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GRADUATE SCHOOL OF ARTS AND SCIENCES

Dissertation

**INVESTIGATING THE MIGRATION AND FORAGING ECOLOGY OF
NORTH ATLANTIC RIGHT WHALES WITH STABLE ISOTOPE
GEOCHEMISTRY OF BALEEN AND ZOOPLANKTON**

by

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requirements for the degree of
Doctor of Philosophy

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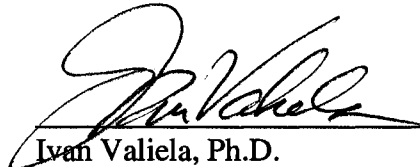
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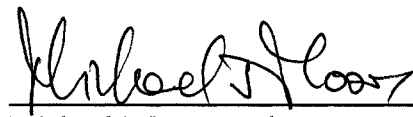
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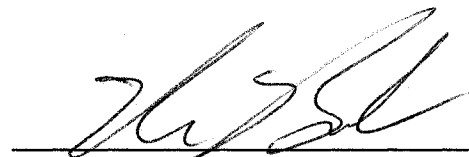
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DEDICATION



Jessie Evelyn Willett Stewart

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This volume is dedicated to my Grammy, Jessie Stewart. She was never able to attend college, despite a strong lifelong desire to do so. I am grateful to have had the opportunity to live out one of her dreams through my own pursuit of higher education. The memory of her unfailing optimism and appreciation for all of the beauty in the world continues to be an inspiration to me.

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**INVESTIGATING THE MIGRATION AND FORAGING ECOLOGY OF
NORTH ATLANTIC RIGHT WHALES WITH STABLE ISOTOPE
GEOCHEMISTRY OF BALEEN AND ZOOPLANKTON**

(Order No.)

NADINE STEWART J LYSIAK

Boston University Graduate School of Arts and Sciences, 2009

Major Professor: Ivan Valiela, Professor of Biology

ABSTRACT

The foraging grounds of the endangered North Atlantic right whale (*Eubalaena glacialis*) are protected under management rulings, but several datasets suggest that right whales use habitats far beyond these areas. In 2005, the National Marine Fisheries Service published a Right Whale Recovery Plan citing the “characterization and monitoring of important habitats” as high research priorities.

Stable isotopes ratios in animal tissue are intrinsic tags of migration, as they vary regionally in the environment, and are assimilated via trophic transfer. This dissertation describes carbon, nitrogen, oxygen, and hydrogen stable isotope ratios in baleen and zooplankton collected in the Gulf of Maine, and their application in determining the migration patterns and foraging ecology of *E. glacialis*.

The Gulf of Maine stable isotope landscape was examined through analysis of zooplankton samples from seven *E. glacialis* habitats. Cape Cod Bay, Great South Channel, and the Bay of Fundy represent distinct isotope sources to right whales. All

other habitat areas were statistically indistinguishable, and seasonal right whale movements between these areas cannot be resolved with stable isotope geochemistry.

Isotope records in *E. glacialis* baleen, like those of other large whale species, contain annual oscillations that correspond to broad-scale north/south migrations. To examine right whale movement patterns at seasonal time scales, baleen isotope records, the *North Atlantic Right Whale Catalog* sighting records, and habitat-specific zooplankton stable isotope values were compared. Poor correlations were found between observed and expected baleen isotope values, likely because of the confounding contribution of body nutrient pools that were de-coupled from diet (i.e. non-essential amino acids).

Comparisons of recently collected *E. glacialis* baleen data with isotope records from late 19th – early 20th century baleen revealed a long-term decrease in carbon and increase in nitrogen isotopes. The observed trends are attributed to increasing anthropogenic inputs of carbon dioxide and nitrogen species, climatic forcing from the North Atlantic and Pacific Decadal Oscillations, and poor overall health in the present-day right whale population.

The results of this study revealed that right whales use “historic habitat” areas more frequently than currently assumed, and demonstrates both the spatial/temporal limitations of the stable isotope method and the confounding effect of fluctuating biogeochemical signals in the environment.

TABLE OF CONTENTS

DEDICATION.....	iv
ACKNOWLEDGEMENTS.....	v
ABSTRACT.....	viii
TABLE OF CONTENTS.....	x
LIST OF TABLES.....	xiii
LIST OF FIGURES.....	xiv
LIST OF ABBREVIATIONS.....	xvi
CHAPTER 1: INTRODUCTION.....	1
Figures.....	12
CHAPTER 2: VARIABILITY IN THE STABLE ISOTOPE RATIOS OF GULF OF MAINE ZOOPLANKTON AND THEIR UTILITY IN STUDYING BALEEN WHALE MIGRATION.....	14
Abstract.....	15
Introduction.....	17
Materials and Methods.....	22
Results.....	28
Discussion.....	31
Conclusions.....	38
Acknowledgements.....	39
Tables.....	40
Figures.....	46

CHAPTER 3: STABLE ISOTOPE RATIOS OF BALEEN AS INTRINSIC MARKERS OF NORTH ATLANTIC RIGHT WHALE MIGRATION.....	55
Abstract.....	56
Introduction.....	58
Materials and Methods.....	64
Results.....	71
Discussion.....	75
Conclusions.....	84
Acknowledgements.....	85
Tables.....	87
Figures.....	92
 CHAPTER 4: EXAMINING LONG-TERM HABITAT USE AND THE INFLUENCE OF ENVIRONMENTAL CHANGE ON STABLE ISOTOPE RECORDS IN NORTH ATLANTIC RIGHT WHALE BALEEN.....	 108
Abstract.....	109
Introduction.....	111
Materials and Methods.....	112
Results and Discussion.....	117
Conclusions.....	126
Acknowledgements.....	128
Tables.....	129

Figures.....	133
APPENDIX 1: ZOOPLANKTON STABLE ISOTOPE RATIOS.....	149
APPENDIX 2: RIGHT WHALE BALEEN STABLE ISOTOPE RECORDS.....	158
LITERATURE CITED.....	178
CURRICULUM VITAE.....	195

LIST OF TABLES

Chapter 2

Table 2.1	Overview of zooplankton tows.....	40
Table 2.2	Spatial variation in Gulf of Maine zooplankton stable isotope ratios.....	42
Table 2.3	Temporal variation of Gulf of Maine zooplankton isotopes.....	43
Table 2.4	Trophic enrichment of zooplankton: oxygen.....	45

Chapter 3

Table 3.1	Right whale life history data and baleen sampling plan.....	87
Table 3.2	Elemental abundances and stable isotope ratios in right whale baleen.....	89
Table 3.3	Growth rates of adult right whale baleen.....	90
Table 3.4	Trophic enrichment between right whales and zooplankton, by habitat.....	91

Chapter 4

Table 4.1	Right whale life history data and baleen sampling plan.....	129
Table 4.2	Elemental abundances and stable isotope ratios in right whale baleen.....	130
Table 4.3	Statistical comparisons of historical and present-day right whale baleen isotope ratios.....	131

LIST OF FIGURES

Chapter 1

- Figure 1.1 Map of primary right whale habitats and timeline of seasonal habitat use.....12

Chapter 2

- Figure 2.1a-b The Gulf of Maine: study area and tow locations.....46

- Figure 2.2 $d^{13}C$ lipid normalization of zooplankton samples.....48

- Figure 2.3 Spatial trends in Gulf of Maine zooplankton: carbon and nitrogen isotopes.....49

- Figure 2.4 Spatial trends in Gulf of Maine zooplankton: oxygen and hydrogen isotopes.....51

- Figure 2.5a-f Contour maps of the Gulf of Maine isotope landscape.....53

Chapter 3

- Figure 3.1 Map of right whale habitat areas in the northwest Atlantic.....92

- Figure 3.2 Adult right whale baleen stable isotope records.....94

- Figure 3.3 Immature right whale stable isotope records.....96

- Figure 3.4 Calf right whale stable isotope records.....98

- Figure 3.5 Habitat-specific trophic enrichment between zooplankton and right whales: $d^{13}C$ and $d^{15}N$100

- Figure 3.6 Trophic enrichment between lactating females and right whale calves.....102

- Figure 3.7 Stable isotopes as a tracer of right whale migration.....104

- Figure 3.8 Demographic separation of stable isotope ratios in right whales.....106

Chapter 4

Figure 4.1	Nitrogen and carbon stable isotope ratios in right whale baleen, 1882-2005.....	133
Figure 2.2	Carbon and nitrogen stable isotope values of historical (1882-1915) vs. present-day (1986-2005) baleen plates.....	135
Figure 4.3	Atmospheric carbon dioxide concentrations: 1832-2005.....	137
Figure 4.4	Nitrogen and carbon stable isotope measurements of right whale baleen: 1986-2005.....	139
Figure 4.5	Trends in atmospheric and oceanic carbon dioxide.....	141
Figure 4.6	Right whale migration patterns.....	143
Figure 4.7	Right whale reproductive success.....	145
Figure 4.8	Climatic oscillations: NAO, AMO, PDO, ENSO.....	147

LIST OF ABBREVIATIONS

AMO	Atlantic Multi-decadal Oscillation
ANOVA	Analysis of variance
BoF	Bay of Fundy
°C	Celsius
C	Carbon
C5	<i>Calanus finmarchicus</i> , fifth stage copepodite
CCB	Cape Cod Bay
<i>C. finmarchicus</i>	<i>Calanus finmarchicus</i>
cm	Centimeter
CO	Carbon monoxide
CO ₂	Carbon dioxide
CPR	Continuous Plankton Recorder
CTD	Conductivity-Temperature-Depth instrument
D	Deuterium
DIC	Dissolved inorganic carbon
<i>E. glacialis</i>	<i>Eubalaena glacialis</i>
ENSO	El Niño Southern Oscillation
GC	Gas chromatograph
GoM	Gulf of Maine
GSC	Great South Channel
GSL	Gulf of St. Lawrence

H	Hydrogen
H ₂ O	Water
IRMS	Isotope ratio mass spectrometer
JL	Jeffrey's Ledge
km	Kilometers
LSW	Labrador Slope Water
m	Meter
µg	Microgram
mg	Milligram
ml	Milliliter
mm	Millimeter
MOCNESS	Multiple Opening and Closing Net Environmental Sensing System
<i>n</i>	Sample size
N	Nitrogen
N ₂	Atmospheric nitrogen
NAO	North Atlantic Oscillation
NEGB	Northeast peak of Georges Bank
O	Oxygen
PDB	PeeDee Belemnite
PDO	Pacific Decadal Oscillation
RB	Roseway Basin
SD	Standard deviation

SE	Standard error
SEUS	Southeast United States
SLW	Slope water
SST	Sea surface temperature
SSW	Scotian Shelf Water
VSMOW	Vienna Standard Mean Ocean Water
WSW	Warm Slope Water
yr	Year

CHAPTER 1

INTRODUCTION

Motivation

Despite protection from targeted commercial whaling, North Atlantic right whales (*Eubalaena glacialis*) remain one of the world's most endangered species (IWC 2001a). Studies of North Atlantic right whale demography have shown that, given its small population size, even single mortality events are significant. Therefore preventing the deaths of two females per year could considerably reduce the species' mortality rate and extinction probability (Fujiwara and Caswell 2001). In light of this analysis, a string of right whale mortalities that occurred between February 2004 and May 2005 greatly alarmed researchers (see Kraus et al. 2005). In that sixteen month period, eight whales were found dead, three of which were carrying full term fetuses (Right Whale Consortium 2008a). Five of these cases could be attributed to human activities, as diagnostic necropsies demonstrated that the whales were killed by vessel strike or fishing gear entanglements (Moore et al. 2006, Campbell-Malone et al. 2008).

Vessel strikes and entanglement in fishing gear are the primary forms of large whale anthropogenic mortality (Knowlton and Kraus 2001, Moore et al. 2005, Nelson et al. 2007), and these sources account for 64% of documented right whale mortalities¹ (Right Whale Consortium 2008a). Additionally, 75.6% of right whales bear scars indicative of interactions with fishing gear (Knowlton et al. 2005), suggesting that few right whales have escaped an encounter with gear and that entanglements are likely under-reported. In addition to the conservation risk they pose, these forms of anthropogenic mortality are also issues of animal welfare. For example, observations of

¹ Statistic calculated from post-mortem examinations of 42 right whale carcasses between 1970 and 2007 (Right Whale Consortium 2008a).

free-ranging whales and post-mortem examinations of carcasses have demonstrated that whales can die slowly from both classes of mortality, especially gear entanglements (Moore et al. 2005, Moore et al. 2006, Campbell-Malone et al. 2008).

Researchers and managers agree that reducing anthropogenic mortalities is of the highest priority for right whale recovery plans (Kraus et al. 2005, NMFS 2005). Yet, the implementation of effective conservation measures has been slow given the socio-economic impact of regulating the activities of fishing and shipping industries. In order to draft effective management plans that can reconcile the interests of these industries with the ultimate goals of whale conservation, accurate and detailed information regarding where and when right whales occur is needed.

With respect to our understanding of right whale ecology, significant knowledge gaps in the areas of migratory connectivity and habitat use exist despite directed research effort since the 1980s. Given the population's small size and high anthropogenic mortality rate, this is concerning. Since conservation and management initiatives are only as sound as the science upon which they are based, these knowledge gaps are a significant hindrance to successful right whale conservation efforts. In an attempt to close this knowledge gap, a multi-year study was conducted to describe the stable isotope geochemistry of baleen in order to infer patterns of right whale migration. By way of general introduction to this study, the following chapter outlines important information about North Atlantic right whales and stable isotope geochemistry as a method for studying animal migration.

Right Whales: Worldwide Status and Taxonomy

Right whales (genus *Eubalaena*) are a group of mysticete cetaceans characterized by a robust body, broad paddle-like flippers, a narrow and arched upper jaw with a deeply curved jawline, long (~2 m) baleen plates, and a large head relative to their body size (which comprises 30% of their total length) (Kenney 2002). Three right whale species are currently recognized: *Eubalaena australis* (Southern right whales), *Eubalaena japonica* (North Pacific right whales), and *Eubalaena glacialis* (North Atlantic right whales) (Rosenbaum et al. 2000). All three species were targeted in various commercial whaling efforts, and were prized for their high yield of oil and baleen, coastal distribution, and fairly slow swimming speeds. Each species was heavily exploited, such that all were significantly depleted by the beginning of the twentieth century (Tormosov et al. 1998, Clapham et al. 2004, Reeves et al. 2007).

The recovery success of right whales since targeted whaling activities ceased has been species dependent. The different degrees of recovery likely stem from: the varied intensity and timing of exploitation, the degree of industrialization in each species' primary habitat areas, each population's pre- and post-exploitation genetic diversity, the occurrence and severity of disease within each population, and regional differences in food availability (IWC 2001a). Southern right whales have demonstrated the strongest recovery; and the extant population is estimated at 7,500 individuals with a 7-8 % annual growth rate (IWC 2001b). By contrast, North Pacific right whales are so rare (with a population estimate in the dozens to low hundreds) that individual sightings are worthy of publication (e.g. Rowntree et al. 1980, Tynan et al. 2001). Although North Atlantic right

whales were once prolific on both sides of the Atlantic, today right whales in the eastern Atlantic are scarce (Brown 1986). A small relict population, estimated at 400 individuals (Right Whale Consortium 2007), is found in the western North Atlantic. Given these approximations of population size, North Pacific and North Atlantic right whales are considered the most endangered species of large whales in the world due to their apparent lack of recovery despite several decades of international protection from commercial harvest (Clapham et al. 1999).

North Atlantic Right Whales²

Population Biology

In addition to a high anthropogenic mortality rate, a reduced reproductive rate is a major factor hindering right whale recovery (Kraus et al. 2005). Right whale reproductive and population biology are characterized by a low overall reproductive rate, high degree of variability in annual calf production and inter-annual calving intervals, and a significant number of nulliparous adult females (Kraus et al. 2007). Although stereotypical right whale calving events occur on three year cycles (including one year of gestation (Best 1994), approximately one year of lactation (Hamilton et al. 1995), and a year of rest before a subsequent pregnancy) female right whales have experienced longer calving intervals on average. The mean calving interval for the population has also been variable. It is hypothesized that limitations in food availability, disease, and the consequences of low genetic variability are potential factors contributing to the poor

² Given the focus of this dissertation, the term “right whale” will herein refer to the northwest Atlantic stock of *Eubalaena glacialis*

reproductive success of the right whale population (Greene and Pershing 2004, Frasier et al. 2007, Kraus et al. 2007).

Foraging Ecology

Right whales are zooplankton specialists, and feed primarily on the calanoid copepod *Calanus finmarchicus* (Murison and Gaskin 1989, Mayo and Marx 1990, Beardsley et al. 1996, Baumgartner and Mate 2003). *C. finmarchicus* is the dominant copepod species of the boreal North Atlantic, and is characterized by a life history cycle that includes a resting stage known as diapause. In preparation for diapause, late stage copepodites sequester lipids in a membrane-bound organelle (oil sac). The oil sac grows as lipids accumulate, and can eventually fill over half of the volume of the body (Miller et al. 1998), making *C. finmarchicus* an energy rich prey item. During diapause, fifth stage copepodites (C5) migrate to depth and enter a state of arrested development which allows them survive periods of low food availability (Hirche 1996).

In contrast to other mysticete cetaceans, right whales exhibit no behaviors that serve to corral their food; instead they rely completely on the environment (or the zooplankton themselves) to concentrate their prey into dense, exploitable patches (Baumgartner et al. 2007). Right whale feeding behavior is quite basic; an individual simply opens its mouth and swims forward. The hundreds of baleen plates in a whale's mouth filter zooplankton from the water column in a very efficient manner (Werth 2007). Right whales have been observed feeding in this manner at the surface (known as skim feeding, Mayo and Marx 1990) or at various depths below the surface. Using suction-cup

mounted time-depth-recorder tags, Baumgartner and Mate (2003) demonstrated that during sub-surface feeding bouts, right whales foraged on thin dense layers of C5s, which were often concentrated at the bottom mixed layer. In both surface and sub-surface feeding scenarios, right whales seem highly attuned to the density of plankton in their feeding path and modify their depth or trajectory in order to exploit the densest patches of plankton.

Distribution and Migration

For a significant portion of each year, North Atlantic right whales are found in the coastal waters of the eastern United States and Canada. Four primary feeding habitats are used seasonally by a large proportion of the right whale population (Fig. 1.1). These include: Cape Cod Bay (CCB, from January – April), the Great South Channel (GSC, from April – July), the lower Bay of Fundy (BoF, from July – October), and Roseway Basin (RB, from July – October) (Kraus et al. 1986a, Winn et al. 1986, Murison and Gaskin 1989, Hamilton and Mayo 2001 Hamilton et al. 2007). Right whales are also found, in fewer numbers, in: Chaleur Bay/Gulf of St. Lawrence (GSL, in the summer and fall, Y. Guilbault, pers. comm.); Jeffrey's Ledge (JL, from October – November, Weinrich et al. 2000); the northeastern flank of Georges Bank (NEGB, in the summer months, Niemeyer et al. 2008); and the central GoM (winter months, Cole et al. 2007). The only known calving ground is located in the southeast US (SEUS), in the coastal waters off Georgia and Florida, and is occupied from November – February (Kraus et al. 1986a, Hamilton et al. 2007).

Analyses of multiple datasets (including survey, photo-ID/mark-recapture, and genetic) suggest that right whales may use areas which are ancillary to their recognized habitats. Five right whale habitats (Cape Cod Bay, Great South Channel, Bay of Fundy, Roseway Basin, and southeast US) are protected, to various degrees, by management rulings such as vessel speed restrictions, re-routed shipping lanes, or fishing gear modifications. The characterization and monitoring of additional habitats has been cited as a research priority by managers (NMFS 2005). Given the high level of anthropogenic mortality that is already observed in the North Atlantic right whale population, a better understanding of right whale distribution, and the threats they face therein, is urgently needed to improve their conservation and recovery potential.

Stable Isotope Geochemistry

Stable isotope analysis has become an established method for examining the flow of nutrients through ecosystems (Peterson and Fry 1987), and many studies utilize it to reconstruct trophic relationships (Kelly 2000). Organisms acquire stable isotope signatures from their diet and the isotopic value of animal tissues are predictably enriched compared to those of their food source (DeNiro and Epstein 1978, 1981). Additionally, stable isotope values in the environment, which are controlled by a variety of abiotic factors, are incorporated into food webs by producers (Rubenstein and Hobson 2004). Therefore, stable isotope data can provide a metric of what and where an animal has recently eaten.

The tissue that is chosen for stable isotope analysis determines what kinds of ecological questions a study can answer. Since the degree of a tissue's metabolic activity dictates its isotopic turnover rate, tissues like blood and liver having fast turnovers (on the order of days to weeks) representing short feeding histories, and tissues like skin and muscle having slower turnovers (weeks to months) and integrating longer feeding histories. In contrast, the stable isotope values of metabolically inactive tissues, such as keratin structures, do not change after they are formed (Hobson 2005). New growth is tagged by the most recently acquired food source. Accreting keratin structures, such as hair, baleen, claws, and feathers, can therefore become temporal records of stable isotope ratios if they are sampled incrementally (Bowen et al. 2005b).

Baleen, composed of keratin, is an ideal tissue for stable isotope analysis. It is metabolically inactive, and is formed from blood metabolites (amino acids) and thus new growth responds relatively quickly to dietary changes (Ayliffe et al. 2004). It accretes continuously over each year (Lubetkin et al. 2008) yet also wears away at the tip such that the longest plates in some species contain over ten years of isotope data, thus providing a decadal-scale record of migration behavior.

Large whales are well suited for isotope studies because they consume large amounts of prey over extensive areas, thereby incorporating the seasonal and geographic variations of stable isotopic ratios of their prey into their own tissues as they move from one region to another. Previous studies have applied stable isotope analysis to the baleen of gray (Caraveo-Patino and Soto 2005, Caraveo-Patino et al. 2007), minke (Mitani et al. 2006), bowhead (Schell et al. 1989, Schell and Saupe 1993), and Southern right whales

(Best and Schell 1996); and have demonstrated the utility of this approach for describing annual movement patterns. In all mysticete species studied to date, annual oscillations in the carbon and nitrogen stable isotope ratios of baleen have been observed. These oscillations can be differentiated into seasonal nutritional sources, corresponding to observed annual migrations by each whale species between high and low latitude habitats. Stable isotope measurements have been useful in determining residence time or the relative amount of nutrition each whale species derives from its respective seasonal habitats (Lee et al. 2005).

Two preliminary studies measured stable isotope ratios in baleen collected from a total of six individual North Atlantic right whales (Wetmore 2001, Summers et al. 2006). Both studies observed annual oscillations in baleen carbon and nitrogen stable isotope ratios, but were unable to resolve right whale migration behavior at small spatial or short temporal scales. Akin to previous studies with the baleen from other species, these analyses were only been able to differentiate movement of individuals between winter and summer habitats. In the following study, additional stable isotope ratios will be measured in baleen collected from a greater number and diversity of individuals, and migration behavior will be examined at finer scales.

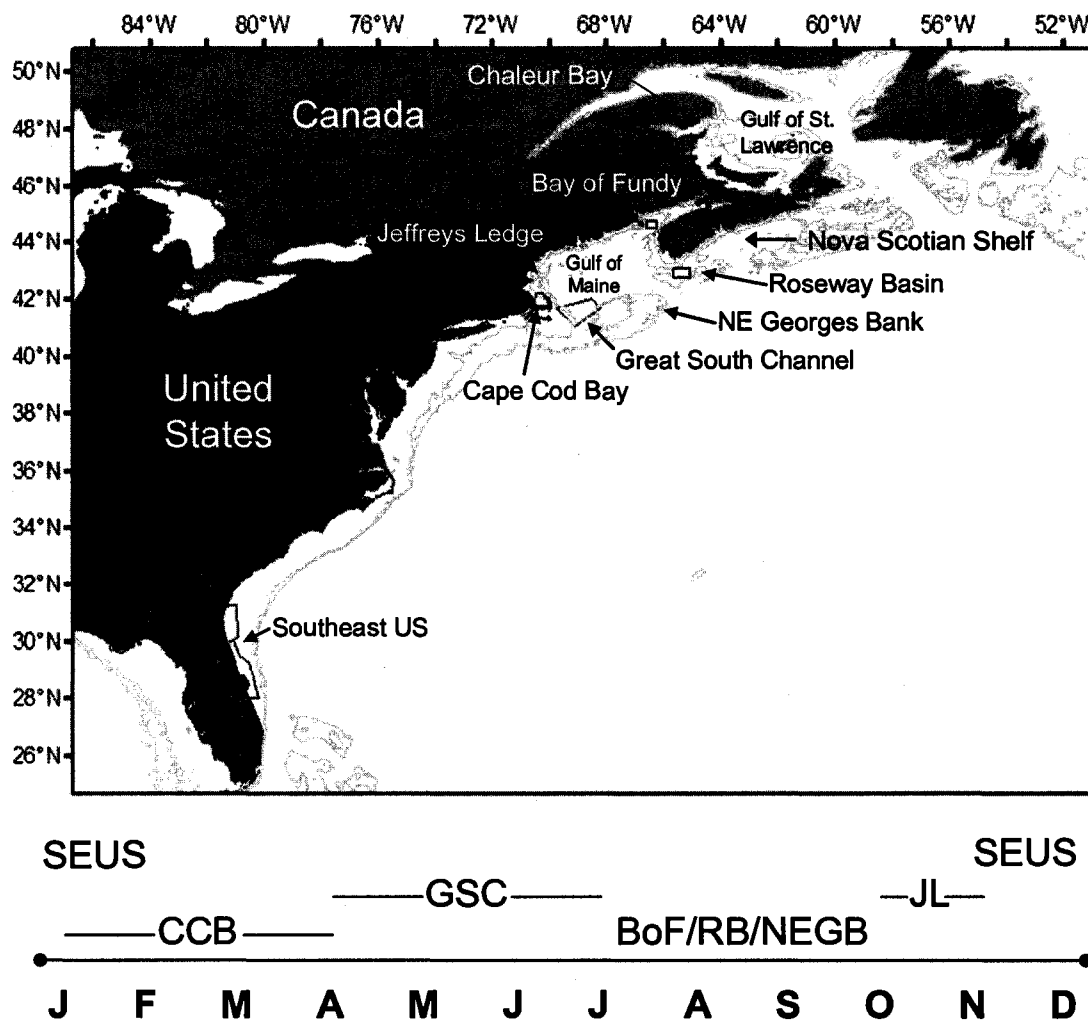
Dissertation Overview

This dissertation examines stable isotope ratios in baleen and zooplankton, as they relate to North Atlantic right whale migration and habitat use. It is composed of four

sections: **(1)** Characterization of the spatial and temporal variability in the C, N, O, and H stable isotope values of zooplankton collected in the Gulf of Maine; **(2)** Examination of the trends and patterns of stable isotope ratios in right whale baleen plates; **(3)** Comparison of baleen stable isotope signatures with right whale biological data such as age, reproductive events, and sighting records; **(4)** Comparison of baleen stable isotope signatures collected from present-day and historical specimens.

Figure 1.1: Map of Primary Right Whale Habitats and Timeline of Seasonal Habitat Use. Four habitats in the Gulf of Maine (Cape Cod Bay, Great South Channel, Bay of Fundy, and Roseway Basin) and the only known calving ground (southeast US) are demarcated by polygons. Two other important habitat areas, Jeffreys Ledge Chaleur Bay, and the northeast peak of Georges Bank, are shown with arrows. The timeline below the map outlines the seasonal occupation of these habitats by right whales. Cape Cod Bay (CCB) is used from January – April, Great South Channel (GSC) is used from April – July, the Bay of Fundy/Roseway Basin/NE Georges Bank are used from July – October, Jeffreys Ledge (JL) is used from October – November, and the southeast US (SEUS) is used from November – February.

Figure 1.1: Map of primary right whale habitats and timeline of seasonal habitat use



CHAPTER 2

**VARIABILITY IN THE STABLE ISOTOPE RATIOS OF GULF OF MAINE
ZOOPLANKTON AND THEIR UTILITY IN STUDYING BALEEN WHALE
MIGRATION**

ABSTRACT

Stable isotope analysis of animal tissues can be used as an intrinsic marker of migration, but this method relies on the unambiguous identification of the isotopic landscape over which an animal roams and derives nutrition. Several basin-scale carbon, nitrogen, oxygen, and hydrogen stable isotope landscapes have been described for the greater North Atlantic, demonstrating the large isotope gradients present in the marine environment. While these gradients can be exploited to examine the high-low latitude migrations of many nektonic species, it is unclear if there is enough variation between individual seasonal feeding habitats for resolving animal movement patterns at smaller spatial/temporal scales using stable isotopes. The zooplanktivorous North Atlantic right whale (*Eubalaena glacialis*) and its foraging habitats in the Gulf of Maine (northwest Atlantic) were examined as a system with which to assess the utility and limitations of stable isotope analysis as a method to assess seasonal baleen whale migration.

To examine the spatial and temporal variation of the Gulf of Maine stable isotope landscape, zooplankton samples were collected from 1998-2007 at seven sites, four of which are recognized *E. glacialis* seasonal feeding habitats. Carbon and nitrogen stable isotopes were measured in all samples, while oxygen and hydrogen isotopes were measured in a subset of the samples. Of the seven areas sampled, three habitat areas (Cape Cod Bay, Great South Channel, and the Bay of Fundy) represented isotopically distinct habitats, and these differences were more pronounced when examining multiple isotopes. The results of this study demonstrate that habitat-specific zooplankton isotope values can be differentiated within the Gulf of Maine feeding ground. However, within

habitat inter-annual temporal variation in the stable isotope ratios was greater than the differences between mean regional isotope values in some areas. This points to the need to temporally couple animal and diet/environmental isotope measurements when conducting stable isotope investigations of animal migration for accurate assessments of habitat use.

INTRODUCTION

Stable isotope analysis has proven to be a practical method for describing trophic dynamics in various food webs (Michener and Schell 1995), and as an intrinsic marker of animal migration (Hobson 2007). To that end, studies utilizing stable isotope geochemistry to track the migration habits of wildlife, especially in the marine environment, have increased substantially in recent decades. This method has enhanced our understanding of the movement patterns and foraging ecology of often cryptic marine predators such as sharks (Kerr et al. 2006), cetaceans (Schell et al. 1989a, Best and Schell 1996, Mitani et al. 2006, Caraveo-Patino et al. 2007), pinnipeds (Burton and Koch 1999, Kurle and Worthy 2001, Tucker et al. 2007), and seabirds (Hobson et al. 2004, Kakela et al. 2007).

Since stable isotope values of most consumer tissues are derived from their diet, the identification of the isotopic landscape over which an individual roams and derives nutrition is necessary for the successful application of stable isotope analysis in animal migration studies (Rubenstein and Hobson 2004). Delineating unambiguous stable isotope values to an animal's specific foraging habitats can be difficult, as these signals may vary over several spatial and/or temporal scales (Matthews and Mazumder 2005). Previous studies using stable isotopes as migration tracers in the marine environment have been most successful in cases where habitat areas exhibit a high degree of isotopic contrast (e.g. marine vs. estuarine, inshore vs. offshore, high vs. low latitude; Hobson 2007).

Several broad-scale carbon, nitrogen, oxygen, and hydrogen stable isotope landscapes have been described recently for the North Atlantic (Schmidt et al. 1999, Englebrecht and Sachs 2005, McMahon et al. in prep.), each of which demonstrate that large gradients are present. Given the high degree of spatial variation in stable isotope ratios found in the marine environment, either in seawater or at low trophic levels such as plankton, it is reasonable to hypothesize that an animal feeding and traveling over large geographic distances in the North Atlantic would encounter a significant range of isotope values along its migration route. Therefore, migration studies using stable isotope analysis might be successfully implemented in the North Atlantic ecosystem.

The conservation plans for several threatened marine mammal, fish, and seabird species hinge on the understanding of their habitat range and migration behavior. In the case of marine mammals, specifically baleen whales (mysticetes), many populations exhibit complex migration patterns that can be examined at multiple spatial and temporal resolutions. At large spatial (1000s of km) and temporal (annual) scales, several mysticete species feed in the productive coastal waters of the North Atlantic during the spring and summer months, and then migrate to lower latitudes for calving during the winter (Bowen and Siniff 1999). At smaller spatial (100s of km) and temporal (seasonal) scales, baleen whales often migrate between habitat areas within a “feeding ground” (Kraus et al. 1986, Winn et al. 1986, Clapham 2000). Although observational studies have given much insight into the migration behavior of whales at both of these spatial and temporal scales, the movement of these animals at even finer scales has been difficult to resolve.

While the basin-scale variation in North Atlantic stable isotope ratios can be exploited to examine the high-low latitude migrations of baleen whales, it is unclear if there is enough variation between individual seasonal feeding habitats for resolving the movement patterns of cetaceans at smaller spatial/temporal scales with stable isotopes. The zooplanktivorous North Atlantic right whale (*Eubalaena glacialis*) and its foraging habitats in the Gulf of Maine (northwest Atlantic) were used as a system with which to examine the utility and limitations of stable isotope analysis as a method to study baleen whale migration. This dissertation chapter describes an investigation of the carbon, nitrogen, oxygen, and hydrogen stable isotope landscape present in zooplankton collected from several regions, including known right whale seasonal feeding habitats, within the Gulf of Maine.

Study Area

The Gulf of Maine (GoM), a semi-enclosed continental shelf sea situated between the northeastern United States and southwest Nova Scotia (Fig. 1a), is the primary feeding ground for North Atlantic right whales (Winn et al. 1986). The majority of the right whale population migrates between several habitats within the Gulf from the late winter to early fall (March – October). Right whales feed exclusively on zooplankton, primarily *Calanus finmarchicus*, a calanoid copepod which dominates the zooplankton biomass in the North Atlantic (Meise and O'Reilly 1996). Specifically, right whales target fifth stage *C. finmarchicus* copepodites (C5) and their occupation of seasonal habitats within the GoM often coincides with peak C5 abundance (Baumgartner et al.

2007). C5s are known to sequester lipids in a membrane-bound oil sac in preparation for a resting state known as diapause (Hirche 1996). The oil sac becomes larger as lipids accumulate, and the sac can eventually fill to over half of the volume of a copepod's body (Miller et al. 1998). Zooplankton samples collected near feeding right whales in several habitats within the GoM have been near mono-specific *C. finmarchicus* and they represent a significant caloric energy source (Murison and Gaskin 1989, Wishner et al. 1995, Baumgartner et al. 2003, Michaud and Taggart 2007).

