

IMPACTS OF CLIMATE-ASSOCIATED CHANGES IN PREY AVAILABILITY ON NORTH  
ATLANTIC RIGHT WHALE POPULATION DYNAMICS

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IMPACTS OF CLIMATE-ASSOCIATED CHANGES IN PREY AVAILABILITY ON  
POPULATION DYNAMICS OF THE NORTH ATLANTIC RIGHT WHALE

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Today's oceans are undergoing rapid and unprecedented changes resulting from anthropogenic impacts. The North Atlantic right whale, one of the most endangered baleen whales with just over 500 animals remaining in the species, is one example of a species at risk resulting from human influence. Modern right whale research is focused on elevated mortality rates due to vessel collisions and fishing gear entanglement. Although understudied, depressed calving rates also contribute significantly to slow growth. Here we analyze the effect of climate-driven fluctuations in prey abundance on right whale reproductive dynamics since 1980.

*Calanus finmarchicus*, the lipid-rich copepod that right whales prey on, were anomalously abundant in the 1980s and 2000s, while concentrations were low in the 1990s. These fluctuations in copepod abundance were driven remotely by freshwater pulses from the Arctic Ocean, and by changes in advective supply to the Gulf of Maine related to North Atlantic circulation patterns. Synchronized with the low prey regime, right whale calf production in the 1990s was depressed relative to the surrounding decades.

In a series of matrix population models, physical variables tied to basin-scale oceanographic mechanisms, climate indices and Continuous Plankton Recorder-derived *C. finmarchicus* abundance anomalies were tested in the prediction of right whale calf births over the time series 1980-2007. While several lagged physical variables and the annual *C. finmarchicus* anomaly outcompeted the prey-independent calf prediction model, the best reproduction model was driven by a combination of bimonthly anomalies in sub-regions spanning the southern Gulf of Maine. The objectively-selected regions and seasons of prey anomalies driving the best reproduction model correspond well with known right whale feeding and breeding habits.

The full demography of the right whale population was analyzed using capture-recapture techniques, demonstrating that prey availability has an observable effect on interannual variations in reproduction but not on mortality. Population size was projected over a 100-year period under three different observed decadal prey regimes, with positive population growth predicted under each scenario. However, a future northward shift in *C. finmarchicus* habitat due to rising sea temperatures may increase the frequency of low prey scenarios for right whales, leading to population decline.

## BIOGRAPHICAL SKETCH

Erin Meyer-Gutbrod was born and raised in Euclid, Ohio, two blocks south of Lake Erie. During high school, Erin worked part-time writing scripts for a local .com company. She graduated 3<sup>rd</sup> in her class at Euclid High School in 2004, and received awards as the top student in science and computer science in her class of 400. After graduation, she spent her summer as a volunteer deckhand aboard the US Brig Niagara as it sailed through the Great Lakes. Following her first summer in college, she worked as boatswain aboard the Schooner Amistad and learned to love the open sea.

Erin earned a BS in physics at the University of Notre Dame in 2008, adding a second major in philosophy and a minor in Spanish to widen her liberal arts education. All four years at college she worked as the Introduction to Astronomy teaching assistant, running the school observatory. In the summer following her sophomore year, Erin worked at the US Naval Observatory in Flagstaff, AZ in an REU program, developing methods for using the black hole at the center of our galaxy as a gravitational lens to improve intragalactic distance estimates. She presented her work as a poster at the American Astronomical Society conference in Seattle, WA in January 2007. During her junior year, Erin studied physics, philosophy and Spanish abroad at the Universidad Catolica in Chile.

After college, Erin spent a year working as a scientific editor in Eugene, OR, where she also volunteered at the raptor rehabilitation center. She briefly joined a field work team vaccinating prairie dogs in Badlands National Park to conserve the black-footed ferret. Then she worked as an intern zookeeper in the Audubon Zoo in New Orleans, LA. In an effort to combine her interest in wildlife conservation with her quantitative skills and education, Erin started a PhD

program in the Ocean Resources and Ecosystems program under Dr. Charles Greene at Cornell University in 2010.

During her time in graduate school, Erin assistant taught multiple semesters of Introductory Oceanography and Satellite Remote Sensing of Biological Oceanography, and received the Outstanding Teaching Award in 2012. She participated in two field courses: Field Marine Science at Shoals Marine Lab on Appledore Island, NH, and Marine Bioacoustics at Friday Harbor Marine Lab on San Juan Island, WA. At Cornell, she took extensive coursework in marine ecology, quantitative ecology and statistics. Erin received several honors and grants including the Earth and Atmospheric Science Research Excellence Award, the National Defense Science and Engineering Fellowship and the Atkinson Center Sustainable Biodiversity Fellowship.

*Dedicated to Joshua, the light of my life.*

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After taking me out to lunch on my first day at Cornell, Bruce Monger quickly became a good friend. Bruce walked into my office each day to provide a ready smile and a funny story. We had a great time teaching IDL and Python side by side, and watching his Oceanography course grow into the largest class at Cornell. My children loved meeting Bruce in the late afternoons for dog walks, or going to his house for pesto pasta dinners. Both Chuck and Bruce were my advocates in dealing with Cornell bureaucracy, even paying me out of pocket as a part-time employee during my maternity leave when the graduate school would not provide support.

Pat Sullivan has been both an amazing fountain of statistical and ecological knowledge and one of the kindest people I have ever met. His courses on multivariate statistics, fisheries



populations and spatial statistics provided much of the background knowledge necessary for my research. Pat also took me into his lab group as one of his own, giving me the opportunity to pester him with questions and learn from him on a regular basis and to benefit from the wisdom of his graduate students and postdocs in the Natural Resources department.

Chris Clark provided biological expertise and a long history of research experience with the species of interest in my research: right whales and *Calanus finmarchicus*. He cheerfully asked questions about right whales I would never have thought to ask and told stories of his time with the North Atlantic right whale population in the Gulf of Maine and the Southern population off the Argentine coast. I was truly lucky to find an advisor and committee members that valued and encouraged me as both a scientist and a person.

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## CHAPTER 1

### INTRODUCTION: ECOLOGICAL IMPACTS IN A CHANGING OCEAN

Anthropogenic influences on the environment and its inhabitants have caused a rapid increase in species extinctions, and scientists have speculated that we may be inciting the sixth mass extinction event in Earth's history (Barnosky et al. 2011). Humans have impacted organism fitness and ecosystem function through direct harvest, habitat destruction, resource depletion, pollution, introduction of invasive species and foreign pathogens, and climate change. While many changes in terrestrial ecosystems are clearly discernable and sampling methods are straightforward, changes in marine ecosystems are less visible and harder to quantify. In this chapter, several of the most threatening impacts of human industry on marine ecosystems are introduced to provide some background on the state of our oceans at this time. Then, a case study of the North Atlantic right whale is presented to demonstrate how human influences have led to the near-extinction of one of the ocean's great baleen whales. Finally, the research presented in this dissertation, which examines the impact of climate-associated fluctuations in prey availability on right whale demography and population dynamics, is summarized. Despite previous beliefs, the ocean is not too big to escape human influence.

#### 2.1 CLIMATE CHANGE

Global temperatures have risen at a rate of 0.2°C each decade over the past three decades as a result of increased anthropogenic emissions of greenhouse gases (Hansen et al. 2006). The global oceans have absorbed over 93% of this increase in heat content (Levitus et al. 2012). The influx of carbon dioxide and rapid accumulation of heat energy have significantly altered Earth's marine ecosystems (Hoegh-Guldberg and Bruno 2010). As warming trends progress towards

increased stratification and a shift towards permanent El Nino-like conditions, evidence suggests that marine primary production, which accounts for half of all global net primary production, will decline (Behrenfeld et al. 2006). Using global satellite-derived chlorophyll data, Polovina et al. (2008) found that the ocean's least productive waters expanded by 15% over an 8-year time series due to increases in vertical stratification near the ocean surface.

Biological responses to warming oceans include shifts in species range distributions and massive coral reef bleaching episodes. Scientists have also documented widespread changes in phenology, or the timing of seasonal activities. In a meta-analysis of over 1700 species, Parmesan and Yohe (2003) found an average poleward range shift of 6.1 km per decade and an advancement of springtime activities of 2.3 days per decade. In the case of pelagic environments, ecosystems such as the North Sea have been impacted by a trophic mismatch as spring phytoplankton blooms occur progressively earlier in response to warming, but secondary and tertiary consumers such as zooplankton and fish larvae, which have evolved to exploit the bloom timing, have not yet altered their behavior (Edwards and Richardson 2004). In a study of 36 demersal fish species in the North Sea, half, in particular the smaller, shorter-lived species, have exhibited northward range shifts (Perry et al. 2005). Fish species with slower life histories and longer maturation times are already susceptible to overexploitation, and with slower adaptation they face greater vulnerability to the effects of warming temperature changes. Many marine species are unable to shift poleward due to abiotic factors, such as geographical barriers or inadequate light levels. For example, the coral species composing tropical reef communities face serious constraints on their adaptability to climate change.

Rising global temperatures are accentuated at upper latitudes and have led to rapid sea ice loss and glacier melt. Decline in Arctic sea ice cover is accelerating, with a current loss of 10%

of perennial ice cover per decade (Comiso et al. 2008). This represents a massive loss of habitat for sea-ice algae and phytoplankton, which account for over half of the total primary production in the Arctic Ocean (Post et al. 2013). Decreased ice extent and warming waters in the Bering Sea have caused upper trophic level demersal fish, historically limited to warmer sub-Arctic waters, to expand their range to Arctic waters. As the Bering Sea shifts from a benthic- to a pelagic-dominated ecosystem, marine mammal and seabird populations that prey on benthic invertebrates will decline (Grebmeier et al. 2006). In the Southern Ocean, sea ice loss has led to a shift towards declining krill densities and increases in salp abundance, effecting the species that prey on krill, including penguins, albatross, seals and whales (Atkinson et al. 2004).

Thermal expansion, coupled with discharge from the melting cryosphere, have increased ocean volume and sea levels are currently rising at a rate of 3.2 mm/year (IPCC: Church et al. 2013). In addition to displacing millions of people living near coasts, sea level rise is expected to have effects on coastal ecology. In areas with steep coastal topography or extensive coastal infrastructure, such as sea walls, loss of intertidal habitat to rising seas may reduce foraging grounds for seabirds (Galbraith et al. 2002). In cases where sea level rise occurs faster than coral reef accretion, reef drowning may occur (Knowlton et al. 2001).

## 2.2 OCEAN ACIDIFICATION

Along with absorbing most of the heat from greenhouse warming, the global oceans also absorb one third of the carbon dioxide released from fossil fuel burning. While this oceanic uptake has reduced atmospheric concentration of carbon dioxide and, in turn, decreased the impacts of global warming, absorption of carbon dioxide has fundamentally altered ocean chemistry (Doney et al. 2009). Carbon dioxide reacts with seawater to form carbonic acid,

lowering ocean pH and decreasing the availability of calcium carbonate needed by calcareous organisms, such as corals and calcifying plankton, to form shells.

In the case of coral reefs, ocean acidification has caused a decrease in the rate of reef building, a decline in skeletal density, and an increase in energy invested in reef building (Hoegh-Guldberg et al. 2007). In addition to warming waters, coral reefs have undergone massive degradation on a global scale by increased disease prevalence and local stressors, such as point-source pollution and outbreaks of predators like the crown-of-thorns starfish. For example, there has been a 50% loss of reef cover on the Great Barrier Reef since 1985 (De'ath et al. 2012).

Commercially important mollusks, such as oysters and mussels, depend on high concentrations of calcium carbonate for both early development and adult reproduction. Economic losses from declines in the US mollusk fishery are projected to range from \$300 million to several billion dollars over the next half century (Cooley and Doney 2009). While ocean acidification causes declines in the growth and condition of calcareous organisms, some fleshy algal species may actually thrive due to increased photosynthetic rates and decreased grazing (Kroeker et al. 2012). A shift towards algal-dominated ecosystems will likely be accompanied by a decrease in biodiversity and altered ecosystem function.

## 2.3 POLLUTION

Marine ecosystems are exposed to toxins in the seawater through riverine discharge, atmospheric deposition and point-source pollution. Human activity including land-use change, infrastructural development and construction, agriculture, shipping and recreation have contributed to marine pollution and resulted in coastal and pelagic ecosystem alterations and

degradation (Islam and Tanaka 2004). For centuries, humans considered the oceans too big to pollute, and operated under the concept that “the solution to pollution is dilution.” However, in recent decades, scientists have discovered myriad devastating effects of pollution in marine environments.

Millions of tons of non-biodegradable plastic have been produced over the past century, becoming the most abundant type of marine debris and posing a serious threat to marine life (Derraik 2002). Marine debris can harm organisms through the mechanisms of entanglement, ingestion, and suffocation. Accumulated in the North Pacific gyre, the great ‘garbage patch’ has a 6:1 weight ratio of near-surface fragmented plastic to plankton (Moore et al. 2001). Floating plastic debris accumulates and concentrates persistent organic pollutants (POPs), such as polychlorinated biphenyls (PCBs) and polycyclic aromatic hydrocarbons (PAHs), making them accessible to marine organisms in much higher concentrations than in typical seawater (Rios et al. 2010). Floating plastic can also be used as a transport mechanism for the dispersal of invasive species (Gregory 2009).

Ten thousand to several hundred thousand tons of crude oil are accidentally spilled into the ocean from tankers and barges each year (ITOPF 2016). Acute-phase mortality events following an oil spill are directly observable and well studied. Sea birds and marine mammals are especially affected due to their need to frequently access the air-sea interface. Contact with surface slicks causes feathers and fur to lose insulation efficiency, causing death by hypothermia. Oiled animals also suffer mortality from smothering, drowning, and poisoning from ingestion. Oil typically penetrates the water column to the benthos, leading to mass mortality of macroalgae and benthic invertebrates due to its toxic effects or smothering (Teal and Howarth 1984). Less understood are the indirect and long-term ecosystem effects following an oil spill. For years

following the Exxon Valdez spill, chronic exposure to PAHs in the sediment affected herring and salmon egg development, and bioaccumulation of toxins in prey increased sea otter and seabird mortality rates (Peterson et al. 2003).

Massive influxes of nitrogen and phosphorous from upstream agricultural fertilization are transported into estuaries and coastal marine ecosystems. Coastal eutrophication has caused harmful algal blooms, rendering shellfish toxic and resulting in human poisoning and death (Smith 2003). Following unbridled algal growth, increased concentrations of particulate organic matter stimulate bacterial production, resulting in increased microbial respiration leading to massive hypoxic zones. The two largest 'dead zones' formed from anthropogenic nutrient loading are the Baltic Sea (49,000 km<sup>2</sup>; Conley et al. 2009) and the Gulf of Mexico (21,000 km<sup>2</sup>; Rabalais et al. 2002). These low oxygen waters are unusable for benthic invertebrates and pelagic species, causing habitat loss and habitat fragmentation (Diaz and Rosenberg 2008).

In addition to chemical pollution, noise pollution has recently been identified as having a deleterious effect on marine ecosystems. A significant portion of anthropogenic noise in the water is an unintentional byproduct of shipping and boating activities or construction and use of offshore platforms for oil and gas wells as well as wind farms. Sound is also used deliberately as a measurement device for navigation, detection of submarines, fish-finding, and seismic reflection profiling for oil exploration (Slabbekoorn et al. 2010). High intensity sounds from activities such as pile driving or air gun use for oil exploration can cause tissue damage, behavioral changes or sudden death in nearby fish and marine mammals (Popper and Hastings 2009, Gordon et al. 2003). Chronic acoustic masking can have deleterious effects on social marine mammals, such as baleen whales, which depend on sound for communication (Clark et al. 2009).

## 2.4 OVERFISHING

More noticeable than ecosystem degradation from unintentional anthropogenic disturbance, the abundance of marine organisms, especially at upper trophic levels, has been impacted directly through human harvesting. Global biomass of large predatory fish has been reduced to 10% of pre-industrial levels as a result of overfishing (Myers and Worm 2003). This trend was true for coastal species such as codfishes, flatfishes, skates and rays, and for pelagic species such as tuna, billfishes and swordfish. Community biomass is typically reduced by 80% of the pre-exploitation value within 15 years of industrialized fishing, and often before any scientific monitoring has taken place.

As the abundance of upper-trophic level fish declines, humans “fish down the food web” targeting lower-trophic level organisms (Pauly et al. 1998). Statistics from the Food and Agricultural Organization show that the mean trophic level of seafood has declined from 1950 to 1994 as markets transition from carrying long-lived piscivorous demersal fish to short-lived, pelagic planktivorous fish and invertebrates. Although the collapse of upper-trophic level fisheries is prevalent, especially in the North Atlantic, middle- and lower-trophic level harvesting is increasing even in areas where top predator catches have not declined, termed “fishing through the food web” (Essington and Beaudreau 2006).

In addition to decreasing marine biomass, overfishing has resulted in unintended ecological consequences such as changes in community structure. The removal of top predators has led to inadvertent trophic cascades. For example, release from predation due to overfishing has caused an increase in grazing by sea urchin populations in the Mediterranean, leading to a transition from erect algal communities to coralline barrens (Sala et al. 1998). In the Black Sea, population surges of both phytoplankton and jellyfish have been attributed to the combined



effects of trophic cascades driven by overfishing and eutrophication (Daskalov 2002). In the Northwest Atlantic, the collapse of benthic fish species, such as cod, haddock and hake, contributed to an increase in small pelagic fish and benthic macroinvertebrates, a decline in large zooplankton and a surge in phytoplankton (Frank et al. 2005). However, the effects of top-down forcing on the lower trophic levels in this system have been called into question (Greene 2012, Pershing et al. 2014).

Another unintended consequence of global fishing is bycatch, or the incidental take of organisms with little or no commercial value. Over 40% of harvested marine organisms are either unused or unmanaged, and therefore classified as bycatch (Davies et al. 2009). Bycatch can occur either when a non-targeted species is caught, or when a non-targeted sex, age or size class of the targeted species is caught. Shrimp trawl fisheries have the highest ratio of bycatch to target species intake by weight, and they account for one third of all bycatch globally (Alverson et al. 1994). Gill-net fisheries are primarily responsible for the bycatch of marine mammals, with a mean take of over 6000 cetaceans and pinnipeds each year in the US fisheries alone (Read et al. 2006). Long-line fisheries are responsible for a tremendous amount of loggerhead and leatherback sea turtle bycatch, resulting in a decline of 80-95% in Pacific populations (Lewison et al. 2004). Sharks and rays are demographically sensitive to threats due to life history characteristics, such as late maturity and low productivity. As a result of targeted fisheries for shark fins (Clarke et al. 2007), minimal regulation of “pest” species and frequent occurrence of bycatch, three-quarters of pelagic sharks and rays are designated as threatened or near-threatened (Dulvy et al. 2008). Large coastal and oceanic shark populations in the Northwest Atlantic, including hammerhead, white and thresher sharks, have declined by over 75% since the 1960s as a result of long-line bycatch (Baum et al. 2003).

Fishing practices over coral reefs have had especially devastating impacts on these fragile and diverse ecosystems. Destructive practices such as cyanide fishing and dynamite fishing are used to stun or kill fish for fishermen to collect once they float to the surface. These practices result in widespread mortality of the organisms and reef structures in the community, far beyond the targeted species. Both the destruction of reef area and the elimination of top predators from overfishing can lead to a phase shift from a coral reef-dominated to an algal-dominated community (McManus 2000). A global assessment in 1997 found that nearly all coral reefs have been degraded by overfishing, as indicated by the low abundance of upper trophic indicator species (Hodgson 1999).

Anthropogenic stressors have caused extensive changes to the physical marine environment and led to significant degradation of marine ecosystems. From the direct effects of harvesting resources from the ocean to the indirect effects of introduced pollution and climate change, marine ecosystems have suffered decreases in both biomass and biodiversity. In response to the rapidly changing marine environment, it is especially essential to monitor marine ecosystems to assess the degree of anthropogenic impact, pinpoint drivers to change and determine what mitigation tactics may be employed.

## 2.5 MARINE MAMMALS AS INDICATORS OF ENVIRONMENTAL CHANGE

Marine mammals serve as remarkable sentinels to environmental change because they “integrate and reflect ecological variation across large spatial and long temporal scales” (Moore et al. 2008). High mortality in the southern sea otter, a keystone species in kelp forest ecosystems, has occurred, partially due to exposure to toxins in the water such as petroleum and POPs (Jessup et al. 2004). As inhabitants of coastal waters, manatees are vulnerable to both

watercraft collisions and disease caused by harmful algal blooms (Bonde et al. 2004). Marine mammals dependent on sea ice, such as the polar bear and the ringed seal, serve as the most blatant examples of ecosystem change resulting from climate change (Hunter et al. 2010; Ferguson and Stirling 2005).

Few cetacean species directly suffer from recent physical changes to their environment such as warming temperatures and melting sea ice because they have adapted to a wide range of physical conditions due to their large habitat range. However, there is evidence of declines in cetacean populations resulting from environmentally driven changes to their prey. Baleen whales especially depend on patches of highly concentrated plankton to sustain their large caloric requirements. Due to the long life histories, high energetic requirements and low productivity of most cetacean species, small changes to the abundance, distribution or patchiness of prey can lead to dramatic changes to cetacean vital rates.

Incidence of starved, beached gray whales increased drastically at the start of the new millennium, likely as a result of reduced prey availability in places such as Chirikov Basin (Moore et al. 2003). Modeling studies have projected that warming temperatures, decreased sea ice extent and an expanding krill fishery in the Southern Ocean will cause a reduction in krill biomass and lead to a significant decline in blue whale birth rates (Weidenmann et al. 2011). Fin whale blubber thickness and birth rates were also shown to vary with environmentally driven changes in prey conditions in Icelandic waters (Williams et al. 2013). Efforts to rebuild the Southern Resident Killer Whale population, which subsists on large quantities of Chinook salmon, directly conflict with efforts to maximize Chinook landings in the Pacific Northwest (Williams et al. 2011).

## 2.6 NORTH ATLANTIC RIGHT WHALES

Nicknamed the “urban whale”, the North Atlantic right whale, *Eubalaena glacialis*, serves as a striking sentinel to anthropogenic change to the marine environment. With a habitat spanning the Eastern seaboard of the US and southern Canada, right whales feed, breed and migrate through waters rife with human activity. Harvested for oil and baleen for centuries, the right whale population was decimated before the start of the 20<sup>th</sup> century (Reeves et al. 1999). Despite the moratorium on commercial whaling in 1935, the North Atlantic right whale remains one of the most endangered large whale species, with a population numbering just over 500 individuals (Pettis and Hamilton 2015).

The most common causes of death for these slow, maladroit creatures are vessel collisions and fishing gear entanglements. Of the 40 right whales necropsied between 1970 and 2006, the cause of death in 53% was determined to be a vessel collision (Campbell-Malone et al 2008). Evidence of entanglement has been documented in 83% of the population, with 26% of adequately photographed individuals exhibiting new signs of entanglement annually (Knowlton et al. 2012).

Like other baleen whales, right whales have a tight-knit social structure and rely heavily on low-frequency calls for communication, navigation, feeding and breeding. Due to the proximity of critical habitat to active shipping lanes, right whales have lost over 60% of their communication space (Hatch et al. 2012). Right whales are also exposed to chemical pollution, including PCBs and neurotoxins from harmful algal blooms, with potential maternal transfer to neonates (Woodley et al. 1991; Doucette et al. 2012).

There is evidence that right whales have also experienced physiological stress resulting from periods of food limitation. While not necessarily increasing mortality rates among healthy

adult whales, low prey availability has the potential to decrease reproductive efficiency or increase prenatal or neonatal mortality rates due to the unusually high energetic demands of mammalian reproduction (Wade and Schneider 1992). Pregnant North Atlantic right whales undergo a significant migration from feeding grounds in the Gulf of Maine to breeding grounds near the coast of Florida, further increasing the demands of reproduction. Miller et al. (2011) found that North Atlantic right whales have significantly thinner blubber layers than their close cousins, the Southern right whale (*Eubalaena australis*), suggesting a difference in nutrition between the two species. North Atlantic right whales experience thinner blubber layers following periods of low prey availability, and blubber layers are thinnest during lactation. Modeled energetic requirements compared with *in situ* prey data demonstrate that lactating females, unlike other demographic groups, may not be acquiring sufficient nutrition (Fortune et al. 2013).

The decline in right whale population growth observed during the 1990s raised serious concerns about population viability (Caswell et al. 1999; Fujiwara and Caswell 2001). However, the resurgence of calf births in the 2000s, mirroring fertility conditions in the 1980s, indicated that a linear trend in population growth was overly simplistic. To improve the management of this critically endangered species, it is essential to better understand the interannual and interdecadal fluctuations in right whale vital rates. In this dissertation, I examine the effects of environmental changes moderated through prey availability on the demography of the North Atlantic right whale.

*Chapter 2: Climate-Associated Regime Shifts Drive Decadal-Scale Variability in Recovery of North Atlantic Right Whale Population*

In Chapter 2, I address large variations in the frequency of North Atlantic right whale calf births which occurred over decadal time periods. In the 1980s, calf production averaged 28 calves \* 100 reproductive females<sup>-1</sup> \* year<sup>-1</sup>. In the 1990s, average calf production declined to 14 calves \* 100 females<sup>-1</sup> \* year<sup>-1</sup>. Then in the 2000s, average calf production increased again to 24 calves \* 100 females<sup>-1</sup> \* year<sup>-1</sup>. This decadal scale variation in breeding rates can be partially explained by climate-associated fluctuations in prey availability in critical right whale feeding grounds.

