Distributions of Euphausia Superba, Euphausia Crystallorophias, and Pleuragramma Antarticum with Correlations to Environmental Variables in the Western Ross Sea, Antarctica

Linnea Brynn Davis

Old Dominion University

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DISTRIBUTIONS OF

_EUPHAUSIA SUPERBA, EUPHAUSIA CRYSTALLOROPHIAS,_

_AND PLEURAGRAMMA ANTARCTICUM_

WITH CORRELATIONS TO ENVIRONMENTAL VARIABLES

IN THE WESTERN ROSS SEA, ANTARCTICA

by

Linnea Brynn Davis
B.S. May 2014, Old Dominion University

A Thesis Submitted to the Faculty of
Old Dominion University in Partial Fulfillment of the
Requirements for the Degree of

MASTER OF SCIENCE

OCEAN AND EARTH SCIENCES

OLD DOMINION UNIVERSITY
December 2016

Approved by:

Eileen E. Hofmann (Director)
Mark J. Butler (Member)
Ari S. Friedlaender (Member)
John M. Klinck (Member)
Peter N. Sedwick (Member)
ABSTRACT

DISTRIBUTIONS OF *EUPHAUSIA SUPERBA*, *EUPHAUSIA CRYSTALLOROPHIAS*, AND *PLEURAGRAMMA ANTARCTICUM* WITH CORRELATIONS TO ENVIRONMENTAL VARIABLES IN THE WESTERN ROSS SEA, ANTARCTICA

Linnea Brynn Davis
Old Dominion University, 2016
Director: Dr. Eileen E. Hofmann

Antarctic krill (*Euphausia superba*), crystal krill (*Euphausia crystallorophias*), and Antarctic silverfish (*Pleuragramma antarcticum*) are key mid-trophic level species in the Ross Sea food web that provide connectivity between primary production and the upper trophic levels. Distributions of these species were constructed from net-based and acoustic observations collected in the western Ross Sea from 1988-2004. Distributions of environmental conditions in the Ross Sea were obtained from a high-resolution circulation model (temperature, mixed layer depth, surface speed) and satellite-derived observations (chlorophyll, sea ice cover). These distributions were analyzed with a range of statistical methods to determine the extent to which species distributions are determined by environmental conditions. The results showed that each species occupies a localized habitat defined by different environmental characteristics. Antarctic krill are concentrated along the northwestern shelf break and prefer deep areas overlying warm water at depth, slow surface speeds, and proximity to the shelf break. Within this habitat, krill biomass is associated with deeper mixed layers. Crystal krill and Antarctic silverfish are concentrated in Terra Nova Bay and prefer southwesterly locations, coastal proximity, cold water temperatures, and slow surface speeds. Within Terra Nova Bay, crystal krill biomass is
associated with cold temperatures and northerly latitudes. Antarctic silverfish biomass is associated with low chlorophyll. The Antarctic krill habitat off the shelf break coincides with the occurrence of Circumpolar Deep Water at depth, which is important for early life stages. The crystal krill and Antarctic silverfish habitat in Terra Nova Bay coincides with the coastal polynya, sea ice, cold water temperatures, and slow surface speeds that are needed for their early life stages. The habitat characteristics obtained for the three species provide a basis for projecting potential changes resulting from climate change. The habitats identified for the three species delineate regions of the Ross Sea that deserve focused management and inform the selection of regions for marine protected areas that support ecosystem level conservation plans.
Copyright, 2016, by Linnea Brynn Davis, All Rights Reserved.
This thesis is dedicated to all the women in science.

And to the researchers who stray from the beaten path of tropical science.

This thesis is also dedicated to the idea that graduate school is easy.

It's like riding a bike.

Except the bike is on fire. And the ground is on fire.

And everything is on fire. And you're in hell.

Just kidding! It's not that bad.

😊
ACKNOWLEDGMENTS

There are many people who have contributed to the success of my master’s degree at Old Dominion University. I would initially like to thank Julie Morgan. Had it not been for her encouragement and welcoming personality at the Oceans Technology meeting in 2012, I would have never met my primary advisor Dr. Eileen E. Hofmann, and maybe never would have gone to graduate school – to you Julie, I owe my success. You paved the pathway of this yellow brick road.

The completion of this master’s thesis would not have been possible without the support from my five committee members: Dr. Eileen E. Hofmann, Dr. John M. Klinck, Dr. Ari S. Friedlaender, Dr. Peter N. Sedwick, and Dr. Mark J. Butler IV. Thank you all for your endless patience and guidance in helping answer my hundreds of questions throughout this research.

I would like to isolate and expressly recognize Dr. Eileen E. Hofmann for her generous support, praise, and supervision over our four-year collaboration. She has gone above and beyond the normal advisor and deserves special recognition. Through her stories, expert advice, recommendations, patience, insight to countless topics including research cruises, extensive knowledge of all ecosystems, and academia, and lastly, her representation and demonstration of what a woman in science can accomplish - she is the reason for my success and I cannot put into words how thankful I am to have worked with her. Most importantly, she has taught me that science is not always a linear trend but more like a roller coaster with many loops and twists. Her strong leadership skills and mentorship have deeply resonated with me and pushed me to become a better scientist. I
am lucky to have worked under her wing and witnessed the work of a wolf in a field of lambs.

The results from my thesis, aka “spectacular contribution to science and life as we know it”, would not be possible without the mathematical guidance, patience, generous Matlab magic, and pure brilliance from Dr. John Klinck. Without you, I would still be attempting to locate the Ross Sea on a map.

I would like to extend my gratitude to my other committee members: Ari Friedlaender – a huge thank you for answering my endless questions relative to ArcGIS and thank you for expressing such interest in my thesis, Peter Sedwick - thank you for your contributions relative to the Ross Sea ecosystem and for your input towards making a stronger thesis, and Mark Butler – thank you for your statistical input and bravery for accepting to be on a committee for a thesis that is far away from your Caribbean research.

I would also like to recognize and thank Mike Dinniman and Andrea Piñones for their encouragement, friendship, and contributions to this thesis. Many of the results and accomplishments from this thesis would not have been possible without your assistance. An enormous and sincere thank you to the both of you!

I would like to thank Nate P. and my family – my loving support system, for always being proud of me, and never once suggesting that girls are not smart enough for science. I would not be where I am today without your emotional and financial support. Thank you Mom and Dad for sending me to college. Every dollar was spent on getting me where I am today - but some did go to beer – and whiskey - all worth it nonetheless.

I would like to recognize my graduate school friends, my confidants: Mary Wolfrey, Amanda Laverty, Rachel McMahon, Andrew Foor, Brett Buzzanga, and Praveen Kumar. We
all started this graduate school roller coaster together and it’s because of our beer, late night study sessions, companionship, words of encouragement, and teamwork that we are still alive. Graduate school wouldn’t be nearly as fun and successful without you amigos.

Lastly I would like to thank Mr. Chesson, my 10th grade oceanography teacher, for introducing me to the magnificent world within the ocean and lighting the fire for my passion of marine science. You were the start of it all.

This study was supported by the National Science Foundation, Office of Polar Programs grant numbers ANT-0944174 and ANT-0838911.
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CHAPTER 1

INTRODUCTION

The Ross Sea (Fig. 1) is one of the most pristine and least anthropogenically affected continental shelf systems on Earth (Halpern et al. 2008). It is among the most biologically productive regions within the Southern Ocean (Arrigo et al. 1998b, Arrigo et al. 2008), contributing about 30% (23.4 ± 9.98 Tg C yr⁻¹) of the annual Southern Ocean shelf production (66.1 Tg C yr⁻¹) (Arrigo et al. 2008). Recent estimates suggest that the Ross Sea is also a major CO₂ sink (Smith et al. 2012). The primary production of the Ross Sea supports a complex and diverse food web that includes a suite of cetacean and other apex predators (Pinkerton et al. 2010, Ballard et al. 2012, Smith et al. 2012). Two species of krill, *Euphausia superba* (Antarctic krill, Fig. 2a) and *Euphausia crystallorophias* (crystal krill, Fig. 2b), and one fish species, *Pleuragramma antarcticum* (Antarctic silverfish, Fig. 2c), account for the majority of the mid-trophic level biomass in the Ross Sea, and provide an important link between primary production and upper trophic levels (Daly & Macaulay 1988, Ainley et al. 2006, Smith et al. 2007, Pinkerton et al. 2010).
Fig. 1. (a) Map of Antarctica showing the study region (red box) in the western Ross Sea and (b) enlarged map of study area showing krill (red circles) and silverfish (yellow circles) sample locations used in this study. Bottom bathymetry data are from NOAA, National Centers for Environmental Information; International Bathymetric Chart of the Southern Ocean and General Bathymetric Chart of the Oceans (GEBCO_08).

Fig. 2. Primary mid-trophic level species in the Ross Sea; (a) Adult *Euphausia superba*, (b) Adult *Euphausia crystallorophias*, and (c) Larval *Pleuragramma antarcticum*. Photo credit: Antarctic Marine Living Resources Program (AMLR)
Many of the upper level apex predators (e.g., penguins, seals, and cetaceans), fish, and other mid-trophic level species in the Ross Sea depend directly or indirectly on krill and Antarctic silverfish as their primary food source (Fig. 3; Pinkerton et al. 2010, Smith et al. 2012, Pinkerton & Bradford-Grieve 2014). This dependency on a few mid-trophic level species sets up a “wasp-waist” foodweb structure in the Ross Sea, in which these few species link and control energy flow between low and high trophic levels (Bakun 1996). The krill and silverfish exert a top-down control on their prey and a bottom-up control on their predators (Ainley et al. 2015). As a result, changes in distribution, abundance, and relative availability of these three species affect all trophic levels. For example, reduced abundance of crystal krill and Antarctic krill in late austral summer resulting from intense foraging by Adélie penguins, minke whales, and fish-eating killer whales, was linked to shifts in penguin diet, increased penguin foraging trip duration, decreased cetacean abundance, and decreased grazing pressure on phytoplankton (Ainley et al. 2006, 2015). A further consequence was that Antarctic silverfish, which also prey on crystal krill, became cannibalistic (Ainley et al. 2006). Reduced availability of krill and Antarctic silverfish can also result in diet switching to food sources with lower caloric value (e.g., squid and salps), which reduces growth rates (e.g., albatross chicks; Clarke & Prince 1980, Prince & Ricketts 1981). These studies illustrate that top down predation pressure can regulate the distributions of krill and silverfish (Ainley et al. 2006, 2015). In turn, the availability of these three species to the food web is influenced by their habitat requirements and environmental conditions.
Fig. 3. Ross Sea food web showing relative trophic levels, flow of organic carbon (arrows), and proportional biomass of individual species and groups (indicated by size of box). Figure from Pinkerton et al. (2010)