The average bottom depth in the GoM is 150m, while several basins exceed 200m. These basins are relatively isolated from one another below the 200m isobath (O'Reilly and Zetlin 1998). Numerous shoals and banks restrict flow between the GoM and the greater North Atlantic, thereby making the GoM a nearly self-contained oceanographic system (Townsend 1998). The prevailing currents move counterclockwise around the Gulf. This circulation pattern is driven by shallow freshwater inputs, the advection of deep water through the Northeast Channel, and amplified tides (Garrett et al. 1978, Smith 1983, Butman and Beardsley 1987). Shallow water entering the GoM is composed of freshwater originating from the Gulf of St. Lawrence (which flows in over the Scotian Shelf) and run-off from numerous rivers in Maine and the Bay of Fundy (Smith et al. 2001). Slope water is the primary deep water mass that enters the Gulf through the Northeast Channel, at depths greater than 100m (Brooks 1985). This circulation scheme may establish differences in the stable isotope signatures specific to "upstream" vs. "downstream" sub-regions within the GoM.

The Gulf of Maine is also situated in a highly dynamic oceanographic transition zone (MERCINA 2001), resulting in physical and biological variability at multiple temporal scales. At relatively long temporal scales (decadal to inter-annual), circulation into the GoM is associated with fluctuating climatic modes such as the North Atlantic Oscillation (NAO, Greene and Pershing 2003). Changes in the relative contribution of slope water sources (Warm Slope Water, WSW vs. Labrador Slope Water, LSW) to the GoM have been associated with phase changes in the NAO such that during positive NAO phases, relatively warm and salty WSW enters the Gulf through the Northeast Channel, while colder and fresher LSW dominates the deep water inflow in during negative NAO phases (Greene and Pershing 2003).

The dominant slope water source to the GoM may result in differential advection of *C. finmarchicus* into the Gulf (MERCINA 2004). A recent decrease in the abundance of *C. finmarchicus*, from 1996 – 2000, has been attributed to a sudden drop in the NAO Index and associated changes in slope water inputs to the GoM (Greene and Pershing 2000). Additionally, variable contributions of warm/salty or cold/fresh slope water may establish oceanographic conditions that cause differential survival of other zooplankton species (MERCINA 2001). Significant changes in zooplankton community composition resulting from variable slope water input could influence the year-to-year stable isotope data collected in each habitat area, especially if the community is altered in such a way that trophic dynamics or the relative trophic level of the zooplankton changes.

At shorter temporal scales (months to weeks), stable isotope values of GoM zooplankton may be affected by events that change the balance of nutrients available to

the food web. These include pulses of new nutrients to the upper ocean, such as increased river runoff, upwelling mixing processes, anthropogenic inputs, and changes in nitrogen sources/sinks (Townsend 1998, McMahon et al. in press.). Given the dynamic nature of the GoM, temporal variation in stable isotope ratios of zooplankton should be expected.

Study Aims

The aims of the study were (1) to characterize the extent of spatial variation in carbon, nitrogen, oxygen, and hydrogen stable isotope ratios within GoM zooplankton and (2) to describe temporal stability of habitat-specific zooplankton stable isotope values at inter-annual scales.

MATERIALS AND METHODS

Field Sampling

Net tows to collect zooplankton were conducted at seven sites in the northwest Atlantic, including several known right whale feeding habitats: Cape Cod Bay, Great South Channel, lower Bay of Fundy, Roseway Basin, Nova Scotian Shelf, the northeast peak (NE) of Georges Bank, and Jeffreys Ledge (Fig. 1a). The sampling plan was designed to incorporate ecological parameters relevant to North Atlantic right whales, since the results of this study will be used to inform an investigation into right whale migration using stable isotope analysis. Tows for zooplankton were linked spatially and temporally with right whale occupation of each area. Furthermore, zooplankton samples

were collected with dual 333 μm mesh nets, which best replicate the capture efficiency of right whale baleen (Mayo et al. 2001).

At six sites (Great South Channel, lower Bay of Fundy, Roseway Basin, Nova Scotian Shelf, NE Georges Bank, and Jeffreys Ledge), double oblique tows were performed using dual nets mounted on 61 cm diameter bongo frame. A Seabird model SBE19 conductivity-temperature-depth instrument (CTD) was affixed to the tow wire approximately 1 m above the bongo nets to relay the sampling depth back to the research vessel in real time. A General Oceanics helical flowmeter was mounted at the center of each bongo to estimate the volume of water filtered during the tow. The nets were lowered at 0.50 ms^{-1} to near bottom (within 5 m) and then hauled in at 0.33 ms^{-1} . The research vessel steamed at 1.5-2.0 knots during the tows. Once on deck, all nets were rinsed into a sieve, and zooplankton were gently removed from the screen. The contents from one net were placed into 50 ml Nalgene jars, which were subsequently frozen. The contents from the second net were preserved in a 10% borate-buffered formalin seawater solution and were archived for later sorting and enumeration.

In addition to the sampling described above, five tows in the Great South Channel (3 in 2005, 2 in 2006) were collected via a single oblique tow to near bottom with a 0.25 m^2 multiple opening-closing net and environmental sensing system (MOCNESS, Wiebe et al. 1976) outfitted with $150 \mu\text{m}$ mesh nets. Once on deck, the nets were rinsed and the concentrated zooplankton were removed from the mesh in the cod end. These samples were placed into 50 ml Nalgene jars, which were subsequently frozen.

In order to sample from within the most likely right whale prey field, surface tows were conducted in Cape Cod Bay as right whales primarily exhibit skim feeding behavior (Mayo and Marx 1990). These tows were collected with a single 333 μm net mounted on a 30 cm diameter metal ring. The net was towed behind the research vessel at approximately 2 knots for 5 minutes. Once on deck, all nets were rinsed into a sieve, and zooplankton were gently removed from the screen. The net contents were placed into 50 ml Nalgene jars, which were subsequently frozen.

Zooplankton samples were collected opportunistically in each habitat area, often in conjunction with other research institutions. This resulted in uneven sampling coverage of each habitat area. Zooplankton collections that took place between 1998-2001 are referenced from an existing thesis (Wetmore 2001), no collections occurred from 2002-2003, and samples from 2004-2007 were collected specifically for this study.

Laboratory Techniques

The samples from each tow were packaged in aluminum foil and dried at 60-80°C until sufficiently desiccated (after approximately 5 days). Each dried sample was then homogenized with a mortar and pestle, and the resulting powder was stored at room temperature in a sterile glass vial. Prior to carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis, 0.8-1.2 mg of each sample was packaged into a 4 X 6 mm tin capsule and crimped shut. All samples were sent to a stable isotope laboratory for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis (1998-2001 samples to the Boston University Stable Isotope Laboratory; 2004-2007 samples to the University of California Davis Stable Isotope Facility).

The samples were loaded into an autosampler and analyzed using an elemental analyzer interfaced to an isotope ratio mass spectrometer (IRMS). Instrumentation at the Boston University laboratory included a Fisons NA1500 elemental analyzer and Finnigan Conflo II interfaced to a Finnigan Delta S IRMS. Instrumentation at the UC Davis laboratory included a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 IRMS. Each sample was pyrolyzed into CO₂ and N₂ gas and then separated on a gas chromatograph (GC) column. The gases were conveyed to the IRMS with a continuous flow of helium carrier gas. Each sample isotope ratio was compared to a secondary gas standard, whose isotope ratio had been calibrated to international standards (PeeDee Belemnite (PDB) for $\delta^{13}\text{C}$, Craig 1957; and atmospheric nitrogen (N₂) for $\delta^{15}\text{N}$, Mariotti 1985).

The total C and N content of each sample were reported along with stable isotope data. C:N ratios and % C and N were calculated from the reported measurements of total C and N content in each sample.

Prior to oxygen ($\delta^{18}\text{O}$) and hydrogen (deuterium, δD) isotope analysis, 0.45-0.55 mg of each sample was weighed and packaged in duplicate into 3.5 X 5 mm silver capsules and crimped shut. All samples were sent to the University of California Davis Stable Isotope Facility for analysis. In order to control for issues related to hydrogen atom exchange, our samples were "air equilibrated" with ambient laboratory air moisture for 2 weeks prior to combustion (Wassenaar and Hobson 2003, Bowen et al. 2005a). After this incubation, samples were analyzed using a Heckatech HT Oxygen Analyzer interfaced to a PDZ Europa 20-20 IRMS. Samples were combusted to CO and H₂O, and

separated chromatographically, as described above. Each sample isotope ratio was compared to a secondary gas standard, whose isotope ratio had been calibrated to the international standard Vienna Standard Mean Ocean Water (VSMOW, Coplen 1994).

All samples are reported relative to international reference standards: carbon isotope values relative to PDB, nitrogen values relative to N₂, and oxygen and hydrogen values relative to VSMOW. Stable isotope measurements are expressed in standard delta (δ) notation, as parts per thousand (per mil, ‰), by the following:

$$\delta^{13}\text{C}, \delta^{15}\text{N}, \delta^{18}\text{O}, \text{ or } \delta\text{D} (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1,000$$

where R_{sample} and R_{standard} are the ratios of ¹³C/¹²C, ¹⁵N/¹⁴N, ¹⁸O/¹⁶O, or ²H/¹H of the sample and standard, respectively (McKinney et al. 1950).

Analytical precision was determined with laboratory working standards of glycine ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), cellulose ($\delta^{18}\text{O}$), and polyethylene (δD), which were analyzed after every 12 zooplankton samples. These standards were calibrated against NIST Standard Reference Materials. Precisions based on the standard deviation of the series of reference checks used in the analysis are as follows: $\delta^{13}\text{C}$ (0.05‰); $\delta^{15}\text{N}$ (0.20‰); $\delta^{18}\text{O}$ (0.43‰); and δD (4.0‰)³.

To control for issues related to hydrogen atom exchange (Bowen et al. 2005a), all sample hydrogen isotope measurements were corrected relative to a laboratory standard,

³ These measurements of precision apply to samples collected from 2004-2007, analyzed at the UC Davis Stable Isotope Facility. Samples collected between 1998 and 2001 were analyzed at the Boston University Stable Isotope Laboratory, which reports an analytical precision of < 0.1 ‰ for carbon and nitrogen isotope measurements.

bowhead whale baleen (BWB2, -105‰). This standard was calibrated against NIST Standard Reference Materials. One BWB2 sample was run for every 24 zooplankton samples.

Data Analysis

$\delta^{13}\text{C}$ data were lipid normalized to examine the potential confounding effect of variable lipid content in our samples, as lipids are depleted in ^{13}C relative to proteins (DeNiro and Epstein 1978). The data were corrected by C:N ratio, which is positively correlated with lipid content (Schmidt et al. 2003). The following equations were used to determine a lipid normalized $\delta^{13}\text{C}$ value for each zooplankton sample ($\delta^{13}\text{C}_{\text{LN}}$).

$$L = 93 / [1 + (0.246 \text{ C:N} - 0.775)^{-1}]$$

$$\delta^{13}\text{C}_{\text{LN}} (\text{‰}) = \delta^{13}\text{C}_{\text{raw}} (\text{‰}) + D [-0.207 + 3.90 / (1 + 287 / L)]$$

where L is a calculation of tissue lipid content, D is the isotopic difference between lipid and protein (estimated at 6 ‰) and $\delta^{13}\text{C}_{\text{raw}}$ refers to uncorrected $\delta^{13}\text{C}$ data (McConnaughey and McRoy 1979).

Statistical analysis was conducted with JMP IN software for Windows.

Zooplankton stable isotope and C:N ratios were compared using one-way ANOVA coupled with Tukey-Kramer HSD post hoc tests or Student's t-tests. Differences in zooplankton stable isotope and C:N ratios among all habitat areas, as well as differences between years within individual habitats were examined.

Referenced Datasets

The NASA Global Seawater Oxygen-18 Database

(<http://data.giss.nasa.gov/o18data/>, Schmidt et al. 1999) was referenced in order to investigate trophic fractionation of oxygen isotopes from seawater to zooplankton. Data associated with seawater samples collected near the Gulf of Maine were acquired from this database, and then compared to zooplankton collected in the Gulf.

RESULTS

The stable isotope ratios of 128 zooplankton tows, collected at seven distinct sites from 1998-2007, were examined in this study (Table 2.1, Fig. 2.1b). The areas identified as seasonal right whale habitats (Cape Cod Bay, Great South Channel, Bay of Fundy, and Roseway Basin) received multi-year sampling coverage, while other areas (Nova Scotian Shelf, NE Georges Bank, and Jeffreys Ledge) were sampled with less frequency. The stable isotope values of samples from all collection habitats/years ranged from -26.86 to -19.46‰ ($\delta^{13}\text{C}_{\text{raw}}$), -25.15 to -18.13‰ ($\delta^{13}\text{C}_{\text{LN}}$), 4.56 to 10.35‰ ($\delta^{15}\text{N}$), 15.07 to 31.55‰ ($\delta^{18}\text{O}$), and -183.06 to -101.32‰ (δD).

Lipid Content and Normalization

Zooplankton C:N ratios from all habitats/years ranged from 3.37 to 11.68, and significant differences between regions were measured (one way ANOVA, $F = 3.36$, $p = 0.004$, Table 2.2). Bay of Fundy zooplankton had higher C:N ratios than Nova Scotian

Shelf zooplankton, and all other areas were statistically indistinguishable. After lipid normalization, zooplankton $\delta^{13}\text{C}_{\text{CLN}}$ values were enriched relative to $\delta^{13}\text{C}_{\text{raw}}$ values in cases where the C:N ratio was > 4 (98% of all cases). $\delta^{13}\text{C}_{\text{CLN}}$ were depleted relative to $\delta^{13}\text{C}_{\text{raw}}$ in 3 cases, where the sample C:N ratio was < 4 (denoting a lower than normal lipid content of the sample, McConnaughey & McRoy 1979). The difference between $\delta^{13}\text{C}_{\text{CLN}}$ and $\delta^{13}\text{C}_{\text{raw}}$ was positively related to C:N ratio (Fig. 2.2).

Inter-annual variation in zooplankton C:N ratios within each habitat area were examined, and Cape Cod Bay (one way ANOVA, $F = 3.87$, $p = 0.044$), the Bay of Fundy (one way ANOVA, $F = 41.43$, $p = < 0.0001$), and Roseway Basin (one way ANOVA, $F = 17.23$, $p = 0.0008$) exhibited statistically different values between collection years (Table 2.3, Appendix 1).

Spatial Variation

Data from multiple sampling years, within each habitat area, were pooled to identify regional $\delta^{13}\text{C}_{\text{raw}}$, $\delta^{13}\text{C}_{\text{CLN}}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$, and δD signatures. There were significant differences in zooplankton stable isotope values between several regions sampled (Table 2.2). Zooplankton $\delta^{13}\text{C}$ values from Cape Cod Bay, the Great South Channel and the Bay of Fundy were statistically different (one way ANOVA, $\delta^{13}\text{C}_{\text{raw}}$: $F = 11.94$, $p < 0.0001$; $\delta^{13}\text{C}_{\text{CLN}}$: $F = 15.89$, $p < 0.0001$; Fig. 2.3). Roseway Basin, Nova Scotian Shelf, and NE Georges Bank $\delta^{13}\text{C}$ values were indistinguishable from Great South Channel/Bay of Fundy (however, note that the zooplankton $\delta^{13}\text{C}_{\text{raw}}$ of the Nova Scotian Shelf was grouped with the Bay of Fundy while $\delta^{13}\text{C}_{\text{CLN}}$ was grouped with Great South Channel/Bay of

Fundy, Fig. 2.3). Jeffreys Ledge $\delta^{13}\text{C}$ was statistically indistinguishable from all habitats areas (Fig. 2.3). There were no differences in the zooplankton $\delta^{15}\text{N}$ values among all habitats sampled (one way ANOVA, $F = 1.36$, $p = 0.24$, Fig. 2.3). $\delta^{18}\text{O}$ values in Great South Channel were significantly lighter than those in Cape Cod Bay/Bay of Fundy/Roseway Basin/NE Georges Bank, while those from Jeffreys Ledge were indistinguishable from all other habitats (one way ANOVA, $F = 7.07$, $p < 0.0001$, Fig. 2.4). δD values in the Great South Channel/NE Georges Bank were statistically different than the Bay of Fundy, while Roseway Basin was similar to all areas sampled (one way ANOVA, $F = 6.92$, $p = 0.0004$, Fig. 2.4). These data are also presented as color contour maps, which illustrate the interpolated spatial variation of stable isotope and C:N ratios across the entire GoM (Fig. 2.5a-f).

Oxygen Fractionation

The mean of GoM seawater $\delta^{18}\text{O}$ values referenced for this study was -1.2‰ ($n = 22$, $SD = 0.6$), while the mean of GoM zooplankton $\delta^{18}\text{O}$ values was 21.7‰ ($n = 58$, $SD = 3.1$). The net trophic enrichment ($\delta^{18}\text{O}_{\text{zooplankton}} - \delta^{18}\text{O}_{\text{seawater}}$) for this system was 22.9‰ (Table 2.4).

Temporal Variation

The inter-annual variation in zooplankton stable isotope values was examined in habitats where multiple years of sampling occurred, and statistically significant differences between years existed in multiple habitat areas (Table 2.3). Comparisons of

the zooplankton $\delta^{13}\text{C}_{\text{raw}}$ values show inter-annual differences in Cape Cod Bay (2001 > 2006), the Bay of Fundy (2000 > 1999, 2006 > 2005) and Roseway Basin (1998 > 1999 > 2000, 2005) (Tables 2.1, 2.3). When lipid-normalized $\delta^{13}\text{C}_{\text{LN}}$ data were examined, only the Bay of Fundy and Roseway Basin isotope values were significantly different among collection years. Zooplankton $\delta^{15}\text{N}$ values were also significantly different among collection years in the Great South Channel⁴ (2006 > 2007) and the Bay of Fundy (1999, 2005 > 2000, 2006), while all other habitat-year combinations were statistically indistinguishable (Tables 2.1, 2.3). Zooplankton $\delta^{18}\text{O}$ values were significantly different among collection years in the Great South Channel (2005, 2006 > 2007) and the Bay of Fundy (2005 > 2006), while all other habitat-year combinations were statistically indistinguishable (Tables 2.1, 2.3). For the majority of isotope-habitat-year combinations described in this study (12 of 21 cases), annual variability in zooplankton $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$, and δD stable isotope signatures within each habitat area was statistically insignificant (Tables 2.1, 2.3). For further examination, the habitat-specific zooplankton stable isotope data is shown graphically in Appendix 1.

DISCUSSION

Zooplankton Lipid Content

High lipid content (proxied by C:N ratios) depletes whole animal $\delta^{13}\text{C}$ values and may be a confounding factor in isotope studies of zooplankton, which are known to change their lipid content seasonally (Matthews and Mazumder 2005). An examination

⁴ Samples collected from the Great South Channel during 2004 ($n = 1$), although represented graphically, were omitted from statistical comparisons of temporal variation.

of the spatial distribution of lipid content in GoM zooplankton demonstrated that zooplankton in most habitats sampled have similar mean C:N ratios (Table 2.2). Zooplankton in the Bay of Fundy have C:N ratios that are significantly higher than those from the Nova Scotian Shelf, while all other areas were statistically indistinguishable from either of these two habitats. This is presumably because lipid-rich C5 *Calanus finmarchicus* (in diapause) were more abundant in Bay of Fundy habitat, as compared to the Nova Scotian Shelf. When examining inter-annual patterns within individual habitat areas, significant variability existed in habitats that were sampled over the longest time intervals. The Bay of Fundy and Roseway Basin habitats were both sampled in the late 1990s and then again in the mid-2000s. The samples in these areas, collected in 1998-2000, had significantly lower C:N ratios than those collected in 2005-2006 (Tables 2.1, 2.3). These measurements coincide with an observed decrease in the abundance of the usually dominant copepod, *Calanus finmarchicus*, during the late 1990s followed by a subsequent increase in the early 2000s (Greene et al. 2003). Abundance data from Continuous Plankton Recorder surveys in the North Atlantic suggest that less lipid-rich copepod genera (i.e. *Oithona* spp., *Centropages* spp., and *Pseudocalanus* spp.) increased in the late 1990s (Pershing et al. 2005), and the water column C:N ratio (as measured in the tows collected for this study) decreased accordingly during this event.

Carbon Isotopes

Cape Cod Bay, Great South Channel, and the Bay of Fundy have statistically different $\delta^{13}\text{C}$ isotope signatures, while other habitats are statistically similar to these

three areas (Fig. 2.3). The differences between these regions remain after the data are lipid-normalized, suggesting that the habitats are characterized by different isotope source values and/or biological parameters which result in diverging stable isotope signatures.

Dissolved inorganic carbon (DIC) is the carbon isotope source for marine food webs. Following a basin-wide survey, Kroopnick (1985) reported a paltry ($\approx 1\text{‰}$) range of variation in $\delta^{13}\text{C}$ values of dissolved inorganic carbon ($\delta^{13}\text{C}_{\text{DIC}}$) throughout the Atlantic. This observed lack of spatial variation is reasonable considering that $\delta^{13}\text{C}_{\text{DIC}}$ is derived from the ubiquitous, well-mixed stable isotope signature of atmospheric CO_2 (via the equilibrium exchange of between the atmosphere and surface ocean (Sharp 2007). While we cannot discount that variation in GoM $\delta^{13}\text{C}_{\text{DIC}}$ might contribute to the observed spatial separation between Cape Cod Bay, Great South Channel, and the Bay of Fundy, it is unlikely that variations in isotope source value alone could explain the 1.36-3.21‰ differences measured between the regional $\delta^{13}\text{C}$ values of the three habitats.

Rather than spatial variation in carbon isotope source values, the differences in GoM regional zooplankton $\delta^{13}\text{C}$ values are likely influenced predominately by biological characteristics of local plankton assemblages. In contrast to the distribution of $\delta^{13}\text{C}_{\text{DIC}}$, phytoplankton $\delta^{13}\text{C}$ values show significant spatial variability and generally decrease with increasing latitude (Rau et al. 1982, Goericke and Fry 1994). As phytoplankton utilize DIC during photosynthesis, several temperature, $[\text{CO}_2]_{\text{aq}}$, or species dependent processes fractionate the $\delta^{13}\text{C}_{\text{DIC}}$ source, ultimately resulting in phytoplankton bulk $\delta^{13}\text{C}$ values. (Hinga et al. 1994, Laws et al. 1995). Net primary production and cell growth rates

influence $\delta^{13}\text{C}$, and higher plankton $\delta^{13}\text{C}$ values are found in coastal regions, especially in upwelling areas or during phytoplankton blooms (Fry and Wainright 1991, Schell et al. 1998, Burton and Koch 1999). Inshore-offshore gradients also exist, since nearshore waters are typically ^{13}C enriched as a result of higher nutrient concentrations, greater overall productivity and inputs from ^{13}C -heavy benthic macrophytes, while pelagic waters are ^{13}C deplete from less nutrient availability, lower productivity and slower phytoplankton growth rates (Kelly 2000, Rubenstein and Hobson 2004). The regional $\delta^{13}\text{C}$ values of the three regions in this study exhibit the inshore-offshore phenomenon: Cape Cod Bay (the shallowest, most inshore habitat) has the highest $\delta^{13}\text{C}$ value, the Bay of Fundy (which contains a deep basin, yet is near the coast) is intermediate, and the Great South Channel (the furthest offshore habitat) has the lowest $\delta^{13}\text{C}$ value (Fig. 2.5c-d).

Characteristics such as plankton species composition could also cause the $\delta^{13}\text{C}$ value of habitats within the GoM to differentiate regionally. At the level of phytoplankton, for example, fast-growing species such as diatoms typically have higher $\delta^{13}\text{C}$ signatures as compared to other species (Fry and Wainright 1991). In this study, given that zooplankton samples were collected from each habitat area in different months, different phytoplankton species could have been supporting each local food web. For example, tows from Cape Cod Bay (collected in March) may have been supported to a larger extent by spring blooming diatoms, while tows from the Bay of Fundy (collected in August) may have been supported by dinoflagellates which typically become abundant after the spring bloom (Tiselius and Kuylenstierna 1996). The zooplankton community

likely differed between the three major habitat areas, specifically those of Cape Cod Bay vs. Great South Channel/Bay of Fundy. During the late winter and early spring, zooplankton in Cape Cod Bay is characterized by a mixed community including *Pseudocalanus* spp., *Centropages typicus*, and *C. finmarchicus* (Costa et al. 2006). The abundance of *C. finmarchicus* in my samples from Cape Cod Bay (collected in March) was relatively low, with this species comprising only 0-17% of the community (D. Osterberg and M. Bessinger, unpublished data). In contrast, *C. finmarchicus* dominated the samples collected from the Great South Channel (in April/May) and the Bay of Fundy (in August). Tows collected in the Bay of Fundy contained 45-92% *C. finmarchicus* (Baumgartner et al. 2003). Changes in species composition between habitat areas may therefore explain a component of the variation in $\delta^{13}\text{C}$.

Nitrogen Isotopes

No significant spatial variation was measured in the nitrogen stable isotope values of zooplankton collected at seven sites in the GoM (Table 2.2, Fig. 2.3). Given that nitrogen isotopes are a robust indicator of trophic position (Michener and Schell 1995), these data confirm that similar trophic levels were sampled in each habitat. There were significant differences in $\delta^{15}\text{N}$ values between years in the Great South Channel and Bay of Fundy (Tables 2.1, 2.3), though these differences were not consistent between the two habitats. Sampling effort overlapped in these areas in 2005 and 2006, and in Great South Channel zooplankton $\delta^{15}\text{N}$ values were statistically equivalent in these two years, while Bay of Fundy zooplankton $\delta^{15}\text{N}$ was greater in 2005 than in 2006. This suggests that

local physical or biological characteristics in each habitat resulted in inter-annual $\delta^{15}\text{N}$ differences. These parameters likely included differences in phyto- or zooplankton community composition, or local fluctuations of nitrogen sources and sinks (McMahon et al. in prep.).

Oxygen Isotopes

Oceanic $\delta^{18}\text{O}$ is affected by the same processes as salinity – including evaporation, precipitation, advection, mixing, and river runoff – and $\delta^{18}\text{O}$ has a positive linear correlation with salinity (Craig and Gordon 1965). Oxygen isotope values of ocean water reflect a mass balance between these processes (Houghton and Fairbanks 2001, Benway and Mix 2004). In this study, zooplankton $\delta^{18}\text{O}$ values separated into two distinct statistical groups, the Great South Channel and Cape Cod Bay/Bay of Fundy/Roseway Basin/NE Georges Bank, with values from the Great South Channel being significantly lower than other areas (Figs. 2.4, 2.5e). The isotope separation of the Great South Channel from the other habitats is likely due to the formation of a seasonal low-salinity surface plume, derived from spring run-off, which forms off of Cape Cod and moves to the Great South Channel each spring (Wishner et al. 1995). An increase in low-salinity water would reduce the regional source $\delta^{18}\text{O}$ value, thereby tagging phytoplankton and zooplankton within the Great South Channel with lower $\delta^{18}\text{O}$ values.

The transfer pathways of oxygen isotopes from seawater to animal tissue is not well understood, and little information is available regarding the trophic fractionation of $\delta^{18}\text{O}$ or $\delta^{15}\text{N}$ variation in animal protein (Koch 2007). Animals (here, zooplankton) could

acquire their $\delta^{18}\text{O}$ value from ambient seawater, from their diet (here, primarily phytoplankton), or from a combination of both sources. Schmidt et al. (1997) report $\delta^{18}\text{O}$ values of 30.4‰ for diatoms collected in Norwegian-Greenland Sea, with surface water values being $\approx 0.1\text{-}0.5\text{‰}$ (Schmidt et al. 1999). Similarly, large enrichments ($\approx 26\text{‰}$) have been reported in the cellulose of submerged aquatic plants, relative to ambient seawater (Cooper and DeNiro 1989). Zooplankton collected for this study in the GoM show an enrichment over seawater of a similar magnitude (22.65‰, Table 2.4), which suggests that after the isotope fractionation between phytoplankton and seawater, there is little trophic fractionation between zooplankton and phytoplankton.

Hydrogen Isotopes

The physical and chemical processes that affect the spatial distribution of marine oxygen isotopes similarly affect hydrogen isotopes, but result in variability at larger scales (McMahon et al. in prep.; Figs. 2.4, 2.5f). Despite the co-variance of meteoric oxygen and hydrogen stable isotope values, the zooplankton δD values measured in the GoM show different spatial patterns than those observed for zooplankton $\delta^{18}\text{O}$. Bay of Fundy/Roseway Basin zooplankton are significantly lighter than zooplankton from the Great South Channel/NE Georges Bank (Figs. 2.4, 2.5f). The δD data conform to the expected spatial structure of surface ocean hydrogen isotopes: a general pattern of lower values at higher latitudes (Englebrecht and Sachs 2005). The lower δD values observed over the Nova Scotian Shelf are also expected, as this is where low-salinity water, derived from the Gulf of St. Lawrence, enters the GoM.

The lack of consistency between δD and $\delta^{18}\text{O}$ is puzzling, given the similar physical and chemical mechanisms that establish each source value. Given that fractionation and trophic transformation of both isotopes are not well understood in mammals (Koch 2007), it is difficult to resolve the lack of consistency between zooplankton δD and $\delta^{18}\text{O}$ ratios. While questions regarding the metabolic transformations of δD and $\delta^{18}\text{O}$ were beyond the scope of this study, the data produced here demonstrate a need to further explore trophic fractionation as a potential confounding factor to animal migration studies with stable isotopes.

CONCLUSIONS

Previous studies have utilized stable isotope ratios in large whale baleen to examine annual movement patterns, but the spatial and temporal scope of these studies has been limited to broad-scale movements between summer/winter grounds. Finer scale tracking of habitat use (i.e. movement between areas within the spring/summer feeding season) have not been reported. The goal of this study was to describe the isotope landscape of the Gulf of Maine, through analysis of zooplankton, to determine if high resolution migration tracking is possible with this method.

To test the spatial and temporal variation of the stable isotope landscape in the Gulf of Maine, carbon, nitrogen, oxygen, and hydrogen stable isotope ratios were measured in zooplankton collected from several sites within the Gulf of Maine. Of the seven habitats investigated, three areas (Cape Cod Bay, Great South Channel, and the Bay of Fundy) represented isotopically distinct habitats, and these differences were more

pronounced by examining multiple isotopes. The results of this study demonstrate that habitat-specific zooplankton isotope values can be differentiated within the Gulf of Maine feeding ground. However, inter-annual temporal variation was present in many habitats, which was greater than the differences between mean regional isotope values in some areas. This points to the need to temporally couple animal and diet/environmental isotope measurements when conducting stable isotope investigations of animal migration for accurate assessments of habitat use. The results of this study suggest the stable isotope landscape of the Gulf of Maine, while not ideal for tracking higher resolution, intra-seasonal movements, does contain spatial differences that should be transferred to right whales as they feed in and move between habitat areas.

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Table 2.1: Overview of Zooplankton Tows. Tow locations, year/month of collection, and sampling frequency of zooplankton within right whale foraging habitats. C:N and stable isotope ratios are presented as annual mean ± 1 SD for each habitat/year combination. (--) denotes no data. Habitat codes are as follows: Cape Cod Bay (CCB); Great South Channel (GSC); Bay of Fundy (BoF); Roseway Basin (RB); Nova Scotian Shelf (NSS); Northeast Georges Bank (NE GB); Jeffreys Ledge (JL).

Region	Month	n	C:N	$\delta^{13}\text{C}_{\text{raw}}$	$\delta^{13}\text{C}_{\text{LN}}$	$\delta^{15}\text{N}$	$\delta^{18}\text{O}$	dD
CCB								
2001	March	12	5.4 ± 0.7	-20.5 ± 0.5	-19.3 ± 0.4	7.5 ± 0.4	--	--
2006	March, April	4	6.5 ± 0.7	-23.3 ± 3.6	-21.6 ± 3.3	7.8 ± 1.9	22.8 ± 0.8	--
2007	March	2	5.2 ± 0.9	-21.0 ± 0.1	-20.0 ± 0.8	8.5 ± 0.1	24.3 ± 0.1	--
GSC								
2004	April	1	4.5	-24.3	-23.8	7.3	25.2	-117.8
2005	May	8	7.0 ± 0.9	-25.3 ± 0.8	-23.4 ± 0.7	7.9 ± 0.7	21.4 ± 2.0	-142.1 ± 10.2
2006	May, June	17	6.1 ± 0.9	-23.9 ± 1.4	-22.4 ± 1.6	8.4 ± 0.9	19.8 ± 1.5	--
2007	May, June	6	6.4 ± 0.9	-24.4 ± 1.5	-22.7 ± 1.1	7.0 ± 0.7	17.6 ± 1.3	--
BoF								
1999	August	9	5.9 ± 0.5	-23.1 ± 0.9	-21.7 ± 0.6	8.6 ± 0.9	--	--
2000	July, August	11	5.2 ± 0.3	-21.9 ± 0.3	-20.9 ± 0.3	7.8 ± 0.4	--	--
2005	August	3	11.4 ± 0.2	-24.8 ± 0.3	-21.7 ± 0.3	9.4 ± 0.5	28.5 ± 2.7	-176.3 ± 6.7
2006	July	9	8.3 ± 1.7	-23.7 ± 0.7	-21.4 ± 0.3	8.2 ± 0.4	22.3 ± 2.4	--
RB								
1998	August	3	4.3 ± 0.2	-23.1 ± 0.2	-22.7 ± 0.1	8.8 ± 1.5	--	--
1999	August	4	6.3 ± 1.4	-22.2 ± 0.3	-20.7 ± 0.4	8.9 ± 0.8	--	--
2000	July, August	3	5.1 ± 0.3	-24.4 ± 0.4	-23.5 ± 0.4	7.3 ± 0.2	--	--
2005	August	2	10.4 ± 1.4	-25.0 ± 0.1	-22.2 ± 0.2	9.6 ± 0.4	25.3 ± 0.4	-169.8 ± 3.0
NSS								
1998	August	11	4.7 ± 0.6	-22.8 ± 1.3	-22.1 ± 1.2	7.8 ± 1.6	--	--
1999	July, August	9	5.2 ± 0.5	-22.9 ± 0.7	-21.9 ± 0.3	8.2 ± 1.2	--	--
NE GB								
2005	August	4	7.8 ± 2.2	-24.0 ± 1.8	-21.9 ± 1.0	8.2 ± 0.6	24.4 ± 2.4	-135.4 ± 24.2
2007	August	4	5.7 ± 0.6	-23.9 ± 0.7	-22.6 ± 0.5	7.4 ± 0.4	--	--
JL								
2006	October, November	3	6.7 ± 4.3	-22.5 ± 1.1	-21.3 ± 0.7	7.7 ± 2.3	22.3 ± 2.3	--

Table 2.2: Spatial Variation in Gulf of Maine Zooplankton Stable Isotope Ratios. Results of one-way ANOVA tests (F ratio and p value) examining the differences between the zooplankton stable isotope values (mean \pm 1 SD) from each habitat area sampled ($\alpha = 0.05$). (-) indicates no data. Habitat codes are as follows: Cape Cod Bay (CCB); Great South Channel (GSC); Bay of Fundy (BoF); Roseway Basin (RB); Nova Scotian Shelf (NSS); Northeast Georges Bank (NE GB); Jeffreys Ledge (JL).

