

UC Santa Cruz

UC Santa Cruz Electronic Theses and Dissertations

Title

Adapted to Environmental Change: Life History, Diet, and Habitat Choice of Krill in Winter

Permalink

<https://escholarship.org/uc/item/65t9345s>

Author

Driscoll, Ryan

Publication Date

2019

Copyright Information

This work is made available under the terms of a Creative Commons Attribution-NonCommercial-ShareAlike License, available at <https://creativecommons.org/licenses/by-nc-sa/4.0/>

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

**ADAPTED TO ENVIRONMENTAL CHANGE: LIFE HISTORY,
DIET, AND HABITAT CHOICE OF KRILL IN WINTER**

A dissertation submitted in partial satisfaction of
the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

OCEAN SCIENCES

by

Ryan M. Driscoll

September 2019

The Dissertation of Ryan Driscoll is
approved:

Professor Marc Mangel, chair

Professor Suzanne Alonzo

Professor Christopher A. Edwards

Jarrold Santora, Ph.D.

Quentin Williams
Vice Provost and Dean of Graduate Studies

Copyright © by

Ryan M. Driscoll

2019

TABLE OF CONTENTS

LIST OF FIGURES	vi
LIST OF TABLES.....	xiii
ABSTRACT.....	xiv
Ryan Driscoll	xiv
ACKNOWLEDGEMENTS.....	iii
INTRODUCTION	1
1.1.1 Euphausiids.....	1
1.1.2 Southern Ocean Euphausiids	2
1.1.3 Seasonal Seas	4
1.1.4 Climate Change.....	6
1.1.5 Thesis Overview	7
1.2 TABLES AND FIGURES	9
2 RESOLVING THE LIFE HISTORY STRATEGY OF <i>THYSANOESSA</i> <i>MACRURA</i> IN WINTER: DEMOGRAPHICS, DIET, AND DISTRIBUTION.....	10
2.1 ABSTRACT.....	10
2.2 INTRODUCTION.....	11
2.3 METHODS.....	16
2.3.1 Study Region.....	16
2.3.2 Hydrographic Sampling.....	17
2.3.3 Net Sampling	17
2.3.4 Density and Distribution.....	18
2.3.5 Length-Frequency.....	20
2.3.6 Biomass.....	20
2.3.7 Stomach Content.....	21
2.4 RESULTS.....	22
2.4.1 Abundance and Distribution	22
2.4.2 Length Frequencies.....	23

2.4.3	Biomass.....	25
2.4.4	Stomach Content.....	25
2.5	DISCUSSION	26
2.6	TABLE AND FIGURES.....	32
3	THE TROPHIC WAVE IN THE DIET OF <i>EUPHAUSIA SUPERBA</i> AND ITS IMPLICATIONS FOR SURVIVAL	48
3.1	ABSTRACT.....	48
3.2	INTRODUCTION.....	49
3.3	METHODS.....	57
3.3.1	Parameters.....	57
3.3.2	The Optimal Rate-Maximizing Diet	59
3.3.3	Estimating Mortality Associated with Prey Choice.....	61
3.4	RESULTS.....	64
3.4.1	Prey Parameters	64
3.4.2	The Rate Maximizing Diet.....	65
3.4.3	Survival Associated with Generalist and Optimal Diets.....	66
3.5	DISCUSSION	67
3.6	TABLES AND FIGUREs	72
4	VERTIKRILL: RESOLVING THE PARADOX OF KRILL AT DEPTH.....	80
4.1	ABSTRACT.....	80
4.2	INTRODUCTION.....	81
4.3	METHODS.....	86
4.3.1	The SDP Model: Model Setting and Model Krill.....	86
4.3.2	The SDP Model: Structure and Behavioral Decisions.....	87
4.3.3	The Environment: Patch Description.....	88
4.3.4	The Environment: Food	89
4.3.5	The Environment: Mortality	90
4.3.6	Physiology: Respiration	91
4.3.7	The SDP Model: Backward Iteration.....	91
4.3.8	The SDP Model: Forward Monte Carlo Simulation	92
4.3.9	Model Runs	94

4.4	RESULTS.....	96
4.4.1	Predicted Vertical Habitat Selection.....	96
4.4.2	Simulated Populations: Habitat Selection.....	98
4.4.3	Forward Monte Carlo Simulation: Changes in Lipid Mass, Mortality, and Habitat Selection.....	99
4.5	DISCUSSION	101
4.6	TABLES AND FIGURES	106
5	CHAPTER 5: CONCLUSION	118
6	REFERENCES	121

LIST OF FIGURES

Figure 1.0.1 Latitudinal distribution of Antarctic and sub-Antarctic euphausiids. (credit: Cuzin-Roudy 2014)	9
Figure 1.0.2 IPCC AR5 Projected global surface temperature changes. (Credit: IPCC)	9
Figure 2.1 Total Biomass Per Recruit (BPR), which is the expected lifetime biomass of a recruit, for <i>Thysanoessa macrura</i> and <i>Euphausia superba</i> over a range of temperatures. M1 and M2 are quadratic growth models with different parameters from (Siegel et al 2014 and Driscoll et al. 2015) and a von Bertalanffy growth model after Driscoll (2013). (from Richerson et al. 2018)	32
Figure 2.2 US AMLR Winter survey stations and areas. Grey boxes mark the boundaries of each sampling area. Drake Passage (DR), West Area (WR), Elephant Island (EI), Joinville Island (JI), Bransfield Strait (BS), Gerlache Strait (GS). Red dots are stations from 2016, actual station locations sometimes varied by a few kilometers between years due to ice conditions.....	33
Figure 2.3 Example of the gamma probability distribution for λ (after Mangel 2006).	34
Figure 2.4 Expected distributions of catch size based on Poisson and negative binomial frequency distributions. (A) The Poisson distribution with a mean of 10. (B, C, and D) The negative binomial distribution with means of 10 and a k overdispersion	

parameter of 0.5, 1, and 5 respectively. Distributions were made in Microsoft Excel using Poisson.dist and Eqn 1. 35

Figure 2.5 Length weight relationship for *T. macrura* for 2010 and 2011 with the mean of the two years in blue based on the power function $W=aL^b$. The relationship was calculated based on the wet mass of individuals or the mean of pooled individuals of the same size. 36

Figure 2.6 *Thysanoessa macrura* mean density for summer (orange) and winter (blue) with standard error. 36

Figure 2.7 Deviations from the mean density for summer (orange) and winter (blue) divided by the standard deviation across years. Dotted line is the regression line for the summer surveys only. 37

Figure 2.8 Estimates of the Negative Binomial Distribution over dispersion parameter k for *Thysanoessa macrura* with *Euphausia superba* for comparison across all water zones. Small values of k indicate a patchy distribution while those greater than 1 indicate a dispersed distribution..... 38

Figure 2.9 Mean length frequencies for the entire survey from summer 1994 to 2010 and winter 2013 and 2014 except for 1997 and 2000, which were not available for analysis. Data are in 1.5 mm bins. Hot color bars correspond to the modes of the distribution. All summer years are dominated by a single mode and in winter 2013 and 2014 there is a second smaller juvenile mode..... 42

Figure 2.10 Winter mean length frequency by sex (individuals/m ³) for 2013 by water zone. Data are in 0.5 mm bins but is presented in line graph format for clarity.....	43
Figure 2.11 Winter mean length frequency by sex (individuals/m ³) for 2013. Data is in 1 mm bins but is presented in line graph format for clarity.....	44
Figure 2.12 Length densities and length weight for summer 2007 and winter 2013..	45
Figure 2.13 <i>Thysanoessa macrura</i> stomach content in frequency of occurrence by sex for 2014.....	46
Figure 2.14 <i>Thysanoessa macrura</i> stomach content in frequency of occurrence by size for 2014.....	47
Figure 3.1. The Trophic Wave Hypothesis. Black lines represent the intensity of predation and grazing. The size of the boxes represent a groups population size relative to other seasons.	72
Figure 3.2. Illustration of the rate maximizing theory of diet selection. In the left-hand panel, I show the predicted rate of energy gain as a function of diet composition. The dashed line represents the point at which including any more prey items decrease the rate of energy return. Items to the left of the dashed line are included in the diet and those to the right are rejected. In the right-hand panel, curve A depicts the diet of a specialist, while curve B depicts a more generalist diet, and in curve C, all potential prey are included in the diet.....	73
Figure 3.3. An example of parachute behavior. In panel A, an individual krill is oriented up is actively feeding. In panel B, an individual is sinking while oriented	

horizontal, with its feeding basket expanded in parachute behavior. (Tarling and Johnson 2006). 74

Figure 3.4 Two perspectives of the ecosystem in terms of proportional abundances by area and season. In column A, prey are arranged by their trophic position reflecting a bottom- up perspective of the ecosystem. In column B prey, are arranged by their energetic profitability to *E. superba* Although the data are the same, each suggests different strategies for *E. superba*. 76

Figure 3.5 The mortality risk of grazing (blue line) and predating (red line) for a range of α 's. Note how grazing becomes more risky, and predating less risky, as α increases. 77

Figure 3.6 The rate of daily energy return depending upon prey included in the diet of *E. superba* for Sub-Antarctic (A), Antarctic Peninsula (B), High Antarctic (C). The order of profitability is the same in all seasons and areas. 77

Figure 3.7 An example of total daily mortality for an optimal diet (top) and a generalist diet (bottom) in each area and season. Here mortality is calculated with an α of 1 which corresponds to a doubling of the mortality risk from grazing and a 50% reduction in mortality risk from predating. 78

Figure 3.8 The relative survival of the optimal diet versus generalizing with increasing α values. 79

Figure 4.1 The probability of encountering food in a given patch for juveniles (A) and adults (B). Model day 0 is the day after spawning occurs, while model day 365 is the

following years spawning event. The surface and epipelagic patches, indicated by the blue and red lines respectively, are calculated from Eqn. 5, while the mesopelagic and benthic patches, yellow and magenta lines respectively, are fixed..... 107

Figure 4.2 The optimal patch choice for juveniles (A,B) and adults (C,D) as a function of state (as lipid mass) and time when krill are restricted to the upper water column (and can inhabit the entire water column (Bottom)). Juvenile state is in mg C x10 with a maximum of 200 mg C x10. Adults have larger body sizes, and therefore larger lipid reserves, so their maximum state is 500 mg C x10..... 108

Figure 4.3 The proportion of juveniles in a simulated population of 10000 individuals in each patch throughout one year, adjusted for loss due to predation and starvation. Because most of the field sampling for *Euphausia superba* was done in summer, in surface water, this has led to the impression that juveniles are restricted to the surface (Top). However, I predict that the mid-water summer and benthic winter habitat may be critical to some juvenile krill (Bottom)..... 109

Figure 4.4 The proportion of adults in a simulated population of 10000 individuals in each patch throughout one year, adjusted for loss due to predation and starvation. Because most of the field sampling for *Euphausia superba* was done in summer surface water this led to the impression that krill are primarily an epipelagic species and efforts in winter have focused on this layer (A). However benthic and mesopelagic habitat may be critical habitat depending on the time of year and body condition of an individual (B)..... 110

Figure 4.5 Juvenile states throughout the year of 40 randomly selected individuals (colored lines) from a simulated population using all patches (A) or only the surface and epipelagic patches (B). All individuals start with the same state equivalent to the average juvenile individual in February. Individuals that drop to 0 die, through either predation (when above 20) or starvation (when state drops below 20). The decision matrix in the background indicates the patches chosen given an individual's state and time. 111

Figure 4.6 Juvenile states throughout the year of 40 randomly selected individuals (colored lines) from a simulated population using all patches with the maximum state increased to 300 C mg C x10..... 112

Figure 4.7 Adult states throughout the year of 40 randomly selected individuals (colored lines) from a simulated population using all patches (A) or only the surface and epipelagic patches (B). All individuals start with the same state, equivalent to the average post spawning lipid mass of an individual in February. Individuals that drop to 0 die through either predation (when above 50) or starvation (when state drops below 50). The decision matrix in the background indicates the patches chosen given an individual's state and time. 113

Figure 4.8 Comparison of the cumulative predation on simulated populations restricted to upper water column versus those utilizing the entire water column juveniles (A) and adults (B)..... 114

Figure 4.9 Simulated adult population with variable starting states. Note that the range of end states is similar to those in Fig. 7A. 115

Figure 4.10 Model scenario for multiple spawning krill. Individuals whose state trajectory crosses the spring reproductive threshold (yellow dotted line) spawn and then begin foraging again. Under delayed spring bloom conditions, winter habitat selection conditions would persist leaving less time in spring to increase state to the minimum threshold thereby lowering the chance for multiple spawning..... 116

Figure 4.11 The number of animals eaten, starved and remaining in the population when (A) respirations costs are the same between habitats ($\alpha_{all} = 2$), and (B) when respiration costs is increased by 1 in the surface habitat only ($\alpha_{surface} = 3$). 117

LIST OF TABLES.

Table 2.1 The total number of stations conducted by the survey for a given year for abundance analysis. The number of stations subsampled for length frequency analysis. The total number of individual <i>Thysanoessa macrura</i> measured from the subsamples. The mean abundance for each year over all areas. The mean length over all areas. Summer mean lengths are for all sexes combined. Winter mean lengths are separated into Male/Female/Combined lengths. The mean SST during the survey. Chlorophyll average integrated down to 100m.....	40
Table 3.1 Model Parameters. Prey are listed in order of their profitability (e_i/h_i). Energy content (e) is for individual zooplankton and for the average number of cells in a 4-minute grazing period for phytoplankton. Handling time (h) is in minutes. Summer and winter abundances (λ) are standardized to μg Carbon/liter. (Atkinson and Ward 1988, Hamner 1988, Price et al. 1988, Froneman et al. 1996 Atkinson et al. 1997, Froneman et al. 1997, Hunt et al. 2011, Borriane and Schlitzer 2013, Garcia et al. 2016).	75
Table 4.1 Model parameters.	106

ABSTRACT

ADAPTED TO ENVIRONMENTAL CHANGE: LIFE HISTORY, DIET, AND HABITAT CHOICE OF KRILL IN WINTER

RYAN DRISCOLL

High latitude oceans are strongly seasonal ecosystems where winter conditions are marked by periods of low primary productivity. These oceans tend to have shortened food webs with relatively few species linking primary production to upper trophic levels. In the case of the Southern Ocean, a single species, *Euphausia superba*, is thought to be this link between trophic levels. The polar regions in both hemispheres are also among the ecosystems heavily impacted by climate change. For example, the western Antarctic Peninsula is experiencing some of the most rapidly changing climate on the planet with changes in temperature, wind, and sea ice durations and extent (Vaughn et al 2003, Stammerjohn et al 2008). Understanding how climate change will affect these ecosystems requires knowledge of trophic structure, its key species, their life history, and their plasticity to environmental variability. In this thesis, I explore the seasonal life history strategies of Antarctic euphausiids. In chapter one, I introduce the high latitude marine ecosystem of the Southern Ocean, Antarctic euphausiids, and climate change and its impact on the ecosystem in this region. In chapter two, I fill in gaps in our knowledge of the life history strategy of the highly abundant, but relatively understudied, *Thysanoessa macrura*, by synthesizing distribution, maturity, and diet data from summer and winter surveys in the Antarctic Peninsula region. I find that krill show knife edge

maturity, can spawn in their first year, are more dispersed and offshore in winter, and are more predatory with increasing size and in winter. In the third chapter I investigate *E. superba* from the perspective of optimal foraging theory to examine when krill generalize or specialize to unify seasonal and regional differences in the diet and feeding behavior of *E. superba* under the Trophic Wave Hypothesis. I predict that krill have a more specialized yet higher mortality risk diet in summer and more of a generalist diet in winter. In chapter four, I ask whether *E. superba* found in benthic and mesopelagic habitats are an aberration or reflect an important part of their life history strategy. In this chapter, I use a Stochastic Dynamic Programming model (VertiKrill) to explore how food, predation, and respiration drive vertical habitat selection across a range body conditions throughout the year. I find that for both juveniles and adults, deep water habitats provide important refuges for avoiding predation and starvation in winter as well as during the transition between seasons. In chapter five I summarize the main findings of each chapter, discuss their implications, and offer future directions for this research.

ACKNOWLEDGEMENTS

I would first and foremost like to thank my advisor Dr. Marc Mangel. Dr. Mangel is well known among his former students for the care and effort he takes in mentorship. This thesis would not have been possible without his dedicated, patient approach to teaching. One of Dr. Mangel's legacies is a family of students who have come out of his lab with a deep understanding of the value in modeling fundamental ecological concepts. I am grateful to Marc for sharing the wisdom he has gained on managing a career in the sciences.

Thank you to my committee members. Dr. Suzanne Alonzo, for letting me temporarily join the Alonzo lab, Dr. Chris Edwards, whose conscientious approach to students is well appreciated and Dr. Jarrod Santora, for his encouragement and belief in this work and whose knowledge of and our shared experience in the AMLR program have proved invaluable. I hope we have more days at sea in the future.

A special thanks to my friends and colleagues at the US Antarctic Marine Living Resource Program for funding, support, encouragement, and experience. Thank you to George Watters for this opportunity and Christin Reiss for just about everything. The US AMLR program does incredible work in the Antarctic year in and year out, yet is not widely known. It is a great example of how much a program can accomplish with a small group of dedicated, passionate scientists.

Thank you to my family and friends for their unwavering support. A special thanks to my parents who always encouraged me to pursue my passion for the ocean.

I would like to thank the Ocean Science Department for their support and assistance and my fellow grad students for their camaraderie, compassion, and sometimes, commiseration.

A special thanks to my co-authors on chapter 2, Kate Richerson and Linsey Sala for their many hours in the lab with me and from whom I have learned so much.

To my wife Sara, whose love and support made this all possible. I love my wife.

INTRODUCTION

1.1.1 Euphausiids

Euphausiids (krill) are a major component of the world's marine ecosystems. They form some of the planet's largest aggregations of biomass and often make up the largest component of regional zooplankton biomass (Brinton and Reid 1985, Siegel 2011, Tarling and Fielding 2016). Krill are found throughout the world's oceans. They inhabit neritic and pelagic environments, are circumpolar in both the Arctic and Antarctic oceans, and are found at nearly all depths (Mauchline 1980, Siegel 2011).

Euphausiids are critical links in many pelagic ecosystems, serving both as grazers and predators as well as food for upper trophic levels, thus playing an important role in the carbon cycle both regionally and globally (Marr 1962, Hopkins 1985, Siegel and Loeb 1995, Mangel and Nicol 2000, Atkinson et al. 2008a).

Euphausiids may themselves be key pathways in nutrient cycling by moving iron to the surface from depth either directly through vertical migration or indirectly through the foraging habits of krill predators (Hopkins 1985, Lavery et al. 2010, Schmidt et al. 2011). The success of many top predators, such as penguins (Trivelpiece et al. 2010), salmonids in the California current (Dorman et al. 2015), pollock in the Bering Sea (Hunt et al 2011) and Antarctic seal populations (Reiss et al. 2017) is directly tied to the population dynamics of krill species. Krill are omnivorous, and their feeding mechanisms can handle prey items with two orders of magnitude in size difference

(Schmidt and Tarling 2016). The grazing mechanisms of krill are so efficient they can exhibit control on phytoplankton populations (Schmidt et al. 2011) and successfully predate on larger copepods (Schmidt and Tarling 2016, Hopkins 1985).

1.1.2 Southern Ocean Euphausiids

In the Southern Ocean, euphausiids are highly abundant and have a collective biomass of 100 - 300 million tons (Loeb 2007, Atkinson et al. 2008a). Of the 11 species of euphausiids in the Southern Ocean five are endemic to Antarctic waters: *Euphausia triacantha*, *E. frigida*, *E. crystallorophias*, *E. superba*, and *Thysanoessa macrura* (Mauchline 1980)(Figure 1.0.1). The latter four species are the most abundant. Relatively little is known about *E. triacantha* and *E. frigida*, but *E. crystallorophias* is most abundant in high latitude neritic environments where it is an important prey item (Thomas and Green 1988). *Euphausia superba* is often considered the main trophic link between primary productivity and higher trophic levels like fish, marine mammals, and seabirds (Atkinson et al. 2008b). *Thysanoessa macrura* is also an important prey species for many predators, including fish (Williams 1985, Saunders et al. 2015), whales (Nemoto & Nasu 1958), seabirds (Bocher et al. 2000, Connan et al. 2008), and penguins (Deagle et al. 2007, Niemandt et al. 2015). *Thysanoessa macrura* is smaller than *E. superba* but numerically dominant and has the broadest distribution across the Southern Ocean (Mauchline 1980). As Nordhausen (1992) noted, the ecological importance of *T. macrura* is likely underappreciated relative to other euphausiids.

Southern Ocean krill exhibit temperature and food dependent growth that varies between species. For example *E. superba* is relatively stenothermic with a narrow temperature range for growth (-1.8 to 5 °C; Cuzin-Roudy et al. 2014) and optimal temperature for growth is around 0.5 °C (Atkinson et al. 2006). In contrast, *T. macrura* is relatively eurythermic, able to tolerate waters -1.8 to 8 °C (Cuzin-Roudy et al. 2014), and its optimal temperature for growth is at least 2.5 °C (Driscoll et al. 2015). The growth rate of *E. superba* is also positively correlated with phytoplankton availability (Atkinson et al. 2006), while *T. macrura* growth in summer is not correlated with phytoplankton or copepod availability (Nordhausen 1992, Driscoll et al. 2015).

Southern Ocean euphausiids also vary in their diet among both species and seasons. For example, *Euphausia triacantha* is mainly thought to be a predator while gut content analyses indicate that *E. superba* diets are dominated by diatoms and (to a lesser extent) metazoans (Schmidt et al. 2006). In summer, *T. macrura* consume high numbers of copepods, particularly *Calanoides acutus* and *Metridia gerlachei*, as well as diatoms, tintinids, and a wide variety of other zooplankton and microzooplankton (Hopkins 1985, Hopkins & Torres 1989). Seasonal variation in diets revealed by lipid analysis are different between species and isotopic analysis and suggest that *E. superba* shifts to smaller phytoplankton, detritus, and microzooplankton while *T. macrura* is primarily a predator in winter (Reiss et al. 2017).

1.1.3 Seasonal Seas

Winter in high latitude marine environments poses unique challenges to its inhabitants. The decreasing daylight, onset of seasonal sea ice, and reduced mixing lead to a dramatic reduction in primary production and changes in phytoplankton community composition (Montes-Hugo et al. 2009). Pelagic zooplankton have developed a range of adaptations to survive winter, such as increasing lipid stores, prey switching, migration, reducing metabolism, diapause, and facultative changes to behavior (Meyer 2012). High latitude ecosystems tend to have simple, relatively short food webs with only a few species or groups providing the main energy flow between primary production and upper trophic levels (Murphy et al 2016). In the Southern Ocean, this wasp-waist type food web is assumed to be dominated by one species, *E. superba*, with *E. crystallarophias* and *Pleuragramma antarctica* (Antarctic silverfish) replacing *E. superba* locally, and with *T. macrura* and *Themisto gaudichaudii* serving as secondary energy pathways (Murphy et al. 2016). A successful winter strategy for adults may lead to better body condition heading into spawning season, while winter survival for larvae and juveniles leads to strong recruitment. *Euphausia superba*'s overwintering strategy has become a critical area of Southern Ocean research given that there is a growing fishery and current interest establishing Antarctic Marine Protected Areas.

Euphausia superba exhibit a number of adaptations to deal with changes in its environment. The current paradigm, in brief, supposes that *E. superba* builds lipid stores during summer and then slows its metabolism to conserve energy as primary

production slows down moving into winter (Meyer 2012). These physiological changes may be the result of an internal clock mediated by a change in day light length (Meyer 2012). Adults supplement their stored lipids by grazing on remaining algae including ice algae and may switch to a more predatory diet in winter (Jia et al. 2016). Larval and juvenile individuals cannot store as much lipids as adults and are obligated to graze on entrained ice algae and/or phytoplankton in open water, returning under the ice to avoid predators (Meyer 2012, Meyer et al 2017). Lipid stores are depleted at the end of winter, making the energy provided by the spring bloom necessary for reproductive development. Individuals spawn through mid-summer and then work to rebuild lipid stores for the coming winter.

There are several inconsistencies between the current overwintering paradigm and recent field observations. If larvae depend on ice algae for survival, then we should see a successful larval cohort appear as juveniles in the summers following a good ice year. However larval abundances show a weak correlation to sea ice and larval cohort abundances in winter are not correlated to their subsequent summer or winter populations (Kinzey et al. 2019). Recent winter surveys in the Antarctic Peninsula region show that adult *E. superba* undertake large migrations inshore in winter and diel migration to twice the depth as in summer, have been found in benthic habitats as deep as 2000 m, and lipid percentages, while reduced, are not nearly depleted by winter's end (Schmitt et al. 2011). These energetically costly movements, along with the maintenance of lipid stores, are not what would be predicted for a species conserving its energy reserve for survival. The existing theories on *E. superba*

behavior in winter do not fully explain observations of the movements and conditions of natural populations.

1.1.4 Climate Change

Evidence for climate change is irrefutable, yet there is a lack of understanding about its impact on pelagic ecosystems. Climate change may cause shifts in habitat boundaries and extent, variations in abundance and annual reproductive success (Southward 1995), and alter phenology (Parmesan and Yohe 2003) for both terrestrial and marine organisms. This can have dramatic consequences for food webs, ecosystem structure and function, and ecosystem benefits to humans (Anisimov et al. 2007). In aquatic ecosystems, climate change impacts are especially important in areas where bottom-up processes may control the dynamics of species important to higher trophic levels, including zooplankton. In these ecosystems, climate change impacts on environmental parameters (seasonal heat flux, irradiance, and nutrient cycling) can alter the conditions necessary for primary productivity (Quetin & Ross 2001). Given that species specific responses to climate change are unknown for many taxa, and responses will likely vary in both magnitude and direction, a more complete understanding of the life history of taxa that are dominant in numbers, biomass, or occurrence is required to understand the likely ecosystem changes that will result from global climate change (Helmuth et al. 2005).

Among the ecosystems most impacted by climate change are the polar regions in both hemispheres. For example, the western Antarctic Peninsula region of the Southern Ocean is experiencing the most rapidly changing climate on the planet

(Vaughn et al 2003, Stammerjohn et al. 2008), with measurable changes in primary production (Hewes et al. 2009), increases in sea surface temperatures (Gille 2002) and seasonal air temperature (Meredith and King 2005), and decreases in sea ice duration and extent (De La Mare 1997a, Stammerjohn et al. 2008). Projections of continued warming based on models developed by the Intergovernmental Panel on Climate Change (IPCC)(Figure 1.0.2) show that the western Antarctic Peninsula air temperature could increase an additional 2°C over the next 30 years. Such continued and dramatic changes will likely further impact regions where primary production was historically tied to seasonal sea ice dynamics. The magnitude and timing of the sea ice melt affects the timing and strength of the spring bloom, which in turn affects the overlap between production and consumption by zooplankton grazers (primarily euphausiids) in the spring (Atkinson et al. 2001, Loeb 2008). Variability in annual sea ice extent, duration, and type may also affect larval overwinter survival (Meyer et al. 2017).

1.1.5 Thesis Overview

This thesis has two broad aims: First, elucidate the life history of species that may provide alternative energy pathways to *E. superba* and second, apply basic ecological theory to provide context to the wide range of behaviors exhibited by *E. superba* across regions and seasons. I address the first aim in chapter two, where I fill in gaps in our knowledge of the life history strategy of the highly abundant, but relatively understudied, *T. macrura*. I synthesize distribution, maturity, and diet data from summer and winter surveys in the Antarctic Peninsula region. I address the second aim

in chapters three and four. In chapter three, I ask whether *E. superba* is always a generalist forager by using Optimal Foraging Theory models to elucidate seasonal and regional differences in the diet and feeding behavior of *E. superba* under the Trophic Wave Hypothesis. In chapter four, I ask whether *E. superba* found in benthic and mesopelagic habitats are an aberration or reflect an important part of their life history strategy. In this chapter, I use a Stochastic Dynamic Programming model (VertiKrill) to explore how food, predation, and respiration drive vertical habitat selection across a range body conditions throughout the year.

1.2 TABLES AND FIGURES

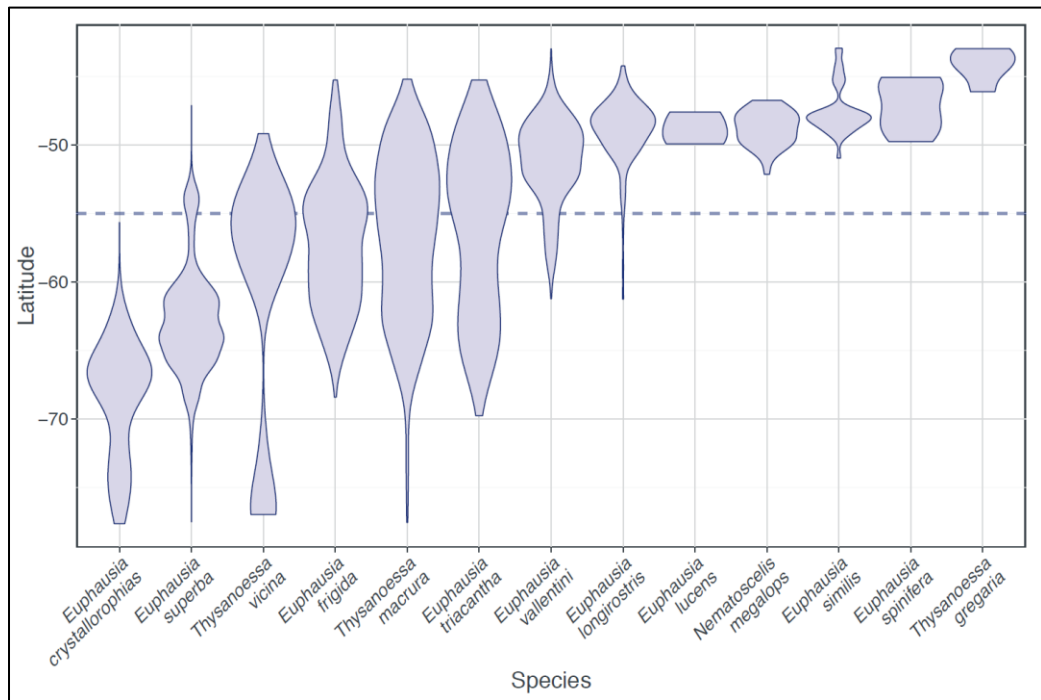


Figure 1.0.1 Latitudinal distribution of Antarctic and sub-Antarctic euphausiids. (credit: Cuzin-Roudy 2014)

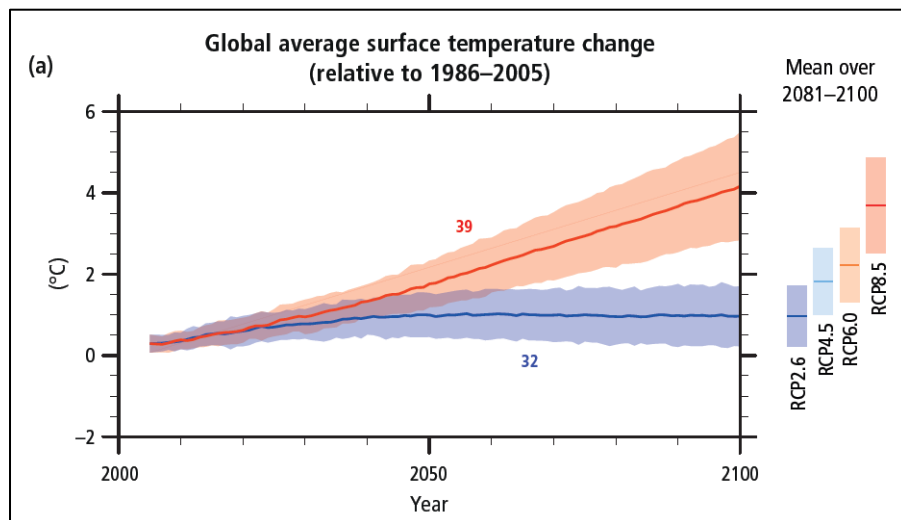


Figure 1.0.2 IPCC AR5 Projected global surface temperature changes. (Credit: IPCC)

2 RESOLVING THE LIFE HISTORY STRATEGY OF *THYSANOESSA MACRURA* IN WINTER: DEMOGRAPHICS, DIET, AND DISTRIBUTION¹

2.1 ABSTRACT

Thysanoessa macrura is the most numerically abundant euphausiid in the Southern Ocean. *Euphausia superba* dominates in biomass, but its populations are either steady or declining, while those of *T. macrura* are increasing. Recent studies show that under future climate change scenarios, increased biomass from *T. macrura* may compensate for the decline in the biomass of *E. superba*. However, *T. macrura* is understudied relative to *E. superba* and key aspects of its life history (specifically, age at maturity, length at age, and winter behavior and diet) make it difficult to accurately assess the species response to climate change. In this chapter, I fill in gaps in our knowledge of the life history strategy of the highly abundant *T. macrura* by synthesizing distribution, maturity, and diet data from summer and winter surveys in the Antarctic Peninsula region. I find that *T. macrura* show knife edge maturity, can spawn in their first year, are more dispersed and offshore in winter than *E. superba*, and are more predatory with increasing size in winter than *E. superba*.