To demonstrate this association, I built a simple three-stage reproduction model following adult female right whales as they step between years of resting, pregnant and lactating. Time series of right whale life history data were taken from the North Atlantic Right Whale Consortium photographic ID (Right Whale Consortium 2011). Transitions between reproductive stages were modeled independently and as a function of food availability. As a proxy for prey abundance, I used late stage *Calanus finmarchicus* anomalies taken from the Continuous Plankton Recorder (CPR) transect running from Boston, MA to Cape Sable, Nova Scotia. The CPR transect was broken into 4 distinct regions: Cape Cod Bay, West Gulf of Maine, East Gulf of Maine and Scotian Shelf, and *C. finmarchicus* data was parsed into bimonthly anomalies.

A demographic matrix model was used to predict a time series of calf births from 1980-2007. Models dependent on spatially- and temporally-resolved prey anomalies performed better than the prey-invariant null model or the model dependent on annually averaged, transect-wide *C. finmarchicus* anomalies. The regions and seasons driving the best resolved model correspond well with known right whale feeding and mating grounds. These prey-dependent reproduction models indicate a tight coupling between *C. finmarchicus* abundance in the Gulf of Maine and right whale reproductive success.

*Chapter 3: Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population*

In Chapter 3, the three state right whale reproduction model was examined more rigorously, assessing various environmental variables that may impact calf rates through the mechanism of prey abundance. Prey-driven variations in right whale calf production are linked to both circulation changes in the North Atlantic and temperature and salinity changes stemming from the Arctic Ocean. A period of low Arctic Ocean Oscillation (AOO) index in the 1990s corresponded to a massive export of cold, freshwater, marked as a Great Salinity Anomaly in the Northwest Atlantic. This transport led to changes in the timing and extent of stratification, altering the phytoplankton and zooplankton assemblages in the Gulf of Maine (MERCINA 2012). This remotely driven, ecosystem-wide regime shift coincided with lower birth rates throughout the decade. An extremely negative phase of the North Atlantic Oscillation during the winter of 1996 led to a decline in the Gulf of Maine *C. finmarchicus* population (Greene and Pershing 2003; Greene and Pershing 2004). This additional decline in copepod abundance coincided with a near cessation in right whale reproduction in 1999 and 2000. At the end of the 1990s, the Arctic Ocean shifted back to a regime of increased freshwater storage in the Beaufort Gyre, and the NAO reverted back to a positive phase. As *C. finmarchicus* rebounded in the early 2000s, right whale fertility increased to levels seen in the 1980s, and the population entered a period of growth.

To analyze the connection between these physical phenomena and the interannual variation in right whale reproduction, the effects of six other variables tied to Gulf of Maine ecology, in addition to CPR-derived late stage *C. finmarchicus* anomalies were tested. Calf births from 1980-2007 were predicted as a function of the NAO, Regional Slope Water Temperature,

Arctic Oscillation, AOO, Regional Shelf Water Salinity and CPR-derived autumn phytoplankton color index. Each variable was tested with time lags varying from zero to five years.

Calf births were best predicted by the four-year-lagged Regional Slope Water Temperature, likely because this index describing the Northwest Atlantic's coupled slope water system captures and explains the drop in reproduction at the end of the 1990s, which is the most significant anomaly observed in the three decade period of study. The 2- and 3-year lagged AOO index as well as the unlagged Autumn phytoplankton anomaly also perform well, capturing the variability in calf births driven by altered seasonal stratification resulting from remote Arctic forcing.

Out of all variables and time lags compared, the reproduction model driven by regionally and seasonally resolved, CPR-derived late-stage *C. finmarchicus* anomalies performed optimally. Some inferences about right whale reproductive biology can be made regarding the shape of the probability functions as reproductive females transition between states. The probability of a female becoming pregnant increases gradually from 20% to 40% with increasing prey concentrations in the Western Gulf of Maine in November/December, a known breeding ground, and across the entire CPR transect in March/April. These results may indicate the combined importance of blubber reserves built during spring feeding and high prey concentrations in the late fall bringing the population together for mating opportunities. The probability of a pregnant female transitioning to lactation, i.e. being observed with a live calf, behaves like a step function with increasing prey in the Eastern Gulf of Maine in July/August. This function indicates that a specific threshold of prey availability is required for successful gestation and neonate survival.

Model predicted calving intervals are estimated for each year from 1980-2007 using the regionally- and seasonally-resolved prey-dependent reproduction model. Each theoretical calving



interval can be interpreted as a snap-shot of reproductive efficiency given that year's prey conditions. In 1998 and 1999, the anomalously low prey concentrations corresponded with a near cessation in reproduction, with theoretical calving intervals exceeding the expected lifetime of a right whale. If the environmental conditions observed over this time period persisted, the population could decline rapidly. Although climate-driven regime shifts in the Northwest Atlantic are unpredictable, right whale feeding grounds occupy the southernmost boundary of the region inhabited by *C. finmarchicus*. As sea temperatures rise, Reygondeau and Beaugrand (2011) predict a northward shift in *C. finmarchicus* habitat, potentially increasing the frequency of low prey scenarios for right whales, or consequently forcing the species to shift their own habitat.

*Chapter 4: A species on the brink: Effects of prey-driven fecundity and anthropogenic mortality rates on demographic projections of the North Atlantic right whale population*

Expanding on the previous chapters, I develop the North Atlantic right whale reproduction model into a full demographic model representing all life stages for male, female, and unknown sex individuals. Using the photographic-ID database (Right Whale Consortium, 2014), each confirmed whale sighting corresponds to a “capture” event, and capture-recapture techniques are used to model the transitions between life stages. Capture probabilities are estimated for each demographic group as a function of annual survey effort. Probabilities of transitioning between demographic states are modeled as constants, then as a function of CPR-derived late-stage *C. finmarchicus*. Using the female states of the full demographic model, I project right whale population growth into the next century under different prey availability and mortality scenarios.

In the time-invariant model, the population growth rate over the time period 1980-2012 is positive, with  $\lambda=1.026$ . Averaged over the time series, approximately one quarter of available females breed each year. Prey dependence was tested in each state transition, but only the inclusion of prey in the transition from adult female resting to breeding significantly improved the model.

The right whale population was projected forward 100 years under three different resampled prey scenarios: high prey concentrations in the 1980s, low prey concentrations in the 1990s, and high prey concentrations in the 2000s. Under the two high prey scenarios, the population grows faster with a narrower range of variability in  $\lambda$  than in the low prey scenario. However, even in the low prey scenario resampled from the 1990s, population growth remains positive. Given these demographic results, right whales appear to be in a period of recovery, and the outlook for this species is hopeful.

Since right whales are vulnerable to anthropogenic mortality resulting from ship strikes or entanglement in fishing gear, it is essential that this species continues to be closely managed. Although population growth remains positive under all prey projection scenarios tested here, viability is a function of both reproduction and mortality rates. Should a change in shipping or fishing gear policies lead to an increase in mortality, population growth cannot be guaranteed. In a scenario where 12 additional whales are killed each year, or just over 2% of the population, the growth rate becomes negative under typical prey concentrations. With the compounding effects of both low prey availability and a small increase in mortality rates, the population could become vulnerable again.

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## CHAPTER 2

# CLIMATE-ASSOCIATED REGIME SHIFTS DRIVE DECADAL-SCALE VARIABILITY IN RECOVERY OF NORTH ATLANTIC RIGHT WHALE POPULATION

### *Abstract*

Despite an elevated mortality rate from lethal interactions with humans, the North Atlantic right whale population has continued to grow during the first decade of the new millennium. This unexpected population growth is the result of a 128% increase in female-specific reproduction relative to the 1990s. Here, we demonstrate that the recent increase in annual right whale calf production is linked to a dramatic increase in the abundance of its major prey, the copepod species *Calanus finmarchicus*, in the Gulf of Maine. The resurgence of *C. finmarchicus* was associated with a regime shift remotely forced by climatic changes in the Arctic. We conclude that decadal-scale variability in right whale reproduction may be largely driven by fluctuations in prey availability linked to climate-associated ecosystem regime shifts.

(Originally published as Meyer-Gutbrod 2014)

### 2.1 INTRODUCTION

Humans began hunting the North Atlantic right whale (*Eubalaena glacialis*) nearly a millennium ago. By the end of the 19th century, the population was so depleted that it was of little commercial value to the whaling industry (Allen, 1908). In 1935, the right whale population first received protected status from the League of Nations, and, since 1949, a complete moratorium on hunting has been in place and overseen by the International Whaling Commission (Best et al., 2001). Despite the end of commercial whaling in the mid-20<sup>th</sup> century, the recovery of this endangered population has been gradual and highly variable. Accurate demographic

studies only became possible after an extensive and ongoing effort was initiated during the 1970s to photograph and catalog all individuals in the population (Kraus et al., 1986). Subsequent analyses of the demographic data indicated that the population's growth rate increased gradually during the 1980s, but then declined sharply during the 1990s (Fujiwara and Caswell, 2001). Demographic projections based on data from the early 1990s suggested that the population was on a trajectory that would lead to its eventual extinction in less than 200 years (Fujiwara and Caswell, 2001).

As news of these demographic projections spread within the right whale research community, a consensus view emerged that the population would continue to decline unless the right whale's elevated mortality rates associated with ship strikes and entanglement in fishing gear could be significantly reduced (Fujiwara and Caswell, 2001; Kareiva, 2001; Waring et al., 2001). In contrast to this expectation, the right whale population began to recover during the following decade. Despite high mortality rates and even more dire demographic projections during the decade of the 2000s (Kraus et al., 2005), the population grew from ~340 animals at the beginning of the decade to ~486 animals by 2010 (Figure 2.1[Top]). A major factor in this recovery was the 128% increase in female-specific average annual calf production between 2001 and 2010 relative to the previous decade (Figure 2.1[Bottom]). Here, we use a data-driven, stochastic reproduction model to explore the ecological underpinnings for this dramatic increase in right whale reproduction.

## 2.2 METHODS

### 2.2.1 *Right Whale Population Data*

North Atlantic right whales have been photographically cataloged in a consistent manner since 1980 and are identified using unique markings, scars and callosity patterns (Kraus et al., 1986).

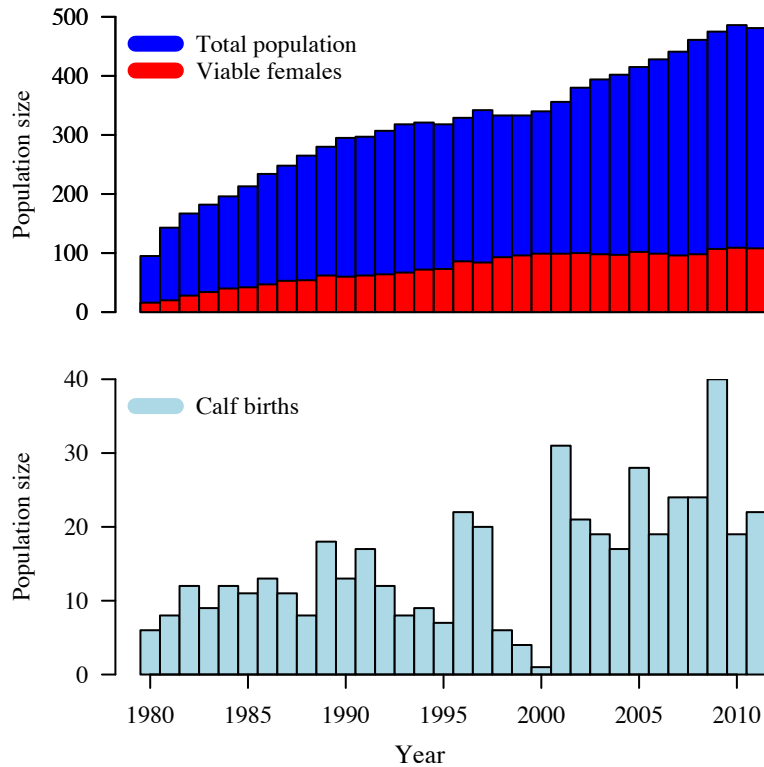


Figure 2.1: Time series of North Atlantic right whale population size from 1980 to 2010. [Top]: total number of all whales (dark blue), number of reproductively viable females (red), and [Bottom]: number of calf births (light blue).

Population growth rates reported in this paper use what are considered to be the best estimates of the total population and numbers of reproductively viable female whales. The North Atlantic Right Whale Consortium (NARWC; <http://www.narwc.org/>) provided us with a list of all known whales along with the years in which they died or were last sighted. Six years missing is the standard used by the NARWC to define a whale that is presumed to have died. Annual estimates of the total number of whales presumed to be alive therefore include any whales on the list that are not known to have died or have not gone missing for six or more years without a subsequent sighting. Because of the potential for bias in using this six-year rule, we only used population data up until 2007 in our models. Among whales presumed to be alive, females considered reproductively viable are ones known to have given birth or to have reached nine years of age,

the average age of first parturition (Hamilton et al., 1998). Whales categorized as senescent are also removed from the time series of reproductively viable females (Knowlton et al., 1994).

The time series of annual calf production used in this study includes all known calf births, regardless of whether the mother was known and/or whether the calf survived its first year of life. Due to high survey effort in the mid-Atlantic region, mother/calf pairs have an especially high sighting probability; therefore, it is assumed that all newborn calves have been observed.

### 2.2.2 Right Whale Reproduction Model

The stochastic reproduction model used in this study assigns reproductively viable females into three states: (1) recovering, (2) pregnant, or (3) nursing (Figure 2.2). Recovering females can remain in the resting state ( $1 - \emptyset_{21}$ ) or become pregnant ( $\emptyset_{21}$ ). Pregnant females can give birth and enter the nursing state ( $\emptyset_{32}$ ) or abort the pregnancy and reenter the recovering state ( $1 - \emptyset_{32}$ ). Nursing females can only transition to the recovering state ( $\emptyset_{13}=1$ ).

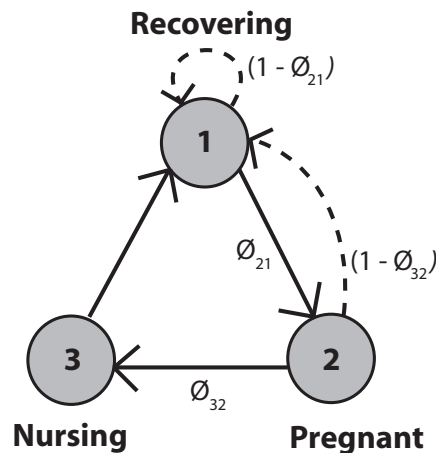


Figure 2.2: North Atlantic right whale reproduction model. Reproductive females can be in the (1) recovering state between pregnancies, (2) pregnant, or in the (3) nursing state. Transitional probabilities between states are determined as functions of *C. finmarchicus* abundance in the Gulf of Maine.

Using this sequence of three reproductive states, we constructed the following transitional probability matrix:

$$A = \begin{pmatrix} 1 - \phi_{21} & 1 - \phi_{32} & 1 \\ \phi_{21} & 0 & 0 \\ 0 & \phi_{32} & 0 \end{pmatrix} \quad [\text{Equation 2.1}]$$

Each element  $A_{ij}$  in the matrix is the probability of a reproductively viable female transitioning from state  $j$  to state  $i$  in a year. The projection matrix  $A$  is multiplied by the female abundance vector  $N_{t-1}$ , or the number of living viable females in each of the three reproductive states during year  $t-1$ , to estimate the female abundance vector  $N_t$  during the following year  $t$ .

$$N_t = [A] * N_{t-1} \quad [\text{Equation 2.2}]$$

The two probabilities optimized in this study are  $\phi_{21}$  and  $\phi_{32}$ , which represent the probability of a female transitioning from the recovering state (1) to the pregnant state (2), and the probability of a female transitioning from the pregnant state (2) to the nursing state (3), respectively.

Transitional probabilities were estimated as logistic functions dependent on *C. finmarchicus* abundance. Model parameter vectors were optimized to yield a predicted calf production time series that best fits the observed one provided by the NARWC.

The transitional probabilities were estimated as logistic functions to constrain the probabilities between 0 and 1 while offering flexibility in the shape of the function:

$$\phi_{21} = \frac{e^{\beta_{21} * X}}{1 + e^{\beta_{21} * X}} \quad [\text{Equation 2.3}]$$

$$\phi_{32} = \frac{e^{\beta_{32} * X}}{1 + e^{\beta_{32} * X}} \quad [\text{Equation 2.4}]$$

where the vector notation  $\beta_{21} * X$  and  $\beta_{32} * X$  each represent a linear combination of an intercept and coefficient(s) multiplied by the independent prey variable(s),  $X$ . These transitional probabilities were fit into a demographic matrix model, and the parameter vectors  $\beta_{21}$  and  $\beta_{32}$

were estimated to yield a predicted annual calf production time series most closely resembling the observed time series.

The model estimates of  $\beta_{21}$  and  $\beta_{32}$  predict different functional responses of the transitional probability  $\emptyset_{21}$  and the transitional probability  $\emptyset_{32}$  as functions of prey abundance.  $\emptyset_{21}$  increases gradually with increasing values of *C. finmarchicus* abundance index, yielding a relatively linear relationship. However,  $\emptyset_{32}$  behaves like a quasi-step function, with the transition to nursing a calf changing abruptly from highly improbable to highly probable over a narrow range of *C. finmarchicus* abundance values. This abrupt transition occurs at abundance values slightly below the climatological average for that bimonthly time period.

*Calanus finmarchicus* abundance indices were estimated from Gulf of Maine Continuous Plankton Recorder (CPR) survey data collected from 1980-2007 (Greene et al., 2013). Despite the sampling limitations of the CPR and the averaging out of spatial and temporal patchiness, this index has proven to be a remarkably useful proxy for characterizing inter-annual to inter-decadal variability in *C. finmarchicus* abundance (MERCINA, 2001, 2004; Greene et al., 2008). Six bimonthly *C. finmarchicus* abundance indices were determined for the entire Gulf of Maine region and for each of four geographical subregions: Massachusetts Bay (MB), Western Gulf of Maine (WGOM), Eastern Gulf of Maine (EGOM), and Scotian Shelf (SS) (Figure 2.3). An annual average *C. finmarchicus* abundance index was also determined for the entire Gulf of Maine region and for each subregion. Combinations of all indices were added and evaluated in a stepwise fashion to determine the best overall model fit to the annual calf production time series.

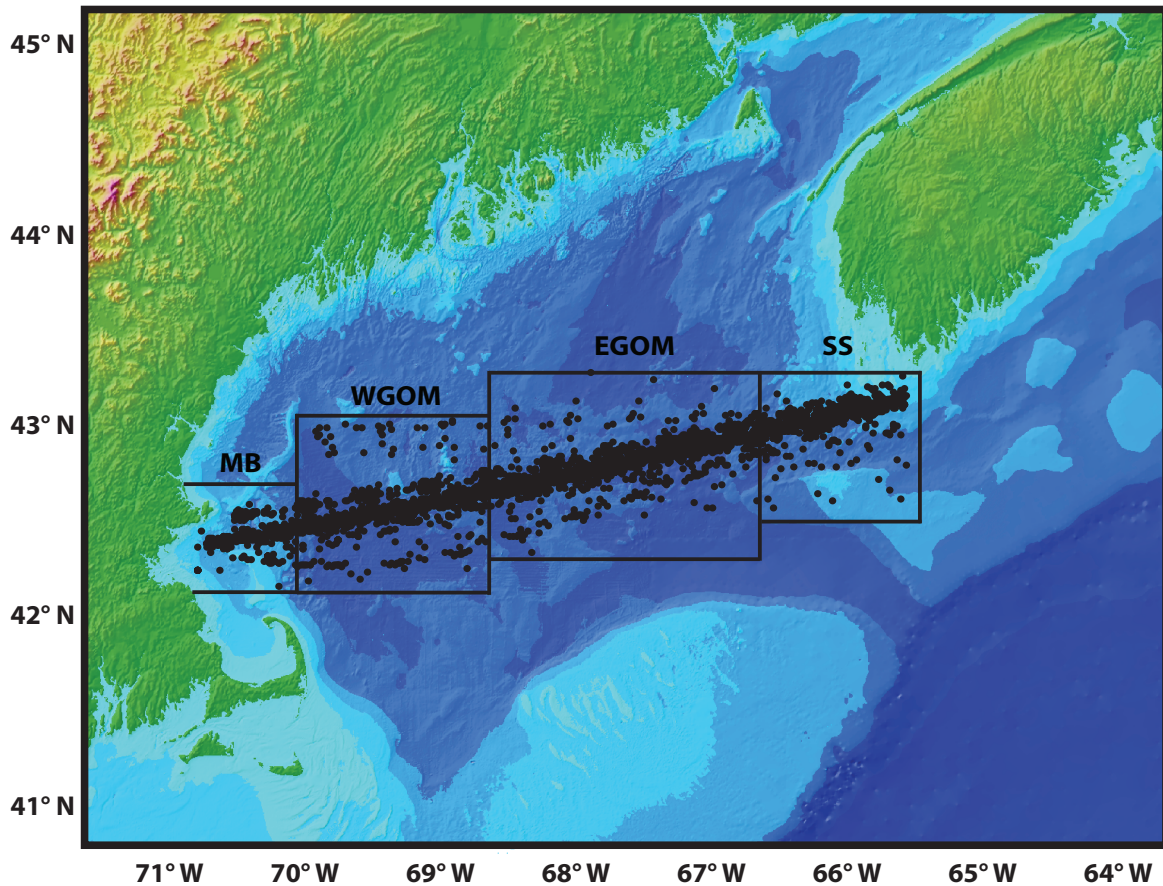


Figure 2.3: Gulf of Maine CPR survey area used to characterize prey availability to right whales. CPR survey area is divided into four geographical subregions: Massachusetts Bay (MB), Western Gulf of Maine (WGOM), Eastern Gulf of Maine (EGOM), and Scotian Shelf (SS). CPR survey sampling (black circles) in the Gulf of Maine occurs at approximately monthly intervals.

## 2.3 RESULTS

Annual calf production estimates from our model demonstrate the tight coupling between right whale reproduction and prey abundance over the past three decades (Figure 2.4[Top & Middle]). Results from the model incorporating bimonthly and regional variations in prey abundance (Figure 2.4[Middle]) fit the observed data better than results from a temporally and spatially averaged version of the model (Figure 2.4[Bottom]), similar to the one previously reported by Greene et al. (2003). The additional information on prey temporal and spatial



distributions incorporated in the new model are consistent with independent observations of whale foraging patterns (Kenney et al., 2001), increasing confidence that the new model captures the relevant features of this predator-prey interaction.

In our best-fit model, the probability of reproductively viable females transitioning from the resting state to the pregnant state is driven primarily by *C. finmarchicus* abundance in the WGOM during November/December. This time frame spans the peak mating season for right whales, and the western and central Gulf of Maine have been identified as a likely mating ground (Cole et al., 2013). The probability of reproductively viable females transitioning from the resting state to the pregnant state is driven secondarily by *C. finmarchicus* abundance in the entire Gulf of Maine during March/April. This time frame corresponds to a period when high right whale abundance is observed in Cape Cod Bay (Pendleton et al., 2009), Massachusetts Bay (Schevill et al., 1986), and the Great South Channel (Kenney et al., 1995). Finally, the probability of reproductively viable females transitioning from the pregnant state to the nursing state is driven by *C. finmarchicus* abundance in the EGOM during July/August. Since right whales are typically found nearby in the lower Bay of Fundy during late summer (Mate et al., 1997), this relationship suggests that the EGOM subregion may be a significant feeding ground for pregnant females.