Region	C:N				$\delta^{13}\text{C}_{\text{raw}}$				$\delta^{13}\text{C}_{\text{LN}}$			
	n	Mean \pm 1 SD	F	p	n	Mean \pm 1 SD	F	p	n	Mean \pm 1 SD	F	p
CCB	18	5.6 \pm 0.8			18	-21.2 \pm 2.0			18	-19.9 \pm 1.7		
GSC	32	6.3 \pm 1.0			32	-24.4 \pm 1.4			32	-22.8 \pm 1.1		
BoF	32	6.8 \pm 2.2			32	-23.0 \pm 1.1			32	-21.3 \pm 0.5		
RB	12	6.2 \pm 2.3	3.36	0.004	12	-23.4 \pm 1.1	11.94	<0.001	12	-22.2 \pm 1.2	15.89	<0.001
NSS	20	5.0 \pm 0.6			20	-23.1 \pm 1.1			20	-22.0 \pm 0.9		
NE GB	8	6.8 \pm 1.9			8	-24.0 \pm 1.2			8	-22.2 \pm 0.8		
JL	3	6.7 \pm 4.3			3	-22.5 \pm 1.1			3	-21.3 \pm 0.7		

Region	$\delta^{15}\text{N}$				$\delta^{18}\text{O}$				δD			
	n	Mean \pm 1 SD	F	p	n	Mean \pm 1 SD	F	p	n	Mean \pm 1 SD	F	p
CCB	18	7.7 \pm 0.9			6	23.3 \pm 1.0			-	-		
GSC	32	8.0 \pm 1.0			32	20.1 \pm 2.2			9	-139.4 \pm 12.5		
BoF	32	8.3 \pm 0.8			12	23.8 \pm 3.7			3	-176.3 \pm 6.7		
RB	12	8.6 \pm 1.1	1.36	0.238	2	25.3 \pm 0.4	7.07	<0.001	2	-169.8 \pm 3.0	6.92	0.004
NSS	20	8.0 \pm 1.3			-	-			-	-		
NE GB	8	7.8 \pm 0.6			4	24.4 \pm 2.4			4	-135.4 \pm 24.4		
JL	3	7.7 \pm 2.3			2	22.3 \pm 2.6			-	-		

Table 2.3: Temporal Variation of Gulf of Maine Zooplankton Isotopes. Results of one-way ANOVA tests examining the differences between zooplankton stable isotope values among years within individual habitat areas. Gray boxes highlight significant relationships ($\alpha = 0.05$), (-) indicates no data. *Student's t-tests were performed when only 2 years of data were available. Habitat codes are as follows: Cape Cod Bay (CCB); Great South Channel (GSC); Bay of Fundy (BoF); Roseway Basin (RB); Nova Scotian Shelf (NSS); NE Georges Bank (GB); Jeffreys Ledge (JL)

Table 2.4: Trophic Enrichment of Zooplankton: Oxygen. Mean (± 1 SD) oxygen stable isotope signatures of zooplankton and seawater from the Gulf of Maine are shown. (n) denotes sample size. Net trophic enrichment of zooplankton (Δ , ‰) as compared to seawater was calculated for zooplankton samples collected in the Gulf of Maine. Trophic enrichment was calculated after: $\Delta = \Delta_{\text{zooplankton}} - \Delta_{\text{seawater}}$.

Group	n	$\delta^{18}\text{O}$ (‰)	Δ (‰)	Reference
Zooplankton	58	21.7 ± 3.1	22.9	This study
Seawater	22	-1.2 ± 0.7		Schmidt et al. 1999

Figure 2.1a-b: The Gulf of Maine: Study Area and Tow Locations. **(a)** The Gulf of Maine with relevant topographical features and bathymetry (50 fathom/91m and 200m isobaths). Inset shows the area that is enlarged. **(b)** Locations of individual zooplankton tows (▲) and seawater samples (■). Boxes surround recognized seasonal feeding habitats of the North Atlantic right whale. Habitat codes represent: Cape Cod Bay (CCB), Great South Channel (GSC), Bay of Fundy (BoF), Roseway Basin (RB), Nova Scotian Shelf (NSS), Northeast Georges Bank (NE GB), and Jeffreys Ledge (JL).

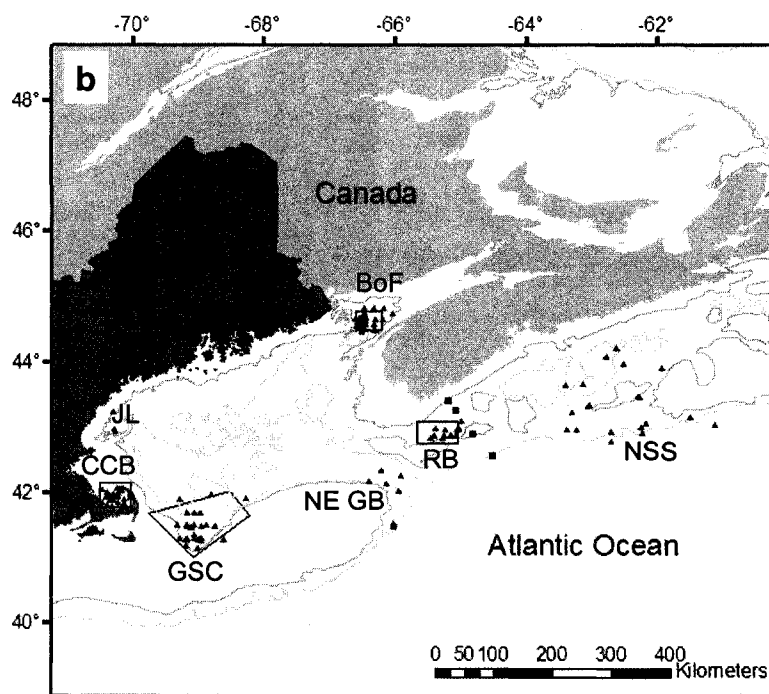
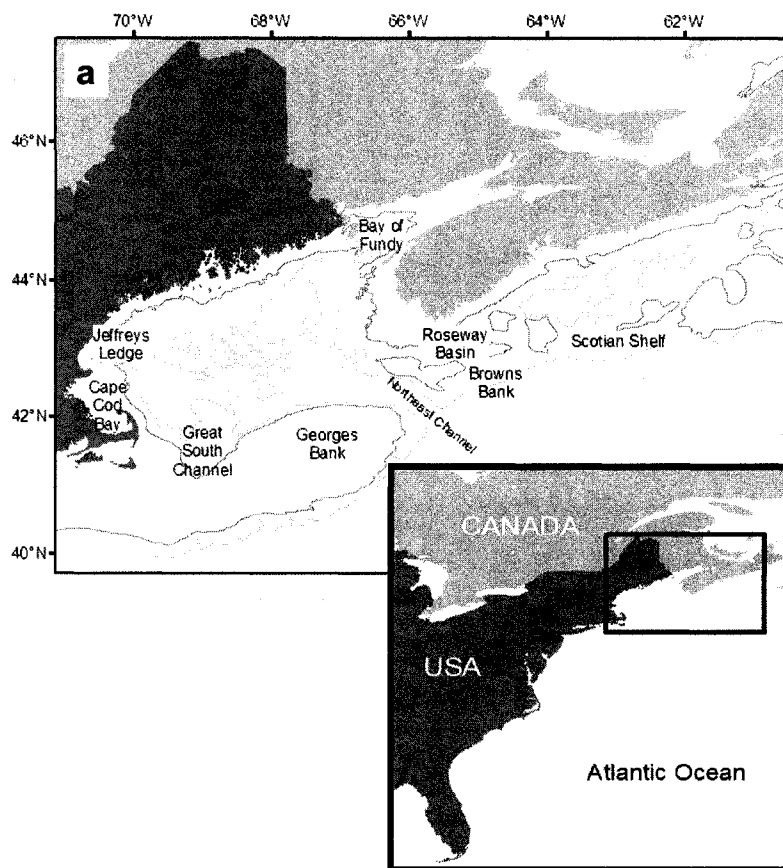


Figure 2.2: $\delta^{13}\text{C}$ Lipid Normalization of Zooplankton Samples. Zooplankton carbon isotope values were normalized by C:N ratio to account for the confounding effects of tissue lipids, which deplete the carbon isotope ratio in raw samples. This plot illustrates the relationship between C:N ratio and enrichment of $\delta^{13}\text{C}_{\text{LN}}$ relative to $\delta^{13}\text{C}_{\text{raw}}$.

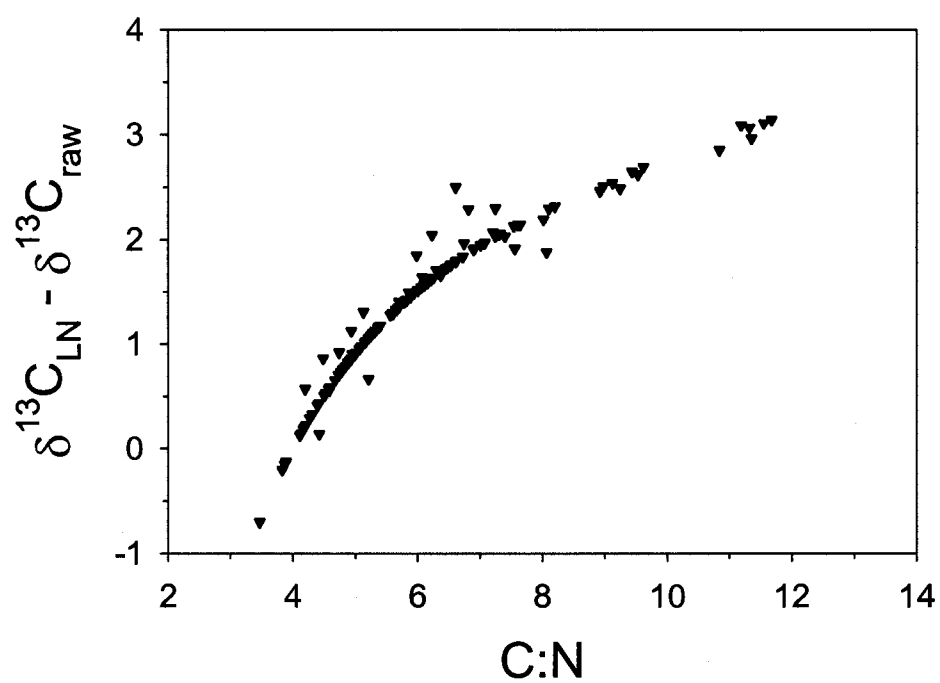


Figure 2.3: Spatial Trends in Gulf of Maine Zooplankton: Carbon and Nitrogen

Isotopes. Timeline describes North Atlantic right whale seasonal habitat use in the Gulf of Maine. Habitat-specific zooplankton carbon and nitrogen stable isotope values (mean ± 1 SD) are plotted by the month in which collections occurred. Zooplankton samples from the Bay of Fundy, Roseway Basin, Nova Scotian Shelf, and northeast Georges Bank were all collected in August, and these data are jittered to enhance visibility. Numbers above the stable isotope data illustrate statistical relationships between regions, with unique numbers denoting statistically significant differences ($\alpha = 0.05$), and the “x” label denotes statistically similar groups. Timeline and symbol labels are as follows: Cape Cod Bay (CCB, C), Great South Channel (GSC, G), Bay of Fundy (BoF, B), Roseway Basin (RB, R), Nova Scotian Shelf (NSS, N), Northeast Georges Bank (NEGB, GB), and Jeffreys Ledge (JL, J).

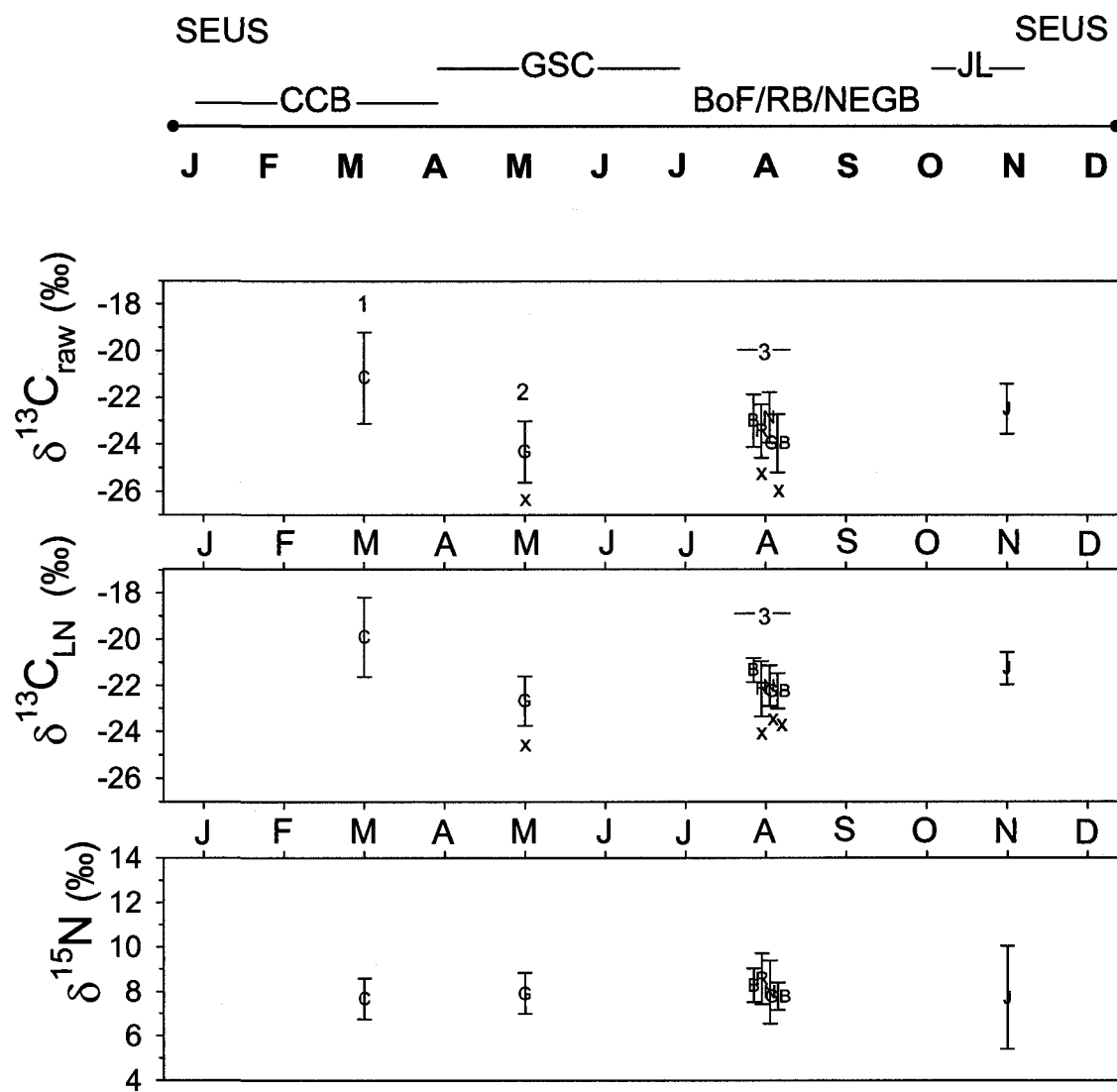


Figure 2.4: Spatial Trends in Gulf of Maine Zooplankton: Oxygen, and Hydrogen Isotopes. Top panel illustrates the shallow and deep water circulation schemes for the Gulf of Maine (redrawn from Bigelow 1927, Brown & Beardsley 1978) with zooplankton sampling locations labeled as 0-6 according to their relative distance “downstream” in the surface circulation mode. Bottom panel shows regional stable isotope values (mean \pm 1 SD) for zooplankton collected in seasonal right whale foraging habitats. Numbers above the stable isotope data illustrate statistical relationships between regions, with unique numbers denoting statistically significant differences ($\alpha = 0.05$), and the “x” label denotes statistically similar groups. X-axis labels are as follows: Nova Scotian Shelf (NSS, 0); Roseway Basin (RB, 1); Bay of Fundy (BoF, 2); Jeffreys Ledge (JL, 3); Cape Cod Bay (CCB, 4); Great South Channel (GSC, 5); and NE Georges Bank (NE GB, 6).

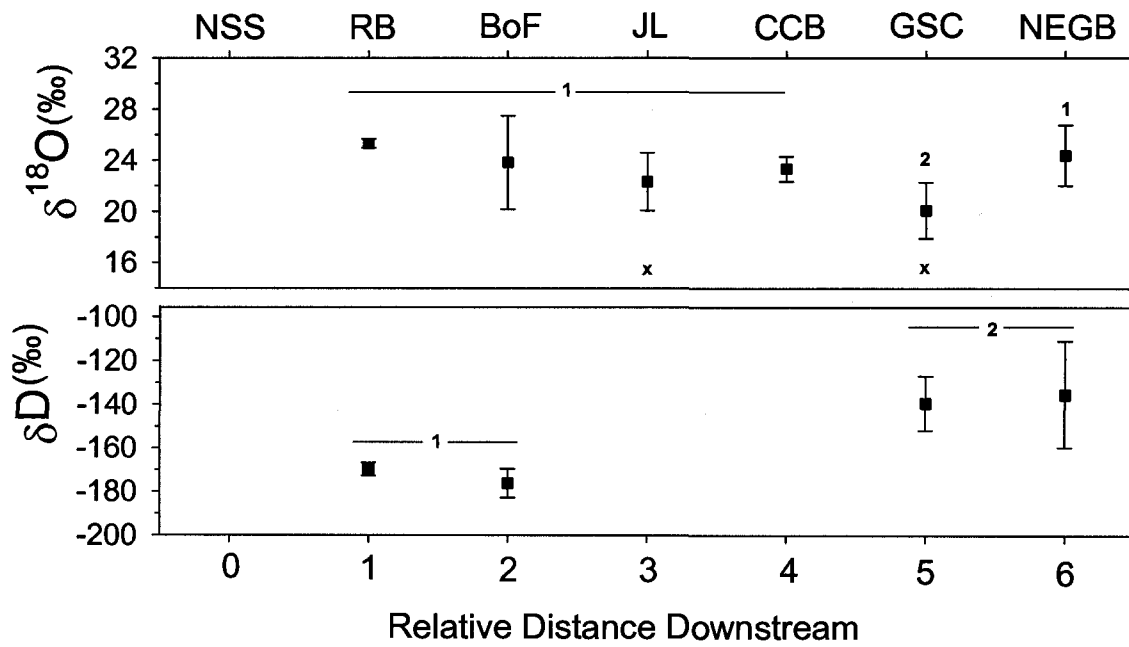
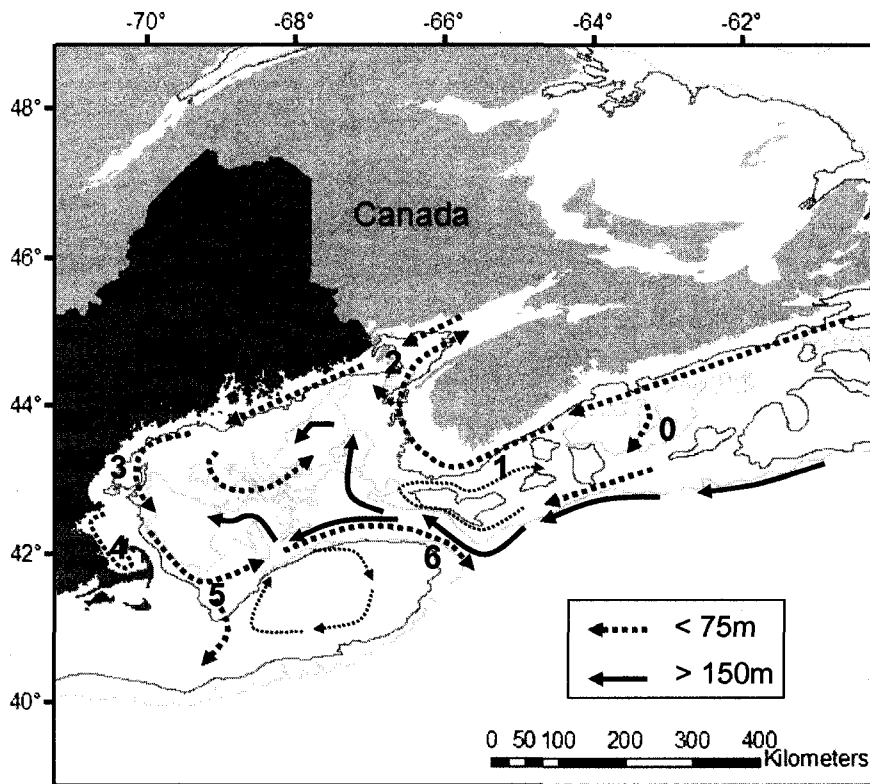
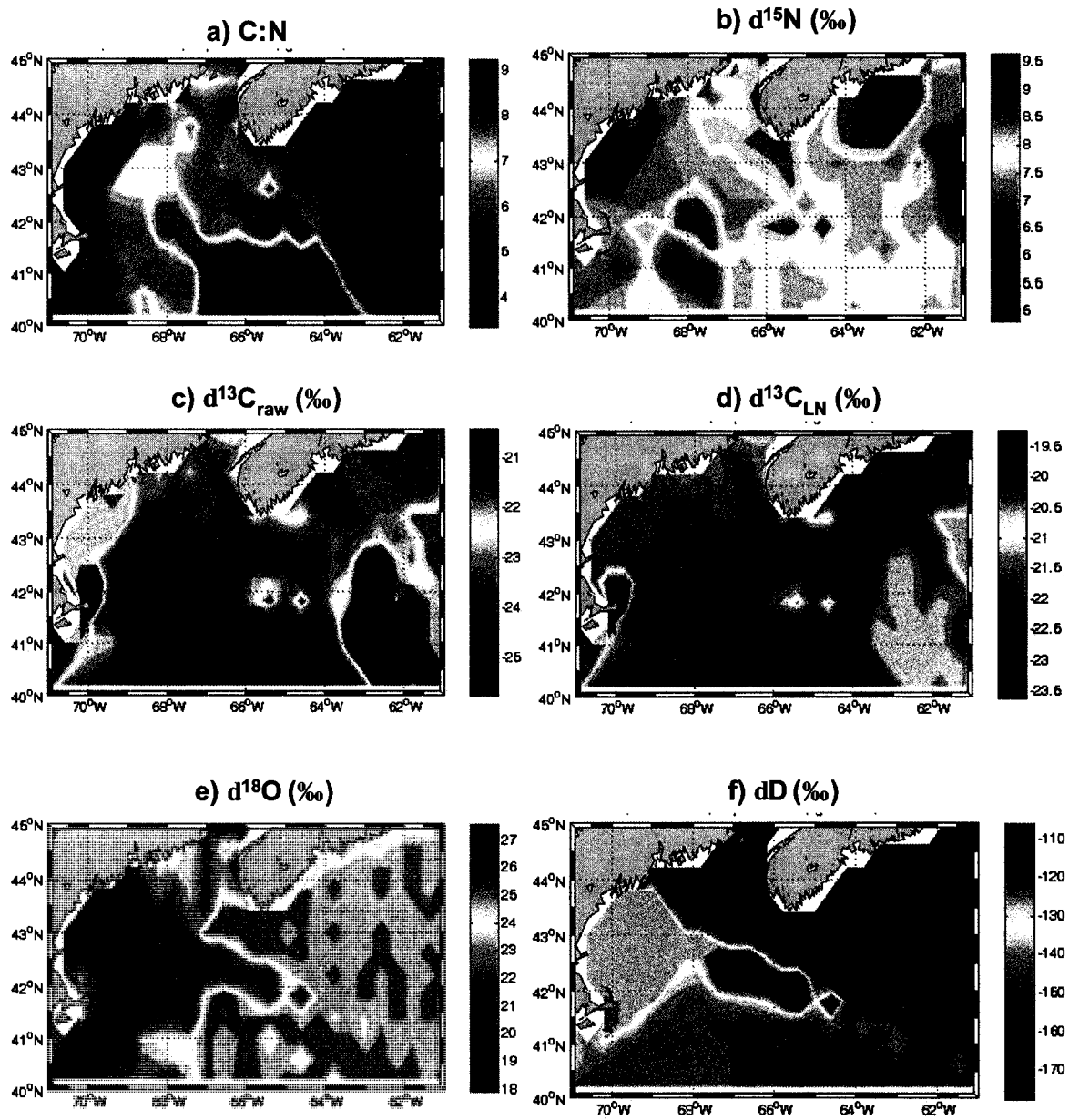


Figure 2.5a-f: Contour Maps of the Gulf of Maine Isotope Landscape. **(a)** C:N and **(b-f)** stable isotope ratios of zooplankton collected in the Gulf of Maine.



CHAPTER 3

STABLE ISOTOPE RATIOS IN RIGHT WHALE BALEEN: INDICATORS OF TROPHIC POSITION AND MIGRATION PATTERNS

ABSTRACT

Although right whales are observed seasonally along the eastern coasts of the United States and Canada, several datasets suggest that they use additional habitat areas. Rare, present-day sightings of right whales in historical whaling grounds offer clues as to the location of such habitats. In 2005, the National Maine Fisheries Service published a Recovery Plan for the critically endangered North Atlantic right whale (*Eubalaena glacialis*), and cited as a high research priority the “characterization and monitoring of important habitats.” Here stable isotopes ratios in right whale baleen are utilized as intrinsic tags of migration, as these isotopes vary regionally within the marine environment and are assimilated via trophic transfer.

This chapter describes carbon, nitrogen, oxygen, and hydrogen stable isotope ratios in baleen plates and zooplankton collected from several right whale foraging sites in the Gulf of Maine, and their application in determining the migration patterns and foraging ecology of *E. glacialis*. Trophic fractionation of carbon, nitrogen, oxygen, and hydrogen between right whales and their zooplankton prey were calculated for baleen formed in the Gulf of Maine. On average, right whales are enriched approximately 2‰ (carbon and nitrogen), -2.3‰ (oxygen), and 30.6‰ (hydrogen) relative to their diet, but trophic enrichment was variable between habitats.

Isotope records in *E. glacialis* baleen, like those of other large whale species, contain oscillations that correspond to annual broad-scale north/south migrations. To examine right whale movement patterns at seasonal time scales, baleen isotope records, the *North Atlantic Right Whale Catalog* sighting records for individual whales, and

habitat-specific zooplankton stable isotope values were compared. Poor correlations were found between the latitude of sighting and baleen isotope signature, likely because of the confounding contribution of body nutrient pools that were de-coupled from diet (i.e. non-essential amino acids) and rapid movement by the whales between habitat areas.

INTRODUCTION

Broad-scale survey effort along the east coasts of the United States and Canada have demonstrated that the majority of North Atlantic right whales right whales (*Eubalaena glacialis*) utilize several seasonal feeding habitats in the Gulf of Maine (GoM) (including Cape Cod Bay, Great South Channel, lower Bay of Fundy, Roseway Basin, and Jeffreys Ledge), while primarily mother/calf pairs occupy a calving ground off the southeast United States coast (SEUS) during the winter months (Kraus et al. 1986b, Winn et al. 1986, Weinrich et al. 2000, Brown et al. 2007; Fig. 3.1). Right whales are also observed (in smaller densities) in the Gulf of St. Lawrence/Chaleur Bay (Y. Guilbault, pers. comm.) and the northeastern flank of Georges Bank in the summer and early fall (Niemeyer et al. 2008).

North Atlantic right whales can be individually identified by raised cornified patches of skin on the rostrum (called callosities) and unique body scars which are easily photo-documented (Kraus et al. 1986a). This led to the creation of a photographic catalog of individuals (herein referred to as the *Catalog*), which has grown over time to contain thousands of photographs and multi-year sighting records for hundreds of individual right whales. Whales in the *Catalog* are given four digit identification numbers, preceded by an “Eg” (denoting the species’ binomial nomenclature, *Eubalaena glacialis*). In recent years, genetic analysis of skin and fecal samples has added an additional component to the *Catalog*, such that the majority of cataloged individuals also have a high resolution genetic profile. The *Catalog* facilitates estimates of population

size, and is frequently referenced for studies of right whale demography, reproductive parameters, and habitat use (Hamilton et al. 2007).

Alternative Habitat Use Hypothesis

Several lines of evidence support an underlying hypothesis of this study: that right whales use habitats that are ancillary to their major feeding and calving grounds in the Gulf of Maine and southeast US (the “alternative habitat use hypothesis”). The most basic forms of these are present-day, opportunistic sightings of right whales on historic whaling grounds. These rare, but intriguing sightings have occurred in the waters off Newfoundland (Lein et al. 1989, Knowlton et al. 1992), Norway (Jacobsen et al. 2004), and in the Cape Farewell Ground (between Greenland and Iceland; Knowlton et al. 1992, Brown et al. 2007). Given that survey effort in these areas has been quite limited, it is unknown if these sightings are indicators of alternative habitats or if they are of individuals occasionally moving through the original range of this population.

The mark-recapture data contained in the *Catalog* demonstrates that after right whales leave their summer feeding grounds, a large proportion of the non-calving population is not sighted during the winter months (Right Whale Consortium 2008b). Given that the peak in right whale calving occurs in January (Knowlton et al. 1994), and that the gestation period is estimated at one year (Best 1994), it is likely that mating activities occur in the winter months. Recent aerial surveys flown over the central Gulf of Maine during the winter have documented individuals and small surface active groups of right whales (Cole et al. 2007, T. Cole, pers. comm.), and a small number of right

whales (tens) can be seen in Cape Cod Bay in the late winter (in January and February, (Hamilton and Mayo 2001). However, a centralized wintertime foraging and/or breeding habitat containing a high density of right whales has not been identified.

The *Catalog* sighting records of many individual whales are characterized by gaps between sighting events which vary in duration from months to several years (Right Whale Consortium 2008b). The longest documented sighting gap is 17 years, although 99% of cataloged whales have gaps of 6 years or less (Hamilton et al. 2007). Survey effort has remained *nearly* consistent over the past 25 years, so these sighting gaps cannot be solely attributed to variable survey effort (Brown et al. 2007). Although it is possible that whales used the Gulf of Maine/southeast US habitats during these sighting gap years and were simply missed by researchers, the frequency of sighting gaps in a large proportion of cataloged right whales lends further support to the alternative habitat use hypothesis.

Recent genetic analyses also substantiate the alternative habitat use hypothesis. Paternity tests using right whale genetic profiles have demonstrated that genetically profiled males (roughly 70% of all cataloged males) were responsible for paternities of only 51% of the sampled calves (Frasier et al. 2007a). Therefore, to account for the unsampled (and likely un-cataloged) males responsible for the other 49% of paternities, the population must be larger than currently estimated (Frasier et al. 2007a). Given the level of survey and sampling effort in the GoM and SEUS seasonal habitat areas, it is likely that these additional males are primarily using other habitat areas.

Analysis of genetic and observational data has also revealed that right whales exhibit maternally directed site fidelity, which has resulted in genetic sub-structuring within the population (Malik et al. 1999). Most new mothers bring their calves to the Bay of Fundy habitat in the summer months, such that this area is considered a nursery habitat. These whales are known as Fundy mothers. In contrast, some mothers never bring their new calves to the Bay of Fundy (non-Fundy mothers), while others bring some but not all of their new calves to the Bay of Fundy (Fundy-some mothers). It is unclear whether non-Fundy and Fundy-some mothers congregate at an alternative nursery habitat, or if several areas are used. One study documented a mother/calf pair in the Labrador Basin in August 1989 (Knowlton et al. 1992), but such sightings of mother/calf pairs in non-Bay of Fundy in the summer and early fall are rare. If there are one or more centralized alternative nursery habitats, they have yet to be identified.

Migration Potential

Long-distance movements of right whales have been studied using satellite-monitored radio tags. Right whales were tagged in the Bay of Fundy in the summers of 1989-1991 and 2000 (Mate et al. 1997, Baumgartner and Mate 2005). These tracking studies have effectively invalidated the assumption that right whales are slow-moving, exclusively coastal animals (Mate et al. 2007). For example, after leaving the Bay of Fundy habitat two tagged individuals traveled thousands of km, at high speeds, to “new” habitat areas (Mate et al. 1997). One animal swam offshore to a Gulf Stream warm-core ring, while a mother/calf pair traveled south to the coast of New Jersey. Perhaps the most

surprising result of these tracking studies was the discovery that right whales are highly mobile. After leaving the Bay of Fundy, the tagged right whales ranged widely through the GoM, Scotian Shelf, northern mid-Atlantic bight, and continental slope. Tagged animals moved at an average speed of 79 km day^{-1} . At this rate, a right whale could effectively circumnavigate the Gulf of Maine and return to the Bay of Fundy in as little as 15 days (Baumgartner and Mate 2005). Right whales were previously thought to have substantial residence times within seasonal habitats, but satellite tag data demonstrated that right whales make frequent excursions in and out of the Bay of Fundy within a season (Mate et al. 1997). In short, we must be careful in generalizing the movement patterns of right whales, as they do not necessarily adhere to our simplistic perception of their migration behavior.

Sighting data from the *Catalog* and position data acquired from satellite telemetry demonstrate that right whales have plastic migration behaviors, such that significant variability in habitat use patterns may exist between individuals as well as inter-annually within individuals. Continuous, multi-year tags of the migration behavior of multiple individuals would be ideal to determine the geographic extent of North Atlantic right whale distribution as well as the degree of inter-annual variability of habitat use within individuals. Although satellite telemetry delivers invaluable results with successful deployments, it is also at the mercy of low encounter rates with one of the rarest of large whales, technological malfunctions, and relatively short attachment periods (< 1 year). An alternative method, stable isotope analysis of baleen, can provide a continuous long-

term record of intrinsic geochemical markers which can be translated into a whale's multi-year migration patterns.

