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The Influence of Seasonal and Decadal Trends in Coastal Ocean Processes on
the Population Biology of the krill species *Euphausia pacifica*: Results of a
coupled ecosystem and individual based modeling study

By

Jeffrey G. Dorman

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:
Professor Thomas M. Powell, Chair
Professor Mary E. Power
Professor Mark Stacey

Fall 2011

The Influence of Seasonal and Decadal Trends in Coastal Ocean Processes on
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Abstract

The Influence of Seasonal and Decadal Trends in Coastal Ocean Processes on the Population Biology of the krill species *Euphausia pacifica*: Results of a coupled ecosystem and individual based modeling study

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University of California, Berkeley

Professor Thomas M. Powell, Chair

Krill of the California Current play a crucial role in the transfer of primary production up to many commercially important higher trophic levels. Understanding the short time scale (weeks to seasonal) and long time scale (decadal) variability in abundance, condition, and spatial patterns that results from changes in ocean conditions is critical if we hope to manage the fishery of any higher trophic levels from more than a single species approach. I have coupled a suite of models in an attempt to understand the impacts of changing ocean conditions on this important prey item. The coastal ocean was simulated with a commonly used oceanographic model (Regional Ocean Modeling System) coupled with an ecosystem model (Nutrient, Phytoplankton, Zooplankton, Detritus). The coastal ocean was simulated from Newport, OR to Point Conception, CA over an 18-year period (1991 – 2008). These model results were used to force a 3-dimensional individual based model (IBM) that was parameterized to represent the krill species *Euphausia pacifica*. Biological processes of the IBM (growth, life-stage progression, mortality, reproduction, vertical migration) were compared to laboratory data and field data under varying food and temperature conditions to understand how well the model can reproduced known biological rates and processes. The model performs well at simulating growth, life stage progression, and reproduction, as these are the areas from which there is an abundance of data from which to parameterize the model. Results from simulations of larval and adult populations indicated the greatest amount growth in both larval and adult populations was over the six-month period from April through October. Mortality was greatest for larvae during the winter (when food resources are typically lowest), but mortality was greatest for adults during summer due to offshore transport of individuals to regions of warmer surface waters and reduced food concentration. Condition of individuals and mortality of individuals correlated positively with the more productive phase of the Pacific Decadal Oscillation and the North Pacific Decadal Oscillation, providing evidence the impact of ocean basin scale atmospheric conditions on krill. The impacts of atmospheric forcing on *E. pacifica* are important factors that

control the distribution, abundance and productivity of this important prey item for many commercially important fisheries of the West Coast of the United States.

Table of Contents

<i>List of Tables and Figures</i>	ii
<i>Acknowledgements</i>	vi
Introduction	1
Chapter One: Climate change impacts on the productivity of California’s coastal ocean	
Introduction	3
Impacts of Climate Change	4
Implications for Policy and Management	9
References	12
Chapter Two: Development and analysis of a individual-based model of the krill species <i>Euphausia pacifica</i>, coupled with the Regional Ocean Modeling System (ROMS) oceanographic model	
Introduction	16
Methods	18
Results	23
Discussion	24
References	29
Appendix	34
Chapter Three: Advection and Starvation cause krill (<i>Euphausia pacifica</i>) decreases in 2005 northern California coastal populations: Implications from a model study	
Introduction	40
Methods	41
Results	42
Discussion	43
References	45
Chapter Four: Seasonal and decadal trends in krill (<i>Euphausia pacifica</i>) population biology in the northern California current and implications for higher trophic level predators	
Introduction	54
Methods	56
Results	58
Discussion	61
References	66
Conclusions	97

List of Tables and Figures

Chapter One: Climate change impacts on the productivity of California's coastal ocean

Figure 1.1. 15
Tracing the impacts of increased atmospheric carbon dioxide through the physical and biological ocean.

Chapter Two: Development and analysis of a individual-based model of the krill species *Euphausia pacifica*, coupled with the Regional Ocean Modeling System (ROMS) oceanographic model

Table 2.1. 35
Model critical concentration of phytoplankton at 12° C for various size classes of individuals.

Table 2.2. 35
Thresholds that individual *Euphausia pacifica* must progress beyond to advance to the next life-stage.

Figure 2.1. 36
Development time from egg to metanauplius life-stage and resultant meta-nauplius weight of *Euphausia pacifica* at temperature ranging from 1 to 20° C.

Figure 2.2. 36
Critical concentration of chlorophyll *a* needed for *Euphausia pacifica* to achieve maximum growth rate.

Figure 2.3. 37
Minimum concentration of chlorophyll *a* needed for *Euphausia pacifica* to maintain weight due to metabolism.

Figure 2.4. 37
Modeled developmental time to various life stages at 8° C , 10.5° C , and 12° C.

Figure 2.5. 38
Reproductive weight gained under a full food ration.

Figure 2.6. 38
Brood size and interbrood period under a full food ration.

Figure 2.7. 39
A comparison of particle tracking in ROMS and the IBM POPCYCLE.

Chapter Three: Advection and Starvation cause krill (*Euphausia pacifica*) decreases in 2005 northern California coastal populations: Implications from a model study

Figure 3.1.	49
January, February, and March mean surface currents during 2001 and 2005.	
Figure 3.2.	50
Mean weekly chlorophyll a concentration within 100 km of the coastline during 2001 and 2005.	
Figure 3.3.	51
Individual density within 100 km of the coastline during 2001 and 2005.	
Figure 3.4.	52
Individual distribution and individual weight on 1 February, 1 March, and 1 April during 2001 and 2005.	
Figure 3.5.	53
Starvation location of furcilia IV-VII, juvenile and adult <i>Euphausia pacifica</i> during 2001 and 2005.	

Chapter Four: Seasonal and decadal trends in krill (*Euphausia pacifica*) population biology in the northern California current and implications for higher trophic level predators

Table 4.1.	71
Observed and NCEP/NARR alongshore wind data at eight coastal National Data Buoy Center buoy locations.	
Table 4.2.	71
Observed and NCEP/NARR air temperature data at eight coastal National Data Buoy Center buoy locations.	
Table 4.3.	72
Observed and ROMS model sea surface temperature data at eight coastal National Data Buoy Center buoy locations.	
Table 4.4.	72
Observed and ROMS model sea surface chlorophyll a data at eight coastal National Data Buoy Center buoy locations.	

Figure 4.1.	73
A map showing the extent of the ROMS model domain and the initial seeding location of the ~10,500 individuals that were put into each model run.	
Figure 4.2.	74
A schematic representation of a “suite” of model runs.	
Figure 4.3.	75
Time series and correlation of NCEP-NARR forcing and observed alongshore wind speed at location of NDBC Buoy 46013 (10 km offshore of Bodega Head, California).	
Figure 4.4.	76
Time series and correlation of NCEP-NARR forcing and observed air temperature at NDBC Buoy 46013 (10 km offshore of Bodega Head, California).	
Figure 4.5.	77
Time series of ROMS sea surface temperature and ROMS chlorophyll <i>a</i> concentration compared to observations at location of NDBC Buoy 46013 (10 km offshore of Bodega Head, California).	
Figure 4.6.	78
Larval and adult average population weight at the end of the 180 day model runs.	
Figure 4.7.	79
Larval and adult average weight of the 100 individuals that grew the most over the course of the 180 day model runs.	
Figure 4.8.	80
Larval and adult starvation mortality at the end of the 180 day model runs.	
Figure 4.9.	81
Advection of larval and adult individuals out of the northern boundary of the model domain.	
Figure 4.10.	82
Advection of larval and adult individuals out of the southern boundary of the model domain.	
Figure 4.11.	83
Number of eggs produced by the entire population and from the top 100 individuals that grew the most over the course of the model run from the adult ‘suite’ of runs.	
Figure 4.12.	84
Phase of the PDO and NPGO from 1991 to 2008.	

Figure 4.13.	85
Monthly anomalies of mean population weight of larvae and adults.	
Figure 4.14.	86
Correlation between larval weight anomaly at the end of 180-day model runs and the PDO and the NPGO.	
Figure 4.15.	87
Correlation between adult weight anomaly at the end of 180-day model runs and the PDO and the NPGO.	
Figure 4.16.	88
Monthly anomalies of mean weight of the top 100 larvae and adults that grew the most over the course of the 180-day model run.	
Figure 4.17.	89
Correlation between larval weight anomaly of the 100 individuals that grew the most over the course of the 180-day model runs and the PDO and the NPGO.	
Figure 4.18.	90
Correlation between adult weight anomaly of the 100 individuals that grew the most over the course of the 180-day model runs and the PDO and the NPGO.	
Figure 4.19.	91
Monthly anomalies of the number of larval and adult individuals that starved over the course of the 180-day model run.	
Figure 4.20.	92
Correlation between larval starvation mortality over the course of the 180-day model runs and the PDO and the NPGO.	
Figure 4.21.	93
Correlation between adult starvation mortality over the course of the 180-day model runs and the PDO and the NPGO.	
Figure 4.22.	94
Monthly anomalies of the number of larval and adult individuals advected out of the southern model boundary over the course of the 180-day model run.	
Figure 4.23.	95
Correlation between number of larval and adult individuals advected out of the southern boundary of the model domain and the NPGO.	
Figure 4.24.	96
Correlation between the number of eggs produces over the course of the 180-day model runs and the PDO and the NPGO.	

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Introduction

The most productive regions of the world's oceans are the coastal upwelling zones located off the coast of Peru, California, South Africa, and Spain. Despite occupying less than 1% of the surface of the ocean, these regions account for upwards of 20% of global fisheries. Their importance to humans as a food resource makes our understanding of the ecosystem processes that underlie those fisheries critical and there has been a substantial amount of research on coastal upwelling zones. The link between the underlying physical oceanographic conditions to higher trophic levels was evident from early on in our study of coastal upwelling zones and resulting in the establishment of one of the world's longest run oceanographic projects. The California Cooperative Oceanic Fisheries Investigation (CalCOFI) program began in the 1940's to understand the driving factors behind the drastic reduction in sardine catch in California over the course of that decade. The CalCOFI program showed great foresight by examining both the physical and biological conditions of the California Current ecosystem and laid the groundwork for our understanding of this coastal upwelling region.

Just as initial research forays into our coastal ocean resources were driven by our commercial interests in fishery resources, much of our current research is also focused on maintaining those same resources and managing them in the most effective way possible. California commercial fish landings represent an important revenue and job source for California with over 350 million pounds of commercial marine harvest during 2009, worth over 150 million dollars (<http://www.dfg.ca.gov/marine/landings09.asp>). In the effort to manage our coastal resources using best practices, there has been a concerted effort, mandated by the Sustainable Fisheries Act, to move from a single species management approach to a more ecosystem based approach. This is particularly important to implement in upwelling regions where bottom up forces are so important to overall productivity. Effective implementation of ecosystem based fishery management will need to consider the known variability in atmosphere and ocean dynamics on a seasonal and multi year time scale and the impacts of that variability on key intermediate prey species.

The work that has been conducted as part of this thesis fills a gap in our knowledge about an important prey item in the coastal upwelling region. The variability in the krill species *Euphausia pacifica*, and other large primary consumers, has been observed to lead to collapses in higher trophic levels, yet we know little about what drives interannual variability in krill. These organisms occupy the "middle zone" in terms of their life history and their ability to respond to important upwelling cues. They have longer life spans than short lived phytoplankton and small zooplankton that can quickly respond to favorable conditions, and whose abundance is controlled by temporally recent events. Krill have much shorter life spans than many commercial fishes whose population abundances might be more controlled by annual recruitment that was influenced

by past environmental conditions much more than by current upwelling conditions. Krill are driven by variations in conditions that have occurred in the past, influencing cohort strength, and present conditions that impact growth and abundance. Because they are the primary link between primary production and many higher trophic levels in the California Current, understanding their response to environmental forcing will guide ecosystem-level understanding for managing our fisheries.

The thesis is centered around the impact of climate variability on biological productivity in the California Current. Natural climate variability occurs on many different time scales (daily, seasonal, Interannual, decadal) and we are introducing long-time scale climate variability in the form of anthropogenic climate change. Understanding the sequence of climactic events that can lead to high and low productivity of *Euphausia pacifica* will allow us to better estimate future prey availability for higher trophic levels. Chapter 1 delves into the future of biological productivity under a warming climate. I have pulled together research on the various impacts of increased atmospheric carbon dioxide on primary producers and biological productivity more generally. In some cases the impacts are fairly straightforward and past research gives us a clear indication of how the ecosystem will respond (increased hypoxic events), and in other cases there is still quite a bit of uncertainty (changes in upwelling strength). Chapter 2 outlines the development of an individual based model of the krill species *Euphausia pacifica*. Models such as this will hopefully serve as numerical laboratories in which we will ultimately be able to examine some of the uncertainty regarding climate change and the way it will impact an important prey species of the California Current. Chapter 3 employs the individual based model that has been coupled with physical oceanographic conditions to examine a few critical months of anomalous conditions during the winter and spring of 2005 that impacted higher trophic level productivity and fisheries through the end of the decade. Finally, chapter 4 examines known trends in climate variability, from seasonal to decadal, and their impact on the population biology of *Euphausia pacifica*. Short of understanding the impacts of anthropogenic climate change on this critical species, understanding how they respond to long time scale events, will give us insight into the potential changes we might expect due to anthropogenic climate change.

Chapter One

Climate Change Impacts on the Productivity of California's Coastal Ocean

Introduction

Climate Change and the Ocean. California's history and culture are intertwined with the Pacific Ocean. The ocean was an important food resource to native coastal Californians, a gateway to settlement in the 1800's, and it continues to be an entryway for global goods and services and an important commercial and recreational resource today. The 2011 population of California is greater than 37 million people. With the majority of the population living in counties that border the ocean, there is much pressure being exerted on our ocean ecosystems by coastal development (i.e. land use, water use, water quality) and by heavy use of our coastal resources (both recreational and commercial). These stresses in addition to global climate change due to increased levels of carbon dioxide (CO₂) in the atmosphere will likely have large impacts on our coastal resources.

As almost all of the anthropogenic CO₂ released is emitted into the air, climate change is often thought of as an atmospheric issue. Yet, the ocean plays an equal role to the atmosphere in the global carbon cycle and the planet's temperature regulation, exchanging CO₂ and heat with the atmosphere based on local gradients between the atmosphere and ocean. While the two systems (atmosphere and ocean) are similar in many respects, the relatively slow circulation of the ocean, compared to the atmosphere, and the higher heat capacity (amount of energy required to change the temperature of a substance) of the ocean will cause the effects of increased atmospheric CO₂ to be felt for hundreds to thousands of years after we have stopped emitting anthropogenic CO₂.

Oceanic impacts of climate change will vary regionally around the globe, but there are some general trends that should hold true for most regions. Sea surface temperatures will increase as the atmosphere warms. Ocean chemistry will become more acidic (lower pH) and carbonate will become under saturated in the surface ocean as CO₂ diffuses into the ocean and reacts with water. Increases in sea level are expected as water warms and expands and as land glaciers melt. These processes will affect all aspects of the coastal ocean including the physics (currents, temperature, density), chemistry (salinity, pH), biology (overall productivity, species traits and performances), and coastal geology (sedimentation) of the region. This chapter is focused on the impacts of climate change on the biology of California's immensely productive coastal ocean. There is no discussion of the impacts of rising sea level, changes in freshwater flow from rivers, or changes in sediment loads from rivers as the emphasis is on pelagic ecosystems over the continental shelf and further offshore. These ecosystems are where the majority of primary productivity in California's coastal ocean occurs, which provides a substantial base for a productive food web. Climate driven change to these regions should concern all

who use and rely upon California's coastal ocean as a recreational and commercial resource.

Coastal Upwelling Regions. The California Current System (CCS) is one of four major coastal upwelling regions in the world's oceans. The cold nutrient-rich water that characterizes upwelling regions is a result of global and local wind patterns, making them among the most productive in the world's oceans, contributing to over 20% of the global commercial fish catch. Within California, there are over 100 commercial fisheries that account for annual revenues over 100 million dollars (Pacific Fisheries Information Network - Report #308) and large numbers of coastal jobs. As such, it is of great interest to understand how climate change will impact these important coastal resources.

In most of the world's oceans, primary productivity in surface waters is limited by a lack of nutrients required for photosynthesis and plant growth. Upwelling regions, including the California coastal pelagic ecosystem, support large amounts of biomass (i.e. are more productive) due to the upwelling of cold nutrient-rich water from depth. The upwelling process is driven by winds that force surface water offshore, resulting in nutrient-rich water being drawn up from depth to replace it. The upwelled nutrients are quickly used by small plant species (phytoplankton), which create "blooms" of phytoplankton in surface waters. The phytoplankton are fed on by small zooplankton (copepods, euphausiids) and small fish (anchovy and herring), which are in turn fed upon by many commercially important species (hake, salmon, rockfish, sablefish, squid). Without the wind-driven upwelling of nutrients, the base of the food chain (phytoplankton) would not be nearly as abundant and productive and the resulting higher trophic level productivity would be greatly reduced. The nutrient driven phytoplankton blooms and the small number of trophic steps from plant to commercially important predator species are the primary reasons that the CCS is one of the most productive regions for commercial fisheries in the world.

As atmospheric forcing is an important driver of the productivity of upwelling systems (winds bringing nutrient-rich water to the surface), any changes in atmospheric conditions due climate change will affect biological productivity of coastal regions. Regional modeling studies on the CCS indicate that changes in atmospheric conditions are likely (Snyder et al. 2003) and as the following sections illustrate, these changes will affect physical attributes of the water (density structure, currents), individual organism physiology (metabolic rates and larval duration), species populations (larval dispersal, size structure, range shifts) and entire communities (changes in predator prey dynamics). Understanding how specific organisms and the entire ecosystem will respond to these changes will be critical to managing California's coastal resources in a changing climate.

Impacts of Climate Change

Changes in Coastal Wind Patterns. Coastal wind patterns are important forcing agents in the CCS. Summertime warming of the continental land mass creates a low-pressure system over the land, while a high-pressure system generally sits over the cooler ocean. This sets up alongshore wind patterns

(from the north), which results in upwelling along the California coast. Increased surface heating due to climate change is expected to have a greater impact on the land than on the ocean, resulting in a greater atmospheric pressure differential and stronger upwelling favorable wind patterns. Wind data shows that upwelling favorable wind strength has been increasing along the coast of California (Bakun 1990) and regional modeling studies suggest that we can expect wind strength to continue to increase, along with a shift of the annual timing of peak wind strength, as atmospheric CO₂ increases (Snyder et al. 2003). As the dominant biological patterns of the CCS are a result of wind driven coastal upwelling, changes to wind patterns could have great impacts on overall ecosystem productivity.

Increases in Upwelling Strength. Increases in upwelling favorable winds will result in increased upwelling of nutrient rich water providing greater resources for phytoplankton growth. However, increased upwelling will also cause increases in alongshore and offshore surface currents, which remove small organisms (phytoplankton and zooplankton) from over the continental shelf. Depending on the strength of the currents this can result in greater advective losses of productivity than result from the increase in nutrients. Modeling studies of nutrient-phytoplankton-zooplankton (NPZ) dynamics in a coastal upwelling region have suggested that productivity over the continental shelf increases with wind strength up to some threshold, and then decreases beyond that threshold due to advective losses of primary productivity (Botsford et al. 2003). Other factors such as ocean bathymetry and coastline topography can also influence the offshore vs. retentive nature of surface currents leaving the net impacts of increased wind strength on shelf productivity unclear.

Stronger wind-driven upwelling conditions may also increase the frequency of hypoxia in California's coastal ocean. Hypoxic conditions occur normally within the CCS in the oxygen minimum zone (OMZ) due to oxygen consumption by bacterial breakdown of sinking organic matter from the productive shelf region. The OMZ is typically located offshore of the continental shelf at depths of 200 to 1000 meters and is defined by water with oxygen levels below 0.5 ml l⁻¹. There is spatial variability in the depth and thickness of the OMZ with latitude (Helly & Levin, 2004) and temporal variability has been associated with changing atmospheric conditions such as El Nino events.

Incidents of hypoxia at locations inshore and shallower than the normal OMZ have become increasingly common off the Oregon coast since 2000 (Grantham 2004, Chan 2008) and a shoaling of the hypoxic boundary (by up to 90 meters) has been observed over the time period 1984-2006 off Southern California (Bograd et al. 2008). During exceptionally strong upwelling, onshore currents at depth draw the oxygen-depleted water of the OMZ further up onto the shelf than normal. Potentially compounding the lack of oxygen are resultant phytoplankton blooms from the stronger upwelling. If zooplankton species (i.e. primary consumers) are not present in sufficient numbers to graze down the bloom, much of the resultant phytoplankton will sink and be decomposed by bacteria, further depleting bottom waters of oxygen. Hypoxic conditions in 2002 on the Oregon continental shelf resulted in high mortality of commercially fished

crab species and other benthic dwellers, and extensive habitat change of pelagic fish (Grantham et al. 2004). In the strong upwelling regions off Africa's west coast, hypoxic conditions are common and it has been suggested that native clupeid fish (herring, sardine) are helpful in decreasing the "overabundance" of phytoplankton during intense upwelling (Bakun & Weeks 2004). These fish are highly mobile (not affected by strong currents) and efficient grazers, which keep the phytoplankton in the marine food chain, reducing oxygen depleting bacterial decomposition of sinking phytoplankton.

It is expected that climate driven increases in wind strength will intensify the frequency and magnitude of hypoxic and anoxic events over the continental shelf. As hypoxic events can have dramatic impacts on pelagic and benthic fisheries, increases in low oxygen conditions highlight the importance of managing fisheries from an ecosystem perspective. The potential for a native commercial fish (clupeids) to decrease the intensity or frequency of these events is even further argument for an integrated ecosystem approach to managing these regions.

Changes in the timing of upwelling. Changes in ecosystem primary productivity resulting from increased upwelling strength will likely be an important bottom-up control on overall abundance of higher trophic levels. Primary consumers (copepods, krill, small fish) and higher trophic levels have evolved life history strategies that take advantage of the prevailing patterns of primary productivity (i.e. timing of peaks). There is always some variability in those patterns from year to year and Cushing (1974, 1990) has shown how variability in the timing of peak prey productivity can impact higher trophic level biomass in the North Atlantic. Thus, the amount of "match-mismatch" between trophic levels is an important source of variability in the transfer of energy to higher trophic levels. With increasing atmospheric CO₂, regional climate models predict that peak periods of coastal upwelling off California may be delayed by up to a few months, due to climate change (Snyder et al. 2003). A permanent delay in the peak periods of upwelling of this magnitude has the potential to interrupt the dominant trophic pathways (i.e. creating a permanent mismatch among current trophic pathways). These changes may result in unconsumed primary productivity (which can impact hypoxia, see above), reduce the energy transfer to higher trophic levels, and redistribute the dominant species in the ecosystem food web. In the CCS in 2005, anomalous atmospheric conditions delayed the onset of spring upwelling by over a month and the impacts were observed throughout all levels of the food web (see "Warm Ocean Conditions in the California Current in Spring/Summer 2005: Causes and Consequences", Special Issue of *Geophysical Research Letters*, Vol 33, No. 22, 2006). At the highest trophic level, the Farallon Island breeding population of Cassin's Auklets experienced total reproductive failure in spring 2005, likely because of a mismatch with common prey resources (Sydeman et al. 2006). These poor ocean conditions also contributed to historically low salmon returns on the Sacramento River in 2007 and 2008 (Lindley et al. 2009) resulting in the closure of the commercial salmon fishery for multiple years. Anomalous years, such as 2005, offer insight into potential future conditions of the CCS under a warmer climate if the onset of

upwelling conditions shifts to later in the year as regional atmospheric models predict.

Increased Sea Surface Temperature. One of the most direct impacts of a warmer atmosphere will be a warmer ocean due to the transfer of heat at the air-sea interface. Trends of increased sea surface temperatures up to 1° C have been observed in the CCS over the past 50 years (McGowan et al. 1998, Bograd & Lynn 2003). The observed temperature increase corresponds with the warm phase of the Pacific Decadal Oscillation (PDO, warm phase from 1978-1999), but is also likely due to warmer atmospheric temperatures from climate change over these same years. This period of warmer coastal ocean conditions can provide insight into the impacts of a warmer sea surface temperature on the biological productivity of the CCS.

Increasing stratification of water column. Water temperature is the primary factor in determining seawater density and the density structure of the water column play's an important role in ecosystem productivity. When a vertical column of water is one constant density from top to bottom, there are no barriers to vertical mixing and nutrients (and anything else in the water) can freely mix up or down in the water column. The amount of energy required to mix the water depends on the strength of the temperature driven density gradient (the thermocline). The thermocline acts as a physical barrier to mixing between deep and surface waters. Warming of the oceans surface waters due to climate change creates a greater barrier to upwelling of nutrients via a stronger thermocline. This can ultimately result in reduced primary productivity at the base of the food web. Increases in coastal stratification have been observed in the CCS since the 1950's, corresponding to a period of reduction in zooplankton biomass by 80% (Roemmich & McGowan 1995, Palacios et al. 2004).

Range shifts in organisms. Warming surface temperatures will also likely impact distributions of species. Those organisms that can move freely in the ocean will likely move to regions of the ocean where the physical conditions are within their desired tolerances. Those that can not move freely will likely experience reduced productivity under more stressful environmental conditions, and invasive sub-tropical and tropical species who may be able to tolerate warmer temperatures will likely increase in numbers (Stachowicz et al. 2002). During previous El Niño events off California, pelagic tropical species were observed well north of their normal ranges and suites of zooplankton species switched from a cold-water northern group to a warmer-water sub-tropical group off of Oregon (Peterson et al. 2002). Movements of organisms will change trophic interactions and energy pathways by interrupting traditional predator-prey relationships and introducing new competitive interactions. These types of temperature driven changes in species abundance, especially to key species in the food web, have been observed to cause total restructuring of food webs and energy pathways (Sanford 1999). The end results to changes in food web dynamics are difficult to anticipate as the changes are based on how each individual organism (among potentially hundreds of organisms) will respond to warming temperatures and how those changes will impact others.

Changes in organism physiology. The effect of temperature change on metabolic rates will also impact marine organisms of the CCS. Temperature controls the rates at which enzymatic activity occurs (warmer temperatures result in faster enzyme activity) at the cellular level and thus impacts the whole organism metabolic rate. A warmer ocean environment will result in higher organism respiration rates and metabolic demands, leaving less consumed energy available for growth and a resulting smaller overall body size (Gillooly et al. 2001). Development rates (from larvae to adult) are also sped up under warmer temperatures and many laboratory studies have shown more rapid larval development of marine species under warmer conditions (Gillooly et al. 2002). Recent work (O'Connor et al. 2007) has highlighted the commonality of decreased body size and increased developmental times under warmer temperatures among marine species from many different phyla. In the marine environment where many organisms rely on a planktonic larval stage to disperse larvae over large distances, more rapid larval development will result in reduced dispersal distances. From the general model described by O'Connor based on a suite of marine species, larval dispersal distances could decrease on average by 45% in response to a 4° C temperature increase (Duarte 2007). Dispersal of marine populations rely on other factors aside from temperature and to be accurately gauged need to be determined on a species by species basis, but a general reduction in marine larval dispersal could result in changing patterns of species abundance, species diversity, genetic diversity, and more isolated populations. These sorts of changes could have policy implications on placement of marine protected areas (MPA) and the potential for the MPA network to adapt and change as the climate warms.

Ocean Acidification. Ocean acidification due to rising atmospheric CO₂ is occurring worldwide and oceanic pH has already decreased by 0.1 in the surface ocean relative to pre-industrial levels (Caldeira & Wickett 2003). pH is expected to drop by another 0.3-0.5 units in the next 50 to 100 years with the Southern Ocean experiencing the greatest change (Caldeira & Wickett 2003). Acidification occurs due to the chemical reaction between CO₂ and water (H₂O), which results in bicarbonate (HCO₃⁻¹) and a hydrogen ion (H⁺). The released hydrogen ion decreases ocean pH, thus making the ocean more acidic.

Undersaturation of calcium carbonate. The expected biological impact of ocean acidification will be on those organisms that incorporate calcium carbonate (CaCO₃) into their external body structures. CaCO₃ is normally in abundance (supersaturated) in the upper ocean and thus readily available to those organisms which need it for growth (most notably mollusks, arthropods, echinoderms). Increased hydrogen ions in the ocean bond with free carbonate ions (CO₃⁻²), reducing the number of carbonate ions available to form CaCO₃. As pH decreases, calcium carbonate will become undersaturated in the ocean, making biological secretion of CaCO₃ structures more difficult and potentially causing dissolution of existing CaCO₃ structures. Experimental work exposing pteropod shells to water undersaturated in calcium carbonate resulted in corrosion of the shell surface in only 48 hours (Orr et al. 2005).

Recreational and commercially important species in California waters that could be directly impacted by ocean acidification include oysters, urchins, mussels, crab, and abalone. Research on urchins (Miles et al. 2007) and shellfish (Gazeau et al. 2007) highlight the detrimental impacts increased CO₂ can have on these types of organisms. Effects on higher trophic levels could result from impacts to the many species that function as part of the ecosystem food web. Experimental work on copepods, an important primary consumer, showed no impacts on adult growth, but hatching success was reduced below 5% (Mayor et al. 2007). Coccolithophores, a plentiful and important calcareous primary producer, showed little change to the presence of increased CO₂ (Cubillos et al. 2007, Langer et al. 2006), while the cyanobacteria *Trichodesmium* exhibited increased growth and nitrogen fixation (Levitan et al. 2007). While laboratory studies using manipulated pH conditions (and in some studies, extreme pH levels) do not always translate to larger more complex ecosystems, the results of these studies are able to give us a rough understanding of the potential impacts of ocean acidification.

Implications for Policy and Management

This chapter has outlined the ways that global climate change is expected to impact California's coastal pelagic ocean. While there is uncertainty in the expected biological impacts, California's coastal ocean has already begun to respond to climate change, experiencing warmer surface waters, greater upwelling favorable winds, and increasing ocean acidification. Resource managers and marine policy makers can not wait for a greater understanding of the overall impacts to act, but need to begin to explore mitigation and adaptation strategies now. Acting now to manage coastal resources for climate change will require a more rapid implementation of "ecosystem based fishery management (EBFM) principals, an emphasis to increase the amount of research on the impacts of climate change on coastal resources, and the flexibility to incorporate new findings into our management strategies.

Traditionally, fisheries management in the United States has been practiced using methods that ignore ecosystem variability, such as single species modeling, and focus on species-scale variability. These techniques are valuable, but are insufficient by themselves in light of the potential ecosystem wide changes that will result from climate change. Ecosystem-scale assessments must also be incorporated into fisheries management to make sense of system variability and the large-scale impacts of climate change. The framework for EBFM was laid out by the Ecosystem Principles Advisory Panel (1999) in response to the Sustainable Fisheries Act (SFA) of 1996, which calls for fisheries to be managed while taking the biological complexities and the overall health of the ecosystem into account. EBFM is a move away from single-species fisheries models to a more holistic view of the ecosystem that may incorporate prey species population dynamics, habitat conditions, and environmental variation into account. Where data on these parameters is not available or uncertain (i.e. climate change), the SFA urges error on the side of caution. Implementing of

EBFM is an ongoing process in California and will be essential to managing fisheries in response to climate change¹.

The primary hindrance to effective implementation of EBFM is the uncertainty regarding the basic ecosystem changes that are expected (Figure 1.1).

Research to clarify the impacts of climate change on biological productivity of the coastal ocean is needed in the following areas:

a. Ocean Ecosystem Response: Significant work has been accomplished towards understanding the impacts of climate change on the global atmosphere using large-scale climate models. As California's coastal ocean is primarily atmospheric driven, emphasis is also needed in applying these warmer atmospheric conditions to California's upwelling system. Ocean models forced by an atmosphere containing increased CO₂ concentrations will enable a better understanding of the oceanographic conditions necessary (currents, nutrients, temperature, pH, oxygen) to predict lower trophic level biological responses (phytoplankton and zooplankton productivity) using knowledge of ecosystems and individual species. It should be noted that many of these models do not take pH or temperature into consideration, but they can provide a first approximation of the impacts of climate change on primary producers and consumers.

b. Species Specific Response: There are many commercially important species in California's coastal ocean and each species will have a unique biological response to climate change. For example, species that have calcareous exoskeletons or shells may be more susceptible to changing ocean pH levels (increased mortality), while pelagic fish may be impacted by increasing temperature (range shifts, changes in physiology). Research on the dominant species responses (physiology, range and phenology shifts, population biology, etc.) to changing ocean conditions needs to be a priority if we are to effectively manage these populations and the pelagic ecosystem with climate change considerations

c. Food Web Response: Perhaps the biggest void in our understanding of how climate change may impact coastal ecosystems, relates to how food web dynamics will change in response to a warmer climate and more acidic ocean. A greater understanding of changing species interactions (competition and predator-prey dynamics) based on changing abundances and spatial ranges are critical to understanding the flow of trophic energy to the highest levels. Putting together the species-specific research on the major components of the coastal food web will be an important step in understanding the impacts of climate change on California's coastal ocean.

Finally, managers of marine resources will need to maintain flexibility in management plans to incorporate new understandings of the impacts of climate change on the coastal ocean. Marine protected areas (MPA's) may not serve their designed purpose under a warmer ocean (decreased larval dispersal distances) or if located in regions of increased hypoxia. Fishery seasons may need to be adjusted later or earlier as shifts in the timing of

¹ A thorough accounting of the legal history, impediments to, and successful implementation of ecosystem-based fisheries management was written by Field (2006).

reproduction or migration occur. Adaptive management of these resources will be crucial to maintaining sustainable fisheries as atmospheric CO₂ increases.