The close relationship between annual calf production and *C. finmarchicus* abundance in the Gulf of Maine is reflected in the decadal variability observed for both (Figure 2.4[Top & Middle]). Since complete records began in 1980, statistically significant changes in calf production and *C. finmarchicus* abundance were observed at the beginning of each decade (Greene et al., 2013). Corresponding, statistically significant changes were also observed each decade in calf production per 100 reproductive females (Figure 2.5). During the 1980s, *C.*

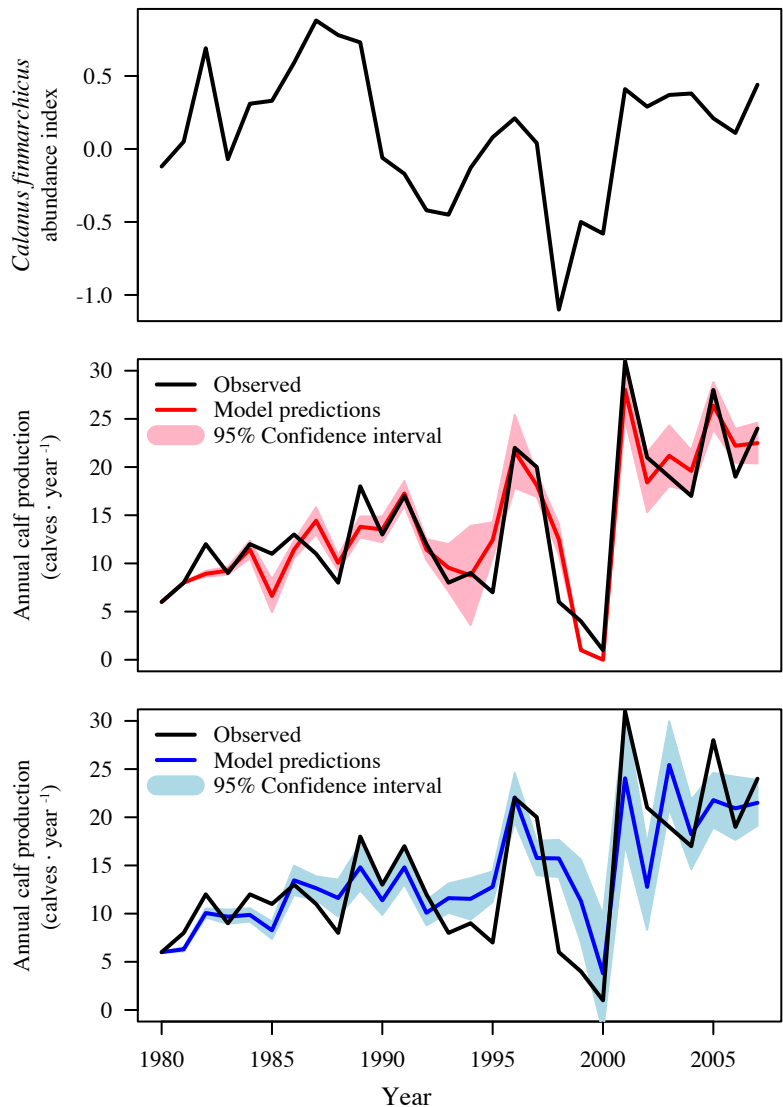


Figure 2.4: [Top]: Time series of *C. finmarchicus* annual abundance index (Greene et al. 2013) estimated for entire Gulf of Maine CPR survey area. [Middle & Bottom]: Time series of annual calf production (calves · year<sup>-1</sup>) observed (black line) and [Middle]: predicted by model driven by bi-monthly- and geographic-specific abundance estimates of *C. finmarchicus* in the Gulf of Maine (red line) and [Bottom]: predicted by model driven by annual abundance estimates of *C. finmarchicus* averaged for entire Gulf of Maine (blue line). The pale red and blue shading surrounding the model predictions correspond to the 95% confidence intervals.

*finmarchicus* was abundant, and right whale calf production averaged  $28 \text{ calves} \cdot 100 \text{ females}^{-1} \cdot \text{year}^{-1}$ . During the 1990s, there was a large decline in *C. finmarchicus* abundance, and the average right whale calf production rate decreased to  $14 \text{ calves} \cdot 100 \text{ females}^{-1} \cdot \text{year}^{-1}$ . During the 2000s, *C. finmarchicus* abundance surged again, and the average right whale calf production increased to  $24 \text{ calves} \cdot 100 \text{ females}^{-1} \cdot \text{year}^{-1}$ .

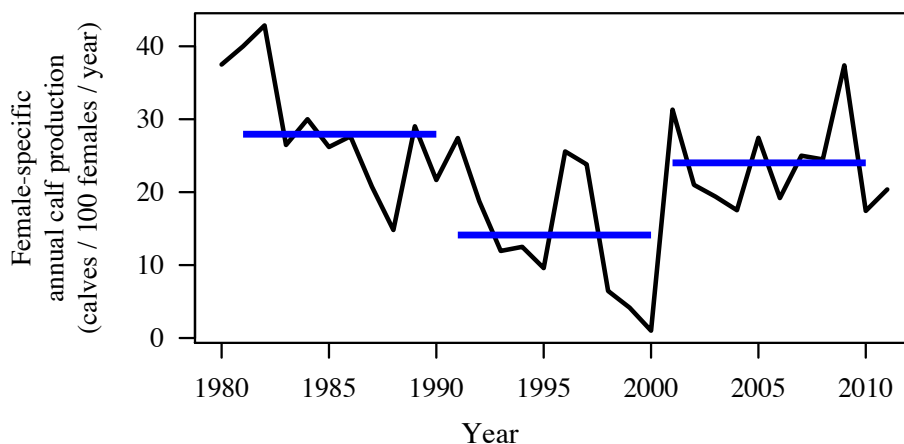


Figure 2.5: Time series of female-specific annual calf production ( $\text{calves} \cdot 100 \text{ females}^{-1} \cdot \text{year}^{-1}$ ). Decadal averages of female-specific annual calf production are shown with blue lines.

## 2.4 DISCUSSION

These correlated changes in *C. finmarchicus* abundance and right whale calf production have been linked to ecosystem responses in the Gulf of Maine to both basin- and hemispheric-scale climate forcing (Greene et al., 2013). The elevated abundance of *C. finmarchicus* in the Gulf of Maine during the 1980s was due to a favorable combination of high local productivity and sufficient advective supply into the region from upstream source regions (MERCINA, 2004). At the end of the 1980s, the Arctic climate system underwent a regime shift that triggered a large-scale export of freshwater out of the Arctic Ocean and into the North Atlantic (Greene et al., 2008; MERCINA, 2012). The resulting Great Salinity Anomaly of the 1990s led to a

sequential reduction of salinities in shelf ecosystems throughout the Northwest Atlantic (Greene et al., 2008; MERCINA, 2012). In the Gulf of Maine, the low-salinity waters altered the timing and extent of water-column stratification, which subsequently impacted the production and seasonal cycles of phytoplankton, zooplankton, and higher-trophic-level consumers in the ecosystem (Greene and Pershing, 2007; Greene et al., 2008; MERCINA, 2012). The abundance of *C. finmarchicus* declined precipitously after this climate-driven ecosystem regime shift, and right whale annual calf production soon followed after a one- to two-year time lag (Figure 2.4[Top & Middle]). During the late 1990s, *C. finmarchicus* abundance declined even further after the 20<sup>th</sup> century's largest drop in the North Atlantic Oscillation (NAO) Index was observed during winter 1996. Large-scale circulation changes in the slope and shelf waters of the Northwest Atlantic were observed during the subsequent two years (MERCINA, 2001; Greene and Pershing, 2003), and these were hypothesized to have been major contributing factors to the crash of *C. finmarchicus* in 1998 and the subsequent reproductive failure of right whales in 1999 and 2000 (Figure 2.4[Top & Middle]) (Greene et al., 2003; Greene and Pershing, 2004).

At the end of the 1990s, the Arctic climate system underwent another regime shift, this time entering a period favoring enhanced freshwater storage in the Arctic Ocean that persisted throughout the first decade of the 2000s (MERCINA, 2012). The corresponding reduction in freshwater export from the Arctic Ocean resulted in elevated salinities throughout Northwest Atlantic shelf ecosystems. In the Gulf of Maine, the plankton shifted back to resemble the assemblage characteristic of the 1980s regime, including a resurgence of *C. finmarchicus* abundance. Primed with a large number of females that had not reproduced during the poor prey conditions of the late 1990s, the relatively large portion of resting females responded with a rapid increase in annual calf production during the early 2000s, which remained at an elevated level

for the remainder of the decade. Rather than facing the prospect of eventual extinction, as was forecast at the beginning of the decade, the right whale population in 2010 was on a positive trajectory towards recovery. It should be noted, however, that continued elevated rates of right whale calf production are contingent upon favorable future prey conditions.

## 2.5 CONCLUSION

The North Atlantic right whale population's recovery during the past decade demonstrates that factors affecting both reproduction and mortality must be considered when projecting the fate of an endangered species. In retrospect, there is evidence supporting the hypothesis that decadal-scale variability in the population's recovery rate is strongly driven by climate-associated ecosystem regime shifts. Specifically, this variability is a reflection of large fluctuations in annual calf production as it responds to changes in the ecosystem that affect prey availability. This conclusion does not mean that anthropogenic sources of mortality are unimportant and that their mitigation should not be adopted as major elements in a conservation management plan. In fact, a plan that can reduce mortalities associated with ship strikes and entanglement in fishing gear will only serve to hasten the population's recovery. What our conclusion does mean is that climate variability and change will introduce a level of uncertainty into demographic projections that must be taken into consideration when the goals of a conservation management plan are set and evaluated.

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## CHAPTER 3

### CLIMATE-ASSOCIATED CHANGES IN PREY AVAILABILITY DRIVE REPRODUCTIVE DYNAMICS OF THE NORTH ATLANTIC RIGHT WHALE POPULATION

#### *Abstract*

Considered one of the most endangered cetacean species, the North Atlantic right whale (*Eubalaena glacialis*) suffered declining abundance during the 1990s due to a high rate of anthropogenic-associated mortality and a low rate of reproduction. Previous studies have suggested that the reproductive rate is tightly coupled to the abundance of *Calanus finmarchicus* in the Gulf of Maine (GOM), which has been shown to respond to ecosystem regime shifts associated with decadal-scale climate forcing from the Arctic. Given the endangered status of the right whale population, it is vital to determine how climate-associated changes in prey availability will affect this species in the future. Here, we investigate a 3-state reproduction model that explores multiple environmental proxies as potential predictors of annual calf production during the period from 1980 to 2007. The model achieves its best fit to observations using temporally and spatially resolved *C. finmarchicus* abundance data derived from Continuous Plankton Recorder (CPR) surveys of the GOM. Building on previous research, this prey-dependent model, which uses bimonthly and geographically specific abundance anomalies of *C. finmarchicus*, significantly improves estimates of annual calf production relative to a null model. The temporal and geographic distributions of prey objectively chosen for inclusion in the new version of the model correspond well with observed right whale seasonal distribution patterns, providing further evidence that the model captures essential features of right whale reproductive ecology. (Originally published as Meyer-Gutbrod 2015)

### 3.1 INTRODUCTION

The North Atlantic right whale population was severely impacted by persistent whaling pressure from the 11th to the 20th century (Aguilar 1986, Reeves et al. 1999), and the remaining members of the population now occupy a greatly reduced range in the Northwest Atlantic. Despite the introduction of international regulations protecting right whales from commercial whaling in 1935, the North Atlantic population has failed to recover due to a combination of variable birth rates and high mortality rates (Fujiwara & Caswell 2001, Greene & Pershing 2004). The high mortality rates are largely anthropogenic in origin, with right whales being especially vulnerable in coastal waters to ship strikes and entanglement in fishing gear (Gaskin 1987, Knowlton & Kraus 2001). With an estimate of only 522 individuals remaining in the population (Pettis & Hamilton 2014), the North Atlantic right whale has been designated as ‘endangered’ under the US Endangered Species Act and by the International Union for Conservation of Nature.

Caswell et al. (1999) developed a stochastic model of North Atlantic right whale population growth from 1980 to 1996. According to their model, a declining population growth rate was attributed to a decrease in survival probability and an increase in the calving interval. Given the population growth rate estimated for the mid 1990s, Caswell et al. (1999) projected that the North Atlantic right whale was on a trajectory towards extinction in less than 200 yr. Using a full demographic population model, Fujiwara & Caswell (2001) found a significant decline in female life expectancy, likely attributed to the proximity of females to shipping lanes and fishing gear during their migration to, and time spent on, calving grounds off the coast of Florida and Georgia (Kraus et al. 1986). Additionally, a change in the calving interval, the mean interval between births for reproductive females, provided strong evidence that the conception

rate was declining and the frequencies of prenatal and neonatal mortalities were increasing (Knowlton et al. 1994, Kraus et al. 2001, Browning et al. 2010).

In comparison, the southern right whale (*Eubalaena australis*) population off the coast of South Africa exhibits higher growth rates and shorter mean calving intervals (Knowlton et al. 1994, Best et al. 2001). Brown et al. (1994) report that only 38% of the reproductive females in the North Atlantic had calved, compared to 54% in the southern population. These differences suggest that the North Atlantic right whale may be capable of higher growth rates and reproductive output under improved environmental conditions.

Greene et al. (2003b) and Greene & Pershing (2004) hypothesized that fluctuations in prey availability associated with climate-associated changes in the ocean environment could explain the high reproductive variability observed in the population. This hypothesis is consistent with the high energetic costs associated with pregnancy and lactation in right whales (Fortune et al. 2013), and prey availability has been linked to body condition and pregnancy rate in other cetacean species (Lockyer 2007, Ward et al. 2009, Williams et al. 2013). In light of the increasing support for this prey-limitation hypothesis, a more thorough and quantitative investigation of the relationship between changes in prey availability and right whale reproduction is warranted.

### 3.1.1 Effects of prey availability on North Atlantic right whale nutrition and reproduction

North Atlantic right whales derive most of their nutrition from the older developmental stages (i.e. copepodites) of the copepod species *Calanus finmarchicus* (Mayo et al. 2001, Baumgartner et al. 2003). A conservative estimate of right whale daily energetic demand reveals that an average-sized right whale (40 000 kg) must consume approximately 100 million late-

stage *C. finmarchicus* copepodites each day (Kenney et al. 1986). To meet this demand, right whales must selectively feed on high-density patches of *C. finmarchicus* to ensure net positive energy intake (Kenney et al. 1986). Consistent with this need for high prey abundance, the seasonal spatial distributions of right whales are significantly correlated with those of *C. finmarchicus* (Michaud & Taggart 2007, Pendleton et al. 2012). There are 4 recognized major feeding grounds for the North Atlantic right whale population, beginning with Cape Cod Bay and Massachusetts Bay during the spring, transitioning seasonally to the Great South Channel during the late spring and summer, and to the Bay of Fundy and Roseway Basin during the late summer and autumn (Hlista et al. 2009). However, the whales have also been observed to desert feeding grounds during periods when the abundance of this prey species becomes too low (Kenney 2001, Patrician & Kenney 2010).

Owing to the extreme energetic demands of pregnancy and nursing, female mammals generally do not reproduce unless they are physically robust, which typically coincides with favorable feeding conditions (Wade & Schneider 1992). Among right whales, reproductive females are especially vulnerable to nutritional limitations due to the foraging hiatus pregnant cows must undergo during the 3-mo period spent migrating to, and residing on, the coastal calving grounds located in Florida and Georgia (Fortune et al. 2013). Recent analyses of blubber thickness in North Atlantic and southern right whales have revealed significantly thinner blubber layers in the North Atlantic species, suggesting that this species' reproduction may be nutritionally compromised in comparison to its southern hemisphere counterpart (Miller et al. 2011). This suggestion is consistent with findings that North Atlantic right whale blubber thickness is positively correlated with *C. finmarchicus* abundance (Miller et al. 2011), and both

are correlated with annual calf production (Pettis et al. 2004, Klanjscek et al. 2007, Miller et al. 2012).

### 3.1.2 Role of prey availability in mediating climate effects on North Atlantic right whale population dynamics

The abundance of *C. finmarchicus* in the Gulf of Maine (GOM) has been linked to ecosystem regime shifts associated with decadal-scale climate forcing from the Arctic (MERCINA 2012, Greene et al. 2013). During the 1980s, *C. finmarchicus* abundance was elevated due to a favorable combination of high local productivity and advective supply into the region from upstream source regions (MERCINA 2004). Towards the end of the decade, the Arctic climate system underwent a regime shift that resulted in the export of large quantities of low-salinity water from the Arctic Ocean into the North Atlantic (Greene et al. 2008). The resulting salinity anomaly progressed downstream in 2 major pulses during the 1990s, leading to a sequential reduction of salinities in Northwest Atlantic shelf ecosystems from the Labrador Sea to the Middle Atlantic Bight (Greene et al. 2008). The invasion of low-salinity water altered the timing and extent of stratification in these ecosystems, which subsequently impacted the production and seasonal cycles of phytoplankton, zooplankton and higher trophic level consumers (Greene & Pershing 2007, Greene et al. 2008).

This climate-driven ecosystem regime shift lasted throughout the 1990s in the GOM. Associated with it, the abundance of early-stage *C. finmarchicus* copepodites increased significantly, while the abundance of late-stage copepodites declined. The exact mechanism underlying this decline in abundance is uncertain; however, it has been hypothesized that

changes in the ecosystem resulted in an increase in planktivorous fish, especially herring, and their size-selective predation on *C. finmarchicus* (Greene et al. 2013).

Correlated with the decline in late-stage *C. finmarchicus* abundance, right whale annual calf production also decreased significantly at the beginning of the 1990s (Greene & Pershing 2003). Annual calf production remained lower throughout the decade relative to the 1980s. In 1999 and 2000, calf production per reproductive female plummeted to an all time low since the start of rigorous demographic observations on the species (Fig. 1B). Greene & Pershing (2003) hypothesized that the reproductive failure observed during these 2 yr was driven by a crash of the *C. finmarchicus* population in the GOM during 1998 (Fig. 1A). They associated this crash with a decrease in the advective supply of *C. finmarchicus* to the GOM after the 20th century's largest drop in the North Atlantic Oscillation (NAO) index during winter 1996 altered slope and shelf water circulation patterns in the Northwest Atlantic (Greene & Pershing 2003).

At the end of the 1990s, the Arctic climate system underwent another regime shift, which persisted throughout the first decade of the 2000s (MERCINA 2012). A reduction in freshwater export from the Arctic Ocean led to elevated salinities over the Northwest Atlantic shelf. In the GOM, the plankton shifted back to resemble the assemblage characteristic of the 1980s, including a resurgence in the abundance of late-stage *C. finmarchicus* copepodites (Fig. 3.1[Top]). Right whale annual calf production increased rapidly and remained at an elevated level for the remainder of the decade (Fig. 3.1[Bottom]).

Given the North Atlantic right whale's status as an endangered species and the large reproductive variability observed from one decade to the next, it is vital to determine how changing climate and corresponding changes in prey availability affect the population dynamics

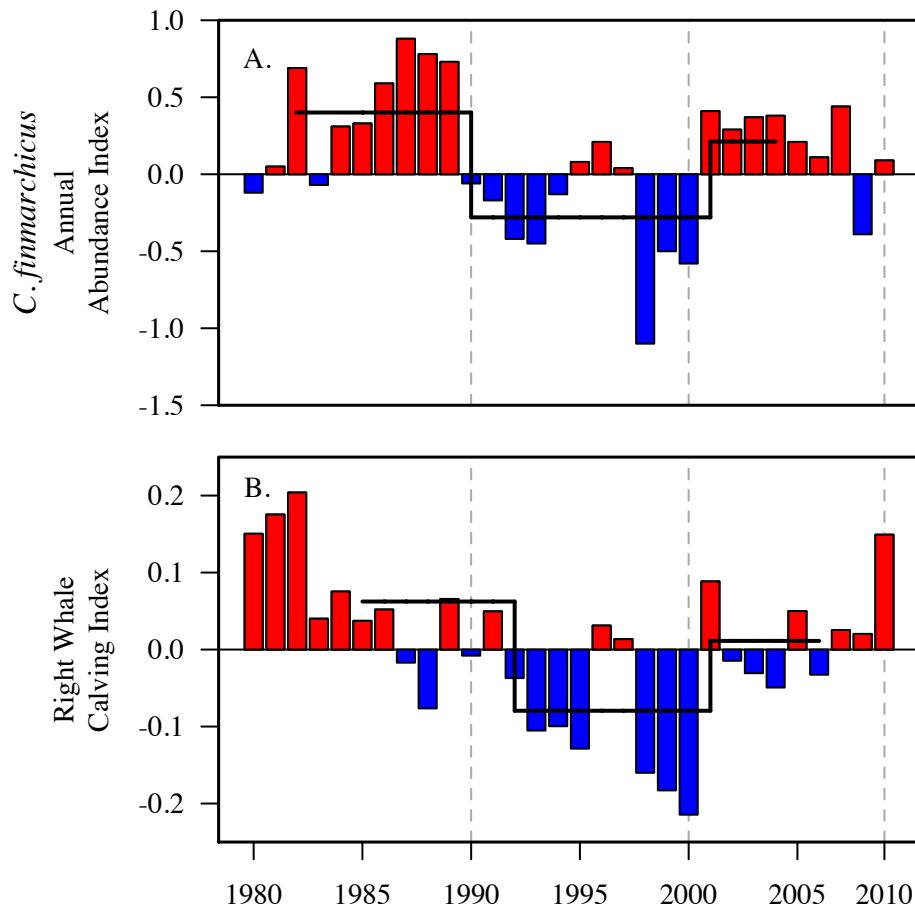


Figure 3.1: [Top]: Late-stage *Calanus finmarchicus* annual abundance anomaly index estimated for the entire GOM CPR survey area and [Bottom]: female-specific annual right whale calf production (annual calf births/annual viable female population size). Positive values of indices above the climatological mean are shaded in red; negative values below the climatological mean are shaded in blue. A sequential t-test analysis of regime shifts (Rodionov 2004) was applied to each of the time series, and regime shifts that are significant at the  $\alpha = 0.05$  level are shown by black lines

of this species. This type of long-term, multi-species research is difficult to accomplish in any ecosystem, but is especially challenging in pelagic marine systems that are relatively large and open. Fortunately, for this particular ecosystem, over 30 yr of co-occurring, but independently collected, right whale demographic data and climate-associated environmental data are available for analysis.

Here, we report results from an analysis of right whale reproduction, which uses a 3-state matrix model to explore how well a number of environmental variables, including *C.*

*finmarchicus* abundance, perform as potential predictors of annual calf production. Within this modeling framework, we tested the predictive skill of these environmental variables against one another and against a null model that assumes a constant calving rate. In the case of *C.*

*finmarchicus*, we compared the model's predictive skill using abundance estimates for the late-stage copepodites averaged over the entire year for the full GOM versus abundance estimates resolved into bimonthly time periods and for specific geographic subregions. Such temporal and spatial resolution may yield additional insights into what times of year and which geographic locations are most important to right whale reproduction.

## 3.2 MATERIALS AND METHODS

### 3.2.1 Right whale demographic monitoring data

The North Atlantic Right Whale Consortium (Right Whale Consortium 2011) identifies right whales by using unique markings, scars and callosity patterns. The corresponding database of identifications has been photographically cataloged in a consistent manner since 1980. This database provided the foundation for our studies of right whale reproduction. First, we used the database to develop a time series of annual calf production. This time series included all known



calf births, regardless of whether the mother was known and whether the calf survived its first year of life. Owing to high survey effort near the calving grounds off the coasts of Florida and Georgia, mother/calf pairs have an especially high sighting probability, and we assumed that all newborn calves have been observed (Kraus & Rolland 2007). Next, we used the database to develop a time series of reproductively viable females. A female is considered reproductively viable if she has been known to give birth or has reached 9 yr of age. A female is considered nulliparous or senescent if she has not reproduced for 9 consecutive years while in the viable pool. A female is considered missing if she has not been sighted in 5 consecutive years and is presumed dead after the 5th yr (Knowlton et al. 1994). Females that have been categorized as senescent or missing were removed from the time series of reproductively viable females.

### 3.2.2 Continuous Plankton Recorder survey data

The Continuous Plankton Recorder (CPR) is an instrument towed behind ships of opportunity to collect and preserve plankton filtered through a 270- $\mu\text{m}$  mesh silk gauze for subsequent analyses in the laboratory (Warner & Hays 1994). Since 1961, the NOAA National Marine Fisheries Service has operated a CPR survey of the GOM running between Boston, Massachusetts and Cape Sable, Nova Scotia, at approximately monthly intervals (Fig. 2.3) (Jossi & Kane 2013). Although the CPR is not an ideal instrument for quantitative and synoptic estimates of plankton species abundance due to the limited geographic, depth and temporal coverage of the sampling, its consistent use in long-term surveys of the region has provided an invaluable data set for studying relative abundance patterns on seasonal to decadal time scales (e.g. Greene et al. 2013). Our hypothesis that the *C. finmarchicus* abundance index serves as a good proxy for right whale prey availability is supported in studies by Pendleton et al. (2009)

and Pershing et al. (2009), which demonstrate that regional scale, near-surface *C. finmarchicus* abundance measured with the CPR is significantly correlated with right whale sightings in the GOM. We used only the abundance of late-stage *C. finmarchicus* copepodites (stage 5 and adults) as a proxy for food availability due to the importance of these stages in the diet of right whales (Mayo et al. 2001).

For evaluating the model's predictive skill when using yearly averaged *C. finmarchicus* abundance estimates for the entire GOM, we used data from samples collected along the full CPR transect (Fig. 2.3). Late stage *C. finmarchicus* abundance index anomalies were calculated from the seasonal climatological cycle as described by Pershing et al. (2005).

For evaluating the model's predictive skill when using temporally and spatially resolved *C. finmarchicus* abundance estimates, data were averaged into temporal bins spanning 2 mo to yield 6 seasonal indices of plankton abundance corresponding to the averages of January and February, March and April, May and June, July and August, September and October, and November and December. Bi-monthly averages provide sufficiently fine temporal resolution to demonstrate seasonal variations in prey abundance while still averaging over sufficient time to avoid data gaps in the survey time series. The *C. finmarchicus* abundance estimates were spatially resolved by breaking the CPR transect into 4 distinct subregions: Massachusetts Bay (MB), Western GOM (WGOM), Eastern GOM (EGOM) and Scotian Shelf (SS) (Fig. 2.3). This geographic breakdown coincides reasonably well with some of the most common right whale feeding grounds, with MB encompassing Cape Cod Bay, WGOM lying just upstream of the Great South Channel, EGOM lying just downstream of the Bay of Fundy and SS being representative of prey conditions on the shelf and in the nearby Roseway Basin. A total of 35

seasonal and subregion-specific variables were explored ([4 subregions + 1 full transect area] × [6 seasons + 1 annual average] = 35 indices).