Stable Isotope Geochemistry of Baleen

Stable isotope analysis is used widely in animal foraging and migration studies (Hobson 1999b, Rubenstein and Hobson 2004, Hobson 2007) as animals incorporate the stable isotope signature of their prey and water source into their own tissues, and are enriched by predictable factors relative to their diet (Michener and Schell 1995). Isotope gradients in the marine environment – formed by abiotic factors such as temperature, salinity, and nutrient concentration – are also transferred from the ambient environment to an animal's tissues via food webs (Rubenstein and Hobson 2004, McMahon et al. in prep.). Therefore, new growth is given a regional tag which allows interpretation of an animal's feeding location and, by extension, its movement patterns.

Accreting keratin structures, such as hair, baleen, claws, and feathers, can become temporal records of stable isotope ratios if they are sampled incrementally (Bowen et al. 2005b). Baleen is composed of keratin, an ideal tissue for stable isotope analysis. It is metabolically inactive, and is formed from blood metabolites (amino acids) and thus new growth responds relatively quickly to dietary changes (Ayliffe et al. 2004). It accretes continuously over each year (Lubetkin et al. 2008) yet also wears away at the tip such that the longest plates in some species contain over ten years of isotope data, thus providing a decadal-scale record of migration behavior.

Study Aims

The aims of this study were to (1) characterize the carbon, nitrogen, oxygen, and hydrogen stable isotopes in right whale baleen collected from multiple individuals, (2) determine trophic fractionation between right whales and their prey by comparing stable isotope values of baleen to Gulf of Maine zooplankton, and (3) examine right whale migration patterns through a comparison of baleen stable isotope measurements with right whale sighting records.

MATERIALS AND METHODS

Baleen plates were collected during diagnostic necropsies from 17 North Atlantic right whale carcasses that had either stranded or been recovered at sea. In the laboratory, all connective tissue was removed and each baleen plate was cleaned with a coarse brush and soap to remove oil and surface dirt. All plates were sampled down the midline, at 2 cm intervals, with a multi-speed drill. The resulting powder shavings from each sampling interval were collected on a clean square of weighing paper, and placed into a sterile 20 ml scintillation vial for storage. The baleen and drill were cleaned thoroughly with ethanol in between each sampling interval.

In preparation for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope analysis, 0.8-1.2 mg of each sample was packaged into a 4 X 6 mm tin capsule and crimped shut. All samples were sent to the University of California Davis Stable Isotope Facility for analysis. During $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis, the samples were loaded into an autosampler and were individually analyzed using a PDZ Europa ANCA-GSL elemental analyzer

interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (IRMS). Each sample was pyrolyzed into CO₂ and N₂ gas and then separated on a gas chromatograph (GC) column. The gases were conveyed to the IRMS with a continuous flow of helium carrier gas. Each sample isotope ratio was compared to a secondary gas standard, whose isotope ratio had been calibrated to international standards (PeeDee Belemnite (PDB) for $\delta^{13}\text{C}$, Craig 1957; and atmospheric nitrogen (N₂) for $\delta^{15}\text{N}$, Mariotti 1985). The total C and N content of each sample were reported along with stable isotope data. C:N ratios and % C and N were calculated from the reported measurements of total C and N content in each sample.

Prior to oxygen ($\delta^{18}\text{O}$) and hydrogen (deuterium, δD) isotope analysis, 0.45-0.55 mg of each sample was weighed and packaged in duplicate into 3.5 X 5 mm silver capsules and crimped shut. All samples were sent to the University of California Davis Stable Isotope Facility for analysis. In order to control for issues related to hydrogen atom exchange, our samples were “air equilibrated” with ambient laboratory air moisture for 2 weeks prior to combustion (Wassenaar and Hobson 2003, Bowen et al. 2005a). After this incubation, samples were analyzed using a Heckatech HT Oxygen Analyzer interfaced to a PDZ Europa 20-20 IRMS. Samples were combusted to CO and H₂O, and separated chromatographically, as described above. Each sample isotope ratio was compared to a secondary gas standard, whose isotope ratio had been calibrated to the international standard Vienna Standard Mean Ocean Water (VSMOW, Coplen 1994).

All samples are reported relative to international reference standards: carbon isotope values relative to PDB, nitrogen values relative to N₂, and oxygen and hydrogen

values relative to VSMOW. Stable isotope measurements are expressed in standard delta (δ) notation, as parts per thousand (per mil, ‰), by the following:

$$\delta^{13}\text{C}, \delta^{15}\text{N}, \delta^{18}\text{O}, \text{ or } \delta\text{D} (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1,000$$

where R_{sample} and R_{standard} are the ratios of $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, $^{18}\text{O}/^{16}\text{O}$, or $^2\text{H}/^1\text{H}$ of the sample and standard, respectively (McKinney 1950).

Analytical precision was determined with laboratory working standards of glycine ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), cellulose ($\delta^{18}\text{O}$), and polyethylene (δD), which were analyzed after every 12 baleen samples. These standards were calibrated against NIST Standard Reference Materials. Precisions based on the standard deviation of the series of reference checks used in the analysis are as follows: $\delta^{13}\text{C}$ (0.05‰); $\delta^{15}\text{N}$ (0.20‰); $\delta^{18}\text{O}$ (0.43‰); and δD (4.0‰).

To control for issues related to hydrogen atom exchange (Bowen et al. 2005b), all sample hydrogen isotope measurements were corrected relative to a laboratory standard, bowhead whale baleen (BWB2, -105‰) after analysis. This standard was calibrated against NIST Standard Reference Materials. One BWB2 sample was run for every 24 right whale baleen samples.

Temporal Context

The stable isotope records derived from North Atlantic right whale baleen were assigned temporal context using two methods. First, the endpoint of each time series (the whale's date of death) was determined/estimated using the necropsy report and field

notes associated with all individuals sampled in this study (Right Whale Consortium 2008a).

Based on studies of other balaenid whales, baleen stable isotope records form oscillating patterns that are annual in nature (Schell et al. 1989, Best and Schell 1996, Hobson and Schell 1998, Wetmore 2001). The period, or annual growth rate, was estimated using both qualitative and quantitative methods. First, the number of data points (i.e. distance) between the annually-occurring “peaks” in each baleen isotope time series was determined as a qualitative estimate of annual growth rate. This technique was conducted on the $\delta^{15}\text{N}$ baleen records, as these showed the most pronounced periodicity of all available isotopes. The period of each isotope time series was also determined statistically, and non-parametric estimators of the annual growth rate were generated for the baleen data from eight adult whales (Hall et al. 2000). For each whale’s baleen time series, the data considered under the following parameters: g denotes a periodic function with period θ_0 , and (X_i, Y_i) , are successive observations for $1 \leq i \leq n$, and $0 < X_1 \leq \dots \leq X_n$, and ϵ_i represents independent random variables with zero means and finite variance.

$$Y_i = g(X_i) + \epsilon_i$$

To estimate θ_0 and g , a nonparametric estimator (\hat{g}) was constructed, and the function S was minimized to θ :

$$S(\theta) = \sum_{i=1}^n \{Y_i - \hat{g}(X_i | \theta)\}^2$$

From the many possible iterations of this function, the best estimation of period for each time series was determined using a goodness-of-fit test.

Sighting and Calving Records

Several of the whales that were sampled in this study were able to be visually or genetically matched to animals recorded in the *North Atlantic Right Whale Catalog* (<http://rwcatalog.neaq.org/>). Sighting and calving records associated with these animals were obtained from researchers at the New England Aquarium (Right Whale Consortium 2008b). These records included the date and latitude/longitude of sighting, associated behaviors, presence of a calf, and other relevant observations (such as the presence of entangled gear or a satellite tag). The sighting records from the *Catalog* were used to give each baleen isotope value spatial and biological context.

Sighting events were assigned to the corresponding temporally-resolved baleen isotope data point. In some cases, a data point represented a period of time for which an individual was sighted multiple times. In such situations, the mean latitude/longitude of the whale was computed by pooling sighting records for the data point. In all of the cases where multiple sighting events were encompassed by a single data point, the sightings were all located within a single habitat area. Therefore, the average positions that were computed can still be considered reliable indicators of habitat use (i.e. if a whale had been sighted in the southeast US and Gulf of Maine within a single isotope data point, the average position of the whale would appear to be in the mid-Atlantic, and would not be an accurate reflection of the animal's actual habitat use).

The ages of the whales sampled for this study were determined/estimated from sighting records in the *Catalog*, and were then used to create demographic categories with which to compare baleen isotope data points. Several individuals were documented

as new calves in the southeast US calving ground, and their ages were then computed accordingly. Other individuals were first observed as juveniles or adults, and so their age is given as minimum estimate. These estimates were determined by the date of the whale's first sighting, its body length and other morphometrics, and the date of the first observation of the animal in surface active groups. In the case of adult females, calving events also aid in determining estimates of minimum age, as sexual maturity is estimated to occur at 9 years (Kraus et al. 2001).

The baleen isotope data were labeled with one of several categories, depending on the whale's age. Baleen isotope data points were categorized as FETUS if they were laid down before the animal was born. Birth (and subsequent nursing) is indicated prominently in the isotope records by a sharp increase in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Baleen isotope data points were then categorized as CALF at the initiation of nursing, or if the animal was less than one year old (age = 0) when the isotopes were laid down. It was assumed that the animal was nursing during most its first year, as weaning is estimated to occur at 8-12 months (Hamilton et al. 1995). Baleen isotope data points were categorized as YEARLING if they corresponded to the period following the animal's weaning through its second year (age = 1). The tell-tale isotopic indication of weaning (a sharp decrease in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios) was used to mark the transition from the calf to yearling states. The next category was JUVENILE, which encompasses baleen isotope values that were laid down during the intervening years before sexual maturity (age = 2-8). After sexual maturity, separate categories were used to differentiate males and females. Male whales 9 years and older were categorized as [mature] MALE. Although the age of sexual

maturity for males is not well understood (some studies suggest that 9 years might be an underestimate, Frasier et al. 2007a), for the purposes of this study, 9 years was used as a threshold for maturity.

Mature female whales (age ≥ 9) were labeled as NULLIPAROUS, PREGNANT, LACTATING, or RESTING given their individual reproductive status. For the adult females sampled in this study, sighting records from the *Catalog* were used to determine an individual's reproductive state associated with each baleen isotope data point. In most cases, calving events were characterized by a sighting of the female with a young calf in the southeast US calving ground. The mother/calf pairs were then usually sighted in the spring feeding habitats in the Gulf of Maine, or during the summer in the Bay of Fundy. The right whale gestation period is estimated at one year, so female right whales were categorized as PREGNANT in the 12 months preceding a calving event. Given the estimated timing of weaning, females were categorized as LACTATING in the 12 months following a calving event. Females that could not be classified as pregnant or lactating were categorized as RESTING if they had calved in the past or NULLIPAROUS if they had never calved. Data points that were formed when whales were calves, yearlings, and juveniles were excluded from statistical comparisons of reproductive state.

Trophic Fractionation

Right whale baleen and Gulf of Maine zooplankton data (Chapter 2) were compared to examine food web relationships and to determine trophic fractionation

between right whales and their prey. Trophic fractionation (or enrichment: $\Delta^{13}\text{C}$, $\Delta^{15}\text{N}$, $\Delta^{18}\text{O}$, and ΔD) was determined by calculating the difference between the mean isotope value of zooplankton collected in the Gulf of Maine and right whale baleen data that could be connected to a sighting in the Gulf of Maine ($\Delta = \delta_{\text{whales}} - \delta_{\text{zooplankton}}$).

Furthermore, habitat-specific trophic enrichment was determined for Cape Cod Bay, Great South Channel, and the Bay of Fundy. The trophic enrichment between lactating females and calves was also examined, using only the data that could be classified as LACTATING or CALF (after $\Delta = \delta_{\text{calf}} - \delta_{\text{lactatingfemale}}$). This comparison resulted in pooled data from multiple whales during multiple years. Given the sample population, direct comparison between mother/calf pairs was not possible.

RESULTS

Stable Isotope Ratios

Baleen plates from 17 North Atlantic right whales were sampled for stable isotope analysis in this study (Table 3.1). Carbon, nitrogen, oxygen, and hydrogen stable isotope ratios ranged widely in right whale baleen: $\delta^{13}\text{C}$ (-21.8 to -16.7‰), $\delta^{15}\text{N}$ (7.0-12.1‰), $\delta^{18}\text{O}$ (14.8-35.8‰), and δD (-154.5 to -71.2‰) (Table 3.2). Elemental abundances (mean \pm 1 SD) of carbon (adults = $47.1 \pm 2.2\%$, juveniles = 47.1 ± 2.3 , and calves = 46.7 ± 3.3), nitrogen (adults = 14.1 ± 0.8 , juveniles = 14.4 ± 0.9 , and calves = 14.0 ± 1.1), and C:N ratios (adults = 3.35 ± 0.13 , juveniles = 3.27 ± 0.14 , and calves = 3.35 ± 0.14) were similar among all three demographic groups (Table 3.2).

The carbon, nitrogen, oxygen, and hydrogen stable isotope records of adult right whale baleen were characterized by multiple oscillations, which are hypothesized to be annual in nature (Fig. 3.2). Although intra-individual variability was present regarding the exact location (i.e. Julian Day) of the peaks and valleys in the isotope records, peaks generally occurred in the winter and valleys occurred in the spring (Fig. 3.2). These patterns were most highly visible in the nitrogen data, which contained oscillations spanning several per mil units in single years. Carbon data showed similar periodicity, but oscillated to a smaller vertical extent. In several individuals, carbon isotope data demonstrated a sustained decrease, while maintaining the seasonal oscillating pattern (discussed at length in Chapter 4). Oxygen data also followed the periodicity seen in nitrogen and carbon data, but was highly variable with some timeseries containing multiple peaks in a single year. Hydrogen data was available for two individual whales, and the observed range and patterns in the data varied greatly between animals. One whale (Eg1004) did not have marked oscillations in its baleen hydrogen data, while the hydrogen data from another whale (Eg2143) contained dramatic oscillations. When comparing all available isotope records from each adult right whale ($n = 8$), intra- and inter-individual variability in the location of peaks/valleys as well as the amplitude of these features were observed (Fig. 3.2, all other whales shown in Appendix 2).

Stable isotope records from immature right whales were characterized by several indications of ontogenetic diet switches, including a transition into a long flat section (indicative of birth and the commencement of nursing), and a dramatic decrease in nitrogen isotopes (marking weaning and the transition to planktonic prey) followed by

one or more oscillations near the end of the record (Fig. 3.3, Appendix 2). Calf baleen isotope records contained no repetitive oscillations, and were characterized by the isotopic indication of birth and the commencement of nursing (an increase in nitrogen isotope value and transition to a long flat section in the baleen record, Fig. 3.4, Appendix 2).

Baleen Growth Rates

Two independent estimates of annual baleen growth were generated for the isotope time series for each adult whale ($n = 8$, Table 3.3): one by counting the distance between isotope peaks in the $\delta^{15}\text{N}$ data, and another using a non-parametric estimator of a periodic function. In seven of the eight cases examined, the two estimates of annual growth rate were in close agreement. In one case (Eg2301), there was an 8.5 cm yr^{-1} difference between the estimations derived from the two methods. The non-parametric estimator was used as the measure of annual growth rate for the Eg2301 data, since the statistical method is assumed to be more robust than the counting method. In general, immature whales had faster annual baleen growth rates than adults. Baleen growth appears to plateau in adulthood, at approximately 24 cm yr^{-1} .

Trophic Enrichment

Trophic enrichment (Δ) between right whales and their zooplankton prey was calculated by comparing the stable isotope value of zooplankton collected in the Gulf of Maine and right whale baleen data that were associated with a sighting in the Gulf of

Maine. On average, right whale $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and δD were enriched relative to Gulf of Maine zooplankton ($\Delta^{13}\text{C} = 2.1\text{‰}$, $\Delta^{15}\text{N} = 2.2\text{‰}$, and $\Delta\text{D} = 30.6\text{‰}$; Table 3.4). Right whale $\delta^{18}\text{O}$ was depleted relative to zooplankton ($\Delta^{18}\text{O} = -2.3\text{‰}$, Table 3.4). Habitat-specific trophic enrichment between right whales and zooplankton was also calculated in Cape Cod Bay ($\Delta^{13}\text{C} = 0.8\text{‰}$, $\Delta^{15}\text{N} = 2.8\text{‰}$, $\Delta^{18}\text{O} = -4.3\text{‰}$), the Great South Channel ($\Delta^{13}\text{C} = 2.7\text{‰}$, $\Delta^{15}\text{N} = 1.7\text{‰}$, $\Delta^{18}\text{O} = -0.2\text{‰}$, and $\Delta\text{D} = 33.3\text{‰}$), and the Bay of Fundy ($\Delta^{13}\text{C} = 1.7\text{‰}$, $\Delta^{15}\text{N} = 2.7\text{‰}$, $\Delta^{18}\text{O} = -5.0\text{‰}$, and $\Delta\text{D} = 57.9\text{‰}$) (Table 3.4, Fig. 3.5). The trophic enrichment between calves and lactating females was small, with calves being enriched relative to females by only 0.3‰ ($\Delta^{13}\text{C}$) and 0.5‰ ($\Delta^{15}\text{N}$) (Fig. 3.6).

Migration and Habitat Use

Right whale baleen data ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$ and δD) that encompassed a *Catalog* sighting record in the Gulf of Maine were regressed against the latitude of that sighting (Fig. 3.7) in order to examine trends in migration. Weak correlations were present for all four isotopes when the data from adult whales was examined together. The data were further compared by examining the baleen δ values by latitude of corresponding data by individual and by reproductive categories (NULLIPAROUS, PREGNANT, LACTATING, RESTING, and MALE). These comparisons were unremarkable, resulted in similarly weak correlations, and are not shown here.

Differential habitat use by age and reproductive classes was examined by pooling all available data and determining a mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value for each category (Fig. 3.8), such that the value assigned to each life history category contains data from multiple

whales while they could be assigned to each relevant category. The top panel of Figure 3.8 displays the mean \pm 1 SD of these categories, and shows the large degree of overlap between groups. For enhanced visibility, the same data are shown as means \pm 1 SE, with a smaller vertical and horizontal scale. In general, calves and yearlings were enriched in carbon and nitrogen relative to adults, and males were enriched in carbon and nitrogen relative to females. Reproductive females (lactating and pregnant) were lighter in carbon but heavier in nitrogen than resting or nulliparous females. An adult that was chronically entangled in fishing gear was enriched in nitrogen, but depleted in carbon. This animal was emaciated at death as a result of its entanglement, and its high nitrogen isotope values should be considered the result of starvation and chronic stress.

DISCUSSION

Baleen Isotope Records

Like other consumers, right whales acquire their stable isotope ratios from their diet (Michener and Schell 1995). After ingesting their zooplankton prey, the stable isotopic values of that zooplankton are fractionated via right whale metabolic activity, and the modified zooplankton isotope signature is then incorporated into right whale tissue. In the case of baleen, which grows continuously, new growth obtains the isotope signature of what has been recently ingested while old baleen continues to carry the isotope signature of the prey that was ingested when it was formed. As right whales move to new habitat areas that carry distinct isotope signatures (see Chapter 2), they obtain variable isotope values along the length of their baleen. One can see the

manifestation of this process when the incremental stable isotope records of right whale baleen are examined (Fig. 3.2). The oscillating patterns are formed as whales move through several feeding habitats (that represent different stable isotope sources) along their migration route. For example, as whale feed in Cape Cod Bay in the late winter (the most ^{13}C enriched habitat area, Chapter 2) their carbon baleen isotope ratios are relatively high. Then, as the whales move offshore in the spring to feed in the Great South Channel (the most ^{13}C deplete habitat area, Chapter 2), their carbon baleen isotope values fall and approach the valley of the annual oscillation. Into the summer months, as the whales move north into Canadian waters, their isotope signatures rise in concordance with the zooplankton collected in the Bay of Fundy/Roseway Basin/Nova Scotian Shelf/northeast Georges Bank (Chapter 2). Finally, as the whales cope with limited food during the winter months (while migrating to the southeast US to calve, or continuing to feed in the Gulf of Maine or elsewhere) their baleen stable isotope signature is composed of a combination of zooplankton-derived and internally-derived isotope sources. This migration/foraging process structures each the isotope signature of each element examined, with regional differences among habitat areas influencing the range of isotopic variation observed in each baleen time series.

When the baleen stable isotope records of multiple whales were examined for this study, a high degree of inter- and intra-individual variability was observed. If the stable isotope signature of whale baleen is indeed primarily structured by whales changing their foraging location, then this variability is to be expected. Analysis of sighting records in the Catalog demonstrate that although right whales follow stereotypical migration

patterns through the Gulf of Maine (Fig. 3.1), there are also many exceptions to this rule. Appendix 2 shows individual whale baleen records in detail, with their sighting records denoted over the isotope data. For many individuals, there are multiple years where there are no sighting events (e.g. Eg 1004, Eg1014, and Eg1623), or years where the whale is sighted in only one of the seasonal habitat areas (e.g. all adult whales). By contrast, there are also individuals that are seen every year, in almost every habitat (e.g. Eg2143, Eg2301, and Eg2617). The commonality between all of these whales is their common tendency to migrate seasonally; the differences are their individual variations in habitat choice, arrival/departure, and associated life history parameters. Therefore, this study provides further evidence that mysticete whales obtain the basic structure observed in baleen stable isotope records from foraging along an extensive migration route.

It can be argued that male and female right whales have remarkably different agendas: females are subject to major physiological demands associated with reproduction (including putting on enough fat storage to support a calf, carrying a growing fetus, nursing a young calf, and sustaining their own metabolic needs) and exhibit a remarkable change in body condition to correspond with this process (Angell 2005); while males simply need to maintain their metabolic needs. Observational studies of right whales have noted differences in habitat use among adult whales, such that resting females (which are in theory feeding at an accelerated rate to prepare for pregnancy) are sighted with less frequency than other adult right whales in the primary Gulf of Maine habitats (Brown et al. 2001).

To demonstrate how these different agendas (based on life history status) might affect stable isotope ratios, I first compared baleen carbon and nitrogen data that was associated with sighting events in the southeast US habitat. The data that fit these constraints were from 2 males (Eg1238 and Eg1623) and 4 females (Eg1004, Eg1223, Eg2143, and Eg2301). Of the available sample population, no resting females were sighted in the southeast US. Males sighted in the southeast US calving ground had a mean (± 1 SD) $\delta^{13}\text{C}$ value of -19.3 ± 0.02 and $\delta^{15}\text{N}$ value of 11.4 ± 0.8 . Similarly, nulliparous females in the southeast US (Eg2143 and Eg1223) had a mean (± 1 SD) $\delta^{13}\text{C}$ value of -19.3 ± 0.6 and $\delta^{15}\text{N}$ value of 11.4 ± 0.2 . Conversely, reproductively active (pregnant or lactating) females sighted in the southeast US (Eg1004, Eg1223, Eg2143, and Eg2301) had had a mean (± 1 SD) $\delta^{13}\text{C}$ value of -20.5 ± 0.9 and $\delta^{15}\text{N}$ value of 9.7 ± 0.9 . These results suggest that whales not involved in calving (males and nulliparous females) had higher carbon and nitrogen values; while reproductively active females (still pregnant and recent mothers) had lower carbon and nitrogen values. In isotopic studies of humans, Fuller et al. (2004) found that during pregnancy the nitrogen value of hair decreased substantially during pregnancy, independent of the mother's diet. These authors suggest that during periods of rapid tissue anabolism (such as pregnancy), amino acids are redirected to tissue synthesis rather than excretion, and $\delta^{15}\text{N}$ subsequently decreases.

To examine isotopic differences (and potential indicators of variable habitat use) among all life history groups, the mean baleen carbon and nitrogen signature of these groups were calculated. Resting females had the lowest observed nitrogen values, putting

them in the closest proximity to the stable isotope value of their zooplankton prey. As consumers ingest a higher proportion of prey, the isotope value of their tissues should more closely approach that of their prey (Lee et al. 2005). As described above, during times of rapid tissue anabolism (also occurring in resting females), their positive nitrogen balance could result in a decreased $\delta^{15}\text{N}$ signature, independent of diet (Fuller et al. 2004) or habitat use.

Despite the fact that all adult whales are feeding on zooplankton, these findings suggest that other life history classes are supplementing their diet, to some degree, with internal stores of carbon and nitrogen, which would result in a slightly elevated nitrogen signature (Hobson et al. 1993). This is supported by the isotopic observations from an entangled whale, which has a substantially higher nitrogen isotope value than other life history categories. The data from the entangled whale should be considered an isotopic manifestation of a stress response.

Trophic Enrichment

The dogma of stable isotope analysis is that “you are what you eat plus 1‰ ($\delta^{13}\text{C}$) and 3‰ ($\delta^{15}\text{N}$)” (Fry 2006). Recent reviews of trophic fractionation within a variety of species and ecosystems has reinforced this notion, but also demonstrated that there is considerably variability in the amount of species-dependent isotope enrichment between trophic steps (Vander Zanden and Rasmussen 2001, Vanderkluft and Ponsard 2003). Given the uncertainty surrounding estimates of trophic fractionation, the importance of ground-truthing a study using controlled diet experiments has become clear (Gannes et al.

1997). In the case of large whales, it is not possible to control upon what and where animals are feeding. To circumvent this issue, this study utilized *Catalog* sighting records of right whales along with baleen stable isotope data. This method facilitated the comparison of a habitat-specific whale baleen isotope value and a zooplankton isotope value. Carbon and nitrogen trophic fractionation between right whales and zooplankton in the Gulf of Maine was approximately 2‰ (Table 3.4), which is above ($\delta^{13}\text{C}$) and below ($\delta^{15}\text{N}$) the range of currently established estimates in other animals (Michener and Schell 1995).

Interestingly, when examining trophic fractionation between whales and zooplankton in specific habitat areas (Cape Cod Bay, Great South Channel, and Bay of Fundy), different estimates of trophic enrichment were found for each habitat (Table 3.4, Fig. 3.5). The estimate of $\Delta^{13}\text{C}$ was highest in the Great South Channel and Bay of Fundy, while it was lowest in Cape Cod Bay. This may be evidence of isotopic routing, which occurs when specific fractions of the diet are sent to build specific consumer tissues (Koch 2007). In the case of whales, amino acids and other carbon skeletons derived from the diet may be used to build baleen, while diet-derived lipid is shunted directly to the blubber. Zooplankton from the Great South Channel and Bay of Fundy habitats have higher lipid content than those from Cape Cod Bay (Chapter 2), so if diet-derived lipids are more available to right whales in these two habitats we would expect a higher degree of isotopic routing (and a larger offset between whales and zooplankton) to occur.

Trophic fractionation of oxygen was approximately -2.5‰ , with right whales being depleted relative to their zooplankton food source (Table 3.4). Hydrogen trophic fractionation was large ($\Delta D = 30.6\text{‰}$), and right whales were heavier than zooplankton from their Gulf of Maine habitats (Table 3.4). The transformation of oxygen and hydrogen within animal proteins is not well understood (Koch 2007), and the large contribution of body water to an animal's oxygen isotope signature has recently been described (Podlesak et al. 2008). As discussed in Chapter 2, there is a large fractionation between the seawater stable isotope value and that of zooplankton, and most of this fractionation is likely by phytoplankton (Cooper and DeNiro 1989, Schmidt et al. 1997). The uncertain nature of oxygen and hydrogen fractionation in animals makes the interpretation of foraging location difficult with these elements.

Trophic fractionation associated with a known diet switch (from milk to plankton) could be examined in right whale calves and juveniles. Depending on its age and timing of weaning, most juvenile right whale baleen plates carry the record of this switch (Fig. 3.3). Many of the baleen plates examined had a small hump in the record, not far from the end (left). This was interpreted to be the animal's birth, when it switched from maternally-derived nutrition in utero to nursing. The subsequent flat, long phase of the stable isotope record is hypothesized to represent nursing, as the animal is receiving a stable lipid rich diet at that time. This period is followed by a decrease in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which represents weaning, when the animal begins to feed at a lower trophic level (zooplankton rather than its mother's tissue). Calf baleen plates only contain the fetal growth and nursing component of baleen (Fig. 3.4). Although nursing calves are

technically feeding at a higher trophic level than the rest of the population, they are not significantly enriched relative to lactating females ($\Delta^{13}\text{C} = 0.3\text{‰}$ and $\Delta^{15}\text{N} = 0.5\text{‰}$; Fig. 3.6). This has been noted in other marine mammal species, as milk is isotopically lighter in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than other maternal tissues (Jenkins et al. 2001). This results in no perceived trophic enrichment even though a trophic shift has occurred.

Isotopes As Migration Tracers

Studies of the isotopic landscape of the Gulf of Maine (Chapter 2) demonstrated that there are three isotopically distinct habitats within the Gulf that could be resolved with stable isotope analysis. The poor separation between habitat-specific baleen stable isotope signatures and the latitude of a whale's sighting within the particular habitat suggests that other factors influence right whale baleen isotope signatures, besides the variation created via the whale's migration (Fig. 3.7). Within the whales themselves, the effects of amino acid pool turnover may have a significant impact on the bulk isotope value of keratin. Keratin is composed of a mixture of amino acids, some of which are derived directly from the diet (essential) and some of which are synthesized by the body (non-essential). Essential amino acids have a short residence time in the body, that is, once they are ingested, they are quickly used in building new tissue. Non-essential amino acids, by comparison, can have longer residence times in the body and thus more opportunities to fractionate and carry a slightly heavier isotope signature.

As a whale moves into a new habitat to feed, it garners essential amino acids from its zooplankton prey that carry the specific isotope value of the foraging habitat. Baleen

that is synthesized at that moment will be made of a mixture of the newly acquired essential amino acids, as well as a smaller fraction of non-essential amino acids that have been cycling through the body and carry a slightly different signature. As whales supplement their zooplankton diet with internal stores of carbon and nitrogen, the amino acids (now exclusively derived from the whale rather than zooplankton) fractionate during metabolism and tissue synthesis, resulting in a different isotopic signature of the bulk tissue. Further study of the stable isotope ratios of amino acids within the bulk baleen tissue would be useful for determining the degree to which zooplankton vs. whale carbon and nitrogen sources change along the baleen isotope records.

Besides issues with internal fractionation of habitat-specific zooplankton signatures, short term right whale movement patterns may also serve to confound the interpretation of foraging location from isotope data. As described in an earlier section, right whales are highly mobile. Although a right whale may have been documented in a particular habitat on a particular date, it does not mean that it did not travel extensively before or after that sighting. The resolution of this study is such that each baleen isotope data point in adult whales represents approximately two weeks of data. Satellite tagging studies have shown that right whales are capable of making excursions on the order of 100s to 1,000s of kms in that amount of time (Baumgartner and Mate 2005). If an animal did travel extensively within a baleen isotope data point, the resulting signature would be an average of all the isotope sources that the animal had encountered recently.

At the start of this dissertation chapter, several lines of evidence were outlined as support of an “alternative habitat use hypothesis.” Although I did not observe a direct

correlation between foraging location and baleen stable isotope ratios, this study does give some evidence to the alternative habitat use hypothesis. Within the adult baleen isotope records, sighting events rarely occur at the extreme peaks and valleys of the stable isotope records (Appendix 2). Baleen stable isotope data points that are associated with sightings in the Gulf of Maine tend to occur in the middle values contained in the stable isotope signatures. For the “unknown” baleen isotope values, those that are not connected to a sighting event, the majority of these data points fall into the range represented by isotope data that we know was formed in the Gulf of Maine. The observation that the remaining “outlier” isotope values are not connected with a sighting record or an extrapolated Gulf of Maine isotope signature suggests that these data points were likely formed elsewhere. Based on a meta-analysis of zooplankton stable isotope values throughout the North Atlantic (McMahon et al. in prep.), zooplankton located off the coast of the United Kingdom, Spain, and northern Africa carry stable isotope signatures which could account for the extreme carbon peaks observed in baleen. Likewise, zooplankton collected off the coasts of Iceland, Greenland, and Norway carry stable isotope signatures that could account for the extreme valleys observed in right whale baleen. These areas also happen to be historical right whale habitat areas (Smith et al. 2006, Reeves et al. 2007). Therefore, right whale baleen stable isotope records lend further support to the alternative habitat use hypothesis.

CONCLUSIONS

Due to the high anthropogenic mortality rate observed in the right whale population, it is essential to determine when and where right whales occur in order to establish effective conservation measures. The primary goal of this study was to employ stable isotope ratios as migration tracers. Isotope records in *E. glacialis* baleen, like those of other large whale species, contain annual oscillations that correspond to broad-scale north/south migrations. To examine right whale movement patterns at seasonal time scales, baleen isotope records, the *North Atlantic Right Whale Catalog* sighting records for individual whales, and habitat-specific zooplankton stable isotope values were compared. Poor separation was seen between the latitude of sighting and baleen isotope signature, likely because of variable trophic enrichment between habitat areas, the confounding contribution of body nutrient pools that were de-coupled from diet (i.e. non-essential amino acids), and rapid movement by the whales between habitat areas. Baleen stable isotope values were observed that could have been formed in historical habitat areas. To improve right whale fisheries management, future exploratory surveys should be conducted in historical habitat areas.

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Table 3.1: Right Whale Life History Data and Baleen Sampling Plan. ^(a) Whale ID number corresponds to the whale's individual identification number in the *North Atlantic Right Whale Catalog* (Eg#), Smithsonian Institute (NMNH#) or Harvard Museum of Comparative Zoology (HMCZ#) database number, or necropsy field number (MH-##-Eg or EgNEFL#); ^(b) Age (in years) or the estimate of whale's minimum age, (J) denotes juvenile; ^(c) Year of the whale's death; ^(d) Relevant notes about each case, including cause of death and reproductive status. Table also shows which isotope ratios were measured in each baleen plate; (X) denotes sampled, (-) denotes not sampled.

Whale ID ^a	Age ^b	Sex	Year ^c	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{18}\text{O}$	δD	Notes ^d
EgNEFL0603	Calf	F	2006	X	X	X	X	Fishing Gear Entanglement
EgNEFL0602	Calf	M	2006	X	X	X	X	Vessel Collision
Eg2617	9	F	2005	X	X	–	–	Vessel Collision
Eg2301	12	F	2005	X	X	X	–	Chronic Fishing Gear Entanglement
Eg2143	14	F	2005	X	X	X	X	Vessel Collision, Pregnant
Eg1004	34	F	2004	X	X	X	X	Vessel Collision, Pregnant
Eg1238	19	M	2001	X	X	X	–	Acute Fishing Gear Entanglement
Eg1014	30	F	1999	X	X	X	–	Vessel Collision
Eg1623	12	M	1996	X	X	–	–	Vessel Collision
Eg2220	5	M	1996	X	X	–	–	Vessel Collision & Fishing Gear Entanglement
Eg2366 (HMCZ 62052)	2.5	M	1995	X	X	–	–	Chronic Fishing Gear Entanglement
Eg1223	12	F	1992	X	X	–	–	Vessel Collision, Nursing
Eg1504	1	F	1986	X	X	–	–	Vessel Collision
Eg1128	2	M	1983	X	X	–	–	Vessel Collision
MH-79-026-Eg (NMNH 504886)	3	M	1979	X	X	–	–	Vessel Collision
MH-76-056-Eg (NMNH 504343)	Calf	M	1976	X	X	–	–	Vessel Collision
MH-75-044-Eg (NMNH 504257)	J	M	1975	X	X	–	–	Undetermined

Table 3.2: Elemental Abundances and Stable Isotope Ratios in Right Whale Baleen. Range and mean \pm 1 SD of elemental abundances (expressed as % dry weight), stable isotope ratios measured and standards used, and the range and mean \pm 1 SD of stable isotope ratios (δ , ‰) measured in the baleen from adult, immature, and calf North Atlantic right whales. (*n*) denotes number of whales / number of isotope data points collected, (-) denotes no data.