References

- Bakun A (1990) Global climate change and intensification of coastal ocean upwelling. *Science* 247: 198-201
- Bakun A, Weeks SJ (2004) Greenhouse gas buildup, sardines, submarine eruptions and the possibility of abrupt degradation of intense marine upwelling ecosystems. *Ecology Letters* 7: 1015-1023
- Bograd SJ, Lynn RJ (2003) Long-term variability in the southern California current system. *Deep-Sea Research II* 50: 2355-2370
- Bograd SJ, Castro CG, DiLorenzo E, Palacios DM, Bailey H, Gilly W, Chavez FP (2008) Oxygen declines and the shoaling of the hypoxic boundary in the California current. *Geophys Res Lett* 35: L12607, doi:10.1029/2008GL034185
- Botsford, LW, Lawrence CA, Dever EP, Hastings A, Largier J (2003) Wind strength and biological productivity in upwelling systems: an idealized study. *Fish Oceanogr* 12: 1-15
- Caldeira K, Wickett ME (2003) Anthropogenic carbon and ocean pH. *Nature* 425: 365
- Chan F, Barth JA, Lubchenco J, Kirincich A, Weeks H, Peterson WT, Menge BA (2008) Emergence of anoxia in the California current large marine ecosystem. *Science* 319: 920
- Cubillos JC, Wright SW, Nash G, de Salas MF, Griffiths B, Tilbrook B, Poisson A, Hallegraeff GM (2007) Calcification morphotypes of the coccolithophorid *Emiliania huxleyi* in the Southern Ocean: changes in 2001 to 2006 compared to historical data. *Mar Ecol Prog Ser* 348: 47-54
- Cushing DH (1974) A link between science and management in fisheries. *Fish Bull* 72(4): 859-864
- Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match-mismatch hypothesis. *Advances in Marine Biology* 26: 249-293
- Duarte CM (2007) Marine ecology warms up to theory. *Trends Ecol Evol* 22(7): 331-333
- Field JC, Francis RC (2006) Considering ecosystem-based fisheries management in the California current. *Mar Pol* 30: 552-569

Gazeau F, Quiblier C, Jansen JM, Gattuso JP, Middelburg JJ, Heip CHR (2007) Impact of elevated CO₂ on shellfish calcification. *Geophys Res Lett* 34, L07603, doi:10.1029/2006GL028554

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science* 293: 2248-2251

Gillooly JF, Charnov EL, West GB, Savage VM, Brown JH (2002) Effects of size and temperature on developmental time. *Nature* 417: 70-73

Grantham BA, Chan F, Nielsen KJ, Fox DS, Barth JA, Huyer A, Lubchenco J, Menge BA (2004) Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* 429: 749-754

Helly JJ, Levin LA (2004) Global distribution of naturally occurring marine hypoxia on continental margins. *Deep-Sea Research I* 51: 1159-1168

Langer G, Geisen M, Baumann KH, Klas J, Riebessel U, Thoms S, Young JR (2006) Species-specific responses of calcifying algae to changing seawater carbonate chemistry. *Geochemistry Geophysics Geosystems*, vol 7, art no Q09006, doi:10.1029/2005 GC001227

Levitan O, Rosenberg G, Setlik I, Setlikova E, Grigel J, Klepetar J, Prasil O, Berman-Frank I (2007) Elevated CO₂ enhances nitrogen fixation and growth in the marine cyanobacterium *Trichodesmium*. *Global Change Biology* 13: 531-538

Lindley ST, Grimes CB, Mohr MS, Peterson W, Stein J, Anderson JT, Botsford LW, Bottom DL, Busack CA, Collier TK, Ferguson J, Garza JC, Grover AM, Hankin DG, Kope RG, Lawson PW, Low A, MacFarlane RB, Moore K, Palmer-Zwahlen M, Schwing FB, Smith J, Tracy C, Webb R, Wells BK, Williams TH (2009). What caused the Sacramento River fall Chinook stock collapse? Report to the Pacific Fishery Management Council

Mayor DJ, Matthews C, Cook K, Zuur AF (2007) CO₂-induced acidification affects hatching success of *Calanus finmarchicus*. *Mar Ecol Prog Ser* 350: 91-97

McGowan JA, Cayan DR, Dorman LM (1998) Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* 281: 210-217

Miles H, Widdicombe S, Spicer JI, Hall-Spencer J (2007) Effects of anthropogenic seawater acidification on acid-base balance in the sea urchin *Psammechinus miliaris*. *Mar Pollution Bulletin* 54: 89-96

O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for

marine ecology, evolution, and conservation. Proc Natl Acad Science 104(4): 1266-1271

Orr JC et al. (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 439: 681-686

Palacios DM, Bograd SJ, Mendelssohn R, Schwing FB (2004) Long-term and seasonal trends in stratification in the California Current, 1950-1993. J Geophys Res 109, C10016, doi:10.1029/2004JC002380

Peterson WT, Keister JE, Feinberg LR (2002) The effects of the 1997-99 El Niño/La Niña events on hydrography and zooplankton off the central Oregon coast. Prog Ocean 54: 381-398

Roemmich D, McGowan J (1995) Climatic warming and the decline of zooplankton in the California current. Science 267: 1324-1326

Sanford E (1999) Regulation of keystone predation by small changes in ocean temperature. Science 283: 2095-2097

Snyder MA, Sloan LC, Diffenbaugh NS, Bell JL (2003) Future climate change and upwelling in the California Current. Geophys Res Lett 30(15), 1823, doi:10.1029/2003GL017647

Stachowicz JJ, Terwin JR, Whitlatch RB, Osman RW (2002) Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. Proc Natl Acad Sci 99(24): 15497-15500

Sydeman, WJ, Bradley RW, Warzybok P, Abraham CL, Jahncke J, Hyrenbach KD, Kousky V, Hipfner JM, Ohman MD (2006) Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking? Geophys Res Lett 33: L22S09, doi:10.1029/2006GL026736

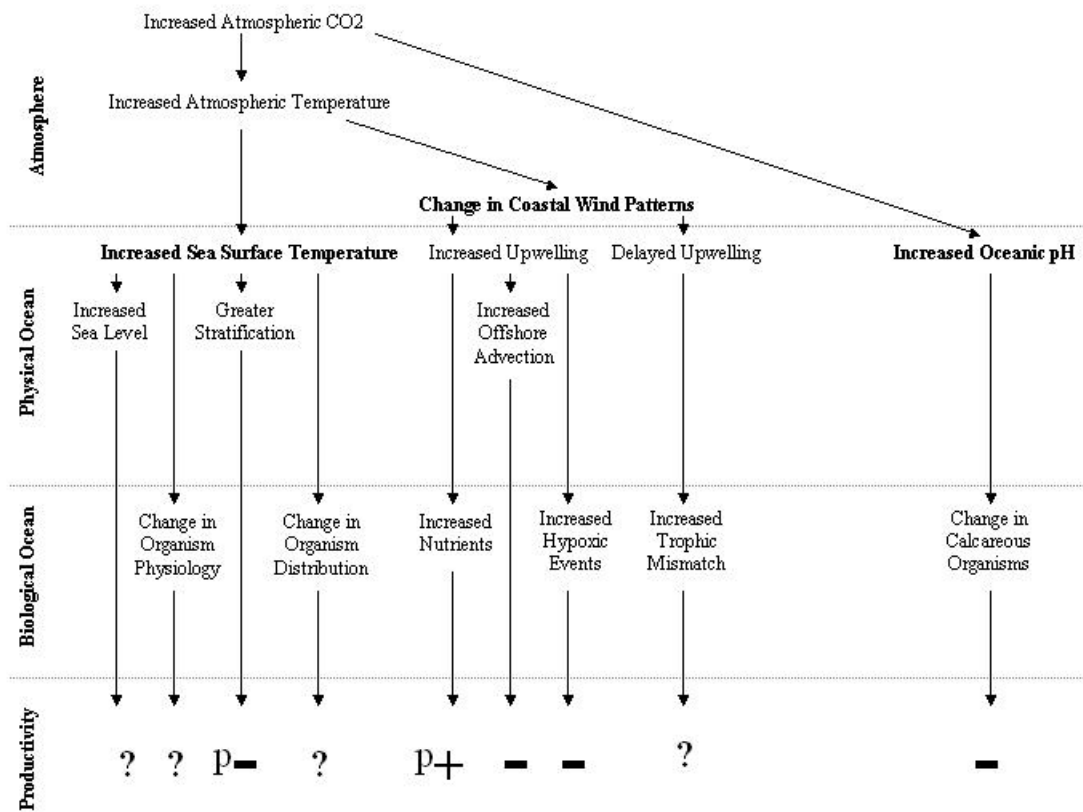


Figure 1.1: Tracing the impacts of increased atmospheric carbon dioxide through the physical and biological ocean. Symbols indicate general trends in shelf productivity and are not meant to represent all species. Those symbols with a 'p' in front of them indicate the response of primary productivity. A (+) indicates an increase, (-) indicates a decrease, and (?) indicates unknown or conflicting changes in productivity.

Chapter 2

Development and analysis of a individual-based model of the krill species *Euphausia pacifica*, coupled with the Regional Ocean Modeling System (ROMS) oceanographic model

Introduction

The use of models to represent plankton populations in the ocean has been an ongoing effort of more than 60 years. The earliest plankton models examined phytoplankton and zooplankton populations using single equations that were driven by external parameters (e.g. nutrients, light, food sources, etc.) with no feedback upon those parameters from the model itself (Riley 1946, 1947a, 1947b). These single equation models were not formulated to represent a specific species of plankton, but were parameterized (nutrient uptake, assimilation, respiration, mortality) to represent the dominant phytoplankton and zooplankton functional groups of the region. Even with such limitations, these models were able to accurately represent observed annual patterns in phytoplankton and zooplankton and recreate the dominant features of the coastal plankton populations (spring bloom and zooplankton response).

As information on processes that control single functional groups became more understood, efforts were made to incorporate multiple functional groups into a unifying set of differential equations representing the major components of an ecosystem. Early plankton ecosystem models typically consisted of three compartments: nutrients, phytoplankton, and herbivorous zooplankton (NPZ) (Steele 1974, Steele & Henderson 1981, Franks et al. 1986). These models explored the abundance of each function group and the energy flow between functional groups and have proven to be effective at capturing a good portion of the variability in lower trophic level ecosystem dynamics. The simplicity in these models does limit the “realistic” nature of results produced, but allows exploration of various parameterizations (respiration, transfer efficiency, grazing, nutrient uptake, mortality) on the system as a whole.

In a quest to explain and model more of the variability in these ecosystems and to incorporate a better understanding of microbial processes, subsequent models split the N, P, and Z compartments into multiple groups and a detritus term (D) was incorporated into many models (Steele & Frost 1977, Pace et al. 1984, Moloney et al. 1986, Fasham et al. 1990). One such successful model that has diversified the traditional compartments of an NPZ model is the NEMURO model (North Pacific Ecosystem Model for Understanding Regional Oceanography) (Kishi et al. 2007). Nutrients modeled in NEMURO include nitrate (NO_3), silicic acid ($\text{Si}(\text{OH})_4$), and ammonium (NH_4). Phytoplankton groups were broken up into size classes that represented small (dinoflagellates) and large (diatoms) organisms. Zooplankton were divided into small and large herbivores, with an additional predatory zooplankton compartment. Three detrital compartments were also included: dissolved organic nitrogen, particulate organic nitrogen, and particulate silica (opal). The resulting model contains eleven

compartments with over 50 defined parameters that determine the fluxes from compartment to compartment. These models of increasing complexity are often able to better represent a specific ecosystem, when compared to a simpler NPZD model, and can clarify and explain the role of important ecosystem processes that were not explored in simpler versions of the model. However, as model complexity increases the specificity of parameters and functional groups, results tend to be more specific to regional ecosystems and are less transferable to other ecosystems. All of these compartmentalized models are also operating on the population or community scale and fail to incorporate any variability that operates on the organism or individual level.

Over the past two decades there has been a growing interest in the use of individual-based models (IBM) to explore population variability in plankton. The use of an IBM to simulate an organism's population biology allows parameters for bioenergetics (ingestion, respiration, assimilation) to vary with attributes of the individual (e.g. size, age, sex), and allows a more accurate representation of discrete events such as reproduction or mortality. If the IBM is incorporated into a 3-dimensional domain, organism movements and behaviors can be included, along with known variability in those behaviors. Early uses of IBM's in plankton populations investigated copepod abundances and stage structure through time without including any spatial component (Batchelder & Miller 1989, Batchelder & Williams 1995). As circulation fields and spatially explicit physical conditions were incorporated into plankton IBM's, these models began exploring how individual variability might influence population distribution (Miller et al. 1998, Batchelder et al. 2002), larval settlement and dispersal (Davidson & DeYoung 1995, Heath et al. 1998), and patchiness (Leising 2001). The choice to use an IBM instead of a compartmentalized ecosystem model provides greater clarity at the population level, with less emphasis on the plankton community as a whole. However, if the species being modeled is of critical importance within the community structure or the ecosystem (e.g. important predator or prey, ecosystem engineer), modeling a single species with an IBM may still provide critical information for the greater ecosystem.

Krill are considered to be a key trophic link in the transfer of energy from primary production to commercially important predators such as hake and salmon in the California Current (Field et al. 2006). The krill species *Euphausia pacifica* is the one of the most commonly found types of krill in the California Current and represents a large amount of the primary consumer biomass of the region. *E. pacifica* are abundant year round in the northern California region, although the majority of growth and reproduction is centered around the spring and summer when upwelling intensity is at greatest. Recent years of lower abundances of krill (including *E. pacifica*) have been hypothesized to have contributed to the collapse of certain predators of the region (Cassin's auklet, Coho Salmon) (Sydeman et al. 2006, Lindley et al. 2009) and highlighted the need to consider the role of prey species in the management of commercially important fisheries (Field & Francis 2006).

Because *Euphausia pacifica* is of such importance to the greater food web of the California Current, there are a considerable number of field and laboratory

studies from which to draw information to parameterize modeling work on this species. Field studies using depth specific nets have clarified the traditional vertical migration patterns of adults, the lack of vertical migration in young larval stages, and the variability that exists in older larval stages (Bollens et al. 1992). Field studies have given us a better understanding of the size structure of the population and field growth rates of cohorts (Brinton 1976, Smiles & Pearcy 1971, Bollens et al. 1992, Shaw et al. 2009), as well as data upon which to ground truth our model against. Laboratory experimental work has produced a robust set of data on the bioenergetics and physiology of *E. pacifica*. There has been extensive work conducted on the timing and variability of stage development of *Euphausia pacifica* under maximum food conditions at 8° C and 12° C (Ross 1981) and at 10.5° C (Feinberg et al. 2006). Direct measurements of growth, molting, reproduction, metabolism and assimilation over a range of stages and weights provides a thorough energy budget of *E. pacifica* under a full food regime (Ross 1982a, 1982b). Experimental work on ingestion rates and food preferences also provides information on energetics under food-limited conditions (Ohman 1984). Information on reproductive parameters (brood size, inter-brood period, egg hatching success) is available from both field (Feinberg & Peterson 2003; Gómez-Gutiérrez et al. 2006, 2007) and laboratory work (Ross et al. 1982, Feinberg et al. 2007).

A synthesis of data on the development, growth, reproduction, and behavior of *Euphausia pacifica* reveal an organism with a highly variable life history. This variability is easily incorporated into the computations of an individual-based model, either through parameter variability or life-stage variability, and makes *E. pacifica* a particularly suitable subject for IBM simulations of population biology.

Methods

Model Interface. The IBM that we have used to represent the species *Euphausia pacifica* is called POPYCLE (Batchelder & Miller 1989, Batchelder et al. 2002) and can be run with physical oceanographic data modeled with the Regional Ocean Modeling System (ROMS) (Shchepetkin & McWilliams 2005, Haidvogel et al. 2008). POPYCLE interfaces with the ROMS model offline, (i.e. models are not run concurrently) by reading in snapshots of saved averaged data. Running the model offline saves computational time as multiple IBM simulations can be run without calculating ocean conditions multiple times. As ROMS data is saved only intermittently, temporal interpretation of the data is necessary and any variability that occurs below the temporal scale of the saved oceanographic data is lost. For each time step of the IBM, data on temperature, salinity, phytoplankton, u-velocity, v-current velocity, w-current velocity, and vertical diffusivity are read in from the preceding and proceeding temporal snapshots of the ROMS model. For each individual, the ocean data corresponding to the individuals location is read from the file and interpolated (using tri-linear) to that location. This occurs for both the preceding and

proceeding data and the resulting two data points are linearly interpolated to the proper time in the model.

Bioenergetics. The bioenergetics of the IBM of *Euphausia pacifica* depend on individuals' sex, size, and life stage, and environmental conditions (temperature and food concentration).

Growth of Non-Feeding Stages.

In the species *Euphausia pacifica*, the egg stage and first two life stages (naupliar I and II) are non-feeding and modeled developmental time is determined by temperature alone. Temperature dependent development is implemented through the physiological-time of each individual, calculated as the temperature a individual is exposed to (°C) multiplied by the time-step duration (days). The sum of a individual's physiological-time is thus a measure of the temperature history that a individual has been exposed to. Stage progression is determined when the sum of the individual's physiological-time exceeds a threshold, thus individuals exposed to colder water will take longer to pass on to the next stage.

Egg hatching time for *Euphausia pacifica* was implemented based on experimental work showing 50% of eggs hatching by day 1.625 at 10.5° Celsius (physiological-time = 17.06 degree days) (Feinberg et al. 2006). Naupliar stage growth of *E. pacifica* depends on yolk reserves. Physiological-time from hatch to metanauplius stage was calculated by averaging 8° Celsius and 12° Celsius stage development data reported by Ross (1982). Total physiological-time to the first feeding stage is 38.28 degree days.

During this period of development to a feeding life-stage, respiration of eggs and naupliar stages was implemented based on stage dependent weight data from Ross (1979, Appendix II). It is expected that higher temperatures would lead to greater metabolic costs and greater weight loss rates (Gillooly et al. 2001), but experimental data of weight loss from egg to metanaupliar stage development measured at 8° C ($0.2092 \mu\text{g C day}^{-1}$) and 12° C ($0.1567 \mu\text{g C day}^{-1}$) did not bear out this expectation. I have assumed that this difference is due to measurement error and an averaged daily weight loss rate of $0.183 \mu\text{g C day}^{-1}$ has been applied to all individuals. Development and respiration of non-feeding stages was capped at a lower limit of 6° Celsius and upper limit of 16° Celsius.

Growth of Feeding Stages.

Growth of all stages beyond the naupliar stages is dependent upon food resources and temperature, both supplied by ROMS model output.

Maximum Growth. An extensive carbon and nitrogen budget has been experimentally measured for *Euphausia pacifica* (Ross 1982a, 1982b) and data from this research has been critical in this modeling effort. This research measured ingestion, metabolism, growth, reproduction, molting, leakage and defecation and weight dependent equations were derived from the data. However, a comparison of measured ingestion and derived ingestion (the sum of the other six measured terms) revealed significant deviations from balance in the

data (Ross 1982b). For this reason, individual growth is modeled using the equation for growth measured directly by Ross (1982a) as opposed to the net result of all terms measured by Ross. As the growth equation was derived under food unlimited conditions the result represents maximum growth where G_{\max} = maximum growth rate ($\mu\text{g C day}^{-1}$) and W = organism weight ($\mu\text{g C}$). Equation 2.1 represents maximum growth for individuals less than 12.5 $\mu\text{g C}$ and Equation 2.2 represents maximum growth for those greater than 12.5 $\mu\text{g C}$.

$$G_{\max} = -0.315 + (W \times 0.198) \quad (\text{Eq. 2.1})$$

$$G_{\max} = 0.216 \times W^{0.617} \quad (\text{Eq. 2.2})$$

Scaling Maximum Growth by Food Resources and Temperature. To implement food dependence on growth, weight gain is scaled based on a relationship between the ingestion rate, critical concentration, and the food threshold at which no growth occurs. Ingestion rate is measured using an experimentally derived equation (Equation 2.3) measured under varying food concentrations (Ohman 1984), where I = ingestion rate, $a = 1.1726$, T_h = handling time ($0.141 \text{ s cell}^{-1}$) and X = prey concentration.

$$I = \frac{a \times X^2}{1 + (a \times T_h \times X^2)} \quad (\text{Eq. 2.3})$$

The critical concentration of phytoplankton (CC) is the level at which an organism is able to achieve maximal growth, is defined as 90% of the maximum ingestion rate, and is dependent upon both organism size and temperature in our modeling study. Ross (1982a) determined critical concentration of three size groups of *Euphausia pacifica* (< 750 $\mu\text{g C}$, 750-1650 $\mu\text{g C}$, and > 1650 $\mu\text{g C}$) and at two temperatures (8° C and 12° C). Model critical concentration at 12° C is calculated based on three size classes as in Table 2.1. Temperature scaling of the critical concentration is determined using the mean Q_{10} value of the three size classes published by Ross (1982a, mean $Q_{10} = 1.59$). The results generally agree with the only other published value of a critical concentration for adult *Euphausia pacifica* (Ohman 1984, CC = 290 $\mu\text{g C}$).

A food scale factor (FSF) is determined using Equation 2.4 by comparing the ingestion rate to the critical concentration.

$$FSF = \frac{I}{CC} \quad (\text{Eq. 2.4})$$

To determine the threshold at which no growth occurs (NGT), the ratio of metabolism to ingestion (i.e. % of ingestion energy accounted for via metabolism) was determined using equations from Ross (1982a). This ratio scales with weight as described by Equation 2.5 for individuals less than 165 $\mu\text{g C}$ and Equation 2.6 for those greater than 165 $\mu\text{g C}$.

$$NGT = 0.5478 + (-0.0723 \times W) \quad (\text{Eq. 2.5})$$

$$NGT = 0.4070 + (-0.0528 \times W) \quad (\text{Eq. 2.6})$$

Adjustment to the food scale factor is made to limit the maximum value to not exceed one, so that growth does not exceed G_{\max} . Food scale factor is also minimally limited to half of the no-growth threshold (Equation 2.5 & 2.6), due to the Type III shape of the ingestion curve (Ohman 1984), indicating a decreased feeding effort under food limiting conditions, reducing metabolic requirements. The food scale factor and no growth threshold are then applied to Equation 2.7 to determine the growth of the individual.

$$Growth = \frac{G_{\max}}{1 - NGT} \times (FSF - NGT) \quad (\text{Eq. 2.7})$$

To scale the growth increment by temperature a Q_{10} value of 3.62 was used (Ross 1982a).

Stage Development

To model the life stage structure and development of *Euphausia pacifica*, thirteen stages of development are included in the IBM. Life stages that exhibit similar behavior have been combined together (both naupliar stages, furcilia 4 and furcilia 5 stages, and juvenile and adult stages). Progression from one life stage to the next is dependent upon physiological time of development for egg and nauplius stages, and weight increase for all other stages. Weight gain beyond a life stage threshold (Table 2.2) determines progression from one stage to the next. Threshold weights were determined using midpoints between average weights of stages reported by Ross (1979, Table 19). An individual that loses weight back below a threshold weight does not regress back to the previous stage.

Reproduction

Reproduction is implemented based on a weight dependent empirical equation of reproductive effort (Ross 1982a) (Equation 2.8). As this equation was derived at a full food ration, scaling of the equation with food resources is done in the same way growth is scaled. Temperature scaling was done using a Q_{10} value of 3.60, which was derived from the experimental data of Ross (1982a).

$$Reproductive\ Weight = 20.37 + ((10.29 \times W) \times 10^{-3}) \quad (\text{Eq. 2.8})$$

While Ross defined her equation for all organisms with a weight greater than 685 $\mu\text{g C}$, for these modeling efforts, reproductive weight gain is not implemented until organisms are 1500 $\mu\text{g C}$ and is maximized when organisms reach 6000 $\mu\text{g C}$. These values roughly equate to reproduction beginning at an individual length

of 13 mm and achieving a maximum reproductive effort at 21 mm length, and agree with field observations from Northern California and Oregon (Dorman et al. 2005, Gómez-Guitérrez et al. 2006). If positive growth is not achieved during the feeding process, but there is reproductive weight associated with the individual, reproductive weight is absorbed back into the body to minimize weight loss.

The release of eggs is only allowed during nighttime, between 1 a.m. to 3 a.m., to ensure that individuals are in surface waters where egg release is most common. Release of eggs is dependent upon a combination of two factors: inter-brood period (IBP) and the ratio of reproductive weight to body weight (RW:BW). IBP is the amount of time between releases of eggs and is set to 10 days. Individuals will release eggs every ten days if reproductive weight is between 2.5% and 7.5% of the body weight. If reproductive weight is less than 2.5% body weight and IBM is greater than 10 days, eggs will not be released until the reproductive weight/body weight ratio is greater than 2.5, resulting in a longer IBP. If the RW:BW ratio is greater than 7.5% and the IBP is less than 10 days, eggs will be released resulting in a shorter IBP. The number of eggs released is equal to the reproductive weight divided by the average weight of an egg (2.58 $\mu\text{g C}$).

Mortality

Starvation mortality is implemented in the model based on weight loss below 70% of each individuals maximum attained weight. Predation and natural mortality is implemented in the model using a uniform random number generator and user inputted stage-specific mortality values ($\% \text{ day}^{-1}$). An individual will be removed from the population if the generation of a uniform random number is less than the stage-specific mortality rate, adjusted for the time increment of the model.

Particle Tracking

Individuals are tracked in the model using a common 4th-order Runge-Kutta method (Butcher 2003) using u, v, and w velocities from the ROMS model. Vertical diffusivity is also incorporated into vertical displacement through a naïve random walk (Visser 1997) to avoid the accumulation of individuals in regions of low vertical diffusivity. Horizontal diffusivity is not implemented in particle tracking as it is considered much too small, when compared to horizontal velocities, to make a perceptible difference in results. Additional vertical movement is added behaviorally through diel vertical migration (DVM) of the individuals. DVM is dependent upon a suite of normalization factors that range from 0-1 and enable or disable vertical migration in the same fashion as Batchelder et al. (2002). A maximum swim speed of approximately 0.1 m s^{-1} (Torres & Childress 1983) is reduced by factors which take into consideration size of the organism (impacting speed and probability of migration), distance from preferred light isolume, level of recent feeding (descent only), distance from surface or bottom, and if the individual is near food (ascent only).

Individuals that leave the model through an open boundary are labeled as such and are removed from the linked list of individuals that is evaluated for each time-step.

Results

Bioenergetics.

Growth of Non-Feeding Stages

Time of development from egg to metanauplius stage is 4.8 and 3.2 days at 8° and 12° C, respectively. Initial metanauplius weight is 1.70 µg C and 1.99 µg C at 8° C and 12° C respectively (Figure 2.1). There isn't any comparative experimental data on developmental rates from egg to metanauplius stage at a single temperature to compare our results with, but resultant metanauplius weights compare favorably to experimentally measured weights of 1.58 µg C and 2.08 µg C at 8° and 12° C, respectively.

Growth of Feeding Stages.

Growth depends on temperature and food resources. Critical concentration increases from a minimum value of 1.58 µg chlorophyll *a* at 6° C to 2.75 µg chlorophyll *a* at 18° C for an organism less than 500 µg C. Maximum critical concentration is 4.74 µg at 6° C and 8.24 µg at 18° C for organisms greater than 2000 µg C.

Minimum food resources to achieve growth (Figure 2.3) ranged from a minimum value of 0.69 µg chlorophyll *a* at 6° C to 0.89 µg chlorophyll *a* at 18° C for an organism less than 500 µg C. Minimum food resources to achieve growth is 1.00 µg at 6° C and 1.05 µg at 18° C for organisms greater than 2000 µg C. Modeled growth results were simulated using maximum food conditions and constant temperatures to be comparable with laboratory studies that were conducted under similar conditions. Developmental time from egg to juvenile stage was modeled slightly faster than experimental data, by 0.9 days at 8° C, by 7 days at 10.5° C, and by 1.1 days at 12° C (Figure 2.4).

Reproduction

Reproductive weight achieved per day under a full food ration ranges from 4 eggs per day at 6° C and 22 eggs per day at 18° C for an organism of minimal reproductive weight (Figure 2.5). An organism greater than 6000 µg C will attain 14 eggs per day and 68 eggs per day at 6° C and 18° C, respectively. Brood size of eggs ranges from a minimum of 20 eggs to a maximum of 366 eggs under a full ration of food, and interbrood period ranged from an average of 8.4 days at 6° C to 2.8 days at 18° C (Figure 2.6).

Mortality

Starvation of individuals under a body weight of 12 µg C, which is the breakpoint at which Ross' allometric equations for growth change from linear to exponential, averaged 5.68 days at 12° C (range of 7.92 days at 6° C and 4.55 days at 16° C). Starvation of furcilia larvae, weighing between 15 µg C and 100 µg C, averaged 15.60 days at 12° C (range of 33.59 days at 6° C and 9.36 days at 16° C). Adult starvation of organisms between 100 and 9000 µg C averaged

218.65 days at 12° C (range of 473.07 days at 6° C to 130.71 days at 16° C). In the model the maximum starvation time was not allowed to exceed 200 days.

Particle Tracking

Individual movement of the IBM using saved daily averaged ROMS data was compared to individuals that were tracked simultaneously with the ROMS model using a particle tracking package (FLOATS) that is built into the ROMS code. For the simulation, 100 individuals were seeded in the coastal domain between 37.5–40° N latitude. Both models were run for 45 days, and diel vertical migration was not implemented in the IBM. The mean individual location of the IBM on day 45 was $40.36 \pm 0.35^\circ$ N latitude (mean \pm 95% confidence interval) by $124.71 \pm 0.09^\circ$ W longitude. The mean individual location of individuals within the ROMS model on day 45 was $40.72 \pm 0.38^\circ$ N latitude (mean \pm 95% confidence interval) by $124.70 \pm 0.10^\circ$ W longitude (Figure 2.7).

Discussion

ROMS Interface

When working with offline data the temporal frequency with which one saves the data output could influence the IBM results if the time-scale at which the data is saved is greater than the time scale of any important physical processes in the ecosystem. In saving the data on the time-scale of one day, we smooth over any processes that occur on the scale of less than one day (e.g. diurnal heating of surface layer). Satisfactory temporal resolution also depends on the questions addressed with the model and the longevity of the species being addressed. In the case of a long lived zooplankton species such as *Euphausia pacifica*, and considering the questions that we are interested in occur on a much larger temporal scale (seasonal, annual, and inter-decadal variability) we are confident that a one-day average of the ocean conditions is sufficient to capture the ecosystem variability that is important for *E. pacifica*. Results comparing daily average oceanographic data to ocean conditions are presented in Chapter 4.

Growth and Feeding

Growth in the POPCYCLE model for *Euphausia pacifica* is implemented based on an equation derived from laboratory studies under controlled conditions. A comparison of model to field growth rates finds that our model is well within the range of observed values. Average adult growth rates of 0.02 and 0.03 mm d⁻¹ (range from -0.07 to 0.14 mm d⁻¹) have been reported for two regions off of Oregon during the summer upwelling season with food sources ranging from approximately 2 to 8 µg chlorophyll a liter⁻¹ (Shaw et al. 2009). A year round study from the same region that examined cohorts over their lifespan found a mean growth rate of 0.065 mm day⁻¹ and a maximum larval growth rate of 0.095 mm day⁻¹ (Smiles & Percy 1971). Using the conversion listed in Appendix 2.1, modeled growth rates of adults at 8° and 12° C and under food unlimited conditions were 0.038 and 0.048 mm d⁻¹, respectively. Under the same conditions, mean growth rate of the entire lifespan was 0.044 and 0.060 mm d⁻¹.

Modeled adult growth rates are slightly higher than shipboard experiment rates measured by Shaw et al. (2009), but considering that field specimens were likely not under food unlimited conditions for the duration of the experiment, a higher modeled growth rate would be expected. The model may be underestimating the absolute maximum growth rate of an individual *E. pacifica*. Differences in the growth rates measured by Smiles & Percy (1971) may be due to their indirect methodology, which assumes sampling of the same population in what is a fairly advective region during upwelling periods. Regardless, our rates show similar trends among life stages (larvae growing faster than adults) and are only 7 to 32 % less than their measured values.

Another potential reason for lower modeled growth rates may be because the modeled *Euphausia pacifica* individuals are feeding only on phytoplankton, while it is known that *E. pacifica* are omnivorous and can feed on smaller zooplankton (Lasker 1966). However, laboratory studies measuring the feeding rate on the copepod species *Pseudocalanus sp.* indicate that adult copepods are a sub-optimal prey item (Ohman 1984) and *E. pacifica* could persist but not grow when feeding solely on adult copepods. Thus, while zooplankton are certainly fed upon by *E. pacifica* in the coastal ocean, it is likely that they are not a significant source of energy and certainly not a preferred prey item during periods of upwelling and phytoplankton blooms. Copepod prey may play a more important role in diet during wintertime or periods of poor primary productivity as a stop-gap measure to reduce weight loss. As individuals in our model feed only on phytoplankton, we recognize that we may be underestimating growth or overestimating starvation in our model.

Stage development in the model is dependent upon weight gain beyond a weight checkpoint and progresses in a similar fashion to published results (Ross 1982, Feinberg et al. 2006). It should be noted that stage progress through calyptopis and early furcilia stages progresses more rapidly in the model than in published laboratory studies. However, there is quite a bit of variability within the stage progression of a natural population (Ross 1979; Feinberg et al. 2006) and the timing of our stage progression is well within measured variability. This type of discrepancy might impact studies that rely heavily on stage specific parameters (e.g. mortality), but the majority of the parameters in the current study are weight based and not specific to stage.

Reproduction

Reproduction is highly variable in both different geographic populations of *Euphausia pacifica* and for individuals within a population. Year round reproduction has been reported in the Southern California Bight region (Brinton 1976), while in colder regions (Oregon, Washington) it is more commonly accepted that seasonal reproduction occurs in sync with regional high primary productivity (Feinberg & Peterson 2003). Experimental work has shown there to be high variability in reproductive patterns (interbrood period and brood size) among individuals of the same population. Interbrood period can range from 1 day to well over a month for organisms maintained under identical conditions and

brood size also can range from just a few eggs to over 400 per brood (Feinberg et al. 2007).

Our model expresses variability in interbrood period and brood size as a function of organism size, food resources and temperature. Experimental data on the median interbrood period (4.5 days) and mean brood size (109 eggs) of *Euphausia pacifica* maintained at 10.5° C under food unlimited conditions (Feinberg et al. 2007) compares favorably with modeled results (IBP = 6.5 days, brood size = 130 eggs) derived under similar conditions (temperature, food conditions and organism size (20 mm or ~ 4400 µg C)). These results are well within the range of reported values from other studies as well (Ross 1982a, Pinchuk & Hopcroft 2006).

Starvation

It is understood that krill can adapt to unfavorable conditions through shrinkage in body weight. The ratio of respiration to ingestion provides us a baseline upon which to define the food concentration at which respiration costs outpace ingestion (see Methods). Food concentrations below this level will result in negative growth and the beginning of the starvation process. The point at which *Euphausia pacifica* starves has not been empirically determined. Experimental work showed negative growth in juvenile *E. pacifica* at temperatures higher than 16.5° C (under food unlimited conditions)(Marinovic & Mangel 1999), but no information is available on the impacts of a lack of food on *E. pacifica*. Starvation parameters used here are derived from laboratory studies on the Antarctic euphausiid *Euphausia superba*. Krill starvation studies on the first feeding stage of the Antarctic species *Euphausia superba* have found a 44-51% loss in body carbon over 10-14 days resulted in the organism reaching a point of no return (PNR), defined as the point at which an organism can not recover from starvation to molt to the next stage even if food conditions improve. Another study on later furcilia stages determined *E. superba* furcila IV larvae reach a PNR at 6-9 days and lose approximately 50% of their body carbon. Starvation studies on decapod zoea larvae determined that a reduction of body carbon by as little as 20% can result in half of the experimental larvae unable to recover, with an average amount of carbon loss in the 25-35% range.

We have chosen a 30% loss in body carbon to represent a starvation point for our model, as *E. pacifica*, which lives in a food rich environment, is likely less resistant to starvation than *E. superba* which is adapted to overwinter under food-limited conditions. This number is also more in line with other crustacean larvae PNR values of 20 to 35% of body carbon loss (Angers & Dawirs 1981, 1982, Dawairs 1983). The resultant starvation times of *E. pacifica* larvae are generally in line with reported time to starvation of *E. superba* larvae. Adult starvation times are likely a bit long under colder conditions, but values in the one hundred to two-hundred day range agree with reports of *E. superba* adults surviving for over two-hundred days without food (Ikeda & Dixon 1982).

Considering the lack of knowledge on the physiological response of *Euphausia pacifica* to food limited conditions, the starvation results from the model should be considered with a critical eye. However, comparison of

starvation results between different model runs does give an indication of the relative impact of primary productivity on the *E. pacifica* population. Further experimental work on starvation and feeding under low levels of food would be very useful for future modeling efforts and in understanding ocean conditions that might lead to poor survival of *E. pacifica* in the California Current.

Predation and Natural Mortality

The IBM has the ability to implement predation and natural mortality, but there is very little data from which to derive the needed stage-specific input parameters (% mortality day⁻¹). The only estimate of natural mortality over all life-stages of *Euphausia pacifica* that I am aware of is presented in Feinberg et al. (2006). However, it is not entirely clear that these rates would apply to a natural population as the population was reared in the laboratory and exposed to quite a bit of handling and potential stress (Feinberg, personal communication).

Predation mortality terms are even more difficult to determine considering the wide variety of organisms that prey on *E. pacifica* as some component of their diet. The model formulation does not apply mortality with any spatial or temporal variability, but assumes that predation is spatially and temporally constant. In ecosystem and IBM population models, predation is often unceremoniously reduced to a closure term that “tunes” the model to accurately represent observed population abundance or size structure (Edwards & Yool 2000). These closure methods may give some idea of the role predation plays to control the populations, though only if confidence is high in the performance of all other model parameters. Predation parameters have not been tested in the model other than determining that the computer coding of the model removes the appropriate proportion of the population as specified by the parameter choice.

Particle Tracking

A comparison of particle tracking within the IBM and particle tracking from within the ROMS model indicates that there is good agreement in individual distribution after 45 days of simulation. Some of the differences in mean individual location at the end of the model run is likely due to the different methodology employed by the two models. The IBM, which uses saved ROMS results, does not incorporate any currents that might occur on a smaller time scale than the daily-averaged files that the IBM uses. Some of this small-scale variability (e.g. diurnal patten in wind strength) can certainly impact population distributions. Additionally, while both ROMS and the IBM use a naïve vertical walk algorithm when considering vertical advection, there is a random component to the algorithm that ensures slightly different results even if the model was re-run using the same ocean conditions. Despite these differences in methodology, the population distribution of each model is remarkably similar.