### 3.2.3 Other environmental variables as predictors of annual calf production

As right whale reproduction appears to be linked to *C. finmarchicus* abundance, and as interannual to interdecadal variability in this species' abundance has been linked to climate-associated ecosystem changes and regime shifts in the GOM/SS region, we also explored how well other environmental variables might be used as predictors of annual calf production. We looked at environmental variables that are associated with 2 basin- to hemispheric-scale mechanisms hypothesized to drive these regional ecosystem changes (Greene et al. 2013).

The first of these mechanisms is a basin-scale phenomenon associated with changes in the phase of the NAO. It has been hypothesized that the NAO is linked to right whale calf production through its effects on the Northwest Atlantic's coupled slope water system and the advective supply of *C. finmarchicus* into the GOM/SS region (Greene & Pershing 2003, 2004, Caswell & Fujiwara 2004, Greene et al. 2013). The Regional Slope Water Temperature (RSWT) index, which is the first derived mode of a principal component analysis of 8 slope water temperature time series anomalies for the GOM/western SS region, serves as an indicator of the state of this coupled slope water system (MERCINA 2001). Negative values of the RSWT index are associated with increased transport of the Labrador Current around the tail of the Grand Banks, contributing more of the colder, fresher Labrador Subarctic Slope Water to the region and displacing the warmer, fresher Atlantic Temperate Slope Water further off the shelf. The abundance of late-stage *C. finmarchicus* copepodites has been correlated with the RSWT index, and it has been hypothesized that this correlation is the result of slope water circulation changes

potentially limiting the advective supply of *C. finmarchicus* into the region (Greene & Pershing 2000, MERCINA 2001, 2004). To explore how this NAO/coupled slope water system mechanism might be linked to right whale annual calf production, the NAO index and RSWT index were each used to drive the reproduction model, with time lags ranging from 0 to 5 yr.

The second of these mechanisms is hemispheric in scale and associated with decadal-scale changes in Arctic climate that regulate freshwater export from the Arctic Ocean into the North Atlantic and subsequently affect stratification and plankton productivity patterns throughout the shelf waters of the Northwest Atlantic (Greene et al. 2008, MERCINA 2012, Greene et al. 2013). Shifts in the atmospheric and oceanic circulation patterns of the Arctic, as measured by the Arctic Oscillation (AO) index and Arctic Ocean Oscillation (AOO) index, respectively, have been linked to the storage and release of freshwater from the Arctic Ocean's Beaufort Gyre. When the Beaufort Gyre weakens and freshwater is released, salinity anomalies can be traced as they exit the Arctic Ocean and propagate down the Northwest Atlantic shelf (Greene et al. 2008). Once they reach the GOM/SS region, such freshwater anomalies can be quantified with the Regional Shelf Water Salinity (RSWS) index, which is the dominant mode of a principal component analysis of shelf-water salinity data from the GOM/SS/Georges Bank region (MERCINA 2012, Greene et al. 2013). The increased buoyancy of the surface waters alters the seasonal patterns of stratification and primary production, which in turn can lead to a regime shift in the plankton assemblage (Greene & Pershing 2007, MERCINA 2012, Greene et al. 2013). The seasonal changes in primary production include an increase in autumn phytoplankton abundance, which can be quantified with an autumn phytoplankton color index derived from the GOM CPR survey samples (Greene & Pershing 2007). Greene et al. (2013) hypothesize that the length and productivity of the phytoplankton growing season affect the

feeding conditions and population abundances for *C. finmarchicus* and the smaller copepod species in the GOM. To explore how this stratification mechanism remotely forced from the Arctic might be linked to right whale annual calf production, the AO index, AOO index, RSWS index and autumn phytoplankton color index were each used to drive the reproduction model, with time lags ranging from 0 to 5 yr (only lags of 0, 1 and 2 yr were analyzed for CPR-derived time series due to some data gaps during the late 1970s).

To examine the likelihood of finding spurious correlations between right whale calf production and the various *C. finmarchicus* and environmental variables, a resampling technique was used to examine the distribution of model Akaike's information criterion indices (AICs) (Akaike 1974, Burnham & Anderson 2002) calculated using bootstrapped data. The moving-block bootstrap method (Wilks 1997) was employed by randomly selecting 4-yr blocks of data with replacement from a single variable to generate a new, resampled time series of the same length. As the time series considered in this study is 28 yr long (from 1980 to 2007), each bootstrapped variable was composed of 7 blocks, with each block consisting of 4 yr of sequential data. This effectively randomizes the relationship between right whale reproduction and prey availability while preserving the short-term autocorrelation in the independent variable. The calf production and viable female time series were not randomized to preserve the demographic relationship between the number of cows and calves, as well as the long-term trend of population growth that can be expected in this system. Each new variable was drawn uniformly from 1 of the 36 genuine lagged and unlagged variables, and tested in the reproduction model. This trial was performed 10 000 times to produce a probability distribution for the AICs.

This resampling scheme provides a conservative evaluation of the likelihood of finding spurious relationships between right whale calf production and each variable being examined.

With such a short time series, only 7 blocks can be randomized while still preserving relevant temporal autocorrelation in the data. Furthermore, given the known occurrence of regime shifts, and the occasional resemblance between regimes, such as that of the 1980s and the early 2000s, the bootstrap-generated time series will resemble the genuine variables more often than with a completely random resampling process.

### 3.2.4 Reproduction model

The reproduction model we employed assigns reproductively viable females to 3 states: resting, pregnant and nursing (Fig. 2.2) (Greene & Pershing 2003, 2004). The resting state corresponds to the period of time between nursing and when the female can be impregnated. In this model, the resting state lasts for a minimum of 1 yr, and can last longer depending on the nutritional state of the female and environmental conditions. The pregnant state in the model lasts 1 yr, which corresponds to the ca. 12-mo gestation period (Best 1994). If a pregnant female experiences a spontaneous abortion or neonatal mortality occurs before the calf is sighted, then the female transitions from the pregnant state back to the resting state. Otherwise, the pregnant female enters the nursing state. The nursing state in the model lasts 1 yr, which corresponds to observations of a ca. 12-mo lactation period. After the nursing state, all females return to the resting state (Fig. 2.2) (Hamilton et al. 1995). In our study, we equate the model-generated time series of nursing females with annual calf production, and model parameters are optimized to fit this time series with the observed calves in the population.

This 3-state reproduction model was implemented with the following transitional probability matrix,  $A$ , (Caswell 2001):

$$A = \begin{pmatrix} 1 - \phi_{21} & 1 - \phi_{32} & 1 \\ \phi_{21} & 0 & 0 \\ 0 & \phi_{32} & 0 \end{pmatrix} \quad [\text{Equation 3.1}]$$

Each element in the matrix  $A_{ij}$  contains the probability of a reproductively viable female transitioning from state  $j$  to state  $i$  in a year. The projection matrix  $A$  is multiplied by the female abundance vector  $N_{t-1}$ , the number of viable females in each of the 3 reproductive states during year  $t-1$ , to estimate the female abundance vector  $N_t$  during the following year  $t$ :

$$N_t = (A) \times N_{t-1} \quad [\text{Equation 3.2}]$$

The 3 elements in  $N$  correspond to the number of resting females, the number of pregnant females and the number of nursing females, respectively, and the number of nursing females is equated with the model-projected number of calves produced that year. Female mortalities (subtractions from  $N$ ) and new recruits into the reproductive pool (additions to  $N$ ) were manually added and subtracted from the population vector at each annual time step to avoid confounding errors in mortality rates with errors in the reproductive transitional probabilities.

The transitions of viable females among the 3 reproductive states were estimated over the time period from 1980 to 2007. This range was chosen because 1980 marks the year when right whale population monitoring methods became standardized, and 2007 is the last year before a gap occurred in the CPR survey data set.

Initial conditions were set to reflect the likely distribution of females among the 3 states in 1980. The 16 known reproductively viable females in 1980 were assigned to the 3 reproductive states by setting the number of females in the nursing state equal to the number of calves born that year, and the number of females in the pregnant state equal to the number of calves born in the following year, 1981. The remaining reproductively viable females identified

in 1980 were assigned to the resting state. While assigning initial conditions always has the potential to introduce some bias into a model, this method performed better than other methods evaluated. In addition, the amount of bias introduced by fixing these initial conditions was very limited because of the small numbers of viable females and calves observed in 1980 relative to later in the time series.

The 2 probabilities optimized in this study are  $\phi_{21}$  and  $\phi_{32}$ , which represent the probability of a female transitioning from the resting state (1) to the pregnant state (2), and the probability of a female transitioning from the pregnant state (2) to the nursing state (3), respectively (Fig. 2.2). The transitional probabilities were estimated as polychotomous logistic functions, as described in Fujiwara & Caswell (2002), to constrain the probabilities between 0 and 1 while offering flexibility in the shape of the function:

$$\phi_{21} = e^{\beta_{21} * X} / (1 + e^{\beta_{21} * X}) \quad \text{[Equation 3.3]}$$

$$\phi_{32} = e^{\beta_{32} * X} / (1 + e^{\beta_{32} * X}) \quad \text{[Equation 3.4]}$$

The parameter vectors  $\beta_{21}$  and  $\beta_{32}$  determine the contribution of the independent prey variable(s),  $X$ , to the transitional probabilities  $\phi_{21}$  and  $\phi_{32}$ . These transitional probabilities were fitted into a demographic matrix model and the parameter vectors  $\beta_{21}$  and  $\beta_{32}$  were estimated in AD Model Builder (Fournier et al. 2012). Parameters were optimized to yield a predicted annual calf production time series that most closely resembles the observed calf time series (Right Whale Consortium 2011).

In determining the best fit for including the temporally and spatially resolved *C. finmarchicus* data into the reproduction model, the 35 *C. finmarchicus* abundance indices (7 time periods  $\times$  5 region/subregions) were tested as predictive variables, both independently and in combination. Each variable was treated objectively and first tested as the sole predictor in both



transitional probabilities simultaneously. The best-performing variable was then fixed as a constant for the first transitional probability, of a female moving from resting to pregnant, while each of the 35 variables was tested for the second transitional probability, of a female moving from pregnant to nursing. Then this process was repeated by fixing the second transitional probability as a constant while all 35 variables were tested for the first transitional probability. The best of these models was selected and the addition of a second predictor, etc., was tested in the same objective manner. Model complexity was increased incrementally until each instance in a suite of models demonstrated a higher AIC than the best-fitting, more parsimonious model. In this way, the temporally and spatially resolved reproduction model was built in a stepwise fashion to objectively select the best-fitting regional and seasonal prey variables to predict calf production.

While each of the 35 regional and seasonal late-stage *C. finmarchicus* indices provides a unique signal of prey abundance in the GOM, some geographically or temporally adjacent variables are highly correlated, as expected. None of the 3 variables present in the best-fit model are strongly correlated, but caution must be applied when interpreting the relative importance of these temporal and regional signatures relative to those that are adjacent. However, some confidence in the model selection process is warranted since the best-fitting variables correspond with known right whale foraging habits.

To rigorously evaluate the prey-dependent case of the reproduction model, we developed a null, prey-independent version of the model for comparison. In the null version, a similar matrix model was developed with time-invariant transitional probabilities. The reproductive transitional probabilities  $\phi_{21}$  and  $\phi_{32}$  were estimated independently using the same optimization method. Logistic functions were fitted as before; however, only the intercepts were estimated.

This method produces a single optimal probability for each transition that does not vary through time. The prey-dependent and prey-independent reproduction models were compared using the AIC, and a difference of more than 2 AIC units was the criterion used to determine an improvement in fitness between 2 models (Akaike 1974, Burnham & Anderson 2002).

### 3.3 RESULTS

The growth rate of the North Atlantic right whale population exhibited considerable interdecadal variability from 1980 to 2007. We hypothesize that this observed variability largely reflects fluctuations in annual calf production brought about as right whale reproductive processes respond to ecosystem changes that affect prey availability. Our model results enable us to examine in detail how these reproductive processes are linked to specific spatial and temporal changes in the feeding environment of right whales.

#### 3.3.1 Calf production null model

The calf production null model is optimized when the transitional probability between the resting and pregnant states,  $\phi_{21}$ , is equal to 0.26, and the transitional probability between the pregnant and nursing states,  $\phi_{32}$ , is equal to 1.0 (Table 3.1). This result means that only a quarter of the viable resting females conceive each year, but each successful conception leads to the production of a calf. Because the null model is prey independent, and therefore transitions are constant through time, the gradual upward trend in the predicted annual calf production time series is driven only by the steady increase in the pool of viable females through the interaction of recruitment, senescence and mortality processes (Fig. 3.2[Top]). The estimated time series of calf production does not exhibit the interannual variability seen in the observed calf births. The

Table 3.1: The intercept and, in the case of the prey-dependent model, the coefficient(s) of prey variability estimated in the logistic equations for the probability of an adult viable female transitioning from the resting stage to the pregnant stage,  $\phi_{21}$ , and transitioning from the pregnant stage to the nursing stage,  $\phi_{32}$ . AIC values and weights for the time-invariant (no-prey) model and the best-fit prey-dependent model are provided. Standard errors are listed in parentheses

	Model	
	No-prey	Resolved prey-dependent
AIC	99.7	64.5
AIC weight	0.0	1.0
$\beta_{21}$ Intercept	-1.063 ( $1.78 \times 10^{-1}$ )	-0.820 ( $1.06 \times 10^{-1}$ )
$\beta_{21}$ Coefficient: WGOM Nov to Dec		0.165 ( $5.61 \times 10^{-2}$ )
$\beta_{21}$ Coefficient: GOM Mar to Apr		0.345 ( $1.37 \times 10^{-1}$ )
$\beta_{32}$ Intercept	13.398 ( $5.93 \times 10^2$ )	108.66 ( $4.00 \times 10^3$ )
$\beta_{32}$ Coefficient: EGOM Jul to Aug		145.74 ( $5.37 \times 10^3$ )

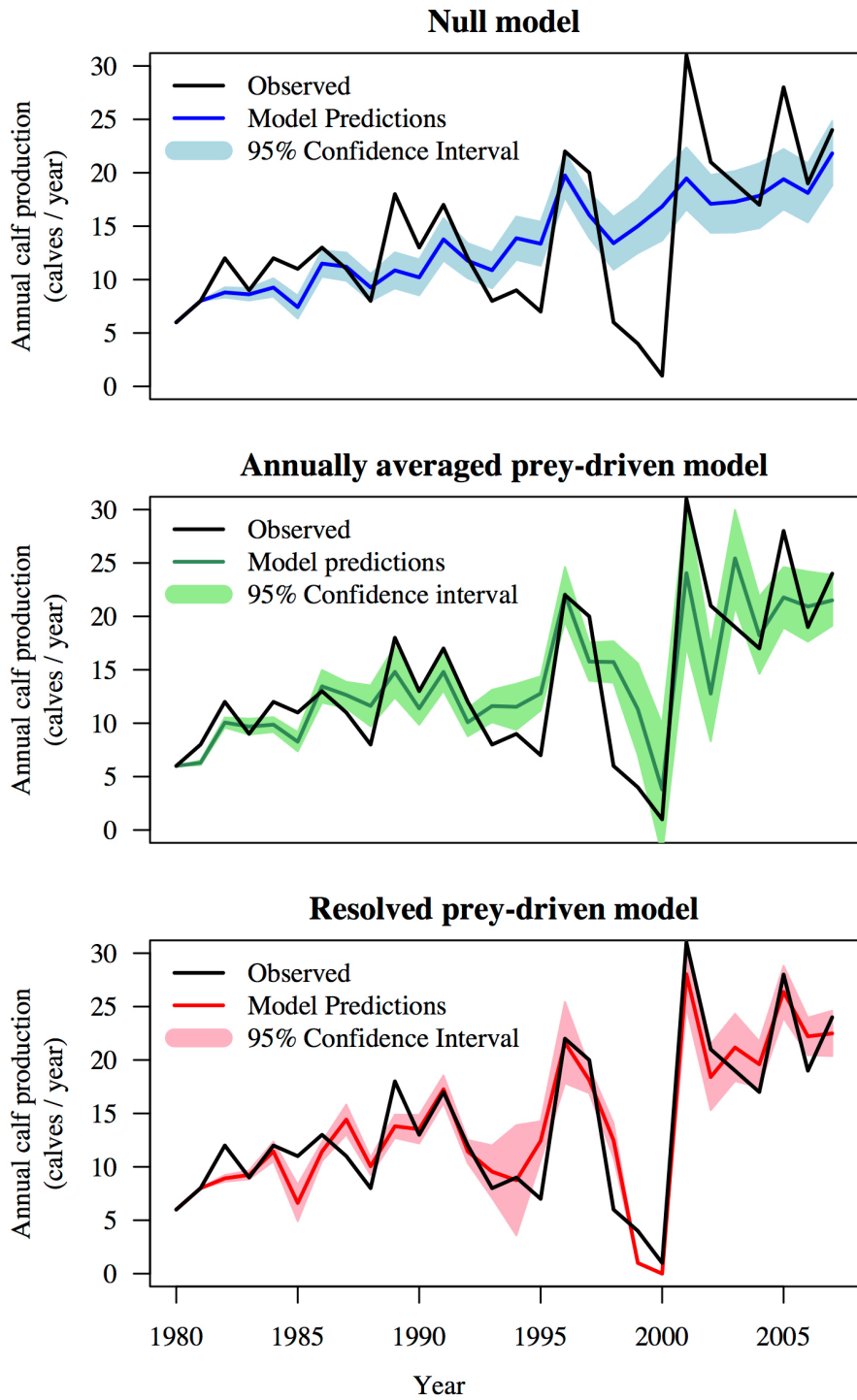


Figure 3.2: Annual calf production for 3 models, with observed number of calf births shown in black. [Top]: Null, prey-independent version of the model estimates (blue), [Middle]: annually and spatially averaged prey-dependent version of the model estimates (green) and [Bottom]: seasonally and spatially resolved prey-dependent version of the model estimates (red). Pale bands surrounding model estimates correspond to 95% CI.

average calving interval for the null model lasts 6 yr, with an average of 4 yr in the resting state prior to conception, and then a year each in the pregnant and nursing states. These results provide a baseline for comparisons with versions of the model that are driven by environmental variables, including prey dependence.

### 3.3.2 Versions of the calf production model driven by annually indexed environmental variables

The results from 36 different versions of the right whale reproduction model driven by annually indexed environmental variables are shown in Fig. 3.3. Of the 36 versions tested, 18 performed better than the null model, given the criteria of a decrease of at least 2 AIC units (null model AIC = 99.7; Table 3.1, Fig. 3.3). Models that performed comparably to or worse than the null model are colored in green (Fig. 3.3). The improvement in fit of many of these environmentally driven versions of the model relative to the null model supports the hypothesis that the environment plays a significant role in right whale reproduction. The unlagged, annually averaged late-stage *Calanus finmarchicus* abundance index derived from the entire CPR transect, which is the most direct measure of right whale prey availability tested, had an AIC of 88.2, more than 10 AIC units lower than the null model (Fig. 3.2[Middle]). Models that performed comparably to the annually and spatially averaged *C. finmarchicus* index are colored in yellow in the AIC heatmap, while those that performed significantly better are shown in orange and red (Fig. 3.3).

In terms of model results, the best performing of the annually indexed environmental variables is the RSWT index lagged by 4 yr, with an AIC of 67.8 (Fig. 3.3). This result is consistent with the hypothesis that the Northwest Atlantic's coupled slope water system regulates

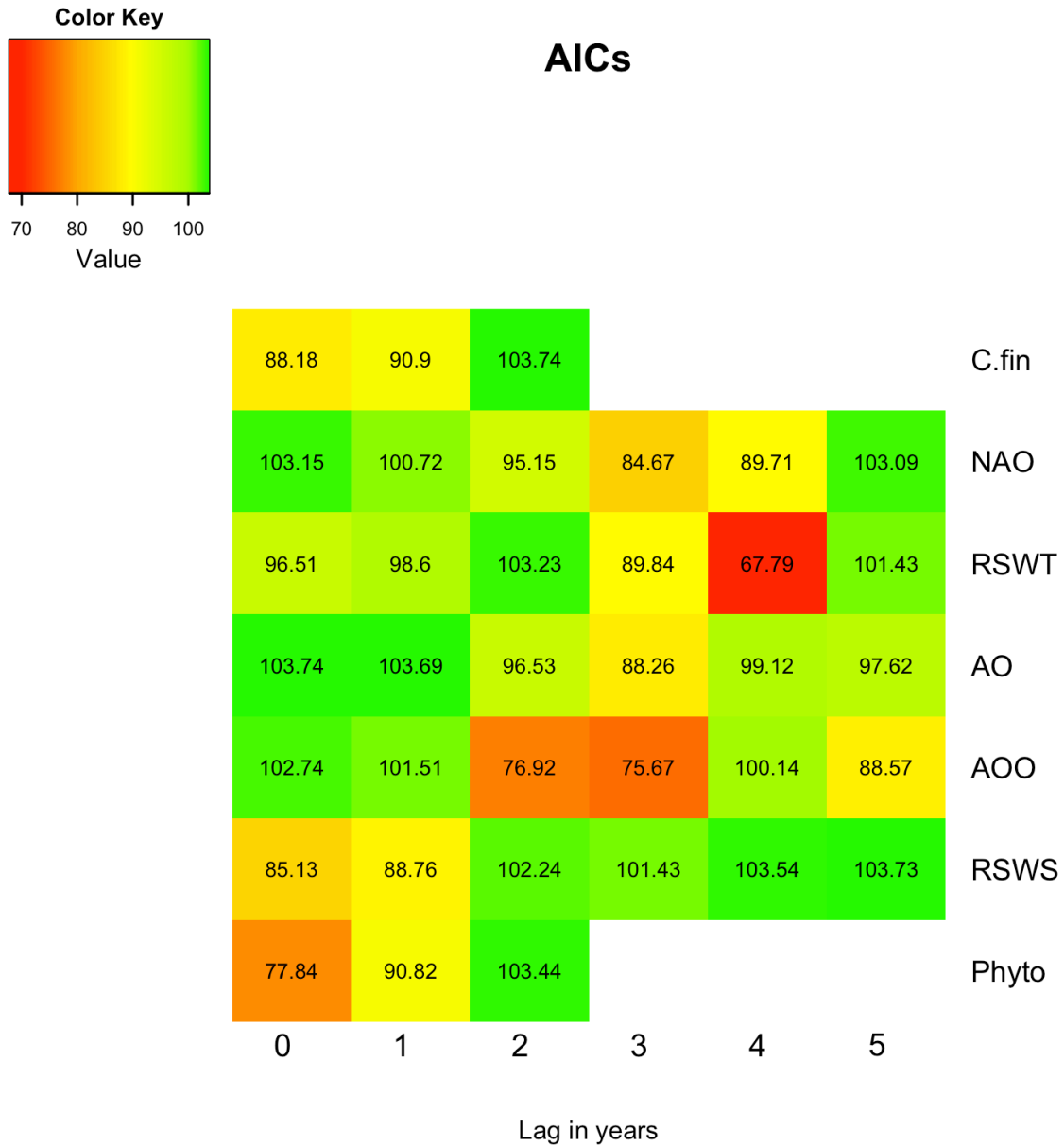


Figure 3.3: AIC values of the environmentally driven versions of the model, showing the environmental variables and the time lag (yr). C. fin: CPR-derived *Calanus finmarchicus* annually averaged GOM transect-wide abundance index; NAO: North Atlantic Oscillation index; RSWT: Regional Slope Water Temperature; AO: Arctic Oscillation; AOO: Arctic Oceanic Oscillation; RSWS: Regional Shelf Water Salinity; Phyto: CPR-derived autumn phytoplankton color index. The best-performing versions of the model (lowest AICs), presented in orange/red boxes, are those that performed better than the version driven by the unlagged, annually averaged *C. finmarchicus* abundance index derived from the entire CPR transect (AIC = 88.2). The poorest-performing versions of the model (highest AICs), presented in green boxes, are those that performed worse than or similar to the null model (AIC = 99.7). Color key is shown in the upper left corner

prey variability in the GOM by altering the advective supply of *C. finmarchicus*. Specifically, GOM *C. finmarchicus* have been known to respond to changes in the coupled slope water system after a lag of 4 yr (Greene & Pershing 2003, Greene et al. 2003a). This version of the model performs especially well because it accurately captures the unusual behaviors in right whale calving efficiency in the late 1990s.

The 2- and 3-yr lagged AOO index and the unlagged autumn phytoplankton color index also perform very well, with AICS of 76.9, 75.7 and 77.8, respectively (Fig. 3.3). These models support the hypothesis that the export of freshwater from the Arctic and the resulting changes in seasonal stratification within the GOM affect right whale calving rates via changes in prey availability. The hierarchy of best-fitting environmental variables associated with changes in seasonal stratification (AO, AOO, RSWS and autumn phytoplankton) exhibits a sequence of time lags consistent with the timing of events driving this phenomenon (Fig. 3.3) (Greene et al. 2013). Interannual to interdecadal variability in late-stage *C. finmarchicus* abundance is most likely driven by a combination of advective processes linked to the Northwest Atlantic's coupled slope water system and changes in seasonal stratification linked to freshwater export from the Arctic. However, the development of a right whale calving model that incorporates both of these mechanisms and their effects on prey availability are beyond the scope of this study.