Element	Composition (%) (Mean \pm 1 SD)	Isotope Ratio (Standard)	δ Range (‰) (Mean \pm 1 SD)	<i>n</i>
Adult Whales (\geq 9 years)				
Carbon	34.8 to 64.4 (47.1 \pm 2.2)	$^{13}\text{C}/^{12}\text{C}$ (PDB)	-21.8 to -16.7 (-19.7 \pm 0.9)	8 / 799
Nitrogen	10.1 to 19.2 (14.1 \pm 0.8)	$^{15}\text{N}/^{14}\text{N}$ (Air)	7.0 to 12.1 (10.3 \pm 0.9)	8 / 799
Oxygen	–	$^{18}\text{O}/^{16}\text{O}$ (VSMOW)	14.8 to 35.8 (19.2 \pm 1.9)	5 / 486
Hydrogen	–	$^2\text{H}/^1\text{H}$ (VSMOW)	-154.5 to -71.2 (-105.5 \pm 18.0)	2 / 211
Immature Whales (1 – 8 years)				
Carbon	35.4 to 63.8 (47.1 \pm 2.3)	$^{13}\text{C}/^{12}\text{C}$ (PDB)	-21.5 to -17.4 (-19.4 \pm 0.6)	6 / 306
Nitrogen	9.9 to 21.1 (14.4 \pm 0.9)	$^{15}\text{N}/^{14}\text{N}$ (Air)	8.2 to 13.2 (11.1 \pm 1.0)	6 / 306
Calves (0 years)				
Carbon	27.6 to 59.6 (46.7 \pm 3.3)	$^{13}\text{C}/^{12}\text{C}$ (PDB)	-20.9 to -18.8 (-19.8 \pm 0.5)	3 / 82
Nitrogen	8.3 to 17.2 (14.0 \pm 1.1)	$^{15}\text{N}/^{14}\text{N}$ (Air)	8.8 to 12.4 (10.6 \pm 0.9)	3 / 82
Oxygen	–	$^{18}\text{O}/^{16}\text{O}$ (VSMOW)	13.7 to 16.9 (15.1 \pm 1.3)	2 / 5
Hydrogen	–	$^2\text{H}/^1\text{H}$ (VSMOW)	-114.4 to -104.5 (-108.7 \pm 4.1)	2 / 5

Table 3.3: Growth rates of adult right whale baleen. The annual growth rates (period) are reported for the baleen isotope time series collected from eight adult right whales. The periods were estimated by determining the average distance between annually-occurring peaks in the baleen isotope records, and by using a statistical non-parametric estimation. These estimates of period were based on N isotope records (counting method) and all available isotope records were used for the statistical estimation (denoted by C, N, O, or H). The mean and best-fit period, in cm yr^{-1} , are reported for each individual.

Whale ID	Age	Sex	Isotopes	Period (cm yr^{-1})	
				Average distance between peaks	Statistical estimate
Eg1004	34	F	CNOH	24.9	24.2
Eg1014	30	F	CN	24.0	24.0
Eg1238	19	F	CNO	34.0	32.0
Eg2143	14	F	CNOH	29.7	28.8
Eg1623	12	M	CN	29.0	30.2
Eg1223	12	F	CN	29.6	29.6
Eg2301	12	M	CNO	30.7	22.2
Eg2617	9	F	CN	33.6	35.6

Table 3.4: Trophic Enrichment Between Right Whales and Zooplankton, by Habitat.

Mean carbon and nitrogen stable isotope signature (δ , ‰) of right whale baleen formed and zooplankton collected in the Gulf of Maine, and trophic enrichment (Δ , ‰) of right whales are reported. Trophic enrichment was calculated after: $\Delta = \delta_{\text{whale}} - \delta_{\text{zooplankton}}$. The same data are also reported by habitat areas (Cape Cod Bay, the Great South Channel, and the Bay of Fundy).

Gulf of Maine			
d Ratio	Whale	Zooplankton	Δ
$d^{13}\text{C}$	-19.6	-21.7	2.1
$d^{15}\text{N}$	10.2	8.0	2.2
$d^{18}\text{O}$	19.2	21.7	-2.5
dD	-115.1	-148.0	30.6
Cape Cod Bay			
d Ratio	Whale	Zooplankton	Δ
$d^{13}\text{C}$	-19.1	-19.9	0.8
$d^{15}\text{N}$	10.5	7.7	2.8
$d^{18}\text{O}$	19.0	23.3	-4.3
Great South Channel			
d Ratio	Whale	Zooplankton	Δ
$d^{13}\text{C}$	-20.0	-22.7	2.7
$d^{15}\text{N}$	9.7	8.0	1.7
$d^{18}\text{O}$	20.0	19.8	-0.2
dD	-139.4	-106.1	33.3
Bay of Fundy			
d Ratio	Whale	Zooplankton	Δ
$d^{13}\text{C}$	-19.7	-21.3	1.7
$d^{15}\text{N}$	10.4	8.3	2.1
$d^{18}\text{O}$	18.8	23.8	-5.0
dD	-118.4	-176.3	57.9

Figure 3.1: Map of Right Whale Habitat Areas in the Northwest Atlantic. Critical habitats and conservation areas are denoted with black polygons. Below the map, a timeline outlines the seasonal progression of right whale habitat use in the North Atlantic. Habitat codes are as follows: Cape Cod Bay (CCB), Great South Channel (GSC), Bay of Fundy (BoF), Roseway Basin (RB), northeast peak of Georges Bank (NEGB), Jeffreys Ledge (JL), and southeast United States (SEUS).

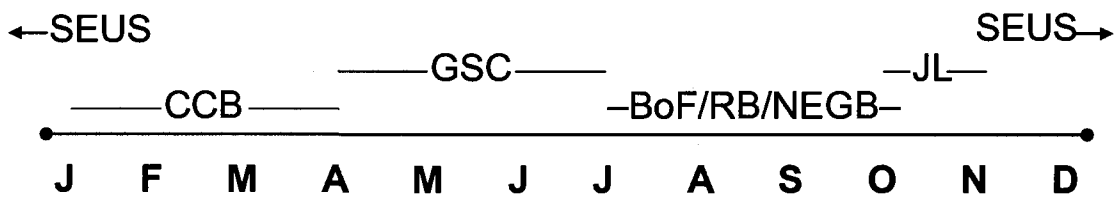
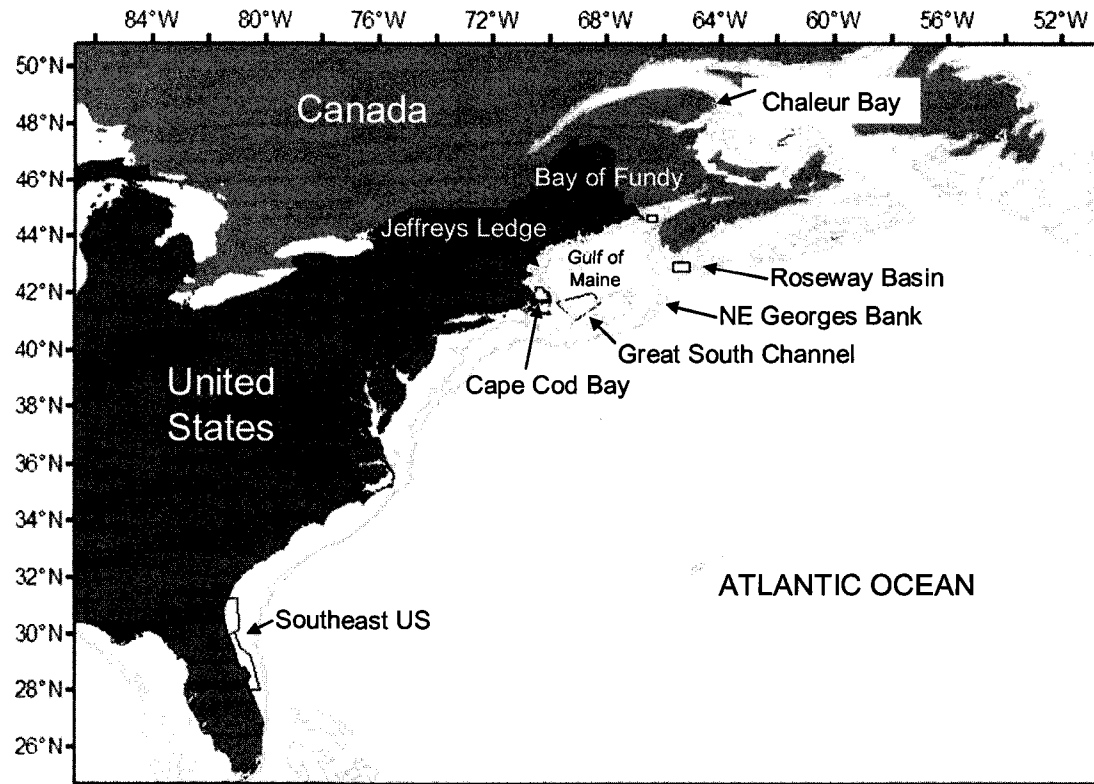


Figure 3.2: Adult Right Whale Baleen Stable Isotope Records. Carbon (a), nitrogen (b), oxygen (c), and hydrogen (d) stable isotope records from the baleen of an adult right whale (Eg1004). The endpoint of each timeseries was assigned as per the whale's date of death, and the dashed gray lines (denoting the January of each year) were placed according to each whale's annual baleen growth rate.

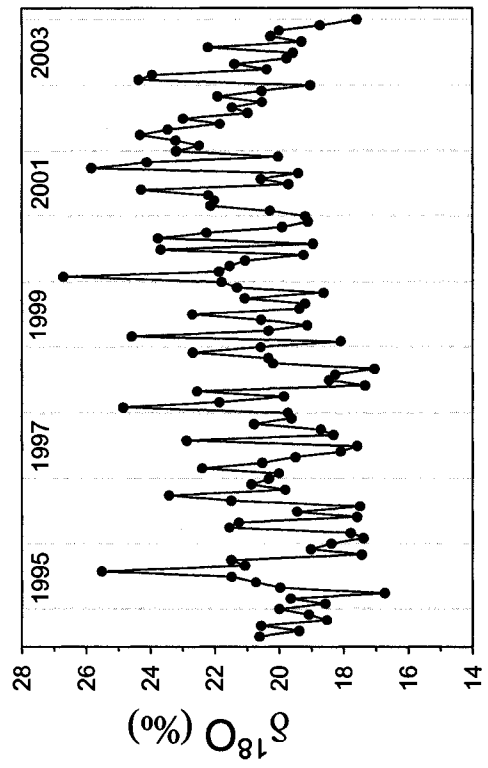
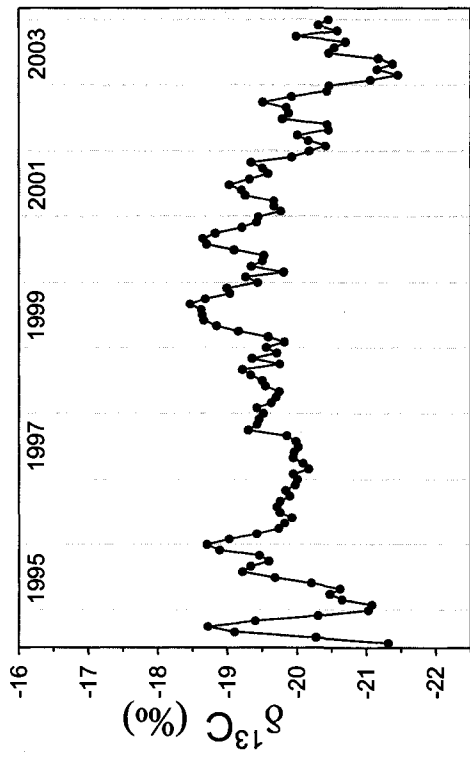
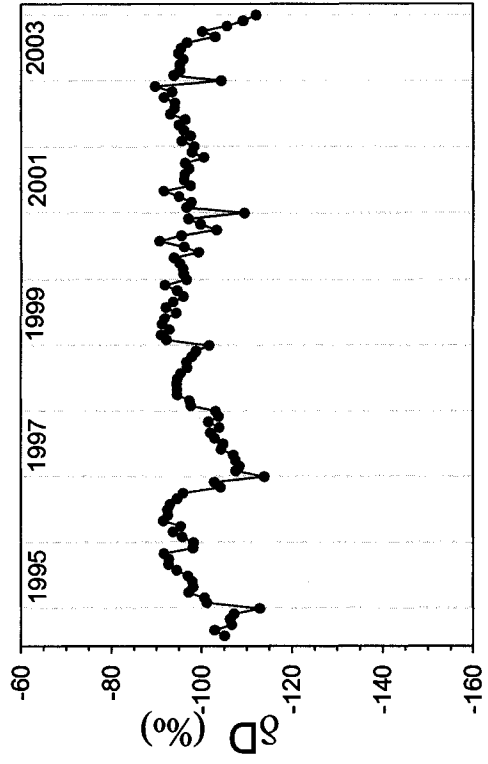
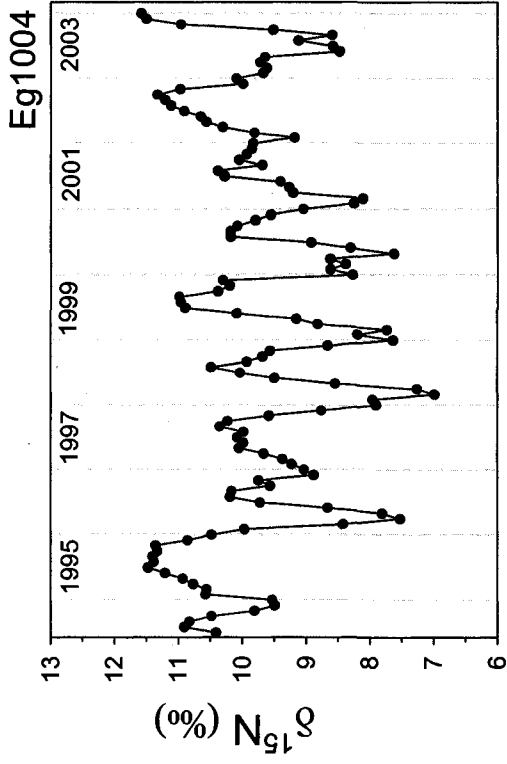


Figure 3.3: Immature Right Whale Stable Isotope Records. Carbon (○) and nitrogen (●) isotope records from the baleen of an immature right whale. Dataset is from Eg1128. The endpoint of each timeseries was assigned as per the whale's date of death, and the horizontal grayscale lines above the data delineate ontogenetic diet shifts that occurred with birth and weaning (designated by vertical dashed gray lines).

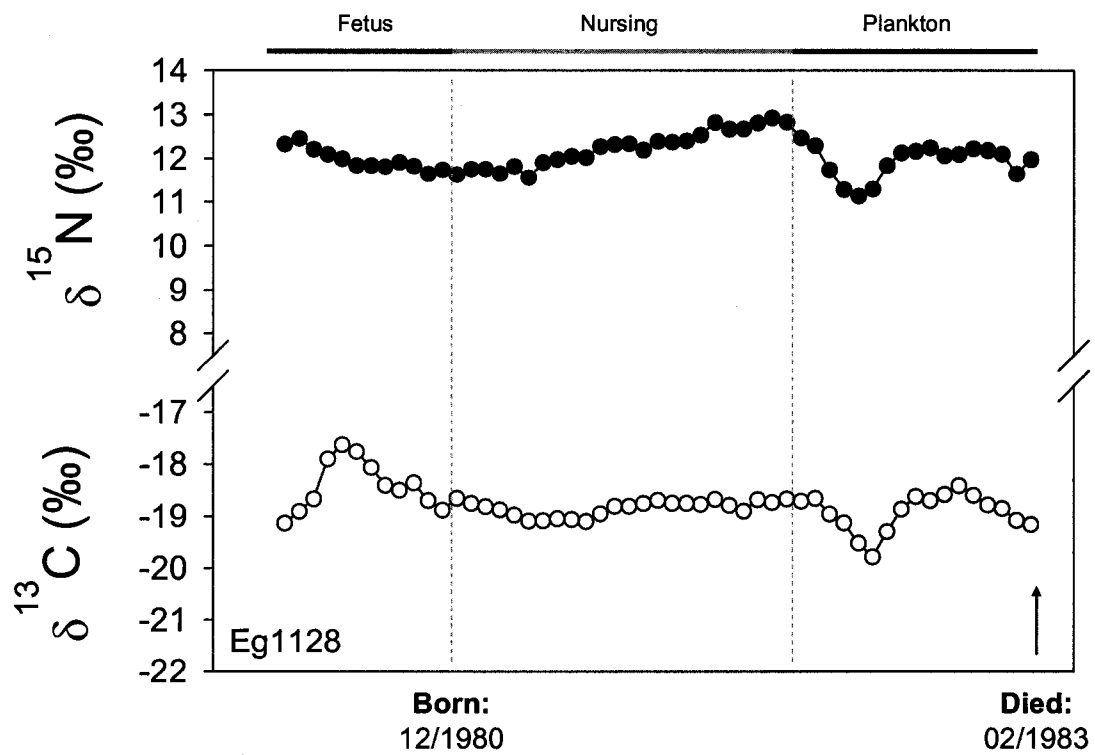


Figure 3.4: Calf Right Whale Stable Isotope Records. Carbon (○) and nitrogen (●) isotope ratios in the baleen of a right whale calf that died in 2006. Dataset is from EgNEFL0603. The endpoint of each timeseries was assigned as per the whale's date of death, and the horizontal grayscale lines above the data delineate ontogenetic diet shifts that occurred with birth (designated by a vertical dashed gray line).

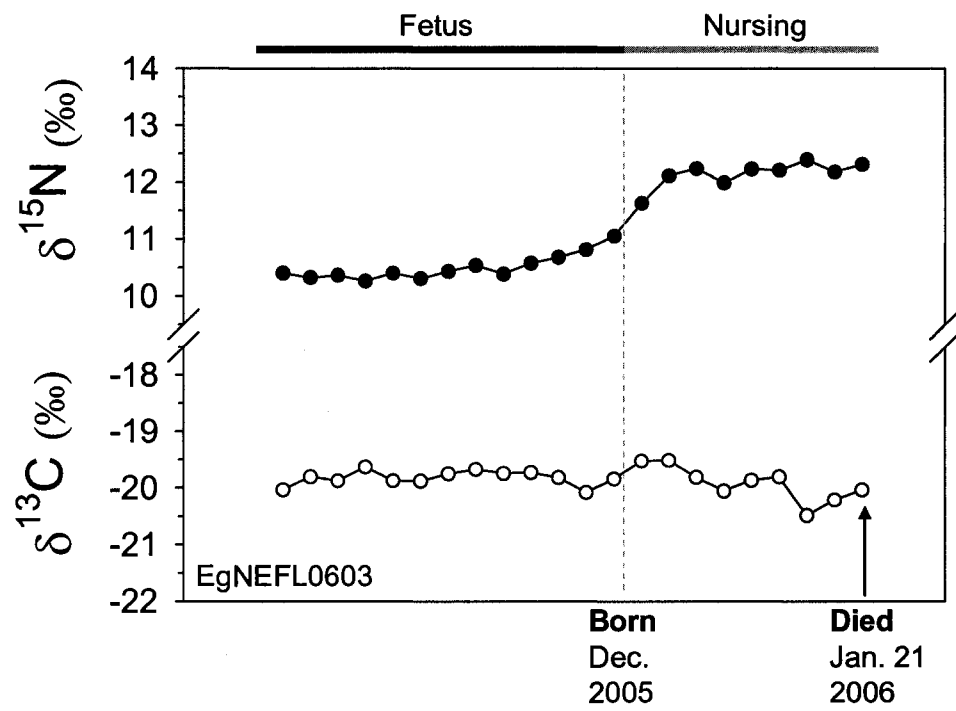


Figure 3.5: Habitat-Specific Trophic Enrichment Between Zooplankton and Right Whales: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of zooplankton (triangles) and right whale baleen (circles) that were collected or formed in Cape Cod Bay, the Great South Channel, or the Bay of Fundy. The right whale data are color-coded by life history status: immature (\circ), female (\bullet), and male (\bullet). Trophic enrichment (Δ , ‰) was calculated after: $\Delta = \delta_{\text{whales}} - \delta_{\text{zooplankton}}$.

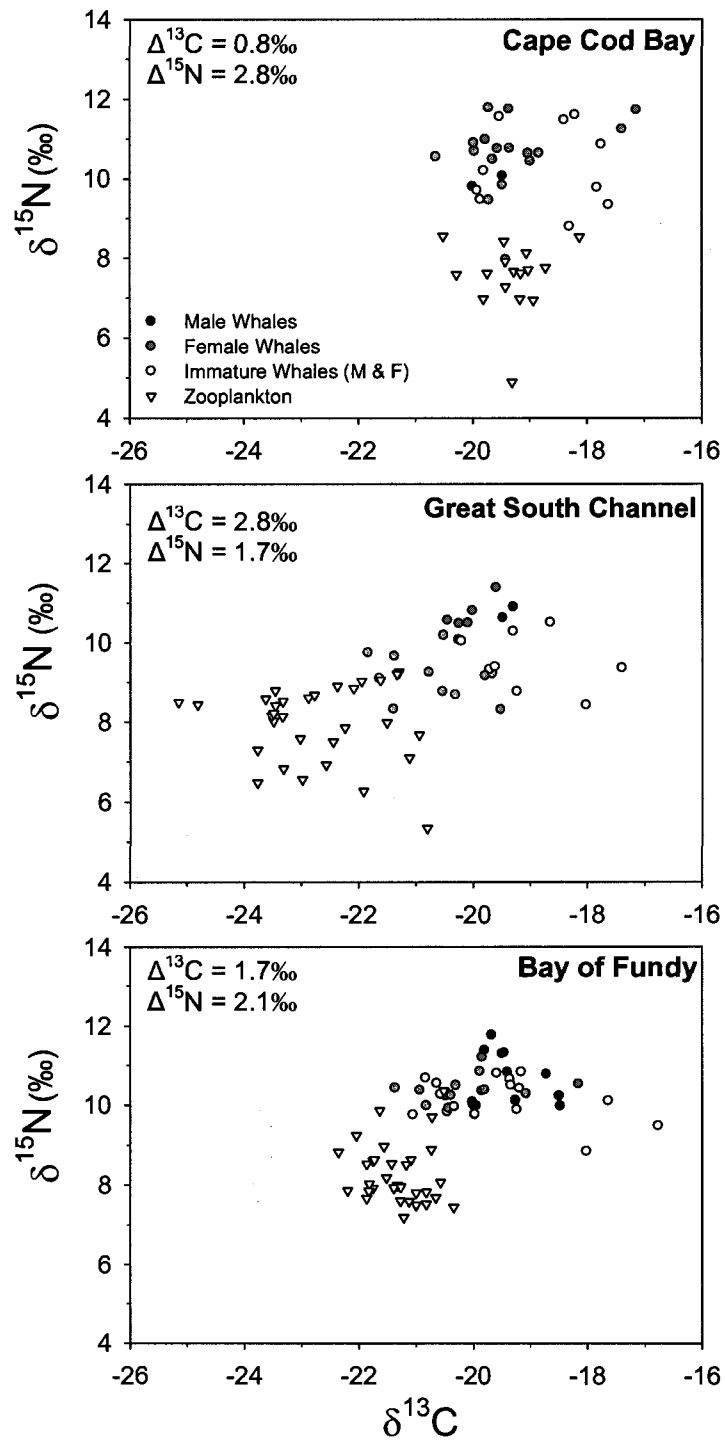


Figure 3.6: Trophic Enrichment Between Lactating Females and Right Whale Calves.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of lactating females (●) and calves (○). Trophic enrichment (Δ , ‰)

was calculated after: $\Delta = \delta_{\text{calves}} - \delta_{\text{fe,a,es}}$.

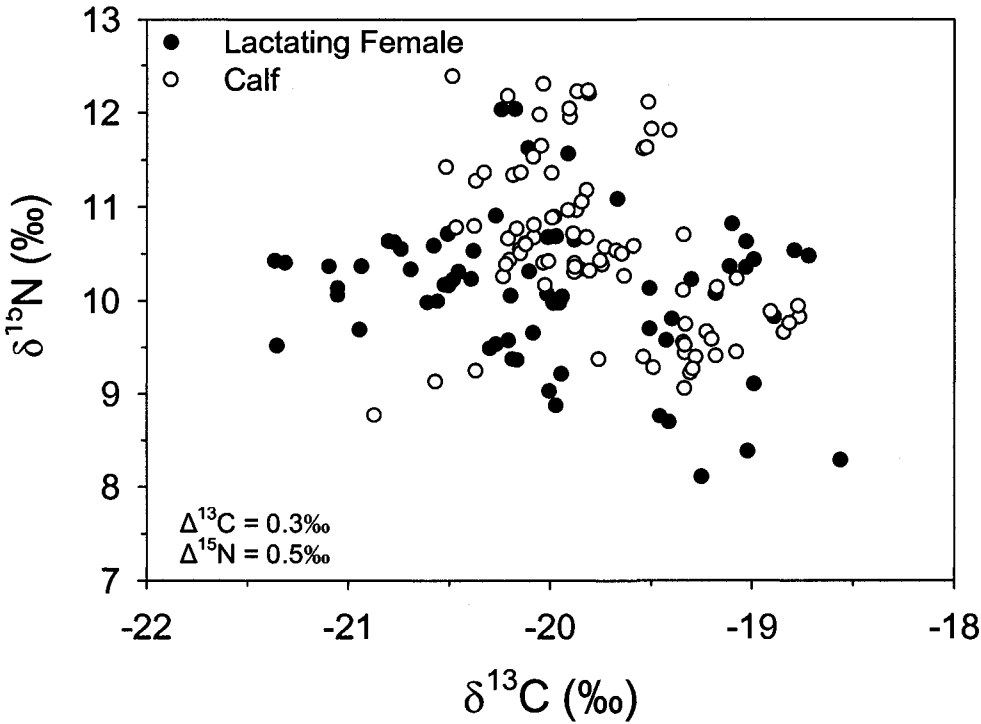


Figure 3.7: Stable Isotopes as a Tracer of Right Whale Migration. Baleen stable isotope ratios (‰) plotted against the latitude of sighting (°N). Linear regression, best-fit equation, and r^2 value are presented.

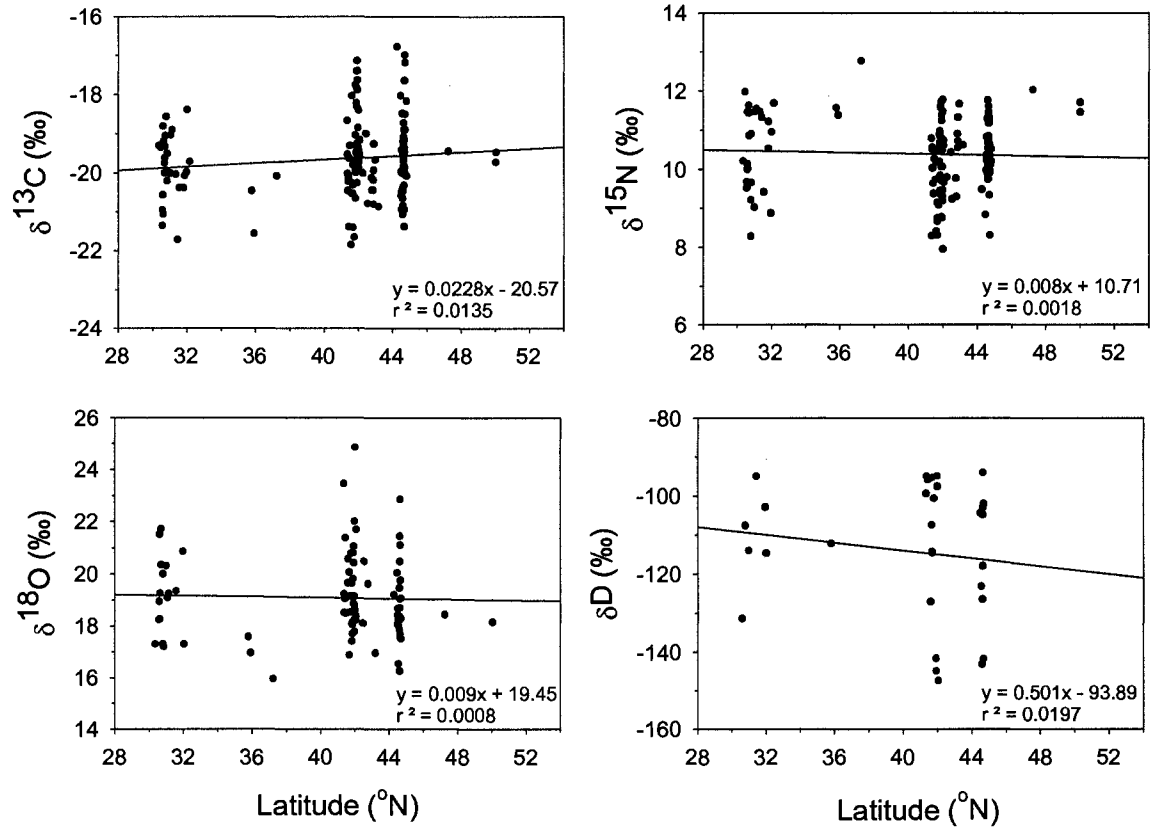
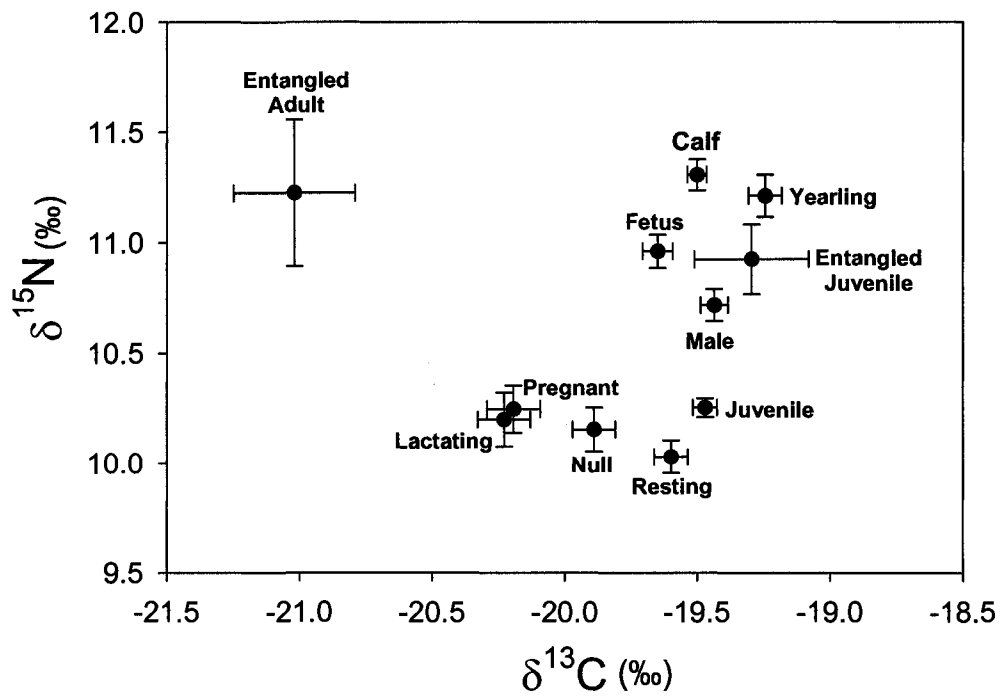
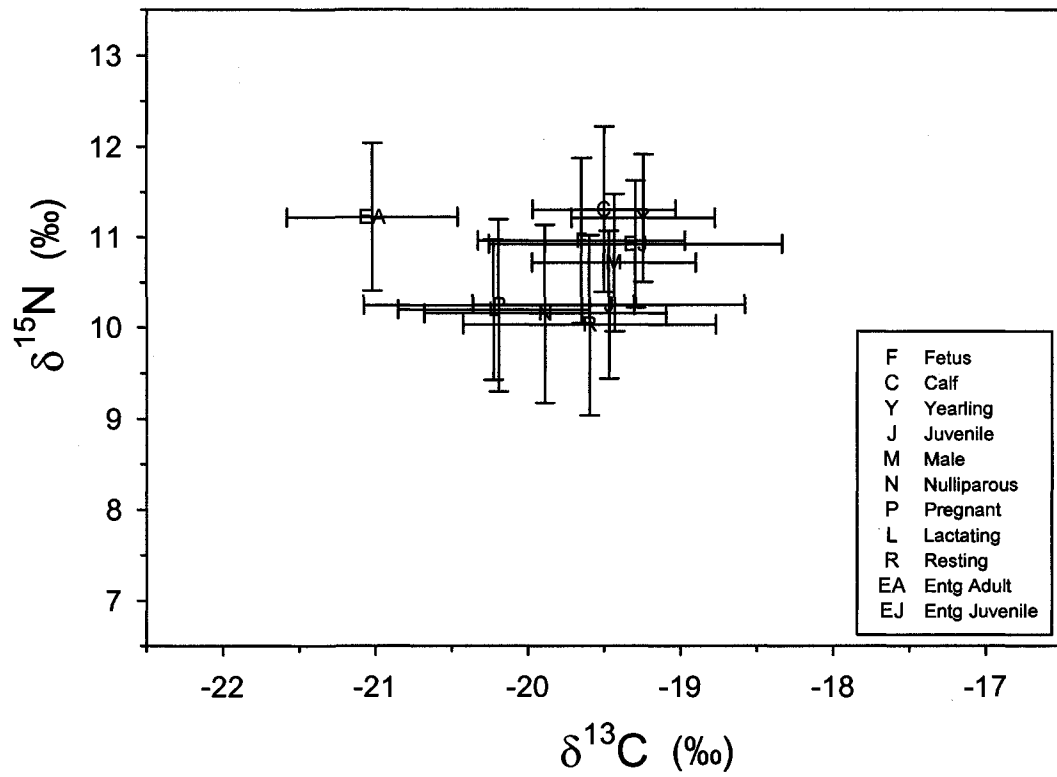


Figure 3.8: Demographic Separation of Stable Isotope Ratios in Right Whales. Baleen stable isotope data were coupled with *North Atlantic Right Whale Catalog* data to examine isotope separation between demographic groups within the population. Top panel shows mean \pm 1 SD for each demographic category. Symbol letters represent the following categories: F = Fetus, C = Calf, Y = Yearling, J = Juvenile, M = Male, N = Nulliparous, P = Pregnant, L = Lactating, R = Resting, EA= Entangled Adult, EJ = Entangled Juvenile. Bottom panel is an enlargement of the data, plotted as the mean \pm 1 SE for visibility.