¹ This work will be published with Kate Richerson, and Linsey Sala, as co-authors for their collaboration with maturity, diet analysis, specimen collection.

2.2 INTRODUCTION

Climate change impacts polar marine environments in ways that pose unique challenges to high latitude marine organisms. These environments experience some of the planet's most rapid climate change, including increases in air and sea surface temperature (Gille 2002, Meredith and King 2005, Whitehouse et al. 2008, Schmidtko et al. 2014), and shifts in meridional winds (Marshall et al. 2006). This has affected the seasonal aspects of sea ice dynamics, including decreases in total sea ice in some regions, and increased variability in the timing and magnitude of seasonal sea ice concentration and primary production (Vaughn 2003, Stammerjohn et al. 2008). Over millennia, polar marine species developed various life histories and overwintering strategies to deal with high seasonal environmental variability (Kennett 1976, Peck et al. 2006), and these species-specific life histories will have different responses to interannual climate variability (Mangel and Nicol 2000, Wiedenmann et al. 2008, Loeb and Santora 2015, Steinberg et al. 2015 Richerson et al. 2018). Resolving the seasonal aspects of the life history of key species, such as euphausiids, is critical to understanding how climate change will impact high latitude marine ecosystems.

Euphausiids show oscillatory responses in population abundance to climate forcing patterns (Pinchuk et al. 2008), as well as long term population trends (Loeb and Santora 2015). In the California Current, *Thysanoessa spinifera* and *Euphausia pacifica*, species adapted to cold water, showed a strong negative correlation with warming due to El Niño indices, while the subtropical, warm water adapted species,

Nyctiphanes simplex, exhibited strong positive correlations and northward range expansions. In the Barents Sea, the euphausiid community is dominated by the warm water *T. inermis* and the cold-water *T. raschii*; each species' range expands and contracts depending on ocean temperature, and is strongly linked to the North Atlantic Oscillation (Orlova et al. 2015). A long-term increase in euphausiid abundance in the Barents Sea is attributed to increased intrusion of warm water, and subsequently warm water species like *T. inermis* and *Meganyctiphanes norvegica* (Orlova et al. 2015). In the Gulf of Alaska, variation in abundance of the herbivorous, episodic spawner *T. inermis* are associated with positive Pacific Decadal Oscillation phases and associated strong spring bloom conditions, while the more omnivorous and broader spawning *T. spinifera* and *E. pacifica* exhibited less variability with climate cycles (Pinchuk et al. 2008).

In the Southern Ocean, the response of euphausiids to environmental change varies by species and region. In the Antarctic peninsula region, *E. superba*, *E. crystallorophias*, *E. frigida*, and *T. macrura* showed positive abundance anomalies to El Niño indices, while *E. triacantha* showed a negative response over a 20-year period (Loeb and Santora 2015, Steinberg et al 2015). Long term trends in abundance from 1992-2013 were positive for *T. macrura* (Steinberg et al. 2015), or showed no significant increase (Loeb and Santora 2015). *E. superba* also showed a positive association with negative anomalies in the Southern Annular Mode, when colder sea surface temperatures lead to anomalously high winter sea ice which provided better larval habitat (Fielding et. al. 2014). In contrast to these findings, one study of all net

data available up to 2004 found a large decline in the abundance of *E. superba* starting in the mid 1970's (Atkinson et al 2004). Several mechanisms have been proposed for the link between *E. superba* and environmental variability. For example, larval recruitment may correlate with anomalously high ice years; these years may provide refuge for larvae and/or positive conditions for reproductive development during the spring bloom (Wiedenman et al. 2008, Meyer et al. 2017, Reiss et al. 2017, Ryabov et al. 2017). Climate modes may change wind and circulation patterns which impact advection and retention patterns within important krill population centers (Fieldling et al. 2014, Loeb and Santora 2015). The mechanisms driving the population dynamics of the other Southern Ocean euphausiids is largely unknown.

The reproductive success or failure of krill predators often follows those of their prey. For example, Barents Sea cod stocks are correlated with successful recruitment years of *T. inermis* (Orlova et al. 2015). In the Southern Ocean, where many regions have relatively simple food webs with one or two species, *E. superba* often serves as the link between primary productivity and upper trophic levels (Atkinson et al. 2008). Consequently, much research in the Southern Ocean has focused on *E. superba*, a species of large biomass and demonstrable importance in the ecosystem (Flores et al. 2012). However, other species, such as *E. crystallorophias* or *Pleuragramma antarcticum* in coastal regions (Hopkins 1985, Cuzin-Roudy et al. 2014) can substitute for *E. superba* as the ecological link between trophic levels, or serve as secondary energy pathways, such as *Themisto gaudichaudii*, copepods, and the ubiquitous *Thysanoessa macrura* (Murphy et al. 2013).

T. macrura is the most numerically abundant euphausiid in the Southern Ocean and an important prey item for seabirds (Bocher et al. 2000), whales (Nemoto and Nasu 1958), and fish (Williams 1985). *T. macrura* is relatively eurythermic compared to *E. superba* and while the populations of the latter are steady or declining, those of *T. macrura* are increasing, and its biomass may compensate for the loss of *E. superba* under future climate change scenarios (Driscoll et al. 2015, Richerson et al. 2017) (see Figure 2.1). For example, Richerson et al. (2017) applied temperature dependent growth models for *E. superba* and *T. macrura* and showed that under future climate change scenarios the biomass per recruit may decrease for *E. superba* but increase for *T. macrura*. However, important gaps remain in the life history of *T. macrura* and hinder our understanding of its potential response to climate change.

T. macrura start spawning in late winter before the spring bloom, and likely spawn several times over a season (Wallis et al. 2017), although the size and age at maturity are not well known. Attempts to determine the length-at-age for *T. macrura* have relied on assigning ages to curves fit to length frequency distributions, a method for which one usually assumes that each mode of a multi-modal length frequency is a different age class (Siegel 1987, Harraldsson and Siegel 2014). However, length frequencies for *T. macrura* tend to be unimodal making the accurate assignment of age groups difficult. Studies of *T. macrura*'s diet in summer indicate they are more predatory than *E. superba*, and a high wax ester composition before spawning suggests they consume micro- and mesozooplankton through winter, although no

direct measurements have been made to confirm their feeding preferences (Hagen and Kattner 1998, Falk-Petersen et al. 2000).

Observations of *T. macrura* near the South Shetland Islands suggest that their distribution from mid- to late summer shifts inshore (Santora and Loeb 2015), however, their winter distribution is unknown in the region. Seasonal shifts in the distribution of *T. macrura* may change predation and grazing pressure on food items, competitive overlap with other euphausiids, and the availability of *T. macrura* to predators. Distribution changes in zooplankton may be geographical, as in the case of a population wide migration, or in patchiness, how concentrated or dispersed individuals are to one another. Repeated spatial surveys can provide information on geographic distribution, and the Negative Binomial Distribution (NBD) can be used to describe the patchiness of a species (Richerson et al. 2017). The NBD describes the probability of discrete events that are clustered in space or time (e.g., the number of *T. macrura* at a station (Mangel 2006)).

Here I use new demographic and diet data from five years of winter surveys in the waters of the South Shetland Islands to ask three important questions in our knowledge of *T. macrura*'s life history. First, Do *T. macrura* abundance and distribution patterns change in winter compared to summer? Second, what is the size and age of maturity for *T. macrura*? Third, what do *T. macrura* eat during winter?

2.3 METHODS

2.3.1 Study Region

I used data from the US Antarctic Marine Living Resource Program (AMLR), which conducted oceanographic summer surveys each January from 1988 to 2011 and winter surveys in August from 2012-2016 around the South Shetland Islands (See Figure 2.2).

Within the study area there are three distinct hydrographic regions that, in summer, can be classified by their dominant water masses (Amos 2001). In general, the Elephant Island (EI) area is dominated by two water zones whose border runs roughly diagonally from the southwest to the northeast. The area north of the South Shetland islands has a relatively broad shelf at the southern edge with pelagic water to the north. The area is composed of the eastward flowing Southern Antarctic Circumpolar Current Front (here denoted as ACC) (Orsi et al 1994) with relatively warm water in summer (2 to 4°C), cold water in winter (0°C, > 100 m), and low salinity (< 34 psu), which persists at depth into summer, and has Upper Circumpolar Deepwater (2°C, > 400 m) beneath it (Amos 2001). The Bransfield strait area, between the South Shetland Islands and the Antarctic Peninsula is characterized by a deep central basin with a broad shelf to the south and none along the north edge. This area is dominated by a clockwise flowing current with intermediate temperature (1.5-2°C) and salinity (33.9 to 34.1 practical salinity units) that is a mixture of Weddell Sea water, Gerlache Strait water from the Western Antarctic Peninsula, and ACC water (Holm-Hansen et al. 1997, Amos 2001). The area south of Elephant Island is

dominated by the western edge of the clockwise flowing Weddell Sea gyre water, characterized by colder (-0.5°C) and saltier (> 34.1 psus) water and water from the Bransfield Strait. In winter, water zone descriptors by Amos (2001) are less accurate (Santora pers comm.) as surface waters cool.

2.3.2 Hydrographic Sampling

Preceding each zooplankton tow, water column temperature, salinity, and oxygen concentration were collected at each station using a Seabird SBE 9/11 Conductivity, Temperature and Depth (CTD) sensor. Each CTD cast was made to a depth of ~ 750 m, or 10 m from the bottom at stations < 760 m depth. Temperature at 15 m depth was used to represent the temperature of the upper mixed layer.

2.3.3 Net Sampling

I focus on archived samples for summer surveys collected starting 1994, when the survey area and gear were standardized with predefined transects and fixed stations either 20 or 40 km apart (Figure 2.2), through 2011, except for 2000 when there was no survey. Samples for length frequencies were limited to the Elephant Island area where consistent sampling provided the longest data set. Winter samples from 2012 to 2016 were collected from all areas with length frequency samples limited to 2013 and 2014. The number of stations varied in each year and area due to ice conditions and research priorities. All samples were obtained using a 1.8 m Isaacs-Kidd Midwater Trawl (IKMT) with 505- μm mesh fished obliquely to either 170 m depth or 20 m above the bottom at stations < 190 m deep. A General Oceanics flowmeter (Model 2030) was used to determine the volume of water filtered during

each tow. The collected samples were sorted aboard ship, and larval and post-larval euphausiids were identified and enumerated. Tows taken at twilight were excluded due to potential differences in diel migration rates of euphausiids by size. Samples were preserved in 5% buffered formalin and transported to Southwest Fisheries Science Center for storage (Loeb et al. 2004).

2.3.4 Density and Distribution

Abundance was corrected for differences in the volume of water filtered during each tow. I divided the total number of individuals caught by the volume of water filtered to report abundances as densities (per 1000 m³).

One of the general characteristics of plankton is their patchiness (McGurk 1986): most sampling locations have no individuals at all but when a spatial location has some individuals, it has many. Krill have this characteristic and tend to aggregate in space in the form of large swarms, with few relatively individuals between patches (Richerson et al. 2017). The consequence of this is that towed net samples often have a variance that is much bigger than the mean. If individuals were randomly distributed in space, their distribution could be characterized by a Poisson process, for which the variance is equal to the mean. On the other hand, plankton samples with the variance larger than the mean are said to be over-dispersed.

The Negative Binomial Distribution (NBD) is one way to capture over-dispersion. It can be derived (e.g. Mangel 2006) that individuals are distributed in space according to a Poisson process with parameter λ but that this parameter itself follows a gamma density. In Figure 2.3, I show some examples of the gamma density.

Combining the Poisson and gamma in this manner leads to the NBD for the number of krill N in a net tow

$$\Pr\{N = n\} = \frac{\Gamma(k + n)}{n!} \left(\frac{k}{k + m}\right)^k \left(\frac{m}{k + m}\right)^n \quad (1)$$

where n is the number of krill in a sample, m is the mean of a given year and k is one of the two parameters of the gamma density. In particular, the coefficient of variation of λ is $\frac{1}{\sqrt{k}}$. I will refer to k as the overdispersion parameter.

If N follows the distribution in Eqn 1, its mean is m and its variance is

$$\text{Var}[N] = m + \frac{m^2}{k} \quad (2)$$

Note that as $k \rightarrow \infty$, the variance in Eqn. 2 approaches m so that large values of k correspond to nearly Poisson distributions of counts. As k decreases (but must be always positive) the variance of N is larger and larger than the mean. In Figure 2.4, I show an example of a Poisson distribution and three associated NBDs.

To assess inter-annual and seasonal differences in the spatial distribution of *T. macrura*, I calculated the overdispersion parameter k of the Negative Binomial Distribution. In particular if S^2 is the variance in abundance and m is the mean of a given year and $S^2 < m$ the method of moments for k is (Richerson et al. 2017)

$$\hat{k} = \frac{m^2}{S^2 - m} \quad (3)$$

where \hat{k} is the estimate of k .

2.3.5 Length-Frequency

I measured *T. macrura* to construct length-frequency distributions for summer surveys using formalin preserved samples from the Elephant Island region from 1994 to 2010, except for 1997, for which the archived samples were not available for processing. For winter surveys, all areas were included in the length frequency using fresh individuals in 2013, and formalin preserved individuals from 2014. For each sample, I selected up to 200 animals randomly for analysis. I did not determine sex or maturity for the summer samples due to logistical constraints at the time of collection. For the winter survey, I sorted individuals from 2013 by sex, and 2014 samples by sex and maturity stage based on Makarov and Deny's (1981) classification of maturity stages for *E. superba*. I used the distance from rostrum tip to telson tip as body length for all post-larval individuals, which is a standardized measure of length for euphausiids and a common measure for *E. superba* (Mauchline 1980, de la Mare 1994). The length frequency from a subsample was used to extrapolate to the entire sample, and the resulting abundance at each size bin were converted to length frequencies. I used the mean frequency of each bin across all subsamples to obtain the length frequency for each year.

2.3.6 Biomass

I constructed a length-weight relationship for *T. macrura* (Figure 2.5) to examine the contribution of different size classes to the biomass of the population. A length-weight relationship for each year was obtained using the power function:

$$\log(W) = \log(a) + b \log(L) \quad (4)$$

where W is weight and L is the length. Given that the length-weight relationship is a power function, I expect larger individuals to have a large contribution to the biomass of the population compared to their abundance. I used this approach because larger individuals can contribute to the biomass disproportionate to their abundance compared to smaller individuals. I constructed length and weights of *T. macrura* in 2010 (263 individuals) and 2011 (219 individuals). Measurements were taken for a separate energetics study which sometimes required up to 7 individual small *T. macrura* to be grouped, in those cases the average weight was used. Growth may vary between years due interannual differences in environmental conditions (temperature and length of season) or food availability. In order to account for this variability, I used the average of allometry for 2010 and 2011 to calculate the weight at each length. This was then applied to the length density for each year to obtain biomass B :

$$B(y) = \sum_{l=\max}^{l=\min} N(l, y)W(l) \quad (5)$$

where N is the number of individuals at length l and year y , and W is the average weight of length class l .

2.3.7 Stomach Content

I conducted stomach content analyses for 2014 using the same samples from which length frequencies were obtained. I removed individuals from formalin, measured and staged them and then removed and separated the stomach from the gastric mill and intestine under a dissecting microscope. I determined gut fullness

visually to the nearest 10% before removing contents. I identified and enumerated stomach contents when possible.

When a prey item was eaten, and how quickly it is digested, affects the ability to both identify and quantify prey. For example, soft bodied prey, such as flagellates, quickly break down making their identification difficult, while small copepods are crushed into many small parts, making enumeration difficult (Hopkins and Torres 1988). In general, I report the presence/absence of prey and use estimates of gut fullness as a qualitative and relative estimate of grazing/predation amount. When relevant, I comment on specific counts and instances of a particular prey.

2.4 RESULTS

2.4.1 Abundance and Distribution

The mean *T. macrura* abundances across all winter years were not significantly different to the mean across all summer years ((122.2/1000 m³, SD=35.47 vs. 116.5/1000 m³, SD=50.54, respectively t(5)=-0.2525, p=0.81) (Figure 2.6). *T. macrura* exhibited a shift from negative to positive anomalies in 1998, except for 2001 and 2011, when abundances were low. However, this trend was not apparent in the winter data (Figure 2.7).

T. macrura were patchier in summer ($\hat{k}=0.419$) than winter ($\hat{k}=1.444$) over all years (t(3)=-2.92, p=0.06) (Figure 2.8). For reference, I plotted \hat{k} for *E. superba* which was first reported by Richerson et al. (2015). *T. macrura* were more dispersed

than *E. superba* in all years in both summer ($t(25)=5.43$, $p<0.01$) and winter ($t(3)=4.15$, $p=0.025$) (Figure 2.8).

2.4.2 Length Frequencies

The length frequencies of *T. macrura* for each austral Summer survey were unimodal and slightly right skewed (mean skewness = 2.21, SD = 0.238) in all years (Figure 2.9). The smallest observed mean size were in 1995 and 2007 (both 15 mm) and the largest mean size occurred in 2006 (18.5 mm). The range of lengths over all years was 10.5 mm to 33.5 mm, with only a few individuals over 27 mm found in the entire 15-yr data set (<0.005% of the total abundance) (

Table 2.1). The narrowest range (12 – 27 mm) occurred in 2001, and the broadest range (10.5 – 33.5 mm) occurred in 2005 (Table 2.1).

Length frequencies of *T. macrura* from the 2013 and 2014 austral winter survey were bimodal with the first modes in both years centered at 8 mm and were comprised almost entirely of juveniles. The second modes centered at 14.5 mm (2013) and 13 mm (2014) and were comprised entirely of adults (

Table 2.1, Figure 2.10, Figure 2.11). Males were smaller on average in both 2013 and 2014 (13.5 mm and 12 mm respectively) than were females (15.5 mm and 14 mm respectively). Though there were relatively few large individuals over all, a larger portion of females exceed 18mm (10%) than males (<3%).

Thysanoessa macrura maturity was knife-edged at 10 mm in both years, where few male (<4%) and female (<2%) individuals in 2013 below 10 mm. In 2014, females were as small as 8.5 mm and few males (<2%) were as small as 9 mm.

Thysanoessa macrura exhibited signs of active spawning in winter in 2014 when the majority of adult males in the entire length range (10 mm to 19mm) had sperm packets, including males as small as 10 mm. The majority of females (>65%) of sizes (11 mm to 24 mm) were found with sperm packets attached, both spent and unspent.

2.4.3 Biomass

Overall summer years, individuals over 19 mm represent 27.6% of the population and 38.9% of the biomass (Figure 2.12). The relative contribution of different size classes to the biomass is dependent on the length density distribution of a given year. For example, in 2007, individuals over 19mm are 18.2% of the population and 30.6% of the biomass, and in winter 2013 juveniles are 15.7% of the population but only 5.6% of the biomass (Figure 2.12).

2.4.4 Stomach Content

Stomach content analyses reveal a diverse diet for male and female *T. macrura* in late winter. Aside from detritus, which includes unidentifiable and

digested food, microzooplankton were the most common prey, primarily foraminiferans and tintinnids, and along with diatoms and dinoflagellates, that made up the grazed portion of the diet. This set of prey accounted for most of the winter diet for small *T. macrura* (under 20 mm) (Figure 2.13). However, both males and females under 20 mm were found with copepod parts in their guts (Figure 2.14). Larger *T. macrura* had a more predatory diet with copepod parts being the third most common item found in the gut. Notably, larger *T. macrura* also preyed on other euphausiid larvae, which were identified by their carapace and ocelli.

2.5 DISCUSSION

I began by asking three broad questions. First, do the abundance and distribution, as pertaining to patchiness, of *T. macrura* change between summer and winter? Second, what is the size and age at maturity for *T. macrura*? And third, what is *T. macrura*'s winter diet?

2.5.1.1 *Seasonal Variability in Distribution and Abundance*

Estimates of \hat{k} show that *T. macrura* is more dispersed than *E. superba*, which forms notably large swarms. The two species exhibit the opposite seasonal pattern in their patchiness, with *T. macrura* becoming more dispersed and pelagic in winter, while *E. superba* becomes more aggregated and coastal. The seasonal and spatial patterns in abundance may reflect seasonal variation in *T. macrura*'s diet, reproduction, and/or changes in predation pressure on *T. macrura*. In summer, individuals may move to areas with high primary productivity closer to the shelf and aggregate to avoid increased predation pressure. In winter *T. macrura* may disperse to

hunt prey and move to the ACC to ensure that eggs are spawned in deep water for ontogenetic migration away from predators.

2.5.1.2 Length-at-age and Maturity

Thysanoessa macrura can mature in their first year of life and have a fairly constrained length-at-maturity at 10 mm. This result indicates that the date of birth/emergence affects whether individuals can spawn in their first year of life and contrasts with *E. superba* which does not spawn in its first year. Length frequencies of winter *T. macrura* were bimodal with one distinct mode that I interpreted as juveniles and another for a single cohort of adults indicating the presence of two cohorts. When adults were separated in winter by sex, their resulting distributions were unimodal with females being significantly larger than males. In summer *T. macrura* adult distributions around the South Shetland Islands have a unimodal length frequency in contrast to the multimodal distributions of other species of krill (Siegel 1987), suggesting that the summer population is primarily composed of a single year class. Adults in summer were 2 mm larger on average than those in winter, suggesting the winter adult year class is the same year class as those found summer but 4 to 5 months younger. The smaller juvenile mode found in winter was not present in the summer length frequencies. Loeb and Santora (2015) suggested that there may be two separate spawning populations in the region, and latitudinal north to south spawning waves have been observed for other euphausiids in the Southern Ocean, where spring bloom conditions occur in the north regions sooner. This timing may account for the juvenile mode found here. Alternatively, if *T. macrura* can spawn multiple times in a

season (Wallis et al 2017), then the juvenile mode may represent late spawning members of the cohort.

Differences between the mean lengths from length-at-age reported here and modal analyses in other studies of *T. macrura* (Siegel 1987, Taki et al. 2008, Haraldsson and Siegel 2014) may be explained in part by regional variations in the time of spawning and differences in the growth rate between males and females. Makarov (1979) and Nordhausen (1992) found later stage *T. macrura* larvae in northern areas and early stage larvae at more southern stations, suggesting a latitudinal spawning progression similar to congeneric euphausiids in the Bering Sea (Smith 1991). In addition, several surveys have found all stages of *T. macrura* larvae (CI to FVI) present in January in both the Ross Sea (Taki et al. 2008) and the waters around the South Shetland Islands (Nordhausen 1992, Loeb 2004), suggesting that a broad spawning period is a consistent feature of the species. Here I found that females were larger on average than males, similar to Haraldsson and Siegel (2014), which leads to a broad unimodal distribution for the population with females forming the majority of the right tail and males the left. However, in Haraldsson and Siegel (2014) and Siegel (1987), multiple modes were fit to the length frequency distribution and interpreted as age classes.

Thysanoessa macrura is likely the most numerically abundant euphausiid in the Southern Ocean (Mauchline 1980, Nordhausen 1992). However, few individuals of the cohort found in summer were found in winter. There are several explanations for this observation. First, it could be that most of the population dies off between

summer and the end of winter, which would require a high mortality rate in the months between summer and the following spring and a large turnover in the population. Second, individuals may be advected out of the study region. If this were the case larger *T. macrura* should appear in surveys occurring in adjoining regions however, they do not. Third, there is some evidence from several recent surveys that indicate that larger *T. macrura* may migrate to waters deeper than 170 m. In the Ross Sea, Taki et al. (2008) estimated that the median depth for *T. macrura* occurred at 200 m for males and at 400 m for females. In the shelf water near Marguerite Bay, Wiebe et al. (2011) found that *T. macrura* had the broadest vertical distribution of the four major euphausiids in the Southern Ocean, with the greatest abundances found between ~150 m to 250 m. In addition, during the summer of 2011, the US AMLR Program (unpublished data) collected a dozen female *T. macrura* > 38 mm, off Livingston Island during a gear test from a depth of 650 m. These observations of large animals at depth suggest it is likely that AMLR's standardized sampling of depths < 170 m is under-collecting the older, larger cohorts. If the largest *T. macrura* are missed by the sampling strategy, then the summertime series largely represents only animals in their second year of life (i.e. recruitment from the previous year's production). The large size and reproductive potential of this under-collected component of the population may constitute a significant portion of the biomass and larval production of this species.

2.5.1.3 Winter Diet and Implications for Life History

A key component of *T. macrura*'s overwintering strategy and phenology is a more predatory diet in winter, including predation on other euphausiid larvae. This strategy allows *T. macrura*, like the other Southern Ocean euphausiids except *E. superba*, to maintain a high percentage of wax esters in its lipid composition. Wax esters can be mobilized for reproductive development in winter. *Thysanoessa macrura* can then spawn one to several more times and use the summer to grow and rebuild its lipid stores. This behavior is similar to the omnivorous and broad spawning *E. pacifica* and *T. spinifera* in the Gulf of Alaska; there, species exhibit reduced variability compared to the herbivorous episodic spawner *T. raschii*, whose strategy is similar to *E. superba* (Pinchuk and Hopcroft 2007).

2.5.1.4 Conclusion

The importance of *T. macrura* to the Southern Ocean ecosystem is likely underestimated. Its mean abundance is estimated to be several times that of *E. superba* in the Antarctic peninsula region, even though several studies have shown that the population is under sampled. Its life history suggests that under future warming scenarios *T. macrura*'s growth rate and population will increase (Richerson et al 2018), potentially providing an alternate source of biomass to *E. superba* for the ecosystem. *T. macrura* may also play an important role as a predator, shaping the zooplankton community and impacting the recruitment of *E. superba* larvae. This study provides the context and motivation with which we can model *T. macrura*'s seasonal behavior and better understand its role in the ecosystem.

2.6 TABLE AND FIGURES

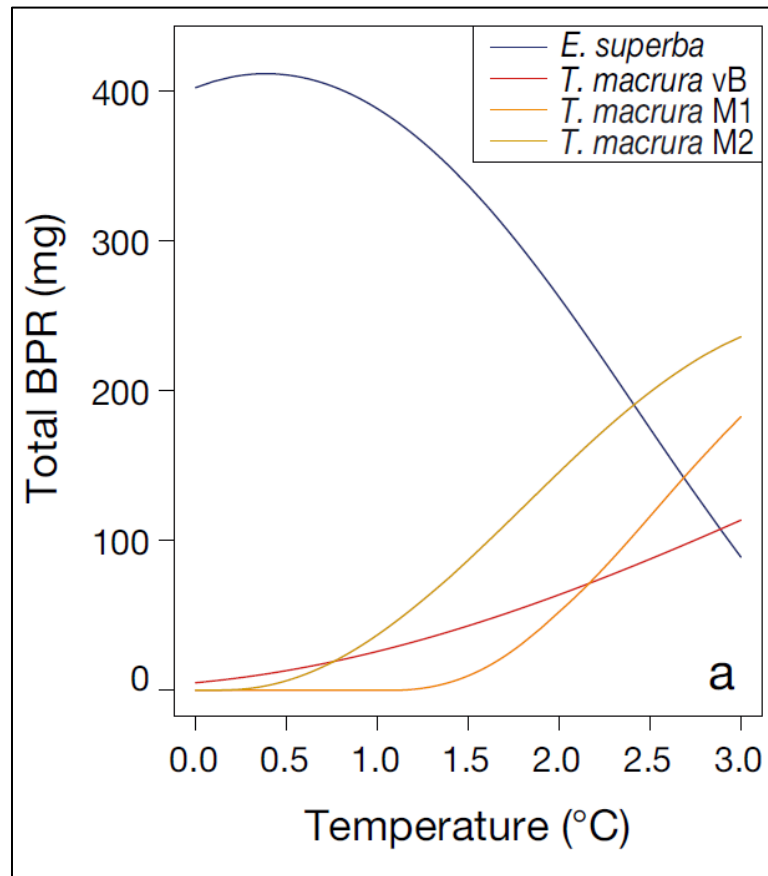


Figure 2.1 Total Biomass Per Recruit (BPR), which is the expected lifetime biomass of a recruit, for *Thysanoessa macrura* and *Euphausia superba* over a range of temperatures. M1 and M2 are quadratic growth models with different parameters from (Siegel et al 2014 and Driscoll et al. 2015) and a von Bertalanffy growth model after Driscoll (2013). (from Richerson et al. 2018)

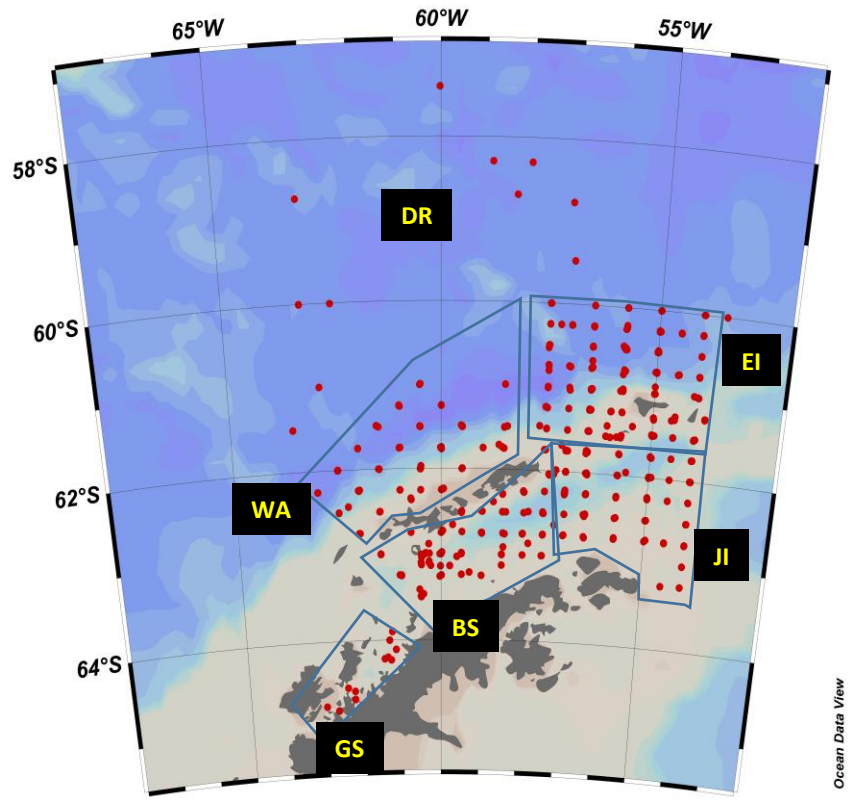


Figure 2.2 US AMLR Winter survey stations and areas. Grey boxes mark the boundaries of each sampling area. Drake Passage (DR), West Area (WR), Elephant Island (EI), Joinville Island (JI), Bransfield Strait (BS), Gerlache Strait (GS). Red dots are stations from 2016, actual station locations sometimes varied by a few kilometers between years due to ice conditions.

