broad scale surveys were useful to describe the temporal trends and overall relationships with the environment, the time series have also been used to link foraging success of predators to krill demographic patterns. It is clear though that these broad- scale surveys provide less information regarding the local scale effects and the predator prey interactions.

To better address questions necessary for understanding the consequences of overlap among krill, predators, and the krill fishery, and to understand the potential effects of changing krill populations owing to climate change in the Southern ocean, an autonomous program of observations may be useful and realistic to implement at this time (Handegard et al. 2012; Guihen et al. 2015; Fielding et al. 2014; Bernard et al. 2015; Heywood et al. 2014). Pivoting monitoring efforts towards a flexible program using moorings and gliders to collect data at finer time and space scales could be made comparable to historical data collected as part of ship-based monitoring efforts. However, such a program requires using both moorings and gliders as moorings can provide data that are highly resolved in time but generally cover a smaller area; in converse, gliders can sample a larger area but at a lower temporal resolution. Using both platforms in combination capitalizes on the strengths of each. Pivoting to an instrument-based research program at sea is timely (given the finer scales at which krill-predator-fishery interactions are now occurring). A revised program of research at sea will also provide data that will be useful to design and evaluate improved, spatially explicit management strategies for the krill fishery (e.g Watters et al. 2013).

An array of moorings that can collect oceanographic and acoustic data in an area where the krill fishery overlaps with penguins and pinnipeds that breed near field camps around the peninsula can be used to examine predator prey fishery interactions, and to determine the flux of krill through the area in order to inform management on the potential for local depletion of krill stocks. At the same time, a fleet of gliders equipped with acoustic instruments to quantify krill biomass, instruments to collect temperature, salinity and fluorescence, can replicate the basic aspects of the ship surveys, albeit at a different time scale given the speed at which gliders transit through the water (25km day).

Around the Antarctic Peninsula such an approach has a high probability of success for several important reasons. First, the pelagic community is largely composed of Antarctic krill, and there are few other taxa (salps, mesopelagic fish, and pteropods) that can dominate the acoustic energy in the water column (Loeb and Santora 2014, Ross et al. 2014). Thus, given the considerable work that has been conducted to describe the acoustic signature of krill over thirty years acoustic relative certainty in the delineation of krill is not a major impediment to this approach (Reiss et al. 2008; Fielding et al. 2010).

Secondly, there is a very strong correlation between the length frequency of krill in the diets of penguins at camps around the peninsula and the length of krill in net tows (Miller et al 2007). A comparison of data from both Livingston Island adjacent to the Antarctic Circumpolar current in the Southern Ocean, and King George Island, within the coastal, relatively sheltered Bransfield Strait shows both areas have strong positive correlations. This correlation means that the length frequency distribution of krill in the diets of these predators can be used to define the length range of krill used in the algorithm to determine relative krill biomass (Miller et al. 2007; Fielding et al. 2010). Finally, occasional scientific surveys, coupled with data collected by fishing vessels could also be used help to ground truth and compare the estimates derived from gliders, moorings and predator diets.

The Antarctic Peninsula continues to change owing climate driven forcing, and this has had large impacts on the ecosystem. Such effects are predicted to continue, and will impact krill populations in a number of direct and indirect ways. At the same time as these impacts on the pelagic ecology are occurring, predator prey interactions and fishery dynamics are also likely to be impacted. Thus it will be critical to understand the potential interactions and to be able to develop management strategies that can ensure that the goals international conventions are met. Increased tagging of upper tropic level krill dependent predators understand their use of habitat is critical to disentangling potential effects of climate change from fishery impacts. A well designed autonomous sampling program can effectively monitor these processes and also can provide a cost effective solution to monitoring long term climate impacts that are likely to impact the structure and function of the krill dominated community.

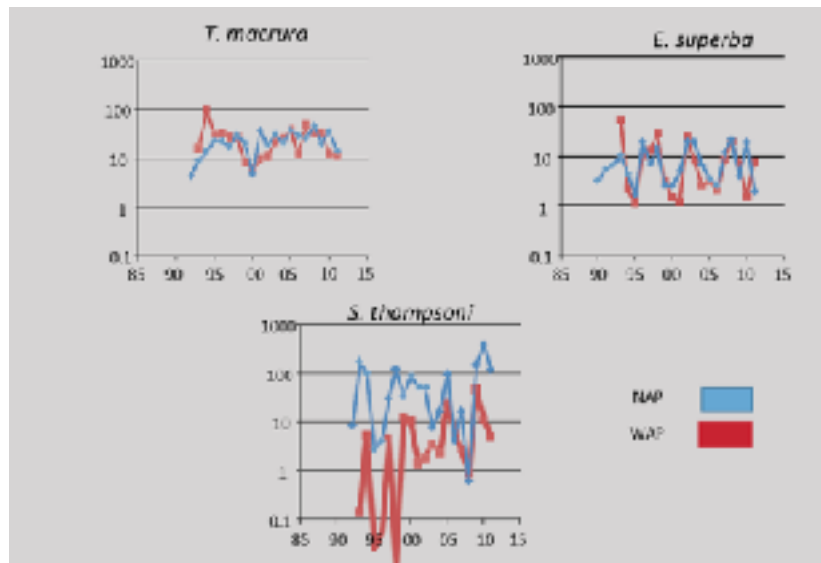


Figure 1. Temporal patterns in the abundance of three species along the northern Antarctic peninsula around the South Shetland Islands, and the western Antarctic Peninsula west of Antarctic peninsula *Thysanoessa macrura*, *Euphausia superba* and *Salpa thompsoni* abundance (no. m⁻²) in two broad areas of the Antarctic peninsula. For some species fluctuations in abundance are uncorrelated, coherent, or reflect changing abundances over time. Impacts of climate change in this region are likely to vary depending on the species of interest (LTER and AMLR unpublished data)