Crystal krill and Antarctic silverfish are associated with sea ice, which provides food and a nursery region for eggs and early life stages (Laws 1985, Kellerman 1986b, Daly & Macaulay 1988), and these ice-obligate species tend to be found in neritic, ice-covered regions (Marr 1962, Hubold 1984, Hubold 1985, Kellerman 1986a, Hubold & Ekau 1987, Thomas & Green 1988, Hosie 1991, Pakhomov & Perissinotto 1996). For Antarctic krill, the presence of warm Circumpolar Deep Water (CDW) at depth is essential for completion of their early life history (Hofmann et al. 1992, Hofmann & Hüsrevoğlu 2003), and this species tends to be found in regions where CDW is present (Quetin & Ross 1984, Azzali & Kalinowski 2000, Sala et al. 2002, Ashijan et al. 2004, Lawson et al. 2004). However, these
general distributions exhibit considerable spatial variability between seasons and across the Southern Ocean (Azzali & Kalinowski 2000, Siegel 2005). Studies have considered relationships between krill abundance with different environmental variables such as temperature, oxygen concentration, and salinity among others. However, predictable relationships that are stable between areas and years have yet to be determined, and the extent to which these organism distributions are related to environmental conditions is unknown.

The warming of atmospheric temperatures along the west Antarctic Peninsula has already affected phytoplankton species assemblages and primary production, and these changes have in turn affected the abundance and availability of Antarctic krill and the distribution of dependent predators (Moline et al. 2004, Montes-Hugo et al. 2009). Projected changes in environmental conditions in the Ross Sea over the next decades to century suggest warming of atmospheric temperatures, reductions in summer sea ice cover, shallower mixed layers, reduced inputs of CDW, and increased primary production (Smith et al. 2014b). Thus, understanding the factors influencing current krill and Antarctic silverfish distributions will allow projections of changes that may occur in their distributions in response to changing environmental conditions in the Ross Sea, and are required to understand associated changes to larger ecosystem and biogeochemical cycles.

This study addresses two specific research questions. The first question, **What are the distributions of the three key mid-trophic level species in the western Ross Sea,** is used to test a hypothesis that these species are or are not randomly distributed. The second question, **To what extent are the distributions of the three mid-trophic level species related to environmental variables,** is used to test a hypothesis about the extent
to which the species’ distributions are correlated with a range of environmental variables. These research questions are addressed by constructing distributions of Antarctic krill, crystal krill, and Antarctic silverfish in the western Ross Sea, and using these with a range of environmental variables that define habitat characteristics develop statistically-based quantitative relationships.

The next chapter provides background information on physical and biological aspects of the Ross Sea. The distributions of the three species were constructed from data sets collected in the western Ross Sea between 1988 and 2004 as described in Chapter 3. The environmental variables were obtained from a range of sources that include satellite and model-based simulations and are described in Chapter 3. This chapter also provides details of the statistical approaches used to describe relationships between the three species and environmental distributions. The distributions and quantitative results of the analyses are given in Chapter 4. Chapter 5 places the results of this study into the context of current understanding of mid-trophic level species’ distributions in the Ross Sea. Chapter 6 provides conclusions from this study.
CHAPTER 2

BACKGROUND ON THE ROSS SEA

2.1 BATHYMETRY AND SEA ICE

The Ross Sea, with an area of nearly 466,000 km², accounts for about 18% of the Antarctic continental shelf (Picco et al. 2000, Smith et al. 2012). It is bounded by Victoria Land to the west (170°E), by the Edward VII Peninsula (155°W) to the east, and the Ross Ice Shelf to the south (Fig. 1). The northern boundary is the westward flowing limb of the Ross Sea gyre, which provides connectivity with the eastward flowing Antarctic Circumpolar Current. The Ross Sea continental shelf is relatively deep (mean depth 450-530 m) and is marked by shallow banks and deep troughs (Picco et al. 2000, Smith et al. 2012).

The seasonal sea ice cycle in the Ross Sea oscillates between nearly complete coverage in the austral winter to open water in summer (January and February), except in the eastern region (Smith et al. 2012). Sea ice begins to develop in March, and retreat begins in late November. The winter sea ice is characterized by polynyas (open regions in sea ice), which are produced by warm water at depth (sensible heat) and by offshore katabatic winds that blow from the Antarctic continent over the Ross Sea (latent heat export). The Ross Sea polynya, which results from both formation processes, is the largest (~25,000 km²) polynya, found along the Ross Ice Shelf, and expands rapidly over the central Ross Sea in December. The Terra Nova Bay polynya in the western Ross Sea remains open during the winter due to the offshore katabatic winds. The polynyas, also known as “ice
factories” (Morales Maqueda et al. 2004), produce and export sea ice to the central Ross Sea.

2.2 CIRCULATION AND WATER MASSES

The circulation just north of the Ross Sea shelf slope consists of the clockwise Ross Sea Gyre, which is composed of the eastward flowing Antarctic Circumpolar Current to the north, a westerly flowing current along the shelf break (Fig. 4), a northern boundary current along the Victoria Land coast in the western Ross Sea, and southerly flow in the eastern Ross Sea (Orsi & Wiederwohl 2009, Smith et al. 2014b). Circulation over the continental shelf consists of two clockwise rotating gyres. Superimposed on this circulation is flow that exchanges shelf and oceanic water across the shelf break (Fig. 4). Circulation along the outer shelf is to the northwest and is associated with the southern limb of the Ross Sea gyre (Fig. 4; Whitworth et al. 1998).
Several water masses are found in the Ross Sea, some of which are formed in this region. At the surface is Antarctic Surface Water (AASW), which undergoes seasonal heating/cooling and salinity variations in response to solar radiation and sea ice formation/decay processes (Carmack 1977). Below AASW is Circumpolar Deep Water (CDW), a warm, salty water mass that rises to about 500 m at the shelf break. This water mass cools during transport around the Ross Gyre and arrives at the shelf break as a modified version of CDW (mCDW) (Jacobs & Giulivi 1999). The mCDW intrudes onto the Ross Sea continental shelf along the troughs that provide deep connections to the outer shelf (Fig. 4) and floods the shelf below 200 m (Orsi & Wiederwohl 2009). Shelf Water (SW) is cold and salty water found at the bottom of the water column, and is formed on the...
continental shelf in combination from sea ice formation and brine rejection. The shelf water is split into two categories: High Salinity Shelf Water (HSSW) and Low Salinity Shelf Water (LSSW). The densest water mass in the Ross Sea is High Salinity Shelf Water (HSSW), which is formed from convective overturning in the polynyas in the western Ross Sea (Jacobs & Giulivi 1998). Antarctic Bottom Water (AABW) is also formed in the Ross Sea by mixing HSSW, cold and dense shelf water, and mCDW (Orsi et al. 2001). This water is exported in the northwestern Ross Sea where it becomes an important component of the large-scale oceanic thermohaline circulation.

2.3 BIOLOGICAL PRODUCTION

The seasonal cycle of phytoplankton biomass in the Ross Sea begins with a rapid increase in November when ice retreats and light increases, exhibits a maximum in late December, and decreases in March as ice cover increases and light levels decrease. The initial phytoplankton bloom typically consists of the haptophyte, *Phaeocystis antarctica*, in its colonial stage. The rapid decline of the *P. antarctica* bloom in January, accompanied by disintegration of the colonies and formation of single cells, may result from iron-limitation (Olson et al. 2000, Sedwick et al. 2000); macronutrients, (nitrate, phosphate, silicate) remain plentiful in the surface waters throughout the growing season (Smith & Gordon 1997, Arrigo et al. 2008). *Phaeocystis antarctica* experiences low grazing pressure and much of the bloom tends to be exported to depth. A secondary diatom bloom typically succeeds the *P. antarctica* bloom (Smith et al. 2012). The progression from *P. antarctica* to diatoms supports a general conceptual description of phytoplankton succession during the growing season in the Ross Sea; the actual progression varies with location and time and can be more complex.
2.4 DISTRIBUTIONS OF MID-TROPHIC LEVEL SPECIES IN THE ROSS SEA

2.4.1 KRILL

Distributions of Antarctic krill and crystal krill in the Ross Sea developed from net and acoustic observations indicate that the two species are mostly spatially segregated (Sala et al. 2002, Taki et al. 2008), but do have limited overlap (Hosie 1991, Ackley et al. 2003). Crystal krill tend to be found in near-shore ice-covered regions (Marr 1962, Mauchline & Fisher 1969, Sala et al. 2002). This distribution is similar to that observed for this species in other areas of the Antarctic (Hosie 1991, Pakhomov & Perissinotto 1996, Amakasu et al. 2011). Antarctic krill tend to be confined to the marginal ice zones in the eastern region (Ackley et al. 2003), and along the outer shelf of the northwest region off Cape Adare (Azzali & Kalinowski 2000, Sala et al. 2002, Azzali et al. 2006, Taki et al. 2008). The limited spatial distribution of Antarctic krill in the Ross Sea is in sharp contrast to the west Antarctic Peninsula where large dense aggregations are found throughout the continental shelf region (Siegel 1988, Lascara et al. 1999, Lawson et al. 2008, Wiebe et al. 2011). Largest concentrations of Antarctic krill are found in the north and eastern sectors of the Antarctic Peninsula that continue into the Scotia Sea and the Weddell Sea (Laws 1985, Atkinson et al. 2004, Siegel et al. 2004). Extensive areas of high Antarctic krill biomass occur around the South Shetland Islands (Hewitt et al. 2003) and South Georgia (Brierley et al. 1997).

An analogous spatial separation in Antarctic and crystal krill distributions has been observed in Prydz Bay (Hosie 1991). Crystal krill are restricted locally to the neritic continental shelf (< 1000m) with highest densities closest to shore (Thomas & Green 1988, Pakhomov & Perissinotto 1996), decreasing with distance to the shelf, while Antarctic krill
are found in the deeper waters at the shelf break and beyond (Thomas & Green 1988, Hosie 1991, Miquel 1991, Lu & Williams 1994). Some overlap in distributions, however, occurs on the continental shelf (Hosie 1991).