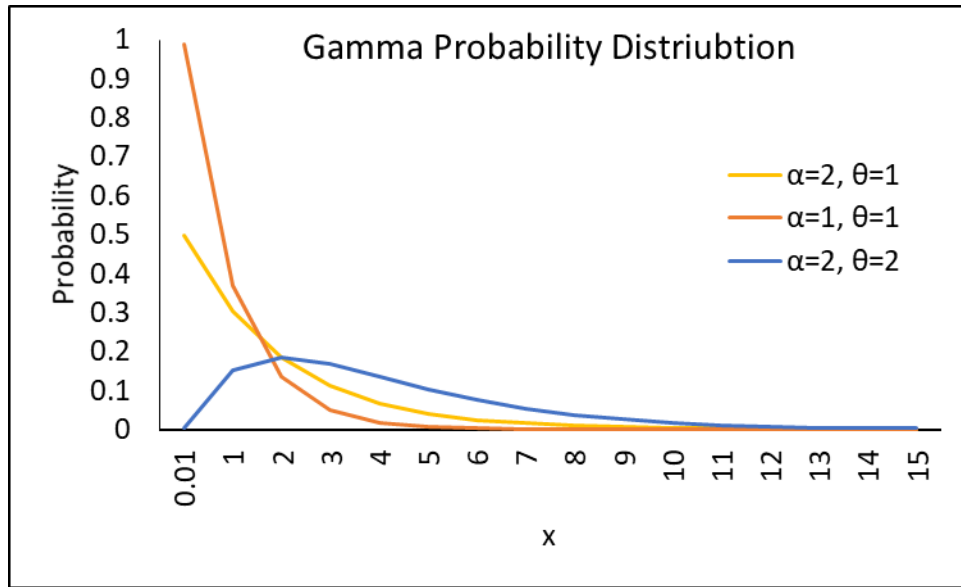


Figure 2.3 Example of the gamma probability distribution for λ (after Mangel 2006).

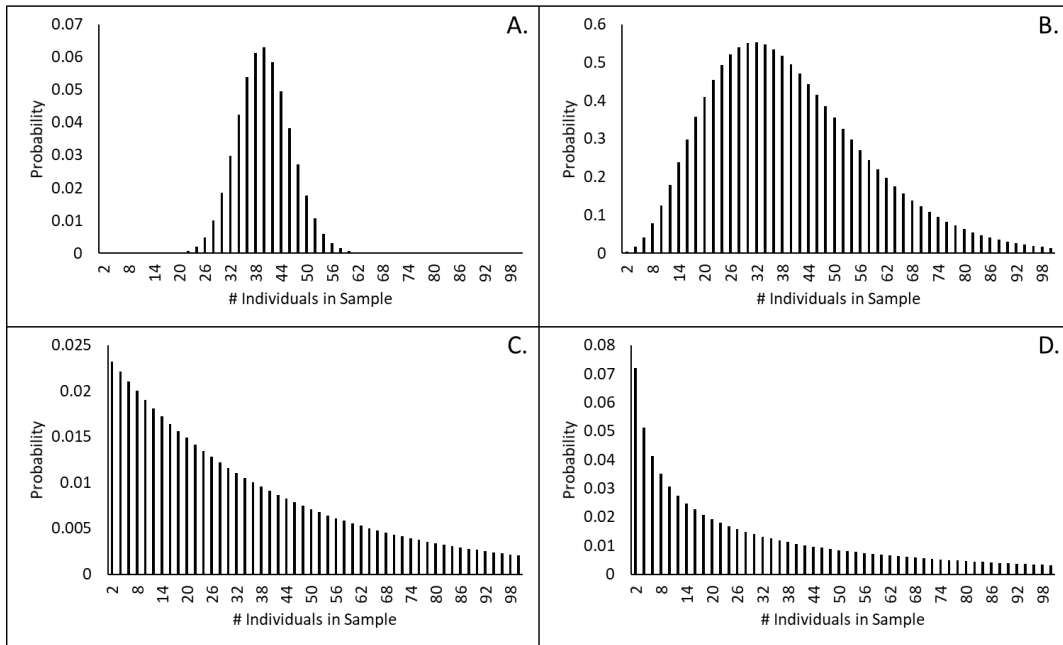


Figure 2.4 Expected distributions of catch size based on Poisson and negative binomial frequency distributions. (A) The Poisson distribution with a mean of 10. (B, C, and D) The negative binomial distribution with means of 10 and a k overdispersion parameter of 0.5, 1, and 5 respectively. Distributions were made in Microsoft Excel using Poisson.dist and Eqn 1.

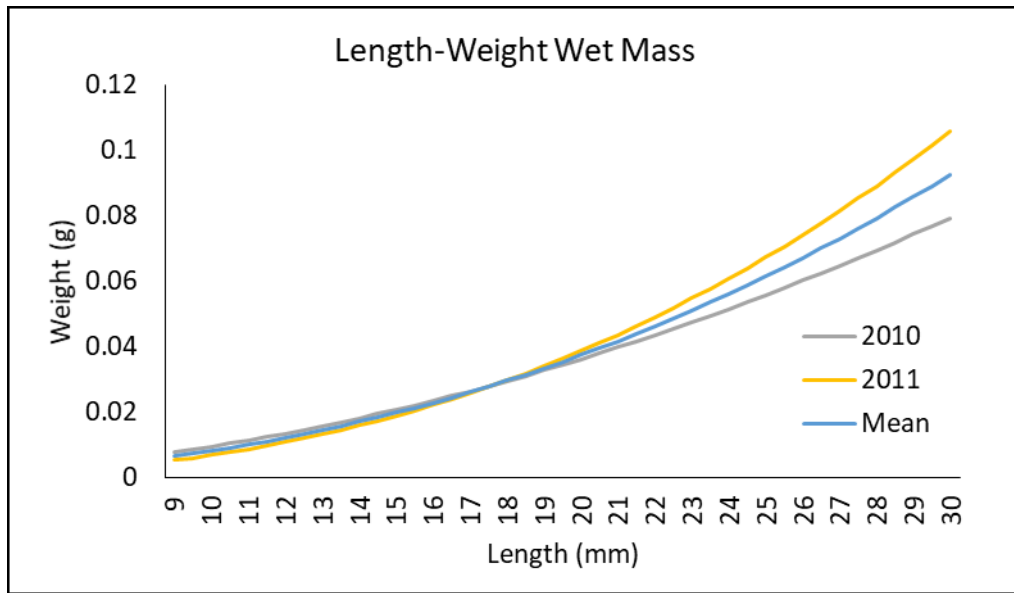


Figure 2.5 Length weight relationship for *T. macrura* for 2010 and 2011 with the mean of the two years in blue based on the power function $W=aL^b$. The relationship was calculated based on the wet mass of individuals or the mean of pooled individuals of the same size.

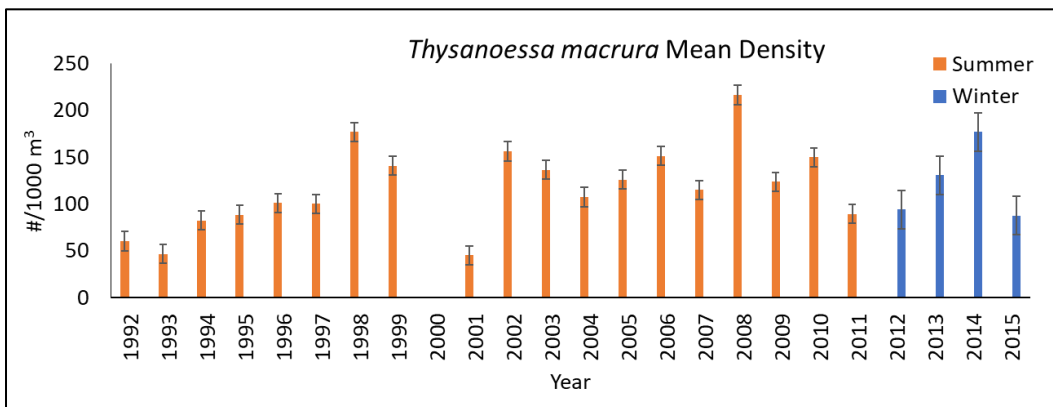


Figure 2.6 *Thysanoessa macrura* mean density for summer (orange) and winter (blue) with standard error.

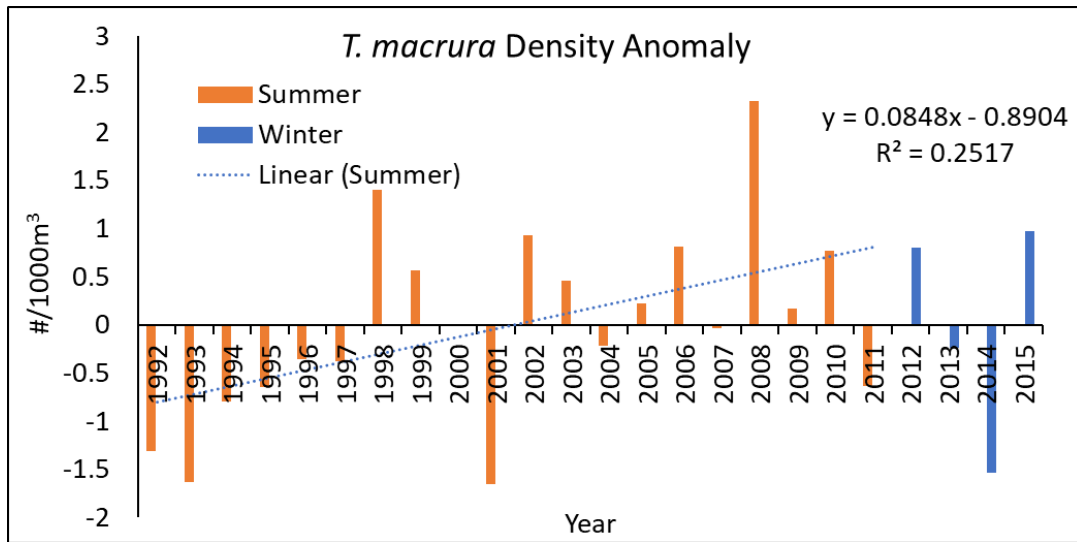


Figure 2.7 Deviations from the mean density for summer (orange) and winter (blue) divided by the standard deviation across years. Dotted line is the regression line for the summer surveys only.

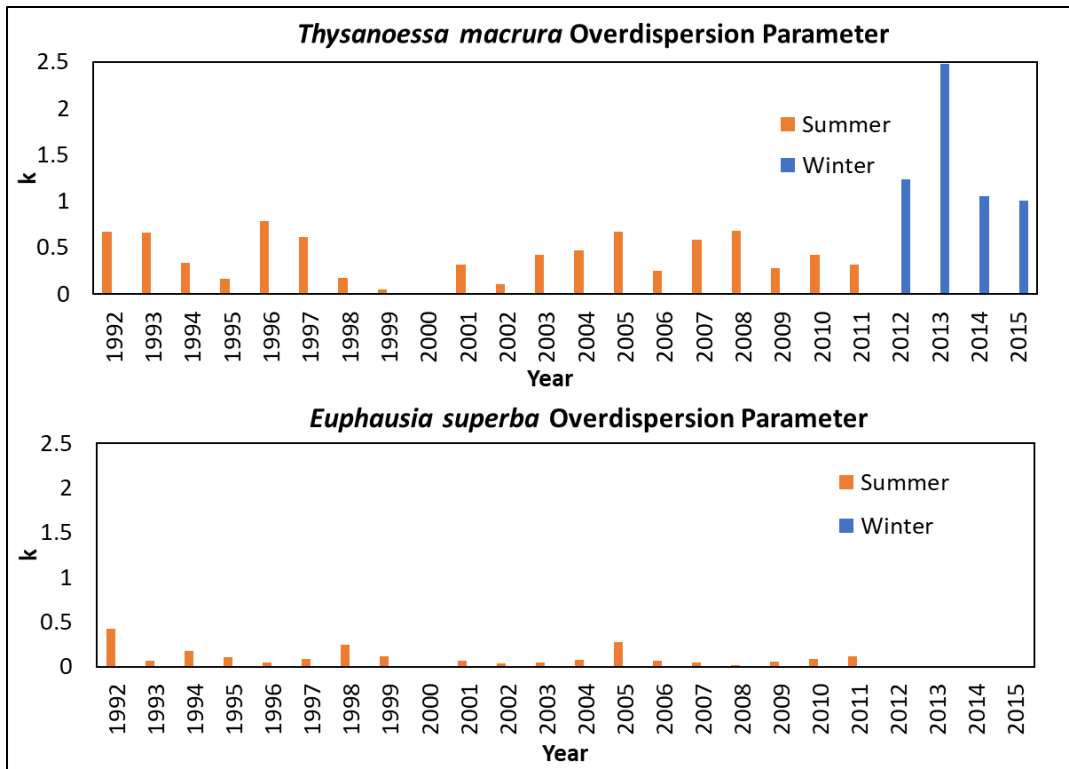


Figure 2.8 Estimates of the Negative Binomial Distribution over dispersion parameter k for *Thysanoessa macrura* with *Euphausia superba* for comparison across all water zones. Small values of k indicate a patchy distribution while those greater than 1 indicate a dispersed distribution

Table 2.1 The total number of stations conducted by the survey for a given year for abundance analysis. The number of stations subsampled for length frequency analysis. The total number of individual *Thysanoessa macrura* measured from the subsamples. The mean abundance for each year over all areas. The mean length over all areas. Summer mean lengths are for all sexes combined. Winter mean lengths are separated into Male/Female/Combined lengths. The mean SST during the survey. Chlorophyll average integrated down to 100m

Year	Total # of Stations	Total Stations Subsampled	Total # measured	Mean Abundance (#/1000m³, sd)	Mean Length (mm)	Mean SST °C	Chl (mg)
1992	63	-	-	60.31±71.54	NA	1.28	33.50
1993	70	-	-	46.60, 52.75	NA	1.65	40.78
1994	63	28	836	82.44, 167.31	16	1.44	31.08
1995	71	23	2550	88.57, 87.75	17.5	1.70	81.69
1996	72	29	3714	101.11, 116.97	16	1.64	52.15
1997	70	0		100.13, 64.13		2.33	53.37
1998	61	38	2894	176.68, 527.90	16.5	1.52	23.36
1999	40	22	1357	140.80, 37.14	18.5	1.40	39.25
2000							
2001	60	26	1646	45.29, 64.23	17.5	1.77	22.94
2002	45	29	1586	156.22, 590.27	17	1.41	43.19
2003	39	34	4384	136.29, 176.94	16	1.65	33.84

2004	46	30	2665	107.27, 178.31	17.5	1.13	41.91
2005	48	28	2836	126.00, 92.36	17.5	1.22	50.29
2006	48	29	3599	151.33, 114.95	18.5	2.56	93.25
2007	49	34	3617	114.75, 147. 17	15.5	1.20	62.60
2008	34	27	4659	216.27, 274.08	15.5	0.85	57.63
2009	47	22	1447	123.55, 49.66	17	1.54	63.00
2010	32	12	932	149.67, 61.32	17.5	1.04	31.51
2011				89.33, 20.81		1.47	39.51
2012				93.90, 28.1		-1.46	6.69
2013	84	42	6090	130.65, 108.35	13.5/15.5/14.5	-1.73	15.07
2014	109	15	2192	176.68, 192.99	12/14/13	-1.68	14.04
2015				87.65, 92.82		-1.59	10.69

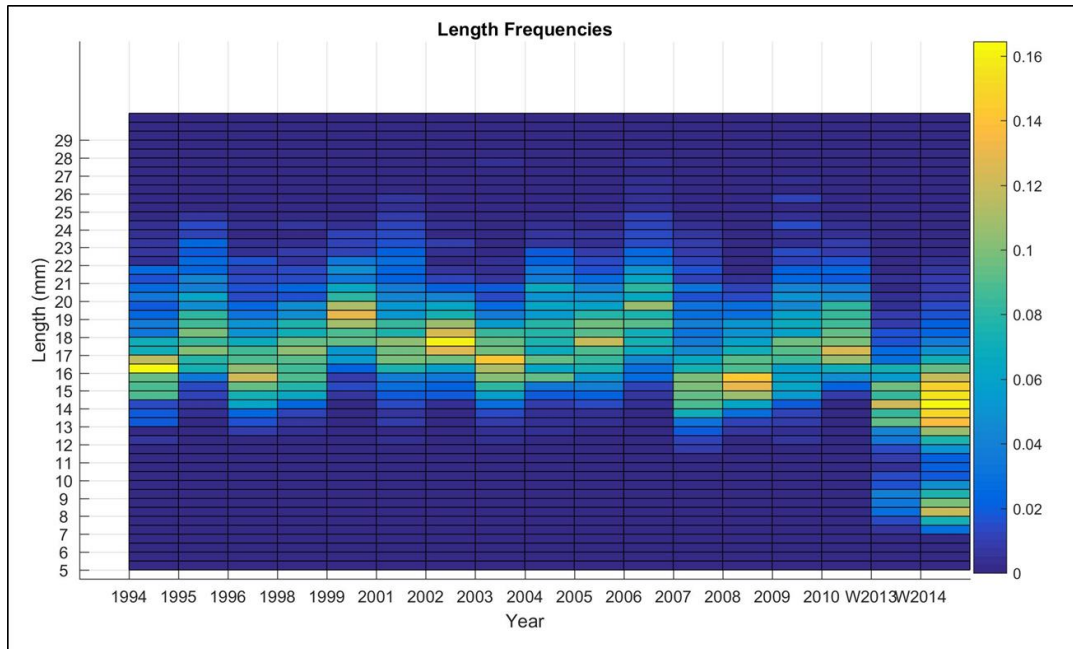


Figure 2.9 Mean length frequencies for the entire survey from summer 1994 to 2010 and winter 2013 and 2014 except for 1997 and 2000, which were not available for analysis. Data are in 1.5 mm bins. Hot color bars correspond to the modes of the distribution. All summer years are dominated by a single mode and in winter 2013 and 2014 there is a second smaller juvenile mode.

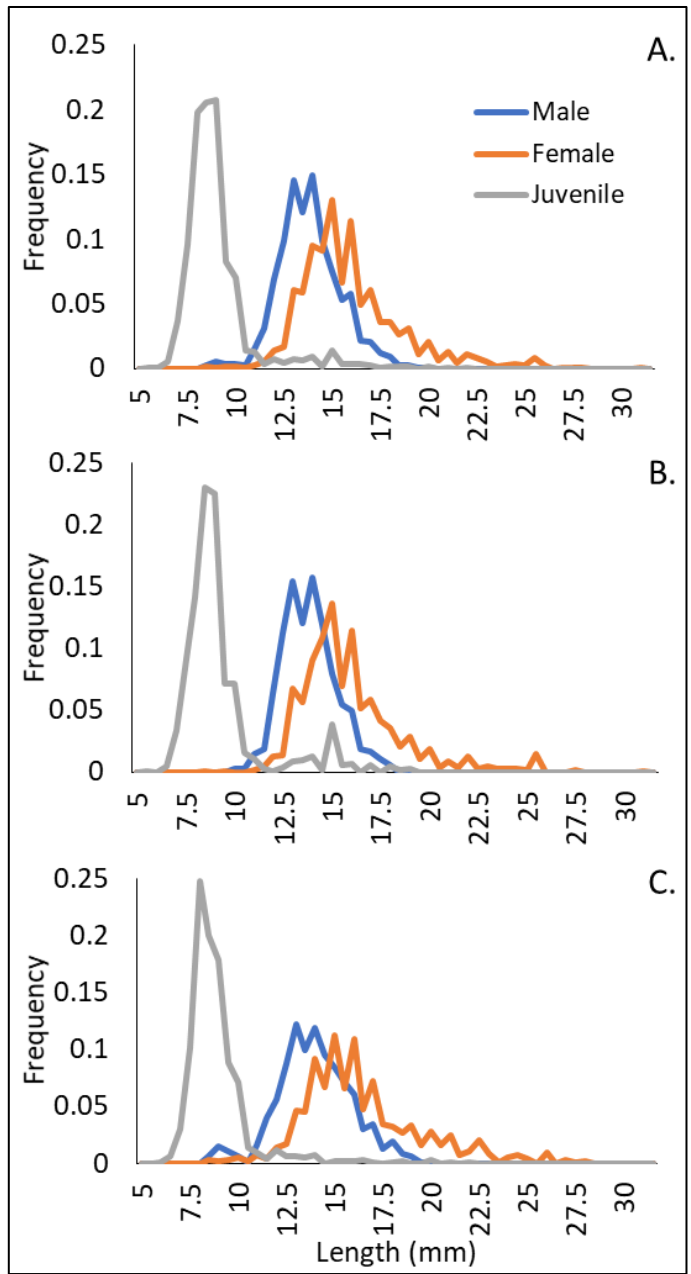


Figure 2.10 Winter mean length frequency by sex (individuals/m³) for 2013 by water zone. Data are in 0.5 mm bins but is presented in line graph format for clarity.

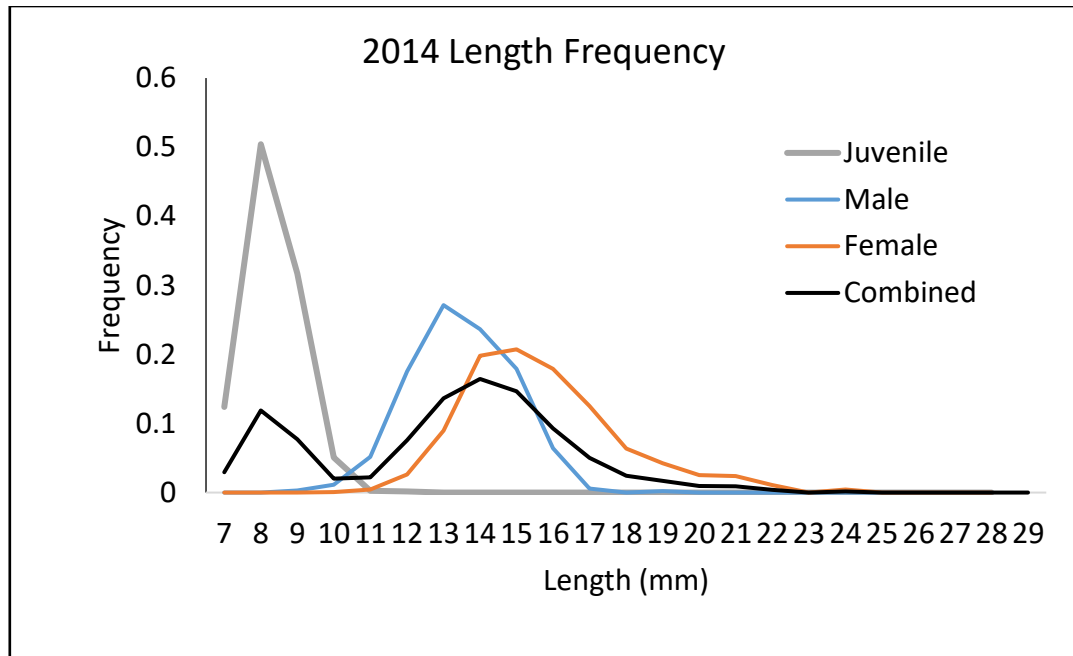


Figure 2.11 Winter mean length frequency by sex (individuals/m³) for 2013. Data is in 1 mm bins but is presented in line graph format for clarity.

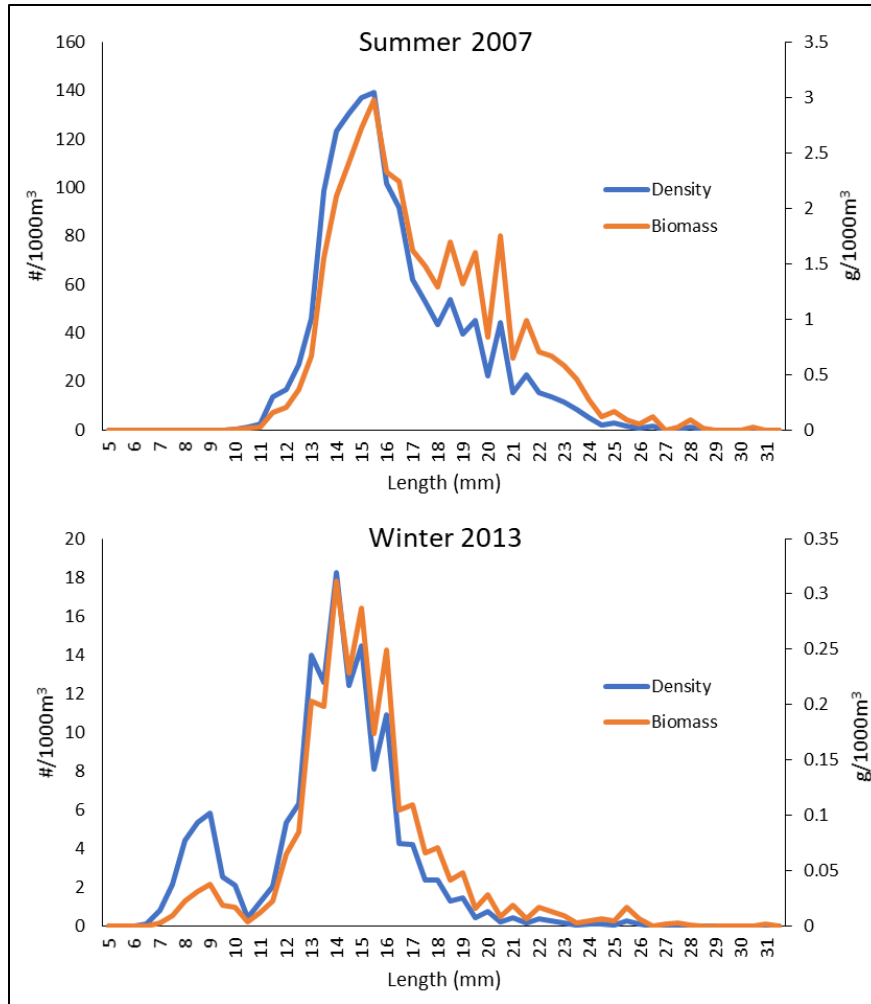


Figure 2.12 Length densities and length weight for summer 2007 and winter 2013.

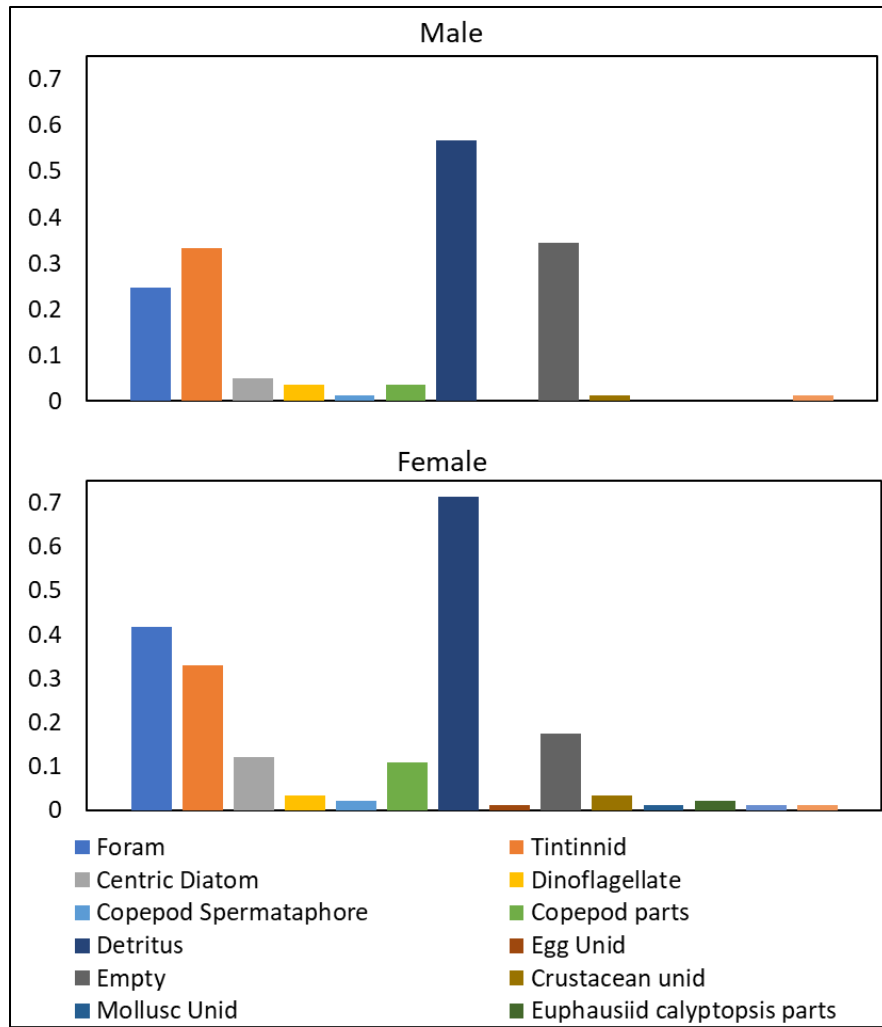


Figure 2.13 *Thysanoessa macrura* stomach content in frequency of occurrence by sex for 2014.