CHAPTER 4

**LONG-TERM HABITAT USE AND THE INFLUENCE OF ENVIRONMENTAL
CHANGE ON STABLE ISOTOPE RECORDS IN NORTH ATLANTIC RIGHT
WHALE BALEEN**

ABSTRACT

Animal stable isotope records that include historical samples can be used as baselines with which to examine changes in a population's habitat use. To examine long-term ecological trends in North Atlantic right whale (*Eubalaena glacialis*) migration and habitat use, carbon and nitrogen stable isotope records were measured from the baleen plates of 12 whales, spanning the period from 1882 to 2005. Two distinct categories were used for data analysis: whales that were alive during the historical (1882-1915) and present-day (1986-2005) period. The nitrogen stable isotope signature of historical right whales was significantly lighter than that of present-day whales, while the carbon isotope signature of historical whales was heavier than that of present-day whales. These differences were attributed to a generally poorer state of health in the present-day population, and the isotopic dilution of atmospheric carbon dioxide due to increasing anthropogenic inputs throughout the study period. The shifts in the stable isotope value between the historical and modern right whales were attributed to factors independent of right whale migration behavior, thereby adding support to the hypothesis that present-day right whales continue to utilize historical habitat areas in the North Atlantic.

Additionally, a rapid 2.25‰ decrease in the carbon stable isotope ratios of the present-day whales was observed. Concurrent to this decrease, which began in 1998, the Pacific Decadal Oscillation switched from a warm to a cool phase, and Southern Oscillation changed from a historically strong El Niño event to a La Niña year. During the baleen $\delta^{13}\text{C}$ decline, right whale calving rates increased, inter-birth intervals decreased, and the abundance of *Calanus finmarchicus* (a major right whale food source)

increased in the Gulf of Maine, yet observed right whale habitat use remained consistent. While the $\delta^{13}\text{C}$ decrease observed in present-day baleen could not be directly attributed to any one factor or event, the results of this study demonstrate that environmental isotopic signals provide variation to animal stable isotope ratios, and should be considered when interpreting stable isotope records.

INTRODUCTION

It is well established that stable isotopes of animal tissue are indicators of animal foraging location and diet (Hobson 2007). Stable isotope ratios in the environment are influenced by biological and biogeochemical processes, and the regionally-specific stable isotope ratios that are formed become integrated into food webs by producers (Rubenstein and Hobson 2004). Consumers derive their stable isotope signature from their food source (Michener and Schell 1995), so as animals move between foraging locations, they acquire the stable isotope signature of their diet and, by extension, the local environment. As a result, two major sources for the stable isotope value of animal tissues are changes in feeding location (e.g. migration) or changes in diet. Stable isotope records, created by sampling many individuals from a population over time, can be used to study long-term trends in a population's foraging ecology and habitat use.

The significance of observed ecological shifts can be evaluated using historical data as a baseline, and these data may then guide contemporary conservation efforts (Newsome et al. 2007a). Studies utilizing pinniped bone and teeth (Hirons 2001, Hobson et al. 2004, Newsome et al. 2007b, Hirons and Potter 2008), fish otoliths (Gao and Beamish 2003), seabird feathers (Hobson et al. 2004), and cetacean baleen plates (Schell 2000) have been used to create such records, some of which represent 50-100 years of data. The goal of the current study was to create a stable isotope record from baleen plates with which to examine long-term trends in right whale habitat use. When compiling a large dataset of baleen carbon and nitrogen records collected to meet this objective, isotope shifts between the historical and present-day samples became apparent,

as did shifts within the present-day samples themselves. To make sense of the dramatic changes in stable isotope signatures in recent years, climatic, physical, and biological datasets were consulted.

MATERIALS AND METHODS

Stable isotope ratios were measured in the baleen of 12 adult North Atlantic right whales (Table 4.1), eight of which were collected recently and represent “**p**resent-**d**ay” data (**PD**, 1986-2005). The other four baleen plates were sampled at museums in the United States and United Kingdom, and were collected in the late 19th or early 20th century (Table 4.1). These four plates represent “**h**istorical” data (**H**, 1882-1915). Previous genetic analysis, using mtDNA sequences, confirmed that these baleen plates are from *E. glacialis* (Rosenbaum et al. 2000). Sample collection, processing, and analysis of the PD baleen plates are described in Chapter 3.

Stable Isotope Analysis of Historical Baleen

Four North Atlantic right whale baleen plates were acquired from archived collections at the Smithsonian Natural History Museum (Washington, D.C., USA), British Natural History Museum (London, UK), and National Museum of Scotland (Edinburgh, UK). Each baleen plate was cleaned thoroughly with repeated ethanol swabs until all surface contaminants were removed. The baleen plates were then sampled down the midline, at 2 cm intervals, with a multi-speed drill. The resulting powder shavings from each sampling interval were collected on a square of clean weighing paper, and

placed into a sterile 20 ml scintillation vial for storage. In preparation for stable isotope analysis, 0.8-1.2 mg of each sample was packaged into a 4 X 6 mm tin capsule and crimped shut.

All samples were sent to the University of California Davis Stable Isotope Facility for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. During analysis, the samples were loaded into an autosampler and were individually dropped into an elemental analyzer interfaced to an isotope ratio mass spectrometer (IRMS). Instrumentation included a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 IRMS. Each sample was pyrolyzed into CO_2 and N_2 gas and then separated on a gas chromatograph (GC) column. The gases were conveyed to the IRMS with a continuous flow of helium carrier gas. Each sample isotope ratio was compared to a secondary gas standard, whose isotope ratio had been calibrated to international standards (PeeDee Belemnite (PDB) for $\delta^{13}\text{C}$, Craig 1957; and atmospheric nitrogen (N_2) for $\delta^{15}\text{N}$, Mariotti 1985). The total C and N content of each sample were reported along with stable isotope data. C:N ratios and % C and N were calculated from the reported measurements of total C and N content in each sample.

All samples are reported relative to international reference standards: carbon isotope values relative to PDB, and nitrogen values relative to N_2 . Stable isotope measurements are expressed in standard delta (δ) notation, as parts per thousand (per mil, ‰), by the following:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1,000$$

where R_{sample} and R_{standard} are the ratios of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ of the sample and standard, respectively (McKinney 1950). Analytical precision was determined with laboratory

working standards of glycine, which were analyzed after every 12 baleen samples. These standards were calibrated against NIST Standard Reference Materials. Precisions based on the standard deviation of the series of reference checks used in the analysis were 0.05‰ ($\delta^{13}\text{C}$) and 0.20‰ ($\delta^{15}\text{N}$).

Baleen Time Series

The temporal context of the PD baleen isotope records was established using the date of each whale's death as an endpoint and two independent estimations of annual baleen growth rate (Chapter 3). The endpoint of the H whale isotope records (i.e. the whale's date of death) could not be determined with the same confidence as in the PD whales, since the month and day of death was not readily available for H whales. The H baleen plates did have an associated collection year within each respective museum's database, and this date was the first order estimate of when the isotope record should end in time. A detailed study of the PD baleen plates revealed that the annual peaks in baleen isotope records occur in the winter, so the annual peaks in the H baleen records were arbitrarily assigned as the starting point of each subsequent year.

To examine shifts in isotope value between H and PD baleen, mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were computed for each individual, and then individuals were used as replicates to statistically test for differences between the grand means of the H and PD categories. The H and PD means were also compared to mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for an Entangled whale (Eg2301). Although this entangled whale is a part of the PD dataset, the portion of the baleen isotope record that encompassed the entanglement (Sept. 2004 – March 2005)

were compared removed from the PD dataset for analysis. All groups (H, PD, E) were compared using a one-way ANOVA test.

Carbon Dioxide

Measurements of atmospheric CO₂ concentrations were collected from the Law Dome Ice Cores (Antarctica, 1832-1978, Etheridge et al. 1998) and at the Barrow Observatory (Alaska, USA, 1971-2005). Data were acquired from the Carbon Dioxide Information Analysis Center (www.cdiac.ornl.gov) and the National Oceanic and Atmospheric Administration Earth System Research Laboratory (www.esrl.noaa.gov) websites, respectively. $\delta^{13}\text{C}$ ratios of atmospheric CO₂ were determined from air samples collected at the Barrow Observatory. These stable isotope samples were analyzed by researchers at the University of Colorado/INSTAAR Stable Isotope Laboratory.

Surface seawater collections took place on research cruises in the waters off Bermuda, associated with the Bermuda Atlantic Time-series Study (BATS, Steinberg et al. 2001). Water from 0-10m was collected in Niskin bottles and analyzed for total CO₂ (ΣCO_2 , $\mu\text{mol kg}^{-1}$). Data from 1985-2005 were downloaded from the Bermuda Institute of Ocean Sciences website (<http://www.bios.edu/research/bats.html>).

Right Whale Migration and Reproduction

Several of the PD whales were able to be visually or genetically matched to animals recorded in the *North Atlantic Right Whale Catalog* (<http://rwcatalog.neaq.org/>) (Table 4.1). The sighting records associated with these animals were obtained from the

New England Aquarium. Additionally, population-wide measures of annual reproductive rates (calving rate and mean calving interval) were compiled by researchers at the New England Aquarium, using *Catalog* data. The calving rate (calves yr⁻¹) is the observed number of calves born each year. The mean calving interval (yr) represents an annual measure of the average number of years between calving events for reproductive females. Stereotypically, female right whales exhibit an inter-birth interval of three years: one year for lactation of a new calf, a year of recovery, and a subsequent year of a new pregnancy, although this has been much higher for North Atlantic right whales in recent years (Knowlton et al. 1994, Kraus et al. 2001, Kraus et al. 2007). All right whale sighting and demographic data were used with permission from the North Atlantic Right Whale Consortium (Right Whale Consortium 2008b).

Climatic Oscillations

Four major climatic oscillations known to influence ocean circulation, temperature, and biological productivity were referenced in this study. The North Atlantic Oscillation (NAO) Index is a measure of the difference in sea-level pressure between the Icelandic Low and the Azores High, and controls the strength of storms and westerly winds in the North Atlantic (Hurrell 1995). An NAO Index was acquired from the National Center for Atmospheric Research website (www.cgd.ucar.edu/cas/jhurrell/indices.html). The Atlantic Multi-Decadal Oscillation (AMO) Index is known as the mode of natural variability occurring in the North Atlantic, and is manifested primarily in sea surface temperature (Kerr 2005). An AMO Index was

acquired from the National Atmospheric and Oceanic Administration Earth System Research Laboratory website (<http://www.cdc.noaa.gov/Timeseries/AMO/>). The El Niño Southern Oscillation (ENSO) Index is calculated from the monthly fluctuations in air pressure difference between Tahiti and Darwin, Australia (Stenseth et al. 2002). Sustained negative phases of the ENSO Index are often deemed El Niño events, while sustained positive phases are La Niña events. The ENSO Index was acquired from the National Center for Atmospheric Research website (<http://www.cgd.ucar.edu/cas/catalog/climind/ENSO.html>). The Pacific Decadal Oscillation (PDO) Index is defined as the leading principal component of North Pacific SST variability (Bond and Harrison 2000). It is similar to the ENSO, though its periodicity is much longer (i.e. approximately 20-30 years between events, rather than < 2 years; Zhang et al. 1997). The PDO Index was acquired from the University of Washington Climate Impacts Group website (<http://jisao.washington.edu/pdo/PDO.latest>). Correlation coefficients were computed between mean annual baleen carbon and nitrogen records and each climatic index at zero, one, two, and three year lags of the isotope data behind the oscillation index.

RESULTS AND DISCUSSION

Baleen Stable Isotope Record

A long-term biogeochemical record, from 1882-2005, was created using right whale baleen stable isotope ratios (Fig. 4.1). Due to a lack of available baleen plates, one small gap (from 1885-1904) and one large gap (from 1915-1986) exist in the record. The

H (1882-1915) and PD (1986-2005) baleen had similar elemental compositions (expressed as % dry weight, Table 4.2) and C:N ratios (H = 3.39 and PD = 3.35). The similarities in these measurements suggest that degradation or diagenesis, which could compromise the stable isotope data (Ambrose and DeNiro 1986), did not occur in the H baleen. The mean $\delta^{15}\text{N}$ value of H baleen was significantly lighter than PD baleen (one-way ANOVA, $F = 7.41$, $p = 0.01$), while the mean $\delta^{13}\text{C}$ value of H baleen was significantly heavier than PD baleen (one-way ANOVA, $F = 50.34$, $p < 0.001$) (Table 4.3, Fig. 4.2). The entangled whale had a significantly lighter $\delta^{13}\text{C}$ signature than both H and PD whales (one-way ANOVA, $F = 50.34$, $p < 0.001$), and had a $\delta^{15}\text{N}$ signature that was heavier than that of H whales but not significantly different than that of PD whales (one-way ANOVA, $F = 7.41$, $p = 0.01$) (Table 4.3, Fig. 4.2). A large, rapid $\delta^{13}\text{C}$ decrease also occurred within the PD baleen record itself. The baleen $\delta^{13}\text{C}$ record decreased 2.25‰ in only 6 years (from -18.84‰ in 1999 to -21.09‰ in 2005; Figs. 4.1, 4.4). This decrease is measured in the carbon isotope records of 4 adult right whales (Eg1004, Eg2143, Eg2301, and Eg2617). In addition to the negative trend, all 4 whales maintain the seasonal patterns/oscillations along the length of their baleen plates.

Nitrogen Isotope Records

In stable isotope studies, $\delta^{15}\text{N}$ is considered to be a marker of trophic position since it increases several per mil units with every trophic step (Minagawa and Wada 1984, Michener and Schell 1995). Therefore, if the $\delta^{15}\text{N}$ value of a species or population increases significantly over time, it is often suggested that a dietary shift to a higher

trophic level has occurred (Hirons 2001, deHart 2006, Tucker et al. 2007). In this case, a large shift ($\approx 1.9\text{‰}$) in $\delta^{15}\text{N}$ occurred between the H whales (mean = 8.4‰) and the PD whales (mean = 10.3‰). While this increase could be interpreted as a trophic shift in the PD population (Vander Zanden et al. 2001), this seems unlikely given that right whales are so highly specialized to feed on mesoplankton (Baumgartner et al. 2007).

$\delta^{15}\text{N}$ values also increase in animal tissue during periods of physiological stress, when animals are in negative N balance and are forced to catabolize their own tissue (Hobson et al. 1993, Fuller et al. 2005). Several lines of evidence suggest that PD right whales are in poor health overall: they are thinner than southern right whales, a sister species (Angell 2005); they are highly inbred (Waldick et al. 2002, Frasier et al. 2007b); they exhibit a depressed reproductive rate (Kraus et al. 2007); and outbreaks of lesions and other external indicators of poor health have been observed in the population (Pettis et al. 2004, Rolland et al. 2007). Some researchers also hypothesize that right whales may be food limited (Reeves 1978). If the present-day right whale population is chronically stressed, their overall $\delta^{15}\text{N}$ signature would increase, despite their foraging at a similar trophic level to the historical population. This assertion is supported by the statistical similarity between the entangled whale (which shows isotopic evidence of nutritional stress) and PD whales.

Carbon Isotope Records

Previous studies of long-term isotope records in marine mammal tissue have reported long-term (50-70 year) sustained decreases in $\delta^{13}\text{C}$. Several of these studies

have analyzed marine mammal tissue originating from the North Pacific, specifically the Gulf of Alaska and Bering Sea regions (e.g. bowhead whales, Schell 2000; Steller sea lions and harbor seals, Hirons 2001, Hobson et al. 2004; and northern fur seals, Newsome et al. 2007a-b). The mechanism(s) behind these sustained decreases is a matter of contention in the scientific literature (for example, see Schell 2000, Cullen et al. 2001, and Schell 2001); with either a decline regional primary productivity or isotopic dilution of atmospheric carbon dioxide being most common explanations. This study provides a potential litmus test for determining which parameter is causing the decline in marine mammal carbon isotope records – as here the geographical scope is widened to include the Atlantic. If similar trends are seen across ocean basins, then North Pacific-specific regional trends in primary productivity would likely not be the cause of observed $\delta^{13}\text{C}$ declines in marine mammals.

Concurrent to long-term decreases in marine mammal $\delta^{13}\text{C}$ records, atmospheric carbon dioxide concentrations have been steadily increasing (Keeling et al. 1998). The majority of this increase in CO_2 can be attributed to anthropogenic inputs and impacts (e.g. fossil fuel burning and land use changes; IPCC 2007). Fossil-fuel derived CO_2 is depleted in ^{13}C relative to ambient, which effectively dilutes the atmospheric carbon pool as its concentrations increase (known as the Suess Effect, Tans 1979). In the sub-polar oceans, this dilution results in a $\delta^{13}\text{C}$ decrease of -0.1‰ decade^{-1} (Sonnerup et al. 1999). During the 123 year period represented by the right whale baleen isotope record, atmospheric carbon dioxide concentrations increased from approximately 293 ppm to 380 ppm (Etheridge et al. 1998; Fig. 4.3). Over this period, the mean $\delta^{13}\text{C}$ of the baleen

record decreased from -19.93‰ in 1882 to -21.02‰ in 2005 (difference = 1.09‰). The expected dilution of marine carbon due to the Suess Effect (over the period represented by the baleen isotope record) is -1.23‰, thereby accounting for the majority of the $\delta^{13}\text{C}$ decrease seen over the extent of the baleen record.

The rapid $\delta^{13}\text{C}$ decrease that occurred within the PD baleen record is not easily explained by the Suess Effect, however. The baleen $\delta^{13}\text{C}$ record decreased 2.25‰ in only 6 years (from -18.84‰ in 1999 to -21.09‰ in 2005; Figs. 4.1, 4.4). Concurrent to this observed decrease, atmospheric CO_2 concentrations increased steadily (from 347 ppm in 1986 to 380 ppm in 2005) and $\delta^{13}\text{C}$ measurements of atmospheric CO_2 decreased steadily (from -7.9 to -8.4‰) (Fig. 4.5). Similarly, total CO_2 ($\mu\text{g kg}^{-1}$) measured in the surface ocean near Bermuda increased slowly during the PD isotope record (Fig. 4.5). From these three records of environmental carbon (atmospheric $[\text{CO}_2]$ and $\delta^{13}\text{C}$, and ocean ΣCO_2), there is no evidence of a sudden increase in the input of carbon dioxide to the marine environment. According to published estimates of the contribution of the Suess Effect, < -0.2‰ of the observed change over the 20 year PD record can be attributed to this phenomenon. To account for the PD baleen $\delta^{13}\text{C}$ decrease, other contributing factors must be considered.

North Atlantic Right Whales

In other studies examining long-term carbon isotope declines in marine mammals, some authors have suggested that the observed isotope declines could be caused by populations foraging progressively farther offshore (Hirons 2001). In general, inshore

waters are more ^{13}C enriched than offshore waters (Hobson 1999, McMahon et al. in prep.). Factors such as phytoplankton species composition and growth rate (Fry & Wainright 1991), inputs from ^{13}C enriched benthic macrophytes, higher nutrient concentrations, and greater overall productivity lead to higher $\delta^{13}\text{C}$ values in coastal regions, especially in upwelling areas or during phytoplankton blooms (Schell et al. 1989; Burton & Koch 1999). By contrast, pelagic waters are ^{12}C enriched, and are characterized by less nutrient availability, lower productivity and phytoplankton growth rates, and an absence of macrophytes. If a marine mammal population increases their reliance on offshore habitats, one would expect an overall decrease in corresponding tissue $\delta^{13}\text{C}$.

To examine trends in right whale movement and habitat use patterns, sighting records of the PD whales from the *Catalog* were examined before and during the $\delta^{13}\text{C}$ decline. In general, PD whales were sighted in similar habitat areas at similar times of year before and during the $\delta^{13}\text{C}$ decline (Fig. 4.6). While this simple comparison does not address if right whales were present in greater densities at alternative habitats (i.e. not their primary habitats in the Gulf of Maine, where survey effort is focused) during one of the two periods, it does demonstrate that the sampled whales were not wholly absent from their primary foraging habitats in the Gulf of Maine before or during the $\delta^{13}\text{C}$ decline.

In the years before the $\delta^{13}\text{C}$ decline, anomalous migration behavior in the right whale population was documented on two occasions. Right whales abandoned two of their seasonal foraging habitats in the Gulf of Maine; Great South Channel in 1992, and

Roseway Basin from 1993-1999 (Kenney 2001, Patrician 2005). Lower concentrations of *Calanus finmarchicus*, the favored prey of right whales, were noted in these habitats during the abandonment periods, suggesting that right whales modified their distribution in years when zooplankton resources were limited (Kenney 2001, Patrician 2005).

Two measures of right whale reproductive rate, mean calving or inter-birth interval (yr) and annual calving rate (calves yr⁻¹), were examined for evidence of changes in population dynamics before and during the $\delta^{13}\text{C}$ decline. In the 1990s, the population-wide calving interval increased steadily, and began to decline in 1999 (Right Whale Consortium 2008b, Fig. 4.7). Annual calving rate was highly variable throughout the entire study period, 1986-2005 (Kraus et al. 2007, Fig. 4.7). Calving rates were lowest in the early and late 1990s (1993-1995 and 1998-2000). In 2001, calving reached a record high, presumably because a large number of females who were unable to calve in previous years were available to do so (Greene et al. 2003, Greene and Pershing 2004). Since females must accumulate sufficient storages of body fat to support a fetus and nursing calf in order to successfully reproduce, food limitation is speculated as a likely factor in the low calving success of right whales in the late 1990s (Greene et al. 2003). Acoustic measurements of right whale blubber thickness, a proxy for body condition, showed that whales were thinner overall during years when their copepod prey was less abundant in the water column (Angell 2005).

Data from Continuous Plankton Recorder (CPR) surveys conducted in and around the primary right whale foraging grounds in the Gulf of Maine demonstrate that [lipid rich, isotopically light] late stage *C. finmarchicus* copepods increased in abundance

beginning in 1998 (Pershing et al. 2005). These data suggest that foraging conditions improved overall for right whales at the onset of the $\delta^{13}\text{C}$ decline. Acoustic measurements of right whale blubber thickness collected from 1998-2002 increased progressively over this period (Angell 2005), presumably as a direct result of improving foraging conditions in the Gulf of Maine. Given the cycle of right whale reproduction, a one to three year lag would occur before the banner foraging conditions translated into an increase in calves born into the population. This was observed in PD right whales, as calving rate increased three years following the 1998 increase in Gulf of Maine *C. finmarchicus* abundance (Fig. 4.6).

Climatic Oscillations

The PD baleen nitrogen and carbon stable isotope records were compared to four climatic indices: the North Atlantic Oscillation Index (NAO), Atlantic Multi-Decadal Oscillation Index (AMO), Pacific Decadal Oscillation Index (PDO), and the Southern Oscillation Index (ENSO) (Fig. 4.8). Correlation coefficients were determined for each isotope-oscillation index combination, and correlations were tested with a zero, one, two, and three year lag of the isotope data behind the oscillation index (Table 4.4). Poor direct correlations were found between the isotope data and climate oscillations, but correlations between $\delta^{15}\text{N}$ and the NAO (lag = 0), AMO (lag = 0, 1, 2), and PDO (lag = 3) were statistically significant. Two oscillations changed phase in the year prior to the $\delta^{13}\text{C}$ decline; in 1998 PDO changed from a warm phase to a cool phase, while the ENSO was characterized by a very strong El Niño event that switched to a La Niña in 1998.

Prevailing climate and atmospheric fluctuations influence a variety of marine ecological processes (Saether 1997). Marine animals are indirectly affected by these fluctuations; temperature, ocean circulation, and weather patterns changes associated with natural climate cycles influence the abundance and distribution of their prey (Stenseth et al. 2002). As seen in this study, direct correlations between animals and climate fluctuation are difficult to quantify, but recent studies have identified linkages between marine mammal reproductive parameters and climate patterns such as the Southern Oscillation (Leaper et al. 2006, Vergani et al. 2008) and the North Atlantic Oscillation (Greene and Pershing 2004).

Climatic fluctuations can induce changes in the physical characteristics of the marine environment (such as temperature, salinity, CO₂ concentration ([CO₂]_{aq}), and N cycling), which are important factors that determine the stable isotope baseline of an environment (see Chapter 2). Given the trophic transfer mechanism of stable isotope ratios, these climate-derived changes would be incorporated into local food webs and then into animal tissues. Climatic oscillations induce physical changes into environment at variable temporal scales. Oscillations such as the PDO is characterized by a long periodicity (20-30 years, Zhang et al. 1997), and phase changes are usually known as regime shifts due to their immense ecosystem impacts and restructuring (Overland et al. 2008). Through analysis of a 60 year (1945-2005) carbon and nitrogen isotope record of northern fur seal teeth, Newsome et al. (2007b) correlated oscillations in the dentin isotope record (characterized by a 22 year period) to PDO phase changes. In the Atlantic,

the NAO is the dominant climate oscillation mode, and it changes phase at shorter time scales.

Given the periodicity of the NAO, we should expect that marine mammal isotope records derived from North Atlantic populations to respond at equally short temporal scales. At semi-decadal or inter-annual temporal scales, circulation into the GoM has been associated with NAO fluctuations (Greene and Pershing 2003). Changes in the relative contribution of slope water sources (Warm Slope Water, WSW vs. Labrador Slope Water, LSW) to the GoM have been associated with phase changes in the NAO such that during positive NAO phases, relatively warm and salty WSW enters the Gulf through the Northeast Channel, while colder and fresher LSW dominates the deep water inflow in during negative NAO phases (Greene and Pershing 2003).

The dominant slope water source to the GoM may result in differential advection of *C. finmarchicus* into the Gulf (MERCINA 2004). The recent decrease in the abundance of *C. finmarchicus*, from 1996 – 2000, and aforementioned subsequent increase in 1998, has been attributed to a sudden drop in the NAO Index and associated changes in slope water inputs to the GoM (Greene and Pershing 2000). To further examine the influence of the NAO on right whale baleen $\delta^{13}\text{C}$, the isotope record needs to be extended to present.

CONCLUSIONS

Historical and present-day isotope records, derived from baleen plates, were examined to address long-term trends in right whale habitat use. Significant differences

in the carbon and nitrogen stable isotope signatures were found between historical and present-day right whales, but these differences could be accounted for by prolonged anthropogenic inputs of carbon dioxide and an overall lower health condition in the present-day population.

A dramatic decrease in carbon stable isotopes was measured in the latter portion of the present-day baleen record. Sighting records confirmed that this isotopic decrease was not due to a significant change in habitat use by the right whale population. Records of zooplankton abundance and right whale calving records provide evidence that foraging conditions improved in the Gulf of Maine just prior to the decline in baleen carbon isotopes. The Pacific Decadal Oscillation and Southern Oscillation both changed phases just prior to the observed decline, yet poor direct correlations were seen between the PDO and ENSO indices and mean annual baleen isotope values. Also, the swift recovery of the NAO following a historical low in 1996 established conditions that facilitated an increase in Gulf of Maine *C. finmarchicus* (a lipid rich, isotopically light copepod species) abundance, and a [lagged] increase in right whale reproductive success. The increase in *C. finmarchicus* and right whale calving success occurred in tandem with the baleen $\delta^{13}\text{C}$ decline.

Several studies have observed similar $\delta^{13}\text{C}$ declines in the stable isotope records of marine mammals (including: northern fur seals, Newsome et al. 2007a-b; Steller sea lions, Hirons 2001, Hobson et al. 2004; Hawaiian monk seals, Hirons 2008; and bowhead whales, Schell 2000, Lee et al. 2005), although the duration of the record and magnitude of the decline vary by species. The interpretation of these studies also varies, but

commonly cited explanations are: a change in foraging/migration behavior from coastal to more offshore habitats (Hirons 2001, Hirons and Potter 2008), an ecosystem-wide decrease in primary production (Schell 2000, Hirons 2001, Newsome et al. 2007b), or the impact of the Pacific Decadal Oscillation (Newsome et al. 2007b). This study adds to the rising number of observed dramatic and rapid decreases in marine mammal $\delta^{13}\text{C}$ records. The wide geographic range represented by these studies (North Atlantic, North Pacific, equatorial Pacific) suggests that a multiple phenomena (both regional (i.e. climatic oscillations and changes in primary productivity) and global (i.e. environmental isotope dilution from anthropogenic inputs) are influencing marine mammal foraging ecology in a variety of marine ecosystems.

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Table 4.1: Right Whale Life History Data and Baleen Sampling Plan. Whale identification numbers correspond to the sample's code in the following museum databases: Smithsonian National Museum of Natural History (NMNH), British Museum of Natural History (BMNH), and National Museum of Scotland (NMS).; or the host whale's identification number in the *North Atlantic Right Whale Catalog* (Eg#). U = unknown.

Whale ID	Age	Sex	Collection Year	Notes
NMNH 22640	U	U	1885	Whaling – Long Island, NY (USA)
BMNH ZD.1891.9.12.1	A	M	1892	Whaling – Iceland
NMS 1907.117.1	U	U	1907	Whaling – Hebrides (Scotland)
NMS 1915.86.1	A	U	1915	Whaling – Hebrides (Scotland)
Eg1223	12	F	1992	Vessel Collision, Nursing
Eg1623	12	M	1996	Vessel Collision
Eg1014	30	F	1999	Vessel Collision
Eg1238	19	M	2001	Acute Fishing Gear Entanglement
Eg1004	34	F	2004	Vessel Collision, Pregnant
Eg2143	14	F	2005	Vessel Collision, Pregnant
Eg2301	12	F	2005	Chronic Fishing Gear Entanglement
Eg2617	9	F	2005	Vessel Collision

Table 4.2: Elemental abundances and stable isotope ratios in right whale baleen. Range and mean \pm 1 SD of elemental abundances (expressed as % dry weight), stable isotope ratios and standards used, and range and mean \pm 1 SD of stable isotope ratios (δ) measured in the baleen from historical and present-day North Atlantic right whales. (*n*) denotes the number of whales samples / number of isotope data points collected.

Historical Whales (1882 – 1915)				
Element	Composition (Mean \pm 1 SD)	Isotope Ratio (Standard)	δ Range (‰) (Mean \pm 1 SD)	<i>n</i>
Carbon	25.8 to 68.1% (48.9 \pm 2.9%)	$^{13}\text{C}/^{12}\text{C}$ (PDB)	-20.7 to -16.9 (-19.0 \pm 0.6)	4 / 344
Nitrogen	4.8 to 11.2 (8.4 \pm 1.5)	$^{15}\text{N}/^{14}\text{N}$ (Air)	7.4 to 19.9% (13.8 \pm 1.0%)	4 / 344
Present-Day Whales (1986 – 2005)				
Element	Composition (Mean \pm 1 SD)	Isotope Ratio (Standard)	δ Range (‰) (Mean \pm 1 SD)	<i>n</i>
Carbon	34.8 to 64.4% (47.1 \pm 2.2%)	$^{13}\text{C}/^{12}\text{C}$ (PDB)	-21.8 to -16.7 (-19.7 \pm 0.9)	8 / 793
Nitrogen	10.1 to 19.2% (14.1 \pm 0.8%)	$^{15}\text{N}/^{14}\text{N}$ (Air)	7.0 to 12.1 (10.3 \pm 0.9)	8 / 793

Table 4.3: Statistical Comparison of Historical and Present-Day Right Whale Baleen Isotope Ratios. Mean \pm 1 SD of Historical, Present-Day, and Entangled right whale baleen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are shown in upper section. Below, results of a one-way ANOVA comparing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of H (n=4) and PD (n=8) whale baleen, as well as an entangled right whale (n=1) are shown. The entangled right whale is from the PD group, but the data that encompass the entanglement were treated separately for this analysis (and removed from the PD group).

Group	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
H	4	-19.0 ± 0.2	8.7 ± 1.2
PD	8	-19.7 ± 0.2	10.2 ± 0.5
E	1	-21.0	11.2

$\delta^{13}\text{C}$					
Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Between Groups	2	3.57	1.79	50.34	< 0.0001
Within Groups	10	0.35	0.04		
Total	12	3.93			

$\delta^{15}\text{N}$					
Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Between Groups	2	7.90	7.89	7.41	0.01
Within Groups	10	5.33	0.53		
Total	12	13.23			

Table 4.4: Correlation of Baleen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Data with Climatic Oscillation Indices.

Correlation coefficients (r) and p-value of correlations between annual mean baleen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ records and climate oscillation indices. Statistically significant correlations ($\alpha = 0.05$) are highlighted in bold. Codes are as follows: NAO, North Atlantic Oscillation Index; AMO, Atlantic Multi-decadal Oscillation Index; PDO, Pacific Decadal Oscillation Index; and ENSO, El Niño Southern Oscillation Index.

NAO	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		PDO	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
	r	P	r	p		r	P	r	p
Lag 0	0.15	0.54	0.45	0.05	Lag 0	-0.19	0.42	0.19	0.43
Lag 1	0.25	0.29	0.21	0.37	Lag 1	0.03	0.91	0.18	0.44
Lag 2	0.11	0.65	0.04	0.87	Lag 2	0.19	0.43	0.42	0.07
Lag 3	0.07	0.80	-0.01	0.97	Lag 3	0.43	0.06	0.45	0.05
AMO	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		ENSO	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
	r	P	r	p		r	P	r	p
Lag 0	-0.41	0.08	-0.55	0.01	Lag 0	0.29	0.21	-0.17	0.47
Lag 1	-0.27	0.24	-0.52	0.02	Lag 1	0.05	0.85	-0.10	0.75
Lag 2	-0.24	0.30	-0.50	0.02	Lag 2	-0.29	0.21	-0.09	0.71
Lag 3	-0.23	0.33	-0.42	0.07	Lag 3	-0.36	0.12	-0.11	0.67

Figure 4.1: Nitrogen and Carbon Stable Isotope Ratios in Right Whale Baleen, 1882 - 2005. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope records collected from the baleen of 12 North Atlantic right whales, with each color representing data from an individual whale. Vertical dashed lines are biennial in frequency.