2.4.2 ANTAGTIC SILVERFISH

Antartic silverfish account for more than 90% of the mid-water fish biomass in the Ross Sea (DeWitt 1970), and have a circum-antarctic distribution (Emslie & McDaniel 2002). This species has a wide distribution throughout the Ross Sea continental shelf (DeWitt 1970, Granata et al. 2000, Ackley et al. 2003, Donnelly et al. 2004, O’Driscoll et al. 2011), but occurs in higher abundance in particular regions. Distributions of Antarctic silverfish constructed from net-based sampling suggested age-based spatial separations (La Mesa et al. 2010). Larvae tend to inhabit the coastal waters of the western and southern sectors of the Ross Sea, and postlarvae were mainly found in the northern and southeastern areas of the western Ross Sea and in Terra Nova Bay. Juveniles were distributed on or near the shallow banks in the Ross Sea (La Mesa et al. 2010). Antarctic silverfish tend to spawn in ice-covered coastal regions, ice shelf areas and polynyas, and use sea ice as a nursery for their eggs and early life stages (Kellerman 1986a, 1986b, Daneri & Carlini 2002).

The distribution of Antarctic silverfish in other regions of the Antarctic is comparable to that in the Ross Sea. This species is the dominant fish biomass over the continental shelf of the Weddell Sea (Hubold & Ekau 1987, White & Piatkowski 1993) with older life stages being found in the colder inner shelf waters (Hubold 1984) and over the continental shelf of Prydz Bay (Lu & Williams 1994).
CHAPTER 3

METHODS

3.1 DATA SOURCES

The krill and silverfish distributions were constructed from data (Table 1) collected from a series of cruises in the western Ross Sea (Fig. 1) made as part of the Italian Antarctic research program between 1988 and 2004. Sampling locations for krill extend from 64°S to 77.5°S and 177°W to 165°E; those for Antarctic silverfish extend from 67°S to 78°S and 175°W to 164°E (Fig. 1). The cruises provided adequate spatial coverage of the western Ross Sea where the three species occur.

3.1.1 KRILL AND ANTARCTIC SILVERFISH DATA SETS

Antarctic and crystal krill biomass was obtained from published acoustic and net-based measurements made over a 12-year period between 1988 and 2000 (Table 1). These cruises mostly occurred during the austral summer (December - February), but some observations were made in late austral spring (November). The data for juvenile and adult euphausiid biomass provided the basis for this study. Larval krill biomass was not included because this stage was under-represented in the net-based data sets and not reported for some cruises (Table 1).

The first cruise in 1988 provided net-based measurements of juvenile and adult euphausiid biomass (Table 1). Subsequent cruises provided acoustic as well as net-based estimates of krill biomass. For the continuous acoustic surveys, the net-based collections provided ground truth information for krill biomass estimates (Table 1), and to apportion
the acoustic returns into Antarctic krill and crystal krill along the cruise tracks. The only exceptions were the 1989 and 1990 cruises, which assumed a mean krill length of 40 mm to convert the acoustic signals to biomass.

Table 1. Summary of cruises, collection method, species sampled, life history stage, measurement units and references for the krill data used in this study. Collection method codes: 1-EZ-NET-BIONESS; 2-HPN (Hamburg Plankton Net); 3-Echosounder; 4-Biosonics 102 Scientific Echosounder; 5-Simrad Three-frequency Echosounder. Azzali et al. (2006) presented a reanalysis of the data in Azzali & Kalinowski (2000). Thus, the November and December 1994 *Euphausia superba* data sets used in Azzali et al. (2006) were excluded from this analysis

Antarctic silverfish biomass was obtained from net-based measurements made over a 16-year period from 1988 to 2004 (Table 2). These cruises mostly focused on the austral summer, but some included late austral spring. The net-based sampling provided biomass
data for the early life history stages of Antarctic silverfish, which include the larval, postlarval, and juvenile stages.

<table>
<thead>
<tr>
<th>Cruise</th>
<th>Cruise Date</th>
<th>Collection Method and Number of Sampling Stations</th>
<th>Life History Stage</th>
<th>Density Units</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polar Queen</td>
<td>Jan. – Feb. 1988</td>
<td>33 Discrete Net Tows</td>
<td>Postlarvae</td>
<td>Ind (100 m$^3$)$^{-1}$</td>
<td>Guglielmo et al. (1997)</td>
</tr>
<tr>
<td>Cariboo</td>
<td>Nov. 1989 – Jan. 1990</td>
<td>57 Discrete Net Tows</td>
<td>Postlarvae</td>
<td>Ind (100 m$^3$)$^{-1}$</td>
<td>Granata et al. (2000)</td>
</tr>
<tr>
<td>ROSSMIZE Itica</td>
<td>Nov. – Dec. 1994</td>
<td>26 Discrete Net Tows</td>
<td>Juvenile</td>
<td>Ind (100 m$^3$)$^{-1}$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Jan. – Feb. 1996</td>
<td>25 Discrete Net Tows</td>
<td>Juvenile</td>
<td>Ind (100 m$^3$)$^{-1}$</td>
<td></td>
</tr>
<tr>
<td>ROSSMIZE</td>
<td>Nov. – Dec. 1994</td>
<td>18 Discrete Net Tows</td>
<td>Larvae &amp; Juvenile</td>
<td>Ind (1000 m$^3$)$^{-1}$</td>
<td>Vacchi et al. (1999)</td>
</tr>
<tr>
<td>Italian Antarctic Expedition</td>
<td>December 1997</td>
<td>35 Discrete Net Tows</td>
<td>Larvae, Postlarvae, and juvenile</td>
<td>Ind (1000 m$^3$)$^{-1}$</td>
<td>La Mesa et al. (2010)</td>
</tr>
<tr>
<td></td>
<td>January 2004</td>
<td>33 Discrete Net Tows</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Summary of cruises, collection method, life history stage, units, and references for the Antarctic silverfish data used in this study. Collection method codes: 1-HPN Hamburg Plankton Net; 2-Krill Midwater Sampling Trawl (KMST); 3-EZ-NET-BIONESS

The krill and silverfish distributions reported from the cruises listed in Tables 1 and 2 were digitized using the Surface Mapping System Software, Surfer 32, to construct individual cruise data sets that include latitude, longitude, and biomass for each species. The data sets from the cruises were then combined to construct a single data set for each species. The resultant data sets consisted of 410 values for Antarctic krill, 359 values for crystal krill, and 548 values for Antarctic silverfish. The biomass of the krill species was reported as either biomass per area or number of individuals (ind) per volume. These units
were converted to metric mT km^{-2} and ind (1000 m^{3})^{-1} respectively. All Antarctic silverfish measurements were reported as individuals per volume, which were converted to ind (1000 m^{3})^{-1}.

The distributions of the two krill species were used to create distributions in terms of biomass per area and number of individuals per volume. However, the sample size of the volumetric data was small (<30 stations), therefore only the distributions given as biomass per area were used for developing environmental relationships. The Antarctic silverfish distributions were reported only as volumetric measurements, and these were used to create the distribution of this species. The cruise tracks from all data sets were also digitized to provide spatial coverage of sampling across the Ross Sea (Fig. 1).

The distributions of the three species were also mapped onto a standard grid of 0.5° latitude by 0.5° longitude. This data set was used with the environmental variables associated with each biomass value (see following sections) to consider possible interactions between the three species.

3.1.2 BATHYMETRY

Bottom topography for the Ross Sea was obtained from a circum-Antarctic data set that was developed using data from the International Bathymetric Chart of the Southern Ocean (IBCSO, 500 m x 500 m resolution) and the General Bathymetric Chart of the Oceans (GEBCO_08, 30 arc-second resolution) (Arndt et al. 2013). The Ross Sea bathymetry data were extracted from the larger data set and imported into ArcGIS, and a bathymetry map for the western Ross Sea was constructed using the ArcGIS mapping tools (Fig. 1).

The bottom topography of the Ross Sea extends from 200 m, along the coast, to >3000 m off the slope break into the Pacific sector of the Southern Ocean. The Ross Sea
continental shelf is relatively deep (mean depth 450-600 m) but has localized regions, such as Terra Nova Bay, in which depths reach ~1200 m. The Ross Sea bathymetry is characterized with deep waters (>1000 m) off the shelf/slope break and ~600 m alongside the Ross Ice Shelf. The Ross Sea bottom topography is irregular and marked with shallow banks (400 m) and deep troughs (~650 m) that intrude onto the continental shelf. These intrusions provide the pathway for deep and relatively warm Circumpolar Deep Water (CDW) to move onto the shelf.

3.1.3 ENVIRONMENTAL DISTRIBUTIONS

Temperature, surface chlorophyll, mixed layer depth (MLD), sea ice coverage, and surface current speed (Table 3) potentially influence krill and silverfish distributions. Distributions of these variables were estimated and mapped onto grids that allow comparative analyses to be made with the krill and silverfish distributions.

<table>
<thead>
<tr>
<th>Environmental Variable</th>
<th>Source</th>
<th>Data Time Range</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum Temperature below 300m (°C)</td>
<td>Ross Sea Circulation Model</td>
<td>Dec. 1 – March 31 2010-2011</td>
<td>Mack (2016)</td>
</tr>
<tr>
<td>Chlorophyll (mg m(^{-3}))</td>
<td>Ocean Color SeaWiFS</td>
<td>Sept. 1997- April 2002</td>
<td>D. McGillicuddy, PRISM project</td>
</tr>
<tr>
<td>Sea Ice (% Coverage)</td>
<td>SSM/I</td>
<td>1988 – 2003</td>
<td>M. Dinniman PRISM project</td>
</tr>
<tr>
<td>Surface Speed (m s(^{-1}))</td>
<td>Ross Sea Circulation Model</td>
<td>Sept. 2010 – Feb. 2012</td>
<td>Mack (2016)</td>
</tr>
</tbody>
</table>

Table 3. Summary of environmental data, source, data time range, and reference. Environmental data were produced from the summer average (December- February). Table abbreviations are: SeaWiFS-Sea-viewing Wide-Field-of-view Sensor and SSM/I-Special Sensor Microwave Imager
3.1.3.1 TEMPERATURE

The maximum temperature below 300 m (Fig. 5a) was extracted from simulated circulation distributions obtained from an implementation of the Regional Ocean Modeling System (ROMS) for the Ross Sea (Mack 2016). The circulation model uses 5-km horizontal grid spacing and 24 vertical layers, with variable thickness (Mack 2016), and has been extensively used for circulation and climate studies in the Ross Sea (Dinniman et al. 2007, 2011, 2012, 2015). The 300-m temperature distribution provides a tracer for Circumpolar Deep Water (CDW). The annual mean temperature field is used because CDW inputs to the Ross Sea do not exhibit seasonal variations (Dinniman et al. 2003).