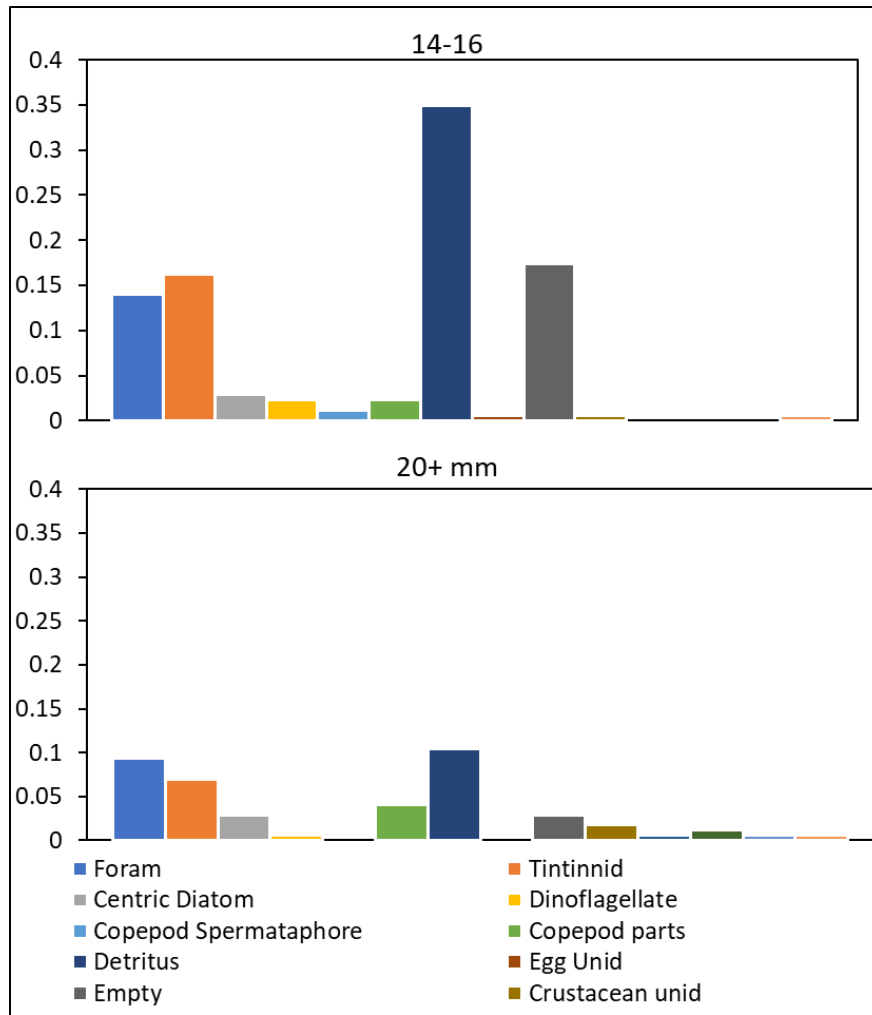


Figure 2.14 *Thysanoessa macrura* stomach content in frequency of occurrence by size for 2014.

3 THE TROPHIC WAVE IN THE DIET OF *EUPHAUSIA SUPERBA* AND ITS IMPLICATIONS FOR SURVIVAL¹

3.1 ABSTRACT

Euphausia superba is a ubiquitous euphausiid subject to extreme changes in its environment between seasons and regions, across the Southern Ocean. A number of adaptations have been suggested for dealing this variability in habitat including; horizontal and vertical migrations, lipid storage, reduced metabolism, and changes in diet. These adaptations can be understood in the context of the seasonal change in the availability of food and the mortality risk of the resulting diet. Here, I assume that *E. superba* follow optimal foraging theory, selecting food that maximizes their rate of energy gain each day, and examine the resulting changes in diet and behavior between seasons and locations. I estimate the risk for each diet based on the time spent foraging and predating given their diet. My major conclusions are i) that depending upon season, *E. superba* are predicted to be either generalist (winter) or specialist (summer) predators; ii) the strength of specialization depends upon location; iii) a specialist diet – which maximizes the daily rate of energy intake – may have lower daily survival than a generalist diet.

¹ This chapter will be submitted, in revised form (with a focus only on energy intake), to *Polar Biology* with the same title and authors Ryan Driscoll and Marc Mangel.

3.2 INTRODUCTION

In general, organisms spend much of their time reproducing, eating, or trying to not be eaten. The latter two can be thought of as simply supporting the first, yet it is in pursuit of these two that an individual will spend most of its life. This triad leads to two fundamental questions: why does an organism eat what it does? and how does an organism avoid being eaten. We ask *why* an organism eat what it does because most animals choose their diet out of many potential food types. One way to address this question is through optimal foraging theory, which proposes that an organism will include only those food types which maximize its rate of energy gain (MacArthur and Pianka 1966, Pyke 1984). We ask *how* an animal avoids being eaten because the question has only one desired outcome, to successfully avoid being eaten. This question is often addressed through behavioral or mechanistic analysis (for example, Diel Vertical Migration (Hays 2003), swarming behavior of krill (Cresswell et al. 2007), or escape response of copepods (Fields and Yen 1997)). Here, I examine why *Euphausia superba* eats what it eats from the perspective of rate maximizing optimal foraging theory (Emlen 1966, Macarthur and Pianka 1966, Schoener 1971, Pyke 1984). After computing the optimal diet for summer and winter across a range of locations, I address the rate of mortality associated with generalist and specialist diets.

High latitude marine environments pose unique challenges to their inhabitants. These ecosystems are strongly seasonal and tend to have simple, relative short food webs with only a few species (*Euphausia superba* in the Antarctic) or groups providing the main energy flow between primary productions and upper trophic

levels (Huntley & Boyd 1984, Helmuth et al. 2005, Flores et al 2012, Murphy et al 2016). The onset of winter brings decreases in primary production, changes in phytoplankton community composition due to decreasing daylight, and the onset of seasonal sea ice which reduces mixing in the upper water column (Montes-Hugo et al. 2009). Pelagic zooplankton have developed a range of adaptations to survive seasonal changes in the environment such as increasing lipid stores (Falk-Peterson et al. 2000), prey switching (Schaafsma et al. 2017), migration (Reiss et al. 2017), reducing metabolism (Meyer 2012), diapause, and facultative changes to behavior (Meyer 2012). A successful winter strategy means maintaining adequate body condition heading into spawning season for adults, and high survival (e.g. higher recruitment) for larvae and juveniles. A successful summer strategy means maximizing growth for adults, juveniles and larvae. Climate change may impact winter strategies in high latitude ecosystems by shifting the timing and magnitude of seasonal production (Parmesan and Yohe 2003, Helmuth et al. 2005). High latitude regions like Antarctic Peninsula in the Southern Ocean have experienced some of the world's most rapid climate change, with increases in air and sea surface temperature (Vaughn 2003, Schmidtko et al. 2014) impacting key species in the food web like euphausiids (Quetin and Ross 2001).

The Southern Ocean ecosystem is dominated by one species, *E. superba*, with *E. crystallarophias* and *Pleuragramma antarctica* (Antarctic silverfish) replacing *E. superba* locally, and *Thysanoessa macrura* and *Themisto gaudichaudii* serving as secondary energy pathways (Murphy et al. 2013, Richerson et al. 2018). *Euphausia*

superba is relatively long lived for a euphausiid (Siegel 1987), omnivorous (Hopkins 1985, Falk-Petersen et al. 2000), stenothermic (Atkinson et al. 2006) and a key prey item for a wide range of predators. At the current time, the general theory for the overwintering strategy of *E. superba* is that it builds lipid stores during summer, begins to slow its metabolism to conserve energy as primary production decreases, and shifts to picoplankton moving into winter (Fiala et al. 1998, Meyer 2012). These physiological changes may be the result of an internal clock mediated by a change in day light length (Meyer 2012). Larval and juvenile individuals cannot store as much lipids or predate as efficiently as adults (Hagen et al. 2001), which obliges small krill to graze on algal picoplankton near the seasonal ice edge, providing refuge from predators in between foraging bouts on free floating and ice entrained algae (Meyer 2017). Adults supplement their lipid supply by grazing on remaining phytoplankton, including ice algae, and may switch to a more predatory diet in winter (Schmidt et al. 2014). At the end of winter lipid stores are depleted, thus making the energy provided by the spring bloom necessary for summer reproduction. After spawning in summer, individuals rebuild lipid stores for the coming winter (Falk-Peterson et al. 2000).

However, there are several inconsistencies between the current overwintering paradigm and field observations. If larvae depend on ice algae for survival, then we predict a successful larval cohort (as juveniles) in the summers after a good ice year. However, larval abundance has a weak correlation to sea ice, and larval cohort abundances in winter are not correlated with their subsequent summer or winter populations (Meyer 2017, Reiss et al. 2017). Recent surveys in the Antarctic

Peninsula region show that adult *E. superba* undertake large migrations inshore in winter, undergo diel migration to twice the depth as in summer (Reiss et al 2017), and have been found in benthic habitats to 2000 m (Clark and Tyler 2008, see Chapter 4). Furthermore, lipid stores, while reduced, are not depleted by winter's end (Schmidt et al. 2014). Energetically costly movement along with the maintenance of lipid stores are not predicted for a species that is conserving its energy reserves for survival. Thus, the existing theories of *E. superba* behavior in winter explain specific responses to local conditions, but do not offer a unifying framework for observations of physiology and behavior across environmental conditions.

One way to view the range of theories on *E. superba*'s regional and seasonal strategies is to place them in the context of maximizing energy gain or reducing the risk of predation. In terms of maximizing energy gain in summer, a period when phytoplankton is highly abundant and blooms are dominated by large diatoms (Fiala et al. 1998), grazing in high productivity waters is an efficient foraging mode for *E. superba*. This strategy may reduce predation pressure by *E. superba* on other mesozooplankton and macrozooplankton. The decreasing density and cell size of the phytoplankton community in winter makes grazing less profitable, so *E. superba* may increase the time it spends preying on other zooplankton.

I hypothesize that *E. superba* is likely to consume large copepods if they can be found. However, more abundant, easier to capture, smaller zooplankton might dominate the diet, followed by less abundant, more mobile, and difficult to capture mesozooplankton. This would result in a Trophic Wave (a shift in relative diet

composition from phytoplankton to small then large mesozooplankton) in the preyscape (Figure 3.1).

An individual's foraging strategy will have a specific mortality risk associated with it through both the risk of starvation, if not enough food is found, and the risk of being consumed by a predator (Leising et al. 2005). Grazing on phytoplankton requires krill to be near the surface, which increases mortality risk by exposing krill to air breathing predators (Schmidt et al. 2011). Predating on copepods may mean krill spend more time in deeper water, thereby reducing predation risk (Leising et al. 2005). Given the high energy value of copepods and the lower risk of being eaten while feeding on them, it seems that copepods would be the preferred food choice. Indeed, krill have been found to select copepods in laboratory feeding experiments (Hamner 1988, Price et al. 1988). The period of high productivity at high latitudes is short, so krill may choose to increase their mortality risk by grazing in summer if it maximizes their energy gain. In winter, low productivity means that that grazing may be both more inefficient, and riskier, than predating. I predict that in each region, the stronger a seasonal pattern is, the riskier the diet will be in summer and the safer it will be in winter. In this chapter, I approach these questions by separately computing the optimal (rate-maximizing) diet and the survival probability associated with a diet. In the next chapter, I provide a unified treatment of a similar topic using stochastic dynamic programming.

The Trophic Wave framework provides a unifying context for several observations of *E. superba*. First, based on the Trophic Wave framework, I predict

changes in body composition, specifically that lipid stores will not be depleted by the end of winter, and that nitrogen isotope values shift to a higher trophic level in winter. Second, I predict that *E. superba* will migrate more both vertically and inshore in winter to search for prey (see Chapter 4). For example, west and north of the South Shetlands, the Antarctic Circumpolar Current threatens to advect species away from near shore retention zones. *Euphausia superba*'s inshore migration in winter would allow them to both avoid advection, and also predate on other zooplankton and larvae retained near shore. Larger vertical migrations in winter might mean that krill are not only avoiding predation, as in summer, but following potential prey items, while deep benthic migrations provide alternative grazing and predation opportunities relative to surface water.

The Trophic Wave hypothesis is predicated on a shift in the foraging behavior of *E. superba* from summer through winter. Specifically, I argue that *E. superba* are not passive omnivores, consuming whatever food items they come across, but rather that they actively choose prey to maximize their rate of energy gain. In nature, krill are true omnivores and their diet shifts regionally and seasonally. However, the consequences of their seasonal diet choices on lifetime mortality are unknown.

I use a series of models to progressively explore seasonal shifts in diet, and associated survival probability, predicted by the Trophic Wave framework from first principles of behavioral ecology.

First, I treat *E. superba* as generalists where diet is be proportional to the ambient prey abundance.

Second, I treat *E. superba* as optimal foragers, choosing prey that maximize their rate of energy gain regardless of other factors. Whether krill specialize on a few prey types or generalize on all prey is dependent on whether some or all prey maximize its energy return. I then compare Optimal foraging krill to generalist krill.

Third, I examine how optimally foraging *E. superba*'s prey choice across its latitudinal range and between seasons, to explore how individuals alter their diet according to local seasonal prey availability.

Fourth, I examine the mortality risk associated with each diet. Predating and grazing have different mortality risks, and the time spent in each foraging mode is proportional to the abundances of prey types in each diet. Thus, each diet will lead to a specific mortality risk and daily survival.

To explore the consequences of krill as generalist omnivores or choosing prey to maximize their rate of energy return, I use a classic rate maximizing model and compute the expected diet composition using summer and winter data on prey abundance. I then compare my results with empirical studies that show that the diet of *E. superba* changes between seasons. If *E. superba* simply consume prey haphazardly, then its diet will be proportional to the ambient prey abundance. If, however, *E. superba* choose prey based on energy gain, then its diet should reflect the combination of prey items that maximizes its energy gain.

In classical optimal foraging theory, one assumes that an individual chooses its diet to maximize the rate of energy gain ((Emlen 1966, Macarthur and Pianka 1966, Schoener 1971). I characterize prey by energy content (e_i) and handling time (h_i) of prey item type i (which is encountered at rate abundance (λ_i)). Handling time is the amount of time it takes to pursue, capture and consume a prey item. It is an opportunity cost in that it reduces the amount of time available to search for prey.

I first rank prey by individual profitability, so that prey items are ordered according to

$$\frac{e_1}{h_1} > \frac{e_2}{h_2} > \frac{e_i}{h_i} \quad (1)$$

If prey type 1 is abundant, I predict krill to specialize on that prey type. However, if prey type 1 is not abundant, then specializing on it may not meet energy requirements. An individual will subsequently add lower profit prey types to its diet until reaching a prey type that leads to a decrease in the rate of energy gain (Figure 3.2). I show how to determine the diet below (equations 6ff).

I let f_i denote the fraction of prey type i in the gut. For generalist krill this fraction is,

$$H_1: (f_1, f_2 \dots f_n) \propto \left(\frac{\lambda_1}{\sum \lambda_i}, \frac{\lambda_2}{\sum \lambda_i}, \dots, \frac{\lambda_n}{\sum \lambda_i} \right) \quad (2)$$

However, if krill choose prey according to rate maximizing consumption (Optimal Foraging Theory), I let f_{max} denote the fraction in the gut of the last prey type added, after which all further prey are rejected. I then predict that:

$$H_2: (f_1, f_2, \dots, f_{max}, 0, 0, \dots) \propto (\lambda_1, \lambda_2, \dots, \lambda_{max}, 0, 0, \dots) \quad (3)$$

I explore the consequences of krill modifying their diet based on season and region by using values for encounter rates (λ_i) specific to a broad latitudinal range of regions and seasons.

To assess the rate of mortality associated with diet, I begin with lifetime survival. Letting M_y denote the yearly mortality rate and A_{max} the maximum age of a krill, I define S_{max} as the survival to maximum age given by

$$S_{max} = e^{-M_y A_{max}} \quad (4)$$

I then determine the rate of mortality by solving equation 4 for M_y . The rate of mortality on smaller time scales is determined in a similar fashion. For example, if N_{days} is the number of days in the average lifetime then the mortality rate for one day, M_{day} , is given by:

$$M_{day} = \frac{-\log(S_{max})}{N_{days}} \quad (5)$$

As described above, I treat grazing and predation explicitly by assuming that grazing on phytoplankton and associated microzooplankton increases M_{day} , while predating on mesozooplankton decreases M_{day} .

3.3 METHODS

3.3.1 Parameters

I separated krill prey into 5 categories: diatoms, small phytoplankton, microzooplankton (ciliates and flagellates), small copepods (e.g. *Oithona*), and large copepods (e.g. *Calanus*, *Rhincalanus*). These categories cover the range of energetic values and functional groups (primary producers, primary and secondary consumers) krill encounter in their diet, and the range of foraging behaviors (grazing and active predation) required to obtain them; see chapter 2 for an example involving *T. macrura*. I used the same parameters for each prey item: energy content (e_i), handling time (h_i) and abundance (λ_i). I used carbon as the model currency since it can be converted easily from the various units of abundance reported the literature (e.g. chl mg/volume, cells/volume, or # individuals/volume).

Thus, energy content in the model is the amount of carbon that will be acquired if krill consume a given category of prey during a discrete period of time. When actively predating, krill capture and consume an individual; therefore the energy content for small and large copepods is the carbon content for individual prey items (Price et al. 1988). When grazing, krill continually consume cells for several minutes and then rest; thus the energy content of grazed items (diatoms, small phytoplankton and microzooplankton) is the total carbon accumulated over several minutes (Hamner 1988). This also sets the minimum time step in which krill choose prey items. I obtained handling times for each prey item either from direct observations (Hamner 1988), or extrapolated from clearance rate experiments on krill (Price et al. 1988).

I obtained prey abundances from literature for summer and winter in three regions that cover the geographic range of krill: the Weddell Sea/Lazarev Sea, the South Shetlands and South Georgia. Ideally, prey abundance obtained for summer and winter in each area would be from the same consecutive years to accurately characterize shifts in the prey field. However, given the logistical constraints of sampling zooplankton in Antarctica, there are few data sets for zooplankton in consecutive seasons. I converted abundances and density values to micrograms carbon per liter.

3.3.2 The Optimal Rate-Maximizing Diet

I use a rate-maximizing model (Mangel 2006) to predict which prey would be included in a diet that maximizes the rate of energy gain given the energy content, handling time, and encounter rate of prey in each season and location. I assume that handling time and energy content do not change across seasons, but that encounter rate does.

I assume that krill feed so that in a single diel foraging period of length T , an individual either searches for (S) or handles (H) food so that

$$T = S + H \quad (6)$$

The total number of prey type i encountered during the foraging period is $\lambda_i S$, where λ_i is the encounter rate for that prey type. The time spent handling prey type i is $h_i \lambda_i S$ where h_i is the handling time for prey type i . The total handling time is the sum of the handling time of all prey included in the diet:

$$H = h_1\lambda_1S + h_2\lambda_2S + \dots h_5\lambda_5S \quad (7)$$

Factoring the S on the right-hand side, the total handling time is:

$$H = S \sum_{i=1}^5 h_i\lambda_i \quad (8)$$

Substituting for H in equation 6 gives:

$$T = S + S \sum_{i=1}^5 h_i\lambda_i \quad (9)$$

so that

$$T = S \left(1 + \sum_{i=1}^5 h_i\lambda_i \right) \quad (10)$$

The amount of energy gained during T from prey type i is by $e_i\lambda_iS$. Thus, the total energy gained during time T is given by:

$$E = S \sum_{i=1}^N e_i\lambda_i \quad (11)$$

Consequently, the rate of energy gain when krill generalizes and includes all 5 prey in their diet (R_5) is:

$$R_5 = \frac{S \sum_{i=1}^5 e_i\lambda_i}{T} \quad (12)$$

I solve equation 9 for S to obtain:

$$S = \frac{T}{(1 + \sum_{i=1}^5 h_i \lambda_i)} \quad (13)$$

so that the rate of energy gain for a generalist diet is:

$$R_5 = \frac{\sum_{i=1}^5 e_i \lambda_i}{1 + \sum_{i=1}^5 h_i \lambda_i} \quad (14)$$

If only the first n prey types (ranked by profitability) are included in the diet, then the specialist analog of equation 14 is

$$R_n = \frac{\sum_{i=1}^n e_i \lambda_i}{1 + \sum_{i=1}^n h_i \lambda_i} \quad (15)$$

The optimal diet consists of choosing the value of n that maximizes the rate of energy gain among the set $\{R_1, R_2, R_3, R_4, R_5\}$.

3.3.3 Estimating Mortality Associated with Prey Choice

The maximum age of *E. superba* in nature is 7 years, and estimated survival is 0.002 (Siegel 1987, 1992). Using an hourly time step and letting M_h denote the hourly rate of mortality gives:

$$e^{-M_h 7 \cdot 265 \cdot 24} = S_{max} \quad (16)$$

and solving for M_h yields:

$$M_h = \frac{-\log(S_{max})}{7 \cdot 365 \cdot 24} \quad (17)$$

The hourly rate of mortality in equation 17 amortizes the different kinds of natural mortality across the lifetime of a krill. Here, I assume that krill are feeding in the upper water column by either grazing or raptorial capture (predating). Krill may also migrate to the sea floor to scavenge on benthos and this behavior requires a different model (see chapter 4).

When grazing, krill are exposed to higher mortality due to proximity to the surface. When predating, krill reduce their mortality by searching lower in the water column or sinking out of surface water while digesting, a practice termed “parachute behaviour” (Hamner 1984, Tarling and Johnson 2006, Figure 3.3). Mortality rates associated with predation versus grazing are unknown for *E. superba*. However, studies on copepod mortality associated with so called “parachute” or foray-foraging behavior show a reduction in mortality of up to 50% (Leising et al 2005). I account for the change in base mortality (M_h) when krill predate by reducing M_h , and increase the baseline rate of mortality when krill are grazing. For simplicity, I assume that when predating on a prey type the rate of mortality is

$$M_i = \frac{M_h}{1 + \alpha} \quad (18)$$

and when grazing on a prey type the rate of mortality is

$$M_i = M_h(1 + \alpha) \quad (19)$$

where, for simplicity, I use a single parameter α to modify the baseline rate of natural mortality.

To estimate how diet effects survival using the risk of mortality associated with different foraging modes and the time spent handling prey, I first obtain the amount of time spent in each foraging mode. Because the time spent searching is:

$$\lambda_i S h_i \quad (20)$$

the total risk of mortality while foraging for prey i when search time is S is:

$$\lambda_i S h_i M_i \quad (21)$$

Since the accumulated mortality from searching is $M_h S$, the daily survival probabilities when krill generalize or follow the rate maximizing diet are, respectively,

$$Pr[\textit{surviving the day}|\textit{generalist}] = e^{-M_h S} \prod_{i=1}^5 e^{-M_i \lambda_i h_i S} \quad (22)$$

and

$$Pr[\textit{surviving the day}|\textit{rate - maximizing}] = e^{-M_h S} \prod_{i=1}^n e^{-M_i \lambda_i h_i S} \quad (23)$$

where n is the least profitable prey included in the diet.

The relative survival of an individual following the rate-maximizing diet is then the ratio of equations 23 and 22; values greater than one indicate that a diet based on optimal foraging theory has a higher survival rate, and values less than one mean that generalizing has a higher survival rate.

3.4 RESULTS

3.4.1 Prey Parameters

I used micrograms carbon per individual obtained from Atkinson et al. (1997) for the energy content of small (<750 μm) and large copepods (>750 μm). I obtained the carbon content per cell for microzooplankton from Atkinson et al. (1997). I used the chlorophyll to carbon ratio reported in Boyd et al. (1984) and Atkinson et al. (1997) for the carbon content of small and large phytoplankton. I computed the total energy as micrograms carbon obtained from grazing on either large or small phytoplankton or microzooplankton from cell ingestion rates (Price et al 1988), or clearance rates (Price et al. 1988, Atkinson et al. 1997) of chlorophyll, in minutes combined with the number of minutes krill graze before stopping to ingest their food (Hamner 1998).

I used clearance and ingestion rates (Boyd et al. 1984, Price et al. 1988 and Atkinsons et al. 1997) to calculate the handling time of prey items. I obtained abundances for phytoplankton by taking chlorophyll in $\mu\text{g}/\text{m}^3$ for each season and location and the proportion of large and small phytoplankton in a season (Atkinson et al. 1997 and Fiala et al. 1998) (see Table 2, Figure 3.4). I then converted chlorophyll from $\mu\text{g}/\text{m}^3$ chlorophyll-a to $\mu\text{g}/\text{m}^3$ Carbon based on Atkinson et al. (1997).

Summer abundances are dominated by diatoms, while winter abundances are dominated by small phytoplankton. Copepods have a relatively low abundance across

seasons and areas compared to phytoplankton and microzooplankton, but they constitute a large proportion of the total biomass in winter.

The maximum age of *E. superba* in nature has been determined by following cohorts over time using mixture distributions at 7-9 years (Siegel 1987) and S_{max} estimated at 0.002 (Siegel 87, 92, Basson 94).

I parameterized the model with α ranging from 0 (no change in mortality with foraging mode) to 9 (so that grazing is very risky and predating and basket-feeding is relatively safe). These values of α correspond to hourly mortalities of $1.0E-4$ to $1.0E-5$ when predating (large and small copepods) and $1.0E-4$ to $9.9E-4$ when grazing (diatoms, microzooplankton and phytoplankton) (see Figure 3.5). The upper bound ($\alpha=9$) exceeds the maximum value found by Kiorboe and Jiang (2012), however, it is useful to see the corresponding total mortality risk of a diet when the mortality risks of grazing and predating are an order of magnitude higher than average.

3.4.2 The Rate Maximizing Diet

Large copepods were the most profitable prey followed by diatoms, small phytoplankton, microzooplankton then small copepods (Table 3.1, Figure 3.6). The large difference in profitability between large and small copepods is explained by feeding experiments that suggest that both small and large copepods have relatively long handling times compared to phytoplankton, but large copepods have 1-2 orders of magnitude more energy. As a result, the model predicts that *E. superba* will

include at least the first 3 prey items in their diet and reject small copepods (Figure 3.6). There were only small differences in the rate of energy gain when microzooplankton, and small phytoplankton were included or rejected in the diet over all areas and seasons. In sub-Antarctic waters I predict that krill have a more specialized diet due to the abundance of large copepods and diatoms that dominate for portions of the summer. In winter, across areas, krill become generalists due to the low abundance of all prey types. Small copepods slightly increase the rate of energy gain in the high Antarctic and have no effect, or a slight decrease, in the Antarctic Peninsula and sub-Antarctic, respectively.

3.4.3 Survival Associated with Generalist and Optimal Diets

In general, the total mortality risk from an optimal diet is higher than that from generalizing across areas and seasons (Figure 3.7). The lower mortality from a generalist diet is due to the inclusion of the least profitable prey item, small copepods, in the diet. Predating on copepods is less risky than grazing, thus including small copepods in the diet means less time grazing and therefore lower mortality risk. In summer the risk of mortality is higher than in winter and similar across areas. This is true whether on a generalist diet or an optimal diet due to more time spent engaging in high risk grazing behavior because of the abundance of diatoms, and their primacy as a share of energy in either diet in all areas. The total mortality risk was lower in all areas in winter due to both an overall lower abundance of food, and the proportionally higher abundance of low risk copepods. The sub-Antarctic is relatively mild compared to the other two coastal Antarctic regions, allowing *E. superba* to graze

effectively in winter leading to higher mortality in winter than the South Shetlands or Sub-Antarctic.

I further explored the consequences of mortality associated with foraging modes by running the model with a range of potential risks for grazing and predating. In the summer and year-round productive waters, as the risk of grazing increases, the total mortality risk from an optimal diet increases and the survival advantage of an optimal diet decreases. In winter in the South Shetlands and High Antarctic water, the survival advantage is still low for optimal diets but increases with increasing α . However, because abundances of grazed prey are low, the change in total mortality between a high and low α is less than that in summer (Figure 3.8)

3.5 DISCUSSION

I have shown that *E. superba* maximizes its daily rate of energy gain if it specializes when productivity is high (summer and sub-Antarctic). When productivity is low (higher latitudes in winter), I predict that *E. superba* will switch to a generalist diet (Figure 3.6). I also found that the diets predicted by optimal foraging theory carry a higher risk of predation than a generalist diet, with a greater difference in summer and in sub-Antarctic regions than in winter. This conclusion calls for integrating energy intake and mortality risk into a common framework of daily survival, which can be done using Stochastic Dynamic Programming. I give an example of such an approach in the next chapter.

Euphausia superba are faced with an interesting diet choice. Their most profitable food type (mesozooplankton) is also the safest, but too low in abundance to meet their energy demands, while low profit food types (phytoplankton) have a relatively high risk, yet are often high enough in abundance to meet their energy requirements. I predict that the default diet includes copepods if they are either high in abundance or phytoplankton is low in abundance. This condition may be true regardless of season. Krill may choose this riskier diet when a region has a short season of high productivity and therefore a short period in which krill can obtain sufficient energy to reproduce and grow. In the model, I assume a homogenous day both spatially and temporally for simplicity. However, both zooplankton and phytoplankton are patchy in time and space within a season. Large krill swarms can locally deplete food which may require krill to change its foraging strategy. This might lead to winter like behavior in seasons other than winter, where individuals choose to predate on copepods and avoid grazing in temporally high risk, low return surface water.

I predict that in productive sub-Antarctic habitats, such as South Georgia, *E. superba*'s optimal diet is more specialized than in higher latitude habitats. In these regions, krill can afford to be choosy. The rate maximizing curves in Figure 3.6 are flattened for the Antarctic Peninsula and the High Antarctic suggesting that krill have a flexible diet when grazing in moderate abundance habitat. The rate maximizing curves in winter suggest that when food is low, higher trophic levels, such as heterotrophs, mixotrophs and small copepods are important components of the diet.

This holds true in the few diet studies that have been conducted on winter krill, where isotopes and lipid profiles suggest a more predatory diet in winter (Meyer 2012). Schmidt et al. (2014) found that copepods are found in the diet of *E. superba* year-round and concluded that copepods are not a “switch” food. However, the inclusion of copepods in winter likely reflects a shift in foraging effort as *E. superba* must devote more time to capturing and consuming fast-moving prey when they are in low abundance.

The diet predicted by optimal foraging theory included large copepods, diatoms and microzooplankton, excluded small copepods, with little to no effect of including small phytoplankton. Small copepods are encountered more often than large copepods and have relatively high energy content compared to phytoplankton and microzooplankton, yet were not included in summer diets in all areas. One reason for this is that clearance rates experiments on copepods suggest that time spent actively chasing and capturing a copepod is similar for large and small species, while the difference in energy content of species can be 2 orders of magnitude (Atkinson et al. 1997). Copepods are a diverse group in terms of size, habitat selection and behavior. For example, some small copepods hang motionless to avoid detection and so are consumed incidentally during grazing, while others vary in the magnitude of the vertical migration, which affects their availability to krill (Atkinson et al. 1997, Marrari et al. 2011). As a starting point for the model, I chose copepod sizes that reflect common prey krill encounter. Including more categories of copepods in future models may provide better resolution on the range of profitability of potential prey.