The distribution of model AICs calculated using moving-block bootstrapped data is shown in Fig. 3.4. When ranked from lowest (best fit) to highest (worst fit), the AIC is 86.3 at the 5th percentile and 90.2 at the 10th percentile. Of the 36 versions of the model fit by an annually indexed environmental variable, lagged or unlagged, 6 (17%) perform better (i.e. have a lower AIC) than the 5th percentile and 12 (33%) perform better than the 10th percentile, including the model driven by the unlagged, CPR-derived late-stage *C. finmarchicus* abundance

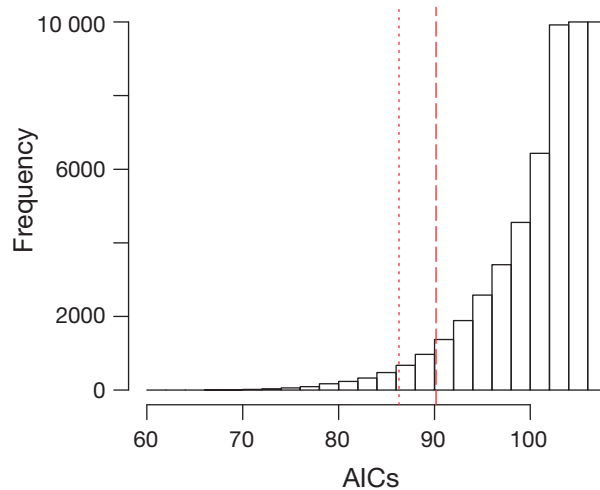


Figure 3.4: The cumulative frequency plot of AIC values from the 10,000 models run in the resampling test. Each model was driven by a unique, randomized 4-yr moving-block bootstrap. The dotted vertical red line marks the value of the 500th ranked AIC (the 5th percentile; AIC = 86.3) and the dashed vertical red line marks the value of the 1000th ranked AIC (the 10th percentile; AIC = 90.2)

index. The improved performance of our actual set of 36 environmental variables in comparison to the 10,000 randomly generated environmental variables provides confidence that the relationships between right whale calf production and environmentally determined prey availability are not spurious.

### 3.3.3 Temporally and spatially resolved prey-dependent calf production model

The temporally and spatially resolved prey-dependent version of the model was fitted through an iterative process to incorporate the optimal combination of *C. finmarchicus* abundance data resolved by subregion and bi-monthly time period. The predicted calf time series from this version of the model captures the largest portion of the interannual variation in calf production compared to all other versions of the model tested (AIC = 64.5; Table 3.1, Fig. 3.2[Bottom]).



In this version, the transitional probability between the resting and pregnant states,  $\phi_{21}$ , is a logistic function dependent on *C. finmarchicus* abundance in the WGOM during the November to December time period and in the whole GOM region during the March to April time period (Fig. 3.5[Middle]). All parameters optimized for this transition are statistically significant (Table 3.1). The transition between pregnant and nursing states,  $\phi_{32}$ , is a logistic function that is exclusively dependent on *C. finmarchicus* abundance in the EGOM during the July to August time period (Fig. 3.5[Bottom]). The large coefficients in this logistic function create a quasi step function, demonstrating that when the *C. finmarchicus* abundance index in the EGOM during July and August falls below a threshold value of  $-0.75$ , the probability of encountering nursing females the following year drops from 1.0 to 0.0 over a narrow range of prey abundances (Fig. 3.5[Bottom], Table 3.1). Owing to the large coefficient size of the 2 parameters calculated for this transitional probability, the associated standard errors cannot be computed precisely (Pampel 2000). However, by comparing this model with a similar one, in which the probability of transitioning between resting and pregnant states is prey dependent but the probability of transitioning between pregnant and nursing states is not, the results reveal that prey dependence in both transitions drastically improves the model's fit (AIC = 64.5 vs. AIC = 96.2).

The prey-dependent model's predicted probabilities of conception and successful delivery for each year in the time series are shown in Fig. 3.5[Top]. These results indicate that under ideal prey conditions, a female in the resting state has a relatively low conception probability (mean probability = 0.314 over the 27-yr time period), but a relatively high probability of successfully delivering a calf once pregnant (mean probability = 0.908). For the time period considered in this study, summertime prey abundances in the EGOM fell below the threshold value of  $-0.75$  a total of 3 times. On each of these occasions, the model predicted that a

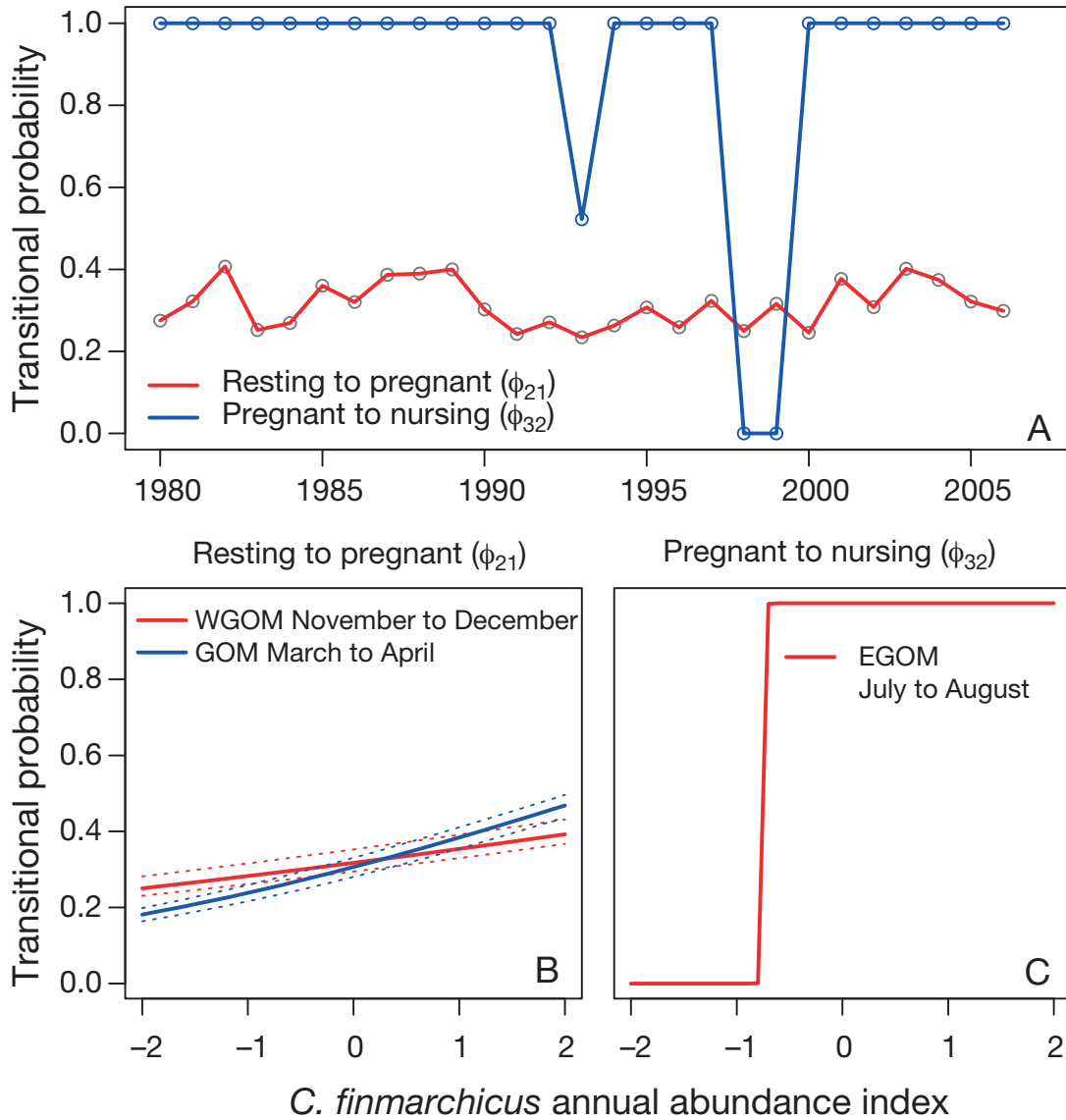


Figure 3.5: [Top]: Transitional probabilities for the temporally and spatially resolved prey-dependent reproduction model, showing  $\phi_{21}$  (red) and  $\phi_{32}$  (blue). [Middle & Bottom]: Transitional probabilities estimated in the prey-dependent reproduction model as functions of the associated *Calanus finmarchicus* abundance indices; [Middle]:  $\phi_{21}$  as a function of the WGOM November to December index and the GOM March to April index and [Bottom]:  $\phi_{32}$  as a function of the EGOM July to August index. Two functions are shown for  $\phi_{21}$  [Middle]: the transitional probability as a function of the WGOM November to December prey abundance index while the GOM March to April prey abundance is held at the upper quartile, median and lower quartile abundances averaged over 1980 to 2006 (upper dashed line, solid line and lower dashed line, respectively) is shown in red; the transitional probability as a function of the GOM March to April prey abundance index while the WGOM November to December prey abundance is held at the upper quartile, median and lower quartile abundances averaged over 1980 to 2006 (upper dashed line, solid line and lower dashed line, respectively) is shown in blue.

significant percentage of pregnancies would result in prenatal or neonatal mortalities (Fig. 3.5[Top]).

The prey-dependent model's predicted distribution of viable females in each of the 3 reproductive states is shown in Fig. 3.6[Top]. As expected, most females are found in the resting state during any given year as they recover from previous pregnancies by restoring lost blubber. The model results demonstrate that during years of higher prey availability the resting and recovery process is accelerated, leading to higher annual calf production. In contrast, during years of lower prey availability, females remain in the resting state for longer, leading to lower annual calf production.

The prey-dependent model's predicted theoretical calving interval for each year in the time series is shown in Fig. 3.6[Bottom]. The theoretical calving interval assumes that prey availability remains constant over a complete reproductive cycle. Therefore, it does not reflect a true calving interval, since a female requires a minimum of 3 yr to complete her reproductive cycle, and prey availability does not remain constant over that length of time. Nevertheless, each predicted calving interval provides a snapshot of the effect of that year's feeding conditions on right whale reproduction. A calving interval of 3 yr is the minimum, given the model constraints, and it is achieved when all viable females are reproducing as fast as physiologically possible, spending only 1 yr in each of the 3 reproductive states. While this minimum value is rarely approached over an extended time period, strong deviations from it are indicative of a bottleneck in right whale population growth. Calving intervals during the good feeding conditions of the 1980s varied between 4 and 6 yr, with a decadal average of 5.0 yr. In contrast, calving intervals during the relatively poor feeding conditions of the 1990s were much more variable. For most of

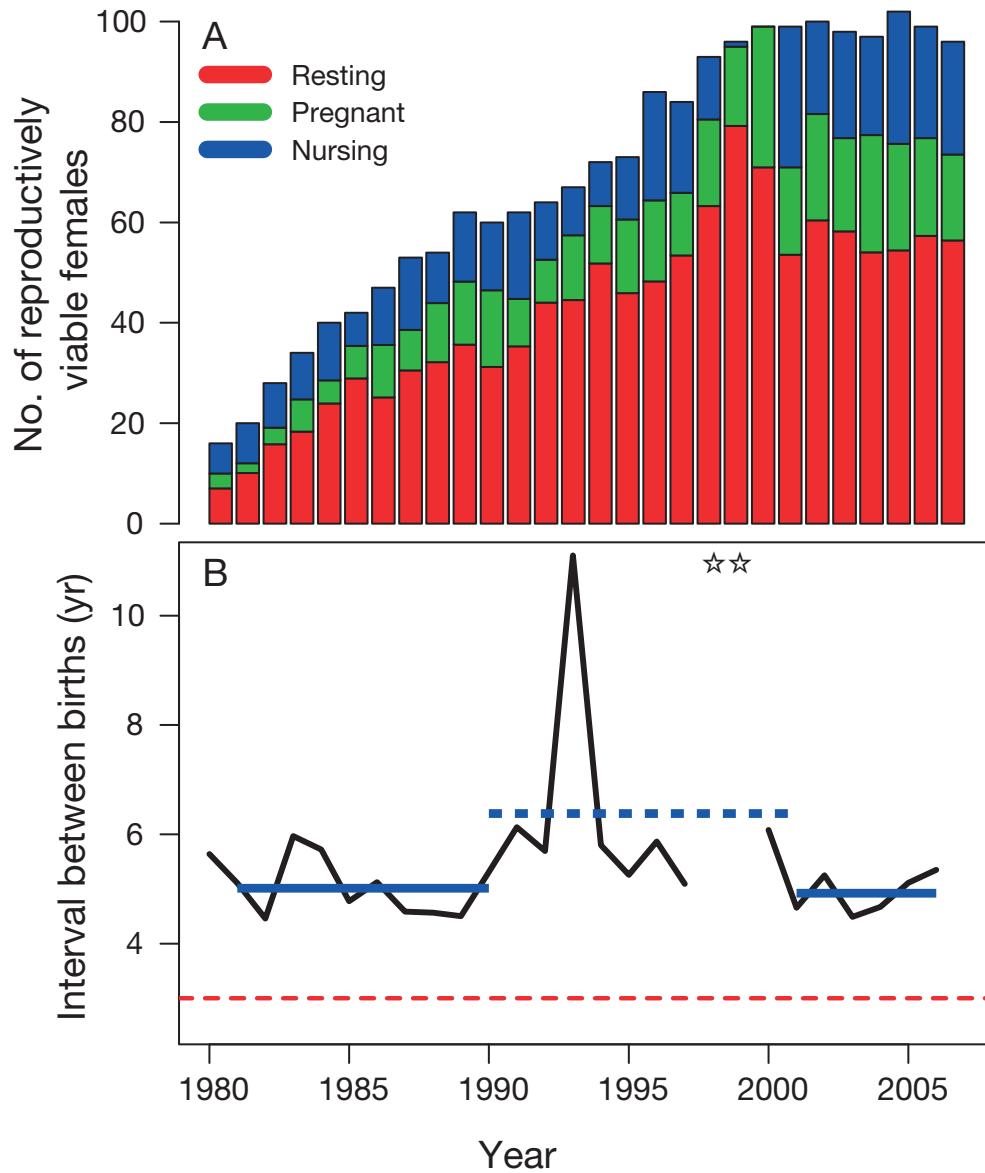


Figure 3.6: [Top]: Model-estimated distribution of reproductive states for the population of reproductively viable right whale females. [Bottom]: Interval between births index (yr) as estimated from the temporally and spatially resolved, prey-dependent version of the model. The red dashed line shows a 3-yr calving interval, the minimum interval length constrained by the model, which corresponds to females spending only 1 yr in each of the 3 reproductive states. Blue lines show decadal averages of female-specific annual calf production and average interval between births. The average interval between births exceeded the lifespan of right whale females in 1998 and 1999 (★★), when prey abundances were unusually low. These values were not included in calculating the decadal average, therefore the blue dashed line is a significant underestimate of the 1990s average model-predicted interval between births

the decade, they varied between 5 and 7 yr, but low *C. finmarchicus* abundance drove the calving interval up to exceed the lifespan of the species during 1998 and 1999. Replacing the 1998 and 1999 calving interval with 61 yr as an estimation of the reproductive life span (70 yr lifespan minus 9 yr, or the age of reproductive maturity) yields a decadal average calving interval of 17.3 yr in the 1990s. When good feeding conditions returned during the 2000s, calving intervals dropped back to varying between 4 and 6 yr, with a decadal average of 4.9 yr.

### 3.4 DISCUSSION

We compared the fit of multiple versions of a right whale reproduction model using direct measures of prey abundance (late-stage *Calanus finmarchicus* abundance anomaly indices derived by the CPR) as well as a number of environmental variables that have been linked to regime shifts and changes in plankton abundance in the GOM ecosystem. The unlagged direct measures of prey abundance tested in this study, both the annually averaged, full GOM *C. finmarchicus* abundance anomaly index and the temporally and spatially resolved abundance anomaly indices tested in combination, provide a very simple mechanistic method of predicting interannual variability in right whale reproduction efficiency.

While the models driven by the lagged environmental variables do not share the same level of mechanistic parsimony as the models driven by prey abundance, they do offer some advantages. The environmental variables chosen for inclusion in this study have links to large ecosystem changes and regime shifts in the GOM and other shelf regions in the Northwest Atlantic that are well supported in the literature. For that reason, these variables may contain more synoptic, broad-scale information on the right whale feeding environment than data from the CPR transect. There is also some uncertainty about the reliability of funding for future

collection and analysis of CPR data in this region. Therefore, these environmental variables may provide the only option for future analyses.

The results from our modeling study provide evidence that not only is the annual calf production of the North Atlantic right whale population dependent on prey availability, this dependence is especially important in specific foraging areas and at specific times. The results provide additional insights into how various reproductive processes may be linked to specific spatially and temporally dependant features in the feeding ecology of right whales.

Of all reproduction models explored, the model driven by temporally and spatially resolved *C. finmarchicus* performed the best (AIC = 64.5). In this model, the *C. finmarchicus* abundance index for the WGOM during November and December is the dominant variable driving the transition of reproductively viable females from the resting state to the pregnant state. This finding is consistent both spatially and temporally with field observations. Although the habits of right whales during late autumn and winter are not well known due to poor weather conditions and visibility, sightings and acoustic monitoring of reproductive females in this region between November and January suggest that the western and central GOM are likely mating grounds (Mussoline et al. 2012, Cole et al. 2013, Bort et al. 2015) during a time period when they are thought to be sexually active (Kraus & Rolland 2007, Cole et al. 2013). We hypothesize that *C. finmarchicus* abundance in this region and during this time period affects the foraging behavior of right whales and their probabilities of conception. For example, during years of low prey availability, the right whale population may disperse in search of better feeding grounds, thereby limiting mating opportunities. Conversely, during years of high prey availability, the population may converge over favorable feeding grounds, thereby fostering improved mating conditions.

The model results also indicate that the transition from resting state to pregnant state is secondarily driven by the *C. finmarchicus* abundance index for the entire GOM during March and April. This time frame corresponds to a period when high right whale abundance is observed in Cape Cod Bay (Winn et al. 1986, Mayo & Marx 1990, Pendleton et al. 2009), Massachusetts Bay (Schevill et al. 1986) and the Great South Channel (Kenney et al. 1995), as well as on Stellwagon Bank (Mussoline et al. 2012). Prey availability in the months before conception has been linked to calving rates in other baleen whales (Lockyer 2007), including the southern right whale (Leaper et al. 2006), a closely related congener of the North Atlantic right whale. In light of these observations, we hypothesize that prey availability throughout much of the GOM during spring likely determines the nutritional condition of reproductively viable females and influences their conception probabilities during the following winter.

The best-fit transitional probability from the pregnant state to the nursing state,  $\phi_{32}$ , is driven by *C. finmarchicus* abundance in the EGOM during July and August. This transitional probability behaves like a quasi step function, indicating that right whale pregnancies tend to be viable except in years when prey abundance falls below a certain threshold (Fig. 3.5[Bottom]).

As right whales are typically observed nearby in the lower Bay of Fundy during late summer (Kraus et al. 1982, Gaskin 1987, Mate et al. 1997), this relationship suggests that the EGOM subregion and the downstream Bay of Fundy may be significant feeding grounds for pregnant females, and *C. finmarchicus* abundance in these areas during summer may play a critical role in determining a female's ability to sustain a pregnancy or nurse a calf.

While each of the 35 regional and seasonal late-stage *C. finmarchicus* abundance indices tested in the temporally and spatially resolved versions of the model provides a unique measure of prey abundance in the GOM, some geographically and/or temporally adjacent indices are

highly correlated (for example, EGOM July and August, and WGOM July and August), as might be expected. Non-adjacent variables in the suite of regional and seasonal prey abundance indices are not strongly correlated, including the 3 variables chosen in the best-fit model. As there is some collinearity among the predictors, one might not expect such predictors to be jointly included in any particular model, as including them together would inflate the variance and result in poorer model performance as measured by standard criteria. While the stepwise regression has resulted in predictors that correspond well with known right whale foraging habits and result in good predictions of annual calf production, there may be other combinations of predictors that result in a comparable level of predictability.

### 3.5 CONCLUSIONS

Strong interannual fluctuations in calf production rate inevitably have a significant influence on the interdecadal variability observed in right whale population growth rate (Meyer-Gutbrod & Greene 2014). Therefore, the ability of our prey-dependent version of the reproduction model to capture a large proportion of the observed variance in annual calf production has important implications for the management of this highly endangered species.

During the 1990s, low prey availability significantly reduced calf production and, in combination with a high mortality rate, the right whale population experienced periods of negative growth. The impact of fewer calf births over the 1990s can be seen in the leveling off in recruitment of viable females in the 2000s (Fig. 3.6[Top]). Persistence of the extremely poor feeding conditions observed during the final years of the 1990s would have resulted in a much more rapid collapse of the population than that projected by Fujiwara & Caswell (2001) due to the near cessation of reproduction, regardless of any changes in anthropogenic sources of



mortality. Fortunately, the feeding conditions of the 1990s did not persist, as an ecosystem regime shift led to a resurgence of the *C. finmarchicus* in the region during the subsequent decade (Greene et al. 2013). In response, the right whale population underwent a notable recovery during the 2000s. This remarkable swing, from heading towards extinction during the late 1990s to being on the path towards a relatively rapid recovery during the 2000s, demonstrates the population's high level of demographic volatility. In retrospect, it is now apparent that much of the decadal variability in the population's recovery rate is driven by changes in prey availability linked to climate-associated ecosystem regime shifts (Meyer-Gutbrod & Greene 2014). Any attempt to characterize the future fate of the right whale population must take these ecosystem regime shifts into account.

The predictability of climate-driven ecosystem regime shifts in the Northwest Atlantic is an active area of research (Greene et al. 2013). Predicting their ecological impacts is much further along than predicting exactly when they will occur. These ecosystem regime shifts have been associated with various natural modes of climate variability; however, additional regime shifts and species range shifts will undoubtedly be modified and/or triggered in the future by anthropogenic climate change. In the context of right whale conservation and management, the recent prediction by Reygondeau & Beaugrand (2011) of a northward range shift of *C. finmarchicus* in response to a warming ocean should raise serious concerns. Such a range shift could greatly limit the availability of prey to right whales in the GOM and surrounding waters over the coming decades. In response, right whales may have to change their behavior to habituate to new foraging grounds, increase the extent of their migration route, or change the location of their calving grounds. Without such behavioral changes, this population may risk a significant decrease in its viability.

As the impacts of climate on right whale demography are mediated by prey availability, specifically the distribution and abundance of *C. finmarchicus*, understanding the responses of this species to such regime shifts will be critical to developing an ecosystem-based management perspective for the North Atlantic right whale population. The shift to such an ecosystem-based management perspective does not alter the importance of implementing policies and regulations that achieve the traditional conservation goals of reducing anthropogenic sources of mortality. After all, reducing the mortalities associated with ship strikes and entanglement in fishing gear will always enhance the population's recovery rate. However, there are at least 2 additional benefits that an ecosystem-based management perspective introduces to developing conservation plans for the right whale population. First, it recognizes that the conservation goals set for management must be regime-dependent. The population's recovery rate is constrained by environmental conditions, therefore measures of success for achieving conservation goals should be expected to vary from one ecosystem regime to another, even if comparable reductions in anthropogenic sources of mortality are achieved. Second, the uncertainty introduced by our limited understanding, as well as the stochastic nature of climate variability and change, will set limits on our ability to predict the recovery of the right whale population. Therefore, rather than relying on a single demographic projection based only on recently observed environmental conditions, an ensemble of projections based on a range of climate and anthropogenic mortality scenarios should be explored. Only then will we have the means to assess the likely fate of this species in the future.

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## CHAPTER 4

### A SPECIES ON THE BRINK: EFFECTS OF PREY-DRIVEN FECUNDITY AND ANTHROPOGENIC MORTALITY RATES ON DEMOGRAPHIC PROJECTIONS OF THE NORTH ATLANTIC RIGHT WHALE POPULATION

#### *Abstract*

In the critically endangered North Atlantic right whale, substantial evidence has linked reproductive efficiency, and consequently population growth, to food availability. Using capture-recapture techniques, we present the demographic dynamics of the right whale population and test the role of prey abundance, specifically Continuous Plankton Recorder-derived late-stage *Calanus finmarchicus* abundance anomalies, on the survival and reproduction of the species. Prey dependence was tested in all demographic transitions for male and female maturation, survival and breeding, and the best model formulation occurred when female breeding probabilities were a function of prey availability and all other transitions remained constant. These results indicate that prey availability has an observable effect on interannual variations in right whale reproduction but not on mortality. Abundant prey has led to a period of population growth at the start of the new millennium, with annual growth averaging 3% in the previous decade (2001-2010). However, a shift in right whale distribution and decline in calving rates in recent years indicate that the population may have shifted back to a regime of lower growth. To assess future viability, right whale growth is projected into the next century under a series of prey and anthropogenic mortality scenarios. Using constant mortality rates averaged over 1980-2012, right whale population size was projected under three different observed decadal prey regimes, with positive growth predicted under each scenario. The population was also projected under scenarios of increasing mortality with prey resampled from the observed annual anomalies

from 1980-2012, and population growth remains positive with up to five additional adult female mortalities annually. With six or more additional adult female mortalities each year, or an increase of 2% in annual mortalities across the population, the species is projected to decline to extinction. Under a regime of decreased prey availability, leading to suppressed breeding rates such as those observed during the 1990s, the population is more sensitive to an increase in mortality.