For this study, the average temperature distribution was imported into ArcGIS and mapped onto the data analysis grid (Fig. 5a). The temperature distribution shows that water temperatures off the shelf break/slope region are mostly >1°C and those over the shelf are mostly less than -1°C (Fig. 5a). The exceptions are the deep regions of the Drygalski, Joides, and Glomar Challenger troughs, where warm modified Circumpolar Deep Water (mCDW) intrudes onto the shelf. The areas of mCDW intrusion along the northwestern Ross Sea shelf coincide with the region that was the focus for the Italian Antarctic research cruises.

3.1.3.2 SURFACE CHLOROPHYLL

Ocean color measurements made from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) from September 1997 to April 2002 were obtained as part of the Processes Controlling Iron Regulation at the Mesoscale (PRISM) in the Ross Sea project and made available for this study (D. McGillicuddy, pers. comm.). Chlorophyll concentrations (mg m⁻³) were estimated from SeaWiFS 8-day Level 3 binned seasonal climatology files, using
the OCv6 algorithm (O’Reilly et al. 1998, 2000). These data were used to construct monthly chlorophyll climatologies (December, January, February) and an average growing season (December to February) climatology.

For this study, the average growing season chlorophyll distribution was imported into ArcGIS and mapped onto the data analysis grid (Fig. 5b). The distribution shows that chlorophyll concentration ranges from 0.07 mg m$^{-3}$ to 0.85 mg m$^{-3}$ across the Ross Sea. Chlorophyll decreases with distance from the Ross Sea Ice Shelf (Fig. 5b), and concentrations in the northwest Ross Sea and along the shelf break/slope region are generally low. The lowest chlorophyll concentrations are associated with the Ross Sea Gyre north of the shelf break (Fig. 5b). Enhanced chlorophyll concentrations occur in the southwestern corner of the continental shelf (Fig. 5b); the enhanced concentrations in the eastern Ross Sea are outside the area covered by the krill and silverfish data sets.

3.1.3.3 MIXED LAYER DEPTH

The mixed layer depth was extracted from simulated circulation distributions obtained from the Ross Sea circulation model (Mack 2016) and made available for this study (M. Dinniman, pers. comm.). The mixed layer depth (MLD), defined as the depth where $\sigma_t$ differs from the surface by $>0.01$ kg m$^{-3}$, was calculated from the simulated daily-averaged temperature and salinity values, and then averaged to provide monthly means. The monthly MLD values for the two summers (September 2010 – February 2012) included in the simulation were then averaged to obtain a summer seasonal MLD climatology. The summer climatology was imported in ArcGIS and mapped onto the Ross Sea grid (Fig. 5c).
The summer mixed layer depth over the continental shelf is relatively shallow, ranging from about 3 to 58 m (Fig. 5c). Shallow mixed layer depths of about 14 m occur over the Drygalski, Joides, and Glomar Challenger troughs, and those around Mawson and Pennell Bank reach maximum depths of 30 m. The deepest mixed layer depths of 58 m occur north of the Ross Sea Ice Shelf. Mixed layer depths in the northwestern Ross Sea are generally shallow (Fig. 5c). However, mixed layer depths in excess of 50 m occur along the innershelf of the western Ross Sea and in Terra Nova Bay. These patterns of shallow summer mixed layer depths in the summer are consistent with patterns reported in Smith et al. (2000, 2014a, 2014b).
Fig. 5. (a) Simulated distribution of the annual maximum potential temperature (°C) below 300 m obtained from the Ross Sea circulation model (Mack 2016; data provided by M. Dinniman)

(b) Average growing season (December – February) chlorophyll (mg m⁻³) climatology derived from SeaWiFS measurements made 1997-2002. Data provided by D. McGillicuddy, PRISM project

(c) Summer average (December-February) mixed layer depth (m) distribution obtained from simulated density distributions (Mack 2016; data provided by M. Dinniman)
3.1.3.4 SEA ICE

The sea ice concentration (Table 3) distributions in the Ross Sea for December, January, and February, and the summer average (December to February), were obtained from Special Sensor Microwave Imager (SSM/I) measurements made between 1988 and 2003 as part of an analysis of sea ice changes in the Ross Sea (Smith et al. 2014b). The monthly and summer sea ice climatologies were mapped onto the grid used for the Ross Sea circulation model. Figure 6a illustrates the average summer (December – February) sea ice concentrations, measured in percent coverage, occurring in the Ross Sea between 1988-2003. The summer average sea ice coverage over most of the Ross Sea is less than 10%, with large areas being essentially ice free (Fig. 6a). The low sea ice coverage that extends from the southwest to the center of the Ross Sea coincides with the Ross Sea polynya. Sea ice coverage along the inner shelf along the western Ross Sea is about 40-50% (Fig 6a). The exception is Terra Nova Bay and surrounding region, which has about 30% sea ice coverage. The northwestern corner of the Ross Sea is characterized by sea ice coverage of 15% or less (Fig. 6a).

3.1.3.5 SURFACE CURRENT SPEED

Estimates of the magnitude and variability of the east-west and north-south components of the velocity field are provided by simulated surface speed distributions that were obtained from the Ross Sea circulation model (Table 3). The simulated daily surface speeds were averaged to obtain monthly (December-February) distributions, which were then averaged to provide a summer distribution (Fig. 6b). Surface speed is variable across the Ross Sea continental shelf with the fastest speeds (up to 0.35 m s⁻¹) occurring along the shelf break (about 1000-m isobath) and along the western flanks of Crary Bank and Ross
Bank (Fig. 6b). Surface speed in the western Ross Sea is generally low with the exception of the area to the north of the Drygalski Ice tongue. Similar low surface speeds are associated with Mawson and Pennell Banks (Fig. 6b).

Fig. 6. (a) Summer (December–February) averaged SSM/I-derived distribution of sea ice concentration (0 -100% coverage) obtained from measurements made between 1988-2003. Sea ice concentration data provided by M. Dinniman. (b) Summer (December – February) averaged surface speed (m s⁻¹) obtained from the simulated circulation distributions (Mack 2016; data provided by M. Dinniman)
3.2 CONSTRUCTION OF DISTRIBUTIONS AND DATA SETS

The krill, Antarctic silverfish, and environmental data sets were imported into the geographic information system package ArcGIS 10.2.2, and the mapping tools were used to: transform the data into point shapefiles (non-topological data format for storing the location and attribute information of geographic features); construct distributions of the individual variables; and overlay combinations of variables (i.e. bathymetry and krill). The environmental data point shapefiles were converted to raster files using the “Point to raster” conversion function in ArcGIS, which allowed the data to be displayed as smooth and continuous surfaces. In the case that more than one point was in the same pixel cell, the most common value found within the pixel would determine the value of the cell.

The location of the coastline, defined by the 0-m isobath, and shelf break, defined by the 700-m isobath, were identified using polylines. The polyline segments were used to estimate distance from the shore and shelf break for each krill and Antarctic silverfish measurement using the ArcGIS function ‘Near’. These additional diagnostic variables were included as part of the environmental variable data set.

Values of the environmental variables that correspond to the location of each krill and Antarctic silverfish measurement were extracted using the ArcGIS function ‘Extract Multi Values to Points’. The krill and silverfish measurements outside the area covered by the environmental variables were assigned a zero value and were not included in the statistical analyses. The attribute table constructed from these data extractions contains all of the environmental values that correspond to the measurement location for each species. This data set was then used for the statistical analyses.
3.3 STATISTICAL ANALYSES

3.3.1 OPTIMIZED HOT SPOT ANALYSIS

The optimized hot spot analysis included as part of the spatial statistics extension in ArcGIS was used to investigate the characteristics of the krill, Antarctic silverfish, and environmental distributions. The optimized hot spot analysis identifies statistically significant spatial clustering of high values (hot spots) and low values (cold spots) within a given data set using the Getis-Ord Gi* statistic (Getis & Ord 1992). The Gi* statistic calculates, for geo-referenced data, the correspondence among the value of a measurement and its nearest neighbors over a distance, and compares this local average to a global average. This identifies a local area that is statistically significantly different from the entire study area.

The Gi* statistic was calculated for the distributions of the three species and the environmental distributions. The volumetric based krill data sets did not include a sufficient number of values (more than 30) for the calculation. The significance of the Gi* statistic for each data value is provided by an associated z-score, p-value, and confidence level bin. The Gi* value for each data point is then partitioned into a bin that reflects its significance level, i.e. confidence intervals of 99% (+/-3 Gi* value), 95% (+/-2 Gi* value) and 90% (+/- 1 Gi* value). The remaining Gi* values are considered to be statistically insignificant.

3.3.2 DATA FREQUENCY

Temperature and bathymetry data values that correspond to each krill and Antarctic silverfish measurement were used to construct histograms to identify relationships in the data sets. The krill and Antarctic silverfish data were partitioned based
on 0.25°C temperature intervals and 100-m bathymetry intervals. The numerous zero values in the data sets for the three species, which reflect absence of the species, biased the histograms. Thus, a second set of histograms were created excluding the zero biomass values from the krill and Antarctic silverfish data sets.

3.3.3 SPATIAL AUTOCORRELATION

The spatial autocorrelation (Moran’s I) analysis included in the spatial statistics extension in ArcGIS was used to measure the similarity of features. The Moran’s I statistic uses the data locations and values to the estimate the degree of similarity in the data and the type of similarity, i.e. clustered, dispersed, or random. The significance of the similarity and pattern is given by a z-score and p-value. A positive Moran’s I Index indicates high values cluster near high values and low values cluster near low values, signifying spatially clustered distributions, and a negative Moran’s I Index indicates no clustering of the data (high values are near low values). Very high or low z-scores associated with significant p-values reflect a non-random pattern in the data. A z-score greater than 2.58 and p-value less than 0.01 indicates that there is less than a 1% likelihood that the clustering pattern is random.