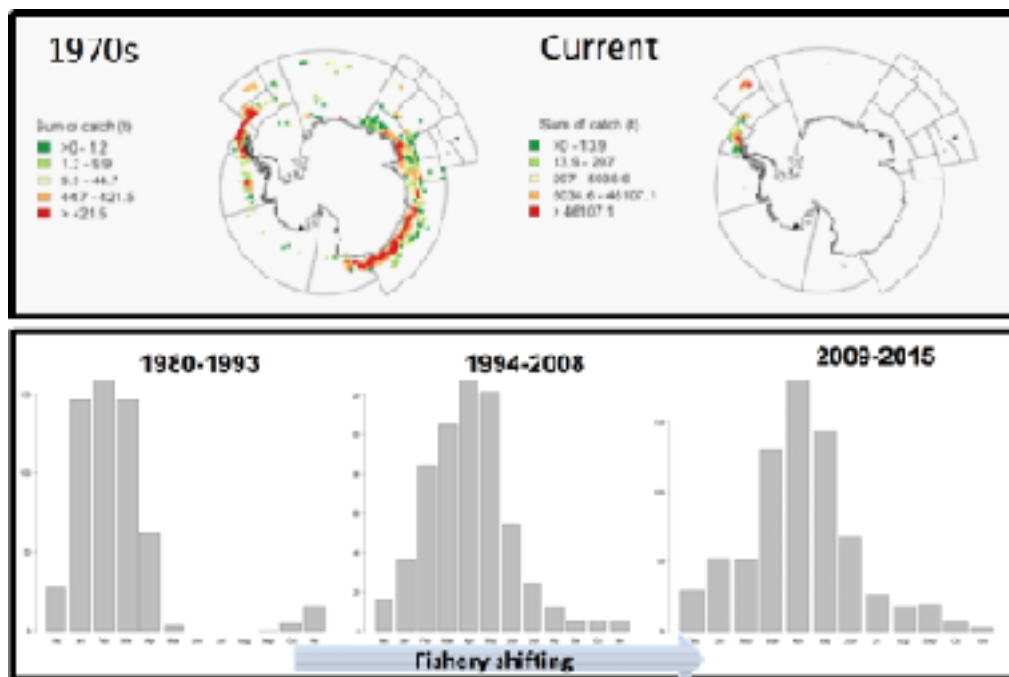


Figure 2. Distributions and sum of the krill catch around the Southern ocean between the 1970s and the mid 2000s. The fishery has concentrated over time increased catch many times in a very few areas in the Atlantic sector of the Southern Ocean. In areas around East Antarctica and the Indian Ocean, the lack of catch also contributes to a lack of knowledge about krill stocks during a period of time when the Antarctic is experiencing large changes in sea ice extent and duration. B) Seasonal shifts in the timing the fishery from mid-summer during the 1980s and 1990s to autumn and early winter reflects changes that fall outside the historical ecosystem monitoring period (both Figures from CCAMLR).

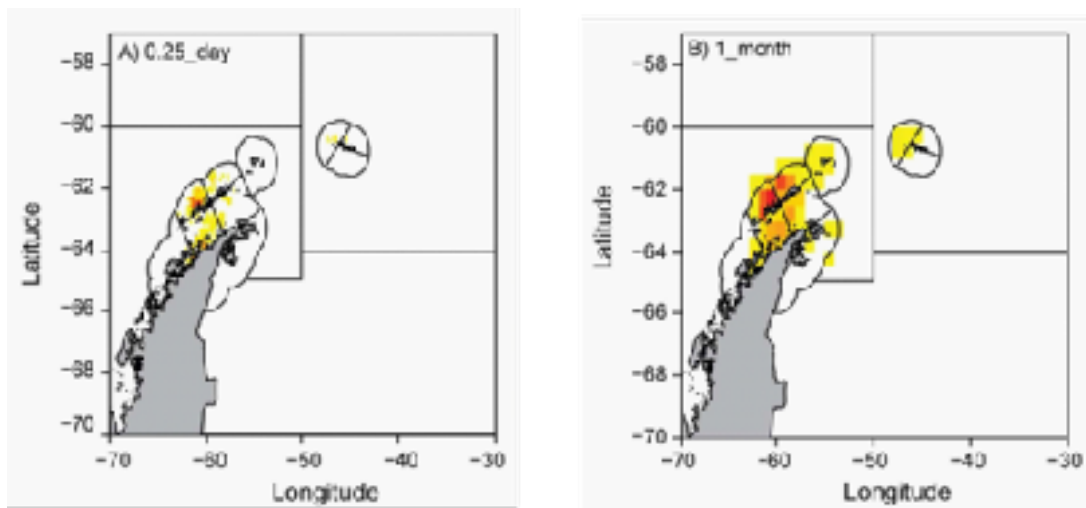


Figure 3. Overlap between predators (seals and penguins) tagged at two sites (Cape Shirreff, Livingston Island, and Copacabana, King George Island) by the U.S. AMLR Program during and after the breeding season and the krill fishery are two spatio-temporal scales A) 0.25 degree spatial grids at a daily temporal scale and (b) a 1 degree spatial grid and a 1 month temporal window. In both cases there are significant interactions between the limited numbers of tags from an extremely small subset of rookeries around the peninsula. Areas of high overlap at both daily and monthly scales (red) are focused near camps and provide ideal locations to better understand predator prey interactions using autonomous instrumentation to monitor the system over the fishing seasons (From Hinke et al. 2017).