Here, I assumed that the clearance/ingestion rates are constant for each prey type regardless of their densities. Clearance rates generally increase with increasing prey density up to a saturation point (Price et al. 1988). However, clearance rate curves for mixed assemblages of prey items are not well understood (Price et al. 1988), therefore average clearance rate values for each prey were chosen when calculating handling times. Similarly, krill may have an easier time locating copepods when phytoplankton densities are high due to the increased grazing behavior, but the relationship is poorly understood (Atkinson et al. 1997) that I did not include it.

The models focus on foraging choices in the upper water column between grazing on phytoplankton and predating on primary and secondary consumers. Recent studies have shown that *E. superba* migrate to benthic habitats throughout the year where they have been observed grazing on benthic detritus (Clark and Tyler 2008, Schmidt et al. 2011). The time and energy required to move between the seabed and the surface imply that krill forage at either the surface, or the bottom during a foraging period. Therefore, including benthic habitat requires a different model to examine the values of different habitats in the water column.

3.5.1.1 Conclusion

Here I show that *E. superba* can maximize their energy gain when foraging, either by generalizing or by specializing, according to location and season. And optimal foraging theory applied continuously through time at a single location leads to a trophic wave. Though the models are simple, they suggest complex behavior with consequences to the species' horizontal and vertical seasonal distribution, diel

migration, availability to predators, and impact on the food web. For example, during summer, *E. superba* maximize their diet through grazing, requiring them to be near the surface, where large swarms can depopulate phytoplankton and, subsequently, increase nutrients. During winter or periods of low phytoplankton abundance, krill include more micro- and mesozooplankton in their diet, which serves to both increase their energy gain and decrease the risk of predation. This may lead to increased diel vertical migration for both *E. superba* and their potential prey.

Climate change is expected force structural changes on the plankton community, and this may lead to changes in krill behavior. For example, climate change may shift phytoplankton communities toward smaller species (Montes-Hugo et al. 2009). Based on my work, I suggest that krill will then spend more time predating and less time grazing near the surface. Changes to the vertical distributions of krill as a consequence of their diet choice may increase the length of foraging trips for krill predators and shift the effort of krill fisheries. Future work would benefit from examining diet choice, predation risk and reproduction in the context of the vertical habitat selection for *E. superba*; a start in that direction is found in the next chapter.

3.6 TABLES AND FIGURES

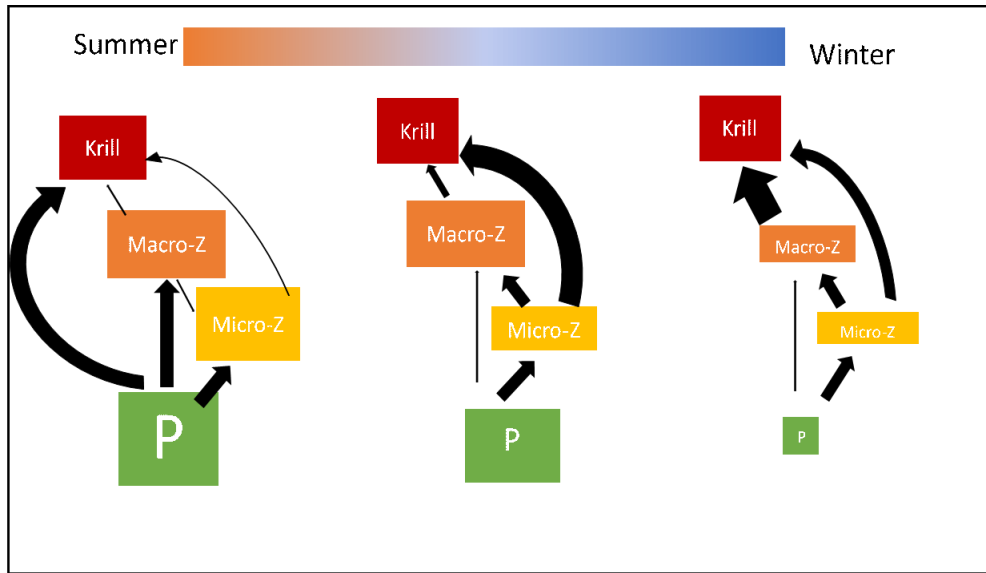


Figure 3.1. The Trophic Wave Hypothesis. Black lines represent the intensity of predation and grazing. The size of the boxes represent a groups population size relative to other seasons.

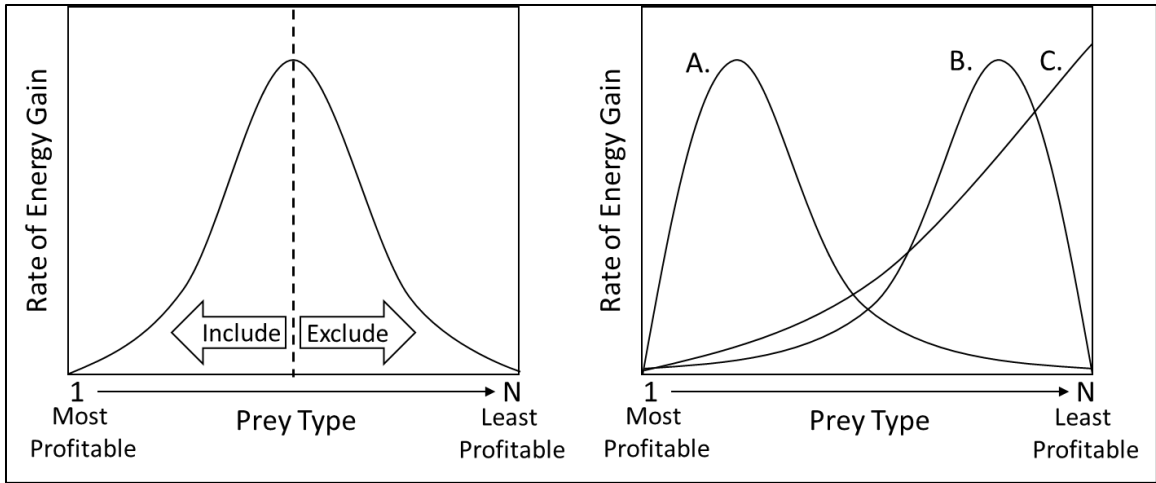
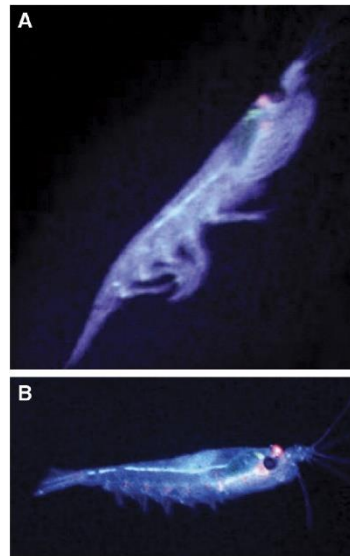


Figure 3.2. Illustration of the rate maximizing theory of diet selection. In the left-hand panel, I show the predicted rate of energy gain as a function of diet composition. The dashed line represents the point at which including any more prey items decrease the rate of energy return. Items to the left of the dashed line are included in the diet and those to the right are rejected. In the right-hand panel, curve A depicts the diet of a specialist, while curve B depicts a more generalist diet, and in curve C, all potential prey are included in the diet.



Current Biology

Figure 3.3. An example of parachute behavior. In panel A, an individual krill is oriented up is actively feeding. In panel B, an individual is sinking while oriented horizontal, with its feeding basket expanded in parachute behavior. (Tarling and Johnson 2006).

Table 3.1 Model Parameters. Prey are listed in order of their profitability (e_i/h_i). Energy content (e) is for individual zooplankton and for the average number of cells in a 4-minute grazing period for phytoplankton. Handling time (h) is in minutes. Summer and winter abundances (λ) are standardized to $\mu\text{g Carbon/liter}$. (Atkinson and Ward 1988, Hamner 1988, Price et al. 1988, Froneman et al. 1996 Atkinson et al. 1997, Froneman et al. 1997, Hunt et al. 2011, Borriane and Schlitzer 2013, Garcia et al. 2016).

Profit	Prey Type	e (μg)	h (min)	Summer λ ($\mu\text{g C/L}$)			Winter λ ($\mu\text{g C/L}$)		
				High Ant.	S. Shetlands	Sub-Ant.	High Ant.	S. Shetlands	Sub-Ant.
194.5	Large Copepods	194.5	1	0.1	0.187	0.2	0.03	0.097	0.033
75	Diatoms	1.25	0.017	35.7	42	40	0.042	0.1	2.5
60	Small Phytoplankton	1	0.017	23.8	28	19	1.68	0.4	10
40	Microzooplankton	1	0.025	11.594	10	10	1	0.2	12
9.72	Small Copepods	3.24	0.333	1.75	2	2.8	0.02	0.024	0.64

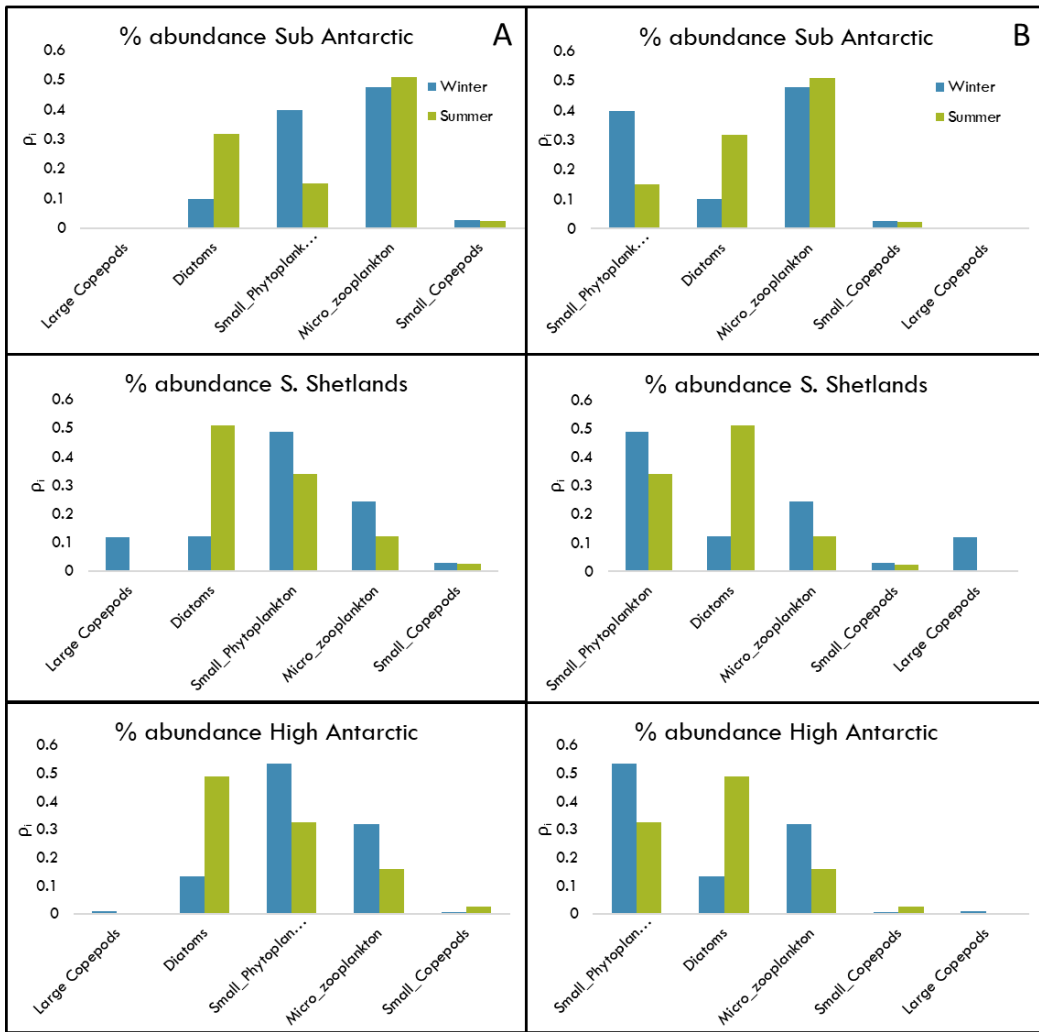


Figure 3.4 Two perspectives of the ecosystem in terms of proportional abundances by area and season. In column A, prey are arranged by their trophic position reflecting a bottom- up perspective of the ecosystem. In column B prey, are arranged by their energetic profitability to *E. superba* Although the data are the same, each suggests different strategies for *E. superba*.

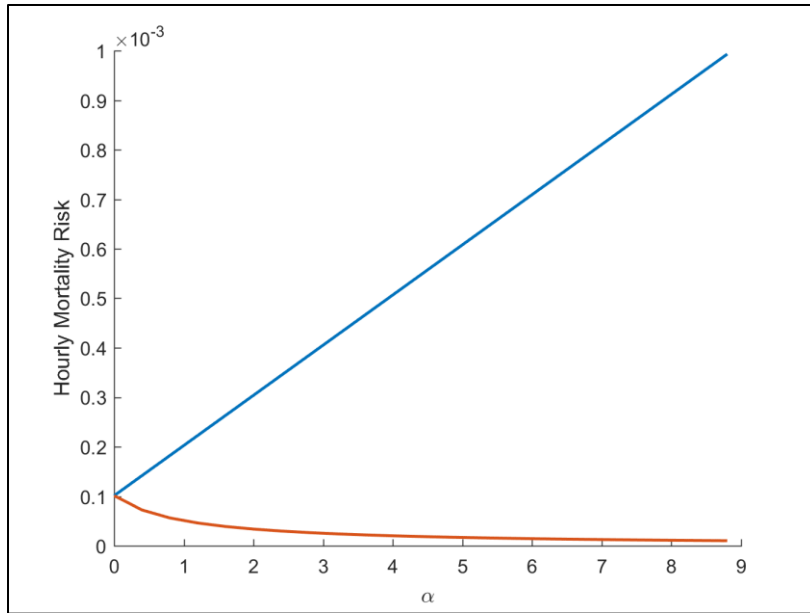


Figure 3.5 The mortality risk of grazing (blue line) and predating (red line) for a range of α 's. Note how grazing becomes more risky, and predating less risky, as α increases.

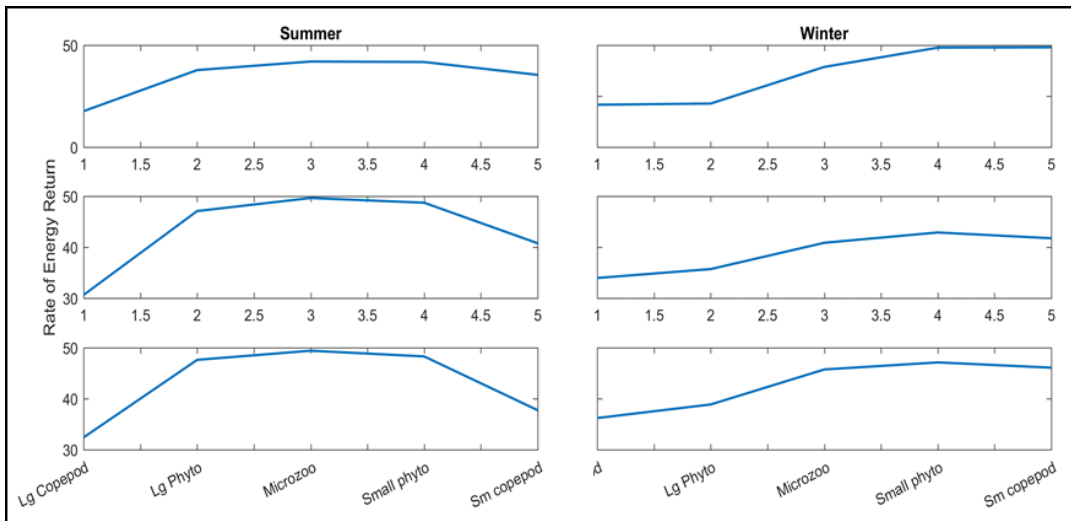


Figure 3.6 The rate of daily energy return depending upon prey included in the diet of *E. superba* for Sub-Antarctic (A), Antarctic Peninsula (B), High Antarctic (C). The order of profitability is the same in all seasons and areas.

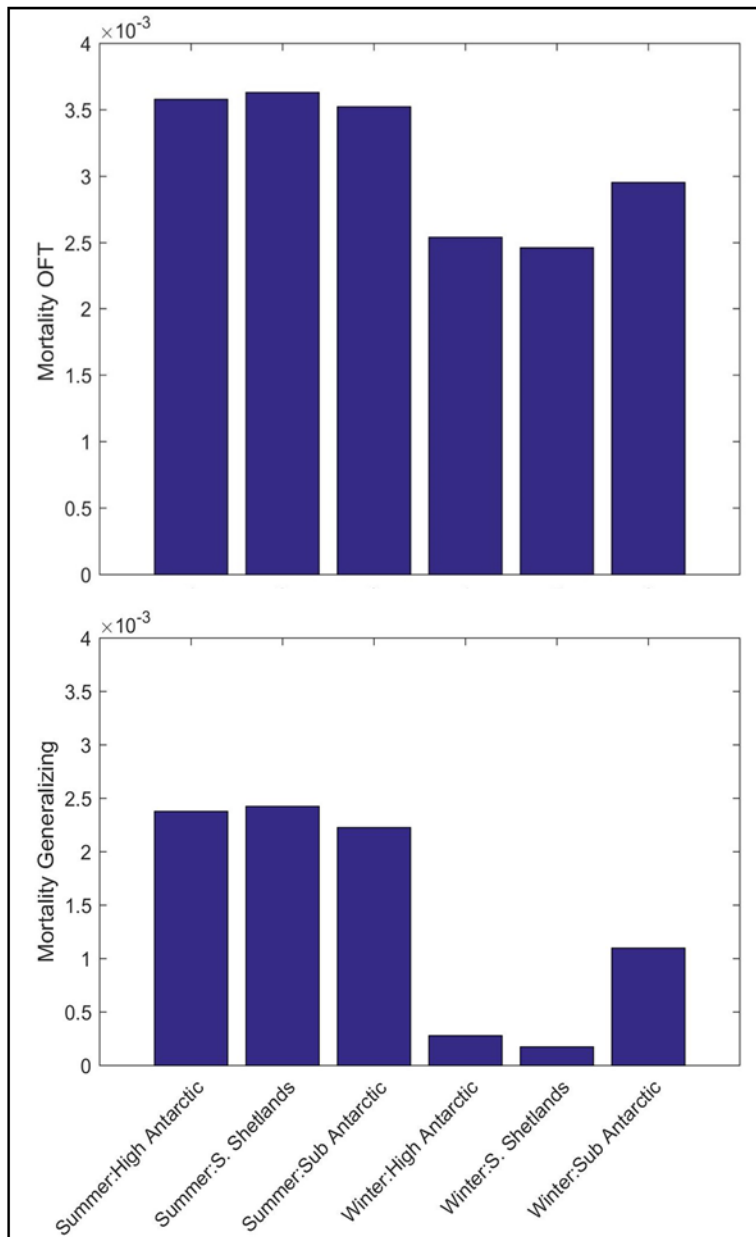
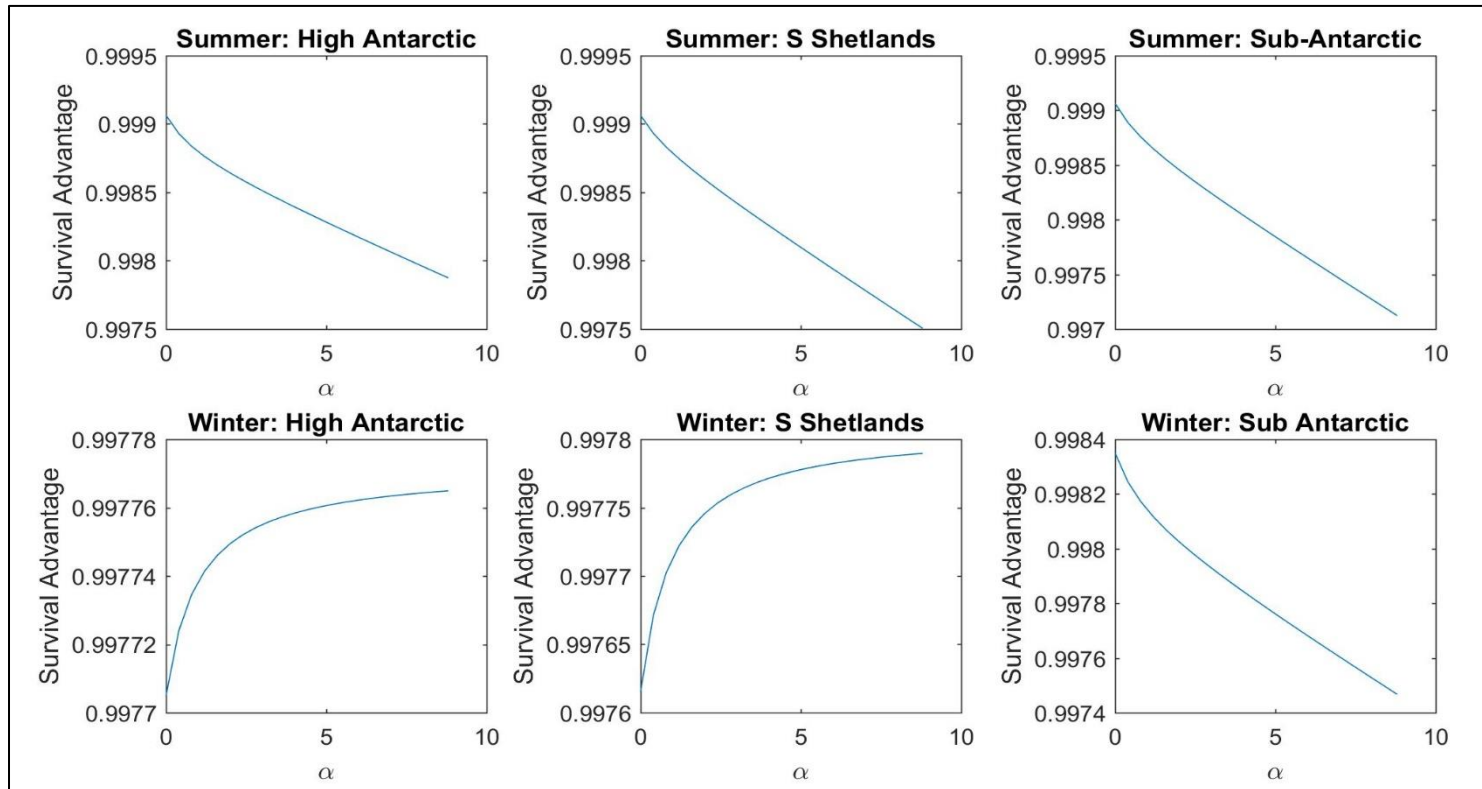


Figure 3.7 An example of total daily mortality for an optimal diet (top) and a generalist diet (bottom) in each area and season. Here mortality is calculated with an α of 1 which corresponds to a doubling of the mortality risk from grazing and a 50% reduction in mortality risk from predating.

Figure 3.8 The relative survival of the optimal diet versus generalizing with increasing α values.



4 VERTIKRILL: RESOLVING THE PARADOX OF KRILL AT DEPTH

4.1 ABSTRACT

Vertical migration of marine zooplankton is a major feature of the world's oceans, involves massive amounts of biomass, and occurs over a variety of spatial and temporal scales. The decision of an organism to move vertically in the water column is often the result of tradeoffs between predation risk, food availability, and physiological stress with depth. In the Southern Ocean, *Euphausia superba* is the key trophic link between phytoplankton and upper trophic levels. The prevailing theory on the vertical distribution of *E. superba* is that, in summer, the majority of the population resides in the upper 200 m of the water column, and the few individuals found in deeper water represented aberrant behavior. Repeated observations of krill below 200 m, including gravid females actively foraging below 2000 m and mating behavior at 700 m, suggest that mesopelagic and benthic habitats are important components of *E. superba*'s environment. Understanding why *E. superba* changes its vertical habitat will increase our understanding of both the population dynamics of krill and their availability to predators. In this chapter, I ask whether *E. superba* found in benthic and mesopelagic habitats are an aberration or reflect an important part of their life history strategy. In this chapter, I use a Stochastic Dynamic Programming model (VertiKrill) to explore how food, predation, and respiration drive vertical habitat selection across a range body conditions throughout the year.

4.2 INTRODUCTION

Vertical migration of marine zooplankton is a major feature of the world's oceans, involves massive amounts of biomass, and occurs over a variety of spatial and temporal scales. For example, diel vertical migration (DVM) of zooplankton occurs over hours and hundreds of meters, while seasonal or developmental migrations may occur on the timescale of months and thousands of meters. Vertical habitat selection can affect populations, impacting growth rates and reproductive success (Mclaren 1974), the availability of prey to upper trophic levels, nutrient cycling (Bianchi et al. 2013), carbon sequestration (Bianchi et al. 2013), and iron fertilization (Schmidt et al. 2011). Therefore, understanding the drivers of vertical habitat selection is key to understanding the population dynamics of marine zooplankton.

The decision of an organism to move vertically in the water column is often the result of tradeoffs between predation risk, food availability, and physiological stress with depth. For example, surface layers are often rich in food but incur higher risk from air breathing predators and increased respiration from higher temperatures. A well-studied example of this tradeoff is the diel vertical migration of copepods, which describes their movement up into phytoplankton rich surface waters at night to avoid visual predators (Gliwicz 1986, Hays 2003). During winter at high latitudes, moonlight can also trigger lunar vertical migration (Last et al. 2016) and some species of zooplankton have adopted a reverse DVM, avoiding overlap with predators by moving to the surface during the day (Ohman and Frost 1983). Seasonal changes in

food availability can drive migrations into mesopelagic and benthic environments. For example, chaetognaths may migrate to near bottom habitats in winter to prey on diapausing copepods (Hirche et al 2016), and the euphausiid *Thysanoessa inermis* moves to the seafloor seeking sedimented phytoplankton or to the mid-water to predate on copepods (Hirche et al. 2016).

Zooplankton also change their vertical distribution as they mature and grow. For example, several species of *Calanus* have been observed near the sea floor during winter diapause (Hirche et al. 2016), and chaetognaths change depth with maturity and season (Conway and Williams 1986). *Euphausia superba* move into mesopelagic water just before spawning, and larvae undergo ontogenetic vertical migration in which eggs sink, hatch in deep water, then larvae migrate to the surface during the first feeding stage (Marr 1962, Hempel and Hempel 1986).

Temperature and oxygen concentration of different water masses also structure the vertical distribution of zooplankton (McLaren 1974, Ambriz-Arreola et al. 2017). For example, early studies on copepod growth, metabolism and DVM showed that by moving into colder water during the day individuals reduce their metabolic cost (McLaren 1974). In a review of euphausiids in the Gulf of California, Ambriz-Arreola et al. (2017) found that temperature, dissolved oxygen and the oxygen minimum zone, along with phytoplankton and copepod prey, were the key variables that explained species' vertical distribution. Climate change is expected to increase sea surface temperature, which will increase the metabolic cost of residing in that layer (McLaren 1974). In regions most impacted by climate change, such as the

Southern Ocean (Gille 2002), these changes in temperature may alter the vertical distribution of zooplankton and their availability to air breathing predators.

In the Southern Ocean, *Euphausia superba* is the key trophic link between phytoplankton and upper trophic levels. Predicting changes in the vertical distribution of *E. superba* will increase our understanding of both the population dynamics of krill and their availability to predators.

The prevailing theory on the vertical distribution of *E. superba* is that in summer the majority of the population resides in the upper 200 m of the water column, and net and acoustic efforts have focused on this layer accordingly (Marr 1962, Jarvis et al. 2010, Reiss et al. 2017). Although krill were known to feed near benthic habitats (Kawaguchi et al. 1986, Gutt and Siegel 1994), and gravid females were found occupying mesopelagic water (Marin et al. 1991), these observations were considered aberrant behavior in the population. However, Lascara et al. (1999) noted that the relatively low abundance of krill in winter compared to summer may be due to individuals migrating below 200 m.

However, recent studies have found that *E. superba* may show greater plasticity in their vertical habitat than previously thought, with significant portions of the population deeper than 200 m in winter (Taki et al. 2005) and occupying both surface and mesopelagic layers (Taki et al. 2008). Further evidence that krill effectively use mesopelagic and benthic habitats came from Clark and Tyler (2008) who found gravid females feeding and molting near the bottom at depths up to 3500

m and Kawaguchi et al. (2011) who recorded mating behavior occurring at 700 m. Schmidt et al. (2011) estimated that, although the density of *E. superba* below 200 m is relatively low, it may make up 20.3 % of the total oceanic population. These findings suggest that the mesopelagic and benthic layers are important habitats for *E. superba*.

In this chapter, I explore the consequences of assuming that *E. superba* inhabit deeper water habitats because they are the optimal tradeoff between predation and food at that point in their life. Schmidt et al. (2011) suggested that, in the Scotia Sea, higher proportions of krill were found near the bottom when close to land, due to high predator concentrations, or far from land, due to low phytoplankton concentrations. At intermediate distances, where phytoplankton was still high and predators low, krill stayed near the surface. Clark and Tyler (2008) observed that krill were found in abyssal depths concurrent with phytodetritus. Similarly, the high densities of krill found in the mesopelagic by Taki et al (2005, 2008) and Kawaguchi et al. (2011) might be explained by individuals with high resource stores seeking the relatively low predation pressure of the midwater. Alonzo and Mangel (2001) used models to predict shifts in habitat use and growth with predation pressure and phytoplankton abundance. However, outside of direct observations of krill at depth, few studies have attempted to understand the drivers of *E. superba*'s vertical habitat selection.

Here I use a Stochastic Dynamic Programming model (SDP) (Mangel and Clark 1988, Alonzo and Mangel 2001), dubbed VertiKrill, to predict the depth an individual krill uses to maximize its annual growth (juvenile) or reproductive success

(adults), given the time of year and current body condition. SDP models allow us to examine how different, and sometimes contrasting, selective pressure affect behavioral decisions across different states and times in an individual's life. I explore how energy requirements, predation pressure, and time of year affect the vertical habitat choice of *E. superba* with the following questions:

- Under what conditions of state and time are benthic and mesopelagic habitats optimal?
- How do those conditions differ between juveniles and adults?
- Are individuals using benthic and mesopelagic habitats more or less successful than those who use surface and epipelagic habitats?
- How does an individual's habitat use history affect its total mortality risk?

I begin with a description of the model, time scale, and aspects of juvenile and adult krill used in the model. The state and end conditions of the model are defined and followed with a description of the patches used and their respective parameters. I then explain the mechanics and structure of the SDP model used for the prediction of habitat selection and the forward Monte Carlo simulations used to estimate the distribution of krill throughout the year. I then modified the basic SDP model to compare krill, using only the surface and epipelagic patches, to those using the entire water column. In the results, I highlight the key differences between the decision matrices and simulated populations. In the discussion, I place these results in the context of the prevailing theory on the vertical distribution of krill and recent findings

on deep water krill. I then relate the results of the model to spatial and temporal variations in the environment, with special consideration to how they relate to reproductive output and growth. I end by suggesting the future potential of the model and how it may help guide empirical work.