#### 4.1 INTRODUCTION

The North Atlantic right whale is a critically endangered species with an estimated population size of 526 individuals (Waring et al. 2015, Pettis and Hamilton 2015). Following three centuries of intense whaling, the population was near extinction with fewer than 200 individuals at the start of the 20<sup>th</sup> century (Reeves et al. 1992, Reeves et al. 1999). Previously coined the “urban whale”, right whales have faced a slow recovery from the whaling era, largely due to anthropogenic factors suppressing population growth (Kraus and Rolland 2007). Recent demographic analyses have targeted declining adult female survival probability as the primary threat to the species and have predicted functional extinction within 200 years (Caswell et al. 1999, Fujiwara and Caswell 2001).

Right whale habitat comprises the eastern coast of the United States and southeastern Canada, with feeding grounds in the Gulf of Maine, Bay of Fundy and Scotian Shelf and breeding grounds along the coasts of Florida and Georgia (Kenney et al. 2001). Whales in these waters face dense commercial shipping traffic, and from 1970-2006, the cause of death of 53% of necropsied right whales was attributed to ship strikes (Kraus et al. 2005, Campbell-Malone et al. 2008). This population also experiences lethal and sub-lethal effects from entanglement in

gear linked to non-mobile fisheries such as lobster pots and gillnets (Kraus et al. 2005, Knowlton and Kraus 2001). Evidence of fishing gear entanglement has been documented for 83% of the population, with an average annual entanglement rate of at least 16% (Knowlton et al. 2012). In this urbanized habitat, right whales are also subjected to high levels of anthropogenic noise and bioaccumulation of toxins, although the effects on population growth are not easy to measure directly (Hatch et al. 2012, Doucette et al. 2012).

In addition to anthropogenic stressors, there is considerable evidence that variable feeding conditions influence right whale health and population dynamics. The effect of prey limitation is most pronounced in reproductive females, which require increased caloric inputs to support pregnancy and lactation (Wade and Schneider 1992, Lockyer 2007). Reproductive females exhibit the widest ranges of variability in individual health scores, with healthier females more likely to calve (Rolland et al. 2016). Fluctuations in reproduction rates concur with changes in adult female blubber thickness, suggesting a nutritional component to calving frequency (Pettis et al. 2004, Miller et al. 2011). In addition to heightened caloric requirements, reproductive females also face decreased access to prey during migration to and time spent on the calving ground (Fortune et al. 2013, Miller et al. 2012). Consequently, calving interval is lengthened in periods of low food availability (Klanjscek et al. 2007, Meyer-Gutbrod et al. 2015).

The chief prey source of the North Atlantic right whale is late-stage *Calanus finmarchicus*, a lipid-rich calanoid copepod (Mayo et al. 2001). Changes in *C. finmarchicus* distribution and abundance has been linked to basin-scale oceanographic fluctuations and regional climate indices through two modes of variability (Greene et al. 2013). In the first mode, a diminished pressure gradient in the North Atlantic, depicted by a strongly negative North Atlantic Oscillation index, can result in a tongue of Labrador subarctic slope water migrating

south, potentially blocking the advection of *C. finmarchicus* into the Gulf of Maine (Greene et al. 2003). This phenomenon is hypothesized to explain the sharp decline in *C. finmarchicus* abundance during 1998 and the subsequent hiatus in right whale births during 1999 and 2000 (Greene and Pershing 2004). In the second mode, the Gulf of Maine ecosystem undergoes a regime shift in response to remote climate forcing from the Arctic. Specifically, anomalously high Arctic sea level pressure, characterized by a positive Arctic Oscillation index, leads to an export of cold, fresh shelf water into the North Atlantic (Greene and Pershing 2007, Greene et al. 2008). These salinity anomalies alter the timing and intensity of water column stratification, impacting shelf ecology by extending the phytoplankton growing season (MERCINA 2012).

Previous modeling efforts demonstrate that right whale reproduction dynamics and calving frequency are linked to *in situ* late-stage *C. finmarchicus* abundance (Meyer-Gutbrod and Greene 2014, Meyer-Gutbrod et al. 2015). In this study, we incorporate these techniques into a full demographic capture-recapture model to test the impact of *C. finmarchicus* on survival and transition among each right whale life history stage. The demographic model is then used to project right whale population growth through the next century under different prey conditions and mortality scenarios.

## 4.2 METHODS

### 4.2.1 Right whale photographic database

The North Atlantic right whale has been photographically catalogued in a consistent manner since 1980. Using unique markings such as callosity patterns and scars from entanglements and ship strikes, individual whales are identified or “captured” and resighted or “recaptured” year after year. These photographs have contributed to a database managed by the

North Atlantic Right Whale Consortium, providing a history of sightings and demographic stages for each known individual (Fig. 4.1)(Right Whale Consortium 2014).

#### 4.2.2 Continuous Plankton Recorder data

The Continuous Plankton Recorder (CPR) is an instrument towed behind ships of opportunity to collect and preserve plankton for subsequent analyses in the laboratory (Warner and Hays 1994). Since 1961, the NOAA National Marine Fisheries Service has operated a CPR survey in the Gulf of Maine running between Boston, MA and Cape Sable, NS at approximately monthly intervals (Jossi and Kane 2013)(Figure 2.3). Although the CPR is not an ideal instrument for sampling absolute abundances of plankton species due to limited geographic, depth, and temporal coverage, its consistent use in long-term surveys in the region has provided an invaluable data set for studying relative abundance patterns through time (e.g., Greene et al. 2013). Despite the stated limitations, Pendleton et al. (2009) and Pershing et al. (2009) demonstrate that regional-scale, near-surface *C. finmarchicus* abundance measured with the CPR is significantly correlated with right whale sightings in the Gulf of Maine, and CPR data has been successfully used as a proxy for North Atlantic right whale prey abundance in multiple studies (e.g. Patrician and Kenney 2010, Miller et al. 2011, Meyer-Gutbrod et al. 2015).

In this study, we focus exclusively on the oldest stages of *C. finmarchicus* (copepodite stages 5 and 6) due to their importance in the diet of right whales (Mayo et al. 2001). Serving as a proxy for annual variations in prey availability, an annually averaged transect-wide index of late stage *C. finmarchicus* abundance anomalies were calculated from the seasonal climatological cycle as described by Pershing et al. (2005). To account for geographic and seasonal variations in zooplankton abundance in the Gulf of Maine, the CPR samples were assigned to four

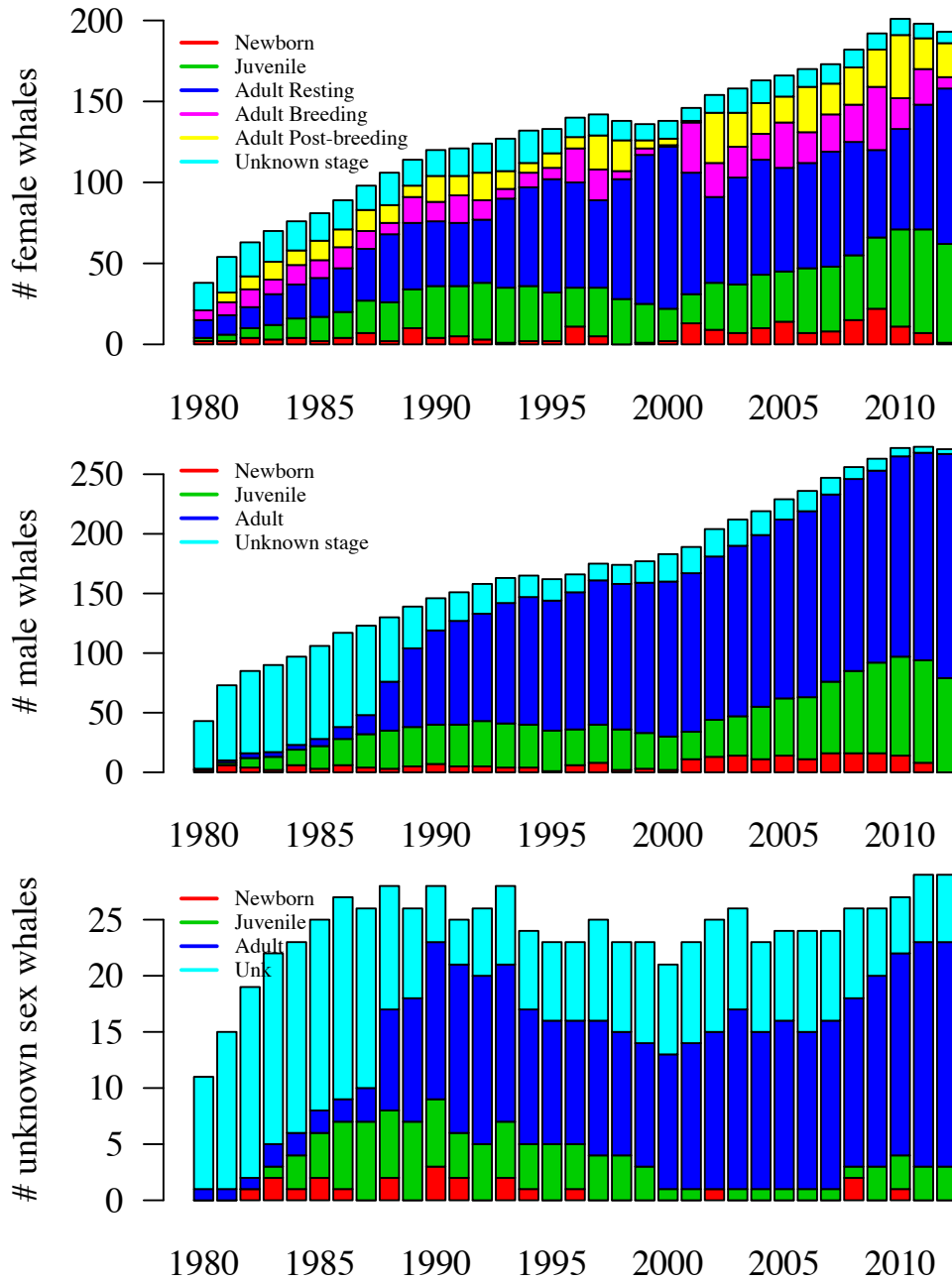


Figure 4.1: Stacked bar graph showing the demographic distribution of known female [Top], male [Middle] and unknown sex [Bottom] right whales over the time series 1980-2012. Demographic stage is denoted by color: red = newborn, green = juvenile, blue = all adults (male) or non-breeding adults (female), purple = breeding female, yellow = post-breeding female, turquoise = unknown stage.

subregions running along a west to east transect: Massachusetts Bay (MB), Western Gulf of Maine (WGOM), Eastern Gulf of Maine (EGOM), and the Scotian Shelf (SS)(Fig. 2.3). Within each subregion and the Gulf of Maine region as a whole, the data were processed into time series of bi-monthly abundance anomalies using the methods described in Pershing et al. (2005). A yearly average time series was also produced for each subregion and the whole Gulf of Maine region.

#### 4.2.3 Capture-Recapture Model

To study the dynamics of the right whale population since 1980, we built a stage-based capture-recapture demographic matrix model (Fujiwara and Caswell 2002, Caswell 2001) (Fig. 4.2). Females transition between 5 living stages: 1-newborn, 2-juvenile, 3-adult, 4-breeding, 5-post-breeding. Males transition between 3 living stages: 1-newborn, 2-juvenile, 3-adult. The newborn stage accounts for the first year of life, and we assume that mortality in this stage is equal for both genders. Whales are classified as juveniles until they reach 9 years of age, have a sighting history of more than 8 years or, in the case of a female, until the year before the first known calving event.

An adult female sighted on the calving grounds with a newborn enters the breeding stage, and in the following year she enters the post-breeding stage. Females never reproduce in consecutive years, and there are only 13 known instances of a female exhibiting a two-year spacing between births out of the 484 known calving events from 1980-2012 (Right Whale Consortium 2014). By adding a one-year post-breeding stage, we are able to account for this difference in the probability of a 2-year birth spacing vs. a longer birth spacing. Due to a lack of



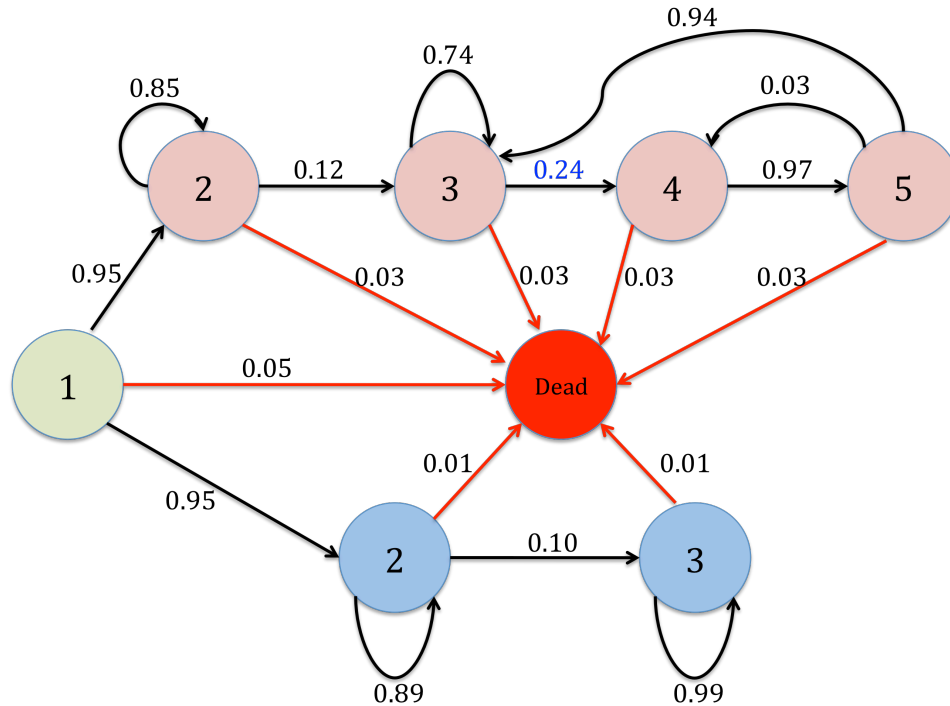


Figure 4.2: Stage-structured model of right whale demography. State 1 (in green) is the newborn state for both males and females. States 2,3,4 and 5 (in pink) represent the female states of juvenile, adult, breeding and post-breeding, respectively. States 2 and 3 (in blue) represent the male states of juvenile and adult, respectively. The red circle in the center of the schematic represents the dead state for both genders. Numbers written next to black arrows represent the probability of transitioning between living states, and numbers written next to red arrows represent mortality rates for each state. All transitional probabilities and mortality rates shown are those estimated in the temporally constant, prey-independent capture-recapture model; however the probability of transitioning from female state 3 to state 4 is written in blue text to signal that in the best model, this transition is prey-dependent, and the probability of transitioning to the breeding state only equals 0.24 when prey are at their mean abundance. See Table 4.1 for confidence intervals.

identified mortality events in breeding and post-breeding females, all adult female stages (adult, breeding and post-breeding) are assumed to have equal mortality rates.

Time steps between demographic stages occur at 1-year intervals based off of the “right whale year” which begins in December rather than January. This definition allows calves born in December to be included with their cohort, since right whale calves are born during the winter months, usually December, January and February.

Capture probabilities, or the likelihood that an individual will be sighted in a given time step, are estimated for each sex and demographic state. Since a newborn sighting is always the first sighting (or “capturing”) of an individual, capture probabilities cannot be estimated for newborns. Due to the high level of survey effort on the calving ground, we assume all calf births are recorded, so the capture probability of a breeding female is fixed at 1.0. The capture probability of an individual in the dead state (state 6 for females, state 4 for males) is fixed at 0.0.

Capture probabilities  $p$  for all remaining demographic states  $i$  are modeled as logistic functions with dependence on annual survey effort, which is designated as the total number of shipboard and aerial survey days each year (Right Whale Consortium 2014):

$$p_i = \frac{\exp(c_1 + c_2 * effort(t))}{1 + \exp(c_1 + c_2 * effort(t))} \quad \text{[Equation 4.1]}$$

The capture probability matrix  $\mathbf{P}$  is a diagonal matrix with each diagonal element  $p_i$  corresponding to the logistic function for that demographic state  $i$ . A separate matrix  $\mathbf{P}$  is constructed for male and female whales. For example,  $\mathbf{P}_f$ :

$$P_f = \begin{pmatrix} p_1 & 0 & \cdots & 0 \\ 0 & p_2 & & 0 \\ \vdots & & \ddots & \\ 0 & 0 & & p_6 \end{pmatrix} \quad [\text{Equation 4.2}]$$

To reduce parameterization, capture probability functions for demographic states that are not significantly different are combined and re-estimated. To that effect, capture probabilities of juvenile males and juvenile females were combined into one function. Similarly, the effects of survey effort for all adult stages (adult male, adult resting female, and post breeding female) were not significantly different and were combined and re-estimated. Capture probabilities with dependence on survey effort are fixed across all transitional probability model formulations. The resulting time series of capture probabilities for all demographic states is shown in Figure 4.3.

Transitional probabilities, or the likelihood of an individual whale transitioning between demographic states during an annual time step, are modeled as a set of polychotomous logistic functions to ensure that the sum of all possible transitions for an individual between consecutive time steps equals 1.0 (Caswell and Fujiwara 2004). In a simple example, here is a set of polychotomous logistic equations in a temporally constant model for a juvenile female transitioning along 3 possible arcs to the following time step: remaining in the juvenile state ( $\phi_{22}$ ), transitioning to resting adult ( $\phi_{32}$ ), or dying ( $\phi_{62}$ ).

$$\phi_{22} = \frac{\exp(c_1)}{1 + \exp(c_1) + \exp(c_2)} \quad [\text{Equation 4.3}]$$

$$\phi_{32} = \frac{\exp(c_2)}{1 + \exp(c_1) + \exp(c_2)} \quad [\text{Equation 4.4}]$$

$$\phi_{62} = \frac{1}{1 + \exp(c_1) + \exp(c_2)} \quad [\text{Equation 4.5}]$$

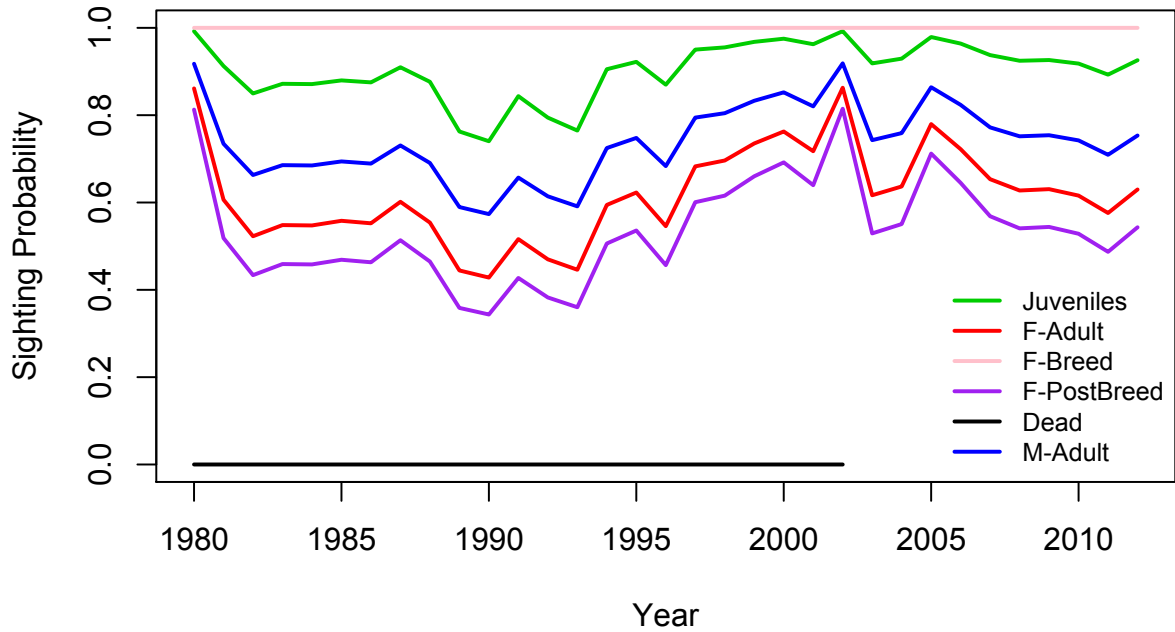


Figure 4.3: Model estimated sighting probabilities for each demographic state over the time series 1980-2012. Sighting probabilities for breeding female state (pink) is fixed at 1.0 and dead states (black) are fixed at 0.0. All other states are modeled as a function of survey effort: male and female juveniles (green), resting adult females (red), post-breeding females (purple) and adult males (blue).

To test for environmental dependence in any of these transitions, a linear combination of parameters and environmental variables, such as prey abundance, can be added into the logistic equation following the example shown for the capture probability  $p_i$  in Equation 4.1.

A separate transition matrix is built for males,  $\Phi_m$ , and females  $\Phi_f$ , where each element corresponds to a possible transition  $\phi_{ij}$  from state  $i$  to state  $j$ , for example:

$$\Phi_f = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ \phi_{21} & \phi_{22} & 0 & 0 & 0 & 0 \\ 0 & \phi_{32} & \phi_{33} & 0 & \phi_{35} & 0 \\ 0 & 0 & \phi_{43} & 0 & \phi_{45} & 0 \\ 0 & 0 & 0 & \phi_{54} & 0 & 0 \\ \phi_{61} & \phi_{62} & \phi_{63} & \phi_{64} & \phi_{65} & 1 \end{pmatrix} \quad \text{[Equation 4.6]}$$

$$\Phi_m = \begin{pmatrix} 0 & 0 & 0 & 0 \\ \phi_{21} & \phi_{22} & 0 & 0 \\ 0 & \phi_{32} & \phi_{33} & 0 \\ \phi_{41} & \phi_{42} & \phi_{43} & 1 \end{pmatrix} \quad [\text{Equation 4.7}]$$

Following the procedure outlined in Caswell and Fujiwara (2004) to calculate the likelihood of the capture history of each individual whale  $k$  over the time series  $t$ , we can calculate the likelihood of the capture history over the whole population as:

$$\text{Log}(L[\Phi, P]) = \sum_k \text{Log}(\ell_k[\Phi, P | X_1, \dots, X_t]) \quad [\text{Equation 4.8}]$$

The numerical estimation of all parameters in the capture-recapture model was performed using AD Model Builder (Fournier et al. 2012), and all subsequent analyses were carried out in R (R Core Team 2015). Model performance is compared using Akaike Information Criteria (AIC; Akaike 1974). For model-derived products such as transitional probabilities, population size and population growth rate, 95% confidence intervals were estimated from 10,000 parametric bootstrap samples generated assuming a normal distribution for all model parameters.

For the prey-independent model, demographic transitional probabilities are modeled as constant over the period 1980-2012. Then to test the impact of prey availability on population dynamics, each demographic transitional and survival probability is tested for dependence on annually averaged *C. finmarchicus* abundance anomalies aggregated across the entire Gulf of Maine CPR transect at a lag of 0-, 1- and 2-years. Finally, a series of capture-recapture models are built to test the effect of seasonally and geographically resolved *C. finmarchicus* abundance anomalies on right whale demographic transitions. Since temporally and geographically resolved prey data are not available after 2007, these models are built for the time series 1980-2007.

Additional formulations of the prey-independent and annually averaged prey-dependent models were built for the 1980-2007 time series for comparison with the resolved-prey dependent model.

#### 4.2.4 Sex and State Uncertainty

The photographic identification of an individual right whale in a given year does not necessarily indicate that the sex or demographic state of that individual is discernible (Fig. 4.1). Nevertheless, the incorporation of all data, even incomplete sightings, is valuable in a capture-recapture analysis (Fujiwara and Caswell 2002). Of the 679 individual right whales that have been photographically identified in the catalog, 63 have an unknown sex. We include the histories of these 63 individuals in the capture-recapture analysis by assuming a 50% likelihood that each individual is either a male or female. Unknown sex individuals are most commonly whales that died at a young age before researchers had a chance to identify the sex; therefore, it is essential to include these individuals in the analysis to avoid underestimating newborn and juvenile mortality rates.

Among all years that an individual was sighted, the demographic state was identified 85% of the time (Fig. 4.1). For the other 15% of sightings, we incorporate state uncertainty into the model to make use of the information. A sighted individual may be classified into an unknown demographic state because it has an unknown birth year and a sighting history of less than 8 years and, in the case of a female, no known reproductive events. To include individuals in an unknown demographic state in the analysis, we assume that the individual is either a juvenile or a non-reproductive adult. We estimate the probability of the individual being either juvenile or adult according to the ratio of known, catalogued whales in those states over the time series 1980-2012, separated by sex. The ratio of known female juveniles over all known female

juveniles and adults is 0.35, so unknown-state females are assumed to have a 35% probability of being juvenile and a 65% probability of being adult. Similarly, the ratio of known male juveniles over all known male juveniles and adults is 0.27, so unknown-state males are assumed to have a 27% probability of being juvenile and a 73% probability of being adult.