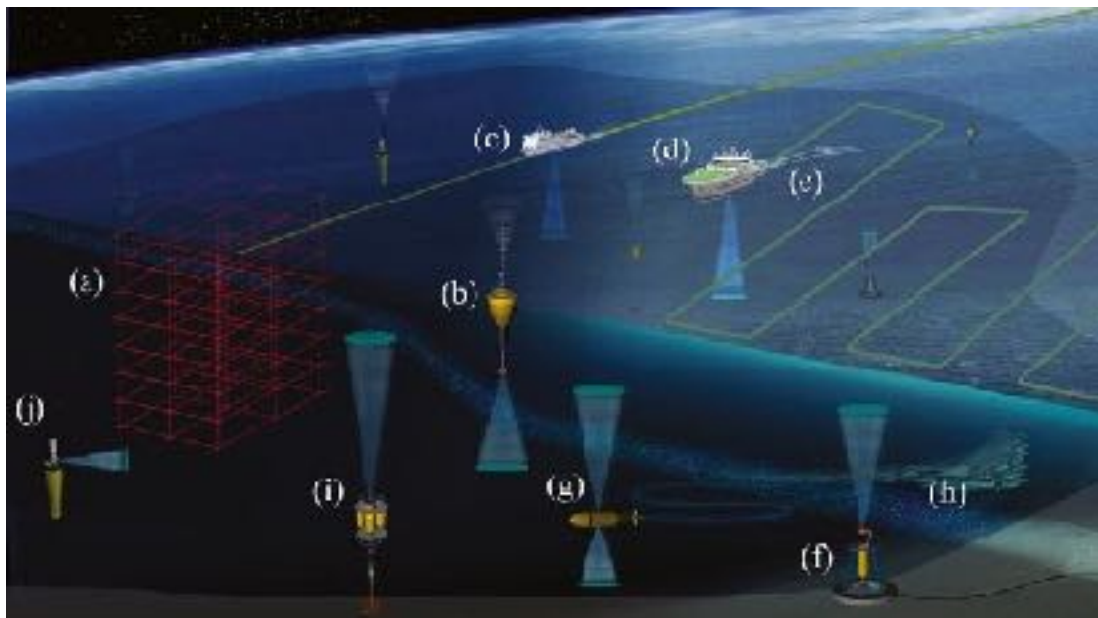


Figure 4. Hypothetical integrated observing system for collection, interpretation and modeling of ocean ecosystems. Different moored and mobile instruments collect data at a variety of spatio-temporal scales that resolve biological processes necessary to develop end to end models of the ecosystem. A) the model grid, B, F, and I, represent different moored instrument types. G, J, D and E represent ship-based or autonomous vehicles that collect data spatially, and for calibration. H represents the kinds of behaviors of the biological observation that can be resolved (modified from Kandegard et al. 2012)

Our Current Understanding of Krill off East Antarctica

Stephen Nicol

The pelagic ecosystems of the waters off East Antarctica have been studied intensively over the last 40 years. The BIOMASS surveys in the early 1980s provided information in several parts of this region (El-Sayed, 1994; Inagake et al., 1985; Miller, 1985; Miller and Montiero, 1988). Surveys of the Cosmonaut the Cooperation Seas (30°E–80°E) were conducted in the 1980s and 1990s (Pakhomov, 1993, 1995, 2000 and Pakhomov et al., 2002). Multiple surveys were conducted in the Prydz Bay region in the 1980s and 1990s (Smith et al, 1984; Hosie, 1994; Nunes-Vaz and Lennon, 1996) and two large-scale summer surveys examined the ecosystems of much of the waters off East Antarctica (30-150°E) south of 62°S (Nicol, 2000 Nicol and Meiners, 2010). More detailed reviews of the pelagic ecosystems off East Antarctica (Nicol et al., 2006, Nicol and Raymond, 2012) should be consulted for a thorough overview. This short overview concentrates on the distribution of Antarctic krill (*Euphausia superba*).

The East Antarctic coastline between 30°E and 150°E is a relatively linear coastline, but it does have some notable geographic features. There is quite extensive latitudinal variation; the coastline is as far south as 70°S in Lützow-Holm Bay and Prydz Bay and as far north as 66°S at Cape Ann (Figure 1). The two major basins, the Enderby Abyssal Plain and the Australian-Antarctic Basin, are separated by the Kerguelen Plateau, which is the major bathymetric feature in this sector. The continental shelf is cut by depressions and submarine canyons, particularly in the 30°E–80°E region. This bathymetry affects the regional oceanic circulation patterns which are, in turn, dominated by the circumpolar flow patterns of the eastward-flowing Antarctic Circumpolar Current (ACC) to the north and the much more constrained westward-flowing Antarctic Coastal Current (Bindoff et al., 2000; Meijers et al., 2010; Williams et al., 2010). These currents interact along the coastline in a series of gyres that are a product of the bathymetry and coastline morphology (Figure 2).



Figure 2. Features of the waters off East Antarctica. Bathymetry from GEBCO (2003); polar front position from Orsi et al. (1995); coastline data from the Antarctic Digital Database (SCAR 2006). The tracks of the BROKE and BROKE-West surveys are overlain on the map. Figure courtesy David Smith of the Australian Antarctic Data Centre. After Nicol and Raymond (2012)

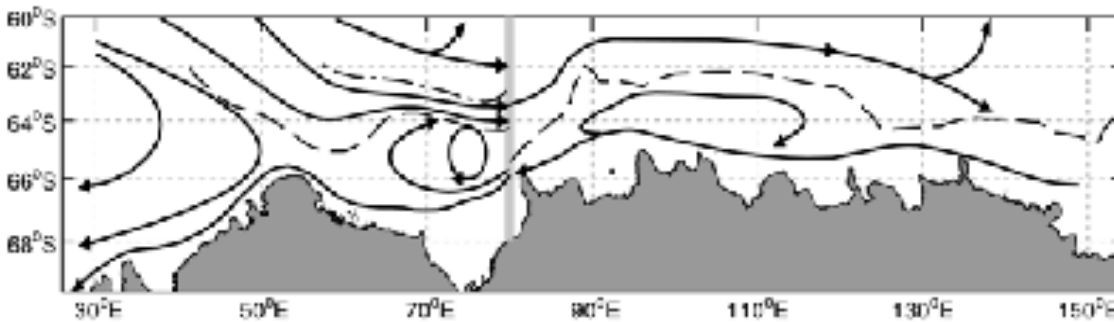


Figure 3. Cartoon of the large-scale circulation patterns off East Antarctica determined from the results of the two BROKE surveys. The dashed lines indicate the position of the Southern Boundary of the Antarctic Circumpolar Current; the dash-dotted line that of the Southern Antarctic Circumpolar Current Front (the position of this front was not determined on the BROKE voyage). The grey line indicates the boundary between the BROKE (to the east) and BROKE-West surveys. After Nicol and Raymond (2012)

This underlying circulation affects the seasonal extent of sea ice (Nicol et al., 2000) which varies considerably across this region from ~58°S at 30°E to ~62°S at 140°E (Figure 3). There are four circum-Antarctic oceanographic fronts (Figures 1 and 2): the Subantarctic Front (SAF), the Polar Front (PF), the Southern Antarctic Circumpolar Current Front (SACCF), and the Southern Boundary of the Antarctic Circumpolar Current (SBACC) (Orsi et al., 1995). The ACC is further subdivided into sub-streams by a series of fronts (Sokolov and Rintoul, 2002). These frontal zones and gyres, and the associated distribution of sea ice, have been implicated in the delineation of biological communities and in the distribution of primary production, herbivores and their predators.

Krill off East Antarctica are rarely found inshore of the shelf break (Figure 4) and there is a sharp delineation between the habitats of Antarctic krill and *E. crystallophias* at the inshore boundary of the coastal current jet (Hosie et al., 2000, Jarvis et al., 2010; Swadling et al., 2010). The Northern boundary of krill habitat is less well-defined. There is little evidence for krill occurring north of the polar front anywhere around the Antarctic (Mackintosh, 1972, 1973; Atkinson et al., 2008) and off East Antarctica suggests krill are rare north of 62°S (Mackintosh, 1973; Pauly et al., 2000; Jarvis et al., 2010). Krill are notably absent from the East Antarctic subantarctic islands; this distinguishes them from the island groups of the South Atlantic. The SACCF may well be the northern limit to krill distribution in this region (Nicol et al., 2010).