Summary

The IBM that has been written and analyzed for the krill species *Euphausia pacifica* is an important first step in understanding the driving forces behind variability in krill population biology in the California Current. These

organisms (and other krill species) are a critical component of the California Current food web and any attempt at management of higher trophic levels from an ecosystem perspective should certainly be aware of the state of the krill community. While there is much we do know about the physiology of *E. pacifica*, there is also a considerable amount of information that is unknown that would improve the model. Most importantly, experiments on the feeding response to varying phytoplankton concentrations (including starvation conditions) on the full spectrum of life-stages would allow us to understand how extreme environmental conditions might impact present (adult) and future (larval) abundances. Using a model such as this to retroactively examine the physical conditions (atmospheric and oceanographic) that have led to anomalous abundances of krill will help us identify conditions in the California Current that may lead to future anomalous krill abundances, and to manage those organisms that are dependent upon *E. pacifica* accordingly.

References

- Anger K, Dawirs R (1981) Influence of starvation on the larval development of *Hyas araneus* (Decapoda, Majidae). *Helgol Meeresunters* 34: 287-311
- Angers K, Dawirs R (1982) Elemental composition (C,N,H) and energy in growing and starving larvae of *Hyas araneus* (Decapoda, Majidae). *Fish Bull* 80: 419-433
- Banse K (1977) Determining the Carbon-to-Chlorophyll ratio of natural phytoplankton. *Mar Biol* 41: 199-212
- Batchelder HP, Miller CB (1989) Life history and population dynamics of *Metridia pacifica*: results from simulation modeling. *Ecol Model* 48: 113-136
- Batchelder HP, Williams R (1995) Individual-based modelling of the population dynamics of *Metridia lucens* in the North Atlantic. *ICES J Mar Sci* 52: 469-482
- Batchelder HP, Edwards CA, Powell TM (2002) Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. *Prog Ocean* 53: 307-333
- Bollens SM, Frost BW, Lin TS (1992) Recruitment, growth, and diel vertical migration of *Euphausia pacifica* in a temperate fjord. *Mar Biol* 114: 219-228
- Brinton E (1976) Population biology of *Euphausia pacifica* off southern California. *Fish Bull US Natl Mar Fish Serv* 74: 733-762
- Butcher JC (2003) Numerical methods for ordinary differential equations. John Wiley & Sons, Chichester, West Sussex, England.
- Davidson FJM, DeYoung B (1995) Modelling advection of cod eggs and larvae on the Newfoundland Shelf. *Fish Ocean* 4: 33-51
- Dawairs R (1983) Respiration, energy balance and development during growth and starvation of *Carcinus maenas* L. larvae (Decapoda: Portunidae). *J Exp Mar Biol Ecol* 69: 105-128
- Dorman JG, Bollens SM, Slaughter AM (2005) Population biology of euphausiids off northern California and effects of short time-scale wind events on *Euphausia pacifica*. *Mar Ecol Prog Ser* 288: 183-198
- Edwards AM, Yool A (2000) The role of higher predation in plankton population models. *J Plankton Res* 22: 1085-1112

- Fasham MJR, Ducklow HW, McKelvie SM (1990) A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *J Mar Res* 48: 591-639
- Feinberg LR, Peterson WT (2003) Variability in duration and intensity of euphausiid spawning off central Oregon, 1996-2001. *Prog Oceanogr* 57: 363-379
- Feinberg LR, Shaw CT, Peterson WT (2006) Larval development of *Euphausia pacifica* in the laboratory: variability in the developmental pathways. *Mar Ecol Prog Ser* 316: 127-137
- Feinberg LR, Shaw CT, Peterson WT (2007) Long-term laboratory observations of *Euphausia pacifica* fecundity: comparison of two geographic regions. *Mar Ecol Prog Ser* 341: 141-152
- Field JC, Francis RC, Aydin K (2006) Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Prog Ocean* 68: 238-270, doi:10.1016/j.pocean.2006.02.010
- Field JC, Francis RC (2006) Considering ecosystem-based fisheries management in the California current. *Mar Pol* 30: 552-569
- Franks PJS, Wroblewski JS, Flierl GR (1986) Behavior of a simple plankton model with food-level acclimation by herbivores. *Mar Biol* 91: 121-129
- Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science* 293: 2248-2251
- Gómez-Gutiérrez J, Feinberg LR, Shaw T, Peterson W (2006) Variability in brood size and female length of *Euphausia pacifica* among three populations in the North Pacific. *Mar Ecol Prog Ser* 323: 185-194
- Gómez-Gutiérrez J, Feinberg LR, Shaw T, Peterson W (2007) Interannual and geographical variability of the brood size of the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* along the Oregon coast (1999-2004). *Deep-Sea Res I* 54: 2145-2169
- Haidvogel DB, Arango H, Budgell WP, Cornuelle BD, Curchitser E, Di Lorenzo E, Fennel K, Geyer WR, Hermann AJ, Lanerolle L, Levin J, McWilliams JC, Miller AJ, Moore AM, Powell TM, Shchepetkin AF, Sherwood CR, Signell RP, Warner JC, Wilkin J (2008) Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modeling System. *J Comp Phys* 227: 3595-3624, doi:10.1016/j.jcp.2007.06.016

- Heath M, Zenitani H, Watanabe Y, Kimura R, Ishida M (1998) Modelling the dispersal of larval Japanese sardine, *Sardinops melanostictus*, by the Kuroshio Current in 1993 and 1994. *Fish Ocean* 7: 335-346
- Iguchi N, Ikeda T (1999) Production, metabolism and *P:B* ratio of *Euphausia pacifica* (Crustacea: Euphausiacea) in Toyama Bay, southern Japan Sea. *Plankton Biol Ecol* 46: 68-74
- Ikeda T, Dixon P (1982) Body shrinkage as a possible over-wintering mechanism of the Antarctic krill, *Euphausia superba* Dana. *J Exp Mar Biol Ecol* 62: 143-151
- Kishi MJ, Kashiwai M, Ware DM, Megrey BA, Eslinger DL, Werner FE, Noguchi-Aita M, Azumaya T, Fujii M, Hashimoto S, Huang D, Iizumi H, Ishida Y, Kang S, Kantakov GA, Kim H, Komatsu K, Navrotsky VV, Smith SL, Tadokoro K, Tsuda A, Yamamura O, Yamanaka Y, Yokouchi K, Yoshie N, Zhang J, Zuenko YI, Zvalinsky VI (2007) NEMURO-a lower trophic level model for the North Pacific marine ecosystem. *Ecol Model* 202: 12-25
- Lasker R (1966) Feeding, growth, respiration and carbon utilization of a euphausiid crustacean. *J Fish Res Board Can* 23: 1291-1317
- Leising AW (2001) Copepod foraging in patchy habitats and thin layers using a 2-D individual-based model. *Mar Ecol Prog Ser* 216: 167-179
- Lindley ST, Grimes CB, Mohr MS, Peterson W, Stein J, Anderson JT, Botsford LW, Bottom DL, Busack CA, Collier TK, Ferguson J, Garza JC, Grover AM, Hankin DG, Kope RG, Lawson PW, Low A, MacFarlane RB, Moore K, Palmer-Zwahlen M, Schwing FB, Smith J, Tracy C, Webb R, Wells BK, Williams TH (2009). What caused the Sacramento River fall Chinook stock collapse? Report to the Pacific Fishery Management Council
- Marinovic B, Mangel M (1999) Krill can shrink as an ecological adaptation to temporarily unfavourable environments. *Ecol Lett* 2: 338-343
- Miller CB, Lynch DR, Carlotti F, Gentleman W, Lewis CVW (1998) Coupling of an individual-based population dynamic model of *Calanus finmarchicus* to a circulation model for the Georges Bank region. *Fish Ocean* 7: 219-234
- Moloney CL, Bergh MO, Field JG, Newell RC (1986) The effect of sedimentation and microbial nitrogen generation in a plankton community: a simulation investigation. *J Plankton Res* 8: 427-445
- Ohman MD (1984) Omnivory by *Euphausia pacifica*: the role of copepod prey. *Mar Ecol Prog Ser* 19: 125-131

- Pace ML, Glasser JE, Pomery LR (1984) A simulation analysis of continental shelf food webs. *Mar Biol* 82: 47-63
- Pinchuk AI, Hopcroft RR (2006) Seasonal variations in the growth rates of euphausiids (*Thysanoessa inermis*, *T. spinifera*, and *Euphausia pacifica*) from the northern Gulf of Alaska. *Mar Biol* 151: 257-269
- Riley GA (1946) Factors controlling phytoplankton populations on Georges Bank. *J Mar Res* 6: 54-73
- Riley GA (1947a) A theoretical analysis of the zooplankton population of Georges Bank. *J Mar Res* 6: 104-113
- Riley GA (1947b) Seasonal fluctuations of the phytoplankton population in New England coastal waters. *J Mar Res* 6: 114-125
- Ross RM (1979) Carbon and nitrogen budgets over the life of *Euphausia pacifica*. Ph.D. thesis, University of Washington. Seattle, WA, 260 p.
- Ross RM (1981) Laboratory culture and development of *Euphausia pacifica*. *Limnol Oceanogr* 26: 235-246
- Ross RM (1982a) Energetics of *Euphausia pacifica*. I. Effects of body carbon and nitrogen and temperature on measured and predicted production. *Mar Biol* 68: 1-13
- Ross RM (1982b) Energetics of *Euphausia pacifica*. II. Complete carbon and nitrogen budgets at 8° and 12°C throughout the life span. *Mar Biol* 68: 15-23
- Ross RM, Daly KL, Saunders English T (1982) Reproductive cycle and fecundity of *Euphausia pacifica* in Puget Sound, Washington. *Limnol Oceanogr* 27: 304-314
- Shaw CT, Feinberg LR, Peterson WT (2009) Interannual variations in the vital rates of copepods and euphausiids during the RISE study 2004-2006. *J Geophys Res* 114, C00B08, doi:10.1029/2008JC004826
- Shchepetkin AF, McWilliams JC (2005) The regional ocean modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Model* 9: 347-404, doi:10.1016/j.ocemod.2004.08002
- Smiles MC, Percy WG (1971) Size structure and growth rate of *Euphausia pacifica* off the Oregon coast. *Fish Bull* 69: 79-86
- Steele JH (1974) The structure of marine ecosystems. Harvard University Press, Cambridge, Massachusetts.

Steele JH, Frost BW (1977) The structure of plankton communities. *Philos Trans R Soc Lond B* 280: 485-534.

Steele JH, Henderson EW (1981) A simple plankton model. *Am Nat* 117: 676-691

Strathman RR (1967) Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. *Limnol Oceanogr* 12: 411-418

Strickland JDH (1965) *Chemical oceanography*. Academic Press, London, England.

Sydeman, WJ, Bradley RW, Warzybok P, Abraham CL, Jahncke J, Hyrenbach KD, Kousky V, Hipfner JM, Ohman MD (2006) Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking? *Geophys Res Lett* 33: L22S09, doi:10.1029/2006GL026736

Torres JJ, Childress JJ (1983) Relationship of oxygen-consumption to swimming speed in *Euphausia pacifica* .1. Effects of temperature and pressure. *Mar Biol* 74: 79-86

Visser AW (1997) Using random walk models to simulate the vertical distribution of particles in a turbulent water column. *Mar Ecol Prog Ser* 158: 275-281

Appendix 2.1

Conversion Equations

Phytoplankton concentration from ROMS is output in units of $\mu\text{mol Nitrogen liter}^{-1}$ and is converted to units of $\mu\text{g carbon liter}^{-1}$ for use in the IBM, and to units of cells ml^{-1} for use in an experimentally derived ingestion equation (Ohman 1984). ROMS phytoplankton output is converted to units of $\mu\text{g carbon}$ with Equation 2.9, using the Redfield ratio of carbon to nitrogen (106 : 16) and the atomic weight of carbon (~ 12) to calculate a ratio of 77 $\mu\text{g carbon} : 1 \mu\text{mol nitrogen}$.

$$\frac{106 \mu\text{mol C}}{16 \mu\text{mol N}} \times \frac{12 \mu\text{g C}}{1 \mu\text{mol C}} \approx 77 \mu\text{g C} (\mu\text{mol N})^{-1} \quad (\text{Eq. 2.9})$$

Further conversion of phytoplankton to units used in the ingestion equation (cells ml^{-1}) was based on the reported ingestion rate of 22950 $\text{cells euphausiid}^{-1} \text{ hour}^{-1}$ (90% of the maximum ingestion rate) being equal to 290 $\mu\text{g C l}^{-1}$ (Ohman 1984). From this data we can determine the average carbon weight of each cell of the diatom used in the ingestion study (*Thalassiosira angustii*) ($661 \text{ pg carbon cell}^{-1}$). Thus modeled phytoplankton ($\mu\text{g liter}^{-1}$) is converted to the prey concentration units of this equation (cells ml^{-1}) using Equation 2.10. This estimate of the phytoplankton carbon cell^{-1} is similar to values for diatoms reported by Strathmann (1967).

$$\text{ModelPhytoplankton} \left(\frac{\mu\text{g C}}{\text{l}} \right) \times \frac{10^6 \text{ pg C}}{1 \mu\text{g C}} \times \frac{1 \text{ l}}{10^3 \text{ ml}} \times \frac{1 \text{ cell}}{661 \text{ pg C}} \quad (\text{Eq. 2.10})$$

Phytoplankton output was further converted to chlorophyll *a* for comparison with observational data using the conversion of 1 $\mu\text{g chlorophyll a}$ per 60 $\mu\text{g carbon}$. There is known variation in the ratio of chlorophyll *a* to carbon (Strickland 1965, Banse 1977) with factors such as light, nutrient concentration and temperature all influencing the ratio. The ratio of 1:60 that is used falls within commonly used values for upwelling regions.

To convert model growth rates ($\mu\text{g C d}^{-1}$) to published growth rates (mm d^{-1}) we assumed that 40% of dry weight of *Euphausia pacifica* is comprised of carbon based on published values between 38.1% and 45.1% (Lasker 1966, Ross 1982a, Iguchi & Ikeda 1999) and used the dry weight to total length relationship published by Feinberg et al. (2007).

Individual Weight ($\mu\text{g C}$)	Critical Concentration ($\mu\text{g C l}^{-1}$)
< 500	125
500 – 2000	$(\frac{1}{6} \times \text{Weight}) + 41.67$
> 2000	375

Table 2.1. Model critical concentration of phytoplankton at 12° C for various size classes of individuals.

Developmental Stage	Threshold	Units
egg hatch	17.06	degree-days
metanauplius	38.28	degree-days
calytopis 1	2.33	$\mu\text{g C}$
calytopis 2	3.52	$\mu\text{g C}$
calytopis 3	6.52	$\mu\text{g C}$
furcilia 1	11.76	$\mu\text{g C}$
furcilia 2	17.70	$\mu\text{g C}$
furcilia 3	32.44	$\mu\text{g C}$
furcilia 4-5	55.77	$\mu\text{g C}$
furcilia 6	70.56	$\mu\text{g C}$
furcilia 7	78.02	$\mu\text{g C}$
juvenile-adult	84.90	$\mu\text{g C}$

Table 2.2. Thresholds that individuals must progress beyond to advance to the next life-stage.

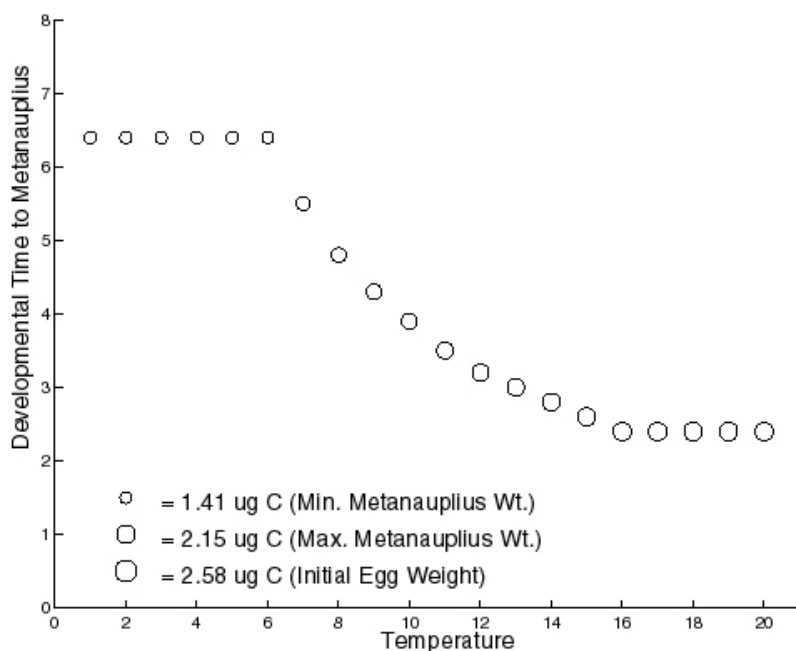


Figure 2.1. Development time from egg to metanauplius life-stage and resultant metanauplius weight of *Euphausia pacifica* at temperature ranging from 1 to 20° C. Minimum and maximum metanauplius weight, and initial egg weight are shown for reference.

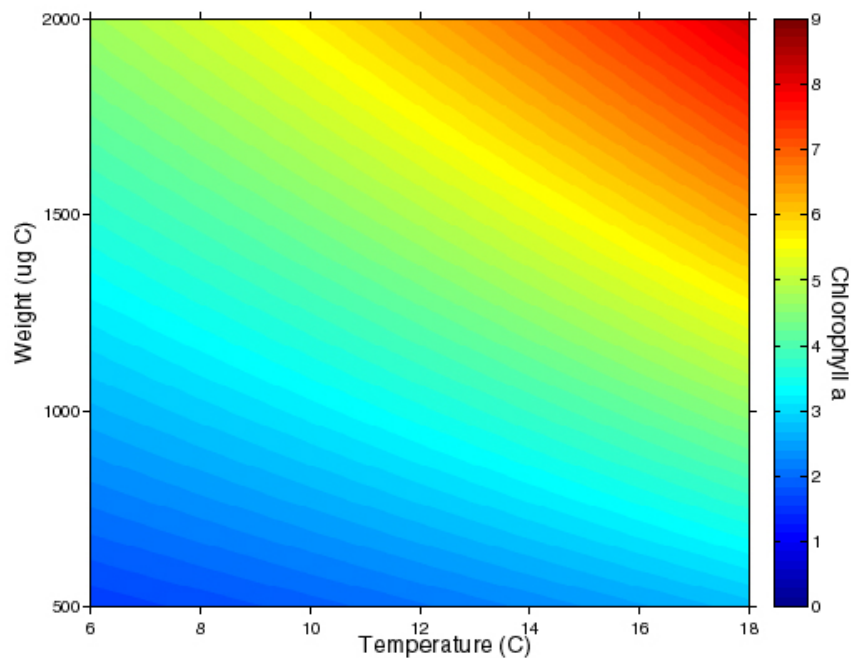


Figure 2.2. Critical concentration of chlorophyll a ($\mu\text{g l}^{-1}$) needed for *Euphausia pacifica* to achieve maximum growth rate under varying temperature (x-axis) and weight (y-axis).

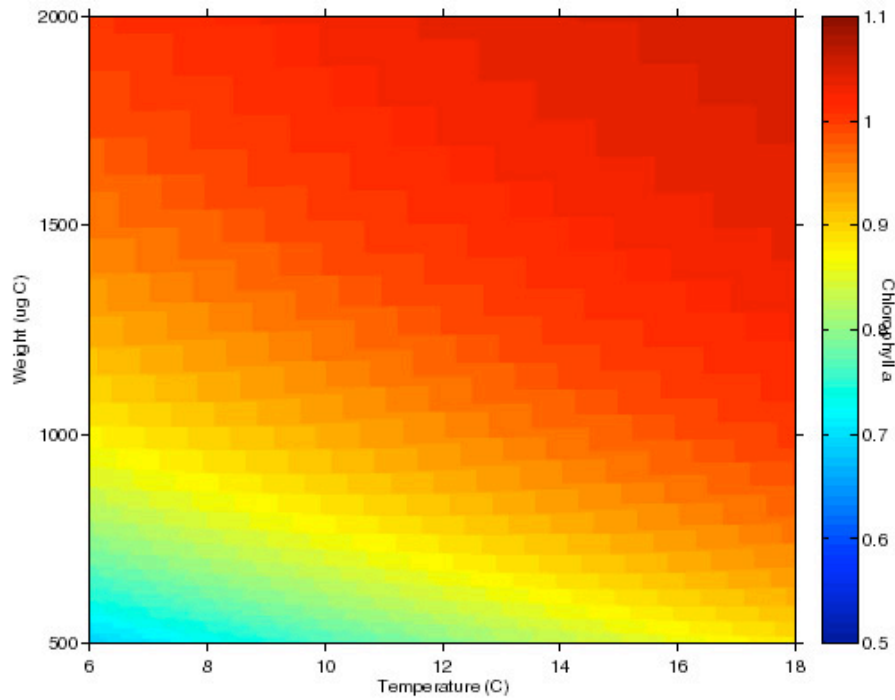


Figure 2.3. Minimum concentration of chlorophyll a ($\mu\text{g l}^{-1}$) needed for *Euphausia pacifica* to maintain weight due to metabolism under varying temperature (x-axis) and weight (y-axis).

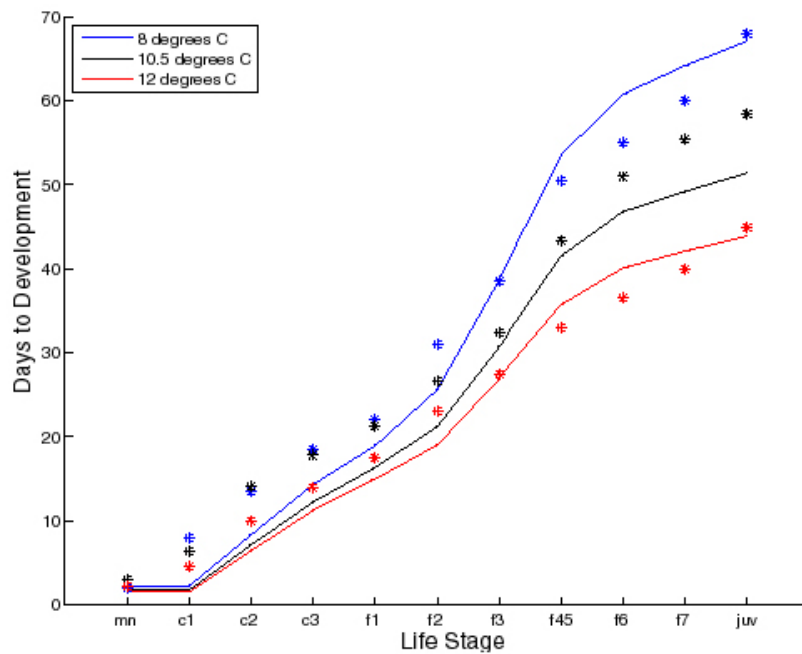


Figure 2.4. Developmental time to various life stages (mn=metanauplius, c#=calyptopis, f#=furcilia, juv=juvenile). Solid lines are published data and asterisks are model results, at 8° C (blue), 10.5° C (green), and 12° C (red).

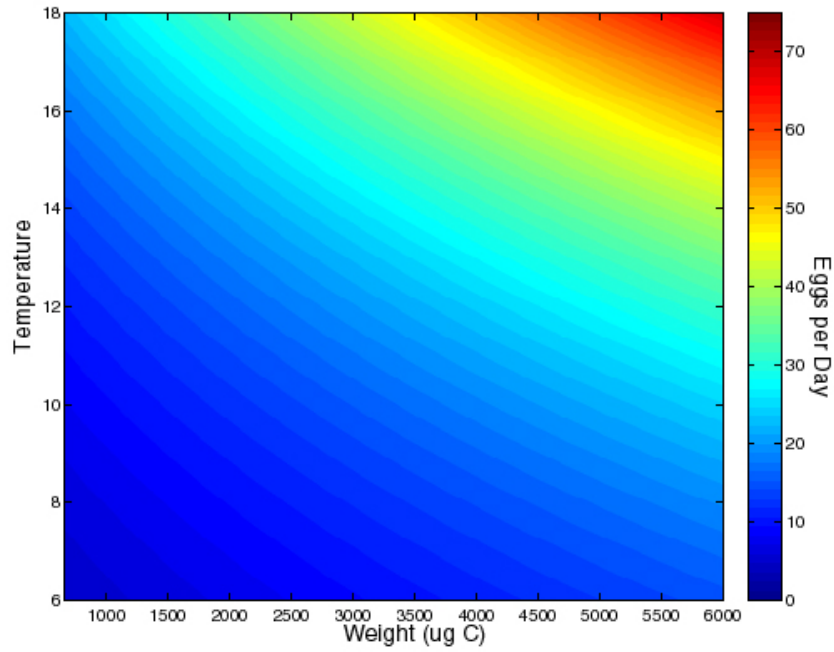


Figure 2.5. Reproductive weight gained (expressed in eggs day⁻¹) under a full food ration under varying weight (x-axis) and temperature (y-axis)..

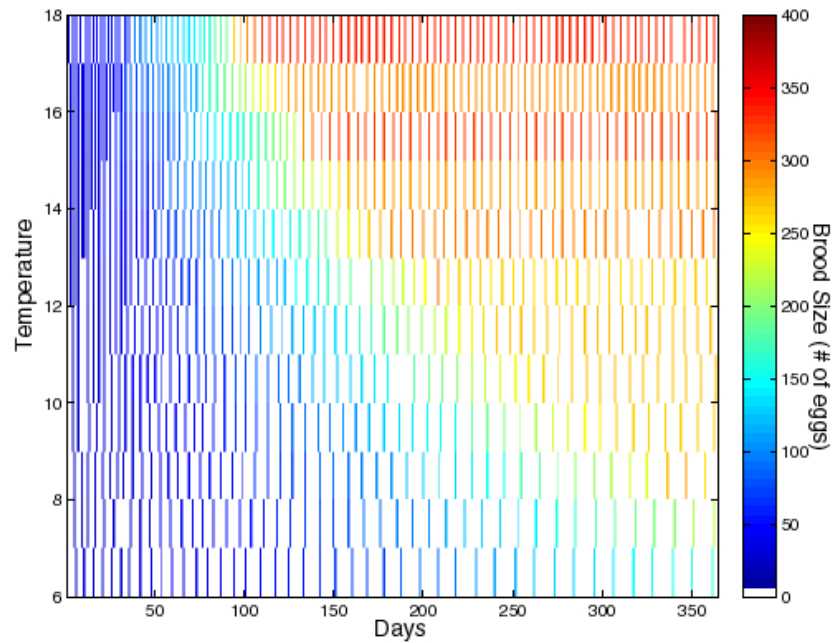


Figure 2.6. Brood size (color axis) and interbrood period (spacing of broods on x-axis) over the course of 365 days of growth under a full food ration at varying temperature (y-axis). Starting individual size is minimum reproductive weight.

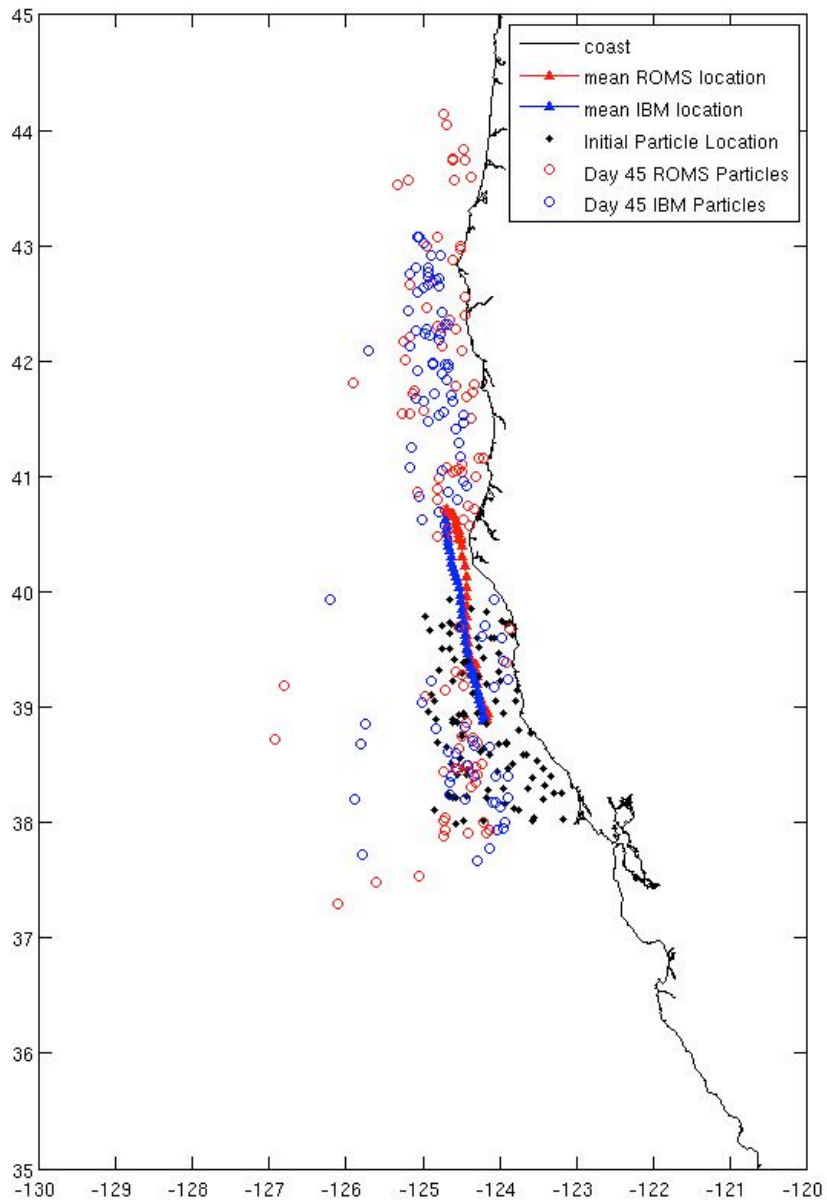


Figure 2.7. A comparison of particle tracking in ROMS (red) and the IBM POPCYCLE (blue). Initial locations (black) of individuals, mean daily location (solid triangles), and location on Day 45 (open circles).

Chapter 3

Advection and starvation cause krill (*Euphausia pacifica*) decreases in 2005 Northern California coastal populations: Implications from a model study.

Abstract

A decrease in krill abundance during 2005 in regions of the California Current was hypothesized to have had immediate (seabird) and long-term (salmon) negative impacts on upper trophic level predators. We use a suite of coupled models to examine the population biology and spatial and temporal distribution of the krill species *Euphausia pacifica* during the winter/spring of 2001, a “normal” year, and 2005, an “anomalous” year, to determine if this hypothesis is supported mechanistically. Ocean conditions were simulated using the Regional Ocean Modeling System (ROMS), which forced an individual-based model parameterized to simulate the population biology of *E. pacifica*. Poleward transport during winter 2005 advected individuals north of Cape Mendocino, away from seabirds and salmon feeding in the Gulf of the Farallons region. Few of the individuals that were advected north in 2005 returned to their region of release throughout the model run time (200 days). Moreover, the “condition” of those individuals remaining within the domain was poor in 2005, with greater mortality from starvation and a decreased mean individual weight. Our results indicate that both physical processes (anomalous northern advection) and biological processes (greater starvation and less weight per individual) contributed to reduced krill availability to predators in the northern California region during 2005, and that the productivity and survival of seabirds and salmonids is dependent on krill during critical life history stages.

Introduction

Krill are important components of the California Current food web, including the most common nearshore species *Euphausia pacifica* (Brinton 1962). This group of zooplankton is an important consumer of large phytoplankton (diatom) biomass, and are fed upon by a diverse suite of higher trophic level organisms including seabirds (Ainley et al. 1996), marine mammals (Croll et al. 2005), and commercially important fishes including salmon, rockfish, and hake (Genin et al. 1988, Yamamura et al. 1998, Tanasichuk 1999). Even organisms that do not feed directly on krill in the California Current are rarely more than two trophic links removed from krill species at some point in their life history (Field et al. 2006). Due to their high connectivity and importance as a prey species to many organisms, the annual availability of krill can have an impact on the productivity and survival of many larger predators.

Krill availability (abundance and spatial distribution) is linked to variability in the timing and amplitude of upwelling (Brinton 1976; Tanasichuk 1998), and resultant primary productivity. Upper trophic level predators demonstrate phenotypic plasticity in breeding or emigration, with limits imposed by photoperiod and other factors (Reed et al. 2009). The degree of match or mismatch in any one year of prey availability and predator demands has been

hypothesized to impact predator productivity for that year (Cushing 1990). The year 2005 in the California Current was anomalous (see special section of Geophysical Research Letters 33, L22S01 – L22S11), with significantly delayed upwelling off the California & Oregon coast (Schwing et al. 2006, Kosro et al. 2006) and low chlorophyll *a* levels from January through May north of 37° N along the West Coast of the United States (Thomas & Brickley 2006). Delayed and reduced upwelling may have led to decreased abundance of krill during 2005, and has been hypothesized to have led to mismatches (both spatial and temporal) between krill (prey) and coastal seabird populations (low reproductive success in 2005 & 2006) (Sydeman et al. 2006) and juvenile salmon entering the ocean (reducing returning adult populations in 2008 & 2009) (Lindley et al. 2009). We used mechanistic models to investigate how wintertime ocean conditions (currents and primary productivity) may have impacted the spatial and temporal distribution and biological condition of *Euphausia pacifica* off northern California in the spring of 2005. The year 2001 is considered as a “normal” year for comparison.

Methods

The coastal ocean was simulated using the Regional Ocean Modeling System (ROMS) (Shchepetkin & McWilliams 2005, Haidvogel et al. 2008), a commonly used tool that has been successfully implemented to model coastal upwelling in the California Current (Marchesiello et al. 2003, Powell et al. 2006, Di Lorenzo et al. 2008). Our ROMS model has 3 km cross-shore resolution, 6 km along-shore resolution, and 40 vertical levels. ROMS was forced with North American Regional Reanalysis (NARR) atmospheric data from the National Center for Environmental Prediction (NCEP) at three-hour intervals. The forcing was parameterized using an approximation detailed by Fairall et al. (1996). Data for initial conditions and boundary conditions is from a monthly climatology from the Estimating the Circulation and the Climate of the Ocean, Phase II (ECCO2) model (Menemenlis et al. 2008). A Nutrient-Phytoplankton-Zooplankton-Detritus (NPZD) ecosystem model was incorporated into ROMS and run simultaneously. NPZD model equations and parameterization are described by Powell et al. (2006) and Fiechter et al. (2009) with the only change in parameterization being the detritus remineralization rate reduced to 0.1 d^{-1} . The ROMS/NPZD model was spun up from initial conditions for one year before the collection of data began and averaged daily values of model variables were saved for analysis. ROMS results were validated using MODIS-A (Moderate Resolution Imaging Spectroradiometer – Aqua satellite) data products.

Euphausia pacifica population biology was simulated using the individual-based model (IBM) POPCYCLE (Batchelder & Miller 1989, Batchelder et al. 2002). POPCYCLE uses output from the ROMS/NPZD model to provide physical ocean conditions and phytoplankton (food source) to the individuals. For each time step, individuals undergo growth according to parameters from Ross et al. (1982a, 1982b). Growth is scaled according to phytoplankton concentration based on an empirical equation of feeding rates of *E. pacifica* under varying food conditions (Ohman 1984). Life stage progression is determined by weight gain

based on laboratory studies of development (Ross 1981, Feinberg et al. 2006). Weight loss beyond the midpoint weight of the previous life stage results in starvation mortality. Diel vertical migration was implemented in a similar fashion to Batchelder et al. (2002) using a maximum swim speed reported by Torres and Childress (1983). Individuals younger than furcilia IV did not vertically migrate, furcilia IV-VII larvae weakly migrated, and juveniles and adults consistently migrated. Individuals were seeded over the continental shelf from the southern model boundary to Cape Mendocino (4,911 total individuals). Individuals representing furcilia III larvae (weight of 40 μg carbon) were seeded on January 5, based on the dominance of early larval stages in January 2002 samples (Dorman et al. 2005). For the results reported in this manuscript, predation mortality and reproduction were not implemented during the model runs.