4.3 METHODS

4.3.1 The SDP Model: Model Setting and Model Krill

I set the SDP model in a pelagic habitat along the Antarctic Peninsula for the following reasons. First, the model examines the conditions and behavioral choices that maximize spawning potential in krill and the Antarctic Peninsula region is a known spawning ground for *E. superba*. Second, I want to model the tradeoff between maximizing energy return and risk of predation, and the region is highly productive in summer with a high concentration of both krill and krill predators. Third, the distribution of krill in the region has been well studied and those studies form the basis of my investigations.

I model the behavior of krill over the course of one year in daily time steps starting immediately after spawning in January. Since I assume that individual *E. superba* will spawn once, a single year represents a single reproductive (See discussion for the model implications on multiple spawning individuals). I chose a time step of one day assuming that krill make decisions about migration and where to feed on the scale of hours, and spend the majority of a single day in one patch (Cresswell et al. 2007). In nature, krill may move between different patches during a

foraging period before settling on a habitat. Since the model predicts the optimal patch given the condition for an individual krill, I assume that individuals in the model have perfect knowledge of the different patches and chose one patch per day.

I model the behavior of two sizes of krill; 30 mm juveniles and 40 mm adults (cf Wiedenmann et al 2008). These sizes represent two life stages at which krill have different fitness-size relations. Juvenile krill (30 mm) do not reproduce by definition, so I assume that they behave to maximize expected growth, where the expectation is chosen over survival. I assume that adult krill (40 mm) behave to maximize expected reproductive success, which means both surviving to reproduce and building up sufficient energy reserves for reproductive development. As a simplification, I assume that length is constant over the year. I use lipid mass, in mg Carbon, as a proxy for body condition. The maximum lipid mass for an individual krill is 50% of its dry weight (Siegel 1992, Hagen 2001) and a minimum lipid composition of 5% of an individual krill's dry weight is appropriate because it is below which cellular function ceases (Saether et al. 1985). The units of the model are in mg C x10 for ease of calculation.

4.3.2 The SDP Model: Structure and Behavioral Decisions

I use the SDP model to predict patch use by an animal that is maximizing expected growth (juvenile) or expected reproduction (adult). I let $X(t)$ denote g C of lipid on day t in the year and T denote the final day of the season.

For juveniles, I let $F(x,t)$ denote the maximum expected final lipid of a juvenile given that $X(t)=x$, that is

$$F(x, t) = E\{X(T)|X(t) = x\} \quad (1)$$

where $F(x,t)$ is the maximum expected reproductive reproduction at time given state x and time t . For adults, I let

$$\phi(x) = \left[\frac{x}{x + x_L} \right] E_{max} \quad (2)$$

denote reproduction at the end of the season given that $X(t)=x$, where E_{max} is the maximum amount of eggs released, and x_L the value of lipids that give half of the maximum reproduction. Then its fitness function for an adult is

$$F(x, t) = E\{ \phi(X(T)) | X(t) = x \} \quad (3)$$

4.3.3 The Environment: Patch Description

I let individuals in the model choose between 4 depth ranges that represent distinct habitats in the water column, each with different food resources, predation pressures and temperatures. I chose the patch structure based on observations of *E. superba* (Siegel 2000, Clarke and Tyler 2008, Wiebe 2011).

Patch #1 represents the surface to the chlorophyll maximum (~50 m). This patch is characterized by high phytoplankton concentrations in summer, intense predation pressure relative to deeper water due to the presence of air breathing predators, and relatively warm water in summer, and very cold water in winter.

Patch #2 is epipelagic and extends from ~ 50 m to ~ 250 m. This patch is characterized by a lower concentration of phytoplankton and sparse but high value prey such as copepods, lower predation pressure, and persistent cold water.

Patch #3 is the mesopelagic layer extending from 250 m to a 100 m from the bottom. This patch has very low food resources, low predation pressure and warmer water than the second patch but colder than the first in summer.

Patch #4 is the near bottom patch. This patch is characterized by abundant but low value food such as detritus, moderate predation pressure from fish and it is of similar temperature to the third patch.

I thus characterize each patch by (Table 4.1, eqn. 8)

- The probability of predation in patch i , β_i ;
- The probability of finding food in patch i at time t , $\lambda_{i,t}$;
- The energetic value of food patch i , Y_i ; and
- The cost of foraging in patch i , α_i .

4.3.4 The Environment: Food

I converted the concentration of food in each patch (Chapter 3) into a probability of encountering food in a given patch at time t . I used encounter rates from clearance rate experiments on krill (See Chapter. 3, Hamner 1988, Price et al. 1988). In order to capture seasonal changes in the environment, I force oscillation in production in the surface and epipelagic patches by the equation

$$\lambda_{i,t} = P_{w,i} + (P_{s,i} - P_{w,i}) \sin \left[2\pi \frac{t}{365} \right] \quad (4)$$

where $P_{s,i}$ is the summer probability of encountering food in patch i and $P_{w,i}$ is the winter probability of encountering food patch i (Figure 4.1).

I measure food value Y_i as the total mass in C mg consumed in a patch i given that food is found. I assigned values assuming that those krill near the surface are primarily grazing on phytoplankton, krill in the epipelagic are primarily predating on copepods, krill in the mesopelagic are grazing on detritus and copepods, and those on the bottom are grazing on detritus. I based the values for Y_i on clearance experiments for copepods and phytoplankton (Hamner 1988, Price et al. 1988, Hofmann and Lascara 2000) and converted to mg C (See Chapter. 3, Boyd et al. 1984, Price et al 1988).

4.3.5 The Environment: Mortality

Mortality β_i is the probability of dying in patch i in a single period and is static through time in the model. Its value was obtained as follows.

I used a maximum of age of *E. superba* in nature of 7 years (Siegel 1987) and assumed survival to that age (S_{max}) is 0.002, that is 0.002% of individuals from a year class survive to age 7. Using a daily time step and letting M_d denote the average daily rate of mortality

$$e^{-M_d \cdot 7 \cdot 365} = S_{max} \quad (5)$$

which, solving for M_d gives:

$$M_d = \frac{-\log(S_{max})}{7 \cdot 365} \quad (6)$$

In order to calculate the difference in mortality based on depth, I assumed that mortality decreases with distance from the surface (Fiksen and Giske 1995, Kiorbo and Jian 2012) so that

$$\beta_i = \frac{M_d}{1 + \gamma_i} \quad (7)$$

where $\gamma_i < 0$ for surface and epipelagic patches and $\gamma_i > 0$ for mesopelagic and benthic patches.

4.3.6 Physiology: Respiration

I set the standard metabolic respiration cost to 2 mg C per day which is base metabolism plus a 1 % increase assuming the krill are moving and feeding (Hoffman and Lascara 2000). This value is fixed for all patches and times.

4.3.7 The SDP Model: Backward Iteration

At each time step in the model, an individual chooses the patch that maximizes its expected future fitness. Each patch is characterized by the probability of predation (β_i), the cost of respiration (α_i), the probability of finding food ($\lambda_{i,t}$) and an increase in its state (Y_i) if it does find food. Because $F(x,t)$ is known at time T it is possible to step backward in time to find $F(x,T-1)$ so that $X(T-1)=x$. If patch i is chosen then the probability of surviving to time T and finding food for patch i is $(1 - \beta_i)\lambda_{i,T-1}$ and the expected fitness is $F(x - \alpha_i + Y_i, T)$. If an individual chooses patch i but does not find food with probability $1 - \lambda_{i,T-1}$ then its expected change of state is

$F(x - \alpha_i), T$. Combining the equations for finding food and not finding food gives the expected future fitness of choosing patch i , called $V(x, T-1)$ is:

$$V_i(x, T-1) = (1 - \beta_i) [\lambda_{i, T-1} F(x - \alpha_i + Y_i, T) + (1 - \lambda_{i, T-1}) F(x - \alpha_i, T)] \quad (8)$$

$F(x, T-1)$ is then the patch which provides the maximum value of $V_i(x, T-1)$. If we continue iterate the model backward in time from $T-1$ to $t=1$ selecting the patch that maximizes $F(x, t)$ we come to the standard SDP equation (Mangel and Clark 1988, reviewed in Mangel 2015):

$$F(x, t) = \max_{i=1,2,3,4} (1 - \beta_i) [\lambda_{i,t} F(x - \alpha_i + Y_i, t+1) + (1 - \lambda_{i,t}) F(x - \alpha_i, t+1)] \quad (9)$$

Because Eq. 9 is linear, I can set $E_{max}=1$ when solving it and interpret the adult fitness to be the maximum expected relative reproduction given $X(t)=x$.

4.3.8 The SDP Model: Forward Monte Carlo Simulation

The solution of Eq. 9 generates the fitness function for juveniles and adults according to the end condition. It also generates the optimal patch $D(x, t)$ for an individual whose state at time t is x for all individuals whose state is greater than the critical lipid level. Those whose state falls below the critical level starve. This decision matrix $D(x, t)$ is essentially a map of which patch an individual is predicted to use given any time t and any state x , in order to maximize expected fitness.

A population of 10,000 individual krill models are run forward through the model from time $t=1$ to T . The individuals choose patches based on their current state and time according to decision matrix created by Eq. 9. Individuals all start at the

state based on the average lipid mass for adults and juveniles in January (Hagen 2001). Stochasticity is introduced in the model through the probability of predation (β_i) and the probability of finding food ($\lambda_{i,t}$) at each time step in the run. This stochasticity is achieved by generating a random number u between 0 and 1 so that when u is less than or equal to β_i the individual dies. Otherwise the individual avoids being eaten. If another uniformly distribute random variable v is less than or equal to $\lambda_{i,t}$ then the individual finds food of value Y_i . Otherwise it survives but doesn't find food.

Pseudocode for the forward iteration proceeds as follows:

- (1) Create a matrix to keep track of state for 10000 individuals k at each time step t , $X(k,t)$.
- (2) Initialize $t=1$ and a starting lipid mass $X_{\text{initial}}=X(1,1)$ for the first individual on the first day.
- (3) Using the decision matrix from Eq. 10 find the optimal patch $D(X(1,1))$; so that $\beta_{D(X(1,1))}$, $\alpha_{D(X(1,1))}$, $\lambda_{D(X(1,1))}$ and $Y_{D(X(1,1))}$ are the patch parameters for patch $D(X(1,1))$ at time 1.
- (4) Given $D(X(1),1)$ choose a random number u_1 so that if $u_1 \leq \beta_{D(X(1),1)}$ the individual dies, $X(1,2)=0$ and the run proceeds with next individual $K(2,1)$. Otherwise if $u_1 > \beta_i$ continue.
- (5) Choose a random u_2 so that if $u_2 \leq \lambda_{D(X(1,1))}$ the individual finds food and $x=x+Y_i-\alpha_i$, otherwise if $u_2 > \lambda_{D(X(1,1))}$ then the individual does not find food and

$x = x - \alpha_i$. If $X(I, I) > X_{max}$ at this point then $X(I, I) = X_{max}$ and if $X(I, I) < X_{crit}$ the animal starves and the run proceeds with next individual $X(2, I)$.

(6) Proceed to $t = t + I$ until T then proceed with the next individual.

The stochasticity of obtaining food means each individual's state will evolve on different trajectories, and therefore patches, over the course of the model year. As a result, individuals will be exposed to different levels of predation risk. In order to keep track of the total amount of risk an individual was exposed to, I first calculate survival for each patch:

$$1 - \beta_i = Pr\{\text{surviving a single day}\} = e^{-m_i} \quad (11)$$

Solving for m_i gives:

$$m_i = -\ln(1 - \beta_i) \quad (12)$$

I then sum m_i over time t for an individual so that the accumulated mortality M_A is:

$$M_A = \sum_{t=1}^{t=364} m_{D(X(k,t))} \quad (13)$$

4.3.9 Model Runs

I use 2 different models for juveniles and adults: one where individuals are limited to the upper 200 m (surface and epipelagic habitats), and another where individuals can move through the entire water column (surface, epipelagic, mesopelagic and benthic habitats). Models of juveniles differ from adults in that respiration cost (α) is lower for juveniles due to their smaller body size, and the

probability of finding food (λ) is lower because their feeding basket is smaller and less efficient at capturing prey. In order to compare the models, all individuals start with the same state. However, the final states, number of animals eaten, and the number starved differ between model runs because the forward iteration uses random number generators for each individual. To account for between run variability, I ran each model 50 times with 10000 individuals each and outputs are reported as means of these runs. For the adults, I explored how variability in starting states would affect the total mortality on the population and end states, in order to better understand how the model might capture natural variability. Specifically, I used the end states of one model as the starting states for the next model year, and ran the model again.

The difference in end states between krill in the upper 200 m only can be compared to those in the entire water column. It is important here to clarify what an individual's state on the final day of the model indicates in terms of that individual's life history. Juvenile krill do not reproduce by definition and thus seek to maximize their body size; thus, the amount of lipid mass at time T is an indicator of their growth potential. For adult krill, the amount of lipid mass at time T is an indicator of reproductive potential. Standard tests of significance are not appropriate for simulated data given that the modeler can control the variance of the model thereby violating assumptions of variability (White et al. 2014). A more appropriate test is Cohen's d statistic which scales the difference between means using the average standard deviation of the models given by (Cohen 1977):

$$d = \frac{|\bar{X}_{all} - \bar{X}_{<200\ m}|}{(SD_{all} + SD_{<200\ m})/2} \quad (14)$$

where \bar{X}_{all} and SD_{all} is the mean and standard deviation of the individuals using all habitats, and $\bar{X}_{<200\ m}$ $SD_{<200\ m}$ is the mean and standard deviation of individuals limited to the upper 200 m. The denominator is the pooled standard deviation, which in this case is the average of the two model outputs. The Cohen's d value is a measure of the effect using all vertical habitats versus the upper 200 m only has on the average final state of the population. Cohen's d values of 0.2, 0.5 and 0.8 are considered benchmarks for small, medium and large effect sizes respectively (Cohen 1992).

4.4 RESULTS

4.4.1 Predicted Vertical Habitat Selection

The decision matrices resulting from Eq. 9 determine the optimal patch E . *superba* are predicted to inhabit for any state and time of year. I will report results for two cases: first, the prevailing view that krill stay only in the first 200 m of the water column and second, my proposal that krill use the entire water column.

4.4.1.1 Forcing Krill to Stay in the Upper 200 m

As I described earlier, the prevailing concept of vertical distribution is that krill primarily inhabit the epipelagic and surface layers (<200m). Under this scenario, I predict that juvenile krill primarily inhabit high-risk, food-rich surface waters in spring summer and fall, except for individuals whose state is >145 mg C x10 for

which the relatively safe epipelagic layer is optimal (Figure 4.2). From late fall through early spring, juvenile patch individuals increasingly choose the epipelagic layer as winter progresses starting with individuals of higher states (i.e. large lipid reserves) with the pattern reversing with spring. Juveniles with very low lipid reserves (state $<50 \text{ mg C} \times 10$) always stay in the surface patch (Figure 4.2).

For adults in summer, the surface is the optimal patch for individuals with states $<355 \text{ mg C} \times 10$ and the epipelagic is optimal for those with higher $\geq 355 \text{ mg C} \times 10$. Individuals transition rapidly to the epipelagic layer in early fall and remain there through late spring (Figure 4.2).

4.4.1.2 Allowing Krill to Use the Entire Water Column

When all habitats are included the model, I predict that the surface is the optimal habitat for juvenile krill in summer and fall for all states except those near the maximum ($>195 \text{ mg C} \times 10$) which take refuge in mesopelagic habitat (Figure 4.2). During the fall/winter transition, the benthic habitat is briefly optimal for most states. As winter progresses, the mesopelagic becomes the optimal patch for juveniles of lower states. Juveniles with very low lipid reserves state ($<50 \text{ mg C} \times 10$) are predicted to stay in the surface patch. For adults in summer the surface patch is optimal across most states ($<425 \text{ mg C} \times 10$) with those closer to the maximum state choosing the safer epipelagic (Figure 4.2). The pattern is similar to that of the upper water column only model except that individuals of all states stay in or switch to the epipelagic patch earlier in the fall. In winter, the optimal habitat for adults with states

>175 mg C x10 is split between the benthic and mesopelagic habitats with those between 50 and >175 mg C x10 staying in the epipelagic.

4.4.2 Simulated Populations: Habitat Selection

I simulated a population of 10,000 individuals and tracked their habitat use for one year. Habitat use is determined by the decision matrices (see Figure 4.2), an individual's state and time of year. Juveniles all start with the same lipid mass (75 mg C x10) on day 1 and therefore all start in the surface patch (Figure 4.3). Juveniles all stayed in the surface during summer. An increasingly large portion of the population moved into the mesopelagic with 50% of individuals in the mesopelagic in mid fall. Individuals are split between the mesopelagic and surface patches in spring before nearly all individuals (>95%) move back to the surface in early summer. The state trajectories of individuals in winter suggests that benthic habitat is briefly important as an energetic bridge between fall and spring. During transitions between seasons, all trajectories exhibit high frequency oscillations due to a relatively narrow range of state.

Simulated adult individuals start at 250 C mg x 10 in the surface patch and remain there for summer before moving to the epipelagic in fall (Figure 4.4). In winter, the population resided primarily in the benthic habitat with only a few simulated adults in the mesopelagic. The transitions between seasons were much more rapid for simulated adults than simulated juveniles and adults showed less oscillation. This may be due to the broader range of state available to simulated adults.

4.4.3 Forward Monte Carlo Simulation: Changes in Lipid Mass, Mortality, and Habitat Selection

I simulated individuals who can choose all habitats, and individuals restricted to the upper water column, with the same starting conditions in order to compare the differences in state trajectories, final state, and mortality. Juveniles restricted to the upper water column ended with a state similar to those open to all habitats ($\bar{X}_{200}=199.16$, $SD=2.25$ Vs. $\bar{X}_{all}=198.85$, $SD=3.08$, Cohen's $d=0.116$), as simulated individuals quickly reached the maximum allowable lipid mass during the summer growth season (Figure 4.5). Juvenile state closely tracked surface production in both models. However, juveniles showed much more variability in state between individuals throughout the year when restricted to the upper water column compared to those using all habitats. In summer, juveniles tend to reach the maximum state. If the maximum state is increased (300 mg C x10) so that the majority of the individuals in the model do not reach the maximum state; there is little effect on the overall state trajectories of the simulated population with similar end states and rates of predation (Figure 4.6). However, 300 mg C x10 is 50% greater than the maximum lipid percentage by bodyweight found in nature (Hagen et al 2001), and individuals at the maximum state of 200 C mg x 10 are devoting resources to growth, which the model does not explicitly treat.

Habitat selection has a greater effect on final state in the adult simulated population (Cohen's $d=0.27$) than in the juvenile population (Cohen's $d=0.116$), although both Cohen's d values indicate the effect of habitat on final state is small.

Adults restricted to the upper water column had a slightly larger state ($\bar{X}_{200}=333.53$, $SD=65.84$) and more variability, than individuals free to choose all patches ($\bar{X}_{all}=316.88$, $SD=57.45$) (Figure 4.7).

One notable difference between krill forced to use only the upper water column, and those using all patches, was in mortality. While very few individuals starved in either model, the number of individuals eaten was consistently higher in the upper 200 m models versus in the entire water column models. The number of juveniles eaten over the course of the year was lower for all habitats ($\bar{X}_{all}=3164$ eaten, $SD=48.2$) than for those in the upper water column ($\bar{X}_{200}=3826$ eaten, $SD=52.2$) suggesting that although they lead to similar states, individuals choosing deeper habitat suffer markedly less mortality. Adults showed a similar pattern, with more predation on upper water column krill ($\bar{X}_{200}=3707$ eaten, $SD=48.9$) versus those also using deeper habitat ($\bar{X}_{all}=3508$ eaten, $SD=45.6$) (Figure 4.8)

Natural variability in starting states was evaluated by using the end states of one year as the starting states for the next year (Figure 4.9). The average end state of the year two model was higher ($\bar{X}_2=358.8$, $SD=64.8$ vs $\bar{X}_1=316.88$, $SD=57.44$), because that the population started from a higher mean state. Variability in starting state had a moderate to high effect on end states (Cohen's $d=0.687$). The mortality for the year two population was lower when adjusted for population size than for populations with the same starting state (19.9% vs 35.1%), indicating that individuals not only maintained a higher state throughout the year but were also better able to avoid predation. This result

is sensible because individuals starting with higher states have more lipid reserves to choose safer patches.

4.5 DISCUSSION

4.5.1.1 Under What Conditions are Krill Predicted to Inhabit Deep Water?

Enough observations of *E. superba* below 200 m exist to recognize that mesopelagic and benthic habitats have a role in their life history. Several authors have suggested that the reproduction (Marin et al. 1991), the availability of food (Gutt and Siegel 1994, Clark and Tyler 2008), and/or predation pressure (Schmidt et al. 2011) may drive vertical distribution. The VertiKrill model shows that deep-water migrations involve tradeoffs between mortality risk and energy gain, and that these tradeoffs depend on the time of year and condition of an individual.

Thus, this relatively simple model predicts complex habitat selection behavior and mimics the seasonal fluctuations in the lipid mass of krill. By using deep water habitats, individuals can lower their mortality risk while maintaining or increasing their energy intake compared to individuals who stay near the surface.

4.5.1.2 VertiKrill in Nature

The VertiKrill model shows that *E. superba* do reside primarily the upper 200 m of the water column in summer when the abundance of food outweighs the risk of predation. Given that most observations of krill come from summer surveys and relatively few surveys in any season sample below 200 m, it is understandable why the misconception that *E. superba* reside primarily near the surface has persisted.

VertiKrill also shows that habitat choice is state-dependent and this also explains misconceptions about seasonal changes in krill body conditions. The prevailing thought is that krill build lipid stores through fall, and use those lipids to build mass and increase survival through the annual nadir of lipid mass in early spring (Hagen et al. 2001, Meyer 2012). However, the model suggests that for krill with relatively high lipid mass at the end of fall, benthic habitat may help individuals limit reductions in lipid mass through winter. Also, individuals with lower lipid masses at the end of fall must risk staying in epipelagic habitat to avoid starvation. Sampling effort has focused primarily on the upper 200 m, meaning that, if the model is consistent with nature, only the most anemic krill in the population are sampled. Even if the benthic population is relatively small, it may represent a refuge for krill with the most reproductive potential.

One of the implications of VertiKrill is that periods or areas of low production may drive krill to deeper water regardless of the time of year. In VertiKrill, I treat production as a smoothly transitioning through the seasons and do account for variability in space. Primary production can be patchy in on the scale of kilometers and days, meaning that, even in summer, there may be periods of “winter” like conditions that drive krill to benthic or mesopelagic habitats. Schmidt et al. (2011) speculated that both high predator populations close to South Georgia, and weak production far from shore, may drive krill into mesopelagic and benthic habitat in summer.

4.5.1.3 The Case of Multiple Spawning Krill

In VertiKrill I assume that individuals spawn only once per season, but some krill may spawn multiple times per season (Couzin-Roudy 2001, Tarling et al. 2007). Tarling et al. (2007) modeled egg production near South Georgia and found that over 60% females may spawn more than once under optimal conditions, but that delayed spring blooms can reduce this production by half. Spawning is energetically costly and can lead to a 30% reduction on body mass (Tarling et al. 2007). In this model the end state represents the magnitude of a single spawning event. We can imagine some minimum lipid state necessary to initiate spawning in spring (Figure 4.10) where individuals who have reached that point begin gonad maturation. Under optimal conditions (e.g. the spring bloom is early), then individuals might spawn earlier and then forage until the minimum lipid state is achieved again, thereby initiating a second spawning event.

4.5.1.4 Vertical Habitat Use and Climate Change

The Southern Ocean has experienced some of the most dramatic effects of climate change, including increasing sea surface temperatures (SST) and variability in the magnitude and timing of the spring bloom (Meredith and King 2005, Montes-Hugo et al. 2009, Schmidtko et al. 2014). VertiKrill results show that these changes may impact juvenile and adult krill in unexpected ways having upstream effects on reliant predators. Juveniles are inefficient predators and rely primarily on phytoplankton until adulthood, restricting their summer foraging habitat to the surface and, to a lesser extent, the deeper epipelagic. Increasing SST will lead to a higher

respiration cost for inhabiting this layer (Wiedenmann et al. 2008). I found that the VertiKrill juvenile model was sensitive to increases in surface respiration cost, with large increases in the number of individuals starving in model runs (Figure 4.11). Individuals were also more variable in state throughout the year, suggesting that the population is vulnerable to both changes in production and respiration cost. Adults have more flexibility in their diet and may respond to increasing SST by moving away from the surface water into the deeper epipelagic water in summer. This may mean reduced state for krill heading into winter and longer foraging trips for their air-breathing predators. Changes in the distribution of *E. superba* will impact Antarctic fishery management decisions both directly, by potentially changing the amount and location of effort of fishing nations, and indirectly, through potential conflict from additional stress placed on krill predators.

4.5.1.5 Conclusion

The broad range of behaviors exhibited by *E. superba* makes it difficult to formulate a single life history strategy for the species. Often, theories about *E. superba* are true locally but not globally, or are not consistent in time (Meyer 2012, Murphy et al. 2013, Reiss et al. 2017). The advantage of relatively simple models like VertiKrill is that they provide context based on first principles of ecology for complex behavior. In doing so, VertiKrill or its extensions can become hypothesis engines for future work on *E. superba*, and provide testable predictions for field studies (Alonzo et al. 2003). Here I used VertiKrill to answer my focal question (are krill at depth an aberration?). In the future, VertiKrill could examine seasonal and

spatial variations in predation pressure and primary production by treating those parameters explicitly. VertiKrill could be modified to explore the direct effect of increasing SST by exploring a range of temperature associated respiration costs. It could predict the conditions for multiple spawning events by exploring the minimum thresholds for reproduction or by modifying the SDP equations (Eqns. 8 and 9) to make spawning before T an adaptive decision. The migrations of *E. superba* to benthic and mesopelagic habitats illustrate how well adapted it is to variability in its environment. It is likely that krill will exhibit a range of behaviors to mitigate the impacts of climate change on its habitat. We can use models like VertiKrill to understand the primary drivers of *E. superba*'s distribution and help predict how these behaviors manifest.

4.6 TABLES AND FIGURES

Table 4.1 Model parameters.

Symbol	Parameter	Value	Unit
$F(x,t)$	Fitness for times $<T$	0-500 (adults), 0-200 (juveniles)	-
$F(x,T)$	Fitness at final time step	0-500 (adults), 0-200 (juveniles)	-
x	body condition as lipid mass	1	$\mu\text{g C x } 10$
xL	Lipid level at 50% of maximum reproduction	250	$\mu\text{g C x } 10$
i	Patch	Surface, Epipelagic, Mesopelagic, Benthic	
T	Final time step		
t	time step $<T$	1	day
α_i	Metabolic cost of patch i	3,3,3,3	$\mu\text{g C x } 10$
β_i	Mortality of patch i	0.0015,0.001, 0.0001,0.001	probability day^{-1}
M_A	Average Daily mortality rate	0.00105	probability day^{-1}
γ	Mortality modifier	-0.9,-0.5,1,1.5	
$\lambda_{i,s,t}$	Food encounter rate	-	probability day^{-1}
Y_i	Food value of patch i	6,10,4,6	$\mu\text{g C x } 10$
$P_{s,i}$	Probability of food in Summer	0.75,0.2,0.15,0.2	-
$P_{w,i}$	Probability of food in Winter	0.5,0.15,0.15,0.2	-

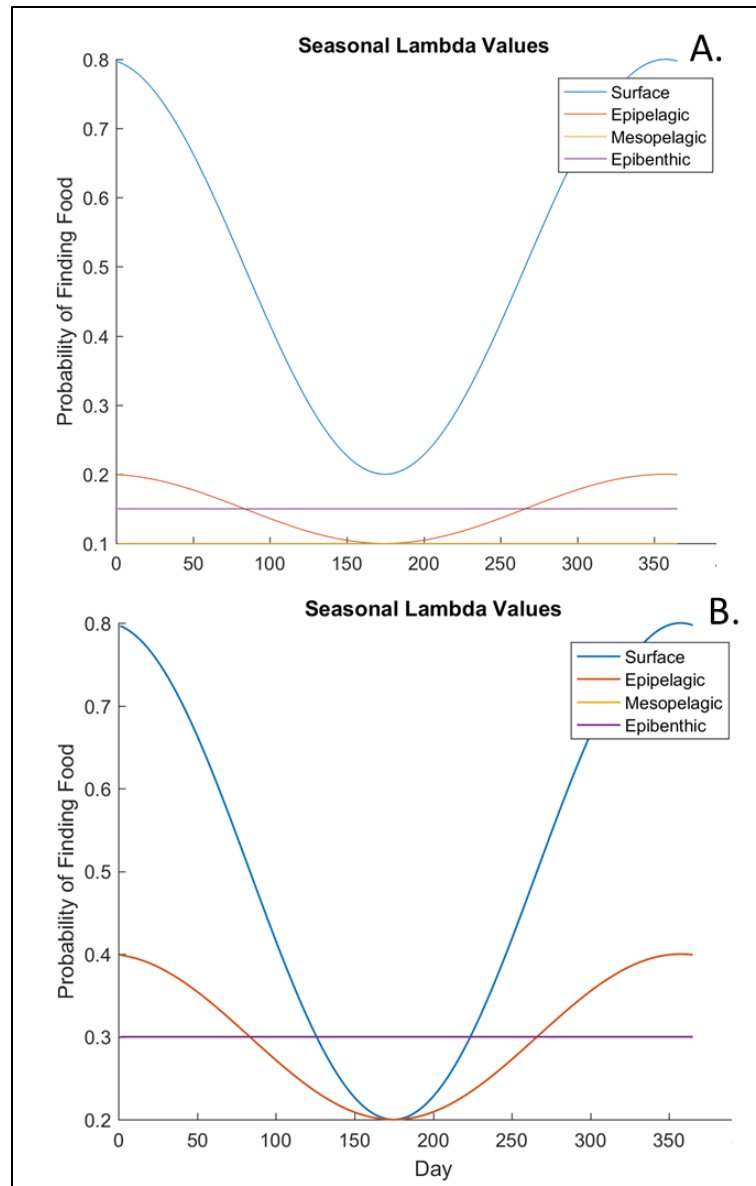


Figure 4.1 The probability of encountering food in a given patch for juveniles (A) and adults (B). Model day 0 is the day after spawning occurs, while model day 365 is the following years spawning event. The surface and epipelagic patches, indicated by the blue and red lines respectively, are calculated from Eqn. 5, while the mesopelagic and benthic patches, yellow and magenta lines respectively, are fixed.