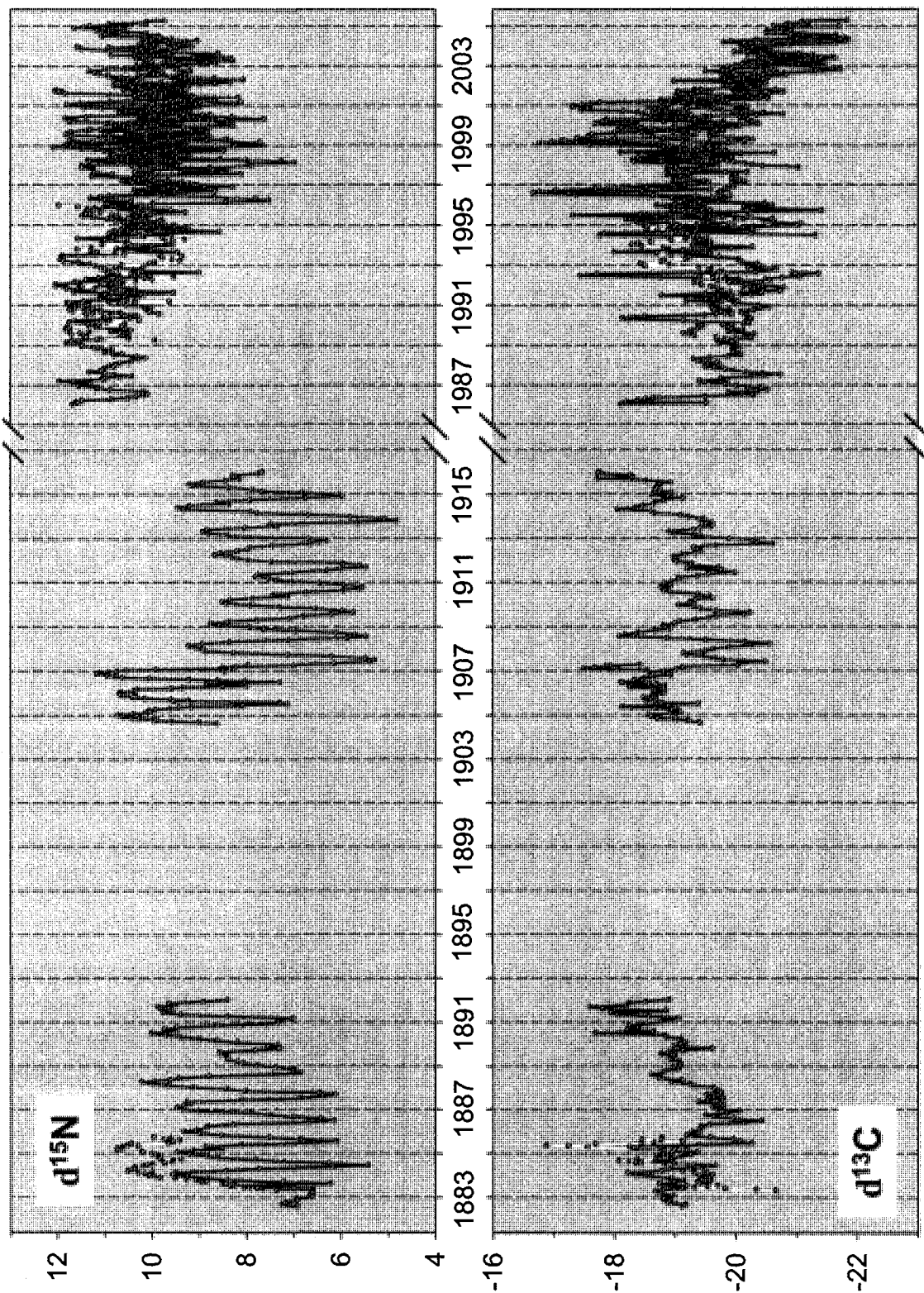


Figure 4.2: Carbon and Nitrogen Stable Isotope Values of Historical (1882 – 1915) vs. Present-day (1986 – 2005) Baleen Plates. Mean (\pm 1 SD) carbon and nitrogen stable isotope values of baleen: (●) = Historical, 1882-1915 and (○) = Present-Day, 1986-2005. (●) denotes the mean carbon and nitrogen isotope signature of an Entangled whale (Eg2301), which was entangled for 6-9 months in 2004-2005. The entangled whale data, although formed during the PD period, was removed from the PD group for analysis.

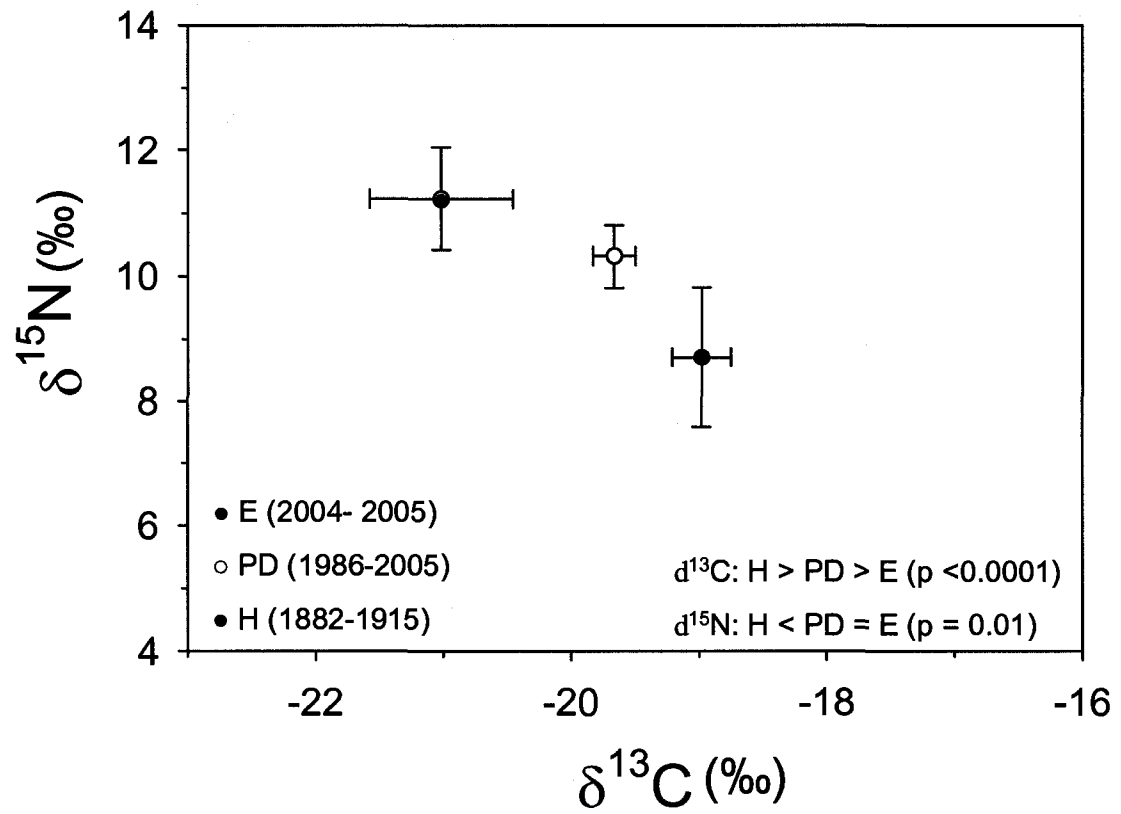


Figure 4.3: Atmospheric Carbon Dioxide Concentrations: 1832-2005. Annual mean atmospheric carbon dioxide concentrations (ppm) analyzed from the Law Dome Ice Cores (Antarctica, 1832-1978) and collected at the Barrow Observatory (Alaska, USA, 1971-2005).

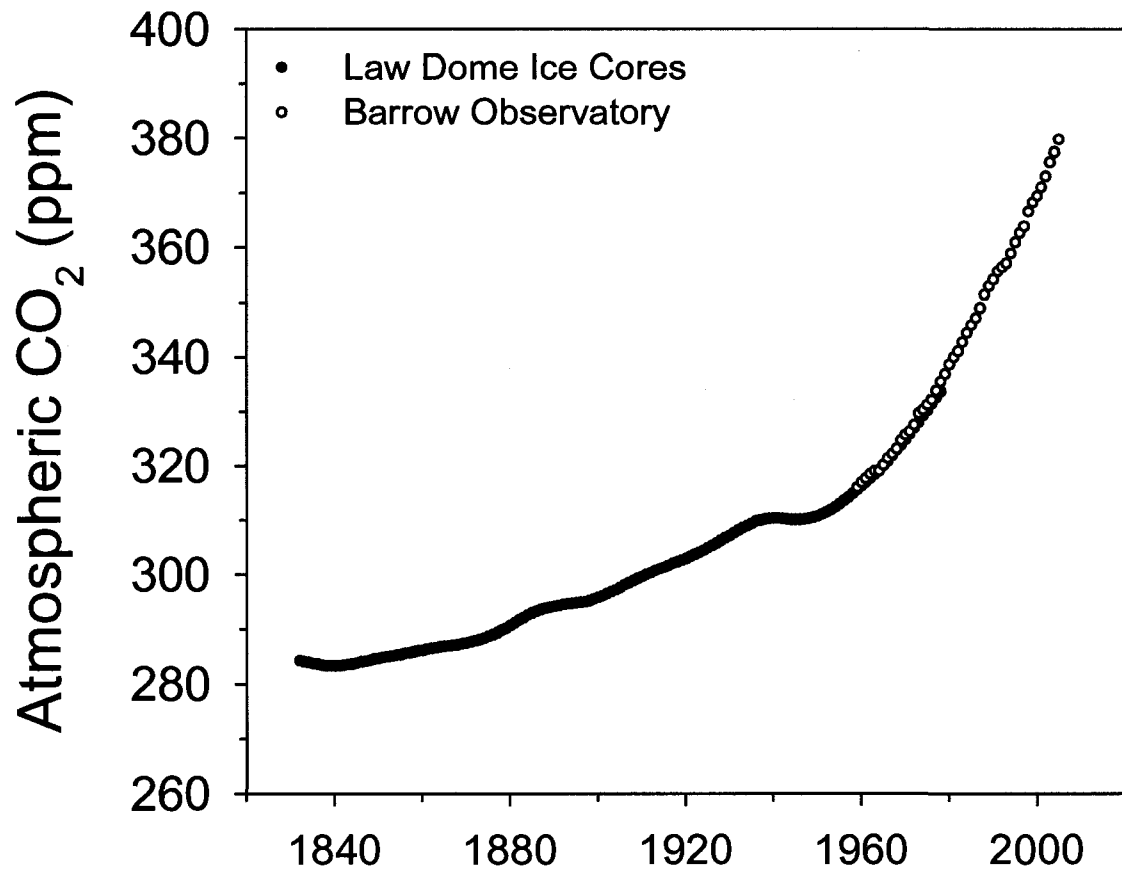


Figure 4.4: Nitrogen and Carbon Stable Isotope Measurements of Right Whale Baleen: 1986-2005. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ baleen values, fit with a running mean, representing baleen formed from 1986-2005. Lower panel illustrates the demographic contingency represented in each year of baleen stable isotope data.

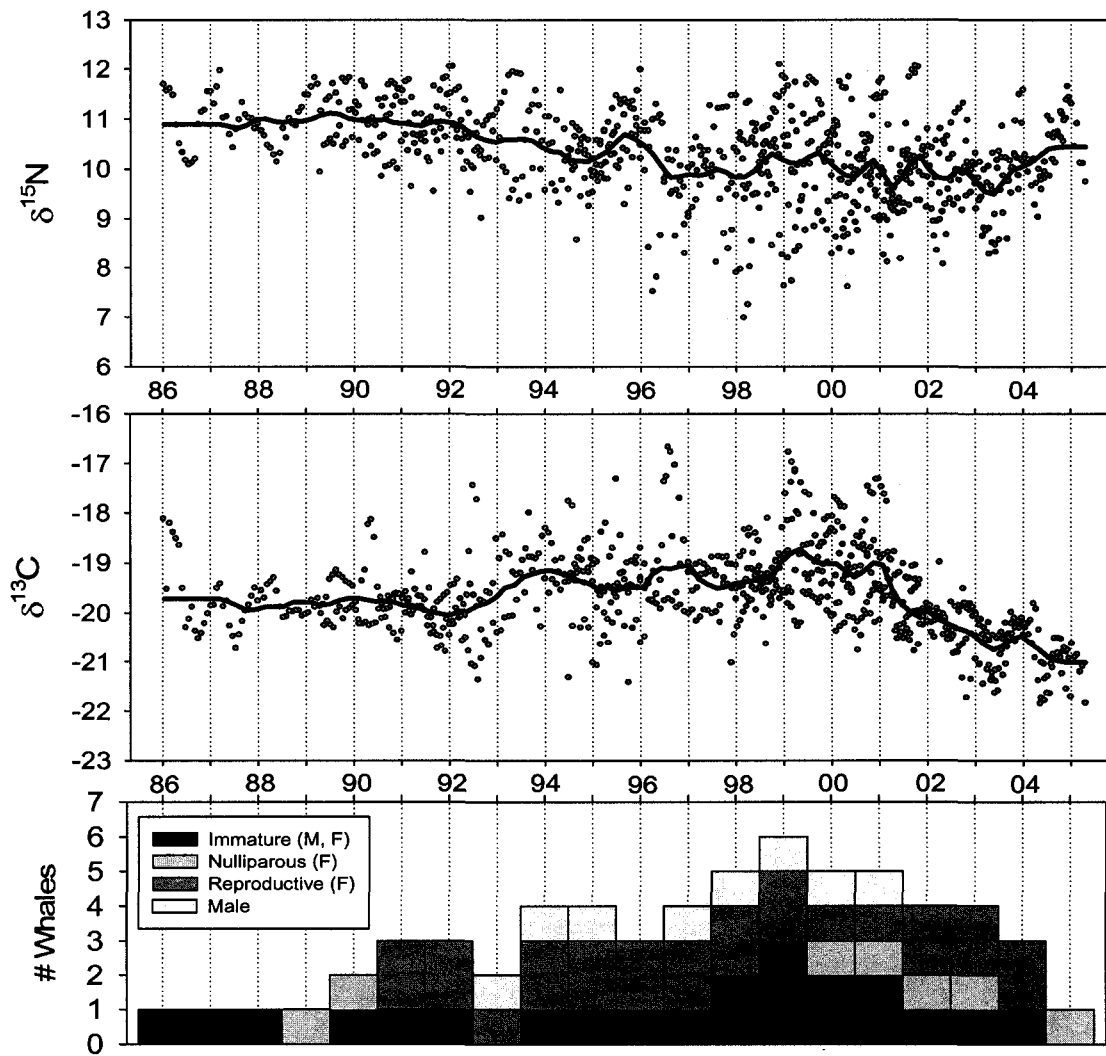


Figure 4.5: Trends in Atmospheric and Oceanic Carbon Dioxide. Annual means of atmospheric CO₂ concentrations (▲, ppm) and δ¹³C (○, ‰) from 1986-2005.

Atmospheric CO₂ was measured from air samples collected at the Barrow Observatory (Alaska, USA). Total dissolved CO₂ (μmol kg⁻¹) was measured from surface (0-10m) bottle samples at Bermuda Atlantic Time Series Stations (Bermuda).

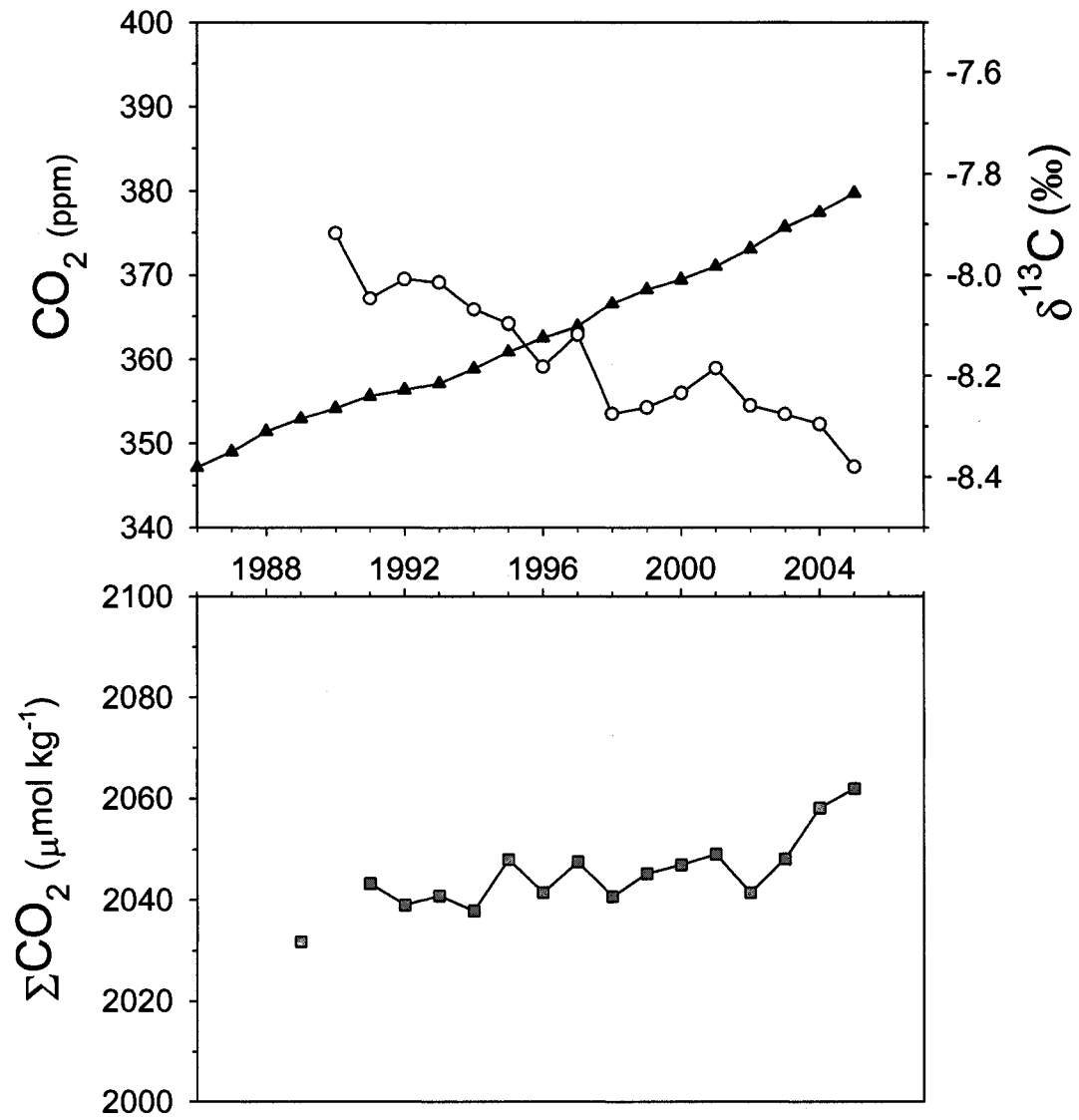


Figure 4.6: Right Whale Migration Patterns. The latitude vs. month of right whale sighting events during (●) 1986-1998 and (○) 1999-2005. Habitat codes are: Cape Cod Bay (CCB), Great South Channel (GSC), Bay of Fundy (BoF), Roseway Basin (RB), Gulf of St. Lawrence (GSL), and Southeast US (SEUS). These data were taken from the *North Atlantic Right Whale Catalog* records for Eg1004, 1014, 1238, 2143, 1623, 1223, 2301, and 2617.

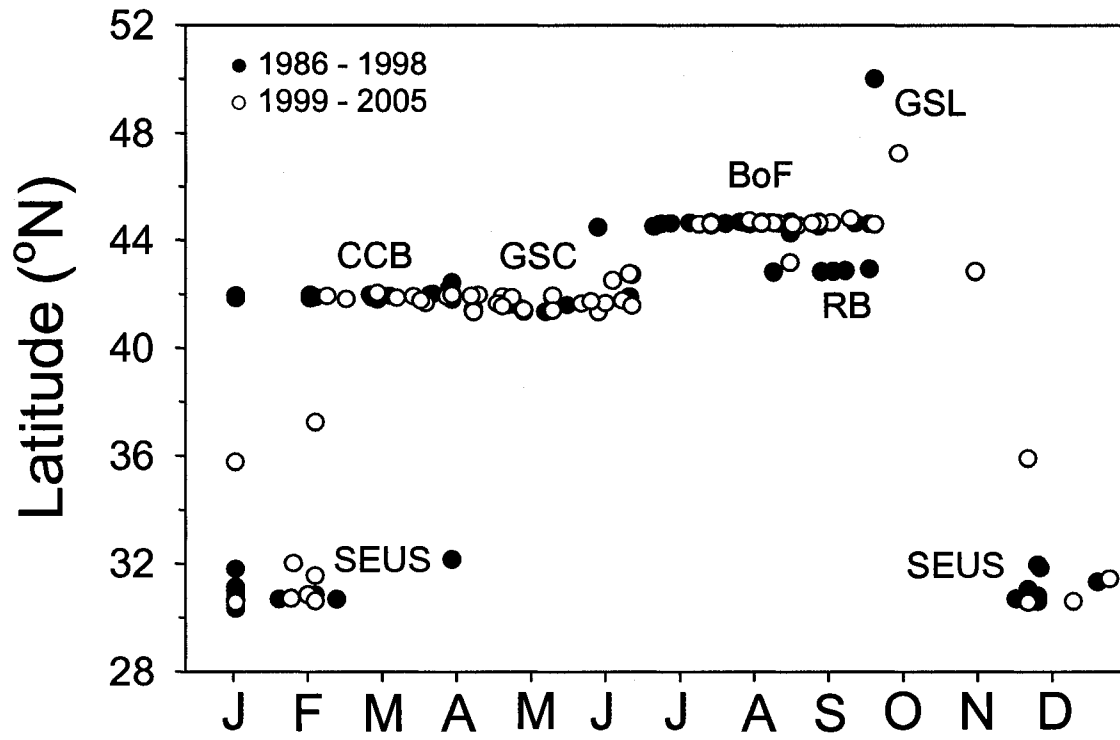


Figure 4.7: Right Whale Reproductive Success. Measures of population-wide reproductive success: Inter-birth interval (■) is an annual count of the mean number of years between calving events for reproductively active females. Error bars represent ± 1 SE. Calving rate (●) is the number of tallied recruits to the population each year. Mean (± 1 SE) inter-birth interval and calving rate are shown for 1986 – 1998 and 1999 – 2005 at the top of each panel.

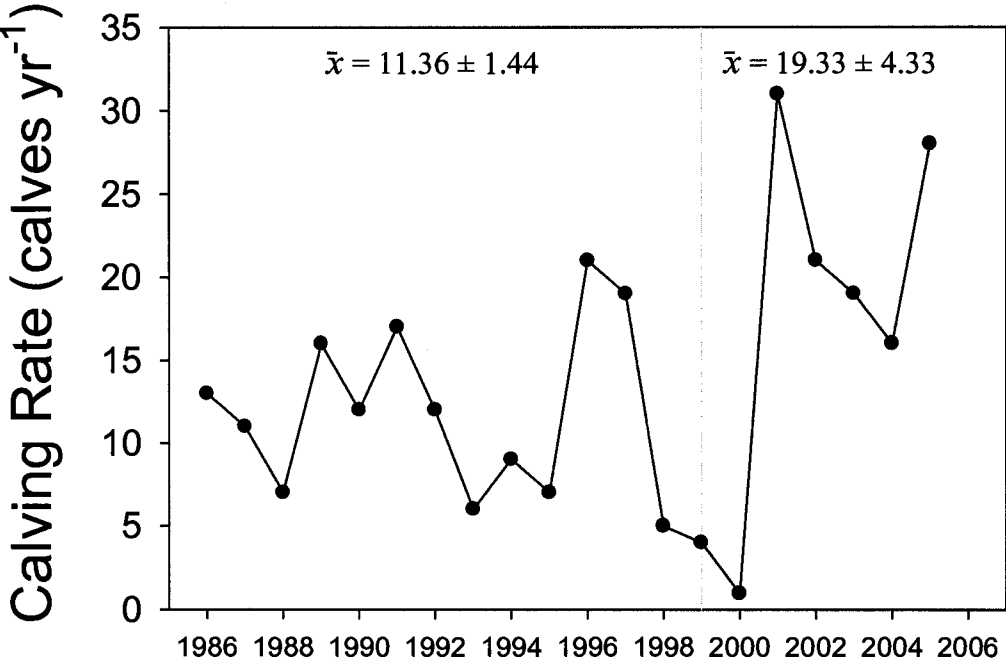
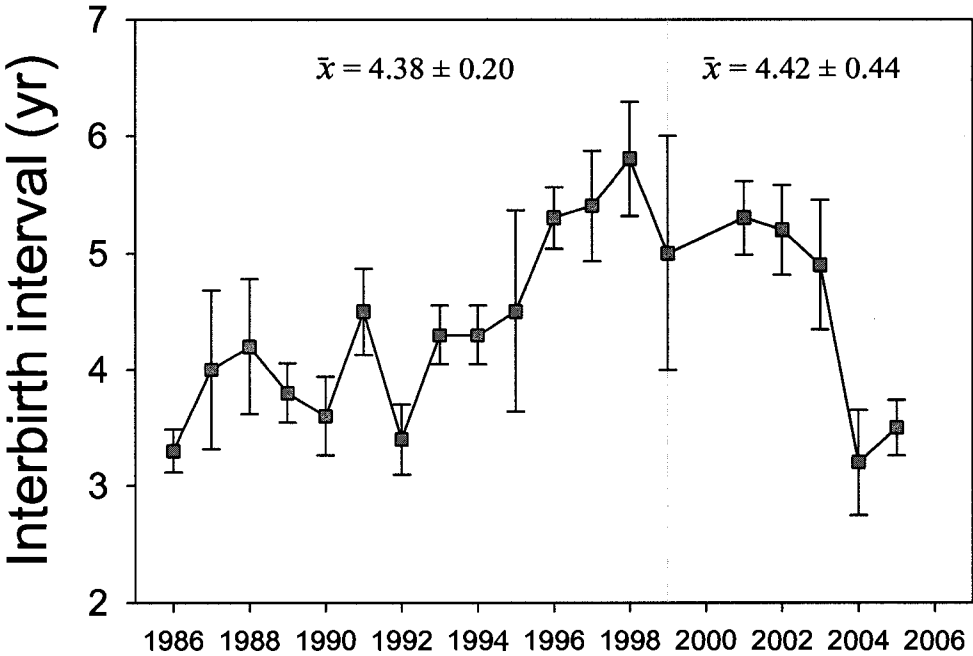
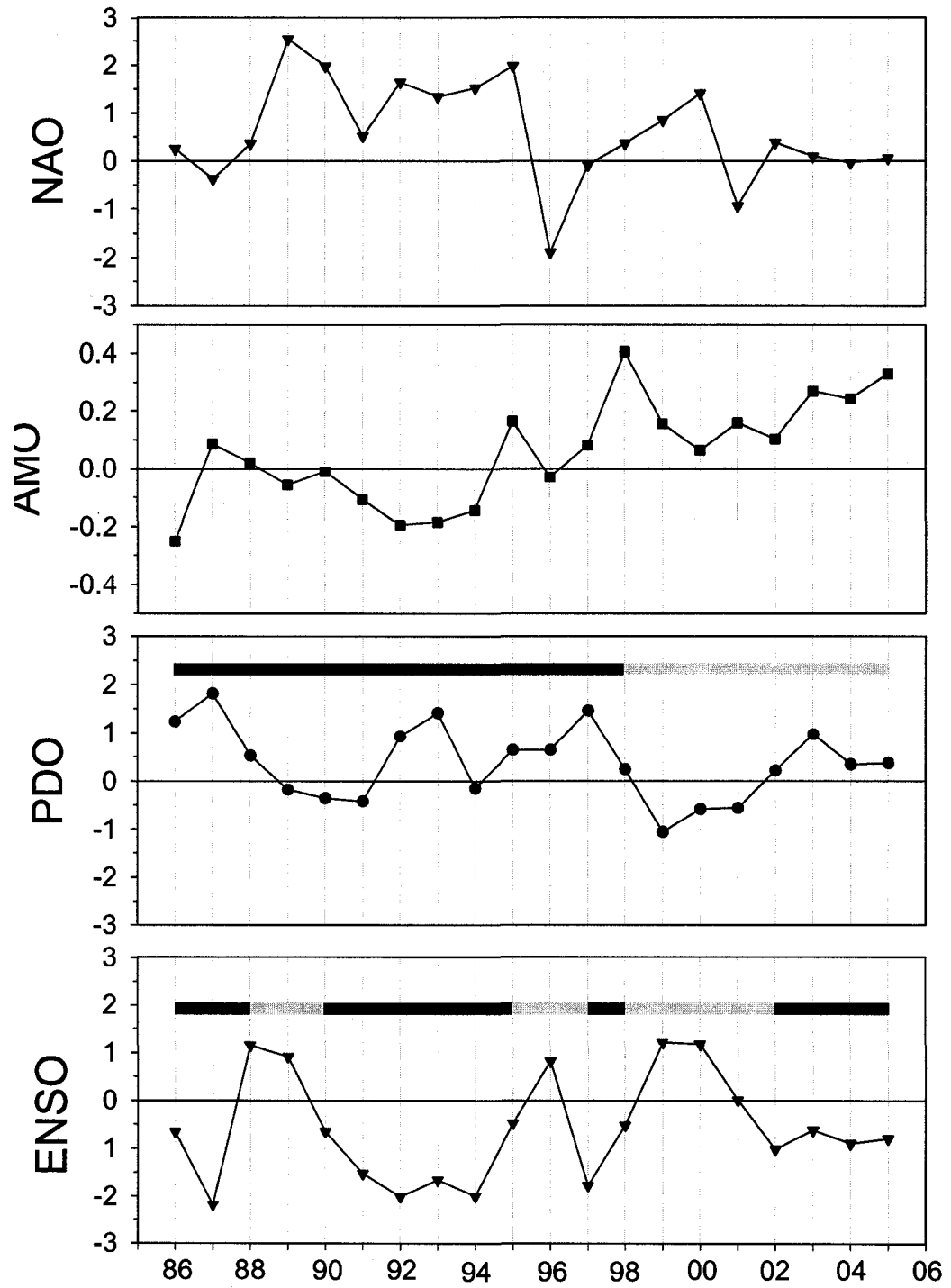


Figure 4.8: Climatic Oscillations: NAO, AMO, PDO, ENSO. The North Atlantic Oscillation Index (NAO), Atlantic Multi-Decadal Oscillation Index (AMO), Pacific Decadal Oscillation Index (PDO), and El Niño Southern Oscillation Index (ENSO) are shown from 1986-2005. Horizontal bars over the oscillation indices represent the warm (black) and cool (gray) phase of the PDO, and El Niño (black) and La Niña (gray) events in the ENSO.

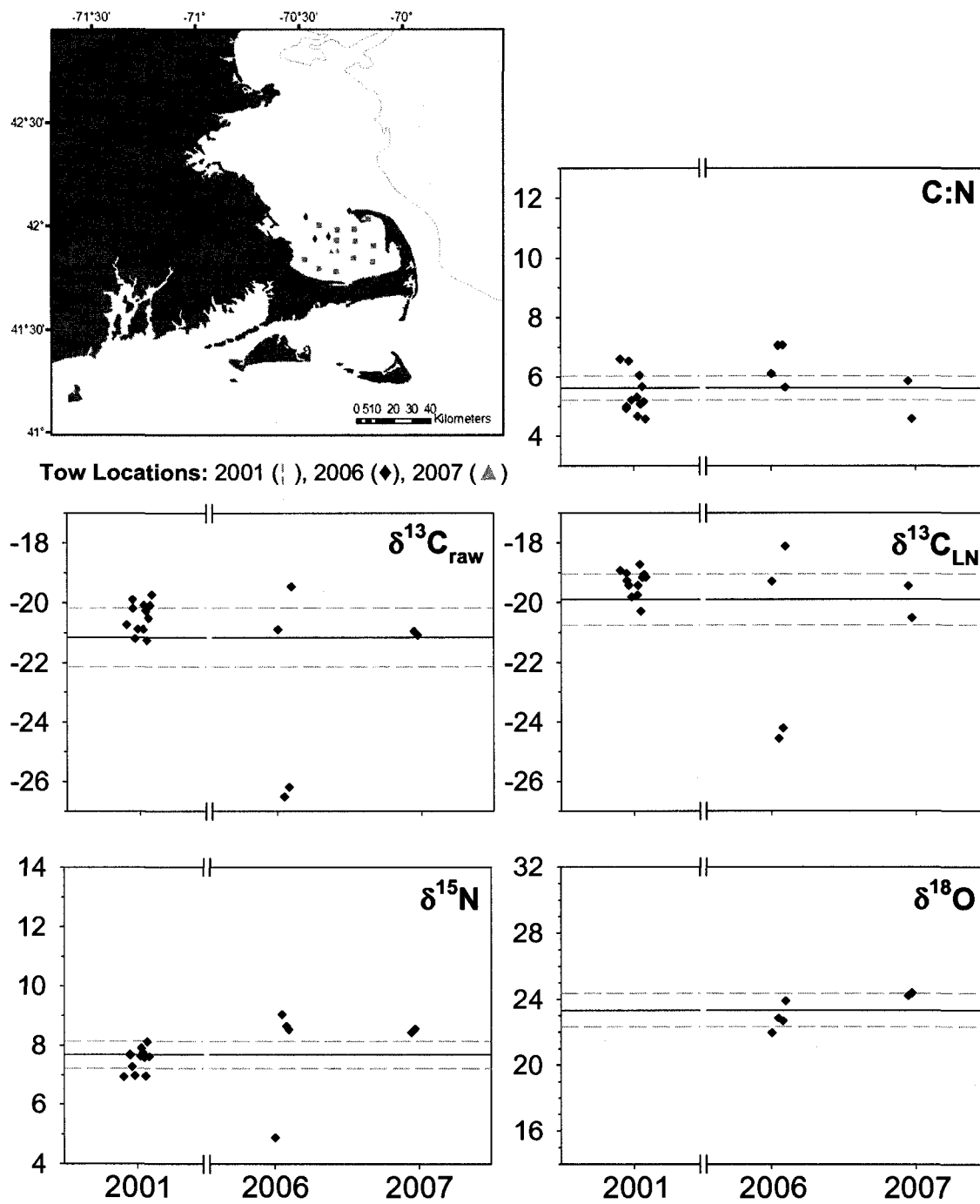


APPENDIX 1

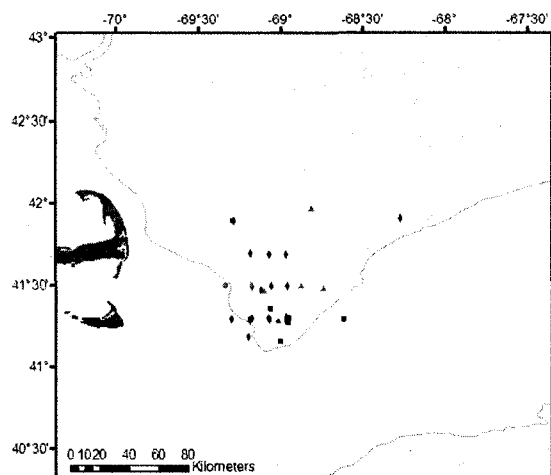
HABITAT-SPECIFIC ZOOPLANKTON STABLE ISOTOPE RATIOS

Appendix 1a-g: Habitat-Specific Temporal Trends in Zooplankton Isotope and C:N Ratios. The upper left panels in each figure are maps of zooplankton tows at individual sampling sites and bathymetry (50 fathom/91m and 200m isobaths). The locations of zooplankton tows are shown by sampling year: 1998 (●), 1999 (◆), 2000 (▲), 2001 (■), 2004 (⊙), 2005 (■), 2006 (◆), 2007 (▲). The remaining panels display C:N and stable isotope ratios (‰) for individual tows from the each collection year, within each sampling site (◆, x-axis plotted with random jitter). The regional mean (—) and 95% confidence interval (- - -) are shown for the pooled data from each sampling area.