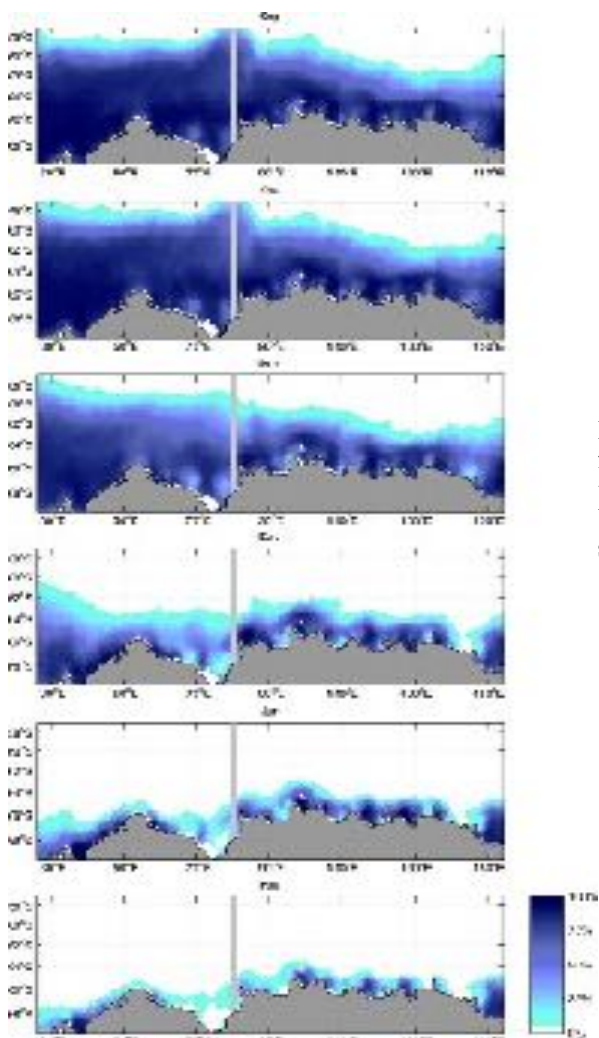


Figure 4. Mean 1979–2008 monthly sea ice concentrations from passive microwave estimates (Cavalieri et al., 1996 updated 2008). The grey line indicates the boundary between the BROKE (to the east) and BROKE-West surveys. After Nicol and Raymond (2012)

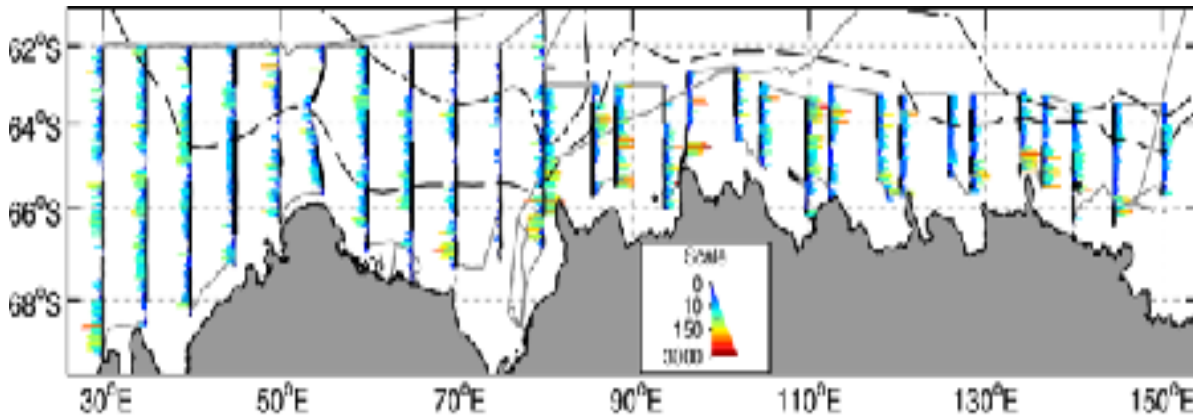


Figure 5. Acoustic estimates of abundances of Antarctic krill *Euphausia superba* from the BROKE and BROKE-West surveys off East Antarctica (Nicol and Raymond 2012). Values given are g/m², integrated over the top 145m of the water column (BROKE; Pauly et al., 2000) and top 252m of the water column (BROKE-West; Jarvis et al., 2010). The dash-dotted line shows the Southern Antarctic Circumpolar Current Front and the dashed line the Southern Boundary of the Antarctic Circumpolar Current (frontal positions from Orsi et al., 1995). After Nicol and Raymond (2012)

Ecosystem Change off East Antarctica.

Information on environmental changes off East Antarctica is less comprehensive than for regions such as the Antarctic Peninsula. There is evidence of warming and freshening of the deep water off the continental slope (Jacobs, 2006). The sea ice regime during the satellite era (1978 – present) has changed (Parkinson, 2004) with both regional increases and decreases in the length of the ice-covered season being observed. The extent of annual sea ice during this same period has slightly increased (Parkinson, 2004). Regional estimates of change in the pre-1978 era using proxy information (Curran, 2003 and de la Mare, 2008) suggest that sea ice extent may have decreased by 1.3-2.2° of latitude across this region in the middle of last century. Overall, although there have been some notable changes in the physical and chemical environment of the waters off East Antarctica, these are nowhere near as great as those changes observed in regions such as the Antarctic Peninsula (Vaughn et al., 2003) and South Georgia (Whitehouse et al., 2008).

There is limited evidence for recent biological changes in the East Antarctic region that might be associated with a changing environment (Hirawake et al., 2005, Takahashi et al., 1998). Krill surveys of the region between 1977–1990 have detected considerable inter-annual variation in densities and demographic parameters but little evidence of a long-term trend (Pakhomov, 2000). There have been no regular surveys for krill off East Antarctica so it is difficult to make inferences about long-term changes in the krill population in this area. Species of krill-dependent vertebrates in the South East Indian Ocean sector have shown evidence of decreases in population sizes (Weimerskirch et al., 2003), population increases (Goldsworthy et al., 2009, Southwell et al., 2015) and stable populations (Weimerskirch et al.,

2003). So, there is no clear signal of changes in the krill based ecosystem in this region.