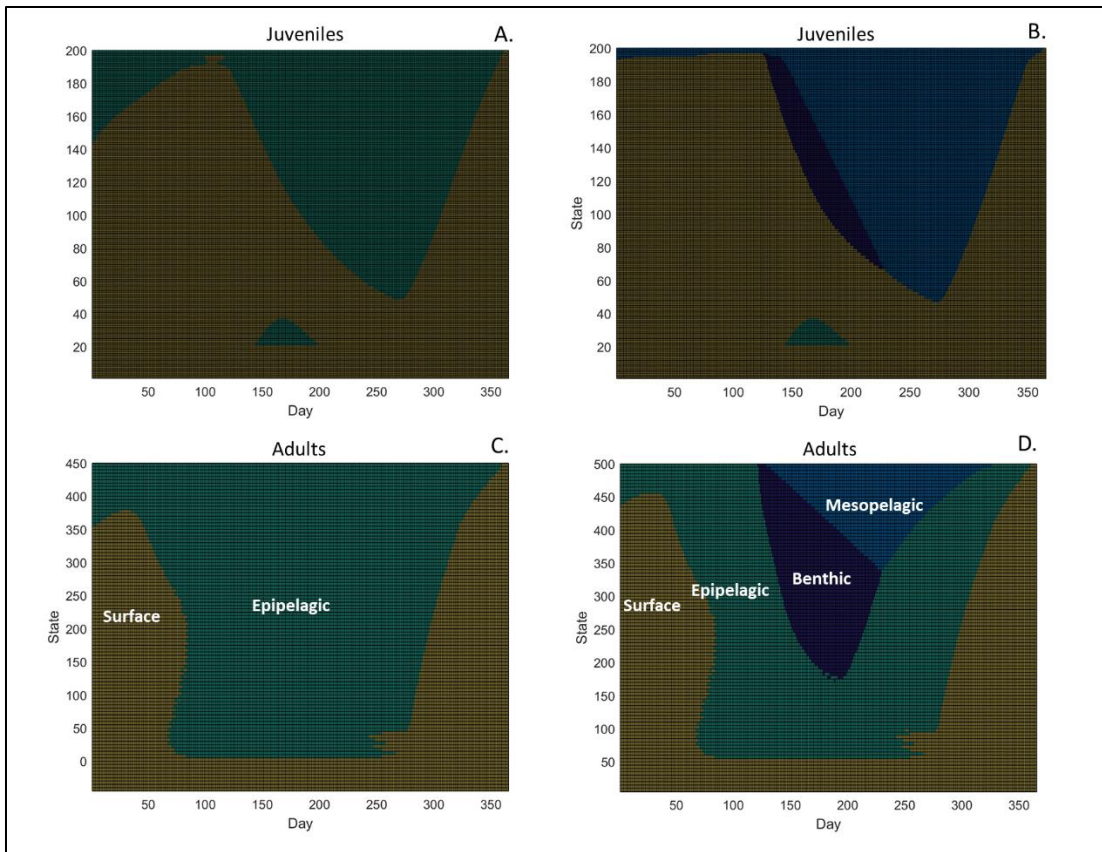


Figure 4.2 The optimal patch choice for juveniles (A,B) and adults (C,D) as a function of state (as lipid mass) and time when krill are restricted to the upper water column (and can inhabit the entire water column (Bottom)). Juvenile state is in mg C x10 with a maximum of 200 mg C x10. Adults have larger body sizes, and therefore larger lipid reserves, so their maximum state is 500 mg C x10.

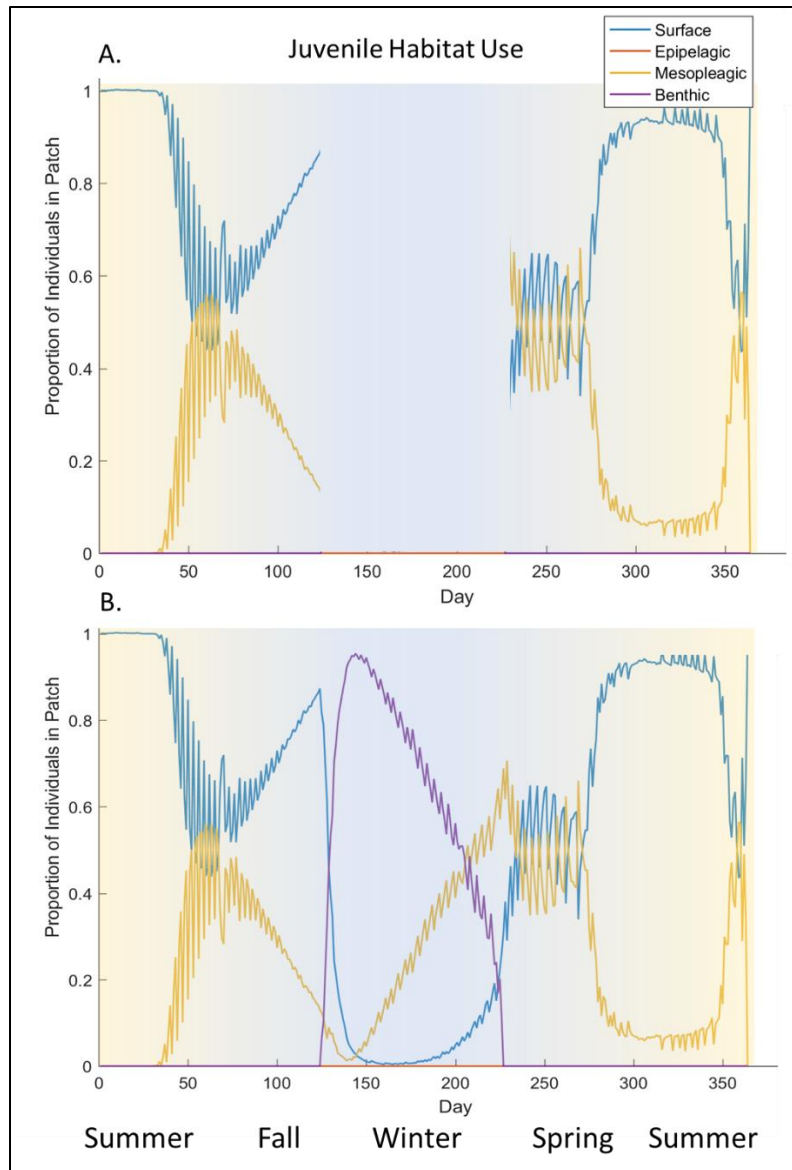


Figure 4.3 The proportion of juveniles in a simulated population of 10000 individuals in each patch throughout one year, adjusted for loss due to predation and starvation. Because most of the field sampling for *Euphausia superba* was done in summer, in surface water, this has led to the impression that juveniles are restricted to the surface (Top). However, I predict that the mid-water summer and benthic winter habitat may be critical to some juvenile krill (Bottom).

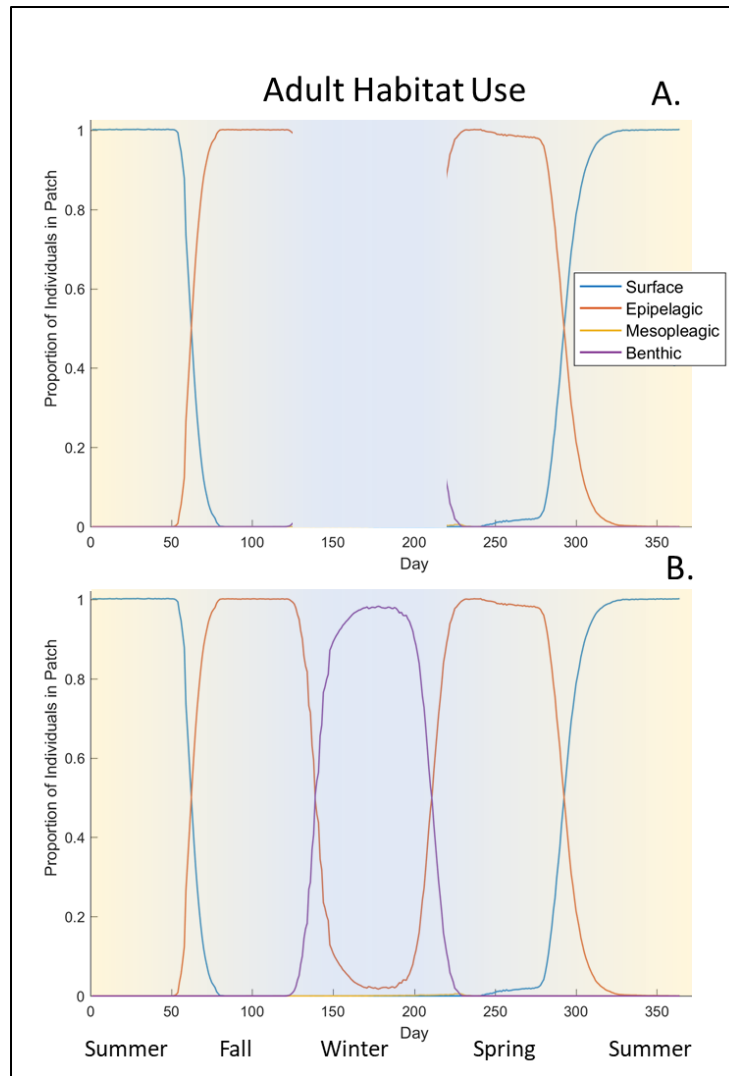


Figure 4.4 The proportion of adults in a simulated population of 10000 individuals in each patch throughout one year, adjusted for loss due to predation and starvation. Because most of the field sampling for *Euphausia superba* was done in summer surface water this led to the impression that krill are primarily an epipelagic species and efforts in winter have focused on this layer (A). However benthic and mesopelagic habitat may be critical habitat depending on the time of year and body condition of an individual (B).

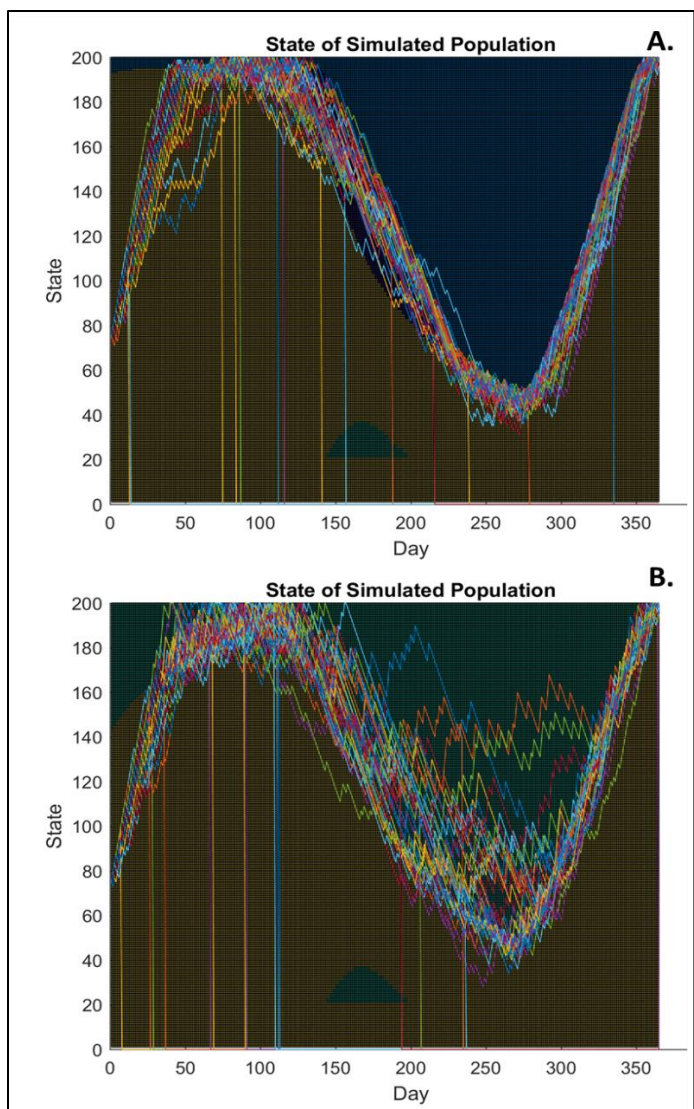


Figure 4.5 Juvenile states throughout the year of 40 randomly selected individuals (colored lines) from a simulated population using all patches (A) or only the surface and epipelagic patches (B). All individuals start with the same state equivalent to the average juvenile individual in February. Individuals that drop to 0 die, through either predation (when above 20) or starvation (when state drops below 20). The decision matrix in the background indicates the patches chosen given an individual's state and time.

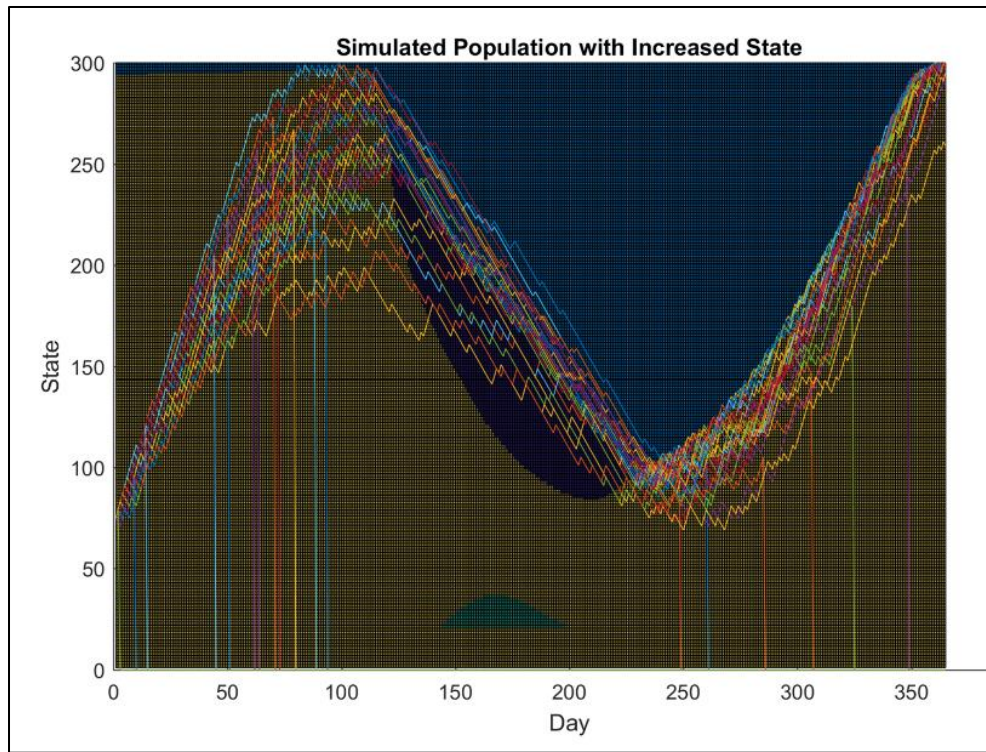


Figure 4.6 Juvenile states throughout the year of 40 randomly selected individuals (colored lines) from a simulated population using all patches with the maximum state increased to 300 C mg C x10.

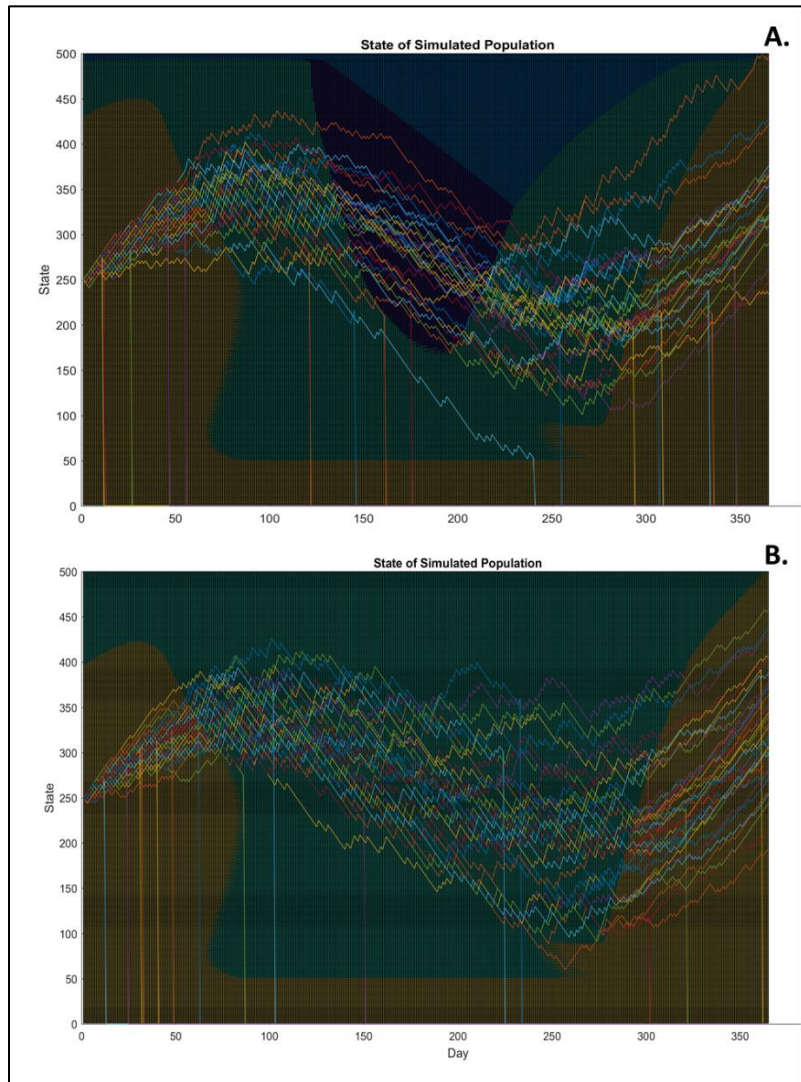


Figure 4.7 Adult states throughout the year of 40 randomly selected individuals (colored lines) from a simulated population using all patches (A) or only the surface and epipelagic patches (B). All individuals start with the same state, equivalent to the average post spawning lipid mass of an individual in February. Individuals that drop to 0 die through either predation (when above 50) or starvation (when state drops below 50). The decision matrix in the background indicates the patches chosen given an individual's state and time.

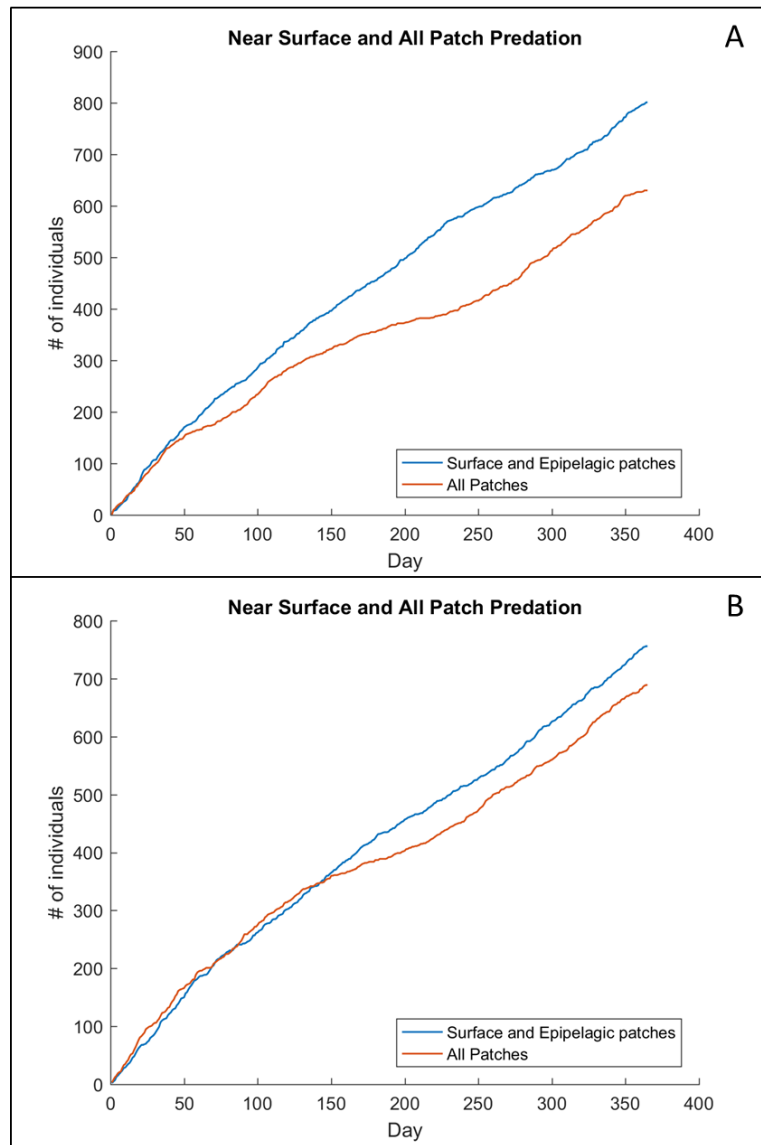


Figure 4.8 Comparison of the cumulative predation on simulated populations restricted to upper water column versus those utilizing the entire water column juveniles (A) and adults (B).

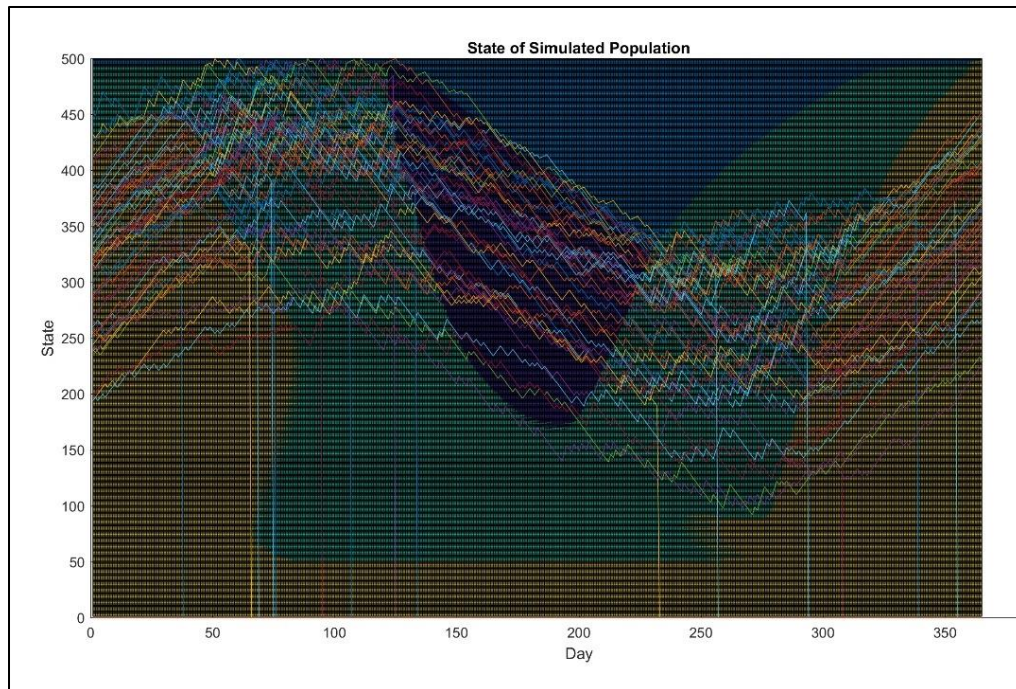


Figure 4.9 Simulated adult population with variable starting states. Note that the range of end states is similar to those in Fig. 7A.

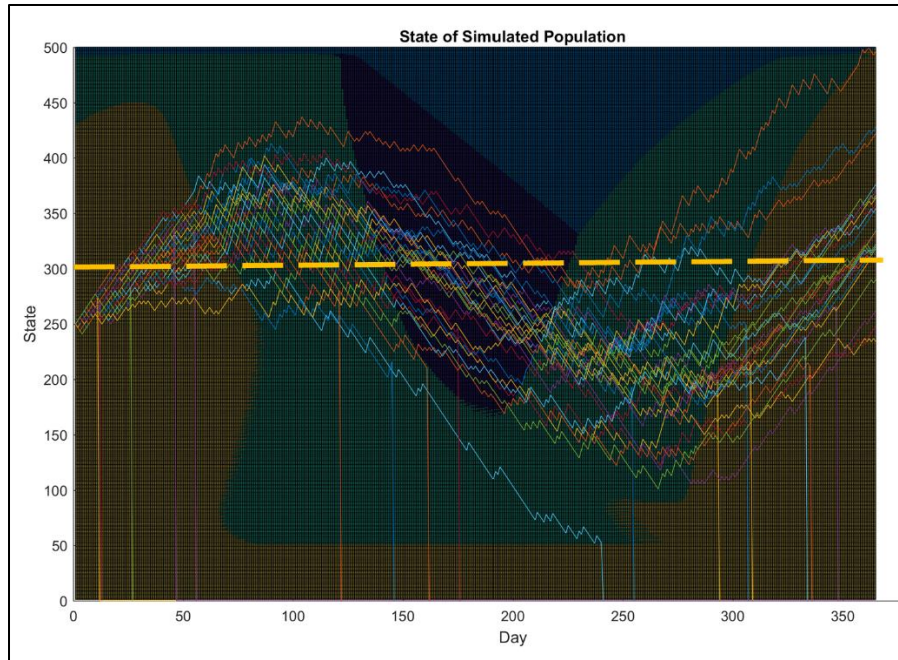


Figure 4.10 Model scenario for multiple spawning krill. Individuals whose state trajectory crosses the spring reproductive threshold (yellow dotted line) spawn and then begin foraging again. Under delayed spring bloom conditions, winter habitat selection conditions would persist leaving less time in spring to increase state to the minimum threshold thereby lowering the chance for multiple spawning.

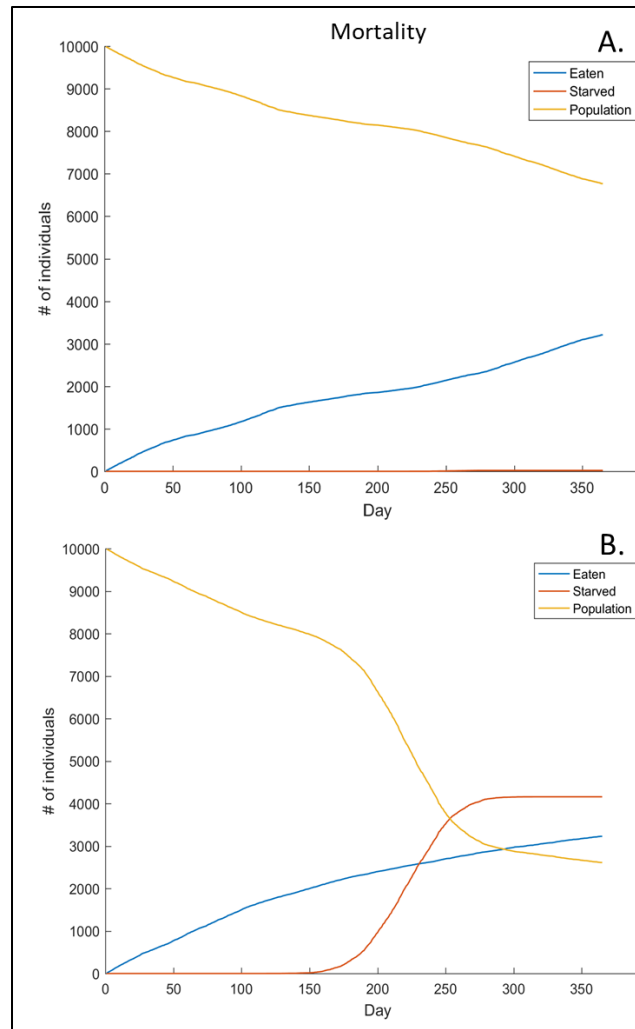


Figure 4.11 The number of animals eaten, starved and remaining in the population when (A) respirations costs are the same between habitats ($\alpha_{all} = 2$), and (B) when respiration costs is increased by 1 in the surface habitat only ($\alpha_{surface} = 3$).

5 CHAPTER 5: CONCLUSION

It is likely that the Antarctic ecosystem was changing before Marr published his seminal work on krill in 1962. The great whales had been nearly exterminated, removing a major group of krill predators (Laws 1977, Willis 2014), and sea ice had precipitously declined (de la Mare 1997). Today, climate change is altering seasonal dynamics (Montes-Hugo et al. 2009) and the great whales are increasing in number (Pallin et al. 2018). This constant change makes it difficult to establish a baseline from which to evaluate species specific responses to climate change. If observations of krill are evaluated against a static point in time or space, then *E. superba* feeding on the bottom and predated at depth in winter is viewed as aberrant behavior instead of natural plasticity in how krill respond to their environment. This also applies to evaluating ecosystem wide responses to climate change where previously understudied species, like *T. macrura*, may play increasingly important roles in the food web. The aim of this work is to understand the range of inter- and intra-specific behavioral adaptations in Antarctic euphausiids in response to environmental variability and their implications on euphausiid life history.

In chapter 2 I showed from observations that the prevailing concept of *T. macrura*'s life history is wrong in two key aspects. First, *T. macrura* can spawn in their first year of life due to a knife-edge maturity at small size relative to *E. superba*. Second, unimodal summer length frequency distributions represent a single cohort in their second summer, which does not appear the following winter or summer. Previous studies assumed that up to three age classes were present in summer

(Haraldsson and Siegel 2014). These results has ecosystem-wide implications because either the most abundant euphausiid in the Antarctic turns over every two years, or some portion of the population is not being sampled. There is some evidence for the latter, and future work should include a habitat selection model, like VertiKrill in chapter 4, to determine the optimal habitat for *T. macrura*. I also showed that larger *T. macrura* predate on euphausiid larvae and, given their high abundance, may impact larval survival of *E. superba*. Chapter 2 illustrates how *T. macrura*'s life history is remarkably different than *E. superba*'s in terms of feeding, reproduction, distribution and growth, and I would expect this species-response to climate change to differ as well.

In chapter 3 I showed, using a model, that *E. superba* switch between specializing and generalizing between seasons, and that the degree of change is regionally dependent. The prevailing theory is that *E. superba* are generalist and optimizing energy return does not drive behavior. I take the view here that known behavior, like vertical migrations, can be viewed in the context of optimal foraging theory. Even if diet composition is similar between seasons, it still reflects a change in foraging effort because *E. superba* are obliged to spend additional time hunting copepods in winter. The change in diet also implies a change in vertical migration as *E. superba* move to predate on copepods, many of whom diapause at depth. I also show that generalizing in winter both increases the rate of energy return and decreases mortality risk.

In chapter 4 I showed, using a model, that *E. superba* inhabiting benthic and mesopelagic depths is not aberrant behavior, but rather an important part of their life history strategy that maximizes future fitness. The prevailing theory on the distribution of *E. superba* is that most of the population is in the upper 200 m. I show that this is only true in summer or when production is high. In winter, benthic and mesopelagic habitats provide important refuges for the fittest individuals. Future models can treat environmental change more explicitly by accounting for metabolic costs associated with increasing SST or changes in productivity patterns. Future models can also explore how climate change may alter the availability of *E. superba* or *T. macrura* to air breathing predators. Extensions of VertiKrill can also provide critical information for management decisions on both the krill fishery and MPA planning.

The Southern Ocean ecosystem will remain in flux as the impacts of climate change, fishing pressure, and new challenges to marine organisms arise. Euphausiids are a key component of Antarctic ecosystem and understanding the range of adaptations in their life history is critical to predicting how the ecosystem will respond to new pressures. Serious gaps remain in our knowledge of the life history of the Antarctic euphausiids that need to be filled. Models based on foundational ecological principals can predict how krill will respond to climate change and help form hypotheses for future research.