The spatial autocorrelation analysis was done for each species and each environmental variable using the entire data set (Ross Sea scale) and using the portion of the data set identified by the 99% confidence interval in the hot spot analysis (hot spot scale). This analysis provided statistically quantitative measures of the patterns observed in the hot spot analysis.
3.3.4 EMPIRICAL ORTHOGONAL FUNCTION ANALYSIS

A traditional Empirical Orthogonal Function (EOF) analysis separates time series measurements at a series of locations into sets of related spatial patterns with certain time histories (Preisendorfer 1988). The EOF implementation used in this study analyzes a set of variables, i.e. the species and environmental distributions, at a series of locations. The EOF yields patterns of related variables, given by the eigenfunction, and locations at which the patterns are dominant, the loading vector. The EOF results reveal locations at which variables are related, allowing inferences to be made about causes underlying the patterns.

The EOF analysis partitions the data sets into 11 modes based on the 10 environmental variables and species’ biomass. The eigenvalue for each mode indicates the fraction of the variance of the data set represented by a given mode. Significant modes are identified by those with eigenvalues that are greater than the mean of all the eigenvalues, i.e., “the average eigenvalue test” (Preisendorfer 1988). These modes were analyzed to determine relationships among variables and locations. The eigenfunctions indicate which variables are related for a given mode and the loading vector indicates the dominance of a pattern. The eigenvector provides the direction of change (positive or negative) relative to the mean.

The EOF analysis was implemented using the distribution of each species and the environmental conditions. The analysis was done using the entire data set (Ross Sea scale), the data set defined as the 99% confidence interval biological hot spot (hot spot scale), and the gridded species interaction data set. The mean value was subtracted from each data set prior to the EOF analysis and the effects of strong trends were removed so that the data variability is better represented. The resultant data was divided by the standard deviation
of the data to create a zero-mean unit variance data set. This detrended and scaled data set was used in the EOF analysis.
4.1 SPECIES’ DISTRIBUTIONS

4.1.1 ANTARCTIC KRILL

The Antarctic krill distribution constructed from the historical data (Table 1) shows that this species is generally found over most of the western Ross Sea continental shelf, along the shelf break, and in the deeper off-shelf waters (Fig. 7a). The inner shelf region is characterized by low biomass (less than 1 mT km$^{-2}$) or absence of Antarctic krill (Fig. 7a). The exception is the southwest inner shelf where Antarctic krill biomass was consistently 1-10 mT km$^{-2}$. Over the central part of the study region, biomass of 10-100 mT km$^{-2}$ is associated with the shallow banks and troughs that extend across the continental shelf. The shallow areas over Mawson and Pennell Banks have the largest biomass of 100-1000 mT km$^{-2}$. Terra Nova Bay has a similar high Antarctic krill biomass (Fig. 7a). Antarctic krill biomass is consistently 100-1000 mT km$^{-2}$ along the shelf break/slope region and in the northwestern corner of the Ross Sea (Fig. 7a). Biomass values in excess of 1000 mT km$^{-2}$ occur in the northwest Ross Sea off the coast of Cape Adare (Fig. 7a). Although fewer samples, the distribution of Antarctic krill biomass reported as ind (1000 m$^{3}$)$^{-1}$ shows a similar pattern, with the largest values occurring along the shelf break/slope region of the northwestern Ross Sea (Fig. 7b).
4.1.2 CRYSTAL KRILL

Crystal krill occur at low biomass levels (less than 1 mT km$^{-2}$) over most of the Ross Sea continental shelf (Fig. 8a). This species is absent in the eastern part of the study region (Fig. 8a and 8b). Localized areas of biomass of 1-10 mT km$^{-2}$ occur over Mawson and Pennell Banks, the southern inner shelf near the Ross Ice Shelf, and the southwestern inner shelf (Fig. 8a). Biomass of 100-1000 mT km$^{-2}$, the highest observed, occurs in and around Terra Nova Bay in the far western Ross Sea. The crystal krill biomass distribution reported
as ind (1000 m$^3$)$^{-1}$ also shows the highest values are associated with Mawson and Pennell Banks, the southwestern inner shelf, and Terra Nova Bay.

Fig. 8. Distribution of crystal krill biomass (purple circles) constructed from the data sources in Table 1 expressed as (a) mT km$^{-2}$ and (b) ind (1000 m$^3$)$^{-1}$. Bottom bathymetry is given in m (black contours)

4.1.3 ANTARCTIC SILVERFISH EARLY LIFE STAGES

The early life stages of Antarctic silverfish are found at low (less than 10 ind (1000 m$^3$)$^{-1}$) biomass levels over most of the continental shelf region and are absent in deeper off-shelf waters (Fig. 9). Localized regions of enhanced biomass occur on the shelf in the
shallower waters over Mawson and Pennell Banks. The largest and most consistent occurrence of Antarctic silverfish is in Terra Nova Bay (Fig. 9), where biomass values exceed 10,000 ind (1000 m³)⁻¹. Just outside of Terra Nova Bay, along the southwestern flank of Mawson Bank, Antarctic silverfish biomass levels are similar to those in Terra Nova Bay (Fig. 9).

Fig. 9. Distribution of Antarctic silverfish early life stage biomass (purple circles) constructed from the data sources in Table 2 as ind (1000 m³)⁻¹. Bottom bathymetry is given in m (black contours)
4.2 DISTRIBUTION ANALYSES

4.2.1 HOT SPOT ANALYSIS

The optimized hot spot analysis indicates that the distribution of Antarctic krill over most of the Ross Sea continental shelf is not significantly different from an average distribution (Fig. 10a). The exception is the northwestern shelf/slope region. The area defined by the 99% confidence level (red circles) outlines a biological hot spot for Antarctic krill along and off the shelf/slope region to the east of Cape Adare (Fig. 10a). The 90% confidence level expands this region to the north and southward onto the outer continental shelf (Fig. 10a).

The crystal krill distribution is relatively uniform over most of the continental shelf, except in Terra Nova Bay (Fig. 10b) where a distinct hot spot occurs. The region outlined by the 99% confidence level includes the inner and northern shelf region of Terra Nova Bay and the outer part of the Drygalski Ice Tongue. The region encompassed by the 90% confidence interval slightly expands the hot spot area (Fig. 10b). The early life stages of Antarctic silverfish are also concentrated in Terra Nova Bay and in the near environs with a distribution that is similar to crystal krill (Fig. 10c).
Fig. 10. Distribution of regions with clustering that is significant at the 99% (red circles), 95% (orange circles), and 90% (light orange circles) significance level for (a) Antarctic krill, (b) crystal krill, and (c) Antarctic silverfish early life stages obtained from the optimized hot spot analysis. Regions that do not have significant clustering are also shown (yellow circles).
4.2.2 DATA FREQUENCY

The frequency distribution of Antarctic krill relative to varying temperature and bathymetry intervals shows that the largest number of Antarctic krill observations are associated with temperatures of 1°C to 1.25°C and depths of 1000 m (Fig. 11a). Secondary peaks occur at temperatures of -1.0°C to -1.5°C at depths of 300, 400, and 500 m. The least number of observations occur at temperatures of 0.0°C to 0.25°C and depths of 600 to 900 m. A similar frequency distribution is obtained when zero biomass values are excluded (Fig. 11b). A chi-square goodness-of-fit test indicates this histogram differs from a normal distribution (p = <0.0005).

Fig. 11. Frequency distribution of Antarctic krill biomass observations as a function of potential temperature (°C) and bottom depth (m) for (a) all biomass observations and (b) biomass observations excluding zero values
The frequency distribution for crystal krill shows the largest number of crystal krill observations are associated with temperatures of -1.75°C to -2°C and depths between 500-800 m (Fig. 12a). A large peak occurs at 0.75°C and 1000 m, which disappears when the zero biomass observations are removed (Fig. 12b). The biomass observation peaks at cold temperatures and 500-800 m remain but are reduced in size (Fig. 12b). A chi-square goodness-of-fit test indicates the histogram differs from a normal distribution (p = 0.0022).

The largest number of observations of the early life stages of Antarctic silverfish are associated with temperatures of 1°C and depths of 1000 m (Fig. 13a). Secondary peaks occur at -1.5°C and -1.75°C at depths of 300 m, 500 m, and 700 m, respectively. Removal of the zero biomass values show peaks at -1.75°C to -2°C and 500-700 m (Fig. 13b). The
fewest observations occur at warm temperatures and depths of 900 m. A chi-square goodness-of-fit test indicates the histogram differs from a normal distribution (p = <0.0005).

![Frequency distribution of Antarctic silverfish early life stage observations as a function of potential temperature (°C) and bottom depth (m) for (a) all biomass observations and (b) biomass mass observations excluding zero values](image)

**Fig. 13.**

4.2.3 SPATIAL AUTOCORRELATION ANALYSIS

The properties of the patterns in the distributions of each species and the environmental variables were obtained from the spatial autocorrelation analysis. For the full data set (the Ross Sea scale), the distribution pattern of Antarctic krill is statistically random (z-score = 0.7597, p-value = 0.4474, Table 4). The distributions of the environmental variables associated with the biomass values are clustered at a statistically significant level (p-value < 0.01), indicating that these distributions have identifiable patterns. In contrast to the Antarctic krill biomass, the biomass distributions of adult
crystal krill and Antarctic silverfish early life stages are clustered at a statistically significant level at the Ross Sea scale (p-value < 0.01, Table 4).

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Table 4. Statistical significance metrics obtained from the spatial autocorrelation analysis for each species and each environmental variable using the entire data set (Ross Sea scale). Statistically significant z-scores and p-values are indicated by bold text.
At the scale of the hot spot, the Antarctic and crystal krill biomass distributions are statistically random (z-score = -0.1272, p-value = 0.8988, z-score = -0.6648, p-value = 0.5062 respectively, Table 5). The Antarctic silverfish biomass distribution is statistically clustered, as are the distributions of environmental variables associated with the biomass distributions (p-value < 0.01, z-score > 2.58, Table 5).

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Table 5. Statistical significance metrics obtained from the spatial autocorrelation analysis for each species and each environmental variable using the data set defined by the 99% confidence interval obtained from the hot spot analysis (hot spot scale). Statistically significant p-values and z-scores are indicated by bold text.
4.2.4 EMPIRICAL ORTHOGONAL FUNCTION ANALYSIS

4.2.4.1 ROSS SEA SCALE ANALYSIS

The eigenvalues obtained from the EOF analysis for each species and associated environmental distributions (Appendix A) show that the first four modes are significant for Antarctic krill and crystal krill (Fig. 14). The first three modes are significant for the early life stages of Antarctic silverfish (Fig. 14) at the Ross Sea Scale.