Summary

The pelagic ecosystems off East Antarctica share many of the features of those off other areas of the Antarctic but there are also significant differences. There are significant oceanographic variations within the region, most notably with respect to the width of the two major current systems, the extent of sea ice and extent of the gyral systems along the coast. All of these features have distinct ecological effects and consequently it is probably appropriate to view this as a series of interrelated subregions, much as is the case for the South Atlantic.

Q/A Discussions

During the Q/A discussion, soon after the four formal presentations, the following two important avenues for further consideration by krill biologists emerged:

- (1) Since the ongoing decline of sea-ice ROUND Antarctica, either activated by EL- NINO Southern Ocean Oscillations or any other driving force, is bound to continue doe decades, more expansion of krill fisheries under CAAMLR regulations will occur. There is an opportunity for krill researchers to work with major krill fisheries operators under the ARK (Association of Responsible Krill Harvesting Companies) that was founded in 2015 to serve as an information HUB that can link CCAMLR and scientific community. This future collaboration with ARK members will enable krill researchers to obtain data not only on *E.superba* but also on other euphausiid species and krill predators (seals, baleen whales and different penguins as well as pteropods and salps. The data procured from these sources can be added to KRILLBASE and other appropriate data-bases.
- (2) The discussion also addressed pertinent questions on krill biology in conjunction with evolutionary changes in the Antarctic marine ecosystems in the light of climate change with changes in both biotic (ecosystem shifts, increase soft-bodied species such as salps, invasion of lithodiid crabs to replace echinoderms on sea floor etc.) and abiotic factors (pCO₂, ph drop, temperature, salinity, oxygen etc). The question of faunal changes, both in pelagic and benthic environment should be investigated side by side in future krill-based research cruises in the Southern Ocean, with emphasis on Ross Sea.

WHAT IS NEXT? DISCUSSION

The Krill Panel recommended the formation of a Krill Working Group that will meet in 2018 to discuss some future research cruises in 2019 and 2020 primarily in Ross Sea and also to define the research questions to be posed in these cruises by an international team of scientists. The names of potential participants are given below.

KRILL WORKING GROUP

WORKING GROUP ON “SPATIAL AND TEMPORAL TRENDS IN DISTRIBUTION AND DENSITY OF ANTARCTIC KRILL *EUPHAUSIA SUPERBA* DANA 1850, CONTRASTING OTHER EUPHAUSIID SPECIES IN THE WORLD OCEANS

1. Working Group Chair: Prof. Robert Y. George, George Institute, North Carolina, USA
2. Working Group Co-Chair - Dr. Simeon Hill, British Antarctic Survey, UK
3. Working Group Co-Chair –2: Dr. Guo-Ping Zhu, Shanghai Ocean University, China
4. Working Group Co-Chair 3. Dr. Enrique Marschoff, Argentine Antarctic Institute
5. Dr. Bettina-Meyer Co-Chair 4, Alfred Wagner Institute, Germany

Full Members*:

6. Dr. Christian Reiss, NOAA Southwest Fisheries Science Center, La Jolla, USA
 7. Dr. Steve Nicol, University of Tasmania, Hobart, Australia
 8. Dr. So Kawaguchi, Antarctic Division, Hobart, Australia
 9. Dr. Hiroto Murase, Japanese Fisheries Research Agency.
 10. Dr. Andrew Brierley, St Andrews University, Scotland
 11. Dr. Olav Rune Gode, Institute for Marine Research, Bergen, Norway
 12. Dr. Keith Reid, CCMLR Secretariat, Australia
 13. Dr. Rod Downie, World Wildlife Fund,
 14. Dr. Jo-Ellen Russell, Arizona Univ., USA
 15. Dr. Kendra Daly, Univ. of South Florida, USA
 16. Dr. Svetlana Kasatkina , Leningrad, Russia
- Those who have published peer-reviewed papers on Krill Advisors: 1. Dr. Osmund Holm Hansen, Scripps, 2. Dr. George Watters, NOAA and 3. Dr. Denzil Miller, Hobart, Australia

Associate members:

1. Dr. Angelika Brandt**, Munich Museum of Natural History, Germany
2. Dr. Rudolfo Werner, Pew Charitable Trust
3. Dr. Chris Langdon, RSMAS, Coral reefs, Univ. of Miami
4. Dr. Saba Grace, Rutgers University
5. Dr. Simon Jarman, Krill Genome Project, Portugal
6. Dr. Jason Hall-Spence***, Cold Corals, Plymouth University, UK
7. Dr. Gesche Winkler****, University of Quebec at Rimouski Canada

** Antarctic Marine Biodiversity *** Ocean Acidification ***** Arctic Krill

YOUNG INVESTIGATORS:

1. Mr. Anthony Cossio, NOAA, USA
2. Ms. Mary Kane, Univ. of Rhode Island, PhD candidate, USA
3. Mr. Jose Seco, Univ. of Aveiro, Portugal
4. Mr. Franki Perry, Plymouth Marine Lab. UK, PhD candate
5. Mr. Gregory D. Larsen, Ph.D. studnert, Duke University, NC, USA
6. Ms. Emlice, Argentinae Antarrcgtic Institute, Buenos Aires, Argentina

TASKS:

- I. Recommend Participants and Projects for the 2019 Ross Sea Expedition for research on Krill, Pteropods & Climate Change
- II. Recommend Participants and Projects for the 2019 Amundson Sea - WAP-South Georgia Expedition. (Krill Fisheries & Climate Change)
- III. Identify “Unanswered Questions and challenges Ahead” on Krill Biology , Krill Fisheries, Climate Change and Inter-annual cycles..

STEERING COMMITTEE

Bob George (Chair), 2. Keith Reid (CCAMLR, Co-chair). 3. Andy Brierfield (St Andrews, Scotland) 4. Simeon Hill (BAS, Cambridge Univ.. 5 Enrique Marschoff (Argentina), 6. G. Zhu (Shangai) 7. Kendra Daly (USF, Florida) 8. Bettina Meyer (Afred Wagoner Institute, Germany) 9 Svetlana Kesakina (Leningrad, Russia,) 10. Steve Nicol (IMAS, Australia) and 11. Rod Downie (WWF) and 12. George Watters (NOAA).

Observers: Nikki Bransome, (PCT) Poly Penhale (NSF) and Christian Fritsen (NSF)

REFERENCES

Agnew, D.J. 1997. The CCAMLR Ecosystem Monitoring Programme. *Antarctic Science*, 9 (3): 235–242

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432: 100-103

Atkinson, A. A., Siegel, V., Pakhomov, E. A., Rothery, P., Ross, R. M., Quetin, L. B., Schmidt, K., Fretwell, P., Murphy, E. J., Tarling, G. A. and Fleming, A. H. (2008). Oceanic circumpolar habitats of

Antarctic krill. *Marine Ecology Progress Series* 362:1–23.