Results

We contrasted along-shore currents in 2005 with those in 2001. In 2001, equatorward (poleward) currents were stronger (weaker) than in 2005 (Figure 3.1). Averaged monthly currents inshore of the continental shelf break (~ 60 km) from Point Reyes to Cape Mendocino exhibited weak equatorward (negative sign) currents during January (-0.016 m s^{-1}) and March (-0.007 m s^{-1}) of 2001, and weak poleward currents during February 2001 (0.035 m s^{-1}). Strong poleward currents were observed in January 2005 (0.131 m s^{-1}), and weak equatorward currents during February (-0.010 m s^{-1}) and March (-0.029 m s^{-1}) of 2005. Mean chlorophyll *a* concentration within 100 km of the coastline was low during winter of both years (Figure 3.2). Increased chlorophyll *a* concentration occurred later in the year during 2005, with only one upwelling event prior to year-day 150 (Figure 3.2).

Individuals released in 2005 moved much further to the north earlier in the year than in 2001 (Figure 3.3, Figure 3.4). On February 1, March 1, and April 1 of 2001, the cumulative number of individuals advected north of 40.5° N latitude (the approximate latitude of Cape Mendocino) was 34 (0.6%), 228 (4.6%), and 528 (10.8%), respectively. On February 1, March 1, and April 1 of 2005, the cumulative number of individuals advected north of 40.5° N latitude was 521 (10.6%), 527 (10.7%), and 731 (14.9%), respectively.

Mortality due to starvation occurred in both years, but was greater in 2005 than in 2001. Starvation of individuals that never progressed beyond the initial seeded stage (furcilia III) was prominent during winter of both years, with 31.9 % and 45.2 % of furcilia III larvae dying in 2001 and 2005, respectively. Starvation of furcilia IV-VII larvae, juvenile, and adult stages was more prominent during 2005, with 3.8% and 21.8% of those individuals that molted beyond the furcilia III stage dying in 2001 and 2005, respectively (Figure 3.5). Starvation of individuals advected north of 40.5° N latitude in January was high in 2001 and 2005 with 82.4% and 92.9% of individuals starving, respectively. Starvation was much lower to the north of 40.5° N latitude in February and March of 2001, with 3.6% and 10.0% of individuals starving, respectively. In this region during 2005, 100% and 31.8% of individuals starved in February and March, respectively.

Discussion

These modeling results do not attempt to explore interannual differences in the krill population biology leading up to January or differences in predation during the winter/spring that might impact our results. By limiting the variability of the initial population, we are able to highlight the impacts of the physical and environmental conditions on the population biology. There is very little wintertime information on the population biology of krill in our region of interest and no data to suggest there would be extreme differences in wintertime populations during 2001 and 2005. Additionally, primary producers and consumers in the northern California Current are generally considered to be controlled by bottom-up (physical) forces (Largier et al. 2006), thus it seems reasonable to omit predation as a variable that impacts our model results.

Differences in winter alongshore currents during the years 2001 and 2005 resulted in variation in the spatial distribution of *Euphausia pacifica* individuals. The most striking advection event during these simulations was in January 2005, when individuals were advected poleward by nearshore northward flowing currents (Figure 3.3b). This event effectively moved all individuals that were seeded below Point Sur, California, to the north of Monterey Bay and advected over 10% of the population north of Cape Mendocino. There is often poleward flow in the California Current during wintertime (Hickey 1998), but 2005 was unique in the strength and duration of the poleward advection. As the upwelling season occurs later in the year as one moves poleward in the California Current, individuals in 2005 were transported into a region of reduced southerly transport that was still months away from upwelling-driven phytoplankton blooms. Thus, these individuals experienced high starvation mortality and weak equatorward currents over the subsequent months, resulting in few of the surviving individuals returning to the south. A poleward advection event in late February of 2001 resulted in much less starvation mortality as food resources were more prevalent at this later time of the year and individuals were ultimately distributed back to the seeded model domain later in the year as persistent equatorward currents developed in the region.

Lower food resources throughout the model domain during 2005 also impacted survivorship and the biological condition of individuals. The initial cohort of individuals (seeded as furcilia III larvae) experienced high mortality within the first 40 days of the model run during both 2001 and 2005 (albeit higher in 2005). The high mortality of larvae observed near day 35 of both years (Figure 3.3) is a byproduct of seeding all individuals the same weight, but high mortality of larvae, with lower energy reserves, is to be expected during winter in the California Current when food resources are generally low and were particularly poor in 2005. Individuals that progressed to late larval (furcilia IV-VII), juvenile and adult stages experienced high starvation mortality during 2005, with individuals starving both nearshore and offshore due to the delayed onset of upwelling-driven primary productivity. During 2001, late larval, juvenile and adult stages rarely experienced starvation except in unproductive offshore regions. Through advection and starvation, fewer individuals remained in the model

domain during 2005, and those individuals that remained had a lower mean weight due to reduced food resources.

Reduced krill availability and decrease in krill condition during 2005 likely impacted many higher trophic level predators that rely on them as a food source. Smaller prey size can impact predators in a variety of ways depending on predator foraging strategies, but in general, smaller prey size requires increased predator foraging effort to achieve comparable energy gain. Seabirds, such as Cassin's auklets (*Ptychoramphus aleuticus*) in the Gulf of the Farallons, require food resources within about 60 km of their colonies to successfully reproduce (Abraham & Sydeman 2004, 2006). Similarly, young salmon entering the ocean require abundant prey for successful first-feeding and initial survival at sea. Our model indicates that the diminished prey availability in the northern California region was due to anomalous poleward transport during winter 2005 and low survival of krill during spring 2005. The effect of these oceanographic anomalies has been long-term, with reductions in salmon populations through at least 2009, resulting in the closure of critical fisheries and causing socio-economic damage in excess of \$1B. The importance of this result and understanding krill population dynamics to societal concerns, therefore, is substantial.

References

- Abraham CL, Sydeman WJ (2004) Ocean climate, euphausiids and auklet nesting: inter-annual trends and variation in phenology, diet and growth of a planktivorous seabird, *Ptychoramphus aleuticus*. *Mar Ecol Prog Ser* 274: 235-250
- Abraham CL, Sydeman WJ (2006) Prey-switching by Cassin's auklet *Ptychoramphus aleuticus* reveals seasonal climate-related cycles of *Euphausia pacifica* and *Thysanoessa spinifera*. *Mar Ecol Prog Ser* 313: 271-283
- Ainley DG, Spear LB, Allen SG (1996). Variation in the diet of Cassin's auklet reveals spatial, seasonal, and decadal occurrence patterns of euphausiids off California, USA. *Mar Ecol Prog Ser* 137:1-10
- Batchelder HP, Miller CB (1989) Life history and population dynamics of *Metridia pacifica*: results from simulation modeling. *Ecol Model* 48: 113-136
- Batchelder HP, Edwards CA, Powell TM (2002) Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. *Prog Ocean* 53: 307-333
- Brinton E (1962) The distribution of Pacific euphausiids. *Bull Scripps Inst Oceanogr* 8: 51-269
- Brinton E (1976) Population biology of *Euphausia pacifica* off southern California. *Fish Bull US Natl Mar Fish Serv* 74: 733-762
- Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling ecosystem. *Mar Ecol Prog Ser* 289: 117-130
- Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match-mismatch hypothesis. *Adv Mar Biol* 26: 249-293
- Di Lorenzo E, Schneider N, Cobb KM, Franks PJS, Chhak K, Miller AJ, McWilliams JC, Bograd SJ, Arango H, Curchitser E, Powell TM, Rivière P (2008) North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophys Res Lett* 35: L08607, doi:10.1029/2007/GL032838
- Dorman JG, Bollens SM, Slaughter AM (2005) Population biology of euphausiids off northern California and effects of short time-scale wind events on *Euphausia pacifica*. *Mar Ecol Prog Ser* 288: 183-198

Fairall CW, Bradley EF, Rogers DP, Edson JB, Young GS (1996) Bulk parameterization of air-sea fluxes for Tropical Ocean-Global Atmosphere Coupled-Ocean Atmosphere Response Experiment. *J Geophys Res* 101: 1295-1308

Feinberg LR, Shaw CT, Peterson WT (2006) Larval development of *Euphausia pacifica* in the laboratory: variability in the developmental pathways. *Mar Ecol Prog Ser* 316: 127-137

Fiechter J, Moore AM, Edwards CA, Bruland KW, Di Lorenzo E, Lewis CVW, Powell TM, Curchitser EN, Hedstrom K (2009) Modeling iron limitation of primary production in the coastal Gulf of Alaska. *Deep-Sea Res II* 56: 2503-2519, doi:10.1016/j.dsr2.2009.02.010

Field JC, Francis RC, Aydin K (2006) Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Prog Ocean* 68: 238-270, doi:10.1016/j.pocean.2006.02.010

Genin A, Haury L, Greenblatt P (1988). Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. *Deep-Sea Res II*: 151-175

Haidvogel DB, Arango H, Budgell WP, Cornuelle BD, Curchitser E, Di Lorenzo E, Fennel K, Geyer WR, Hermann AJ, Lanerolle L, Levin J, McWilliams JC, Miller AJ, Moore AM, Powell TM, Shchepetkin AF, Sherwood CR, Signell RP, Warner JC, Wilkin J (2008) Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modeling System. *J Comp Phys* 227: 3595-3624, doi:10.1016/j.jcp.2007.06.016

Hickey BM (1998) Coastal oceanography of western North America from the tip of Baja California to Vancouver Island. in *The Sea*, vol. 11, edited by A. R. Robinson and K. H. Brink, pp. 345-393, John Wiley, Hoboken, N. J.

Kosro PM, Peterson WT, Hickey BM, Shearman RK, Pierce SD (2006) Physical versus biological spring transition: 2005. *Geophys Res Lett* 33: L22S03, doi:10.1029/2006GL027072

Largier JL, Lawrence CA, Roughan M, Kaplan DM, Dever EP, Dorman CE, Kudela RM, Bollens SM, Wilkerson FP, Dugdale RC, Botsford LW, Garfield N, Kuebel Cervantes B, Koračin D(2006) WEST: A northern California study of the role of wind-driven transport in the productivity of coastal plankton communities. *Deep-Sea Res II* 53: 2833-2849, doi:10.1016/j.dsr2.2006.08.018

Lindley ST, Grimes CB, Mohr MS, Peterson W, Stein J, Anderson JT, Botsford LW, Bottom DL, Busack CA, Collier TK, Ferguson J, Garza JC, Grover AM,

Hankin DG, Kope RG, Lawson PW, Low A, MacFarlane RB, Moore K, Palmer-Zwahlen M, Schwing FB, Smith J, Tracy C, Webb R, Wells BK, Williams TH (2009). What caused the Sacramento River fall Chinook stock collapse? Report to the Pacific Fishery Management Council

Marchesiello P, McWilliams JC, Shchepetkin A (2003) Equilibrium structure and dynamics of the California Current System. *J Phys Ocean* 33: 753-783

Menemenlis D, Campin J, Heimbach P, Hill C, Lee T, Nguyen A, Schodlok M, Zhang H (2008) ECCO2: High resolution global ocean and sea ice data synthesis. *Mercator Ocean*. 31: 13-21

Ohman MD (1984) Omnivory by *Euphausia pacifica*: the role of copepod prey. *Mar Ecol Prog Ser* 19: 125-131

Powell TM, Lewis CVW, Curchitser EN, Haidvogel DB, Hermann AJ, Dobbins EL (2006) Results from a three-dimensional, nested biological-physical model of the California Current System and comparisons with statistics from satellite imagery. *J Geophys Res* 111, C07018, doi:10.1029/2004/JC002506

Reed TE, Warzybok P, Wilson AJ, Bradley RW, Wanless S, Sydeman WJ (2009) Timing is everything: flexible phenology and shifting selection in a colonial seabird. *J Anim Ecol* 78: 376-387, doi:10.1111/j.1365-2656.2008.01503.x

Ross RM (1981) Laboratory culture and development of *Euphausia pacifica*. *Limnol Oceanogr* 26: 235-246

Ross RM (1982a) Energetics of *Euphausia pacifica*. I. Effects of body carbon and nitrogen and temperature on measured and predicted production. *Mar Biol* 68: 1-13

Ross RM (1982b) Energetics of *Euphausia pacifica*. II. Complete carbon and nitrogen budgets at 8° and 12°C throughout the life span. *Mar Biol* 68: 15-23

Schwing FB, Bond NA, Bograd SJ, Mitchell T, Alexander MA, Mantua N (2006) Delayed coastal upwelling along the U.S. West Coast in 2005: A historical perspective. *Geophys Res Lett* 33, L22S01, doi:10.1029/2006GL026911.

Shchepetkin AF, McWilliams JC (2005) The regional ocean modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Model* 9: 347-404, doi:10.1016/j.ocemod.2004.08002

Sydeman, WJ, Bradley RW, Warzybok P, Abraham CL, Jahncke J, Hyrenbach KD, Kousky V, Hipfner JM, Ohman MD (2006) Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual

atmospheric blocking? Geophys Res Lett 33: L22S09,
doi:10.1029/2006GL026736

Tanasichuk RW (1998) Interannual variations in the population biology and productivity of *Euphausia pacifica* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. Mar Ecol Prog Ser 173: 163-180

Tanasichuk RW (1999) Interannual variation in the availability and utilization of euphausiids as prey for Pacific hake (*Merluccius productus*) along the south-west coast of Vancouver Island. Fish Oceanogr 8: 150-156

Thomas AC, Brickley P (2006) Satellite measurements of chlorophyll distribution during spring 2005 in the California Current. Geophys Res Lett 33, L22S05, doi:10.1029/2006GL026588

Torres JJ, Childress JJ (1983) Relationship of oxygen-consumption to swimming speed in *Euphausia pacifica* .1. Effects of temperature and pressure. Mar Biol 74: 79-86

Yamamura O, Inada T, Shimazaki K(1998) Predation on *Euphausia pacifica* by demersal fishes: predation impact and influence of physical variability. Mar Biol 132: 195-208

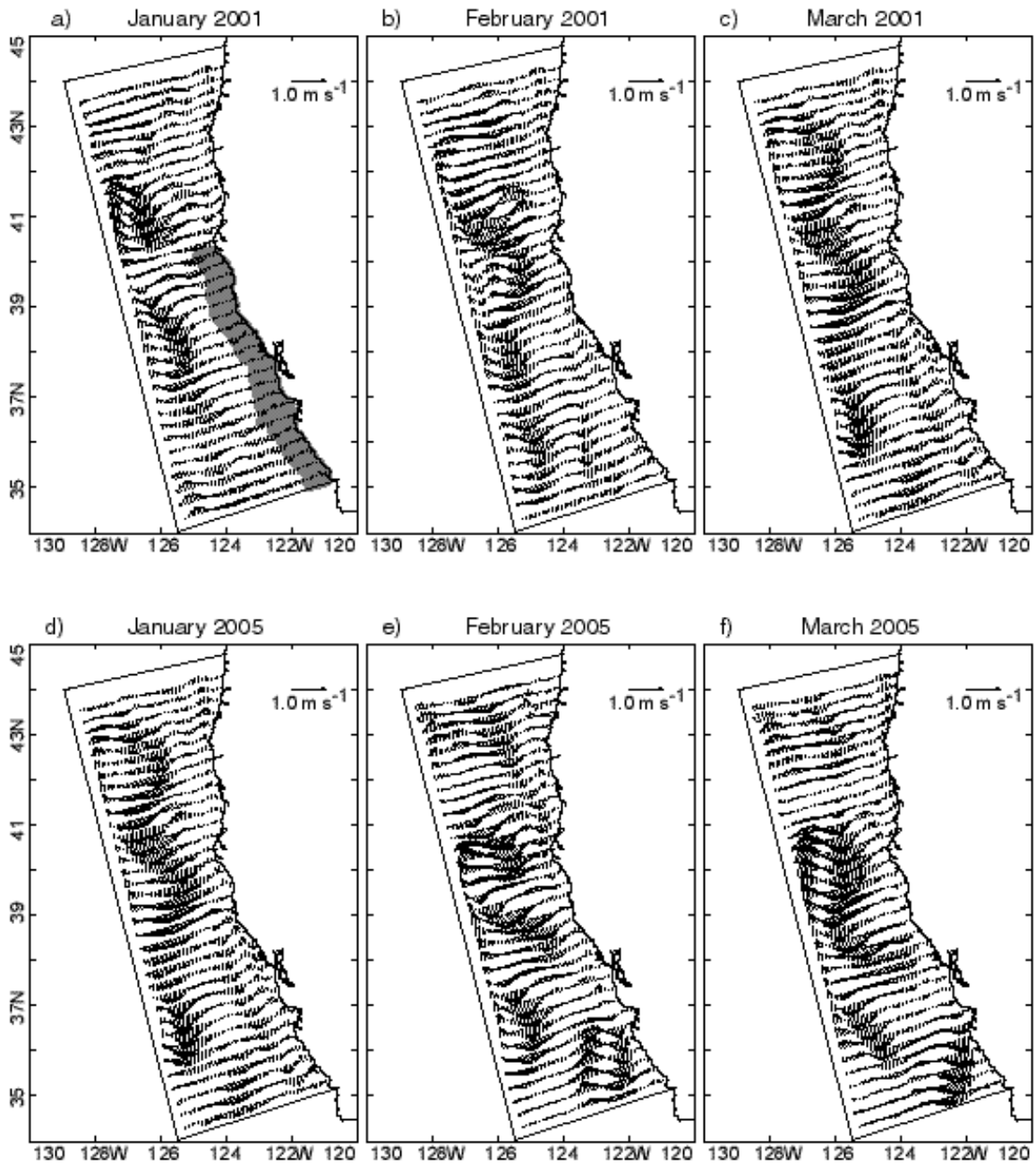


Figure 3.1. January, February, and March mean surface currents during 2001 (a-c) and 2005 (d-f). Initial seeding location on year-day 5 is shown in gray (a).

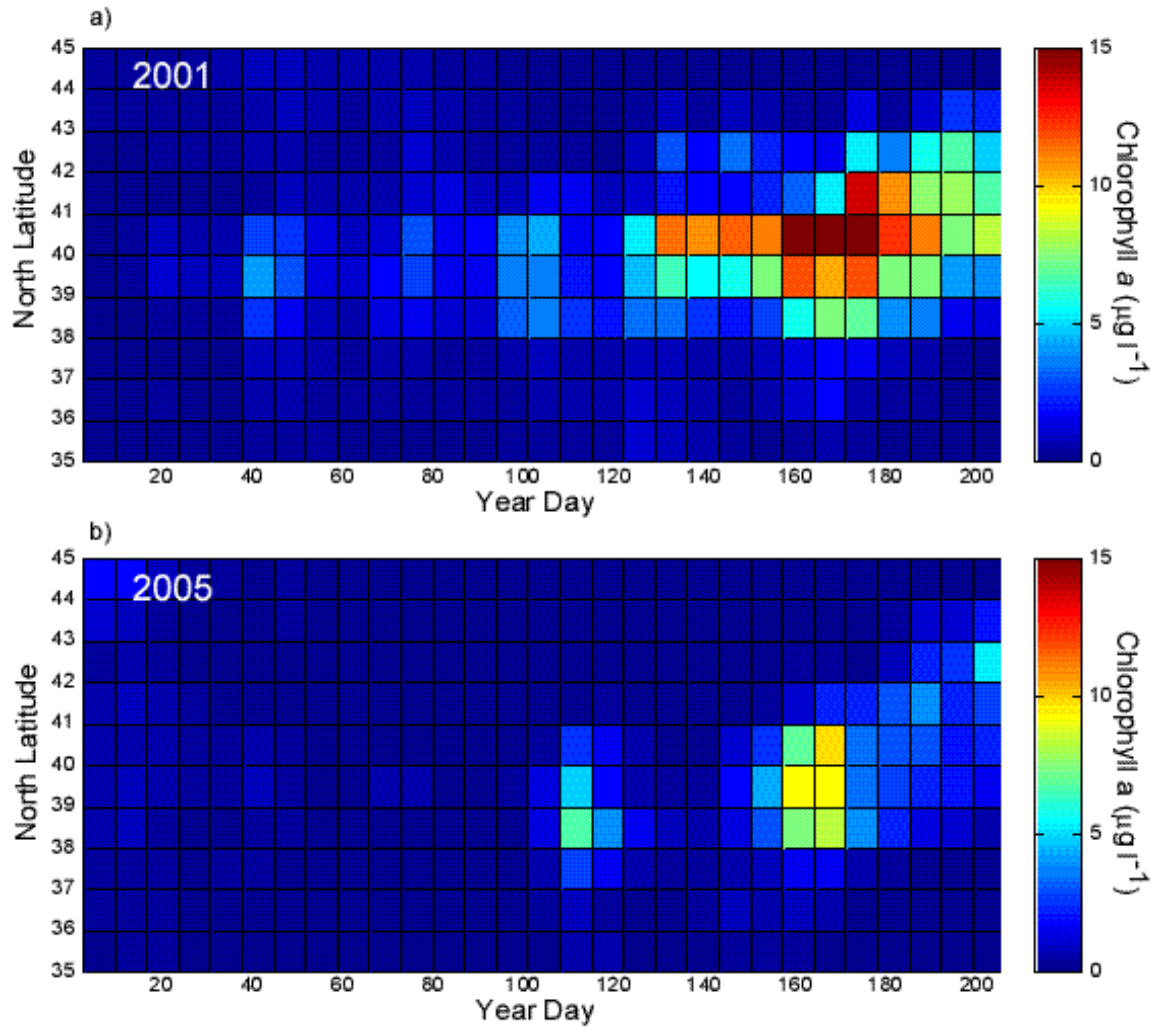


Figure 3.2. Mean weekly chlorophyll a concentration within 100 km of the coastline during (a) 2001 and (b) 2005.

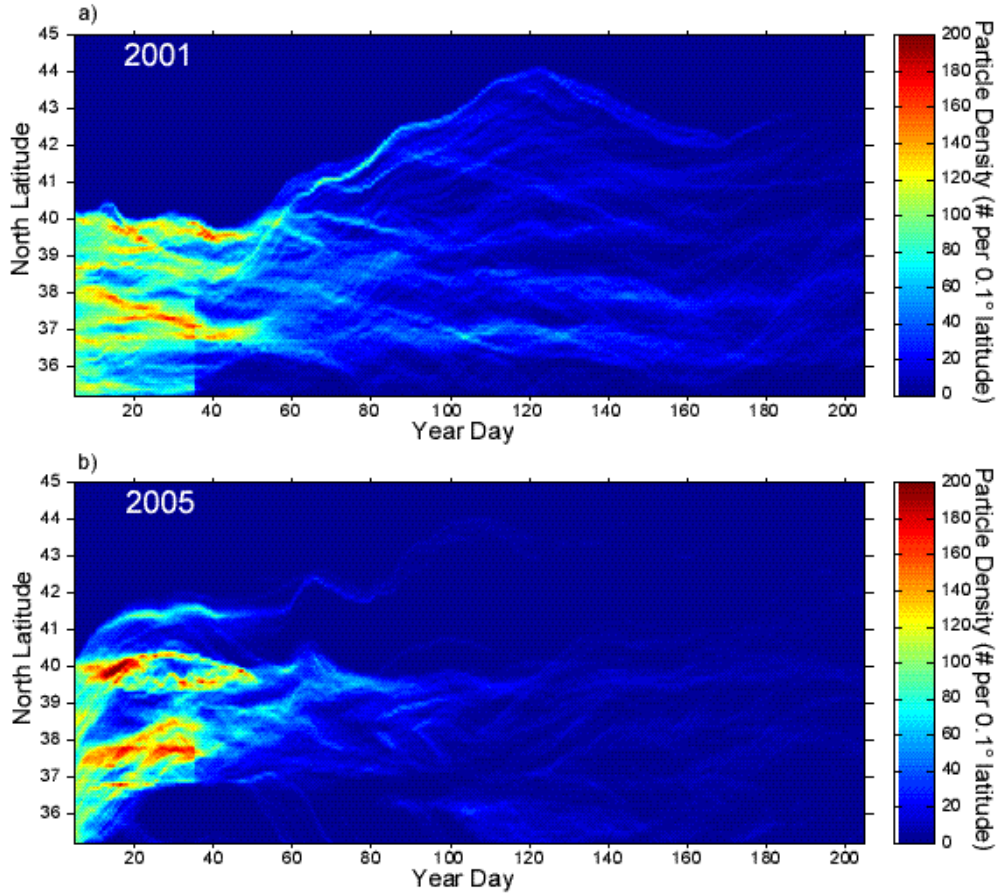


Figure 3.3. Individual density (# per 0.1° latitude) within 100 km of the coastline during (a) 2001 and (b) 2005. Note the northward advection of individuals in January 2005 and greater number of individuals in 2001.

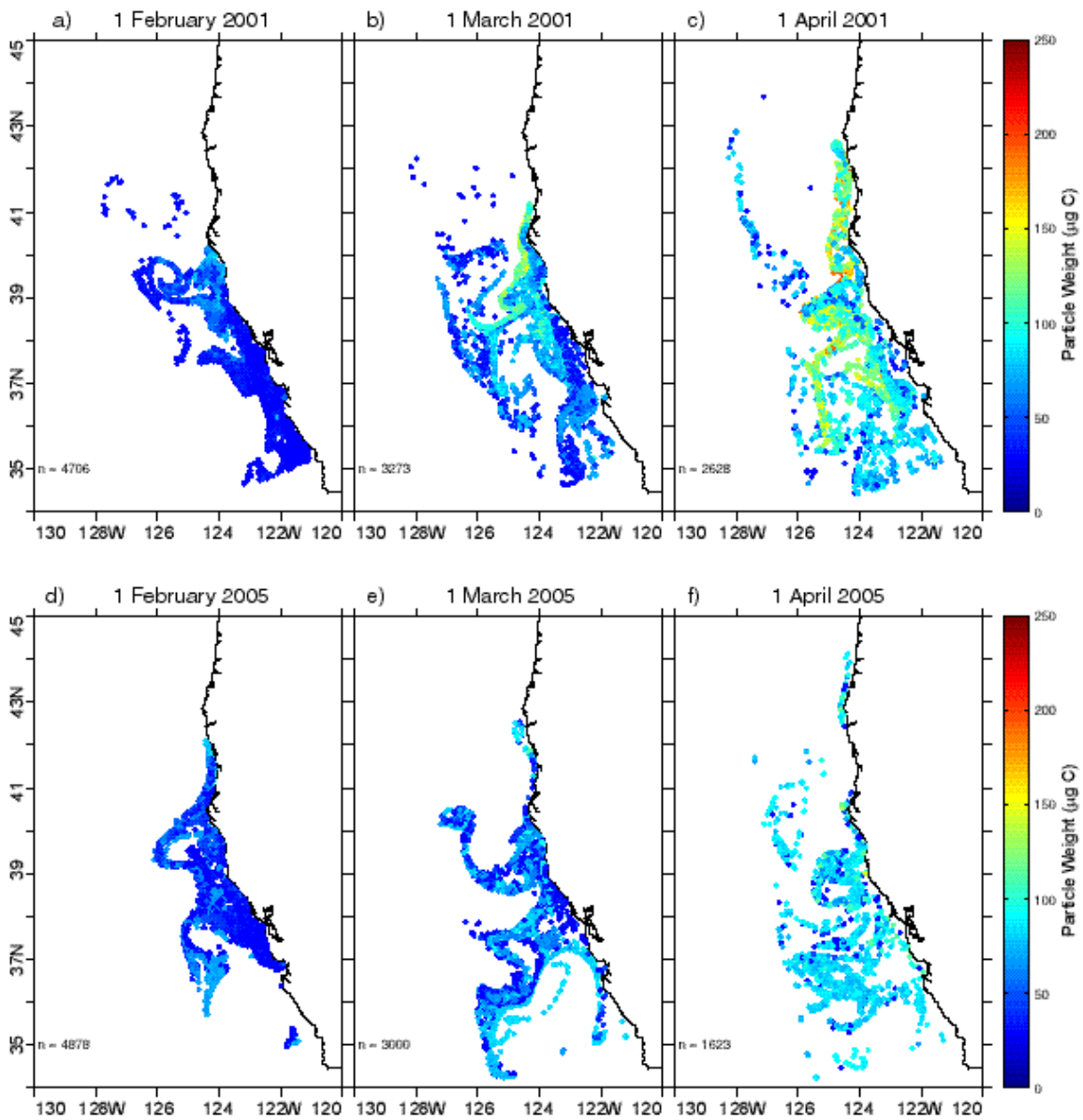


Figure 3.4. Individual distribution and individual weight (color axis) on 1 February, 1 March, and 1 April during 2001 (a-c) and 2005 (d-f).

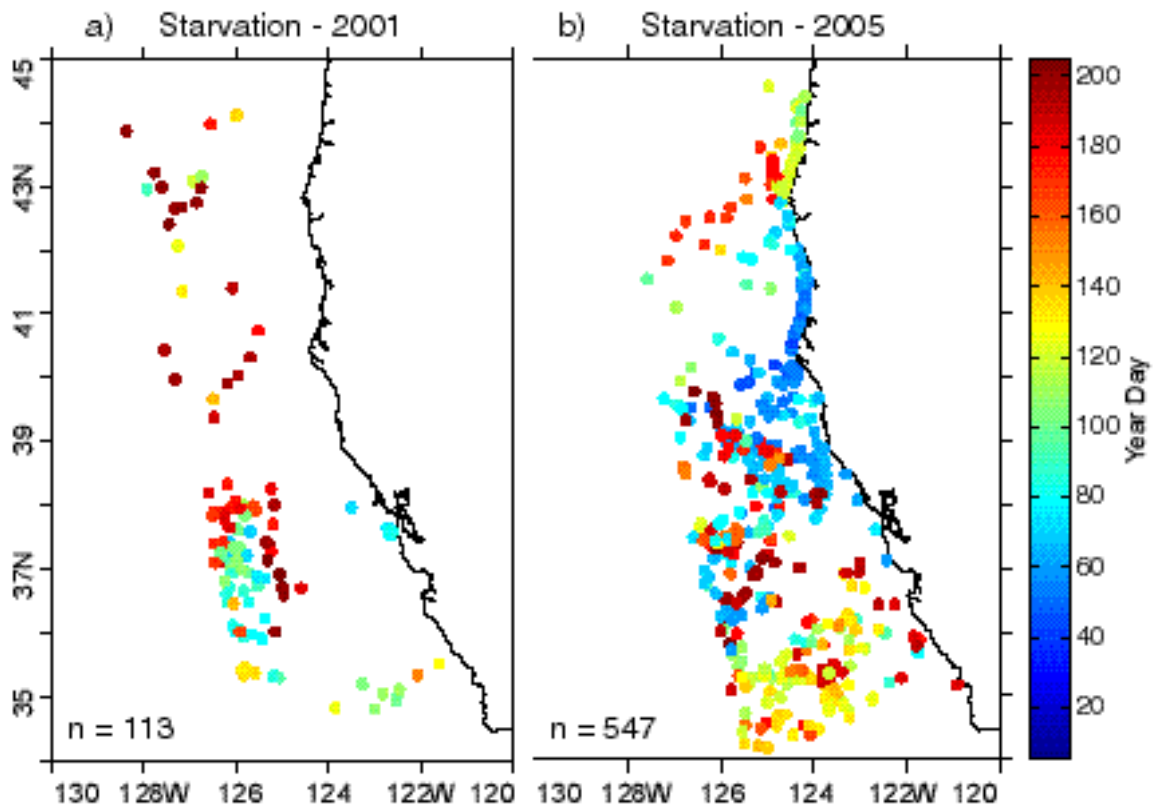


Figure 3.5. Starvation location of furcilia IV-VII, juvenile and adult *Euphausia pacifica* during 2001 (a) and 2005 (b). Color axis shows year-day of starvation.

Chapter 4

Seasonal and decadal trends in krill (*Euphausia pacifica*) population biology in the northern California Current.

Introduction

The upwelling ecosystem off California's coast is one of the most productive regions of the world's oceans (Pauly & Christensen 1994). Southerly winds along the coast of California, move surface water offshore resulting in the upwelling of cold nutrient-rich water, which provides the base of a highly productive food web. Upwelling along the coast is driven entirely by atmospheric conditions and varies on seasonal, interannual, and decadal time scales.

Seasonal variability in upwelling is driven by more intense upwelling favorable winds during the spring and summer months along the northern California coast. Intermittent upwelling favorable and downwelling favorable conditions dominate wintertime months. This seasonal cycle in forcing conditions sets up a seasonal biological response that can be evident up to the highest trophic levels. Primary producers (diatom dominated) and small zooplankton populations (e.g. copepod) can typically respond to seasonal variability in upwelling events via increases in population abundance or productivity on the order of days to weeks. Thus these organisms tend to be in synchrony with intermittent forcing events. Longer lived organisms, such as krill, can respond to these variable forcing events via eggs production and release (Brinton 1976), but are also constrained by development times to reproductive maturity that can last up to one year. Thus, these organisms are equally influenced by longer time scale variability that occurs on a yearly or decadal nature.

The productivity of the California Current is also subject to longer time-scale forcing which impacts overall productivity through changes in atmospheric forcing and through the changes in large-scale circulation patterns into and out of the coastal region. There are three dominant atmospheric regimes that occur in the North Pacific Ocean on a time-scale greater than one year and each have major consequences on the physical and biological conditions in the California Current. El Niño Southern Oscillation (ENSO) events are highly variable events that typically occur every 2-7 years and generally persist from 6 to 18 months. ENSO events impact the California Current primarily through the transport of warmer surface water northward up the west coast of North America, increasing the strength of the thermocline and reducing the amount of cold nutrient-rich water upwelled along the coast. Along with the transport of warmer water from the south comes a more southerly suite of organisms which can drastically change the community composition of both lower and higher trophic levels in the California Current (Brodeur et al. 2003, Mackas et al. 2004, Lluch-Belda et al. 2005). The Pacific Decadal Oscillation (PDO) (Mantua et al. 1997) and the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al. 2008) are two longer-term atmospheric/oceanic conditions that each describes a bi-polar state of the North Pacific Ocean. The PDO has a "warm/positive" phase that is characterized in the California Current by weakened upwelling and warmer sea surface temperatures,

and a “cool/negative” phase characterized by intensified upwelling and cooler sea surface temperatures in the California Current. The PDO has traditionally been viewed as shifting phases on a decadal time scale of 10 to 30 years but recently has shifted phase more rapidly on a sub-decadal scale (Peterson & Schwing 2003). The NPGO operates on a smaller spatial scale and tends to impact the northern and southern regions of the California Current differently. The NPGO, while also associated with sea surface temperature, is more closely associated with upwelling favorable winds, salinity, nutrients, and chlorophyll *a* levels, all variables that are indicators of upwelling of water from depth. Each of these long time scale forcings impact the region both through changing atmospheric conditions and through the increased/decreased transport of water masses, and their associated biological community, into and out of the California Current coastal region.

The California Current upwelling ecosystem is generally considered to be “bottom” forced domain (Largier et al. 2006), thus these short and long time scale variations in atmospheric conditions can have significant impacts on the ecosystem of the region. The krill species *Euphausia pacifica* plays an important role in the California Current ecosystem in the transfer of primary production to higher trophic levels (Field et al. 2006). *E. pacifica* is the most numerous euphausiid in the coastal regions of the west coast of the United States and Canada (Brinton 1976, Tanasichuk 1998, Marinovic et al. 2002, Gómez-Gutiérrez et al. 2005, Dorman et al. 2005) and has been identified as a dominant prey item for many higher trophic level predators including fishes, seabirds, and whales (Brodeur & Pearcy 1992, Reilly et al. 1992, Ainley et al. 1996, Tanasichuk 1999, Croll et al. 2005). There can be a tremendous amount of interannual variability of krill along the California coast (Santora et al. 2011), and periods of low krill productivity have been hypothesized to have major repercussions at higher trophic levels (Sydeman et al. 2006, Lindley et al. 2009).