![Graph showing eigenvalues and associated modes for different species.](image)

Fig. 14. Eigenvalues and associated modes for Antarctic krill (black line), crystal krill (blue line), and Antarctic silverfish (red line) obtained from the entire data set (Ross Sea scale). Modes with eigenvalues greater than the mean (= 1), (magenta line) are significant.
The first mode obtained for the Antarctic krill (Figure 15a, dark blue bars) explains about 38% of the variance (Appendix A) in the data set. This variance is accounted for by the combined effect of latitude, water temperature, chlorophyll, and distance to the shelf break. The eigenvectors associated with these environmental variables indicate correspondences among: southerly latitudes, cold temperatures, higher concentrations of chlorophyll, and increased distance from the shelf break, (Fig. 15a) that characterize a habitat. The relationships among the eigenvectors from mode 1 can also be interpreted as northerly latitudes, warmer temperatures, lower chlorophyll concentrations, and decreased distance from the shelf break. Mode 2 (Fig. 15a, cyan blue bars) explains 17% of the variability in the data set (Appendix A) and the eigenvectors indicate that this is attributed to depth, sea ice, and surface speed. Higher concentrations of sea ice and slower surface speeds occur at deeper depths. Modes 3 and 4 (Fig. 15a, yellow and red bars) account for 11% and 10% of the variance, respectively. The mode 3 eigenvectors suggest a correspondence between longitude and mixed layer depth, with shallower mixed layers occurring at westerly longitudes. Mode 4 eigenvectors show that the variability is attributed to longitude, surface speed, and distance to the coast.

The first mode obtained for crystal krill explains 36% of the variance in the data set (Appendix A) that is attributed to latitude, distance to the shelf break, distance to the coast, and temperature (Fig. 15b, dark blue bars). This mode captures characteristics of the habitat and indicates correspondences among northerly latitudes, increased distance from the coast, decreased distance to the shelf break, and warmer temperatures. Mode 2 accounts for 18% of the variance in the data set, which is attributed to depth, chlorophyll, and sea ice (Fig. 15b, cyan blue bars). Modes 3 and 4 account for 10% and 9% of the
variance, and indicate correspondences between longitude and mixed layer depth (Fig. 15b, yellow bars), and crystal krill biomass, water depth, and mixed layer depth (Fig. 15b, red bars), respectively. Mode 4 indicates decreased (increased) crystal krill biomass is associated with increased (decreased) water depths and deeper (shallower) mixed layers.

The three significant modes obtained for the Antarctic silverfish explain 40%, 22% and 13% of the variance in the data set (Appendix A), respectively. Mode 1 is associated with longitude, distance to the shelf break, distance to the coast, and temperature (Fig. 15c, dark blue bars). This mode suggests a habitat in the eastern (western) part of the study area that is associated with warmer (colder) temperatures, decreased (longer) distance to the shelf break, and increased (decreased) distance from the coast. The eigenvectors associated with mode 2 show that the variance is accounted for by depth, sea ice, and chlorophyll concentration, suggesting associations among deeper depth, increased sea ice coverage, and decreased chlorophyll concentrations (Fig. 15c, green bars). Mode 3 provides an association between depth, surface speed, and mixed layer depth, with slower surface speeds associated with deeper water depths and deeper mixed layers (Fig. 15c, red bars).
Fig. 15. Eigenvectors showing partitioning of variance for each significant EOF mode and environmental variable obtained from the entire data set (Ross Sea scale) for (a) Antarctic krill, (b) crystal krill, and (c) Antarctic silverfish. Environmental variables are abbreviated as: Long-latitude, Lat-longitude, Bio-species’ biomass, Depth-bottom depth, Speed-surface speed, Temp-temperature, Coast-distance to coastline, Ice-sea ice coverage, Chla- chlorophyll concentration, Shelf-distance to shelf break, MLD-mixed layer depth.

4.2.4.2 HOT SPOT SCALE ANALYSIS

The eigenvalues obtained from the EOF analysis for each species and associated environmental distributions at their associated hot spot scale (Appendix B) show that the first four modes are significant for Antarctic krill and Antarctic silverfish (Fig. 16), and the first three modes are significant for crystal krill (Fig. 16).
Fig. 16. Eigenvalues and associated modes for Antarctic krill (black line), crystal krill (blue line), and Antarctic silverfish (red line) obtained from the data set defined by the 99% confidence interval from the hot spot analysis (hot spot scale). Modes with eigenvalues greater than the mean (= 1), (magenta line) are significant.

The first mode obtained for Antarctic krill explains 44% of the variance in the data set (Appendix B). This variance is attributed to an association among depth and water temperature (Fig 17a, blue bars). The mode 1 eigenvectors indicate that deeper depths and warmer temperatures characterize the habitat at the hot spot scale. Mode 2, which accounts for 23% of the variance, highlights the association between decreased sea ice cover and decreased distance to the shelf break (Fig. 17a, cyan bars). Mode 3 accounts for 13% of the data variance, and the eigenvectors for this mode indicate a correspondence
between surface speed and latitude, with increased surface speed occurring at northern latitudes (Fig. 17a, yellow bars) of the hot spot. A correspondence between Antarctic krill biomass and mixed layer depth is given by mode 4 (Fig. 17a, red bars), which accounts for 10% of the data variance. The first three modes suggest the hot spot habitat for Antarctic krill in the Northwestern corner of the Ross Sea shelf break region is defined by deep depths with warm water temperatures, decreased sea ice coverage, and fast surface speeds. Mode 4 of the EOF suggests that within this habitat, increased Antarctic krill biomass is associated with deeper mixed layers.

The three significant modes from the EOF analysis at the hot spot scale for crystal krill explain 40%, 18%, and 15% of the variance in the data set, respectively (Appendix B). The eigenvectors for mode 1 capture the characteristics of the hot spot habitat in Terra Nova Bay, which are defined by longitude, temperature, distance to the coast, chlorophyll concentration, and distance to the shelf (Fig. 17b, blue bars). Mode 2 provides further refinement to the habitat characteristics by including latitude, distance to the shelf, and mixed layer depth (Fig. 17b, green bars). The eigenvectors for mode 3 show an association among crystal krill biomass, water temperature, and latitude, which suggests that increased crystal krill biomass is associated with colder temperatures along the northern side of Terra Nova Bay. The first two modes suggest that the hot spot habitat for crystal krill in Terra Nova Bay is defined by southwesterly locations with cold temperatures, low chlorophyll concentrations, shallow mixed layers, and deeper depths. Mode 3 of the EOF suggests that within this habitat of Terra Nova Bay, increased crystal krill biomass is associated with northerly latitudes and cold temperatures.
Mode 1 explains 48% of the variance in the Antarctic silverfish data set defined by their Terra Nova Bay hot spot. This mode indicates that the characteristics of the Antarctic silverfish habitat are defined by longitude, surface speed, temperature, and distance to the coast and shelf (Fig. 17c, blue bars). Modes 2 and 3 add depth, mixed layer depth, and latitude as additional habitat characteristics, respectively. Mode 4 provides a correspondence between Antarctic silverfish biomass and chlorophyll concentration. These in total suggest that the hot spot habitat for the early life stages of Antarctic silverfish in Terra Nova Bay is defined by southwesterly locations with slow surface speed, cold temperatures, shallow depths, deep mixed layer depths, increased sea ice cover (Fig. 17c). Within the Terra Nova Bay habitat, increased biomass of the early life stages of Antarctic silverfish are associated with low chlorophyll concentrations.

The dominant variables associated with the significant modes for each species at the Ross Sea scale and the hot spot scale are outlined in Table 6.
Fig. 17. Eigenvectors showing partitioning of variance for each significant EOF mode and environmental variable obtained from the data set defined by the 99% confidence level from the hot spot analysis (hot spot scale) for (a) Antarctic krill, (b) crystal krill, and (c) Antarctic silverfish. Environmental variables are abbreviated as: Long-longitude, Lat-latitude, Bio-species’ biomass, Depth-bottom depth, Speed-surface speed, Temp-temperature, Coast-distance to coastline, Ice-sea ice coverage, Chla-chlorophyll concentration, Shelf-distance to shelf break, MLD-mixed layer depth
Table 6. Summary of the dominant variables and direction of change (positive (+), negative (-)) relative to the mean for each species at the Ross Sea scale and the hot spot scale obtained from the EOF analysis. Environmental variables are abbreviated as: Long-longitude, Lat-latitude, Biomass-species’ biomass, Depth-bottom depth, Speed-surface speed, Temp-temperature, Coast-distance to coastline, Ice-sea ice coverage, Chla- chlorophyll concentration, Shelf-distance to shelf break, MLD-mixed layer depth

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<td>4</td>
<td>Biomass (-), Depth (+), MLD (+)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Antarctic silverfish</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Long (+), Temp (+), Coast (+), Shelf (-)</td>
<td>1</td>
<td>Long (-), Speed (-), Temp (-), Coast (-)</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Depth (+), Ice (+), Chla (-)</td>
<td>2</td>
<td>Depth (-), Ice (+), MLD (+)</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Depth (+), Speed (-), MLD (+)</td>
<td>3</td>
<td>Lat (-)</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>4</td>
<td>Biomass (+), Chla (-)</td>
<td></td>
</tr>
</tbody>
</table>

4.2.4.3 GRIDDED SPECIES INTERACTION ANALYSIS

The EOF analysis of the Species Interaction data set yielded three significant modes (Fig. 18). Mode 1 defines the characteristic habitat for the three species in the Ross Sea in terms of longitude, latitude, distance to the coast, distance to the shelf break, and temperature (Fig. 19, blue bars). Mode 2 refines the habitat characteristics of the Ross Sea by inclusion of depth, chlorophyll concentration, and sea ice coverage. These two modes explain nearly 60% of the variance in the data, 36% and 20%, respectively (Appendix C). Mode 2 also shows that crystal krill and Antarctic silverfish biomass are associated with these habitat characteristics, both decreasing (increasing) with decreased (increased) depth, decreased (increased) sea ice coverage, and increased (decreased) chlorophyll concentrations (Fig. 19, green bars). Mode 3, which explains only 10% of the variance
(Appendix C), represents contributions from mixed layer depth and surface speed in addition to depth (Fig. 19, red bars). This mode shows an association with increased surface speed and shallow depths and mixed layers.