Bernard KS, Steinberg DK (2013) Krill biomass and aggregation structure in relation to tidal cycle in a penguin foraging region off the Western Antarctic Peninsula ICES Journal of Marine Science, 70 834–849

Bergmann, H. E. 1945. The development and life history of adolescent and adult krill *Euphausia sueprba*. Discovery Report 23: 105 – 141.

Bindoff, N. L., Rosenberg, M.A., and Warner, M. J. (2000). On the circulation of the waters over the Antarctic continental slope and rise between 80 to 150°E. *Deep-Sea Research Part II: Topical Studies in Oceanography* 47(12-13):2299–2326.

Brierley, A.S., 2008. Antarctic Ecosystem: Are deep krill ecological outliers or portraits of Paradigm shift? *Current Biology* 18(6): 252 – 254.

Clarke, A. and P. Tyler, 2008. Antarctic krill feeding at abyssal depths. *Current. Biology* 18: 282 – 285..

Cavalieri, D., Parkinson, C., Gloersen, P., and H. J. Zwally (1996, updated 2008). *Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I passive microwave data*. Boulder, Colorado USA: National Snow and Ice Data Center. Digital media.

Cooper HL, Potts DC, Paytan A 2017. Effects of elevated pCO₂ on the survival, growth, and moulting of the Pacific krill species, *Euphausia pacifica*. ICES Journal of Marine Science 74:1005-1012.

Curran MAJ, van Ommen TD, Morgan VI, Phillips KL, Palmer AS (2003). Ice core evidence for sea ice decline since the 1950s. *Science* 302:1203–1206.

Deacon, G. E. R., 1982. Physical and biological zonation in the Southern Ocean. *Deep Sea Res.* 29: 1 – 15

Deacon, G. E.R. 1984. Water movement and Antarctic krill. *Journal of Crustacean Biology* 4 (Sec. N0. 1): 13 – 15.

de la Mare, W. K. (2008). Changes in Antarctic sea-ice extent from direct historical observations and whaling records. *Climatic Change*, DOI 10.1007/s10584-008-9473-2.

El-Sayed, S.Z. (1994). History, organization and accomplishments of the BIOMASS Program. In: S.Z. El-Sayed (Ed.), *Southern Ocean Ecology: The BIOMASS Perspective*, Cambridge University

Press, Cambridge, pp. 1–8.

Frazer, F. C. 1936. On the development and distribution of young stages of krill *Euphausia superba* Discovery Report 14: 3 – 190.

Fielding, S., G. Griffiths, and H. S. J. Roe. 2004. The biological validation of ADCP acoustic backscatter through direct comparison with net samples and model predictions based on acoustic-scattering models. ICES J. Mar. Sci. 61:184-200 [doi:10. 1016/ j. icesjms. 2003. 10. 011

Fielding SO, et al. (2010) The ASAM 2010 assessment of krill biomass for area 48 from the Scotia Sea CCAMLR 2000 synoptic survey. CCAMLR document WG-EMM 11/20.

G EBCO (2003). Centenary Edition of the GEBCO Digital Atlas, published on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans; British Oceanographic Data Centre, Liverpool.

George, R. Y. (editor) 1984. The Biology of the Antarctic Krill *Euphausia superba*. Journal of Crustacean Biology Vol 4 (Special No. 1): 337 pages.

George, R. Y. 2017. Potential Impact of Carbonate Chemistry (pCO₂) on krill and krill- based Food-Chain in the Southern Ocean with emphasis on Embryogenesis of Antarctic Krill. *Biogeosciences* (In Press).

George, R. Y. and J. O. Stromberg, 1985. Development of eggs of Antarctic krill *Euphausia superba* in relation to pressure. *Polar Biology* 4: 125 – 133.

George, R. Y. and L. B. Hayden. 2018. Krill distribution in relation to warming as evidenced from a loss of Ice Shelf (1972 – 2003) in Amundsen Sea and threats to krill egg development by changing carbonate chemistry of the Southern Ocean. In: Proceedings of the 3rd International Krill Symposium in St Andrews, edited by Andrew Broderley and Keith Reid. *Canadian Journal of Fisheries and Aquatic Science*.

Goldsworthy, S.D., McKenzie, J., Page, B., Lancaster, M.L., Shaughnessy, P.D., Wynen, L.P., Robinson, S.A., Peters, K.J., Baylis, A.M.M., McIntosh, R.R. (2009). Fur seals at Macquarie Island: post-sealing colonisation, trends in abundance and hybridisation of three species *Polar Biology*, 32: 1437-1486

Guihen D, Fielding S, Murphy EJ, Heywood KJ, Griffiths G. (2014) An assessment of the use of ocean gliders to undertake acoustic measurements of zooplankton: the distribution and density of Antarctic krill (*Euphausia superba*) in the Weddell Sea. *Limnol. Oceanogr.: Methods* 12, 2014, 373–389

Hamner WM, Hamner PP 2000. Behaviour of Antarctic krill (*Euphausia superba*): schooling, foraging, and antipredatory behavior. *Canadian Journal of Fisheries and Aquatic Sciences* 57

(Suppl.3):192–202.

Hinke JT, Cossio AM, Goebel ME, Reiss CS, Trivelpiece WZ, Watters GM (2017) Identifying Risk: Concurrent Overlap of the Antarctic Krill Fishery with Krill-Dependent Predators in the Scotia Sea. PLoS ONE 12(1): e0170132. doi:10.1371/journal.pone.0170132

Hirawake, T. Odate, T. and Fukuchi M. (2005). Long-term variation of surface phytoplankton chlorophyll *a* in the Southern Ocean during 1965–2002. *Geophysical Research Letters*, 32, L05606, doi:10.1029/2004GL021394.

Hosie, G.W. (1994). The macrozooplankton communities of the Prydz Bay region, Antarctica. In: S.Z. El-Sayed (Ed.), *Southern Ocean Ecology: The BIOMASS Perspective*, Cambridge University Press, Cambridge, pp. 93–123.

Hosie, G.W., Schultz, M. B., Kitchener, J.A., Cochran, T.G., and Richards, K. (2000). Macrozooplankton community structure off East Antarctica (80-150° East) during the Austral summer of 1995/96. *Deep Sea Research Part II: Topical Studies in Oceanography* 47:2437–2463.