#### 4.2.5 Population projections

Forward projections can be used to demonstrate the effects of perturbations on population viability. Only female individuals contribute to future population growth through breeding, so population growth and perturbation analysis can be performed on the female portion of the capture-recapture model. The transition matrix  $\Phi$  estimated in the capture-recapture analysis can be converted to population projection matrix  $\mathbf{A}$  following the protocol outlined in Caswell et al. (2004). Briefly, all mortality stages are removed from the female transition matrix, reducing the 6x6 matrix into a 5x5 matrix. Then fertility rates are computed from the transition matrix using the following formulae:

$$A_{13}(t) = 0.5 * \phi_{43}(t) * \sqrt{(1 - \phi_{65}(t + 1))} \quad \text{[Equation 4.9]}$$

$$A_{15}(t) = 0.5 * \phi_{45}(t) * \sqrt{(1 - \phi_{65}(t + 1))} \quad \text{[Equation 4.10]}$$

Where the probability of a resting adult female producing a female calf,  $A_{13}(t)$  is the product of the probability of transitioning from resting to breeding  $\phi_{43}(t)$  multiplied by the probability of the mother's survival during the first 6 months after breeding  $\sqrt{(1 - \phi_{65}(t + 1))}$ , since calf survival is linked to mother survival, and we assume calves must survive 6 months to be catalogued. Finally, the probability of breeding is multiplied by 0.5 under the assumption that only half of the calves produced are female (Equations 4.9). Similarly, the probability of a post-breeding female producing a calf,  $A_{15}(t)$  can be calculated from the probability of transitioning

from post-breeding to breeding  $\phi_{45}(t)$  (Equation 4.10). With the creation of the matrix A, the right whale population can be projected from a known size and demographic distribution  $N_t$  as follows:

$$N_t = [A(t)] \times N_{t-1} \quad \text{[Equation 4.11]}$$

To examine the effect of prey availability on future population viability, population growth was simulated under three different prey scenarios corresponding to the three decades that right whales were monitored for this study. Gulf of Maine transect-wide annually averaged late stage *C. finmarchicus* abundance anomalies were randomly sampled with replacement from 1980-1989 in the first decadal scenario, from 1990-1999 in the second decadal scenario and from 2000-2009 in the third decadal scenario. Prey abundance anomalies were resampled at each annual time step, and each run was projected over a 100-year period.

While changing prey availability can affect population growth rates through its impact on calving rates, right whale mortality rates are known to fluctuate in response to changes in anthropogenic behavior due to ship strikes and gear entanglement. Forward projections are simulated under increasing lethal removal scenarios demonstrating population growth over the following century in the scenario of 0, 2, 4 and 6 annual lethal removals of adult females in addition to the currently estimated mortality rates. A second analysis is conducted under scenarios of 0, 4, 8 and 12 annual lethal removals taken at random from any demographic group in the population. Under these simulations, prey is sampled randomly from the 1979-2011 time series of annually averaged *C. finmarchicus* abundance anomalies.

Under each projection scenario, the distribution of right whales in the initial time step is set to the observed population size and demographic distribution in 2012. To demonstrate stochasticity, 100 simulations were run for each projection scenario.



## 4.3 RESULTS

### 4.3.1 Constant Transitional Probabilities

Transitional probabilities between all states for the prey-independent, temporally constant capture-recapture model were estimated as constant over the time series 1980-2012 (Fig. 4.2)(Table 4.1). The results of this model indicate that the population is growing at a rate  $\lambda=1.026$ . The demographic state with the highest mortality rate is the newborn state ( $\phi_{m,41}=\phi_{f,61}=0.054$ ). Resting adult females have a 24% chance of breeding (Fig. 4.4[Top]), however, the probability of a post-breeding females transitioning into a breeding state (i.e. females following a 2 year calving cycle rather than the typical 3+ year calving cycle) is much less common at 3%.

The right eigenvalue of the projection matrix can be calculated to determine the stable stage distribution of the population. When the population is in equilibrium, the proportion of females that will populate the states in the order of newborn, juvenile, adult resting, adult breeding and adult post breeding is as follows:

$$\text{Stable stage distribution} = \{0.052, 0.289, 0.451, 0.106, 0.101\}$$

The left eigenvalue of the projection matrix can be calculated to determine the lifetime reproductive value of a female in each demographic stage. These values are shown below, scaled to the reproductive value of a female in the newborn stage:

$$\text{Reproductive value} = \{1.000, 1.084, 1.562, 1.417, 1.493\}$$

Mature adult females have the highest reproductive value because they have survived the newborn and juvenile stages and are able to actively reproduce.

Sensitivity and elasticity values of the prey-independent projection matrix are calculated from A and shown in Table 4.1. Sensitivities show the effects of absolute changes in transitional probabilities on the population growth rate. Sensitivities are computed using the stable state

distribution and the reproductive value of each stage, such that the most sensitive transitions are those that affect the largest number of individuals with the highest reproductive value. Since resting adults make up the largest portion of the female population and have the highest reproductive value, resting adult survival is the most sensitive transition, followed by the transition from resting to breeding and then juvenile survival (Table 4.1).

Elasticities show the influence of a proportional change in each transitional probability on the population growth rate. Transitions with the highest elasticities are adult resting survival and juvenile survival (Table 4.1).

#### 4.3.2 Annually averaged prey-dependent models

Dependence on annually averaged transect-wide *C. finmarchicus* anomalies with a lag of 0, 1 and 2 years was tested independently in all transitional probabilities and mortality rates for all demographic stages among both males and females. Only the inclusion of prey in the transition from adult female to breeding resulted in a significant improvement ( $\Delta AIC > 2.0$ ) compared to the temporally constant model. In the transition from adult female to breeding female, dependence upon 1-year lagged prey abundance, for example, occurs when the chance of transitioning from adult female in 1989 to calving in 1990 is driven by prey abundance in 1988. When adding 0, 1 and 2 year lagged prey abundance to the transition from adult female to breeding female, there was significant improvement in fitness of the 1-year and 0-year lagged prey driven models compared to the temporally constant, prey-independent model (prey independent:  $AIC=14619.5$  ( $\Delta AIC=33.9$ ); 0-year lagged prey:  $AIC=14607.6$  ( $\Delta AIC=22.0$ ); 1-year lagged prey:  $AIC =14585.6$  ( $\Delta AIC=0.0$ ); 2-year lagged prey:  $AIC=14621.2$  ( $\Delta AIC=35.6$ )).

Female Temporally Constant Transitional Probabilities						
	Estimate	Upper C.I.	Lower C.I.	Sensitivity	Elasticity	
Phi21	0.946	0.966	0.915	0.041	0.038	
Phi22	0.854	0.917	0.752	0.229	0.19	
Phi32	0.12	0.215	0.062	0.329	0.038	
Phi13*	0.116	0.15	0.086	0.329	0.037	
Phi33	0.73	0.802	0.664	0.514	0.37	
Phi43	0.244	0.307	0.174	0.466	0.107	
Phi54	0.974	0.979	0.968	0.116	0.11	
Phi15*	0.015	0.025	0.009	0.074	0.001	
Phi35	0.944	0.957	0.921	0.115	0.106	
Phi45	0.03	0.052	0.017	0.104	0.003	
Phi61	0.054	0.085	0.034			
Phi62	0.026	0.039	0.017			
Phi63	0.026	0.032	0.021			
Phi64	0.026	0.032	0.021			
Phi65	0.026	0.032	0.021			
Phi66	1					
Male Temporally Constant Transitional Probabilities						
	Estimate	Upper C.I.	Lower C.I.			
Phi21	0.946	0.966	0.915			
Phi22	0.89	0.944	0.789			
Phi32	0.095	0.191	0.045			
Phi33	0.988	0.991	0.983			
Phi41	0.054	0.085	0.034			
Phi42	0.015	0.024	0.009			
Phi43	0.012	0.017	0.009			
Phi44	1					

Table 4.1: Estimates and 95% confidence intervals, sensitivities and elasticities for transitional probabilities in the temporally constant (prey independent) capture-recapture model. \*Denotes transitions derived from the transition matrix,  $\Phi$ , to form the projection matrix,  $A$ .

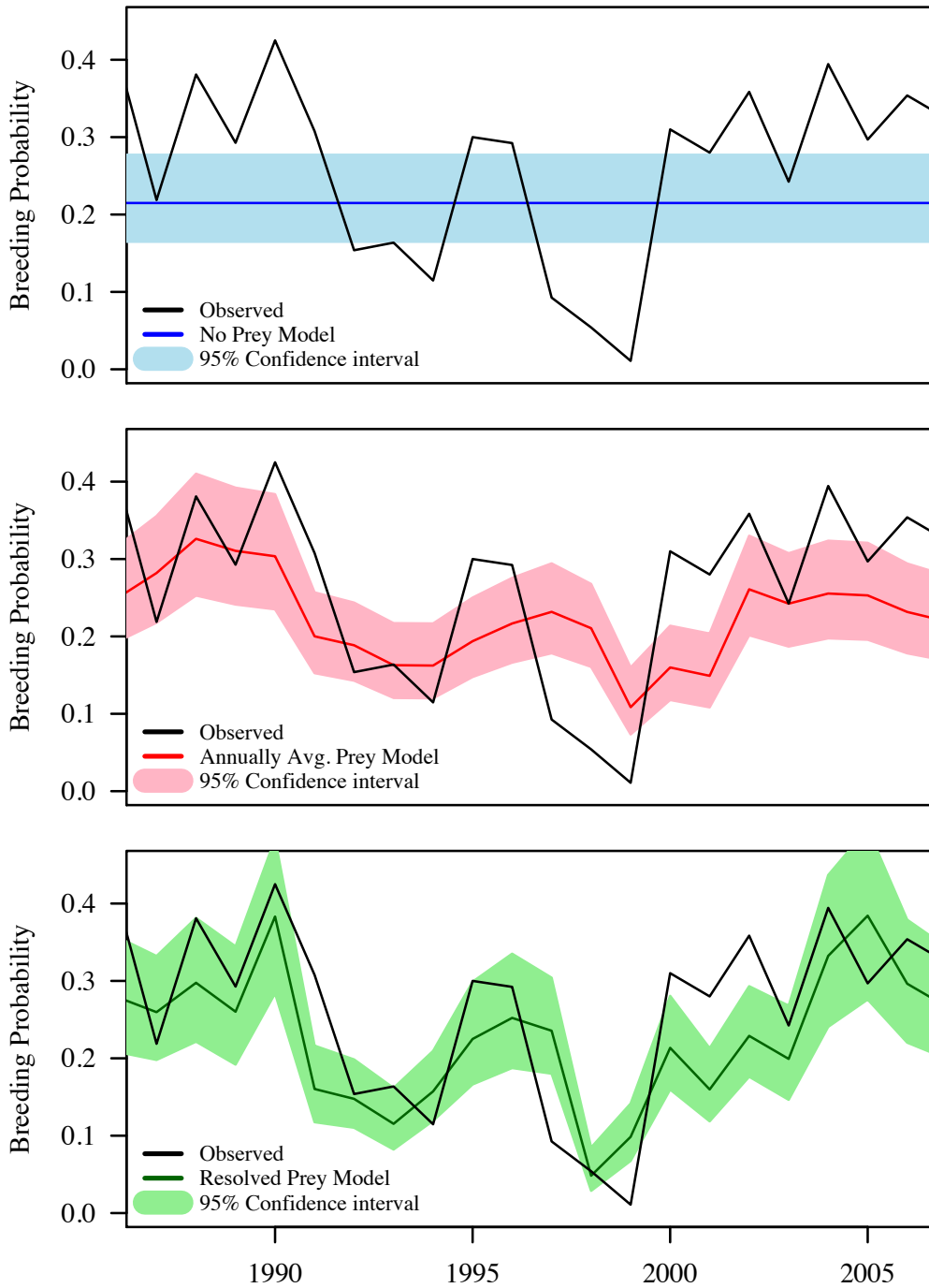


Figure 4.4. Time series plots show the probability (with 95% confidence intervals) of transitioning between the female resting stage and breeding stage as a constant in the no prey model (blue)[Top], as a function of annually averaged *C. finmarchicus* (red)[Middle], and as a function of three geographically and seasonally specific *C. finmarchicus* abundance indices in the resolved prey model (green)[Bottom]. Also plotted in each panel is the ratio of observed breeding females and resting females (black lines).

The probability of a female transitioning from state 3 to state 4 in the annually averaged prey dependent model is shown in Figure 4.4 [Middle]. The probability of breeding over the 1980-2012 time series ranges from a maximum value of 36% in 1988 during the period of high *C. finmarchicus* abundance in the late 1980s to a minimum value of 11% in 1999 following the *C. finmarchicus* crash in 1998 (Fig. 4.5[Top]). The annual population growth rate varies with the change in breeding probability, reaching a maximum of  $\lambda=1.040$  in 1988 and a minimum of  $\lambda=1.004$  in 1999 (Fig. 4.5[Bottom]).

#### 4.3.3 Spatially and temporally resolved prey-dependent models

After testing annually averaged prey dependence in all demographic transitions, only prey dependence in the transition from adult female resting to breeding was a significant improvement over the temporally constant model. To test whether the prey-dependent capture-recapture model could be further improved by including higher spatial and temporal resolution in the prey data, CPR-derived bimonthly and regional late stage *C. finmarchicus* abundance anomalies were tested independently and in combination for the transition from resting to breeding following the protocol outlined in Meyer-Gutbrod et al. (2015). In the best fit resolved prey model, the transition from female adult resting to breeding was driven by 1-year lagged, CPR-derived May/June anomalies in the West Gulf of Maine, September/October anomalies across the entire Gulf of Maine transect and March/April anomalies in the West Gulf of Maine. Since resolved prey data is not available after 2007, the resolved prey-dependent capture-recapture model was fit to the 1980-2007 time series of capture probabilities, and the temporally constant and annually averaged prey-dependent models were reformulated to fit the 1980-2007 time series for comparison with the resolved prey model. Both the annually averaged prey- and

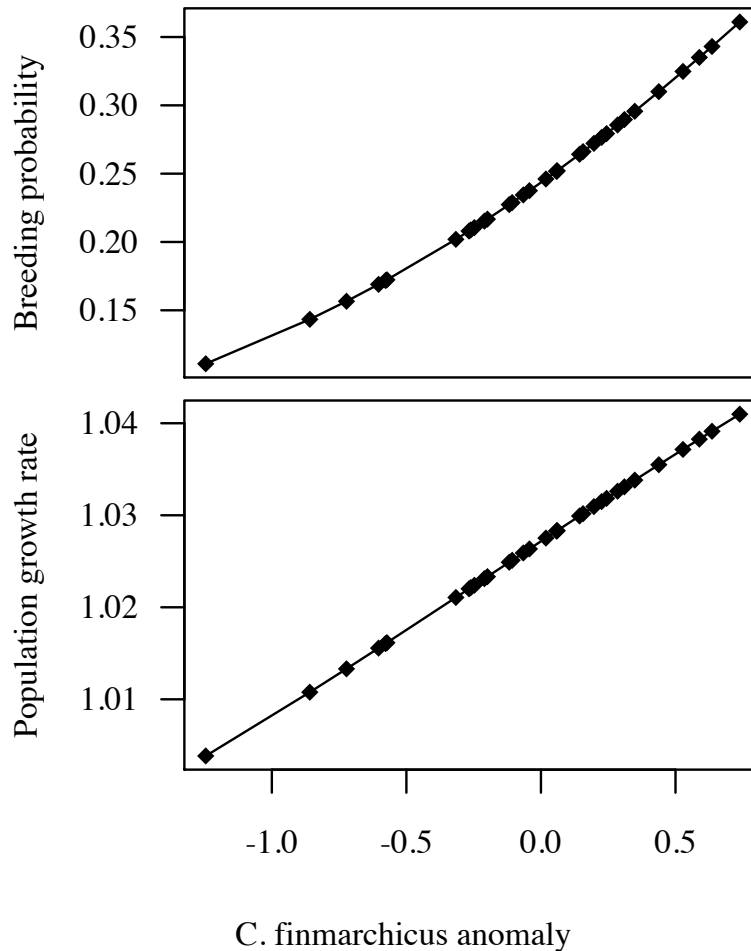


Figure 4.5: [Top]: The probability of a female transitioning from resting to breeding as a function of the annually averaged *C. finmarchicus* abundance anomaly. [Bottom]: The population growth rate ( $\lambda$ ) as a function of the annually averaged *C. finmarchicus* abundance anomaly. Diamonds mark observed annual *C. finmarchicus* anomalies over the time period 1979-2006.

#### 4.3.3 Spatially and temporally resolved prey-dependent models

resolved prey-dependent model formulations performed better than the temporally constant model, with the resolved prey model performing the best (temporally constant model AIC=11481.08 ( $\Delta$ AIC=63.5); annually averaged prey model AIC=11455.2 ( $\Delta$ AIC=37.6); resolved prey model AIC=11417.6 ( $\Delta$ AIC=0.0)).

Modeled breeding probability for the temporally constant, annually averaged prey-dependent and resolved prey-dependent 1987-2007 models is shown in Figure 4.4, plotted alongside the observed ratio of breeding females to resting females in the previous year (black lines). Years prior to 1987 are not shown because observed breeding ratios are inflated due to the discovery curve (Fig. 4.1[Top]). The probability of transitioning from resting to breeding in the temporally constant model is 0.21, which is slightly lower than in the temporally constant 1980-2012 model ( $\phi_{43}$ =0.24). This difference arises because the poor breeding conditions driven by low prey in the late 1990s make up a larger portion of the modeled time series. Figure 4.4 shows that the inclusion of prey allows the capture-recapture model to explain a greater portion of the temporal variability in breeding rates.

#### 4.3.4 Projected population growth under decadal prey scenarios

To examine the potential population trajectories of the North Atlantic right whale under different prey scenarios, we projected the population growth under the annually averaged prey dependent model using prey randomly sampled from the three different decadal prey regimes observed since 1980: the high prey abundance of the 1980s, low abundance in the 1990s and moderate abundance in the 2000s (Fig. 4.6[Top]). Under these projection scenarios, all other transitional probabilities were held constant at the values estimated in the annually averaged, prey-dependent capture-recapture model described previously. The mean, model-estimated,

population growth rate under each of the three decadal regimes is  $\lambda=1.032$  (std=0.0064) in the 1980s,  $\lambda=1.019$  (std=0.0069) in the 1990s, and  $\lambda=1.029$  (std=0.0032) in the 2000s (Fig. 4.6[Bottom]). As evidenced by these projections, and by the annual population growth rate calculated under the observed annual *C. finmarchicus* anomalies (Fig. 4.5[Bottom]), growth is positive even under the worst prey conditions in the 1980-2012 time period.

#### 4.3.5 Projected population growth under increased mortality scenarios

With evidence supporting positive future population growth under all observed prey conditions, we investigated what increase in mortality could lead to population decline in a new forward projection analysis. Population growth was projected over 100 years using the annually averaged prey model with prey randomly sampled with replacement from the 1979-2011 time series. Growth was projected using the demographic dynamics estimated in the annually averaged, prey-dependent, capture-recapture model with no change in mortality rates (black), and with 2 (red), 4 (green) and 6 (blue) additional adult female mortalities each year (Fig. 4.7). With the annual removal of 6 or more adult females, the population will collapse within the next century.

A similar analysis was performed with increasing mortality events taken from the population at large rather than taken specifically from just adult females. Annually averaged prey anomalies were again randomly sampled from the 1979-2011 time series. In these scenarios, population collapse occurred within 100 years under the majority of projected simulations when the total additional removal was 13 whales annually (Fig. 4.8).



### Projected growth under 3 decadal prey regimes

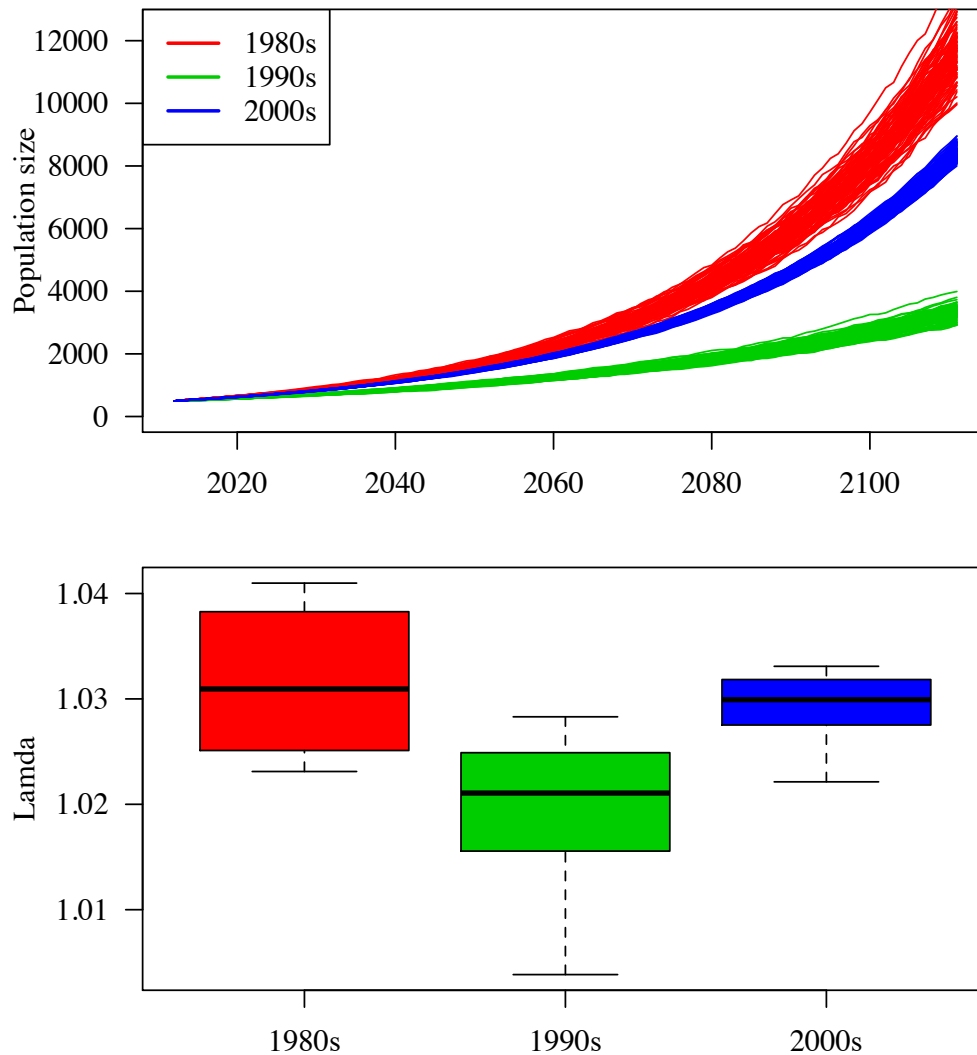


Figure 4.6. Projected population growth of the North Atlantic right whale under three different decadal prey regimes: 1980s (red), 1990s (green) and 2000s (blue). [Top]: Each line corresponds to a 100-year population projection, simulated 100 times under each decadal prey regime. [Bottom]: Box and whisker plots showing the median (thick black bar), first and third quartiles (edges of box) and maximum and minimum (ends of whiskers) values of the population growth rate,  $\lambda$ .

### Projections with non-breeding adult female removals

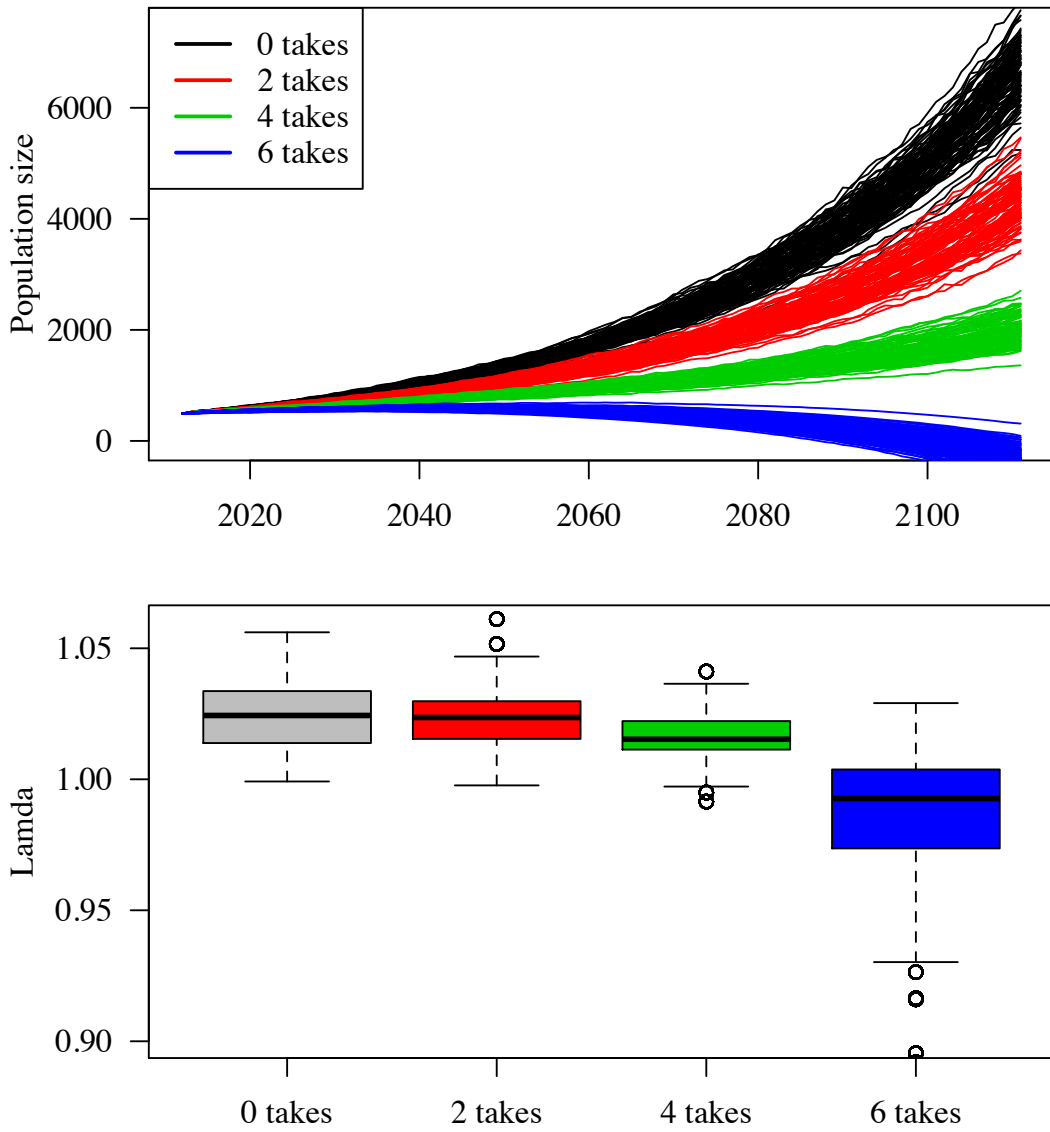


Figure 4.7: Future projections [Top] and box plots of the population growth rate,  $\lambda$  [Bottom] of right whale population size in the annually averaged prey-driven model with prey sampled randomly from 1979-2012. At each annual time step of the projection, 2 (red lines), 4 (green lines), or 6 (blue lines) non-breeding adult females are removed from the population to simulate increased mortality rates. These increased mortality scenarios are shown alongside the current population trajectory (black lines).