![Graph showing eigenvalues and associated modes](image)

Fig. 18. Eigenvalues and associated modes from the EOF analysis that used the species interaction and environmental variable data set. Modes with eigenvalues greater than the mean (= 1), (magenta line) are significant.
Fig. 19. Eigenvectors showing partitioning of variance for each significant EOF mode and environmental variable obtained from the species interaction data set. Environmental variables are abbreviated as: Long-latitude, Lat-latitude, Depth-bottom depth, Speed-surface speed, Temp-temperature, Coast-distance to coastline, Ice-sea ice coverage, Chla-chlorophyll concentration, Shelf-distance to shelf break, MLD-mixed layer depth, AK-Antarctic krill biomass, CK-crystal krill biomass, ASF-Antarctic silverfish biomass.
CHAPTER 5
DISCUSSION

5.1 PERSPECTIVE

The relationships developed to describe correspondences between terrestrial and marine species and environmental conditions take many forms (see review in Elith & Leathwick 2009), but all have the goal of providing quantitative and robust models that allow the prediction of potential effects of changing environmental conditions on species distributions. For the Antarctic marine system, species distribution models have focused on Antarctic krill and top predators because of their importance in the food web, and the availability of observations to describe the distributions and habitat characteristics (Trathan et al. 2003, Atkinson et al. 2008). The early attempts to explain the observed circumpolar distribution of Antarctic krill were based on qualitative comparisons with environmental conditions, such as temperature, sea ice, and bathymetry (Marr 1962, Mackintosh 1973). While providing insights into basic factors affecting Antarctic krill distributions, these qualitative studies lacked the ability to quantify relationships with environmental distributions, and to assess regional differences in controls. More recent studies have developed statistical relationships and models that allow quantification of the relative effects of environmental conditions on circumpolar (Hofmann & Hüsrevoğlu 2003, Atkinson et al. 2004, 2008) and regional distributions of Antarctic krill (Weber & El-Sayed 1985, Witek et al. 1988, Trathan et al. 2003). These studies identified patterns and provided correlations between Antarctic krill and environmental variables, but also
showed that these exhibited considerable variability, which is in part attributed to different space and time scales that are resolved by the observations used in the analyses. Similar studies for other krill species, such as crystal krill, have not been done, except through qualitative analyses that relate presence to ambient conditions (e.g., Fevolden 1980, Brinton & Townsend 1991, Daly & Zimmerman 2004). The general distribution of the early life history stages of Antarctic silverfish is known (review in La Mesa & Eastman 2012), but again correspondences with environmental conditions are based on qualitative analyses (Hubold 1984, Kellerman 1986a, 1986b, Koubbi et al. 2011).

This analysis advances these studies by quantitatively characterizing the habitats of three important mid-trophic level species in the Ross Sea. The use of environmental distributions obtained from a high-resolution circulation model provides a range of environmental distributions at the scale of the Ross Sea that are not possible to obtain from observations. The addition of satellite-derived distributions provides a comprehensive characterization of the environmental conditions, that when combined with ship-based biomass distributions, provide a basis for quantitative assessments of distributional patterns and habitats of each species.

Observations of the three species included in this analysis come from five cruises that are confined to the austral spring and summer. These data capture general characteristics, but are not sufficiently dense in space or time to capture temporal variability. As a result, the primary relationships that emerge from this analysis are those that characterize the physical environment of the Ross Sea. The general characteristics of the distributions of the three species show clear and distinct patterns in the Ross Sea. Each
species occupies a localized habitat that is defined by different environmental characteristics (Table 7).

<table>
<thead>
<tr>
<th>Species</th>
<th>Primary Location</th>
<th>Bathymetry</th>
<th>Temperature</th>
<th>Habitat Characteristics</th>
<th>Biomass Associations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antarctic krill E. superba</td>
<td>Northwest corner of the shelf break</td>
<td>&gt; 1000 m</td>
<td>1°C to 1.25°C</td>
<td>Deep water</td>
<td>No association</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Warm temperature</td>
<td>Deep mixed layer</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Slow surface speed</td>
<td></td>
</tr>
<tr>
<td>Crystal krill E. crystallophias</td>
<td>Terra Nova Bay</td>
<td>500 - 800 m</td>
<td>-1.75°C to -2°C</td>
<td>Southerly latitude</td>
<td>Shallow depth</td>
</tr>
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<td></td>
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<td>Coastal proximity</td>
<td>Shallow mixed layer</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Cold temperature</td>
<td></td>
</tr>
<tr>
<td>Antarctic silverfish P. antarcticum</td>
<td>Terra Nova Bay</td>
<td>500 - 700 m</td>
<td>-1.75°C to -2°C</td>
<td>Westerly longitude</td>
<td>No association</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Coastal proximity</td>
<td>Low chlorophyll</td>
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<tr>
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<td>Cold temperature</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Slow surface speed</td>
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</tbody>
</table>

Table 7. Summary of the habitat locations and characteristics for each species obtained from the analyses in this study. The bathymetry and temperature ranges are from the histogram analysis and the general characteristics are from the EOF analysis. The associations between species biomass and environmental conditions are based on the EOF analysis.

Antarctic krill occupy the habitat along the outer continental shelf break. Crystal krill and the early life stages of Antarctic silverfish occupy similar and overlapping habitats in the Terra Nova Bay region that are distinct from the Antarctic krill habitat. Interactions between crystal krill and Antarctic silverfish in the Terra Nova Bay habitat are not seen from the EOF analysis, but biological interactions such as predator prey responses, are not captured in the data used in this analysis. Some overlap in the distribution of the three species occurs over the continental shelf, but the regions where the biomass is enhanced (i.e. statistically significant) relative to average conditions, the hot spots, are separate and distinct.
5.2 HABITAT CHARACTERISTICS

5.2.1 ANTARCTIC KRILL

Although Antarctic krill are distributed throughout the Ross Sea, the habitat defined by this analysis indicates that this species prefers deep areas overlying warm water at depth, and proximity to the shelf break (Table 7). In the Ross Sea these conditions are found off and along the northwestern shelf/slope region, and coincide with the region of enhanced Antarctic krill biomass. Many studies have shown that Antarctic krill are associated with the shelf/slope region (Trathan et al. 2003, Lawson et al. 2004, Ashijan et al. 2004, Siegel 2005) and note that this area is important to many parts of their life history (Nicol 2006). Moreover, the circumpolar analysis by Atkinson et al. (2008) found that 87% of the Antarctic krill population occurs over deep water and speculated that this habitat protects against intense predation pressure found in shallower shelf regions, where the species is accessible to a range of predators.

The Antarctic krill hot spot region in the northwestern Ross Sea is associated with shelf/slope waters of >1000 m and temperatures of 1°C to 1.25°C. The latter is associated with the presence of warm CDW and mCDW at depth, which is considered to be necessary for Antarctic krill to successfully complete the first phase of their early life history (Ross et al. 1988, Hofmann et al. 1992, Hofmann & Hüsrevoğlu 2003). Intrusions of CDW and mCDW occur along the outer shelf region of the northwestern Ross Sea (Dinniman et al. 2003, Smith et al. 2007) and the Antarctic krill hot spot in the northwestern Ross Sea overlies this area. This region is also a known spawning area for Antarctic krill (Spiridonov 1996) and the circulation found here contributes to their transport and aggregation (Piñones et al. 2015).
Within the regional habitat defined by the hot spot, the Antarctic krill distribution is statistically random. This result suggests that the distribution at this scale is variable and unpredictable, similar to results from studies in other Antarctic regions (Priddle et al. 1988, Sushin & Shulgovsky 1999, Trathan et al. 2003). Daly & Macaulay (1991) suggested that krill are not only structured by environmental conditions (such as currents), but that behavioral and ecological pressures, such as the acquisition of food and avoidance of predators affect variability and regional distributions; factors that are not included in this analysis. The EOF analysis also indicated that enhanced Antarctic krill biomass is associated with deeper mixed layers, which may be related to food supply, although no correspondence with surface chlorophyll emerged from the analysis. Atkinson et al. (2008) found that food supply exerted a stronger influence on the circumpolar distribution of Antarctic krill than shelf area or water depth. The relationship with mixed layer depth in the Ross Sea may be capturing this effect.

The circulation is an important contributor to hot spot formation and maintenance. The slower surface speeds associated with the habitat in the northwestern corner of the Ross Sea potentially retain and aggregate Antarctic krill in this region. This was demonstrated with numerical particles simulations that showed the region offshore and along the shelf break of the northwestern Ross Sea is a retention area for larval and adult stages of krill (Piñones et al. 2015).

5.2.2 CRYSTAL KRILL

over the western Ross Sea continental shelf and are not found in the eastern Ross Sea or offshore of the shelf/slope break. The general habitat characteristics for crystal krill determined from this study consist of high latitude regions near the coast with cold temperatures, which are consistent with other studies. Specifically, crystal krill are associated with temperatures of -1.75°C to -2°C and depths between 500-800 m. These conditions define a primary habitat in Terra Nova Bay, which supports a statistically significant region of enhanced crystal krill biomass. Terra Nova Bay is characterized by a polynya that supports high levels of primary production (Arrigo et al. 1998a). Pakhomov & Perissinotto (1996) suggest that crystal krill have adapted to inner shelf regions with polynyas and that their reproduction is timed to take advantage coastal polynya breakout in the spring.

The crystal krill distribution at the Ross Sea scale is clustered at a statistically significant level; whereas the distribution in Terra Nova Bay is statistically random. This suggests that gradients in environmental variables are structuring the crystal krill at larger scales, but their distributions at smaller scales are responding to ecological and behavioral controls.

The EOF analysis at the Ross Sea scale showed that increased crystal krill biomass is associated with shallower bathymetry, shallower mixed layers, and conditions that are associated with the shallow banks that extend across the continental shelf. These areas exhibit sustained enhanced production (Smith et al. 2014a), potentially providing food resources needed to support growth and reproduction similar to what is provided by the coastal polynyas.
For the Terra Nova Bay hot spot, the EOF analysis indicated that increased crystal krill biomass is associated with colder water temperatures and northerly latitudes. This relationship is consistent with observations that showed that the highest crystal krill biomass in the northerly region of Terra Nova Bay (Guglielmo et al. 2009).