Inagake, D., Matsuura, N., and Kurita, Y. (1985). Stock and quantitative distribution of the Antarctic krill (*Euphausia superba* Dana) in the Antarctic Ocean South of Australia in January and February 1984. *Transactions of the Tokyo University of Fisheries*, 6, 139–147.

Jacobs, S. (2006). Observations of change in the Southern Ocean. *Phil. Trans. R. Soc. A* (2006) 364, 1657–1681

Jarvis, T., van Wijk, E., Kelly, N., Kawaguchi, S., and Nicol, S. (2010). Biomass of Antarctic krill (*Euphausia superba*) off East Antarctica (30-80°E) in January-March 2006. *Deep-Sea Research Part II: Topical Studies in Oceanography* 57, (9-10), 916-933.

Hamner WM, Hamner PP 2000. Behaviour of Antarctic krill (*Euphausia superba*): schooling, foraging, and antipredatory behavior. *Canadian Journal of Fisheries and Aquatic Sciences* 57 (Suppl.3):192–202.

Handegard NO, et al. (2012) Towards an acoustic based coupled observation and modelling system for monitoring and predicting ecosystem dynamics of the open ocean. *Fish Fisher.* 14:605-615

Kawaguchi S, Nicol S, 2007. Learning about Antarctic krill from the fishery. *Antarctic Science* 19, 219–230.

Kawaguchi S, Nicol S, Press AJ (2009) Direct effects of climate change on the Antarctic krill fishery.

Fish Manage Ecol 16:424-427.

Kawaguchi S, Ishida A, King R, Raymond B, Waller N, Constable A, Nicol S, Wakita M, Ishimatsu A (2013) Risk maps for Antarctic krill under projected Southern Ocean acidification. *Nature Climate Change* 7:843-847

Kawaguchi S, Kurihara H, King R, Hale L, Berli T, Robinson JP, Ishida A, Wakita M, Virtue P, Nicol S, Ishimatsu A (2011) Will krill fare well under Southern Ocean acidification? *Biology Letters* 7:288-

Kawaguchi, S., Nicol, S., Virtue, P., Davenport, S. R., Casper, R., Swadling, K. R., and Hosie, G. W. (2010). Krill demography and large scale distribution in the Western Indian Ocean sector of the Southern Ocean (CCAMLR Division 58.4.2) in Austral summer of 2006. *Deep-Sea Research Part II: Topical Studies in Oceanography* 57, 9-10, 934-937.

Loeb VJ and Santora JA 2015. Climate variability and spatiotemporal dynamics of five Southern Ocean krill species. *Progress in Oceanography* 134:93-122.

Loeb VJ and Santora JA 2015. Climate variability and spatiotemporal dynamics of five Southern Ocean krill species. *Progress in Oceanography* 134:93-122.

Mackintosh, N. A. (1972). Life cycle of Antarctic krill in relation to ice and water conditions. *Discovery Rep.*, 36:1–94.

Mackintosh, N. A. (1973). Distribution of post-larval krill in the Antarctic. *Discovery Rep.*, 36:95–156.

Marr, J. W. S. (1962). The natural history and geography of the Antarctic krill (*Euphausia superba* Dana), *Discovery Rep.*, 32:33–464.

Mackintosh, N.C., 1972. Life cycle of antarctic krill in relation to ice and water conditions. *Discovery Reports* 16: 1 – 94.

Meijers, A. J. S., Klocker, A., Bindoff, N. L., Williams, G. D., and Marsland, S. J. (2010). The circulation and water masses of the Antarctic shelf and continental slope between 30 and 80E. *Deep-Sea Research Part II: Topical Studies in Oceanography* 57, 9-10, 723-737.

Micol T. and P. Jouventin (2001). Long-term population trends in seven Antarctic seabirds at Pointe Géologie (Terre Adélie). Human impact compared with environmental change. *Polar Biology* 24:175–185.

Miller, D. G. M. (1985). The South African SIBEX-I Cruise to Prydz Bay region, 1984. *South African Journal of Antarctic Research* 15:33–41.

Miller, D. G. M. and Monteiro, P.M.S. (1988). Variability in the physical and biotic environment of the Antarctic krill (*Euphausia superba* Dana), south of Africa: Some results and a conceptual appraisal of important interactions. In *Antarctic Ocean and Resources Variability*, D. Sahrhage, ed. Springer-Verlag, Berlin Heidelberg, pp. 245–257.

Miller AK, Trivelpiece WZ. Chinstraps alter foraging and diving behavior in response to the size of their principle prey, Antarctic krill. *Mar Biol.* 2008; 154: 201±208.

Nicol, S., Ed. (2000). BROKE: A multidisciplinary survey of the waters off east Antarctica (80-150°E). *Deep-Sea Research Part II: Topical Studies in Oceanography* 47 (12-13):2281–2613.

Nicol, S. 2006. Krill, Currents, and Sea Ice: *Euphausia superba* and Its Changing Environment. *Bioscience* 56 (@): 111 – 120.

Nicol S. and Meiners, K., Eds. (2010). BROKE-West: a multidisciplinary survey of the waters off East Antarctica (30-80E). *Deep-Sea Research Part II: Topical Studies in Oceanography* 57, 9-10, 693-991.

Nicol, S., Pauly, T., Bindoff, N.L., Wright, S.W., Theile, D., Hosie, G.W., Strutton, P.G., Woehler, E. (2000). Ocean circulation off East Antarctica affects both ecosystem structure and sea-ice extent. *Nature* 406:504–507.

Nicol, S., Worby, A. P., Strutton, P. G. and Trull, T. W. (2006). Oceanographic influences on Antarctic ecosystems: a summary of observations and insights from East Antarctica (0°-150°E). Chapter 37 in Volume 14B of *The Sea*, ed. A. Robinson, Harvard University Press, 778pp

Nicol, S. Meiners, K., and Raymond, B. (2010). BROKE-West, a large ecosystem survey of the South West Indian Ocean sector of the Southern Ocean, 30-80°E (CCAMLR Division 58.4.2). *Deep-Sea Research Part II: Topical Studies in Oceanography* 57, 9-10, 693-700.

Nicol, S. and Raymond, B. (2012) East Antarctic Ecosystems. In *Antarctica: An Extreme Environment in a Changing World*, Wiley Press.

Nicol S, Foster J, Kawaguchi S. The fishery for Antarctic krill recent developments. *Fish Fish.* 2012; 13: 30±40.