Considering the importance of krill to many higher trophic levels in the California Current and the degree of variability that has been observed in population abundance of krill, understanding how these physical drivers (from event to inter-decadal scale) impact krill population biology is important for our fisheries management. Field sampling of *E. pacifica* has yielded a significant amount of knowledge about the seasonal variability in the population biology of *E. pacifica*. Seasonal cycles in growth rates (Bollens et al. 1992), stage structure (Dorman et al. 2005), and reproduction (Gómez-Gutiérrez et al. 2007) have all been identified using field methods. The use of field samples with regards to longer time-scale variability such as the PDO or ENSO though, requires extensive temporal data sets of a minimum of over 20 years that are sampled at a minimum of 4 times per year. These types of data sets exist in only two locations on the West Coast of the United States. For over 60 years, the Southern California Region has been extensively sampled by the California Cooperative Oceanic Fisheries Investigations program (CalCOFI) (Bograd et al. 2003). The Southern California region is characteristically very different than the Northern California coast, both in terms of width of the continental shelf (wide, shallow, respectively) and in terms of the timing and magnitude of upwelling

(consistent & weak, seasonal & strong, respectively). The other long-term sampling site on the West Coast of the United States is off Newport, Oregon (Huyer et al. 2007). While this region is similar to northern California in bathymetry and the seasonal nature of upwelling, the northern California region experiences more intense upwelling and intermittent upwelling event year round, while Oregon experiences more strict seasonal summer upwelling and is more influenced by the flow of the northern extension of the North Pacific gyre. Considering the paucity of information on the trends of zooplankton, and specifically *E. pacifica*, in the northern California region on a multi-decadal time scale, the use of models to investigate the response of these organisms to long time-scale atmospheric forcing is necessary.

We will investigate the seasonal and inter-decadal response of the population biology to both seasonal and long-term climate variability in the northern California region. The analysis of the population biology of *Euphausia pacifica* in relation to climate indicators such as the PDO and the NPGO will give insight into the role that large scale climate variability can play on lower trophic level prey in the California Current.

Methods

ROMS. The coastal ocean was simulated using the Regional Ocean Modeling System (ROMS) (Shchepetkin & McWilliams 2005, Haidvogel et al. 2008), a free-surface hydrostatic model with a terrain-following coordinate system that solves the primitive equations of motion. ROMS has been commonly used to model the coastal ocean and upwelling ecosystems such as the California Current (Powell et al. 2006, Di Lorenzo et al. 2008). To model the northern California coastal region, we created a model domain that ranges from Newport, Oregon to Point Conception, California and extends approximately 450 km offshore. The model grid is rotated approximately 20° so that the “north/south” axis is in line with the average coastline angle and model grid resolution is approximately 3 km in the cross-shelf direction and 6 km in the alongshore direction (Figure 4.1). An ecosystem model of nutrients, phytoplankton, zooplankton, and detritus (NPZD) (Powell et al. 2006) was run concurrently with ROMS and model output was saved at daily intervals.

Atmospheric interactions with the ROMS ocean (momentum and heat fluxes) are parameterized using a formulation developed by Fairall et al. (1996). Atmospheric variables needed to force the model are shortwave radiation, downward longwave radiation, air temperature, relative humidity, precipitation, and wind speed. These data were downloaded from the National Centers for Environmental Predictions (NCEP) North American Regional Reanalysis (NARR) database. The data was interpolated from the NARR grid, which is approximately 0.3° longitude resolution, to our ROMS grid using a triangle-based linear interpolation scheme based on Delaunay triangulation of the data. The temporal resolution of the atmospheric forcing data is every three hours.

Physical boundary and initial conditions for the model were obtained from the Estimating the Coastal Circulation of the Ocean (ECCO2) model (Menemenlis et al. 2008). Data obtained from ECCO2 were water temperature,

salinity, and current velocities. These data were interpolated from the ECCO2 grid onto our ROMS grid using the same methods employed for the atmospheric forcing data. In certain locations, primarily in the deep ocean, differences in the grid resolution of the two models (ECCO2 and ROMS) resulted in no data available to interpolate to the ROMS grid. In these instances, interpolated data on the ROMS grid at the nearest grid point was duplicated. Each occurrence of this lack of data occurred in thousands of meters of water, well away from our region of biological interest (surface waters). The temporal resolution of the physical boundary conditions is a monthly climatology.

Biological boundary conditions for the NPZD model were obtained from data collected from the Newport hydrographic line (Huyer et al. 2007) from 1997 through 2004 and downloaded from the GLOBEC data products website. Nitrate and chlorophyll *a* values were averaged into a monthly climatology and interpolated onto the northern boundary. For boundary locations beyond the offshore extent of the Newport hydrographic line (~85 km), the most offshore values of line (station NH85) were used. For boundary grid points deeper than what was sampled on the NH line, the deepest sampled data was used. Zooplankton boundary values were set to 10% of phytoplankton values and detritus boundary values were set to zero. As there is no comparable sampling line near the southern boundary of our model domain, the same values that were derived for the northern boundary were used for the southern boundary. As the majority of the flow through the domain is from north to south, the values at the southern edge of the domain are far less critical for the results within the model domain. Western boundary values for nitrate, phytoplankton, zooplankton and detritus were all set to zero as flow is generally parallel to the model boundary and our interest is more in the coastal realm. Biological initial conditions were constant throughout the domain (17 $\mu\text{mol N}$, 1 $\mu\text{mol P}$, 1 $\mu\text{mol Z}$, 1 $\mu\text{mol D}$).

The ROMS model was run for the years 1991-2008. For each year modeled, ROMS was spun up from initial conditions for six months (July 1 – December 31 of the prior year) before data collection began. The spin up time was determined to be long enough so that biological and physical initial conditions were no longer influencing model results (Powell et al. 2006).

POPCYCLE. The oceanographic model was run to provide forcing to a 3-dimensional individual based model (IBM) called POPCYCLE. POPCYCLE was originally developed as a 1D model to simulate copepods by Batchelder & Miller (1989) and has subsequently been updated to interface with ROMS and track individuals in both 2 and 3-dimensions (Batchelder et al. 2002, Batchelder 2006). We have parameterized the bioenergetics of the model to represent the krill species *Euphausia pacifica*, based primarily on the work of Ross (1979, 1981, 1982a, 1982b), Ohman (1984), and Feinberg et al. (2006, 2007). For a full accounting of the details of the IBM (interface with ROMS, bioenergetics of *Euphausia pacifica*, and particle tracking), please see chapter 2 of this thesis.

To look at long time-scale changes in krill population biology, we ran two “suites” of model runs over the years 1991-2008. Each suite consisted of 144 model runs, eight per year over 18 years, and each model run lasted for 180 days. Model start dates were the first day of February, April, May, June, August,

September, October, and December for each of the years modeled (Figure 4.2). For the “adult suite” of runs, all individuals were placed in the domain as adults at 3000 μg Carbon weight (approximately 17.5 mm length), and for the “larval suite” of runs, all individuals began as eggs at 2.58 μg Carbon weight. For each model run ~10,500 individuals were evenly seeded within 60 km of the coastline throughout the model domain (Figure 4.1).

Analysis. Correlations between NCEP-NARR forcing data and observations were conducted using Pearson’s correlation technique. The residuals were examined for autocorrelation and accounted for using a single iteration of the Cochrane-Orcutt method if necessary. All r and p -values reported have been modified to account for autocorrelation if necessary. Wind speed, air temperature, and sea surface temperature were obtained from the National Data Buoy Center and averaged into 3-hour bins for comparison with NCEP-NARR data (winds, air temperature), and daily bins for comparison with ROMS sea surface temperature. Chlorophyll *a* concentration was downloaded from the MODIS Aqua satellite and ROMS data was averaged into 8-day bins for comparison. No corrections were made for differences in wind speed observational height (5 meters) and NCEP-NARR wind speed height (10 meters) or for differences in air temperature observation height (4 meters) and NCEP-NARR air temperature height (2 meters).

Results

Atmospheric forcing, physical and biological results of the ROMS and NPZD model were compared to data available from satellites and buoys during the year 2005. The relative accuracy with which ROMS models the environment during this year is indicative of the other years modeled.

ROMS. Correlations of NCEP-NARR forcing winds and observed wind data from eight National Data Buoy Center (NDBC) coastal buoys were significant at each station examined (Table 4.1) with the slope of a linear least-squares line not differing significantly from one for the primary range of observed data points. Underestimation of alongshore equatorward wind strength was observed at almost every station, particularly during wind events in excess of 5 m sec^{-1} (Figure 4.3).

Correlation of NCEP-NARR forcing air temperature and observed air temperature was also significant at each station examined (Table 4.2). At most stations there was an approximate 2° C increase in air temperature in the NCEP-NARR forcing data during the summer (Figure 4.4). When data from year-day 180-270 data was excluded from the analysis, correlation improved at all stations but one (NDBC Buoy 46042) and the slope of the least-squares regression line shifted closer to one (Table 4.2).

Correlation of ROMS modeled and observed sea surface temperature was significant at most of the stations examined (Table 4.3). The ROMS model was consistently biased towards warmer sea surface temperatures, with a summer bias of approximately 4° C in certain locations (Figure 4.5). Correlation improved at all stations and the slope of the least-squares regression line shifted closer to

one when data from year day 180-270 was excluded from the analysis (Table 4.3).

Surface chlorophyll *a* concentration was compared to data from the MODIS-A satellite (Table 4.4). Correlation was significant at 6 of the eight locations but the ROMS model consistently underestimated chlorophyll *a* at low levels (Figure 4.5).

POPCYCLE. All mean values reported are from the end of the 180-day model run unless otherwise noted.

Seasonal Results. Larval Suite. Average larval population weight was greatest for those runs that began on October 1 ($157.0 \pm 27.1 \mu\text{g C}$) (mean \pm 95% confidence interval of mean) and least for those runs that began on June 1 ($143.8 \pm 9.1 \mu\text{g C}$). None of the monthly means were significantly different from each other (Figure 4.6). Average larval population weight of the 100 individuals that grew the most over the model run (the 'top 100') was greatest for those runs that began on April 1 ($685.9 \pm 136.2 \mu\text{g C}$) and least for those runs that began on December 1 ($307.9 \pm 71.8 \mu\text{g C}$). The mean larval population weight of the top 100 was significantly greater for model runs beginning the first of April and May than those beginning the first of August, October, and December (Figure 4.7).

Larval mortality did not significantly differ among any of the monthly means. The greatest larval mortality occurred for model runs beginning on the October 1 (6489.1 ± 551.9 individuals) and the least amount of larval mortality occurred for model runs beginning on July 1 (5679.1 ± 584.0 individuals) (Figure 4.8).

Advection of larvae out of the northern boundary was greatest for runs beginning on December 1 (2302.6 ± 453.0 individuals) and least for runs beginning on May 1 (420.5 ± 186.3 individuals). Wintertime runs beginning on the first of October and December had significantly greater advection of larval individuals out the northern boundary than summertime runs that began on the first of April, May or June (Figure 4.9). Advection of larvae out of the southern boundary was greatest for runs that began on May 1 (1139.9 ± 271.9 individuals) and least for runs beginning on August 1 (713.5 ± 194.3 individuals). None of the monthly means were significantly different from each other (Figure 4.10). Advection of larval individuals out of the western boundary of our model domain showed a similar pattern (magnitude and timing) as advection out of the southern boundary (results not shown).

Seasonal Results. Adult Suite. Average adult population weight was greatest for those runs that began on July 1 ($2660.4 \pm 40.1 \mu\text{g C}$) (mean \pm 95% confidence interval of mean) and least for those runs that began on October 1 ($2508.6 \pm 92.2 \mu\text{g C}$). The only significant difference in all the monthly means was between the model runs that began on July 1 and those that began on October 1 (Figure 4.6). Average adult population weight of the top 100 individuals was greatest for those runs that began on May 1 ($3692.1 \pm 255.1 \mu\text{g C}$) and least for those runs that began on October 1 ($3343.0 \pm 177.5 \mu\text{g C}$). There were no significant differences between any of the monthly means (Figure 4.7). Egg production by adults was greatest for runs that began on June 1 (685220 ± 122080 eggs) and least for runs that began on October 1 ($434810 \pm$

95600 eggs). These were the only months in which significantly different numbers of eggs were produced (Figure 4.11). Egg production of the top 100 growing adults was greatest during model runs that began on May 1 (64846 ± 13686 eggs) and least for those that began on October 1 (28120 ± 5146.9 eggs). Significantly more eggs were produced by the top 100 adults for model runs that began on May, June, or July 1 than model runs that began on October, December or February 1 (Figure 4.11).

The greatest adult mortality occurred for model runs beginning on July 1 (2674.1 ± 643.6 individuals) and the least amount of mortality occurred for model runs beginning on December 1 (270.1 ± 172.1 individuals). Model runs that began in the spring and summer months April through August, all had significantly greater mortality than those that began during the winter months, October, December, and February (Figure 4.8).

Advection of adults out of the northern boundary was greatest for runs beginning on December 1 (4098.1 ± 610.1 individuals) and least for runs beginning on May 1 (372.3 ± 129.5 individuals). Model runs beginning on the first of February, August, October, and December all had significantly greater advection of adult individuals out the northern boundary than summertime runs that began on the first of April, May, June, and July (Figure 4.9). Advection of adults out of the southern boundary was greatest for runs that began on April 1 (3354.2 ± 535.3 individuals) and least for runs beginning on December 1 (2152.6 ± 414.4 individuals). Model runs beginning on December 1 had significantly fewer individuals advected out of the southern boundary than model runs that began on April or May 1 (Figure 4.10). Advection of adults out of the western boundary of our model domain showed a similar pattern (magnitude and timing) as advection out of the southern boundary (results not shown).

Decadal Results. Larval Suite. To compare POPCYCLE data with the phase of the Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO) (Figure 4.12), we subtracted the 18-year monthly means (see Figure 4.13 for an example) from each monthly value to create variable anomalies. Average larval population growth anomaly (Figure 4.13) was significantly negatively correlated with the phase of the PDO ($r = -0.20$, $p < 0.05$) (Figure 4.14) and positively correlated with the NPGO ($r = 0.33$, $p < 0.001$) (Figure 4.14). Average growth anomaly of the top 100 larvae (Figure 4.16) was not significantly correlated with the PDO ($r = -0.15$, $p = 0.078$) (Figure 4.17) and was positively correlated with the NPGO ($r = 0.25$, $p < 0.01$) (Figure 4.17). Larval population mortality anomaly (Figure 4.19) was significantly positively correlated with the phase of the PDO ($r = 0.41$, $p < 0.001$) (Figure 4.20) and negatively correlated with the NPGO ($r = -0.42$, $p < 0.001$) (Figure 4.20). No significant trends were observed regarding advection of larval individuals out of any of the boundaries and the PDO. Advection of larval individuals out of the southern boundary (Figure 4.22) was significantly correlated with the phase of the NPGO ($r = 0.28$, $p < 0.001$) (Figure 4.23).

Decadal Results. Adult Suite. Average adult population growth anomaly (Figure 4.13) was significantly negatively correlated with the phase of the PDO ($r = -0.37$, $p < 0.001$) (Figure 4.15) and positively correlated with the NPGO ($r = 0.48$,

$p < 0.001$) (Figure 4.15). Average growth anomaly of the top 100 adults (Figure 4.16) was also significantly negatively correlated with the PDO ($r = -0.40$, $p < 0.001$) (Figure 4.18) and positively correlated with the NPGO ($r = 0.39$, $p < 0.001$) (Figure 4.18). Adult population mortality anomaly (Figure 4.19) was significantly positively correlated with the phase of the PDO ($r = 0.45$, $p < 0.001$) (Figure 4.21) and negatively correlated with the NPGO ($r = -0.55$, $p < 0.001$) (Figure 4.21). No significant trends were observed regarding advection of individuals out of any of the boundaries and the PDO. Advection of adult individuals out of the southern boundary was significantly correlated with the phase of the NPGO ($r = 0.37$, $p < 0.001$) (Figure 4.23). Total number of eggs produced by adult krill was significantly negatively correlated with the phase of the PDO ($r = -0.42$, $p < 0.001$) (Figure 4.24) and positively correlated with the NPGO ($r = 0.38$, $p < 0.001$) (Figure 4.24).

Discussion

ROMS. The analysis of how well the NCEP-NARR forcing data (wind speed and air temperature) correlates with observations gives us insight into how small discrepancies in forcing data can have ramifications up the modeled food chain and the importance of bottom-up forcing in the California Current (Largier et al. 2006). The correlation of the NCEP-NARR alongshore wind to observations from the NDBC buoys was very accurate at moderate wind speeds, but the NCEP-NARR data does not capture the magnitude of upwelling favorable wind events that occur along the northern California coast. Considering that these events are the primary cause of the upwelling of nutrients into the photic zone and that the wind stress, which acts on the ocean to move the water, is proportional to the squared wind speed, the underestimation of upwelling favorable winds is concerning. The intensity of upwelling favorable winds is influenced by the coastal mountain ranges, particularly in the northern California region (Halliwell & Allen 1987). These coastal ranges may not be as accurately resolved in the topography underlying the NCEP-NARR model as the grid resolution is approximately 32 km, perhaps leading to the underestimation of the wind strength.

The discrepancy in air temperature seen in the NCEP-NARR model data, much warmer air temperatures during summer, may be due to the NCEP-NARR model not accounting for a cooler sea surface in the coastal region during summer due to intense coastal upwelling. Underlying sea surface temperatures in the NCEP-NARR model are derived from the “Reynolds” dataset, which is resolved at 1° latitude (Reynolds et al. 2002). This dataset likely does not resolve the spring/summertime upwelling of cold water in the coastal upwelling zone, which would cool the overlying air temperature in the NCEP-NARR model. Further evidence that this problem may be related to unresolved upwelling in the underlying NCEP-NARR sea surface temperature data, is evident in the spatial variability of the timing of increased NCEP-NARR air temperature. Upwelling favorable winds occur earlier in the year in the more southerly regions of the California Current and the discrepancy in air temperature data is evident at stations 46013 & 46014 as early at year-day 150, and not evident until year day

200 at stations north of Cape Mendocino (46022, 46027, 46015) (data not shown).

The impact of these discrepancies in forcing data can be seen in the comparison between ROMS sea surface temperature and phytoplankton with observations. The ROMS model least accurately represents sea surface temperature during summer, when the intensity of upwelling favorable winds is weaker than observed, resulting in weaker upwelling of cool water to the surface layers of the model. In addition to weaker winds, a warmer atmospheric layer over the ocean is also contributing to warmer sea surface temperatures. The resulting greater thermal stratification in the upper ocean requires greater energy to break down and bring colder nutrient rich waters to the surface. Thus, it is not surprising to note that during the late summer, blooms of chlorophyll *a* that are observed in the satellite data are either not present or are of a lesser magnitude in the ROMS model, as the weaker winds are not strong enough to break down thermal stratification and bring nutrients to the surface. Consideration of these discrepancies should be taken into account in our analysis of the POPCYCLE model and especially during upwelling favorable times of year.

POPCYCLE. Seasonal Patterns. Seasonal results from the POPCYCLE model agree with the consensus view of lower trophic level productivity in the California Current. The greatest growth and reproduction of the modeled krill population occurred in response to seasonal upwelling favorable conditions and the resultant phytoplankton blooms during the spring and summer months. While phytoplankton concentration is the primary driver of growth in our model, the influence of temperature on growth and mortality is evident in the model results.

While we would expect that the most productive time of year for *Euphausia pacifica* would be the spring and summer upwelling season, this was not the case in our results when analyzing the entire population. Average larval growth of the entire population was fairly constant over the seasonal cycle (Figure 4.6), despite increases in phytoplankton during the upwelling season (Figure 4.5). Adult mortality peaked during the phytoplankton rich spring and summer months when we might expect mortality to be at a minimum. Average adult growth during each month was significantly less than the starting weight of 3000 $\mu\text{g C}$. These somewhat confounding results are due to increased summer ocean temperatures and the spatial distribution of the entire population. Increases in temperature during summertime leads to increased respiratory costs for the organisms, resulting in loss of weight and ultimately greater starvation mortality. As noted in the discussion above, modeled summer sea surface temperatures were warmer than observed sea surface temperature, which may have exacerbated the weight loss and mortality results. However, the majority of individuals that are placed into the coastal domain are ultimately transported to warm, offshore waters at some point during the model run. These offshore waters are also typically less productive than coastal waters, maintaining low background levels of primary production from diffusion of nutrients up through the thermocline, as well as offshore transport of phytoplankton. Lower levels of food resources (1 to 2 $\mu\text{g l}^{-1}$ chlorophyll *a*) may allow larval populations to survive (thus peak larval mortality during winter), but not grow any faster than a typical

wintertime population. For an adult population, the lower offshore food resources appear to have a greater impact on mortality as their base metabolic needs are greater than larval populations and the background levels of chlorophyll *a* are not sufficient for survival. Laboratory experiments exposing *Euphausia pacifica* to warm temperatures under full rations of food have found that negative growth (respiration cost exceeding food intake) occurred at temperatures greater than 16.5° C (Marinovic & Mangel 1999), lending support to our conclusions. These results emphasize the importance of cool waters in keeping metabolic rates low enough and also importance of spatial dynamics in the model domain.

These results also highlight the importance of focusing and performing analyses on those individuals that are most important to the system. If our questions are centered on krill as a prey resource of higher trophic levels distributed throughout the model domain, interest in the mean condition of the entire population is certainly justified. However when examining the interannual variability of krill population biology, only those organisms that spawn eggs in inshore regions are likely to have those eggs grow to adult krill. Any eggs that are spawned in offshore regions are not likely to be advected back onshore where productivity is highest and will likely not survive. Thus, our interest may be only in those individuals that survive and grow at an above average rate. In the case of krill, and many large brood broadcast spawners, an “average individual” is likely a dead individual. Based on our model results, the average egg that any individual produces is almost certainly going to be either 1) removed from the model domain through advection or 2) is not going to survive to reproductive age. An examination of the seasonal trend in weight of the 100 larval individuals that grew the most over the model run reveals the greatest growth during the traditional spring and summer upwelling months when phytoplankton resources are greatest. The average weight of the top 100 adult individuals also exhibit the greatest growth during spring and summer upwelling and show positive growth during all parts of the year.

Transport of individuals was generally to the south (and offshore) during the spring and summer upwelling periods and to the north during wintertime downwelling conditions. These results conform to the general view of the California Current (Hickey 1998) and validate that our ROMS model is reproducing the large-scale dynamics of the system.

Decadal Patterns. The success of the model to simulate the annual cycle in upwelling and lower trophic level dynamics allows us to look at longer time series to examine how interannual variability in forcing and upwelling dynamics might impact the population biology of this important prey species over long time scales.

Our results show significant correlations between the mortality of *Euphausia pacifica* (Figure 4.20 and 4.21) and the egg production (Figure 4.24) of *E. pacifica* in the California Current and the phase of the PDO and the NPGO. Both of these aspects of the population biology of *E. pacifica* are primarily driven by variability in primary production in the coastal region and can impact the local and future abundance of the species. Regime shifts in the PDO have been shown to impact higher trophic levels through intermediary prey species

(Anderson & Piatt 1999) and considering the important role that *E. pacifica* plays in the food web of the California Current (Field et al. 2006), it is likely that this variability may also impact higher trophic level production both positively and negatively. But variations in preferred prey species can also lead to changes in prey selection, increasing predation pressure on other prey species in the regional food web. The Cassin's auklet, a common planktivorous seabird in the central California region, switches prey from *E. pacifica* to another krill species, *Thysanoessa spinifera*, every year in the spring time (Adams et al. 2004, Abraham & Sydeman 2006). Decreased abundance of *E. pacifica* might cause a switch to *T. spinifera* earlier in the season or the exploitation of another intermediate prey species. Additionally, reduced abundances can result in increased energy expenditure during foraging, and in the case of seabirds that are spatially tied to breeding and rearing sites, further migration in search of prey. All of these consequences may diminish higher trophic level productivity.

The PDO and NPGO also correlated with the amount of growth that occurred over the run-time of the model (Figure 4.15). Increased or decreased growth is essentially a change in the condition of the krill and the energy that it can impart to predators. Changes in the energetic condition of a prey can impact predators in similar ways to changes in prey abundance, but also through the timing of future peaks in abundance (Edwards & Richardson 2004), as smaller adult euphausiids will achieve reproductive maturity later in life. Smaller adults will also produce fewer and smaller reproductive broods (Gómez-Guitérrez et al. 2006, Feinberg et al. 2007), which can result in a carryover effect on population abundance from year to year. As we re-seeded the model with a constant number of individuals for each model run, we could not explore this effect.

Large time-scale climate variability (ENSO, PDO, NPGO) have been cited as drivers of changing zooplankton community composition in the California Current (Marinovic et al. 2002, Peterson & Keister 2003, Hooff & Peterson 2006) through the input of different ocean waters and their associated zooplankton community. These changes in species composition of a region often change the energetic nature of the zooplankton as a food source for higher trophic levels (more lipid rich, less lipid rich). Our results are unique in that they focus on changes within a specific species of zooplankton and its response to the climate drivers as opposed to changes in the community. The species *Euphausia pacifica* extends coastally throughout the North Pacific Ocean, from California up to Alaska and south again to Japan in the western Pacific. A shift in the origin of ocean waters to the northern California region may bring about a shift in some species of the euphausiid community, but *E. pacifica* will almost surely still be an important component of the regional food web. These results lend insight to the within-species changes we might observe in *E. pacifica* in relation to these large-scale climatic events.

In considering the results of this study it is important to remember that the boundary conditions used for ROMS are a climatological monthly mean. Thus, during years in which the phase of the PDO or NPGO is strongly negative or positive, the boundary conditions remain constant and do not reflect the properties of different water masses that move into the our model region.

Similarly, during ENSO events warmer water masses do not move into the southern model domain, as the boundary conditions do not reflect the ENSO event. The only ways in which these long time-scale events are imposed upon the model are through variable atmospheric forcing (wind speed, air temperature, relative humidity, and precipitation). This is the primary reason that we believe that all correlations between the population biology of *Euphausia pacifica* and the NPGO were greater than those correlated with the PDO. The influence of the PDO upon the domain would primarily come from changing boundary conditions and the flow of different water masses into the region, while the NPGO appears to be more directly tied to variability in upwelling favorable winds, especially for the region south of 40° N latitude (Di Lorenzo et al. 2008).

Atmospheric forcing drives the coastal domain of the California Current ecosystem and variability in the climate forcing, from short to long time scales, has been shown to be important in structuring the productivity of the ecosystem. In this modeling study, both short and long-term climate variability has been shown to impact the biological condition, mortality and reproductive potential of a critical prey item of the northern California region. The NPGO in particular was strongly correlated with indices of growth, condition and abundance for the northern California region. Any attempt at management of resources in this region should consider the impacts of these long time scale forcing indices on important lower trophic level prey items such as the krill species *Euphausia pacifica*.

References

- Abraham CL, Sydeman WJ (2006) Prey-switching by Cassin's auklet *Ptychoramphus aleuticus* reveals seasonal climate-related cycles of *Euphausia pacifica* and *Thysanoessa spinifera*. *Mar Ecol Prog Ser* 313: 271-283
- Adams J, Takekawa JY, Carter HR (2004) Stable foraging areas and variable chick diet in Cassin's auklets (*Ptychoramphus aleuticus*) off southern California. *Can J Zool* 82: 1578-1595
- Ainley DG, Spear LB, Allen SG (1996) Variation in the diet of Cassin's auklet reveals spatial, seasonal, and decadal occurrence patterns of euphausiids off California, USA. *Mar Ecol Prog Ser* 137:1-10
- Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar Ecol Prog Ser* 189: 117-123
- Batchelder HP, Edwards CA, Powell TM (2002) Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. *Prog Ocean* 53: 307-333
- Batchelder HP (2006) Forward-in-Time-/Backward-in-Time-Trajectory (FITT/BITT) modeling of particles and organisms in the coastal ocean. *J Atmos Ocean Technol* 23: 727-741
- Bograd SJ, Checkley DA, Wooster WS (2003) CalCOFI: a half century of physical, chemical, and biological research in the California Current System. *Deep-Sea Res Part II* 50: 2349-2353
- Bollens SM, Frost BW, Lin TS (1992) Recruitment, growth, and diel vertical migration of *Euphausia pacifica* in a temperate fjord. *Mar Biol* 114: 219-228
- Brinton E (1976) Population biology of *Euphausia pacifica* off southern California. *Fish Bull US Natl Mar Fish Serv* 74: 733-762
- Brodeur RD, Pearcy WG (1992) Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. *Mar Ecol Prog Ser* 84: 101-119.
- Brodeur RD, Pearcy WG, Ralson S (2003) Abundance and distribution patterns of nekton and micronekton in the Northern California Current Transition Zone. *J Oceanogr* 59: 515-535

Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling ecosystem. *Mar Ecol Prog Ser* 289: 117-130

Di Lorenzo E, Schneider N, Cobb KM, Franks PJS, Chhak K, Miller AJ, McWilliams JC, Bograd SJ, Arango H, Curchitser E, Powell TM (2008) North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophys Res Lett* 35, L08607, doi:10.1029/2007GL032838

Dorman JG, Bollens SM, Slaughter AM (2005) Population biology of euphausiids off northern California and effects of short time-scale wind events on *Euphausia pacifica*. *Mar Ecol Prog Ser* 288: 183-198

Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 403: 881-884

Fairall CW, Bradley EF, Rogers DP, Edson JB, Young GS (1996) Bulk parameterization of air-sea fluxes for Tropical Ocean-Global Atmosphere Coupled-Ocean Atmosphere Response Experiment. *J Geophys Res* 101: 1295-1308

Feinberg LR, Shaw CT, Peterson WT (2006) Larval development of *Euphausia pacifica* in the laboratory: variability in the developmental pathways. *Mar Ecol Prog Ser* 316: 127-137

Feinberg LR, Shaw CT, Peterson WT (2007) Long-term laboratory observations of *Euphausia pacifica* fecundity: comparison of two geographic regions. *Mar Ecol Prog Ser* 341: 141-152

Field JC, Francis RC, Aydin K (2006) Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Prog Ocean* 68: 238-270, doi:10.1016/j.pocean.2006.02.010

Gómez-Gutiérrez J, Peterson WT, Miller CB (2005) Cross-shelf life-stage segregation and community structure of the euphausiids off central Oregon (1970-1972). *Deep-Sea Res II* 52: 289-315

Gómez-Gutiérrez J, Feinberg LR, Shaw T, Peterson W (2006) Variability in brood size and female length of *Euphausia pacifica* among three populations in the North Pacific. *Mar Ecol Prog Ser* 323: 185-194

Gómez-Gutiérrez J, Feinberg LR, Shaw T, Peterson W (2007) Interannual and geographical variability of the brood size of the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* along the Oregon coast (1999-2004). *Deep-Sea Res I* 54: 2145-2169

Haidvogel DB, Arango H, Budgell WP, Cornuelle BD, Curchitser E, Di Lorenzo E, Fennel K, Geyer WR, Hermann AJ, Lanerolle L, Levin J, McWilliams JC, Miller AJ, Moore AM, Powell TM, Shchepetkin AF, Sherwood CR, Signell RP, Warner JC, Wilkin J (2008) Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modeling System. *J Comp Phys* 227: 3595-3624, doi:10.1016/j.jcp.2007.06.016

Halliwel GR, Allen JS (1987) The large-scale coastal wind field along the west coast of North America, 1981-1982. *J Geophys Res C* 92:1861-1884

Hickey BM (1998) Coastal oceanography of western North America from the tip of Baja California to Vancouver Island. in *The Sea*, vol. 11, edited by A. R. Robinson and K. H. Brink, pp. 345-393, John Wiley, Hoboken, N. J.

Hooff RC, Peterson WT (2006) Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California current ecosystem. *Limnol Oceanogr* 51: 2607-2620

Huyer A, Wheeler PA, Strub PT, Smith RL, Letelier R, Kosro M (2007) The Newport line off Oregon – Studies in the North East Pacific. *Prog Oceanogr* 75: 126-160

Largier JL, Lawrence CA, Roughan M, Kaplan DM, Dever EP, Dorman CE, Kudela RM, Bollens SM, Wilkerson FP, Dugdale RC, Botsford LW, Garfield N, Kuebel Cervantes B, Koračin D (2006) WEST: A northern California study of the role of wind-driven transport in the productivity of coastal plankton communities. *Deep-Sea Res II* 53: 2833-2849, doi:10.1016/j.dsr2.2006.08.018

Lindley ST, Grimes CB, Mohr MS, Peterson W, Stein J, Anderson JT, Botsford LW, Bottom DL, Busack CA, Collier TK, Ferguson J, Garza JC, Grover AM, Hankin DG, Kope RG, Lawson PW, Low A, MacFarlane RB, Moore K, Palmer-Zwahlen M, Schwing FB, Smith J, Tracy C, Webb R, Wells BK, Williams TH (2009). What caused the Sacramento River fall Chinook stock collapse? Report to the Pacific Fishery Management Council

Lluch-Belda D, Lluch-Cota DB, Lluch-Cota SE (2005) Changes in the marine faunal distributions and ENSO events in the California Current. *Fish Oceanogr* 14: 458-467.

Mackas DL, Peterson WT, Zamon JE (2004) Comparisons of interannual biomass anomalies of zooplankton along the continental margins of British Columbia and Oregon. *Deep-Sea Res II* 51: 875-896

- Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull Am Meteorol Soc* 78: 1069-1079
- Marinovic B, Mangel M (1999) Krill can shrink as an ecological adaptation to temporarily unfavourable environments. *Ecol Lett* 2: 338-343
- Marinovic BB, Croll DA, Gong N, Benson SR, Chavez FP (2002) Effects of the 1997-1999 El Niño and La Niña events on zooplankton abundance and euphausiid community composition within the Monterey Bay coastal upwelling system. *Prog Oceanogr* 54: 265-277
- Menemenlis D, Campin J, Heimbach P, Hill C, Lee T, Nguyen A, Schodlok M, Zhang H (2008) ECCO2: High resolution global ocean and sea ice data synthesis. *Mercator Ocean*. 31: 13-21
- Ohman MD (1984) Omnivory by *Euphausia pacifica*: the role of copepod prey. *Mar Ecol Prog Ser* 19: 125-131
- Pauly D, Christensen V (1994) Primary production to sustain global fisheries. *Nature* 374: 255-257
- Peterson WT, Keister JT (2003) Interannual variability in copepod community composition at a coastal station in the northern California Current: a multivariate approach. *Deep-Sea Res II* 50: 2499-2517
- Peterson WT, Schwing FB (2003) A new climate regime in northeast pacific ecosystems. *Geophys Res Lett* 30, 1896, doi:10.1029/2003GL017528
- Powell TM, Lewis CVW, Curchitser EN, Haidvogel DB, Hermann AJ, Dobbins EL (2006) Results from a three-dimensional, nested biological-physical model of the California Current System and comparisons with statistics from satellite imagery. *J Geophys Res* 111, C07018, doi:10.1029/2004/JC002506
- Reilly CA, Echeverria TW, Ralston S (1992) Interannual variation and overlap in the diets of pelagic juvenile rockfish (genus: *Sebastes*) off Central California. *Fish Bull* 90:505-515
- Reynolds RW, Rayner NA, Smith TM, Stokes DC, Wang W (2002) An improved in situ and satellite SST analysis for climate. *J Clim* 15: 1609-1625
- Ross RM (1979) Carbon and nitrogen budgets over the life of *Euphausia pacifica*. Ph.D. thesis, University of Washington. Seattle, WA, 260 p.