### Projected growth with removals from random stage

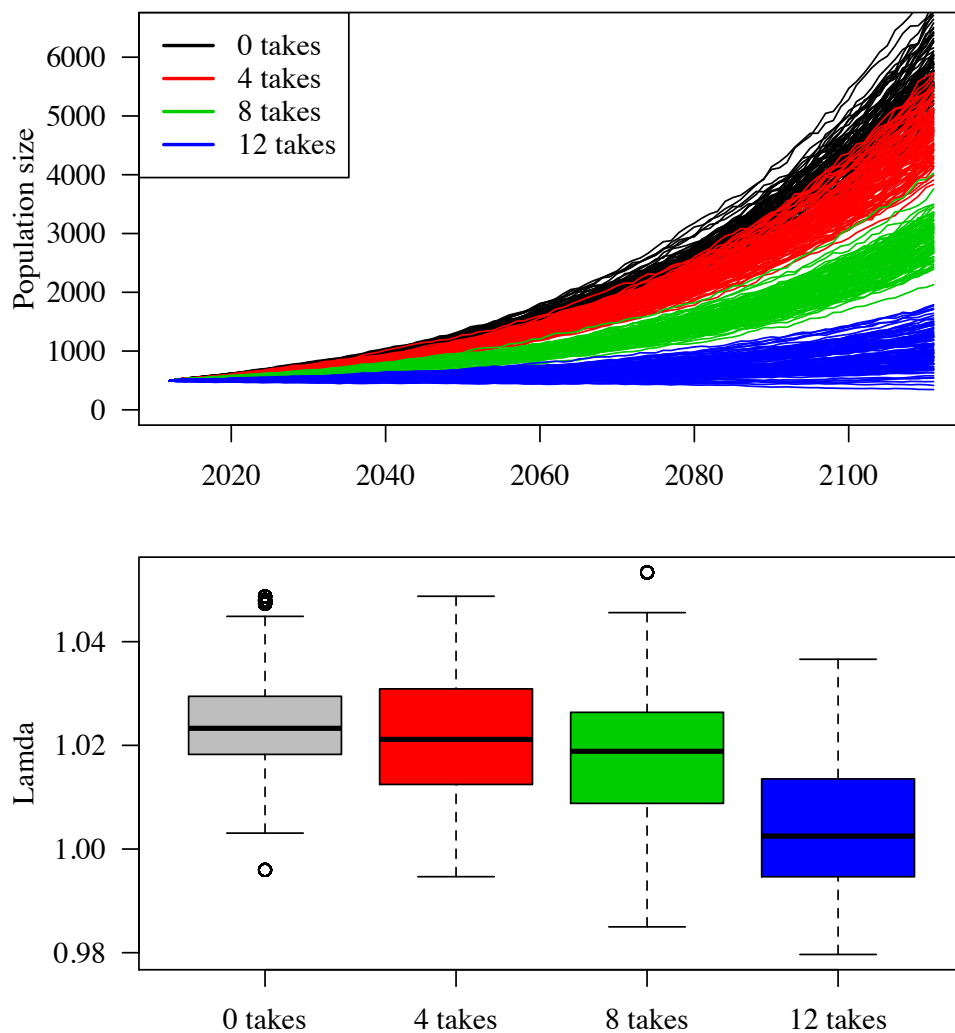


Figure 4.8: Future projections [Top] and box plots of the population growth rate,  $\lambda$  [Bottom] of right whale population size in the annually averaged prey-driven model with prey sampled randomly from 1979-2012 at each year time step. At each annual time step of the projection, 4 (red lines), 8 (green lines), or 12 (blue lines) whales are removed from the population at random to simulate increased mortality rates among all demographic stages. These increased mortality scenarios are shown alongside the current population trajectory (black lines). Population collapse occurs under the majority of simulations at annual removal counts greater than 12 whales.

#### 4.3.4 Projected population growth under combined low prey and increased mortality scenarios

The previous analysis shows how the population growth rate will change with additional annual mortalities given the prey conditions present in the previous three decades. Since two of the previous three decades occurred during regimes of relatively high prey availability (the 1980s and 2000s), reproduction rates were weighted towards shorter calving intervals. However, if low prey conditions such as those observed in the 1990s occur in the future, population growth will be more sensitive to increases in mortality rates.

To analyze the combined effects of low prey abundance and increased mortality, population growth was projected over the next century using the annually averaged prey model with prey randomly sampled with replacement from the 1991-2000 time series and three scenarios of annual non-breeding adult female removals. Growth was projected using the demographic dynamics estimated in the annually averaged, prey-dependent, capture-recapture model with no change in mortality rates (black), and with 2 (red) and 4 (green) additional adult female mortalities each year (Fig. 4.9). Under prey conditions similar to those observed in the 1990s and with the additional annual removal of 4 or more adult females, the population will begin a period of gradual decline.

#### 4.4 DISCUSSION

When tested independently, the addition of both 0-year lagged prey and 1-year lagged prey to the transition from adult female to breeding female significantly improves the capture-recapture model compared to a prey-independent model formulation. These results corroborate findings from a previous study of the influence of prey on right whale calving rates using a 3-state reproduction model, where 1-year lagged prey influenced the rate of conception and 0-year

### Projections with 1990s prey and adult female removals

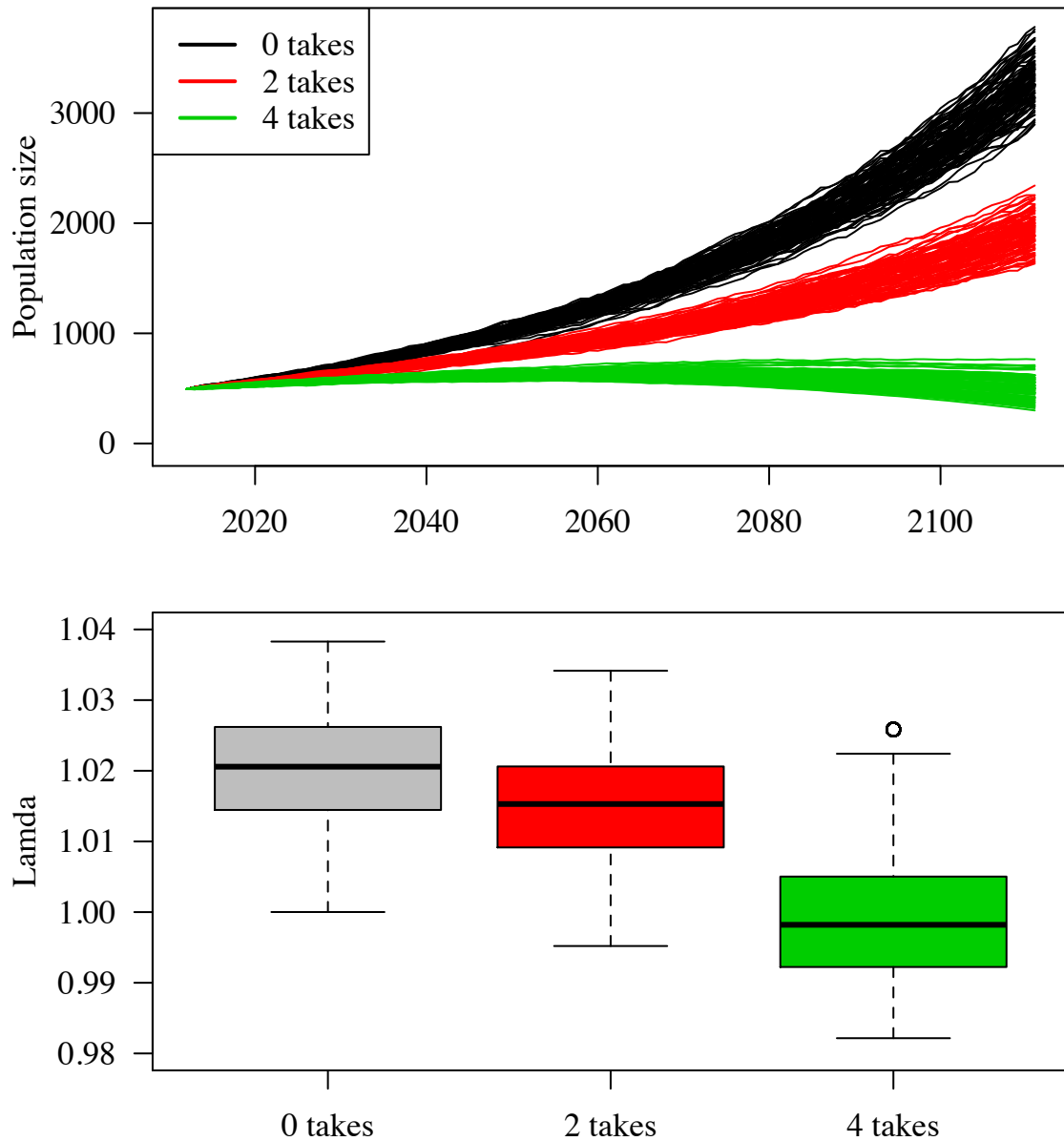


Figure 4.9: Future projections [Top] and box plots of the population growth rate,  $\lambda$  [Bottom] of right whale population size in the annually averaged prey-driven model with prey sampled randomly from the 1990s. At each annual time step of the projection, 0 (black lines), 2 (red lines), or 4 (green lines) non-breeding adult female whales are removed from the population at random to simulate increased mortality rates among all demographic stages. Gradual population decline occurs with an annual removal of 4 adult female whales.

lagged prey influenced the rate of successful calving events among pregnant females (Meyer-Gutbrod et al. 2014). After testing prey dependence in each demographic transition, the inclusion of prey dependence only improved the capture-recapture model when incorporated in the transition from adult female resting to breeding. This indicates that starvation of juvenile and adult whales is not currently a realistic threat to population viability, however periods of low prey availability may reduce calving rates when females are not able to obtain adequate nutrition for breeding and lactation. Changes in visually assessed health conditions across most demographic groups, but most notably for resting females, correspond with interannual fluctuations in recruitment, providing direct evidence of the link between nutritional availability and breeding rates (Rolland et al. 2016).

By incorporating prey availability into a full demographic model, we were able to project right whale population growth into the future and conduct a perturbation analysis. Although the best model fit in this study is the resolved prey model where three bimonthly values of subsections of the CPR transect were used to predict breeding probability, the model incorporating annually averaged transect-wide prey anomalies was selected for use in the population projection and perturbation analysis. Right whales have been known to fluctuate between feeding grounds based on prey availability (Patrician and Kenney 2010), therefore the regions where whales have historically fed will not necessarily be utilized in future decades. Therefore, the annually averaged *C. finmarchicus* abundance anomalies across the GOM may provide a more robust metric for characterizing future prey fluctuations because they are more representative for a greater portion of the feeding habitats, both spatially and temporally. Although the annually averaged model was chosen for more conservative population viability assessment, this decision may mask the severity of prey limitation in anomalous years. For example, the low breeding rate

and population growth rates predicted in the late 1990s by the annually averaged prey model does not fully characterize the decline in reproduction that was observed and which was predicted by the resolved prey model (Fig. 4.4; Meyer-Gutbrod et al. 2014, Meyer-Gutbrod and Greene 2014).

In the forward projections under three different prey scenarios, it is clear that the North Atlantic right whale population is experiencing positive growth even during the worst decadal-scale prey conditions. These results provide an interesting update to the study by Fujiwara and Caswell (2001) which indicated that population growth was in decline, with projected extinction within 200 years. The decline estimated in the late 1990s by Fujiwara and Caswell was based primarily on a temporally-increasing mortality rate among breeding females. However, this model was based upon limited data, since there are very few well-documented instances of mortality among breeding females. Fujiwara and Caswell (2001) cited a mass mortality event of 5 recovered right whale carcasses in 1996 as evidence that the modeled increase in breeding female mortality captures a real biological phenomenon. However, of the five dead whales recovered that year, two were newborns, two were males and the remaining individual was unidentifiable (Waring et al. 1999 Stock Assessment report). For the models presented in this study, all three adult female stages were assumed to have equal mortality rates because there is insufficient data available to accurately estimate separate mortality rates for the breeding and post-breeding states. Without mortality data specific to female reproductive states to populate the model, there is less basis for the population decline predicted by Fujiwara and Caswell (2001).

## 4.5 CONCLUSION

Despite a stagnation in population growth at the end of the 1990s leading to projections of future extinction, the North Atlantic right whale experienced a period of recovery in the early 2000s mediated by high prey abundance and a corresponding increase in reproduction rates. However, following the end of this study period in 2012, right whale population growth has languished, partly due to an observed decline in calf births (Pettis and Hamilton 2015, Kraus et al. 2016). While humans exhibit control over right whale mortality, fluctuations in fecundity driven by changes in prey abundance create a degree of unpredictability, resulting in limited control over the population's fate. Due to funding limitations, CPR data in the Gulf of Maine are not currently being processed. The break in this 50-year time series makes it difficult to update the demographic model presented here to analyze the most recent changes in population trends. This break in data collection comes at a most unfortunate time, with unusual warming in the Gulf of Maine and unprecedented change in global climate patterns.

There are many uncertainties regarding the assessment of recent right whale population performance because whales often have multiple-year gaps in sighting histories. In the past several years, right whale sightings have been at an all time low, dropping from a typical annual sighting rate of 85% of the population down to sighting rates of 74%, 56% and 68% in 2012, 2013 and 2014, respectively (Pettis and Hamilton 2015). This decline in Gulf of Maine sightings combined with three right whale carcasses found in the Gulf of St. Lawrence in the summer of 2015 provide evidence that right whale distributions may be shifting north, possibly in search of denser prey aggregations. This decline in sightings data leaves scientists blind during a time of rapid change, and when small fluctuations in vital rates have the potential to bring irreparable damage to a vulnerable species.



Analysis of population viability under increasing mortality scenarios is useful for the assessment of population dynamics under changing environmental conditions. Fishing gear entanglement remains problematic for the species, with increasing severity of entanglement injuries and a greater risk of mortality (Knowlton et al. 2015, Robbins et al. 2015). Research currently underway suggests that entanglement mortality is both severely underestimated and increasing, potentially as a result of shifts in right whale habitat use (Pettis et al. 2015). With dramatic changes in right whale distribution and increasing entanglement rates, the low prey abundance, high mortality scenario presented in Fig. 4.9 (2 [red] and 4 [green] additional annual adult female mortalities) may be a reflection of current conditions (Kraus et al. 2016). With only 526 individuals in the population, heightened efforts to reduce anthropogenic mortality remain essential to protecting this endangered species.

The South African and Argentine populations of Southern right whales, close cousins to the North Atlantic right whale, have considerably higher growth rates with a 7% annual rate of increase (Cooke et al. 2001; Best et al. 2005) compared to the modest 2-3% rate estimated for the North Atlantic population here. These populations experience faster growth due to decreased mortality rates (annual mortality = 0.019 for Argentine adult females; 0.01 for South African adult females) and shorter calving intervals (mean interval = 3.35 years for Argentine population, 3.15 years for South African population)(Cooke et al. 2001; Best et al. 2005). These vital rates provide further evidence that the North Atlantic right whale population may be biologically capable of a faster recovery if not subjected to the pressures of anthropogenic mortality and inadequate food availability.

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## CHAPTER 5

### CONCLUSION

#### 5.1 OVERVIEW AND RESULTS OF THIS DISSERTATION

The North Atlantic right whale population has experienced net positive population growth over the time series considered in this study, with 255 known individuals in 1986 (Knowlton et al. 1994) to an estimated population size of 526 individuals in 2014 (Pettis and Hamilton 2015). Despite this assurance of positive growth, scientists remain concerned about the population's viability due to high rates of anthropogenic mortality (Campbell-Malone et al 2008, Knowlton et al. 2012), evidence of prey-limited reproduction (Fortune et al. 2013, Miller 2012, Pettis 2004) and vulnerability associated with low population size. In this dissertation, I explored the effects of climate-driven variations in prey abundance on the population dynamics of the North Atlantic right whale, with a focus on variability in breeding rates. In the previous chapters, I present evidence of the following:

- 1) A significant portion of interannual variability in North Atlantic right whale population growth is caused by annual changes in right whale breeding rates.
- 2) Variability in reproduction efficiency is driven by changes in prey availability, as measured by late-stage *C. finmarchicus* abundance anomalies from the Continuous Plankton Recorder transect across the Gulf of Maine
- 3) Fluctuations in reproductive efficiency are correlated with climate indices and oceanographic variables, suggesting that remote forcings from the Arctic Ocean and Northwest Atlantic Ocean are affecting right whale reproduction through climate-associated changes in prey availability.

- 4) Forward projections indicate that right whale population growth will remain positive during the next century under prey conditions characteristic of both high-prey abundance periods in the 1980s and 2000s as well as the low-prey abundance period of the 1990s.
- 5) Forward projections under increased mortality scenarios indicate that the right whale population will decline to extinction if an additional 2% of the population is killed each year. The co-occurrence of low prey availability decreases the mortality rate associated with this extinction threshold.

The connection between prey availability and right whale viability is plain, suggesting that the changes in circulation and stratification that effect *C. finmarchicus* abundance and distribution, both on a local and ocean-basin scale, should be included in future studies of right whale population dynamics. Forward projections currently indicate that under any of the prey conditions resampled over each of the three previous decades, reproduction will occur at a rate consistent with positive population growth. However, prey abundance anomalies have been recorded in a single year, such as 1998, when breeding rates contributed to a decline in population growth.

As ocean temperatures warm, the corresponding dynamics of the Gulf of Maine and Scotian Shelf ecosystems remain uncertain. Using an ecological niche model, Reygondeau and Beaugrand (2011) projected a reduction in *C. finmarchicus* distribution at the southern range of their habitat, with effects most pronounced in the key right whale feeding grounds of Georges Bank and the Scotian Shelf. If right whale prey shifts north, right whale females will either need to increase the distance of their migration between winter breeding grounds and summer feeding grounds, or shift their winter breeding grounds north in response. Given the strong maternally



directed site fidelity noted in these whales (Malike et al. 1999), the former response might be more likely. Careful monitoring of the distribution of *C. finmarchicus* and the corresponding effects on right whale breeding rates will be an essential component to future right whale conservation efforts and management decisions.

## 5.2 RIGHT WHALE CONSERVATION EFFORTS

The recovery of the North Atlantic right whale population can be attributed to a series of policy changes and management decisions designed to protect this vulnerable species. Since 1935, the last time a right whale was intentionally killed in the US, the population has been provided an opportunity for recovery (Kraus and Rolland 2007). In addition to the creation of laws preventing the harvest of right whales, a series of policies have been implemented to encourage population growth.

Repeated aerial and ship surveys as well as passive acoustic monitoring are conducted to identify critical right whale habitats (Clark et al. 2010). A Mandatory Ship Reporting System developed by the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NMFS) has collected valuable ship traffic data near right whale critical habitats off the Northeastern US and Southeastern US coasts (Ward-Geiger et al. 2005). Scientists have worked to develop shipping routes that decrease the risk of vessel collisions with right whales in the Southeastern US (Fonnesbeck et al. 2008) and the Northeastern US (Vanderlaan et al. 2008). As a result of these studies, NMFS implemented a large-vessel speed restriction in right whale critical habitats during seasons of heavy use (NOAA 2008). In addition, NOAA has issued voluntary Area To Be Avoided (ATBA) recommendations and a Traffic Separation Scheme outside of Boston, MA. Modeled risk assessment indicates that the

implementation of vessel speed restrictions has reduced the risk of fatal ship strikes by 80%-90% in the restricted regions and time periods (Conn and Silber 2013).

Due to the detrimental impact of fishing gear entanglements to right whale survival and health, NOAA formed the Atlantic Large Whale Take Reduction Plan (ALWTRP) in 1997. NOAA has implemented a series of fishing gear modifications in an attempt to decrease risk and severity of entanglement events (see <http://www.greateratlantic.fisheries.noaa.gov/protected/whaletrp/> for details). These gear modifications include adding weak links between gillnets or lobster pots and their buoy systems, adding weak links between gillnet panels, and implementing sinking groundlines in place of floating groundlines to connect buoys and gillnets. The ALWTRP has also implemented a large whale disentanglement program to provide training and assist in the formation of a rapid response network to respond to reported entanglement events. Despite these efforts to reduce the risk and severity of entanglement, Knowlton et al. (2012) found no change in annual entanglement rate and an increase in the severity of right whale entanglement events from 1980-2009. Continued efforts to improve fishing gear, update gear modification policies and monitor the efficacy of existing policies are necessary to reduce future entanglements.

While most conservation efforts focus on vessel strikes and entanglement in fishing gear as the largest sources of direct mortality to right whales, several additional conservation efforts have been implemented to improve general management of the species. The North Atlantic right whale has been listed as “critically endangered” under the Endangered Species Act since 1970. NMFS has restricted the approach by vessel, aircraft or other means within 500 feet of a right whale to reduce general disturbance and the risk of vessel strikes (NOAA 1997). Finally, the extensive undertaking of the North Atlantic Right Whale Consortium in managing the databases

of sightings, photo-identification, genetics, contaminants, health assessment, necropsy and blubber measurements has made possible both broad and deep efforts in science, management, education and outreach regarding this species. These conservation efforts provide hope that the recovery of this species, though gradual, may continue into the future.

### 5.3 OCEAN CONSERVATION

More generally, conservation measures being implemented in the oceans, ranging from local to global scale, are providing a glimmer of hope amidst the overall degradation of marine ecosystems. One of the most notable ocean conservation efforts in recent years has been the establishment of Marine Protected Areas (MPAs) or marine reserves where different forms of anthropogenic activities are limited or restricted. MPAs are established to accomplish a wide range of goals, including the conservation of an organism or ecosystem, regulations to prioritize traditional or historical use by indigenous people, or the implementation of sustainable modern harvest (Agardy et al. 2003). Reviews of data collected from over 100 MPAs have demonstrated that they serve to increase the density, biomass, average organism size and diversity within the reserves (Halpern and Warner 2002). Currently, 2.8% of the global ocean is protected by marine reserves, and that figure rises each year (IUCN and UNEP-WCMC 2013).

The Magnuson-Stevens Fishery Conservation and Management Act of 1996 mandated an end to overfishing practices and the rebuilding of depleted fish stocks in the US. In response, fisheries scientists and managers are implementing numerous techniques to address overfishing practices, including setting stock quotas, reducing legal fishing areas and seasons, protecting age- size- and sex-classes that contribute most to recruitment, and modifying fishing gear to reduce bycatch (Board 2013). Although progress has been slow, these techniques have already

led to the successful rebound of several commercially important stocks in US waters, including New England scallops, mid-Atlantic bluefish, Pacific whiting and Pacific lingcod (Rosenberg et al. 2006).

Pollution is a much more diffuse issue and therefore not as straightforward to resolve. Two alternative strategies have been proposed to manage non-point-source pollution from agricultural use of nitrogen and phosphorous: a decrease in fertilizer application rates and the restoration of wetlands to filter nutrients shed from croplands (Ribaud et al. 2001). Numerous approaches have been or are in the process of being developed to address the need for carbon dioxide emission reductions to reduce greenhouse warming and ocean acidification, including improvements in energy-use efficiency, development of alternative, non-fossil based energy sources, and development of carbon dioxide capture and storage technologies (Bille et al. 2013). Although implementation of these strategies has been slow, it is still possible to curb warming below the 2°C threshold recommended by climate scientists and policymakers (Peters et al. 2013).

Under mounting pressure from increased anthropogenic stressors to marine ecosystems, the timely implementation of conservation and management policies is critical to the health of the global ocean and its living inhabitants. While the conservation measures addressed here are promising, nearly all strategies are working too slowly. Increased funding to support science and management efforts will be essential to improving our understanding of these ecosystems and to implementing successful conservation measures. Adaptive changes to modern industry and human lifestyles must occur promptly to reduce anthropogenic stressors on the global ocean and to protect its living resources for future generations.

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