Nunes Vaz, R., and Lennon, G. (1996). Physical oceanography of the Prydz Bay region. *Deep-Sea Research* 43:603–641.

Orsi, A. H., T. Whitworth III, and W. D. J. Nowlin (1995). On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Research* 42:641–673.

Pakhomov, E. A. (1993). The faunistic complexes of macroplankton in the Cooperation Sea (Antarctica). *Antarctica*, 32:94–110 (in Russian).

Pakhomov, E. A. (1995). Demographic studies of Antarctic krill (*Euphausia superba*) in the Cooperation and Cosmonaut Seas (Indian sector of the Southern Ocean). *Marine Ecology Progress Series* 119 (1–3):45–61.

Pakhomov, E. A. (2000). Demography and life cycle of Antarctic krill, *Euphausia superba* in the Indian sector of the Southern Ocean: long-term comparison between coastal and open-ocean regions. *Can. J. Fish. Aqu. Sci.*, 57 (Supplement S3):68–90.

Pakhomov, E. A., Froneman, P.W., and Perissinotto, R. (2002). Salp/krill interactions in the Southern Ocean: spatial segregation and implications for the carbon flux. *Deep Sea Research Part II: Topical Studies in Oceanography* 49: 1881–1907.

Parkinson CL (2004) Southern Ocean sea ice and its wider linkages: insights revealed from models and observations. *Antarctic Science* 16(4):387–400

Pauly, T., Nicol, S., and Higginbottom, I. (2000). Distribution and abundance of Antarctic krill (*Euphausia superba*) off East Antarctica (80-150° East) during the Austral summer of 1996. *Deep Sea Research Part II: Topical Studies*

Reid K, Sims M, White RW, Gillon K. 2004. Spatial distribution of predator/prey interactions in the Scotia Sea: implications for measuring predator/fisheries overlap. *Deep-Sea Research II* 51:1383–96.

Reiss, C. S., A. M. Cossio, V. Loeb, and D. A. Demer. 2008. Variations in the biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996-2006. *ICES J. Mar. Sci.* 65:497-508 [doi:10.1093/icesjms/fsn033]

Ross RR, Quetin LB, Newberger T, Shaw CT, Jones JL, Oakes SA, Moore KJ (2014) Trends, cycles, interannual variability for three pelagic species west of the Antarctic Peninsula 1993–2008 *MEPS* Vol. 515: 11–32, 2014

Ross RM, Quetin LB, Martinson DG, Iannuzzi RA, Stammerjohn SS, Smith RC (2008) Palmer LTER: patterns of distribution of five dominant zooplankton species in the epipelagic zone west of the Antarctic Peninsula, 1993–2004. *Deep-Sea Res II* 55: 2086–2105

Saba GK, Schofield O, Torres JJ, Ombres EH, Steinberg DK (2012) Increased feeding and nutrient excretion of adult Antarctic krill, *Euphausia superba*, exposed to enhanced carbon dioxide (CO₂). *PLoS One* 7: e52224.

Siegel V, Loeb V 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Marine Ecology Progress Series* 123:45-56.

Sperfeld E, Mangor-Jensen A, Dalpadado P 2014. Effect of increasing sea water pCO₂ on the northern Atlantic krill species *Nyctiphanes couchii*. *Marine Biology*, 161: 2359–2370. *Oceanography* 47 (12-13):2465–2488.

Smith, N. R., Zhao Qian, D., Kerry, K.R., and Wright, S. (1984). Water masses and circulation in the region of Prydz Bay, Antarctica. *Deep-Sea Research*, 31:1121–1147.

Sokolov, S. and Rintoul, S. (2002). Structure of Southern Ocean fronts at 140°E. *Journal of Marine Systems* 37(1-3):151–184.

Sokolov, S., and Rintoul, S. R. (2007). On the relationship between fronts of the Antarctic Circumpolar Current and surface chlorophyll concentrations in the Southern Ocean. *J. Geophys. Res.*, 112, C07030, doi:10.1029/2006JC004072

Southwell, C., Emmerson, L., McKinlay, J., Newbery, K., Takahashi, A., Kato, A., Barbraud, C., DeLord, K. and Weimerskirch, H., 2015. Spatially extensive standardized surveys reveal widespread, multi-decadal increase in East Antarctic Adélie penguin populations. *PloS one*, 10(10), p.e0139877.

Stammerjohn SS, Martinson DG, Smith RC, Yuan X, Rind D (2008) Trends in Antarctic annual sea ice retreat and advance and their relation to ENSO and Southern Annular Mode variability. *J Geophys Res* 113: C03S90

Swadling, K., Kawaguchi, S., and Hosie, G. W. (2010). Antarctic zooplankton community structure during BROKE-West (30E – 80E), January – February 2006. *Deep-Sea Research Part II: Topical Studies in Oceanography* 57, 9-10, 887-904

Takahashi K, Tanimura A, Fukuchi M (1998). Long-term observation in zooplankton biomass in the Southern Ocean

Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proc Natl Acad Sci USA* 108: 7625–7628

Vacchi M, DeVries AL, Evans CW, Bottaro M, Ghigliotti L, Cutroneo L, Pisano E (2012) A nursery area for the Antarctic silverfish *Pleuragramma antarcticum* at Terra Nova Bay (Ross Sea): first estimate of distribution and abundance of eggs and lar

Vaughan D. G., Marshall G. J., Connolley W. M., Parkinson C. L., Mulvaney R., Hodgson D. A., King J. C., Pudsey C. J. and Turner, J. (2003). Recent rapid regional climate warming on the Antarctic Peninsula. *Climatic Change* 60(3), 243-274.

Watters GM, Hill SL, Hinke JT, Matthews J, Reid K. 2013. Decision making for ecosystem-based management: evaluating options for a krill fishery with an ecosystem dynamics model. *Ecological Applications* 23:710–25.

Weimerskirch H., Inchausti P., Guinet C., and Barbraud C. (2003). Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science* 15(2):249–256.

Whitehouse, M. J., Meridith, M. P., Rothery, P., Ward, P., and Korb, R. E. (2008). Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: Forcings, characteristics and implications for lower trophic levels. *Deep-Sea Research I* 55:1218– 1228

Williams, G. D., Nicol, S., Bindoff, N. L., Aoki, S., Meijers, A., Marsland, S., Klocker, A., and Iijima, Y. (2010). Surface oceanography of BROKE-West, along the Antarctic Margin of the South-West Indian Ocean (30°-80°E). *Deep-Sea Research Part II: Topical Studies in Oceanography* 57, 9-10, 738-747.