Ross RM (1981) Laboratory culture and development of *Euphausia pacifica*. *Limnol Oceanogr* 26: 235-246

Ross RM (1982a) Energetics of *Euphausia pacifica*. I. Effects of body carbon and nitrogen and temperature on measured and predicted production. *Mar Biol* 68: 1-13

Ross RM (1982b) Energetics of *Euphausia pacifica*. II. Complete carbon and nitrogen budgets at 8° and 12°C throughout the life span. *Mar Biol* 68: 15-23

Santora JA, Ralston S, Sydeman WJ (2011) Spatial organization of krill and seabirds in the central California Current. *ICES J Mar Sci* , doi:10.1093/icesjms/fsr046

Shchepetkin AF, McWilliams JC (2005) The regional ocean modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Model* 9: 347-404, doi:10.1016/j.ocemod.2004.08002

Sydeman, WJ, Bradley RW, Warzybok P, Abraham CL, Jahncke J, Hyrenbach KD, Kousky V, Hipfner JM, Ohman MD (2006) Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking? *Geophys Res Lett* 33: L22S09, doi:10.1029/2006GL026736

Tanasichuk RW (1998) Interannual variations in the population biology and productivity of *Euphausia pacifica* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. *Mar Ecol Prog Ser* 173: 163-180

Tanasichuk RW (1999) Interannual variation in the availability and utilization of euphausiids as prey for Pacific hake (*Merluccius productus*) along the south-west coast of Vancouver Island. *Fish Oceanogr* 8: 150-156

NDBC Buoy	Location	Alongshore Winds						
		obs. mean	model mean	obs. stddev	model stddev.	r	slope	
Buoy 46015	Port Orford, OR	-0.81	-0.22	7.19	6.31	0.79	1.08 ± 0.014	
Buoy 46027	Crescent City, CA	0.30	0.47	5.71	4.87	0.65	1.03 ± 0.023	
Buoy 46022	Eel River, CA	-0.68	-0.99	5.86	4.92	0.67	1.07 ± 0.019	
Buoy 46014	Pt. Arena, CA	-1.90	-3.07	5.79	6.02	0.72	0.88 ± 0.014	
Buoy 46013	Bodega Bay, CA	-3.44	-2.04	5.81	4.28	0.66	1.22 ± 0.021	
Buoy 46012	Half Moon Bay, CA	-2.82	-1.81	5.16	4.45	0.67	1.05 ± 0.018	
Buoy 46042	Monterey, CA	-2.99	-2.43	5.19	4.26	0.72	1.11 ± 0.018	
Buoy 46028	San Martin, CA	-4.44	-4.07	5.31	5.13	0.76	0.96 ± 0.014	

Table 4.1. Observed and NCEP/NARR alongshore wind data at eight coastal National Data Buoy Center buoy locations. Bold *r*-values represent a significant result at the $p < 0.001$ level.

NDBC Buoy	Location	Air Temperature (Air Temperature excluding days 180-270)						
		obs. mean	model mean	obs. stddev	model stddev.	r	slope	
Buoy 46015	Port Orford, OR	11.27 (11.10)	11.94 (11.40)	1.67 (1.71)	1.75 (1.50)	0.32 (0.42)	0.71 (0.96)	
Buoy 46027	Crescent City, CA	11.42 (11.27)	12.23 (11.67)	1.51 (1.62)	1.58 (1.39)	0.32 (0.37)	0.60 (0.83)	
Buoy 46022	Eel River, CA	11.86 (11.70)	12.38 (11.93)	1.42 (1.49)	1.39 (1.27)	0.28 (0.33)	0.70 (0.88)	
Buoy 46014	Pt. Arena, CA	11.98 (11.95)	12.76 (12.44)	1.20 (1.27)	1.19 (1.16)	0.33 (0.39)	0.59 (0.76)	
Buoy 46013	Bodega Bay, CA	12.06 (12.01)	13.00 (12.71)	1.22 (1.30)	1.24 (1.21)	0.33 (0.36)	0.53 (0.65)	
Buoy 46012	Half Moon Bay, CA	13.07 (12.92)	13.15 (12.96)	1.20 (1.24)	0.90 (0.95)	0.32 (0.36)	0.94 (0.99)	
Buoy 46042	Monterey, CA	13.34 (13.12)	13.45 (13.14)	1.14 (1.13)	1.20 (1.16)	0.42 (0.41)	0.66 (0.68)	
Buoy 46028	San Martin, CA	13.68 (13.50)	14.01 (13.60)	1.06 (1.09)	1.26 (1.15)	0.31 (0.32)	0.57 (0.66)	

Table 4.2. Observed and NCEP/NARR air temperature data at eight coastal National Data Buoy Center buoy locations. Bold *r*-values represent a significant result at the $p < 0.001$ level.

Sea Surface Temperature (Sea Surface Temperature excluding days 180-270)									
NDBC Buoy	Location	obs. mean	model mean	obs. stdev	model stdev	r	slope		slope
Buoy 46015	Port Orford, OR	11.30 (11.12)	13.39 (13.06)	1.55 (1.64)	1.73 (1.60)	0.34 (0.39)	0.62 (0.71)		
Buoy 46027	Crescent City, CA	11.39 (11.26)	13.03 (12.84)	1.34 (1.43)	1.52 (1.43)	0.26 (0.24)	0.51 (0.61)		
Buoy 46022	Eel River, CA	11.86 (11.71)	13.94 (13.23)	1.31 (1.39)	1.97 (1.50)	0.08 (0.29)	0.36 (0.56)		
Buoy 46014	Pt. Arena, CA	11.98 (11.95)	13.07 (12.65)	1.05 (1.13)	1.39 (1.13)	0.08 (0.12*)	0.24 (0.42)		
Buoy 46013	Bodega Bay, CA	12.06 (12.01)	14.07 (13.22)	1.08 (1.17)	2.00 (1.34)	0.18 (0.32)	0.21 (0.52)		
Buoy 46012	Half Moon Bay, CA	13.07 (12.91)	14.81 (13.87)	1.09 (1.14)	2.02 (1.17)	0.10* (0.22)	0.25 (0.56)		
Buoy 46042	Monterey, CA	13.35 (13.11)	14.84 (13.79)	1.02 (1.01)	2.31 (1.37)	0.11* (0.16*)	0.24 (0.39)		
Buoy 46028	San Martin, CA	13.68 (13.49)	14.96 (14.09)	0.96 (0.99)	2.11 (1.47)	0.13* (0.20)	0.25 (0.38)		

Table 4.3. Observed and ROMS model sea surface temperature data at eight coastal National Data Buoy Center buoy locations. *Bold r-values represent a significant result at the p<0.001 level. Bold r-values with an asterisk represent a significant result at the p<0.01 level.*

Chlorophyll a									
NDBC Buoy	Location	obs. mean	model mean	obs. stdev	model stdev	r	slope		slope
Buoy 46015	Port Orford, OR	1.81	1.28	2.72	2.07	0.53	0.34		
Buoy 46027	Crescent City, CA	5.57	2.29	7.30	2.86	0.44	0.34		
Buoy 46022	Eel River, CA	2.83	0.63	6.26	0.90	0.36*	0.31		
Buoy 46014	Pt. Arena, CA	2.32	3.46	3.36	7.62	0.44	0.35		
Buoy 46013	Bodega Bay, CA	3.61	2.03	4.52	4.26	0.15	0.10		
Buoy 46012	Half Moon Bay, CA	4.05	0.73	5.74	1.09	0.65	0.64		
Buoy 46042	Monterey, CA	4.44	0.79	6.26	1.55	0.44	0.45		
Buoy 46028	San Martin, CA	1.70	0.55	1.83	0.48	0.22	0.25		

Table 4.4. Observed and ROMS model sea surface chlorophyll a data at eight coastal National Data Buoy Center buoy locations. *Bold r-values represent a significant result at the p<0.001 level. Bold r-values with an asterisk represent a significant result at the p<0.01 level.*

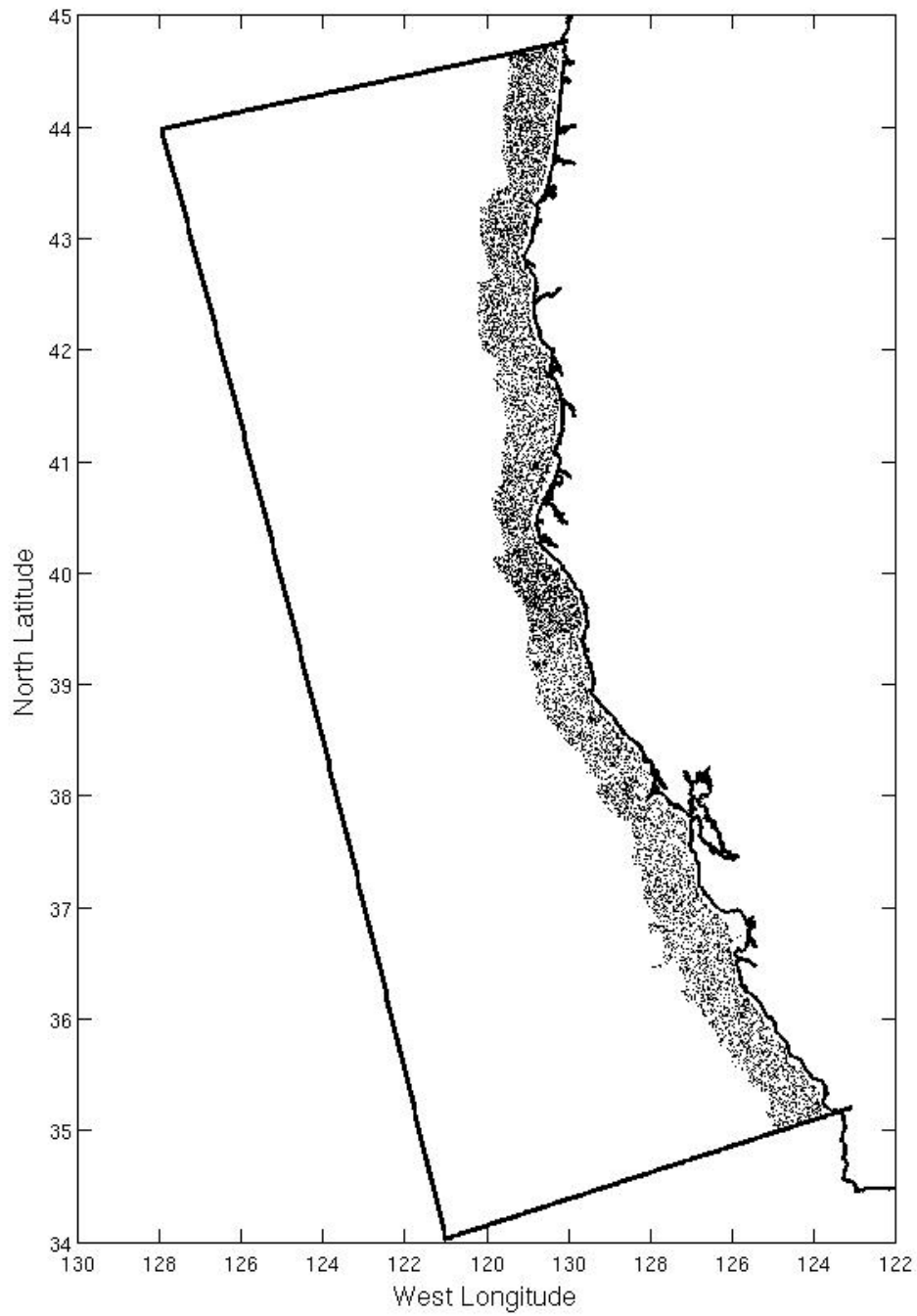


Figure 4.1. A map showing the extent of the ROMS model domain and the initial seeding location of the ~10,500 individuals that were put into each model run.

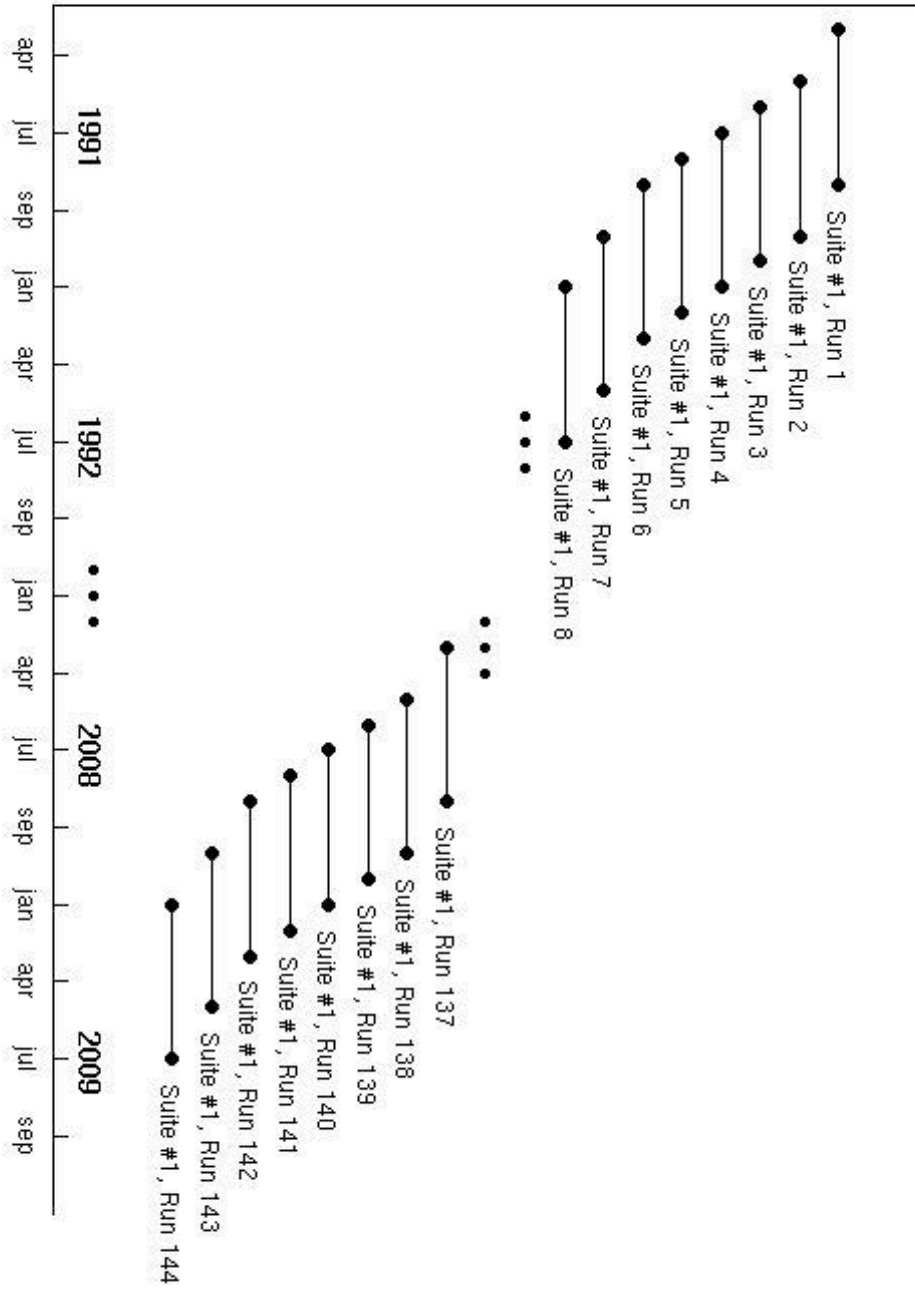


Figure 4.2. A schematic representation of a “suite” of model runs. Each model run was seeded with ~10,500 individuals of an identical weight (adults or eggs) and ran for 180 days. Note the break in time on the x-axis.

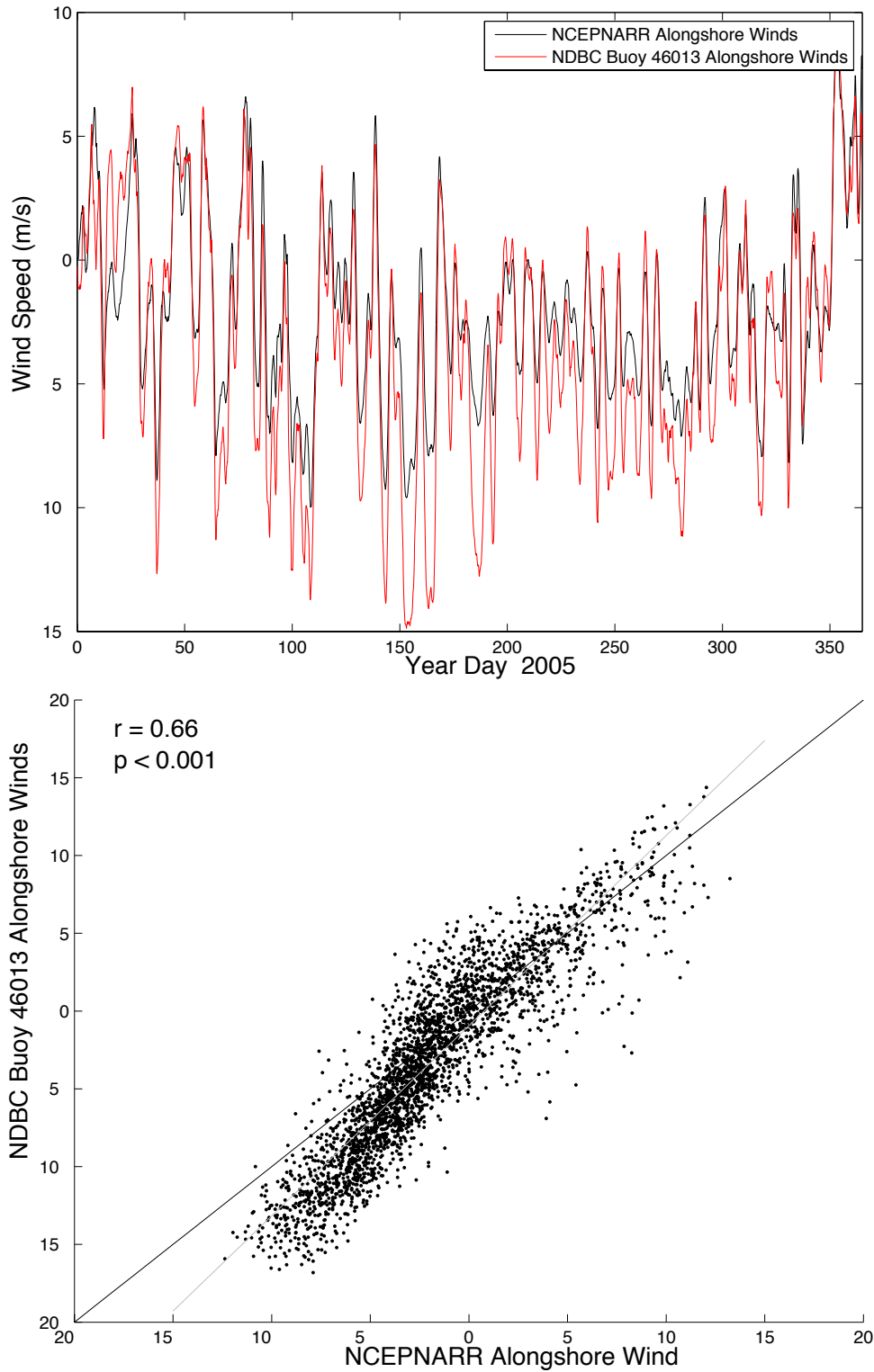


Figure 4.3. Time series (upper) and correlation (lower) of NCEP-NARR forcing and observed alongshore wind speed at location of NDBC Buoy 46013 (10 km offshore of Bodega Head, California).

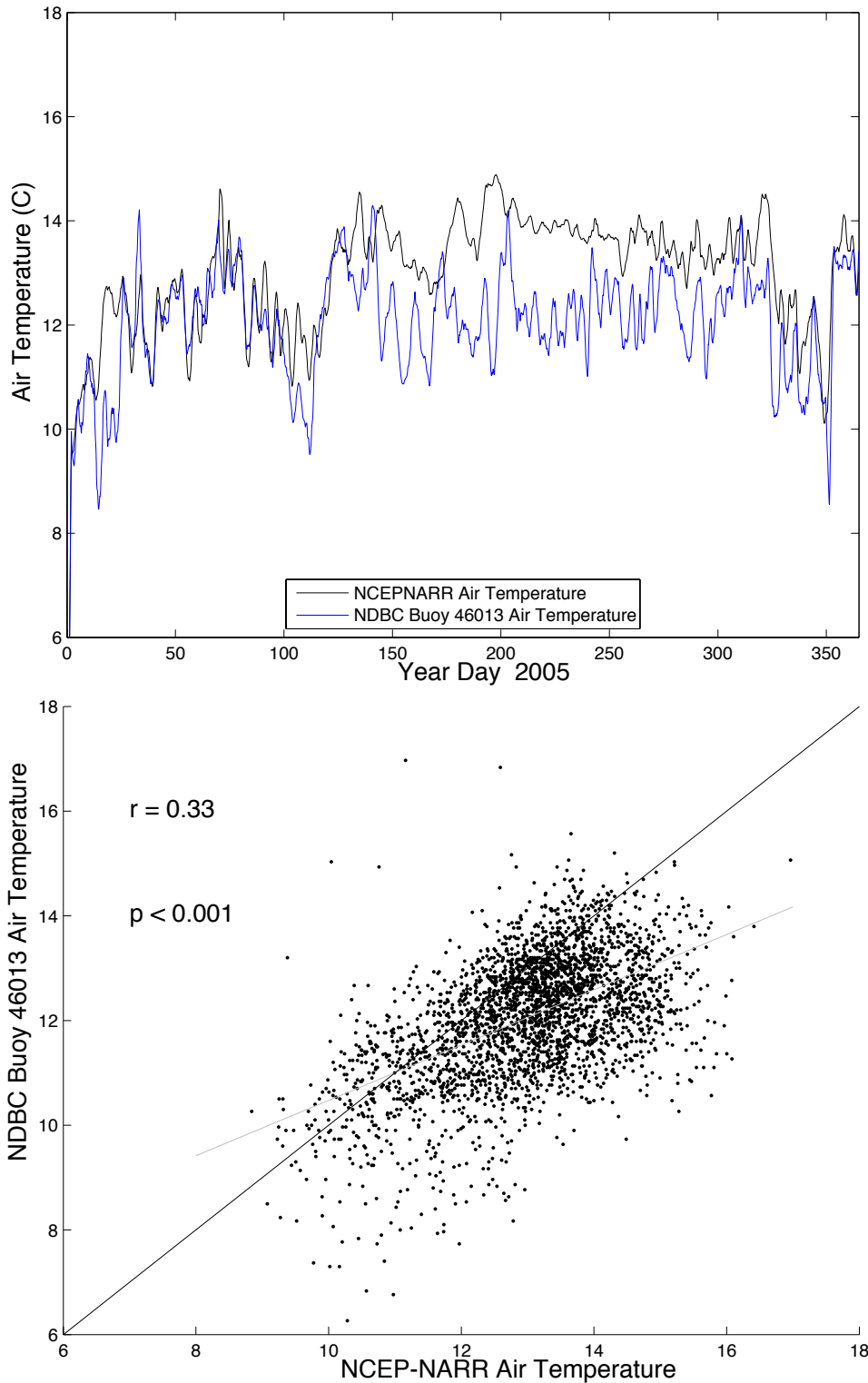
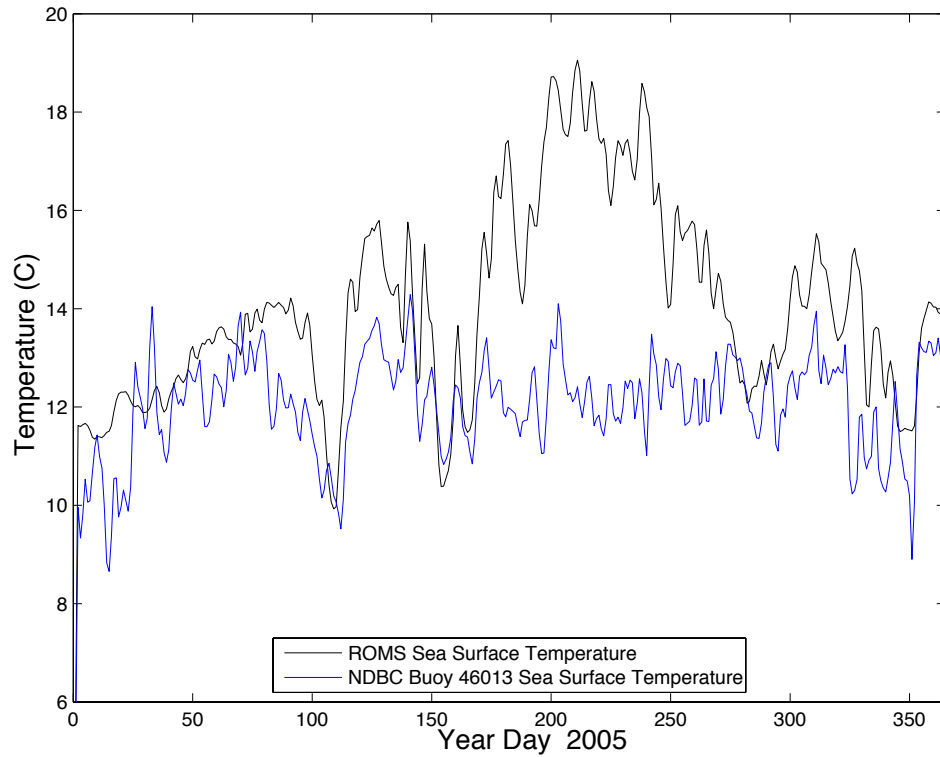


Figure 4.4. Time series (upper) and correlation (lower) of NCEP-NARR forcing and observed air temperature at location of NDBC Buoy 46013 (10 km offshore of Bodega Head, California).



NDBC Buoy 46013

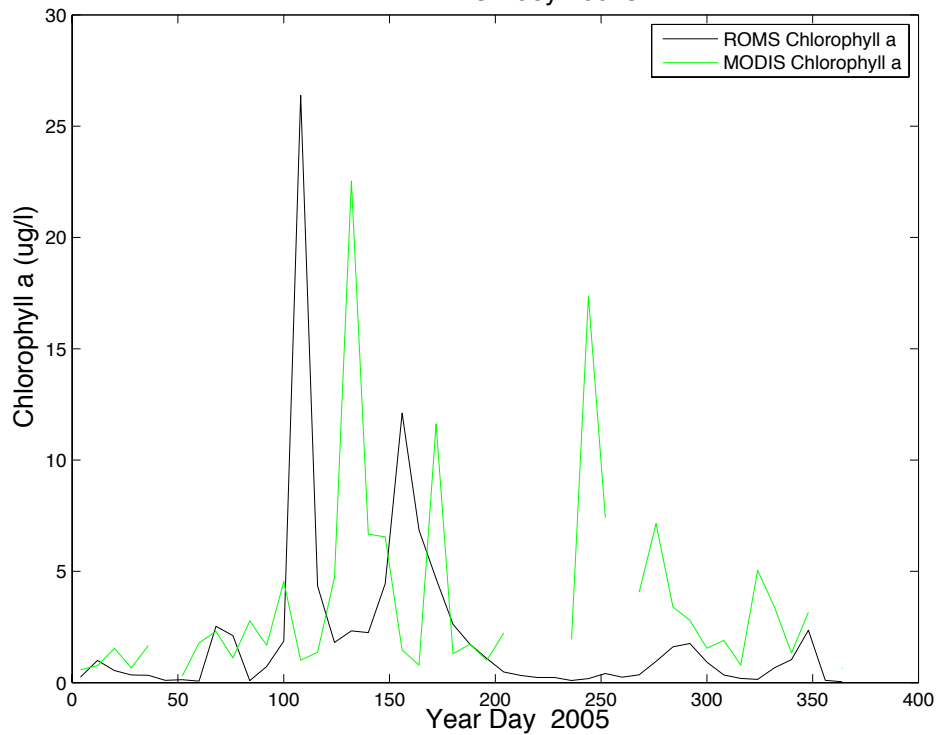


Figure 4.5. Time series of ROMS sea surface temperature (upper) and ROMS chlorophyll a concentration (lower) compared to observations at location of NDBC Buoy 46013 (10 km offshore of Bodega Head, California).

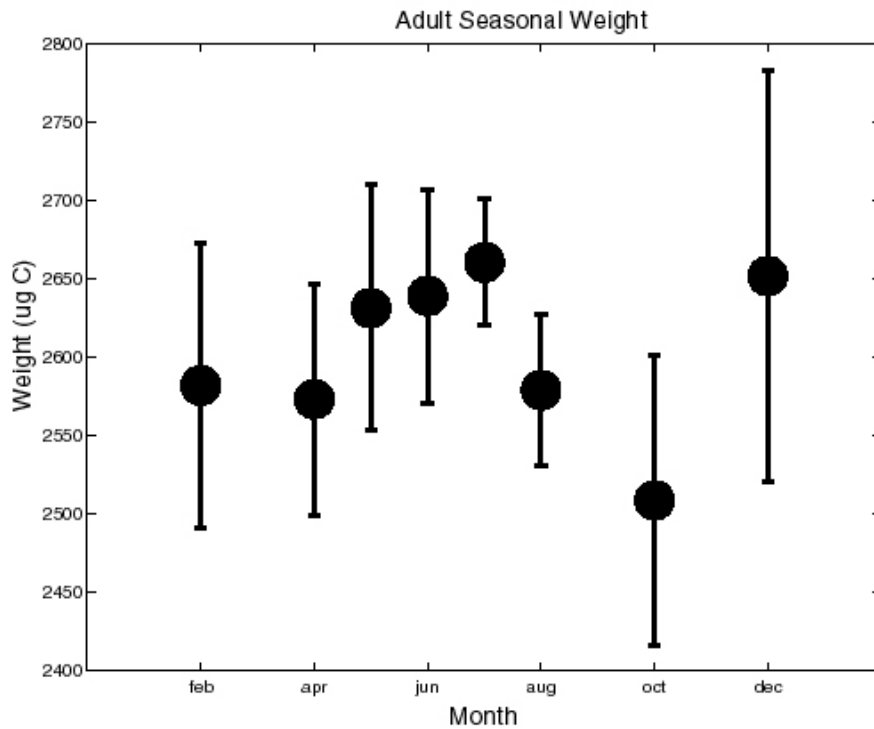
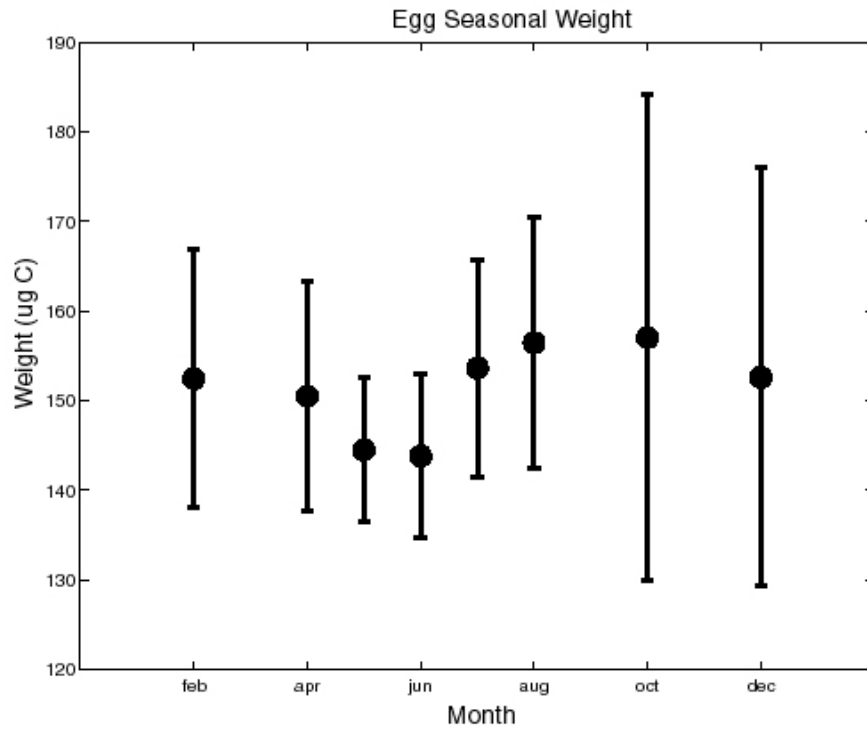


Figure 4.6. Larval (upper) and adult (lower) average individual weight at the end of the 180-day model runs. Monthly means were created by combining 18 years worth of monthly data and plotted on the start month of the 180-day model run. Error bars show the 95% confidence intervals of the mean.

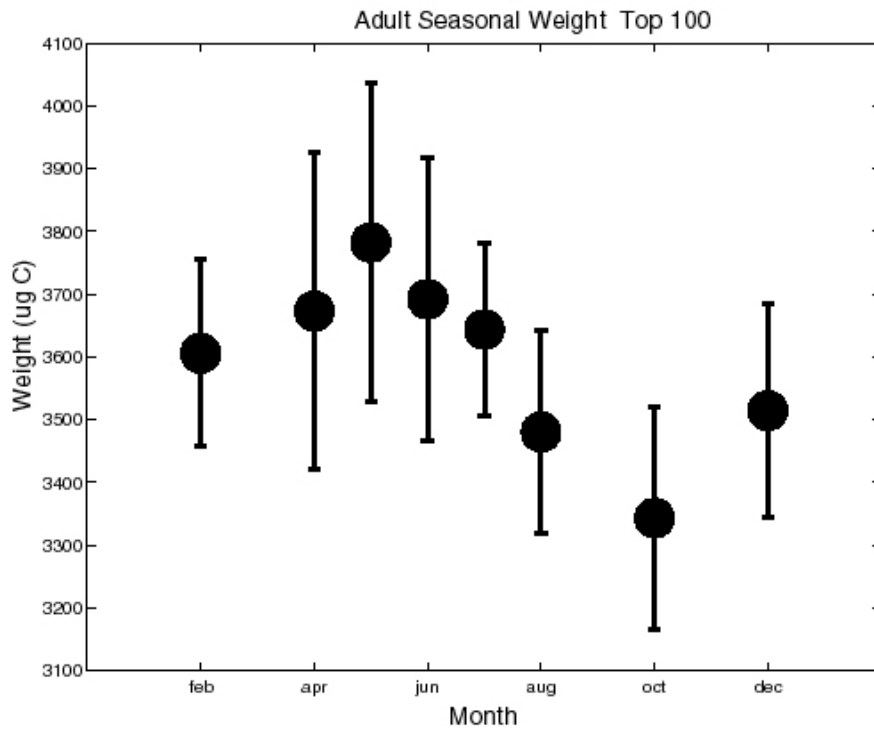
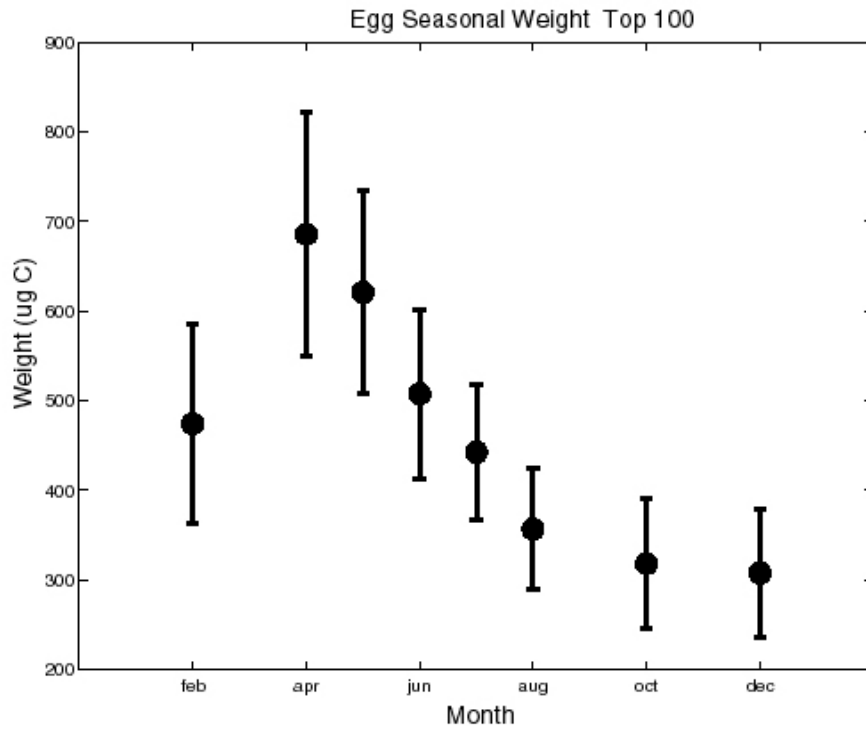


Figure 4.7. Larval (upper) and adult (lower) average weight of the 100 individuals that grew the most over the course of the 180-day model runs. Monthly means were created by combining 18 years worth of monthly data and plotted on the start month of the 180-day model run. Error bars show the 95% confidence intervals of the mean.