The circulation is an important contributor to hot spot formation and maintenance. The surface speeds associated with the shallow banks over the continental shelf and in Terra Nova Bay potentially retain and aggregate crystal krill in these regions. This was demonstrated with numerical particles simulations that showed the shallow banks along the outer Ross Sea Shelf and in Terra Nova Bay are retention areas for larval and adult stages of crystal krill (Piñones et al. 2015).

5.2.3 ANTARCTIC SILVERFISH

Antarctic silverfish are typically found over continental shelf waters throughout the Antarctic (DeWitt et al. 1990, Miller 1993, Trunov 2001, Donnelly & Torres 2008). The early life stages of Antarctic silverfish occur at low biomass levels over most of the Ross Sea continental shelf region and are absent in deeper off-shelf waters. The Antarctic silverfish distributions are clustered at a statistically significant level at the Ross Sea and Terra Nova Bay scales, suggesting similar environmental structuring of their distributions. The highest biomass of Antarctic silverfish early life stages occurs in Terra Nova Bay, which was identified as a statistically significant hot spot. Terra Nova Bay is a known spawning site for Antarctic silverfish and provides conditions that support the early life stages (Vacchi et al. 2004, 2012a).

The Antarctic silverfish habitat is defined by westerly regions near the coast that include cold temperatures and slower surface speeds. In Terra Nova Bay, the habitat is
specifically associated with temperatures of -1.75°C to -2°C and depths of 500-700 m. Antarctic silverfish spawn in the lower water column and embryos, which are slightly positively buoyant, are found associated with platelet ice (Vacchi et al. 2004, 2012a, 2012b). Thus, a habitat characterized by slow surface speeds will facilitate retention of the early life stages in the productive polynya region. The EOF analysis indicated that sea ice was not a strong factor structuring the Terra Nova Bay habitat, which is counterintuitive for a species that depends on sea ice for reproduction and food supply. This result is likely an artifact of the ship-based sampling, which avoids regions with high sea ice coverage.

5.3 CLIMATE CONSIDERATIONS

The habitat characterizations obtained from this study provide a basis for understanding potential changes in the distribution of the three species as climate affects environmental conditions in the Ross Sea. Projections of conditions for 2050 and 2100 that are based on assumed warming trends and changes in wind forcing suggest that the Ross Sea will experience decreased summer sea ice concentration and extent, earlier formation of polynyas, expansion of the Ross Sea polynya, shallower summer mixed layer depths, and a decrease in the advection of CDW onto the shelf. The three species of interest to this study are successful at present, but they are stenothermal (able to tolerate only a small range of temperatures), and have life cycles that are dependent on sea ice, making them potentially sensitive to climatic change.

Summer seasonal sea ice coverage is projected to decrease to 44% of current coverage and that for 2100 is projected to decrease further to 22% of current conditions (Smith et al. 2014b). Habitat observations show that crystal krill and Antarctic silverfish occupy ice-covered regions. Reduction of this habitat may impact both species through
effects on food supply, adult reproduction, and availability of nursery grounds for early
history stages. Both species have life history strategies that are timed with the opening of
polynyas, and earlier polynya formation may result in a mis-match with their required
environmental conditions, producing decreased reproductive success and survival.
Reduced sea ice may favor early spawning by Antarctic krill and increase recruitment
(Siegel & Loeb 1995) due to the extended growth period throughout the summer months.
However, this species also depends on sea ice as an overwintering habitat that provides
food sources and protection for early life history stages (Daly 1990, 2004) as well as older
stages (Siegel & Loeb 1995).

Projected decreases in mCDW inputs to the Ross Sea continental shelf and shallower
mixed layer depths will potentially reduce nutrient supply to the upper water column and
allow the ocean to remain stratified for a longer period of time (Smith et al. 2014b). These
changes may reduce the relative contribution of *Phaeocystis antarcticum* to the continental
shelf production and may favor diatom production (Smith et al. 2014a, 2014b). This may
provide increased food supply for all three species, especially Antarctic krill, which prefer
diatoms as food (Haberman et al. 2003). However, reduced mCDW may adversely affect
the ability of Antarctic krill to complete the descent-ascent portion of their early life
history, which depends on warm water at depth to accelerate embryo and early larval stage
development.

The projected changes in environmental conditions may also alter the present
distribution of hot spots, which are foci for locally intense energy fluxes within the food
web (Atkinson et al. 2001, Murphy et al. 2007). Changes in environmental conditions that
alter hot spot location, size, and persistence, potentially affect the distribution, abundance,
and relative availability of the three mid-trophic level species, that in turn, affect all trophic levels of the Ross Sea food web. Ainley et al. (2006, 2015) show that reduced availability of the two krill species in late austral summer resulted in a trophic cascade that caused diet switching, changes in foraging behavior, and reduced abundance of top predators. The hot spot locations identified in this study are in areas associated with land-based colonies of penguins (Woehler 1993, Ainley et al. 2010b, Smith et al. 2014a) and enhanced abundance of seals and cetaceans (Stirling 1969, review in Smith et al. 2007). Hence, alterations to these sites have potentially large consequences for the Ross Sea food web.
CHAPTER 6
CONCLUSIONS

Habitats are sites of elevated trophic transfers and those defined in this study represent regions where primary production is transferred via three important mid-trophic level species to upper trophic level predators. In these areas of the Ross Sea, the mid-trophic level species are associated with particular physical features and environmental structures. The continental shelf break/slope region provides a productive habitat with features that favor Antarctic krill. Similarly, the inner shelf region within Terra Nova Bay provides a habitat that supports crystal krill and the early life stages of Antarctic silverfish. The localization of energy transfer in these regions provides a defined area for quantifying energy flows in the food web. This localization also makes the food web productivity vulnerable to environmental changes.

This study takes a bottom-up approach to defining habitat characteristics that are based on the assumption that the distributions of the three mid-trophic level species are controlled by environment conditions. However, predation pressure and predator foraging strategies are important top-down controlling factors that need to be combined with environmental controls to account for variability in prey distributions. Prey behavior such as vertical migrations and swarm formations are also biological and behavioral components that may be responsible in structuring the distributions of the three mid-trophic level species. The distribution of early life stages is likely controlled by bottom up factors, such as circulation, but older life stages are more likely controlled by growth potential and predation (Atkinson et al. 2008). Refinement of the habitats identified in this
study requires inclusion of the effects of predation, behavioral and species interactions, such as competition, within and between trophic levels.

The habitats for the three mid-trophic level species identify areas of the Ross Sea that deserve focused management. Environmental changes in these regions coupled with possible pressures from resource use, such as fishing, could alter the balance in the food web and overall production of the Ross Sea. The Ross Sea was the focus for a bioregionalization study, which is the specification of regions of biodiversity that are based on physical measures of habitat heterogeneity (CCAMLR 2007, 2008). This process provided the basis for identification of regions of the Ross Sea for designation as marine protected areas by the Committee for the Conservation of Antarctic Marine Living Resources (CCAMLR) that recognized niche occupation of meso-predator species in the continental shelf break, shelf and slope, and marginal ice zone of the pack ice surrounding the Ross Sea post-polynya as regions that allow large populations of these species to exist (Ballard et al. 2012). The results from this study provide further rationale and support for ecosystem level conservation that underlie the selection of the Ross Sea marine protected areas.
LITERATURE CITED


Bakun A (1996) Patterns in the Ocean: ocean processes and marine population dynamics. California Sea Grant Program, in cooperation with Centro de Investigaciones Biologicas del Noroeste, La Paz, Mexico


Daly KL (1990) Overwintering development, growth, and feeding of larval Euphausia superba in the Antarctic marginal ice zone. Limnol Oceanogr 35:1564-1576


Dinniman MS, Klinck JM, Hofmann EE (2012) Sensitivity of circumpolar deep water transport and ice shelf basal melt along the West Antarctic Peninsula to changes in the winds. J Clim 25:4799-4816


Mack S (2016) Influence of tides and mesoscale eddies in the Ross Sea. PhD dissertation, Old Dominion University, Norfolk, VA


Marr JWS (1962) The natural history and geography of the Antarctic krill (Euphausia superba Dana). Discov Rep 32:33-464


Trathan PN, Brierley AS, Brandon MA, Bone D, Gross C, Grant A, Murphy E, Watkins JL (2003) Oceanographic variability and changes in Antarctic krill (Euphausia superba) abundance at South Georgia. Fish Oceanogr 12:569-583

Trunov IA (2001) Occurrence of Pleuragramma antarcticum (Nototheniidae) off South Georgia Island and the South Sandwich Islands (Antarctica). J Ichthyol 41:549-550

Vacchi M, DeVries AL, Evans CW, Bottaro M, Ghigliotti L, Cutrone L, Pisano E (2012a) A nursery area for the Antarctic silverfish Pleuragramma antarcticum at Terra Nova
Bay (Ross Sea): first estimate of distribution and abundance of eggs and larvae under the seasonal sea-ice. Polar Biol 35:1573-1585


APPENDIX A. Variance, eigenvalue, and eigenvector for each significant mode associated with each species and environmental variable obtained from the EOF analysis using the entire data set (Ross Sea scale).

<table>
<thead>
<tr>
<th>Mode</th>
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<th>Eigenvalue (%</th>
<th>Eigenvector (%</th>
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<td>16.78</td>
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<td>0.1534</td>
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**Antarctic krill**

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<td>4</td>
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**Crystal krill**

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**Antarctic silverfish**

<table>
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from the hot spot analysis (hot spot scale)

APPENDIX B. Variance, eigenvalue, and eigenvector for each significant mode associated with each species and environmental variable obtained from the EOF analysis using the data set defined by the 99% confidence interval obtained from the hot spot analysis (hot spot scale).
APPENDIX C. Variance, eigenvalue, and eigenvector for each significant mode associated with each environmental variable and species' biomass obtained from the EOF analysis using the gridded species interaction data set.
VITA

Linnea Brynn Davis
Department of Ocean, Earth, and Atmospheric Sciences
4600 Elkhorn Ave. Norfolk, VA 23508
Center for Coastal Physical Oceanography
4111 Monarch Way Norfolk, VA 23508
Old Dominion University

EDUCATION

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Thesis: Distributions of Euphausia superba, Euphausia crystallorophias, and Pleuragramma antarcticum with correlations to environmental variables in the Western Ross Sea, Antarctica

PUBLICATIONS


PRESENTATIONS


TEACHING EXPERIENCE

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- Introduction to Oceanography Lab