6 REFERENCES

- Ainley, D.G., Ballard, G., Jones, R.M., Jongsmojit, D., Pierce, S.D., Smith, W.O. and Voloz, S. (2015) Trophic cascades in the western Ross Sea, Antarctica: revisited. *Mar. Ecol. Prog. Ser.* 534:1-16
- Aitchison, J. (1955) On the distribution of a positive random variable having a discrete probability mass as the origin. *J. Am. Statist. Assoc.* 50: 901-908
- Alonzo S.H. and Mangel, M. (2001) Survival strategies and growth of krill: avoiding predators in space and time. *Mar. Ecol. Prog. Ser.* 209:203-217
- Alonzo S.H, Switzer, P.V. and Mangel, M. (2003) Ecological games in space and time: The distribution and abundance of Antarctic Krill and Penguins. *Ecology* 84(6):1598-1607
- Ambriz-Arreola, I., Gómez-Guitierrez, J., Franco-Gordo, M., Palomares-Garcia, J., Sánchez-Velaco, L., Robinson, C. and Seibel, B. (2017) Vertical pelagic habitat of euphausiid species assemblages in the Gulf of California. *Deep Sea Res. I* 123:75-89
- Amos, A. F. (2001) A decade of oceanographic variability in summertime near Elephant Island, Antarctica. *J. Geophys. Res.* 106:401-423
- Atkinson, A. and Ward, P. (1988) Summer-winter differences in copepod distribution around South Georgia. *Hydrobiologia* 167:325:334
- Atkinson, A., Whitehouse M. J., Priddle, J., Cripps G. C., Ward P., and Brandon M.A. (2001) South Georgia, Antarctica: a productive, cold water, pelagic ecosystem. *Mar. Ecol. Prog. Ser.* 216:279-308
- Atkinson, A., Siegel, V., E. Pakhomov and Rothery, P. (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100-103
- Atkinson, A, Shreeve, R., Hirst, A., Rothery, P., Tarling, G., Pond, D., Korb, R., Murphy, E. and Watkins, J. (2006) Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex, and maturity stage. *Limnol. Oceanogr.* 51:973-987
- Atkinson, A., Siegel, V., Pakhomov, E. A., Jessopp, M.J. and Loeb, V. (2008) A re-appraisal of the total biomass and annual production of Antarctic krill. *Deep-sea Res. I.* 56:727-740

- Bianchi, D., Stock, C., Galbraith, E. and Sarmiento, J. (2013) Diel vertical migration: ecological controls and impacts on the biological pump in a one-Dimensional ocean model. *Global Biogeochem. Cycles* 27:478-491
- Basson, M. (1994) Towards a distribution of M/K of krill (*Euphausia superba*) required for the stochastic krill yield model. CCAMLR WG-Krill-94/11
- Bocher, P., Cherel, Y. and Hobson, K.A. (2000) Complete trophic segregation between South Georgian and common diving petrels during breeding at Iles Kerguelen. *Mar. Ecol. Prog. Ser.* 208:249-264
- Borrione, I. and Schlitzer, R. (2012) Distribution and recurrence of phytoplankton blooms around South Georgia, Southern Ocean. *Biogeosciences Discuss.* 9:10087-10120
- Boyd, C., Heyraud, M. and Boyd, C. N. (1984) Feeding of the Antarctic krill *Euphausia Superba*. *J. Crustac. Biol.* 4:123:141
- Brinton, E. and Townsend, A.W. (1984) Regional relationships between development and growth in larvae of Antarctic krill, *Euphausia superba*, from field samples. *J. Crustacean. Biol.* 4:224-246
- Budge, S.M., Iverson, S.J. and Koopman, H.N. (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. *Mar. Mam. Sci.* 22(4):759-801
- Clarke, A. and Tyler, P. (2008) Adult Antarctic krill feeding at abyssal depths. *Curr. Biol.* 18:282-285
- Cresswell, K., Tarling, G. and Burrows, M. (2007) Behavior affects local-scale distributions of Antarctic Krill around South Georgia. *Mar. Ecol. Prog. Ser.* 343:193-206
- Cohen, J. (1977) *Statistical Power Analysis for the behavioural sciences*. Academic Press. New York.
- Cohen, J. (1992) A Power Primer. *Psychol. Bull.*, 112: 155-159
- Connan, M., Mayzaud, P., Trouvé, C., Barbraud, C. and Cherel, Y. (2008) Interannual dietary changes and demographic consequences in breeding blue petrels from Kerguelen Islands. *Mar. Ecol. Prog. Ser.* 373:123-135

- Conway, D. and Williams, R. (1986) Seasonal population structure, vertical distribution and migration of the chaetognath *Sagitta elegans* in the Celtic Sea. *Mar. Biol.* 93:377-387
- Cuzin-Roudy, J., Irisson, J., Penot, F., Kawaguchi, S. and Vallet, C. (2014) Chapter 6.9 Southern Ocean Euphausiids. In: De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', et al. (eds.). *Biogeographic Atlas of the Southern Ocean*. Scientific Committee on Antarctic Research, Cambridge
- Deagle, B.E., Gales, N.J., Evans, K., Jarman, S.N., Robinson, S., Trebilco, R. and Hindell, M.A. (2007) Studying seabird diet through genetic analysis of feces: a case study on macaroni penguins (*Eudyptes chrysolophus*) *PLoS One* 2:e831.
- de la Mare, W. (1994) Estimating krill recruitment and its variability. *CCAMLR Science*. 1:55-69
- de la Mare, W. (1997) Abrupt mid-twentieth-century decline in Antarctic sea-ice extent from whaling records. *Nature* 389:57-59
- Driscoll, R.M., Reiss, C.S. and Hentschel, B.T. (2015) Temperature-dependent growth of *Thysanoessa macrura*: inter-annual and spatial variability around Elephant Island, Antarctica. *Mar. Ecol. Prog. Ser.* 529:49-61
- Edwards, C.A., Batchelder, H.P. and Powell, T.M. (2000) Modelling microzooplankton and microzooplankton dynamics within a coastal upwelling system. *J. Plankton Res.* 22(9):1619-1648
- Emlen, J. (1966) The role of time and energy in food preference. *The Am. Nat.* 100:611-617
- Falk-Petersen, S., W. Hagen, W. Kattner, G. Clarke, J. and Sargent, J. (2000) Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. *Can. J. Fish. Aquat. Sci.* 57: 178-191
- Farber-Lorda, J. (1994) Length-weight relationships and coefficient of condition of *Euphausia superba* and *Thysanoessa macrura* (Crustacea: Euphausiacea) in southwest Indian Ocean during summer. *Mar. Biol.* 118: 645-650
- Fiala, M., Kopyczynska, E., Jeandel, C., Oriol, L. and Vétion, G. (1998) Seasonal and interannual variability of size-fractionated phytoplankton biomass and community structure at station Kerfix off the Kerguelen Island, Antarctica. *J. Plankton Res.* 7:1341-1356
- Fields, D. and Yen, J. (1997) The escape behavior of marine copepods in response to a quantifiable fluid mechanical disturbance. *J. Plankton. Res.* 19:1289-1304

- Fiksen, O. and Giske, J. (1995) Vertical distribution and population dynamics of copepods by dynamic optimization. *ICES J. Mar.* 52:483-503
- Flores, H., Atkinson, A., Kawaguchi, S., Kraffitt, B. A., Milinievsky, S., Nicol, S., Reiss, C., et al. (2012). Impact of climate change on Antarctic krill. *Mar. Ecol. Prog. Ser.* 458:1-19
- Folch, J., Lees, M. and Sloane-Stanley, G.H. (1957) A simple method for the isolation and purification of total lipids from animal tissues. *J. Biol. Chem.* 226:497-509
- Forcada, J., Trathan, P.N., Reid, K. and Murphy, E.J. (2005) The effects of global climate variability in pup production of Antarctic fur seals. *Ecology* 89:2408-2417.
- Franks, P.J., Wroblewski, J.S. and Flieri, G.R. (1986) Behavior of a simple plankton model with food-level acclimation by herbivores. *Mar. Biol.* 91:121-129
- Froneman, P., Perissinotto, R. and McQuaid, C. (1996) Dynamics of microplankton communities at the ice-edge zone of the Lazarev Sea during a summer drogoue study. *J. Plankton Res.* 18:1455-1470
- Froneman, P., Pakhomov, E., Perissinotto, R., Laubscher, R. and McQuaid, C. (1997) Dynamics of the plankton communities of the Lazarev Sea (Southern Ocean) during seasonal ice melt. *Mar. Ecol. Prog. Ser.* 149:201-214
- Garcia, M., Hoffmeyer, M., Celeste Lopez Ababate, M., Barria de Cao, M., Pettigrosso, R., Almandoz, G., Harnando, M. and Schloss, I. (2016) Micro- and mesozooplankton responses during two contrasting summers in a coastal Antarctic environment. *Polar Biol.* 39:123-137
- Gille, S. T. (2002) Warming of the Southern Ocean since the 1950's *Science* 295:1275-1277
- Gliwicz, M. (1986) Predation and the evolution of vertical migration in zooplankton. *Nature* 320:746-749
- Gutt J., Siegel V. (1994) Benthopelagic aggregations of krill (*Euphausia superba*) on the deeper shelf of the Weddell Sea (Antarctic). *Deep-Sea Res.* 41:169–178
- Hamner, M. (1988) Biomechanics of filter feeding in the Antarctic Krill *Euphausia superba*: Review of past work and new observations. *J. Crustac. Biol.* 8:149:163

- Hagen, W. and Kattner, W. (1998) Lipid metabolism of the Antarctic Euphausiids *Thysanoessa macrura* and its ecological implications. *Limnol. Oceanogr.* 43:1894-1901
- Hagen W, Kattner G and Terbrüggen van Vleet, E. (2001) Lipid metabolism of the Antarctic krill (*Euphausia superba*) and its ecological implications. *Mar. Biol.* 139:95–104
- Haraldsson, M. and Siegel, V. (2014) Seasonal distribution and life history of *Thysanoessa macrura* (Euphausiacea, Crustacea) in high latitude waters of the Lazarev Sea, Antarctica. *Mar. Ecol. Prog. Ser.* 495:105-118
- Hays, G., Richardson, A. and Robinson, C. (2005) Climate change and marine plankton. *Trends Ecol. Evol.* 6:337-344
- Helmuth, B., Kingsolver, J G., and Carrington, E. (2005) Biophysics, physiological ecology, and climate change: does mechanism matter? *Annual Rev. Physiol.* 67:177-201
- Hempel I. and Hempel G. (1986) Field observations on the developmental ascent of larval *Euphausia superba* (Crustacea) *Polar Biol.* 6:121-126
- Hewes, C.D., Reiss C.S. and Holm-Hansen, O. (2009) A quantitative analysis of sources for summertime phytoplankton variability over 18 years in the South Shetland Islands (Antarctica) region. *Deep-sea Res. I.* 56:1230-1241
- Hilborn, R. and Mangel, M. (1997) *The Ecological Detective: Confronting Models with Data.* Princeton University Press, Princeton (NJ)
- Hirche, H. Laudien, J. and Bucholz, F. (2016) Near-bottom zooplankton aggregations in kongsfjorden: implication for pelago-benthic coupling. *Polar Biol.* 39:1897:1912
- Hofmann E. and Lascara C. (2000) Modeling the growth dynamics of Antarctic krill *Euphausia superba*. *Mar. Ecol. Prog. Ser.* 194:219–231
- Holm-Hansen, O., Lorenzen, C. J., Holmes, R. W. and Strickland, J. H. (1965) Fluorometric determination of chlorophyll. *J. Cons. Perm. Int. Explor. Mer.* 30:3-15
- Hopkins, T.L. (1985) Food web of an Antarctic midwater ecosystem. *Mar. Biol.* 89:197-212
- Hopkins, T.L. and Torres, J.J. (1989) Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea. *Deep Sea Res.* 36:543-560

- Hunt, B.P., Pakhomov, E.A., Siegel, V., Strass, V., Ciesewski, B., Bathmann, U. (2011) The seasonal cycle of the Lazarev Sea macrozooplankton community and potential shift to top-down trophic control in winter. *Deep Sea Res. II* 58:1662-1676
- Huntley, M and Boyd, C. (1984) Food-Limited Growth of Marine Zooplankton. *Am. Nat.* 124:455-478
- Jarvis, T., Kelly, N., Kawaguchi, S., Van Wijk, E., Nicol, S. (2010) Acoustic characterization of the broad-scale distribution and abundance of Antarctic krill (*Euphausia superba*) off East Antarctica (30–80_E) in January–March 2006. *Deep-Sea Res. II* 57:916–993
- Ji, R., Edwards, M., Mackas, D., Runge, J. & Thomas, A. (2010) Marine plankton phenology and life history in a changing climate: current research and future directions. *J. Plankton Res.* 32:1355–1368
- Jia, Z., Swadling, K.M., Meiners, K.M., Kawaguchi, S. and Virtue, P. (2016) The zooplankton food web under the East Antarctic pack ice- A stable isotope study. *Deep Sea Res.* 131:189-202
- Kattner, G., Hagen, W., Falk-Petersen, S., Sargent, J.R. and Henderson, R.J. (1996) Antarctic krill *Thysanoessa macrura* fills a major marine lipogenic pathway. *Mar. Ecol. Prog. Ser.* 134:295-298
- Kawaguchi, K., Ishikawa, S. and Matsuda, O. (1986) The overwintering strategy of Antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off the Ongul Islands in Lutzow-Holm Bay, Antarctica. *Mem. Natl. Inst Polar. Res.* 44:67–85
- Kawaguchi, S., Kilpatrick, R., Roberts, L., King, R. and Nico, I. S. (2011) Ocean-bottom krill sex. *J. Plankton. Res.* 33:1134–1138
- Kinzey, D., Watters, G. and Reiss, C.S. (2019) Estimating recruitment variability and productivity in Antarctic krill. *Fish. Res.* 217:98-107
- Kiorboe, T. and Jian, H. (2012) To eat and not be eaten: Optimal foraging behavior in suspension feeding copepods. *J. R. Soc.* 10:20120693
- Lascara, C., Hofmann, E., Ross, R., and Quetin, L. (1999) Seasonal variability in the distribution of Antarctic krill, *Euphausia superba*, west of the Antarctic Peninsula. *Deep-Sea Res.* 46:951–984

- Last, K., Hobbs, L., Berge, J., Brierley, A. and Cottier, F. (2016) Moonlight drives ocean-scale mass vertical migration of zooplankton during the arctic winter. *Curr. Biol.* 26:244-251
- Laws, R. (1977) Seals and whales of the Southern Ocean. *Phil. Trans. R. Soc. Lond.* 279:81-96
- Leising, A., Pierson, J., Cary, S. and Frost, B. (2005) Copepod foraging and predation risk within the surface layer during night-time feeding forays. *J. Plankton Res.* 10:987-1001
- Loeb, V., Chambers, K., Daniels, E., Force, M., Gong, N., Jenkins, A., Reum, J., Rowley R. and Sessions, S. (2004) Net sampling. In Lipsky, J. D. (ed.), *AMLR 2003/2004 Field Season Report*. NOAA-TM-NMFS-SWFSC-367: 53-116
- Loeb, V., Hofmann, E. E., Klinck, J. M., Holm-Hansen, O. and White, W. B. (2008). ENSO and variability of the Antarctic Peninsula pelagic marine ecosystem. *Antarct. Sci.* 21: 135-148.
- Loeb, V., Siegel, V., Holm-Hansen, O., Fraser, W., Trivelpiece, W. and Trivelpiece, S. (1997). Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387: 897-900
- MacArthur, R. and Pianka, E. (1966) On optimal use of a patchy environment. *Am. Nat.* 100:603-609
- Macdonald, P. D. M. and Pitcher, T. J. (1979) Age-groups from size-frequency data- versatile and efficient method of analyzing distribution mixtures. *J. Fish. Res. Board. Can.* 36:987-1001
- Mackey, A.P., Atkinson, A., Hill, S.L., Ward, P., Cunningham, N.J., Johnston, N.M. and Murphy, R.J. (2012) Antarctic microzooplankton of the southwest Atlantic sector and Bellinghousen Sea: Baseline historical distributions (*Discovery Investigations*, 1928-1935) related to temperature and food, with projections for subsequent ocean warming. *Deep Sea Res.* 59-60:130-146
- Madsen, L.M., Gaard, E. and Hansen, B. W. (2008). Wax-ester mobilization by female *Calanus finmarchicus* (Gunnerus) during spring ascendance and advection to the Faroe Shelf. *ICES J. Mar. Sci.* 65: 1112-1121
- Makarov, R.R. (1979). Larval distribution and reproductive ecology of *Thysanoessa macrura* (Crustacea: Euphausiacea) in the Scotia Sea. *Mar. Biol.* 52: 377-386
- Makarov, R.R., and Denys, C.J.I. (1981) Stages of sexual maturity of *Euphausia superba*. *BIOMASS Handbook* ser. 11

- Mangel, M. and Clark, C. (1988) Dynamic modeling in behavioral ecology. Princeton University Press. Princeton. 313 pg.
- Mangel, M. and Nicol, S. (2000). Krill and the unit of biology. *Can. J. Fish. Aquat.* 57:1–5
- Mangel, Marc. (2006) The Theoretical Biologists Toolbox: Quantitative Methods for Ecology and Evolutionary Biology. Cambridge University Press, New York
- Mangel, M. (2015) Stochastic dynamic programming illuminates the link between environment, physiology, and evolution. *Bull. Math. Biol.* 77:857-877
- Marin, V., Brinton, E. and Huntley, M. (1991) Depth relationships of *Euphausia superba* eggs, larvae and adults near the Antarctic Peninsula, 1986–87. *Deep-Sea Res.* 38:1241–1149
- Marr, J.W.S, (1962) The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Reports* 32:33-464
- Marrari, M., Daly, K., Timonin, A. and Semenova, T. (2011) The zooplankton of Marguerite Bay, western Antarctic Peninsula-Part II: Vertical distributions and habitat partitioning. *Deep-Sea Res. II* 58:1614-1629
- Marshall G.J., Orr A., Van Lipzig N.P. and King J.C. (2006) The impact of a changing Southern Hemisphere annular mode on Antarctic Peninsula summer temperatures. *J Clim.* 19:5388-5404
- Mauchline, J. (1980) Measurement of body length of *Euphausia superba*. Dana. *BIOMASS Handbook* ser. 11
- Mayzaud, P., M. Boutoute, et al. (2003). Lipid composition of the euphausiids *Euphausia vallentini* and *Thysanoessa macrura* during the summer in the Southern Indian Ocean. *Antarctic Science* 15:463-475
- McGurk, M.D. (1986) Natural mortality of marine pelagic fish eggs and larvae: the role of spatial patchiness. *Mar. Ecol. Prog. Ser.* 34:227-242
- McLaren, I.A. (1978) Generation lengths of some temperate marine copepods - estimation, prediction, and implications. *J. Fish. Res. Board Can.* 35:1330-1342
- Meredith, M.P. and King, J.C. (2005). Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys. Res. Lett.* 32:L19604.
- Meyer, B. (2012) The overwintering of Antarctic krill, *Euphausia superba*, from an ecophysiological perspective. *Polar Biol.* 35:15-37

- Meyer, B., Freier, U., Grim, V., Groeneveld, J., Hunt, B., et al. (2017) The winter pack-ice zone provides a sheltered but food-poor habitat for larval Antarctic krill. *Nat. Ecol. Evol.* 1(12):1853-1861
- Minagawa, M. and Wada, E. (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim. Cosmochim. Acta.* 48:1135-1140
- Montes-Hugo, M., Doney, S. C., Ducklow, H. W., Fraser, W., Martinson, D., Stammerjohn, S. E. and Schofield, O. (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the Western Antarctic Peninsula. *Science* 323:1470-1473
- Murphy, E., Hofmann, E., Watkins, J., Johnston, N., Pinones, a., Ballerini, T, Hill, S., Trathan, P., Tarling, Cavanagh, R., Young, E., Thorpe, S. and Fretwell, P. (2013) Comparison of the structure and function of Southern Ocean regional ecosystems: The Antarctic Peninsula and South Georgia. *J. Mar. Syst.* 109-110
- Murphy E.J., Cavanagh R.D., Drinkwater K.F., Grant S.M., Heymans J.J., Hofmann E.E., Hunt Jr G.L. and Johnston N.M. (2016) Understanding the structure and functioning of polar pelagic ecosystems to predict the impacts of change. *Proc. R. Soc. B* 283
- Nemoto, T. and Nasu, K. (1958) *Thysanoessa macrura* as a food of baleen whales in the Antarctic. *Sci. Rep. Whales Res. Inst.* 13:193-199
- Nicol, S. (2000) Understanding krill growth and aging: The contribution of experimental studies. *Can. J. Fish. Aquat. Sci.* 57:1687-177
- Niemandt, C., Kovacs, K.M., Lydersen, C., Dyer, B.M., Isaksen, K., Hofmeyr, G.J.G., Mehlum, F. and de Bruyn, P.J.N. (2016) Chinstrap and macaroni penguin diet and demography at Nyrøysa, Bouvetøya. *Antarctic Science*, 28(2):91–100
- Nordhausen, W. (1992) Distribution and growth of larval and adult *Thysanoessa macrura* (Euphausiacea) in the Bransfield Strait Region, Antarctica. *Mar. Ecol. Prog. Ser.* 83:185-196
- Nordhausen, W. (1994) Winter abundance and distribution of *Euphausia superba*, *E. crystallorophias*, and *Thysanoessa macrura* in Gerlache Strait and Crystal Sound, Antarctica. *Mar. Ecol. Prog. Ser.* 109:131-142
- Ohman, M. and Frost, B. (1983) Reverse diel vertical migration: an escape from invertebrate predators. *Science* 220:1404-407

- Orsi, A.H, Whitworth III, T. and Nowlin Jr., W.D. (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Res. I.* 42: 641-673
- Pakhomov, E.A., Froneman, P. W., Wassmann, P., Ratkova, T. and Arashkevich, E. (2002) Contribution of algal sinking and zooplankton grazing to downward flux in the Lazarev Sea (Southern Ocean) during the onset of phytoplankton bloom: a langrangian study. *Mar. Ecol. Prog. Ser.* 233: 73-88
- Pallin, L., Baker S., Steel D., Kellar N., Robbins J, Johnston D., Nowacek D., Read A., Friedlaender A. (2018) High pregnancy rates in humpback whales (*Megaptera novaeangliae*) around the Western Antarctic Peninsula, evidence of a rapidly growing population. *Royal Soc. Open Sci.* 5:180017.
- Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual. Rev. Ecol. Syst.* 37: 637-639
- Phleger et al. (2002) Interannual and between species comparisons of the lipids, fatty acids and sterols of Antarctic krill from the US AMLR Elephant Island survey area. *Comp. Biochem. Physiol. B* 131:733-747
- Pinchuk, A. I. and Hopcroft, R. R. (2007) Seasonal variations in the growth rates of euphausiids (*Thysanoessa inermis*, *T. spinifera*, and *Euphausia pacifica*) from northern Gulf of Alaska. *Mar. Biol.* 151:257-269
- Price, H., Boyd, K. and Boyd, C. (1988) Omnivorous feeding behavior of the Antarctic krill *Euphausia superba*. *Mar. Biol.* 97: 67-77
- Pyke, G. (1984) Optimal foraging theory: a critical review. *Ann. Rev. Ecol. Syst.* 15:523-575
- Quetin, L. B. and Ross, R. M. (1991) Behavioral and physiological characteristics of the Antarctic krill, *Euphausia superba*. *Am. Zool.* 31:49-63
- Quetin, L. B. and Ross, R. M. (2001) Environmental variability and its impact on the reproductive cycle of Antarctic Krill. *Am. Zool.* 41:74-89
- Reiss, C., Cossio, A., Santora, J., Dietrich, K., Murray, A., Mitchell, G., Walsh, J., Weiss, E., Gimpel, C., Jones, C. and Watters, G. (2017) Overwintering habitat selection by Antarctic krill under varying sea-ice conditions: implications for top predators and fishery management. *Mar. Ecol. Prog. Ser.* 568:1-16
- Richerson, K.E. (2015) Antarctic euphausiids in space and time: Behavior, distribution, and growth, with implications for predators. (Doctoral Dissertation). Retrieved from ProQuest Dissertations Publishing 3730014

- Runge, J. (1980) Effects of hunger and season on the feeding behavior of *Calanus pacificus*. *Limnol Oceanogr.* 25:134-145
- Ryabov, A., de Roos, A., Meyer, B., Kawaguchi, S. and Blasius, R. (2017) Competition-induced starvation drives large-scale population cycles in Antarctic krill. *Nat. Ecol. Evol.* 1(7):0177
- Saunders R.A., Collins, M.A., Ward, M., Stowasser, G., Hill, S.L. and Shreeve, R., Tarling, G.A. (2015) Predatory impact of the myctophid fish community on zooplankton in the Scotia Sea (Southern Ocean). *Mar. Ecol. Prog. Ser.* 541:45-64
- Schaafsma, F., Kohlbach, D., David, C., Lange, B., Graeve, M., Flores, H. and van Franeker, J. (2017) Spatio-temporal variability in the winter diet of larval and juvenile Antarctic krill, *Euphausia superba*, in ice-covered waters. *Mar. Ecol. Prog. Ser.* 580:101-115
- Schmidt, K., Atkinson, A., Steigenberger, S., Fielding, S., Lindsay, M., Pond, D.W., Tarling, G.A., Klevjer, T.A., Allen, C.S. and Nicol, S. (2011) Seabed foraging by Antarctic krill: Implications for stock assessment, benthic-pelagic coupling, and the vertical transfer of iron. *Limnol. Oceanogr.* 56:1411-1428
- Schmidt, K., Atkinson, A., Pond, D. and Ireland, L. (2014) Feeding and overwintering of Antarctic krill across its major habitats: The role of sea ice cover, water depth and phytoplankton abundance. *Limnol. Oceanogr.* 59:17-36
- Schmidtko S., Heywood K. J., Thompson A. F. and Aoki S. (2014) Multidecadal warming of Antarctic waters. *Science* 346:1227-1231
- Schoener, T.W. (1971) Theory of feeding strategies. *Annul. Rev. Ecol. Syst.* 2: 369-404
- Siegel, V. S. (1987) Age and growth of Antarctic Euphausiacea (Crustacea) under natural conditions. *Mar. Biol.* 96: 483-495
- Siegel, V., Skibowski, A. and Harm, R. (1992) Community structure of the epipelagic zooplankton community under the sea-ice of the northern Weddell Sea. *Polar Biol.* 12:15-24
- Siegel, V.S. (2000) Krill (Euphausiacea) life history and aspects of population dynamics. *Can. J. Fish. Aquat. Sci.* 57:130-150
- Siegel, V. S., Kawaguchi, P. Ward, F. Litvinov, V. Sushind, V. Loeb, and J. Watkins, (2004). Krill demography and large-scale distribution in the southwest Atlantic during January/February 2000. *Deep-Sea Res. II* 51.

- Siegel, V. and Loeb, V. (1995). Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Mar. Ecol. Prog. Ser.* 123:45-56
- Smetacek V. and Nicol S. (2005) Polar ocean ecosystems in a changing world. *Nature* 437:362-368
- Smith, S. L. (1991). Growth, development and distribution of the euphausiids *Thysanoessa raschi* (M. Sars) and *Thysanoessa inermis* (Kroyer) in the southeastern Bering Sea. *Proc. Pro Mare Symp. On Polar Mar. Eco.* 10: 12-16
- Stammerjohn, S.E., Martinson, D.G., Smith, R.C., Yuan, X. and Rind, D. (2008) Trends in Antarctic annual sea ice retreat and advance and their relation to El Nino-Southern Oscillation and Southern Annular Mode variability. *J. Geophys. Res-Oceans.* 113:C03S90
- Stepien, J. C. (1983). Zooplankton in the Weddell Sea, October-November 1981. *Antarctic J. U.S.* 17:109-111
- Stepnik, R. (1982). All-year population studies of Euphausiacea (Crustacea) in the Admiralty Bay (King George Island, South Shetland Islands Antarctic). *Pol. Polar Res.* 3:49-68
- Taki K., Hayashi T. and Naganobu, M. (2005) Characteristics of seasonal variation in diurnal vertical migration and aggregation of Antarctic krill (*Euphausia superba*) in the Scotia Sea, using japanese fishery data. *CCAMLR Sci.* 12:163–172
- Taki, K., Yabuki, T., Noiri, Y., Hayashi, T. and Naganobu, M. (2008). Horizontal and vertical distribution and demography of euphausiids in the Ross Sea and its adjacent waters in 2004/2005. *Polar Biol.* 31: 1343-1356
- Tarling, G. and Johnson, M. (2006) Satiation gives krill that sinking feeling. *Curr. Biol.* 16:83-84
- Tarling, G., Cuzin-Roudy, J., Thorpe, S., Shreeve, R., Ward P. and Murphy E. (2007) recruitment of Antarctic krill *Euphausia superba* in the South Georgia Region: adult fecundity and the fate of larvae. *Mar. Ecol. Prog. Ser.* 331:161–179
- Turner J., Bindschadler R., Convey P., Di Prisco G. et. al. (2009) Antarctic climate change and the environment, Vol. Scientific Committee on Antarctic Research, Cambridge, UK
- Vaughn D. G., et al. 2003. Recent rapid regional climate warming on the Antarctic Peninsula. *Climatic Change.* 60:243-274.

- Vidal, J. (1980) Physioecology of zooplankton. 1. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus sp.* Mar. Biol. 56:111-134
- Wallis, J. (2018) A description of the post-naupliar development of Southern Ocean krill (*Thysanoessa macrura*). Polar Biol. 41(12):2399-2407
- White, J., Rassweiler, A., Samhuri, J., Stier, A. and White, C. (2014) Ecologists should not use statistical significance tests to interpret simulation model Results. Oikos 123:385–388
- Wiebe, P. H., Ashijan, C. J., Lawson, G. L., Pinones, A. and Copley, N. J. (2011) Horizontal and vertical distribution of euphausiid species on the western Antarctic Peninsula U.S. GLOBEC Southern Ocean study site. Deep-Sea Res. II 58:1630-1651
- Wiedenmann, J., Cresswell K. and M. Mangel, (2008) Temperature-dependent growth of Antarctic Krill: predictions for a changing climate from a cohort model. Mar. Ecol. Prog. Ser. 358:191-202
- Wiedenmann, J., Cresswell, K. and Mangel, M. (2009). Connecting recruitment of Antarctic krill and sea ice. Limnol. and Oceanogr. 54:799-811
- Williams, R. (1985) Trophic relationships between pelagic fish and euphausiids in Antarctic waters. Antarctic nutrient cycles and food webs. Springer, Berlin 452-459
- Willis, J. (2014) Whales maintained a high abundance of krill; both are ecosystem engineers in the Southern Ocean. Mar. Ecol. Prog. Ser. 513:51-69
- Vaughn, D. G., et al. (2003) Recent rapid regional climate warming on the Antarctic Peninsula. Climatic Change 60:243-274