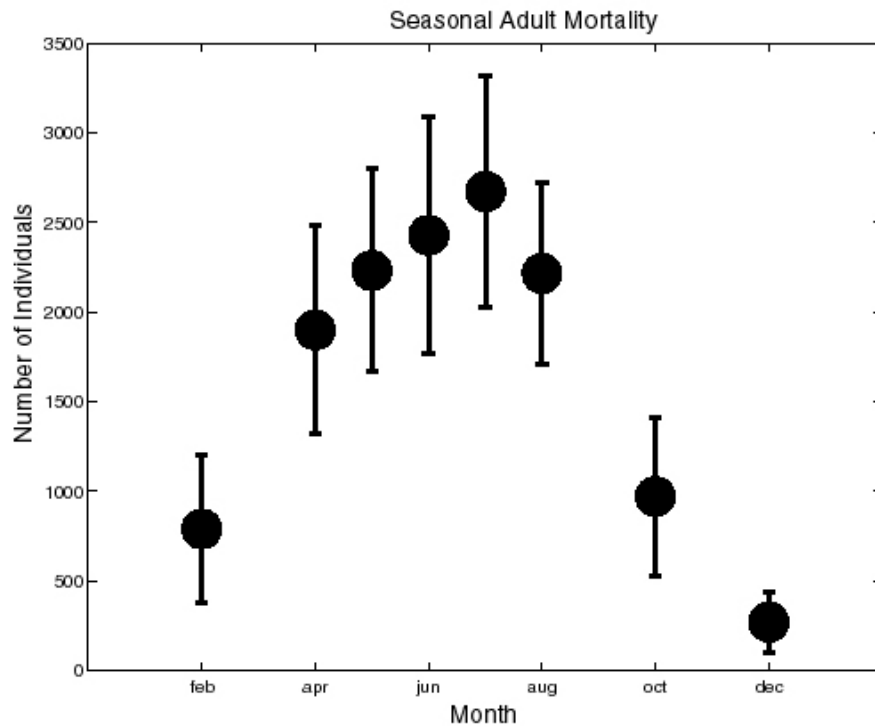
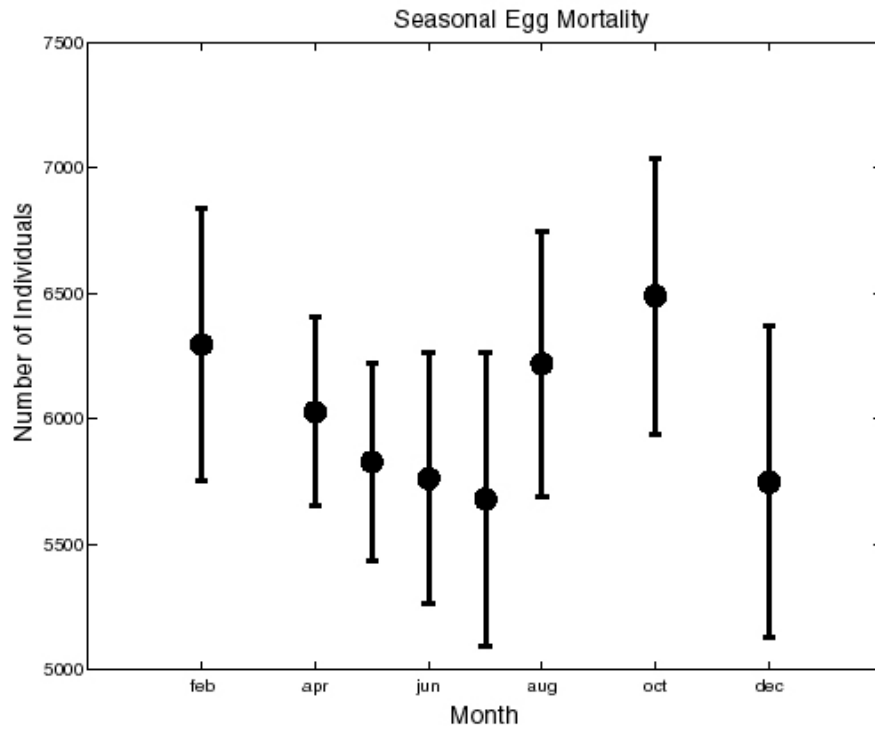


Figure 4.8. Larval (upper) and adult (lower) starvation mortality at the end of the 180-day model runs. Monthly means were created by combining 18 years worth of monthly data and plotted on the start month of the 180-day model run. Error bars show the 95% confidence intervals of the mean.

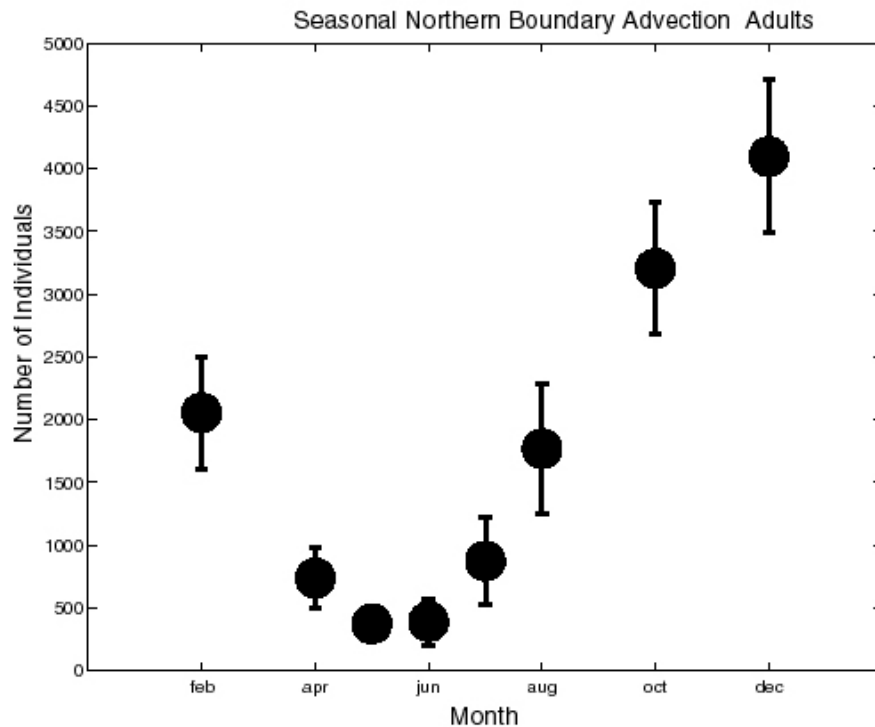
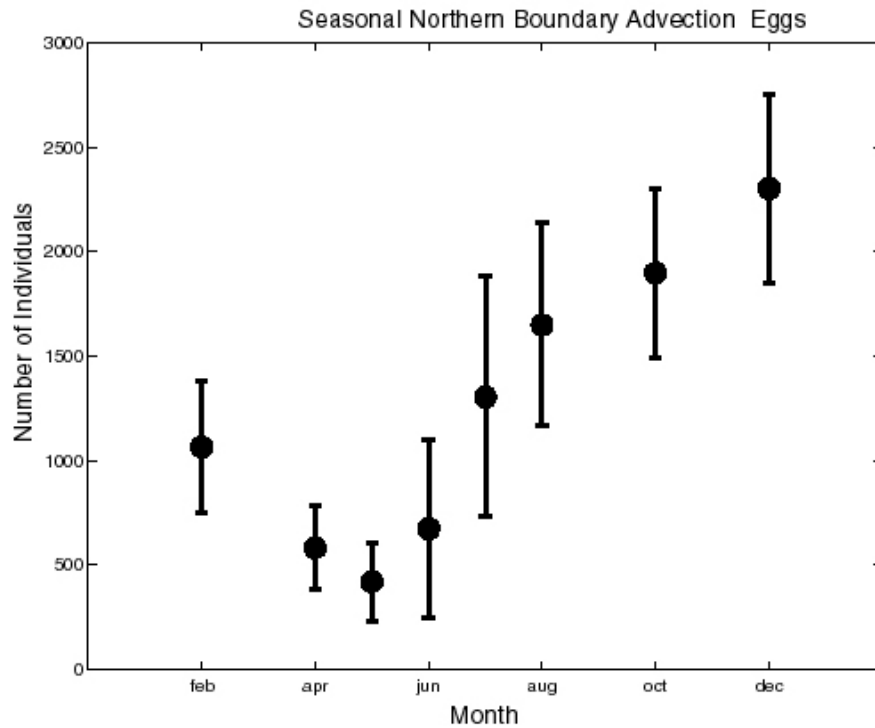


Figure 4.9. Advection of (upper) larval and (lower) adult individuals out of the northern boundary of the model domain. Monthly means were created by combining 18 years worth of monthly data and plotted on the start month of the 180-day model run. Error bars show the 95% confidence intervals of the mean.

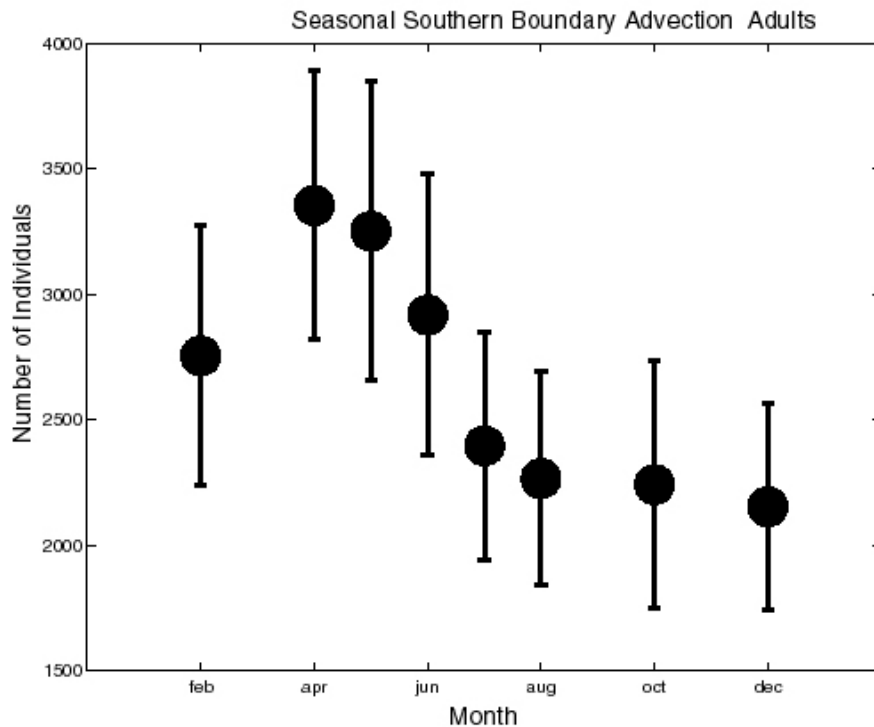
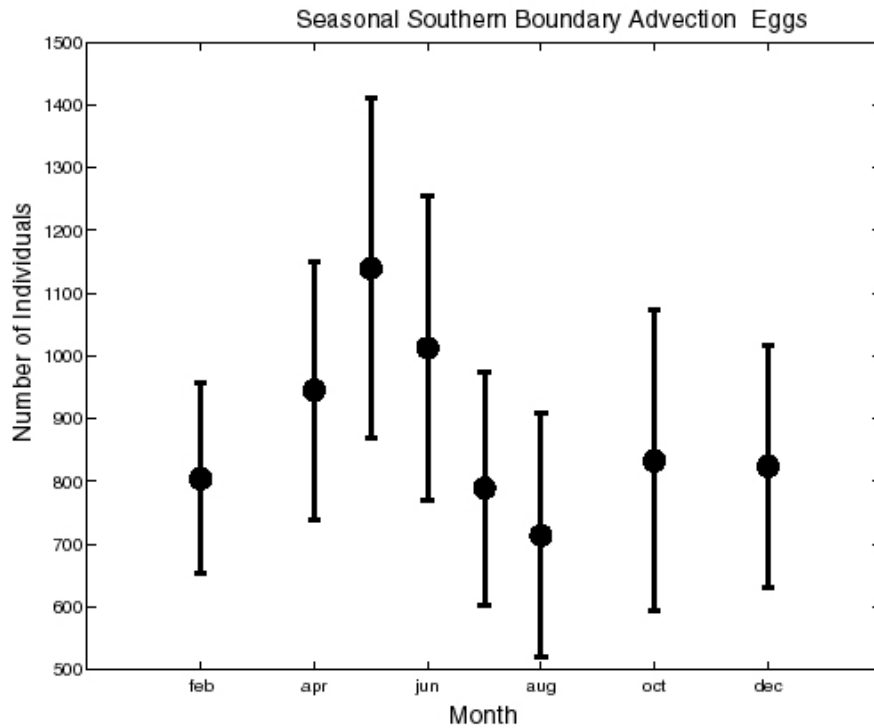


Figure 4.10. Advection of (upper) larval and (lower) adult individuals out of the southern boundary of the model domain. Monthly means were created by combining 18 years worth of monthly data and plotted on the start month of the 180-day model run. Error bars show the 95% confidence intervals of the mean.

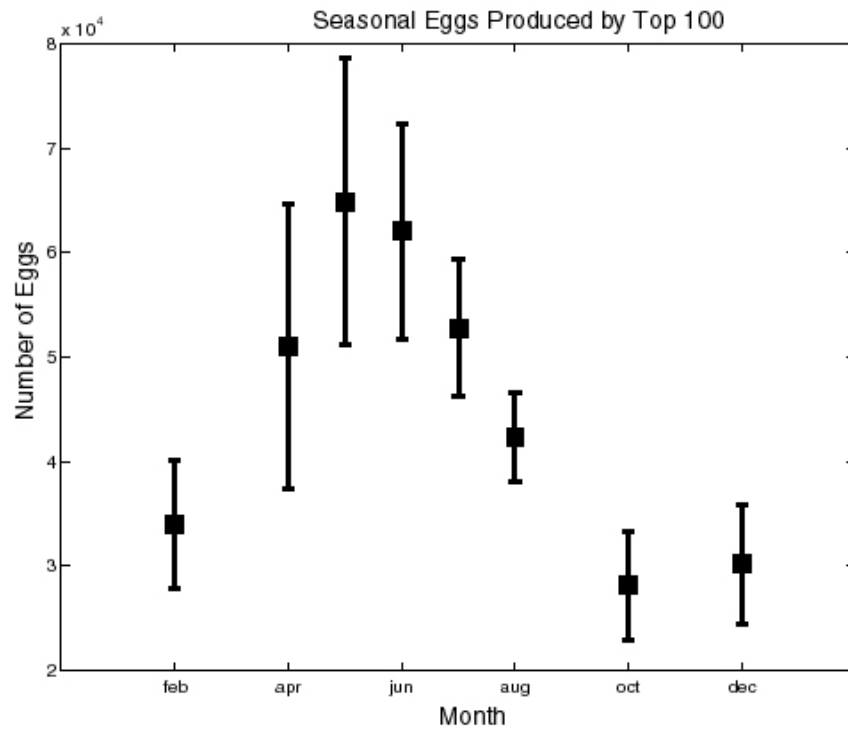
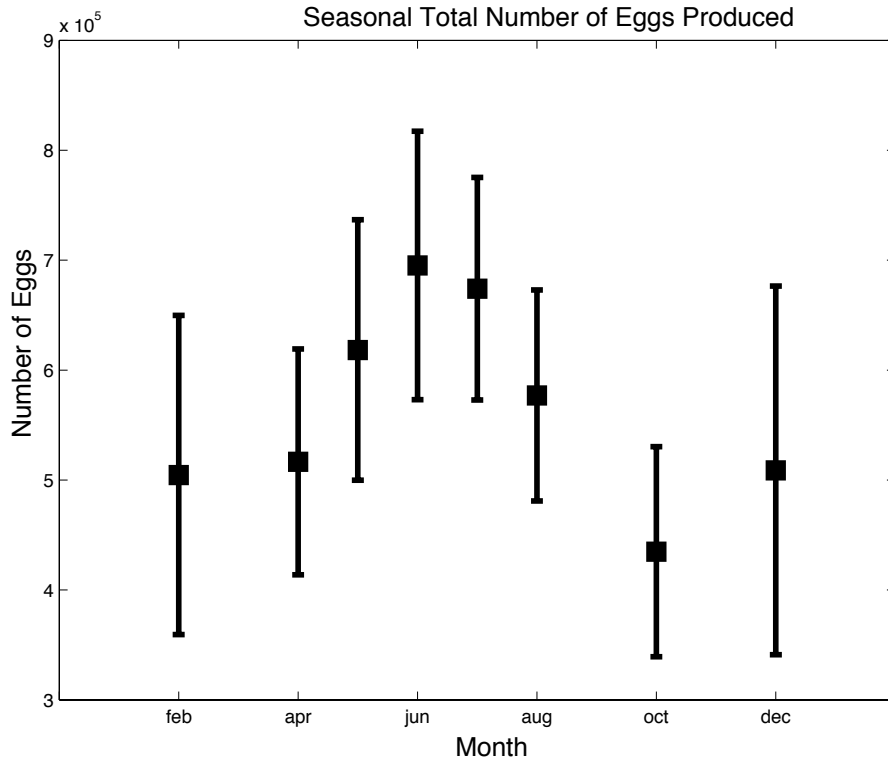


Figure 4.11. Number of eggs produced by the entire population (upper) and from the top 100 individuals that grew the most over the course of the model run (lower) from the adult 'suite' of runs. Monthly means were created by combining 18 years worth of monthly data and plotted on the start month of the 180-day model run. Error bars show the 95% confidence intervals of the mean.

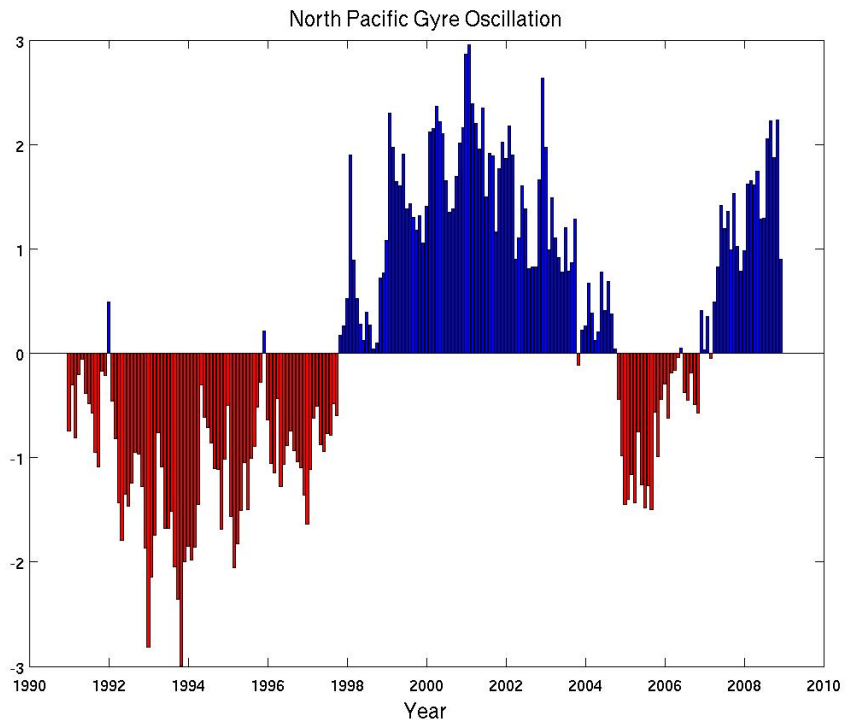
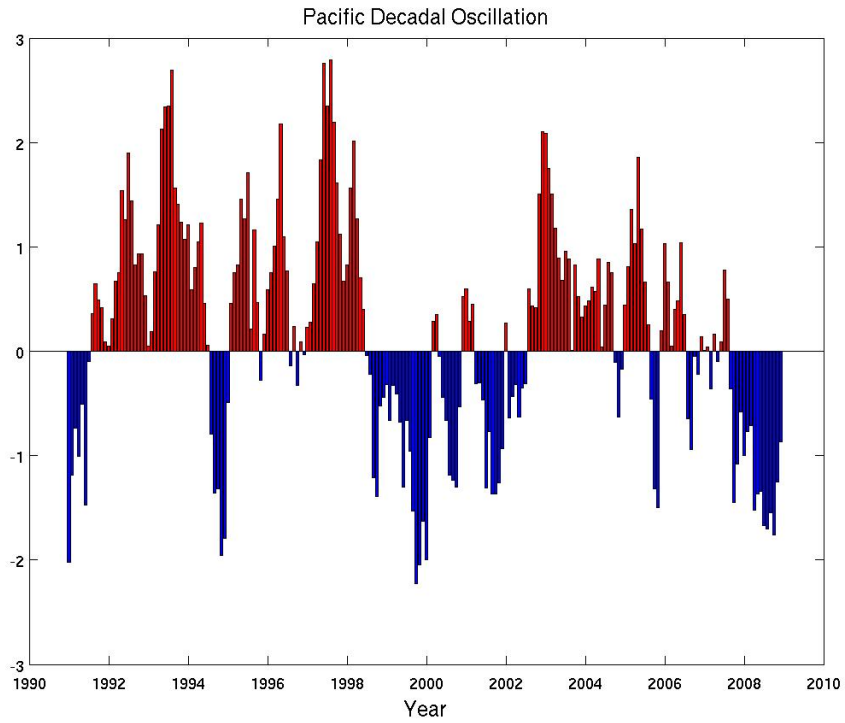


Figure 4.12. Phase of the (upper) PDO and (lower) NPGO from 1991 to 2008. The phase that is considered “more productive” is colored blue in each index.

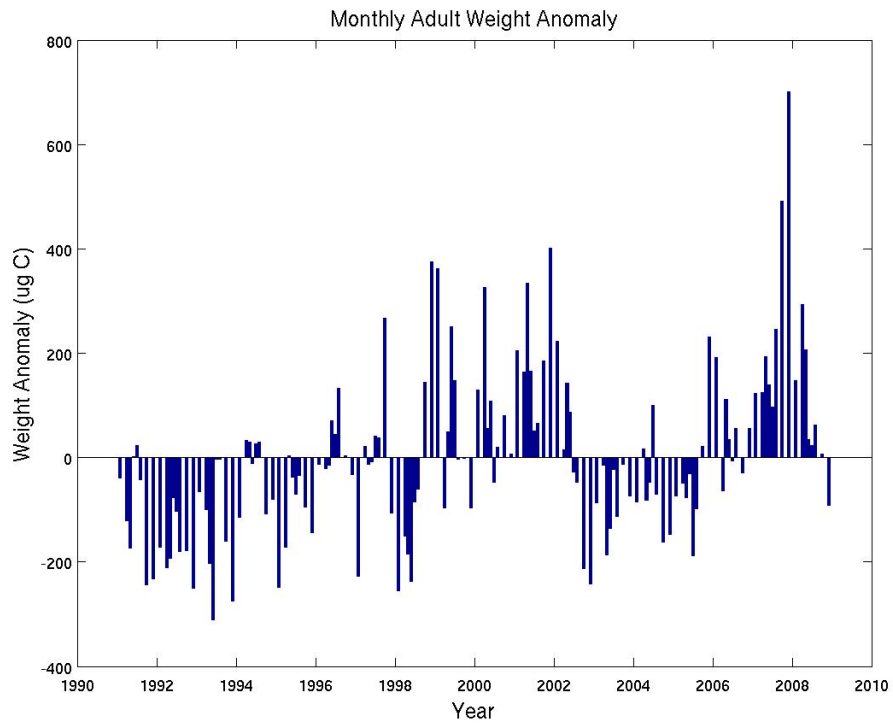
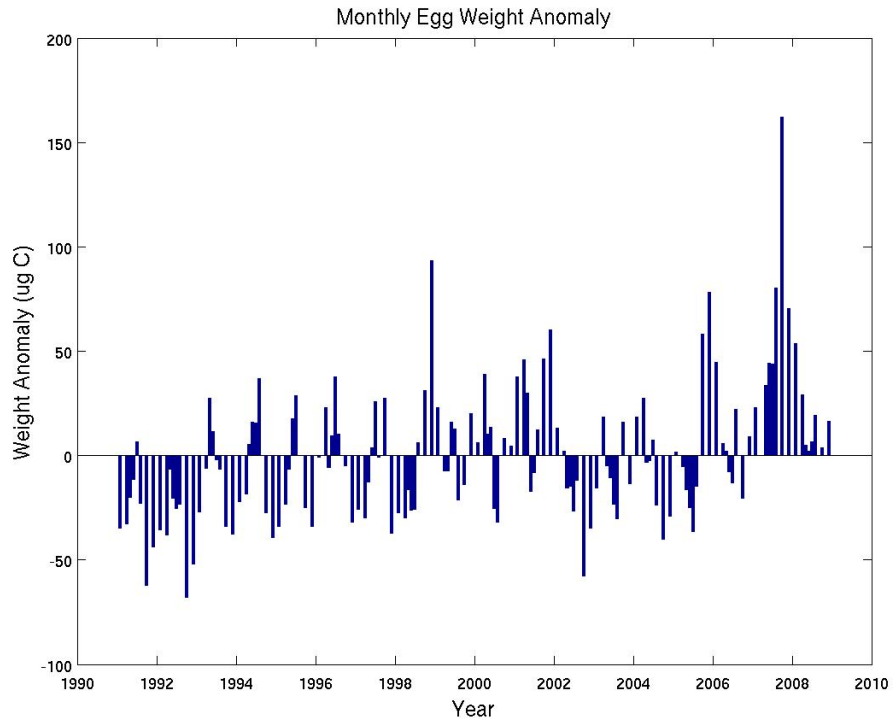


Figure 4.13. Monthly anomalies of mean population weight of (upper) larvae and (lower) adults.

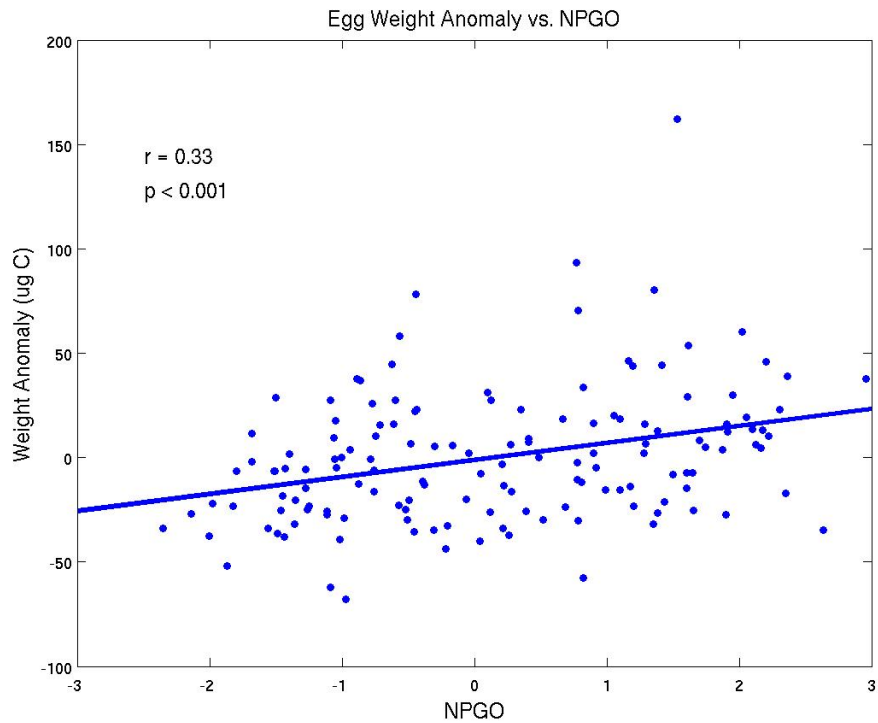
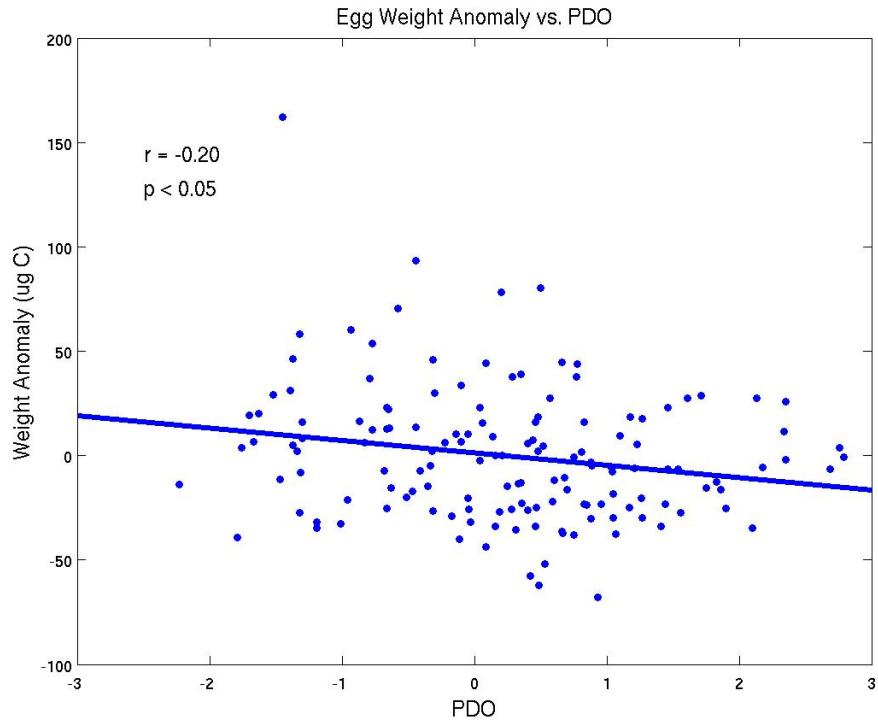


Figure 4.14. Correlation between larval weight anomaly at the end of 180-day model runs and (upper) the PDO and (lower) the NPGO.

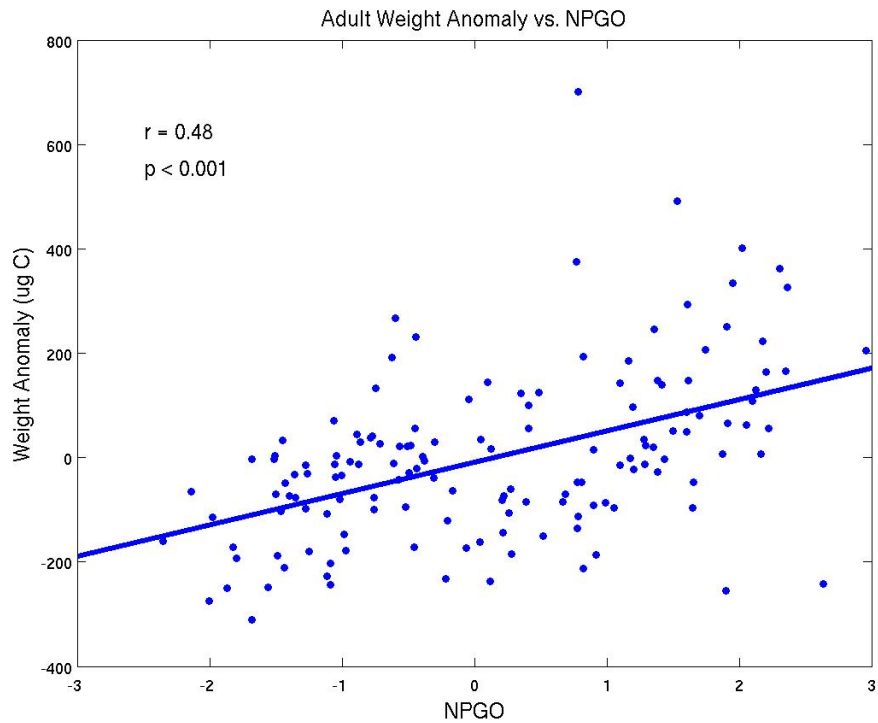
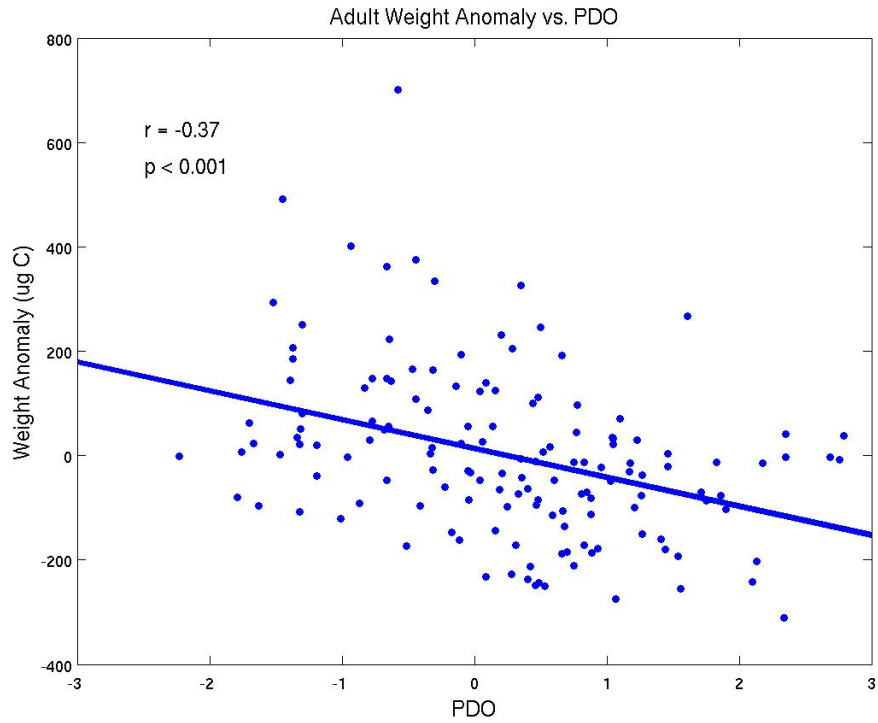


Figure 4.15. Correlation between adult weight anomaly at the end of 180-day model runs and (upper) the PDO and (lower) the NPGO.

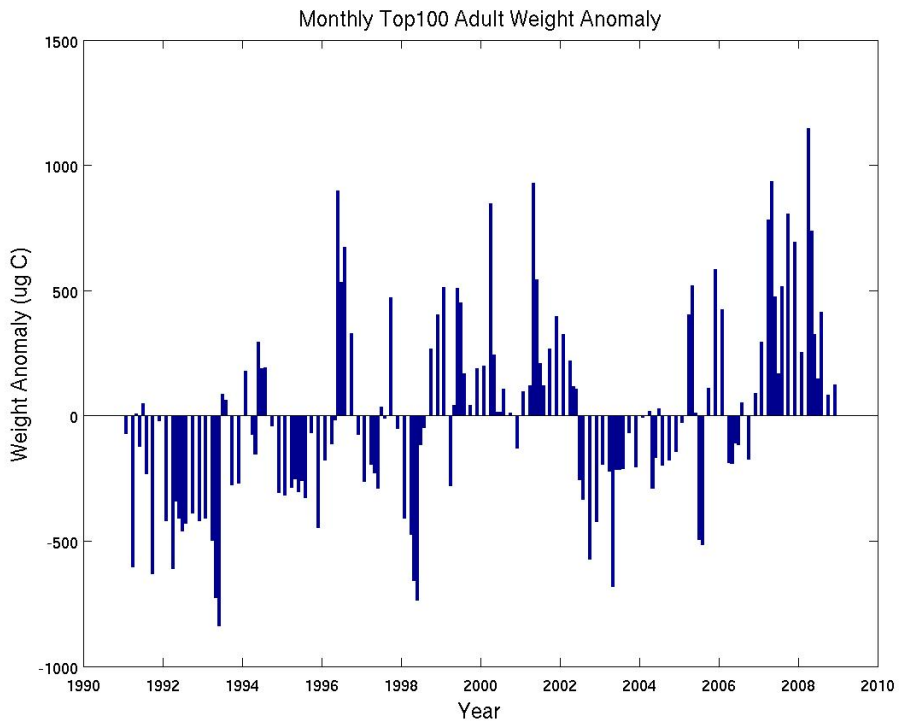
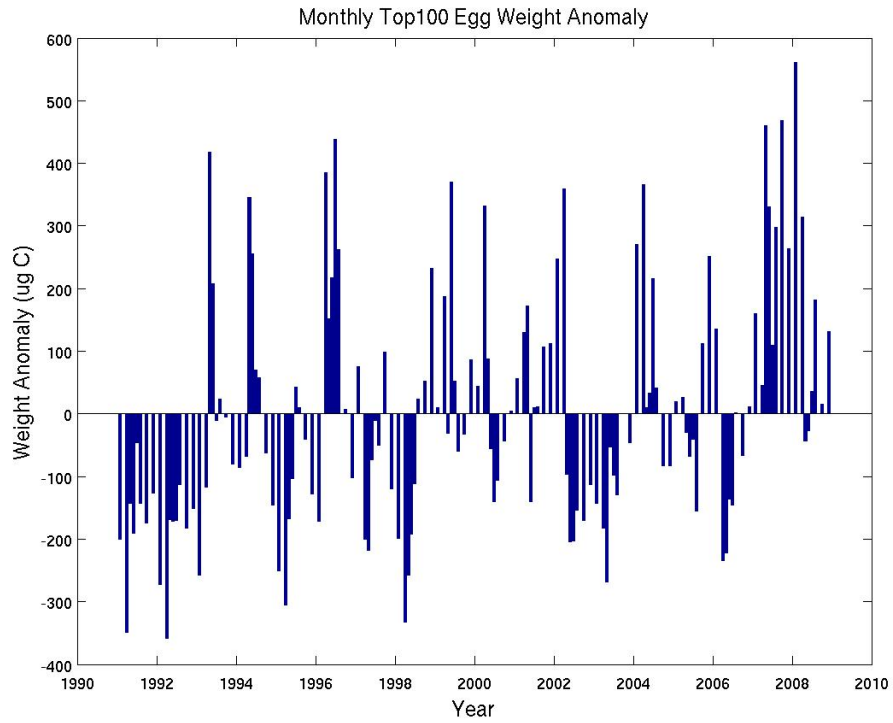


Figure 4.16. Monthly anomalies of mean weight of the top 100 (upper) larvae and (lower) adults that grew the most over the course of the 180-day model run.

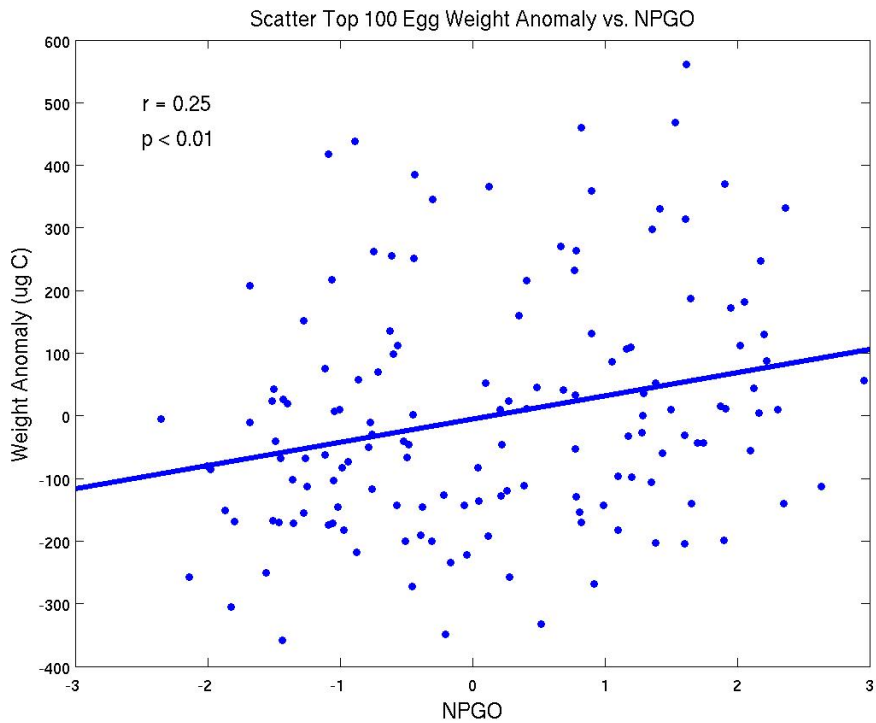
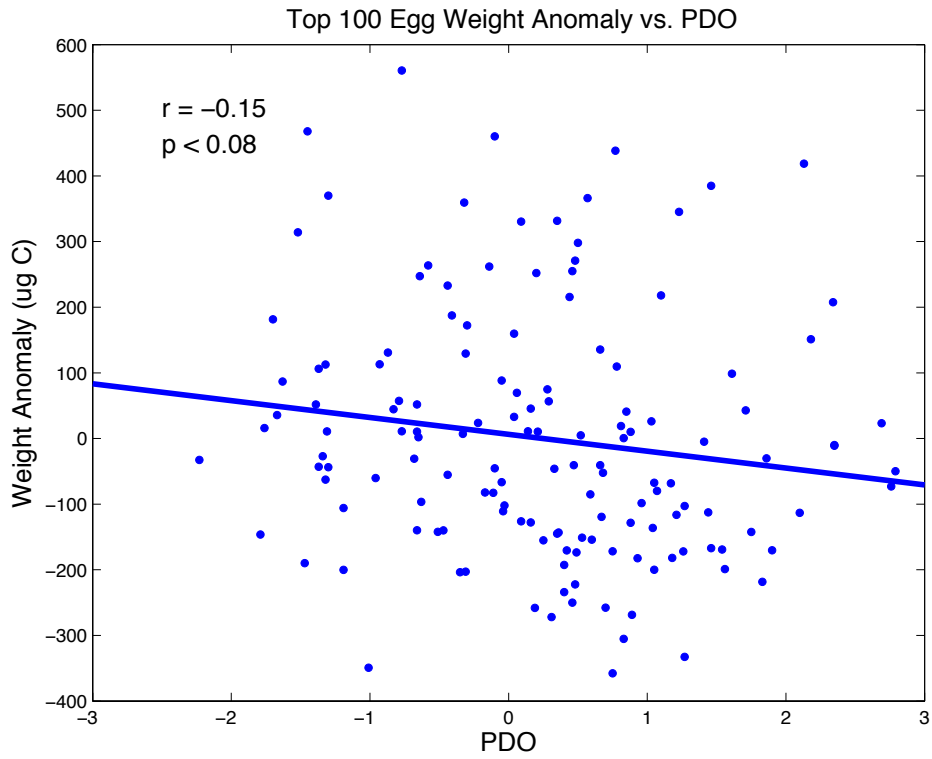


Figure 4.17. Correlation between larval weight anomaly of the 100 individuals that grew the most over the course of the 180-day model runs and (upper) the PDO and (lower) the NPGO.

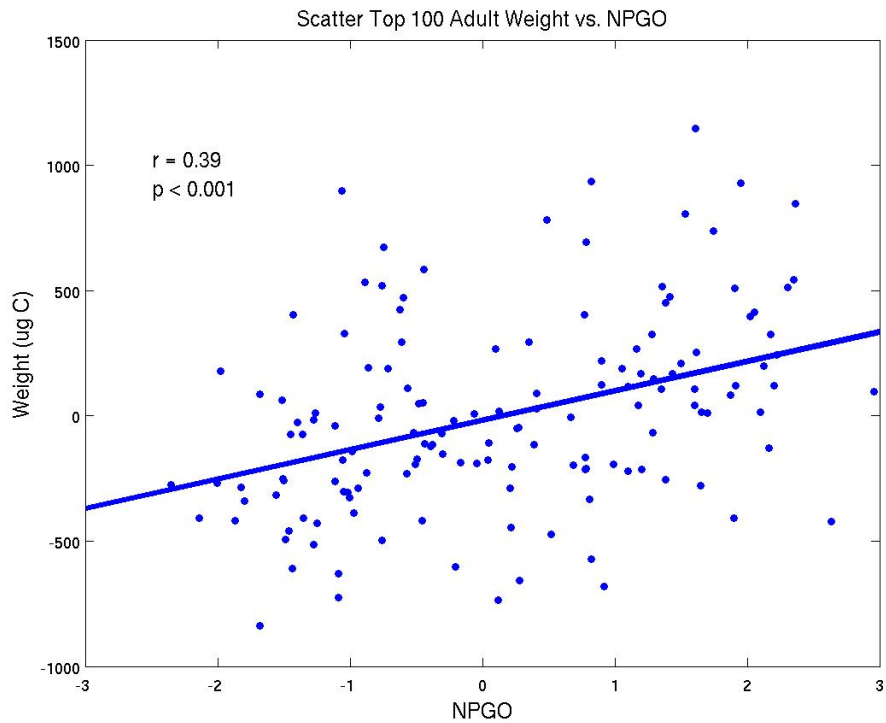
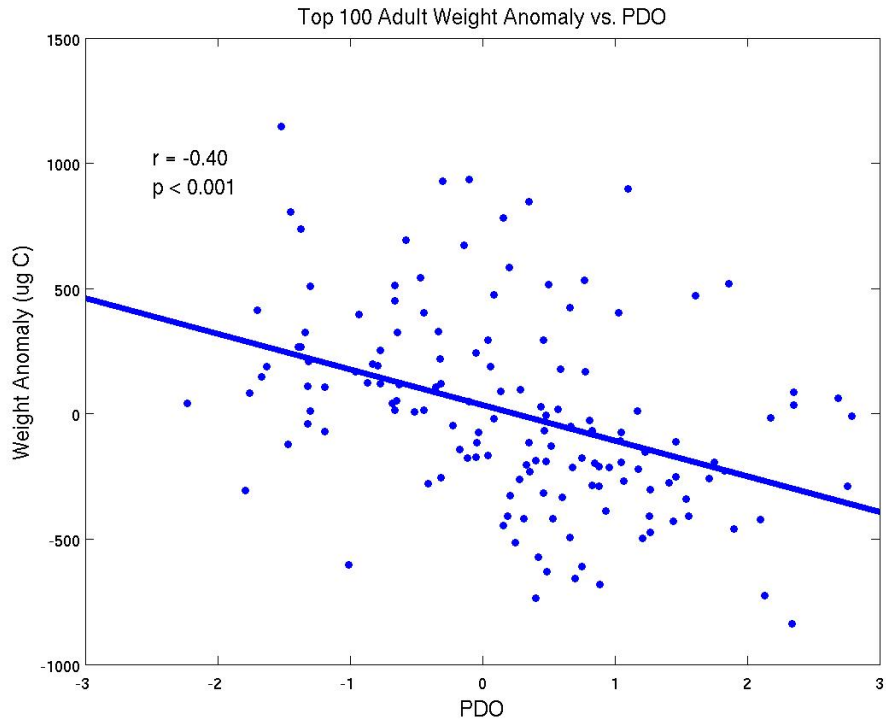


Figure 4.18. Correlation between adult weight anomaly of the 100 individuals that grew the most over the course of the 180-day model runs and (upper) the PDO and (lower) the NPGO.

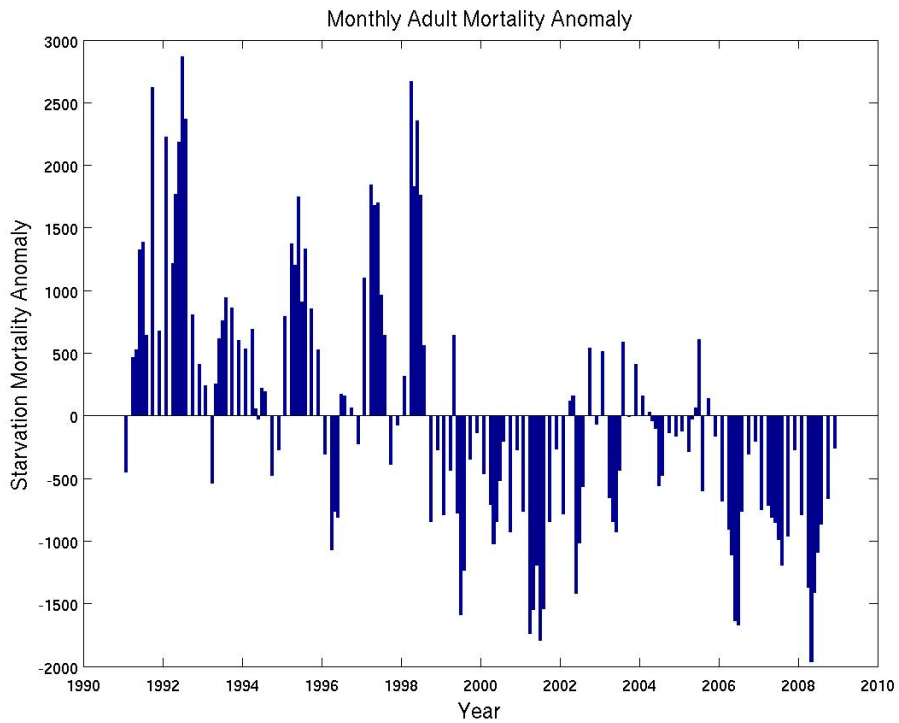
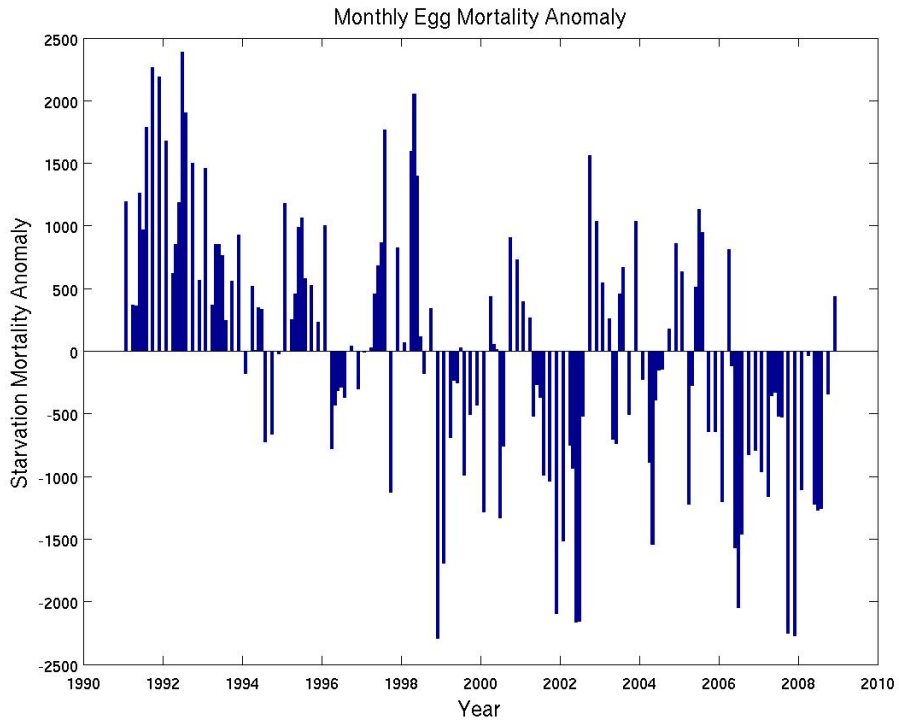


Figure 4.19. Monthly anomalies of the number of (upper) larval and (lower) adult individuals that starved over the course of the 180-day model run.

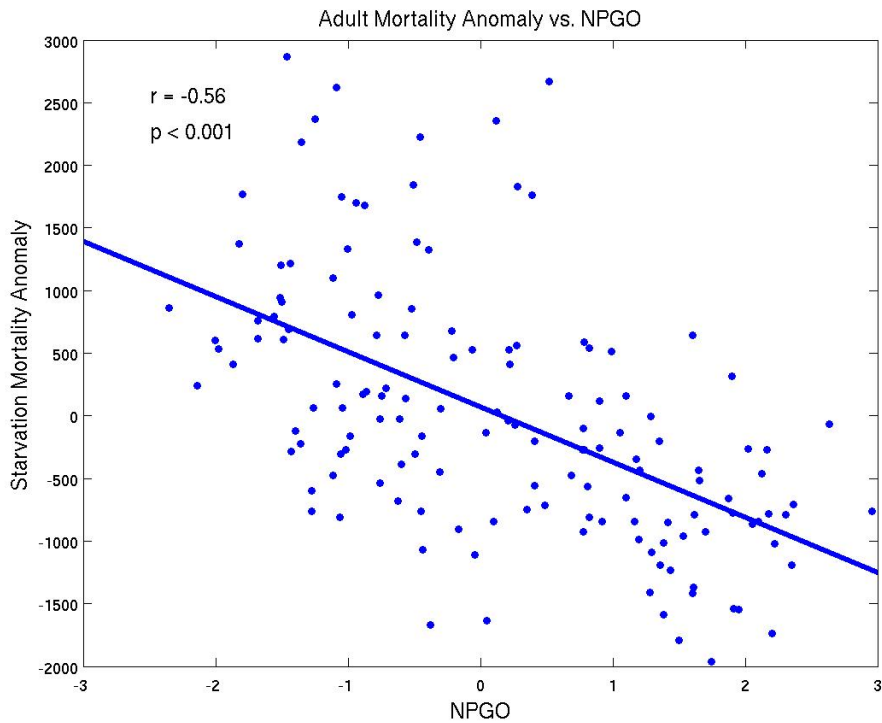
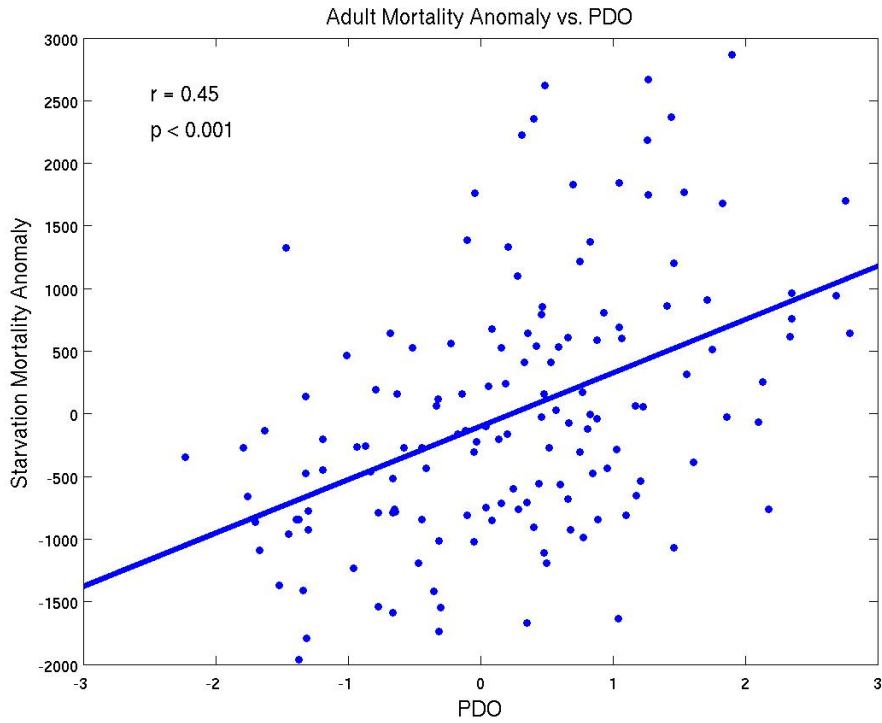


Figure 4.21. Correlation between adult starvation mortality over the course of the 180-day model runs and (upper) the PDO and (lower) the NPGO.

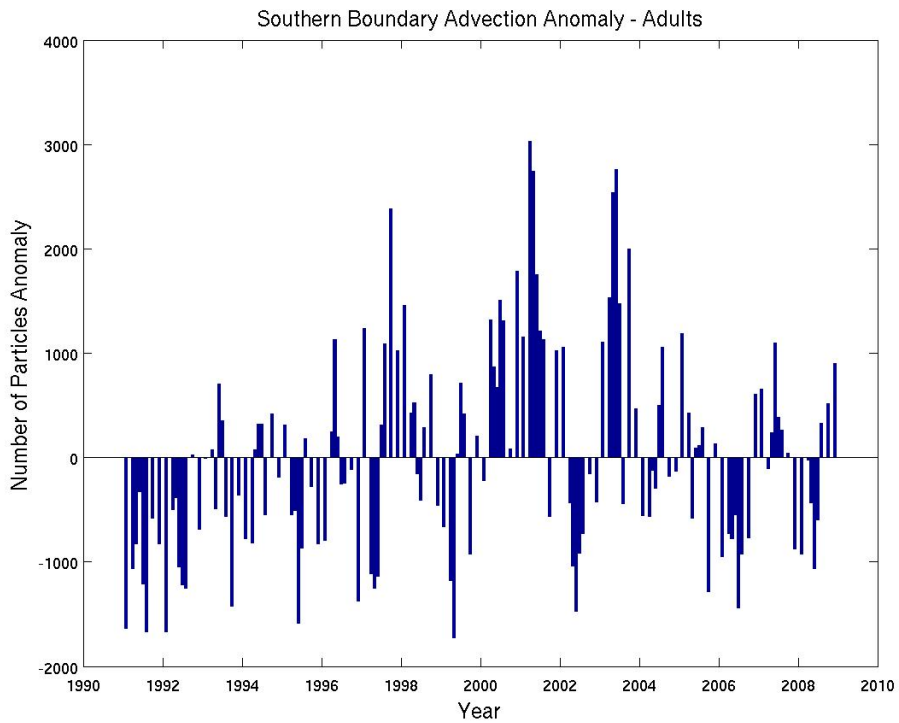
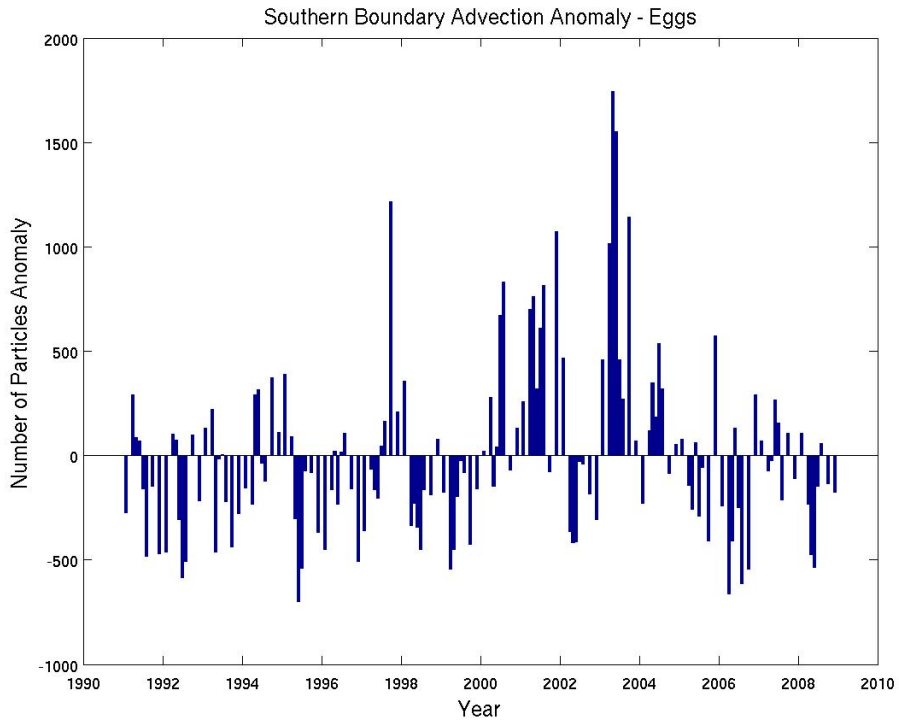


Figure 4.22. Monthly anomalies of the number of (upper) larval and (lower) adult individuals advected out of the southern model boundary over the course of the 180-day model run.

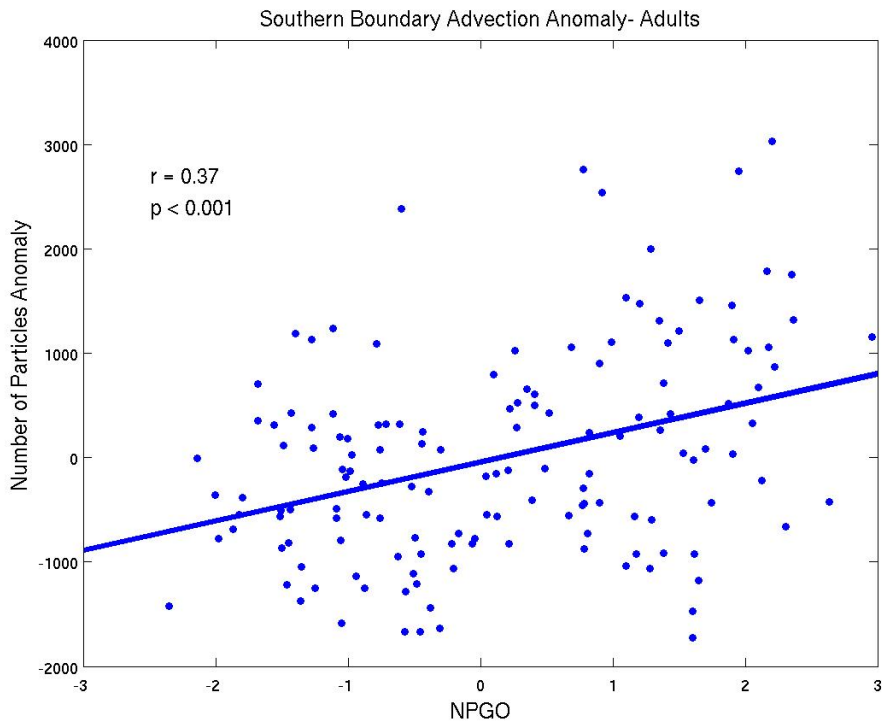
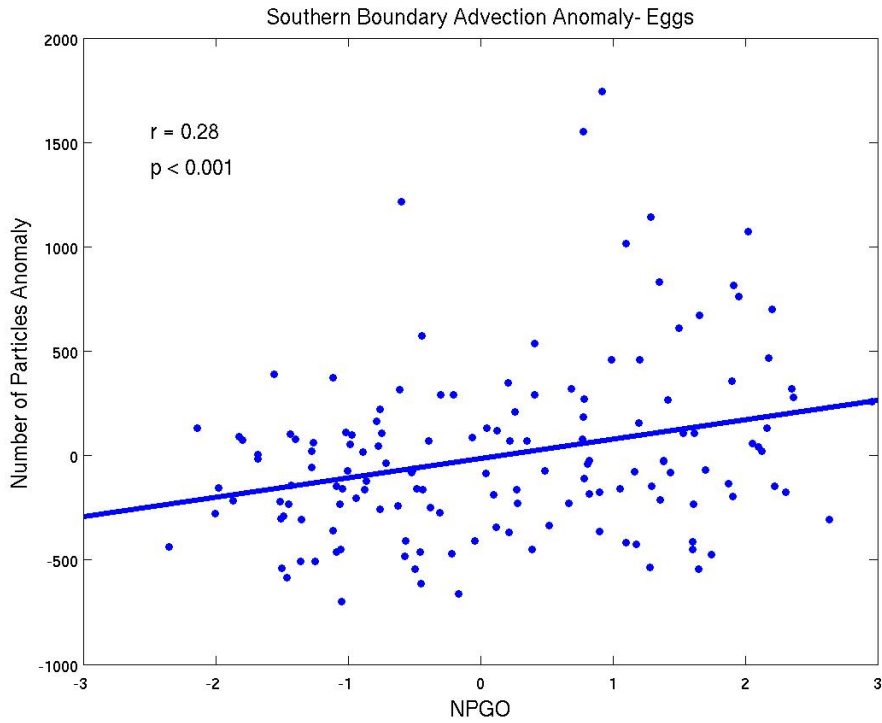


Figure 4.23. Correlation between number of (upper) larval and (lower) adult individuals advected out of the southern boundary of the model domain and the NPGO.

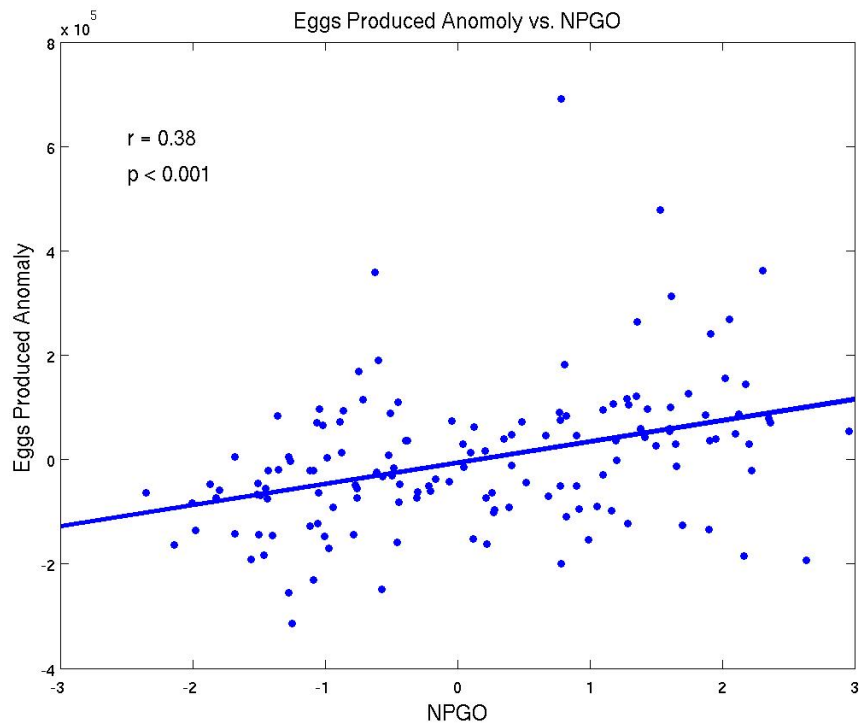
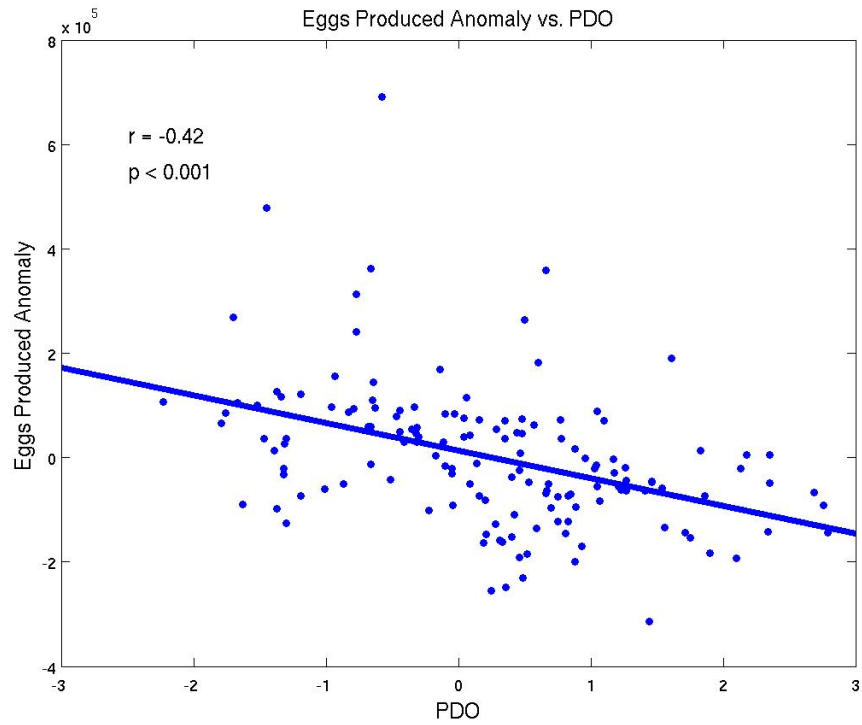


Figure 4.24. Correlation between the number of eggs produces over the course of the 180-day model runs and (upper) the PDO and (lower) the NPGO.

Conclusions

There is still much work still to be done to move the modeling of *Euphausia pacifica* forward to a state where the results will more realistically resemble the population biology of krill. Limitations to our work include the number of individuals that we are effectively able to model into the coastal domain, the spatial scale at which we can resolve the coastal ocean, and a lack of knowledge of particular aspects of the physiology and behaviors of *E. pacifica*. We could tackle some of these issues with greater computing power and storage, but this refrain has likely been said for as long as computers have been commonplace in the sciences. With greater computing power, we could simulate a greater number of individuals, but we could likely never practically represent an entire population of *Euphausia pacifica* over a domain as large as the California Current. Greater computing power would also allow us to run our coastal ocean model at smaller (say 0.5 km) spatial resolution. However, if our forcing data (atmospheric) is still not resolved to smaller than 0.3 degree (~ 30 km.) the results may not fully realize the variability in ocean conditions, and thus population biology of *E. pacifica*, that is possible at the smaller resolution. These sorts of issues emphasize the importance of working together with a wide diverse group of scientists (atmospheric, oceanographic, & ecologists) to achieve the goals of these sorts of oceanographic ecosystem modeling.

Other challenges lie within our ability to parameterize an individual based model with enough relevant information that captures the important characteristics and variability of the organism. *Euphausia pacifica* is one of the most studied species of krill in the North Pacific Ocean, yet there is still large gaps in our knowledge of feeding, mortality, and behavior. Feeding experiments have only been done for adults and not over a range of life stages and temperatures. There is little to no information on the impacts of zero food resources on the various life stages of *E. pacifica*. Our knowledge of behavior in particular is limited to diel vertical migration (DVM), which is included in the model, but without all of the variability (and the unknown causes of variability) that is observed in nature. Other behaviors that result in swarming (observed in nature) and potentially impact the patchy nature of krill distributions are unknown.

In spite of the known deficiencies in our modeling effort, we have succeeded in creating an IBM that is able to represent the growth, life-stage progression, and reproduction of *Euphausia pacifica* in response to environmental cues of food and temperature. This IBM has been coupled to a physical ocean model (ROMS) and ecosystem model (NPZD model) and 18 years worth of data have been generated (1991-2008) over which time there was a full range in variability of conditions (both physical and biological) to explore the response of *E. pacifica*. We have taken the steps of forcing an ecosystem over two decades and teasing out the response of a critical component of that ecosystem on both a short-time scale and longer-time scale to physical forcing. Primary findings of research conducted with this model include:

- Anomalous northward advection and poor feeding conditions during the winter/spring of 2005 resulted in fewer individuals and smaller individuals

retained in the Northern California region during critical feeding times for higher trophic levels.

-In the summertime, warm surface temperatures, primarily in offshore regions, which have lower level of chlorophyll *a*, resulted in greater adult mortality through starvation and a reduction in average population weight.

-Correlation between measures of *Euphausia pacifica* condition, mortality, and abundance and the PDO and NPGO indicate that long time scale atmospheric forcing can play an important role in krill productivity in the California Current.

The ultimate goal of running these types of models would be to predict krill abundances into the future to better inform fishery management decisions. To do so, we need to introduce some sort of carryover or “biological memory” to the model so that the success of one generation has an impact on future generations. Running the model as we have for this thesis research is useful, in that we are able to assess any one run against another, but does not produce results that characterize the actual spatial and temporal distributions of krill. We know that anomalously high or low population growth, reproduction, or recruitment can impact year-to-year variability and introducing this “biological memory” into our future model runs is a high priority.

We also hope to force our model with more accurate atmospheric conditions and with forcing that represents anthropogenic climate change. I feel that modification of the NCEP-NARR data, or using a blended forcing product that is better resolved in the coastal domain, is crucial for any future modeling work in the California Current. Limitations to forcing our model with results from climate models is currently a matter of spatial scale. The horizontal resolution of climate products will continue to decrease over the next years so that the important climate variability is represented in the coast upwelling regions, and I hope to force the ROMS/NPZD/IBM suite of models with these results in the future.