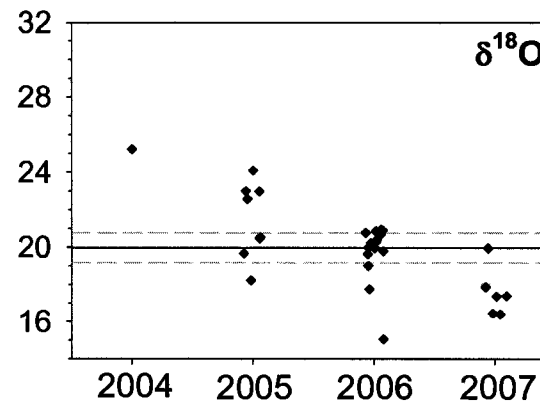
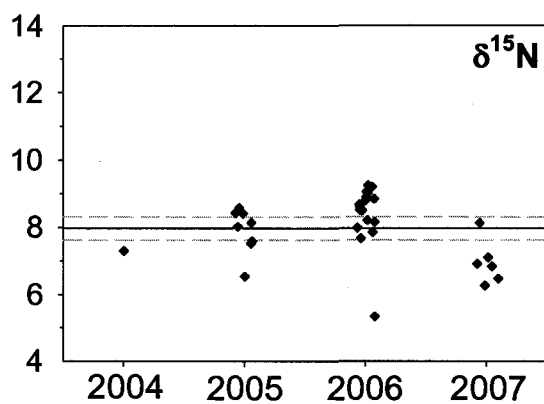
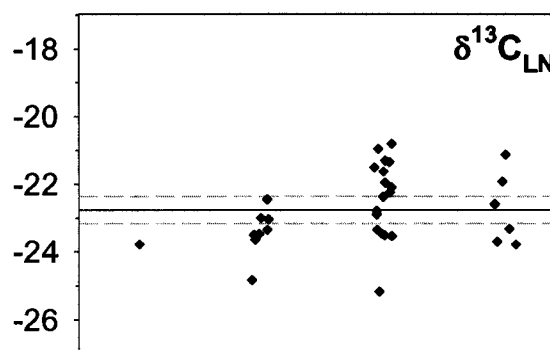
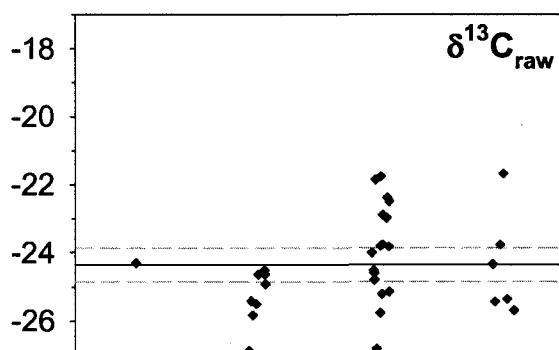
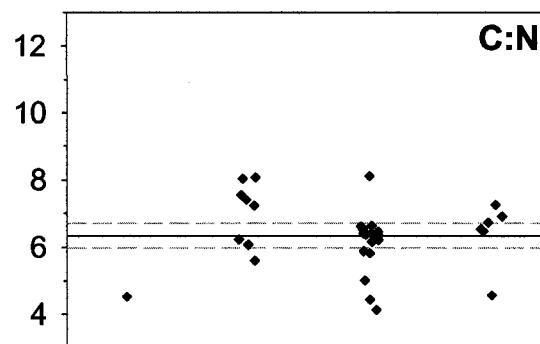
Appendix 1a: Cape Cod Bay.



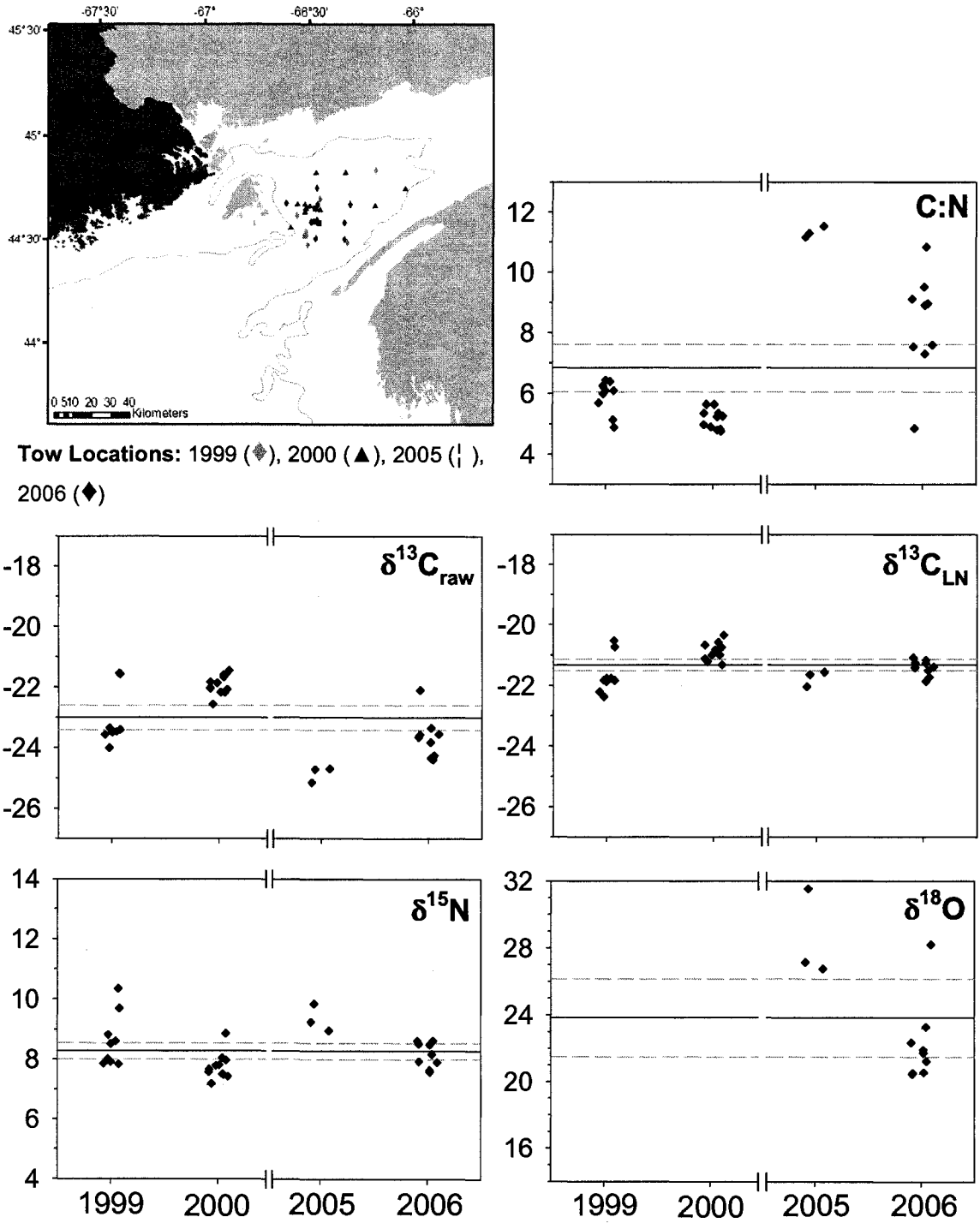
Appendix 1b: Great South Channel.



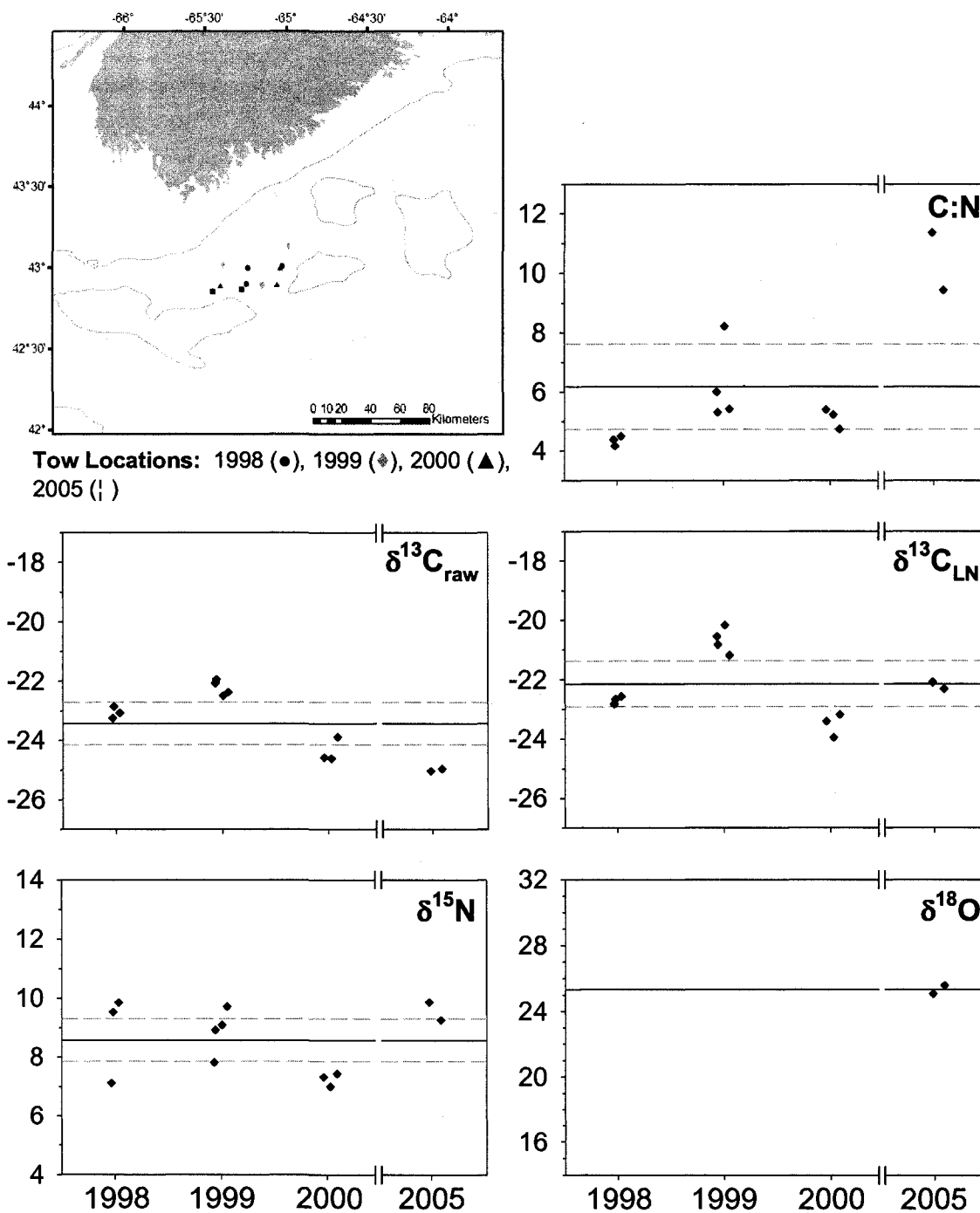
Tow Locations: 2004 (●), 2005 (|), 2006 (◆), 2007 (▲)



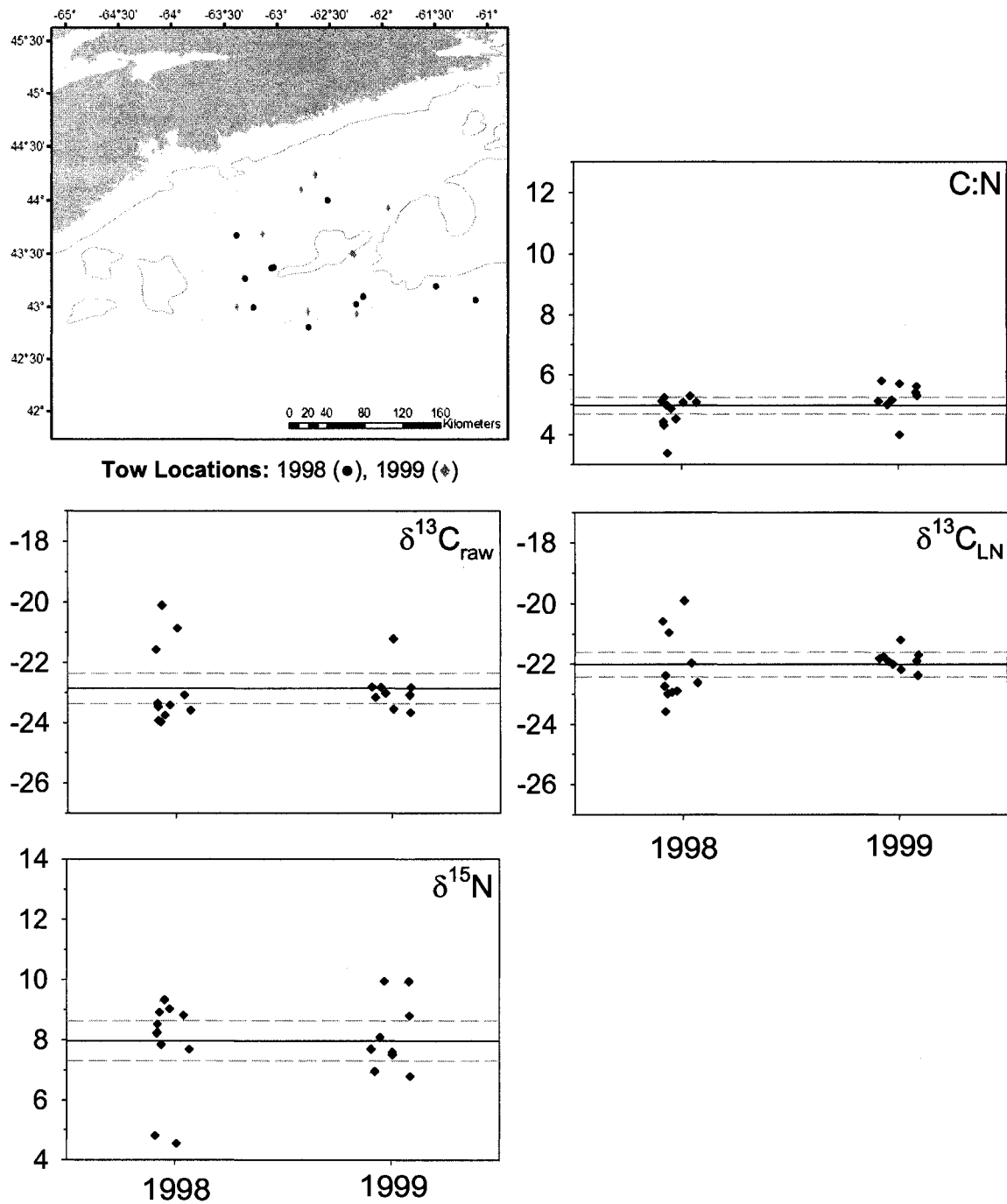
Appendix 1c: Bay of Fundy.



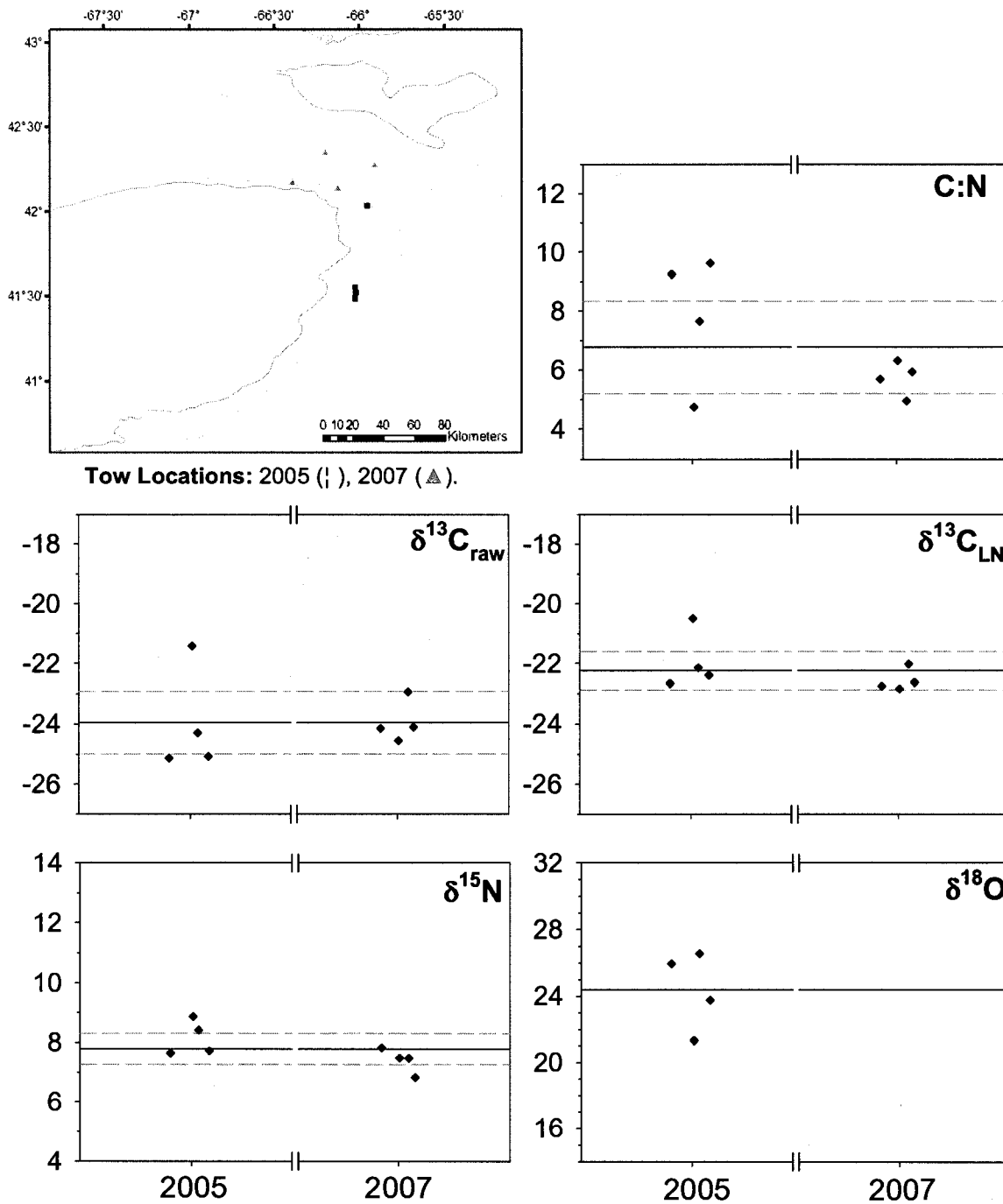
Appendix 1d: Roseway Basin.



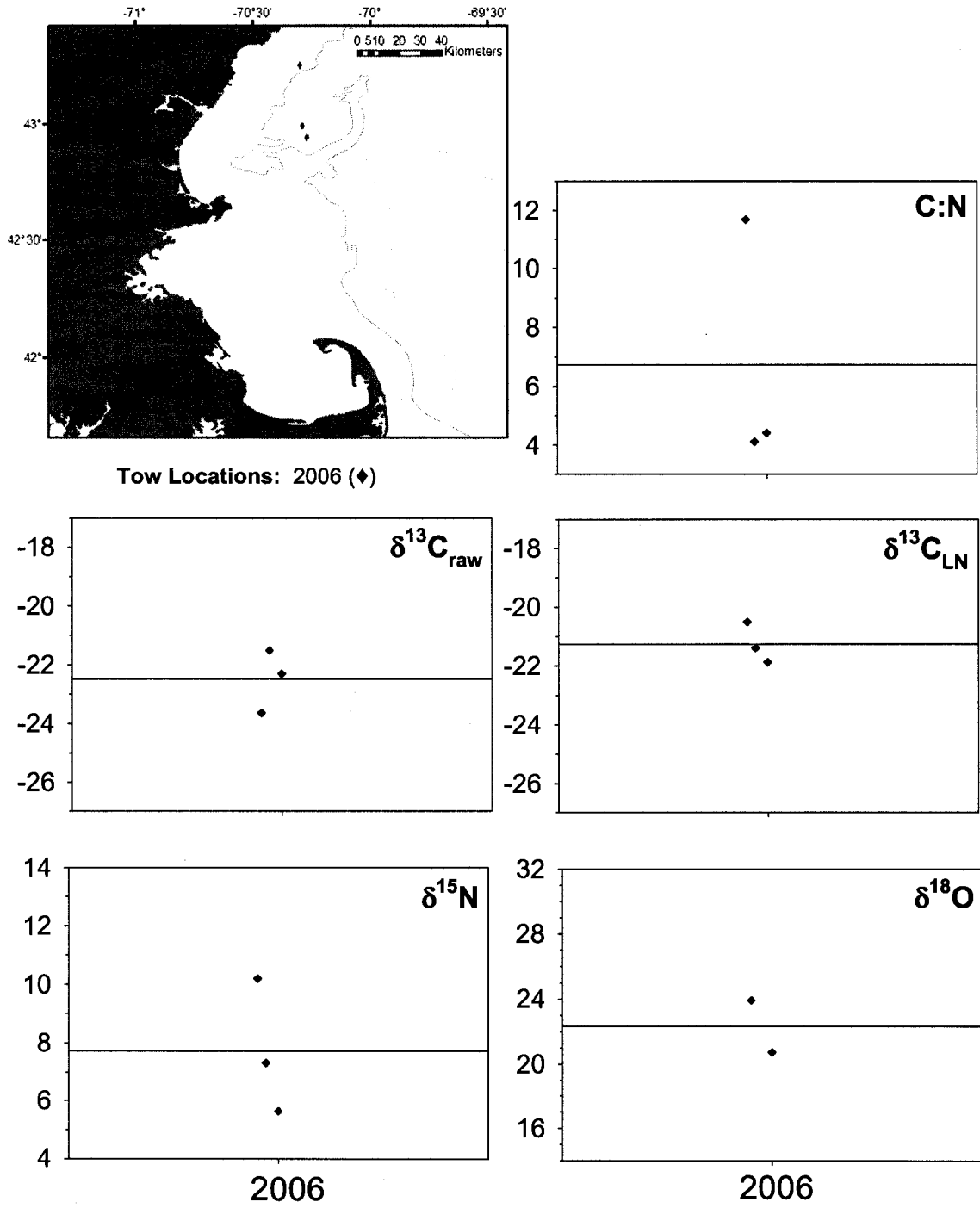
Appendix 1e: Nova Scotian Shelf.



Appendix 1f: Northeast Georges Bank.



Appendix 1g: Jeffreys Ledge



APPENDIX 2

**NORTH ATLANTIC RIGHT WHALE CASE HISTORIES AND BALEEN
STABLE ISOTOPE RECORDS**

CASE HISTORIES

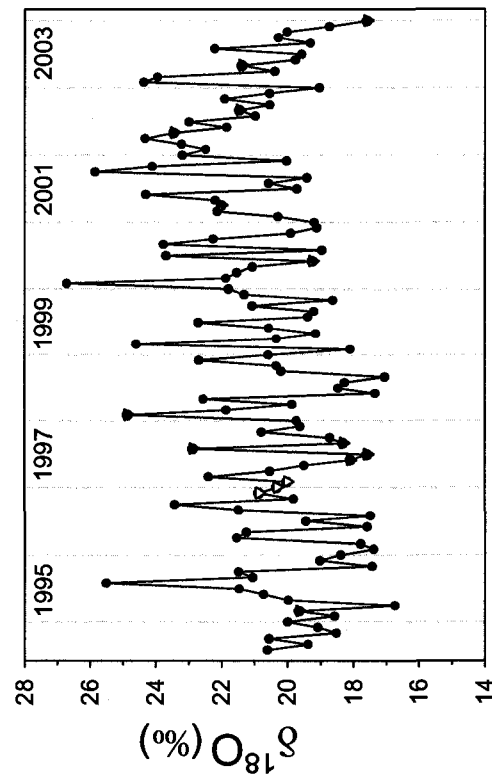
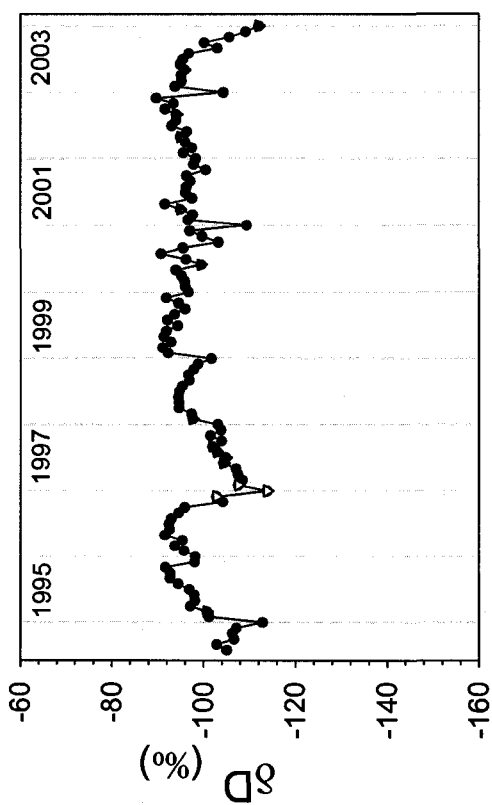
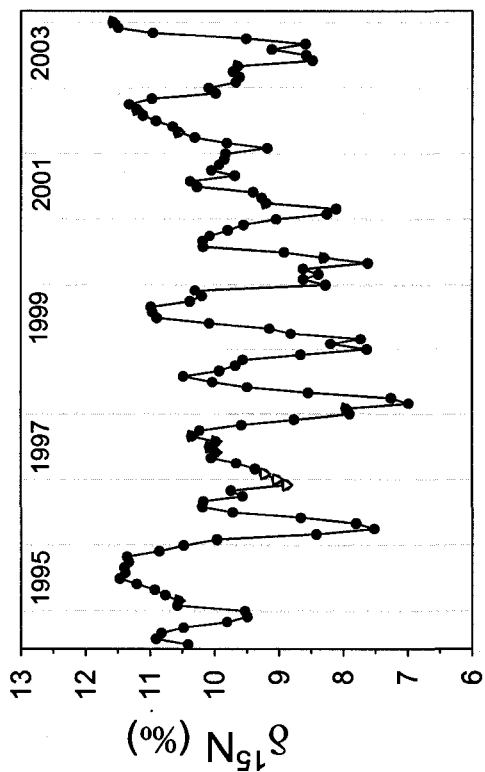
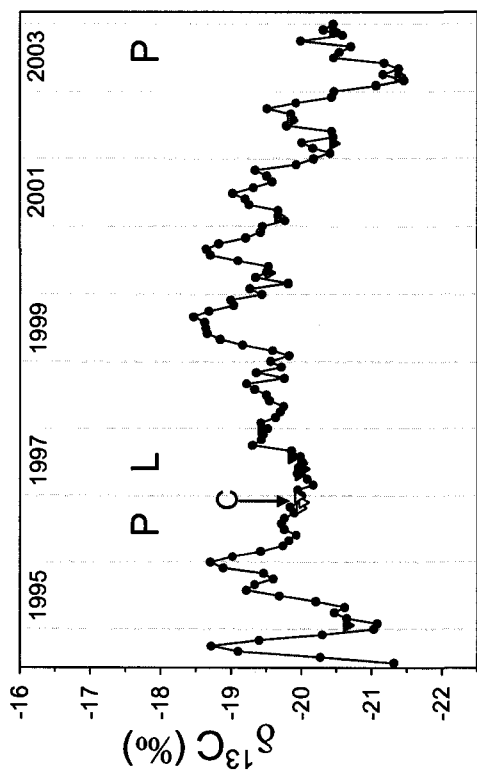
The available life history data and case histories of each whale sampled in this study are described in the following section. Necropsy reports for each whale were referenced (Moore et al. 2005, Right Whale Consortium 2008a), as were individual sighting and calving records contained in the *North Atlantic Right Whale Catalog* (Right Whale Consortium 2008b). All baleen isotope records for each whale are reported here, with the sighting records displayed over the isotope data such that the colored triangles represent an isotope data point that contained a sighting event. In all of the subsequent figures, the color-coding designates the following habitat areas:

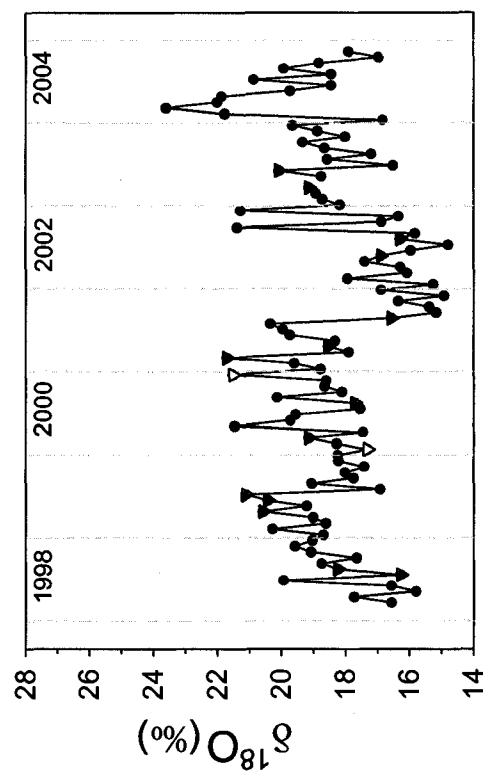
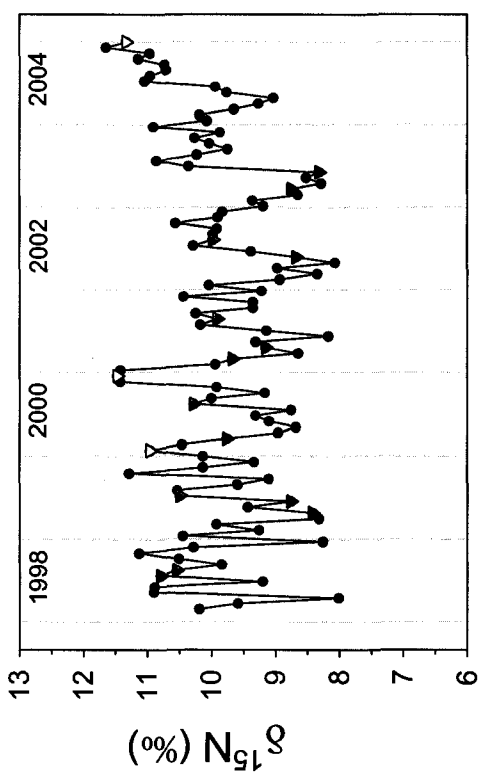
- ▼ = Cape Cod Bay
- ▼ = Great South Channel
- ▼ = Bay of Fundy
- ▼ = Roseway Basin
- ▼ = Jeffreys Ledge
- ▼ = Mid-Atlantic
- V = Southeast US (GA/FL coast)
- = Gulf of St. Lawrence

Life history is also denoted on the baleen isotope records. Reproductive events such as calving (**C**) and the year of pregnancy (**P**) preceding and year of lactation (**L**) following calving events are noted. For immature whales and calves, ontogenetic diet shifts are associated with birth (commencement of nursing) and weaning (commencement of a planktonic diet) are denoted by grayscale bars over the isotope record. Birth and weaning are denoted by vertical dashed gray lines. The month/year of death are shown at the end of each time series. Since baleen growth in young whales is highly variable, no attempts were made to assign individual baleen isotope data points a Julian Day value, nor were

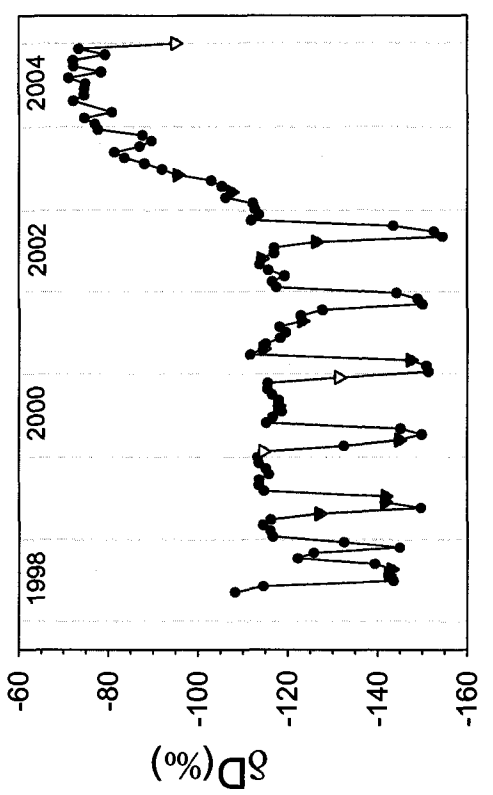
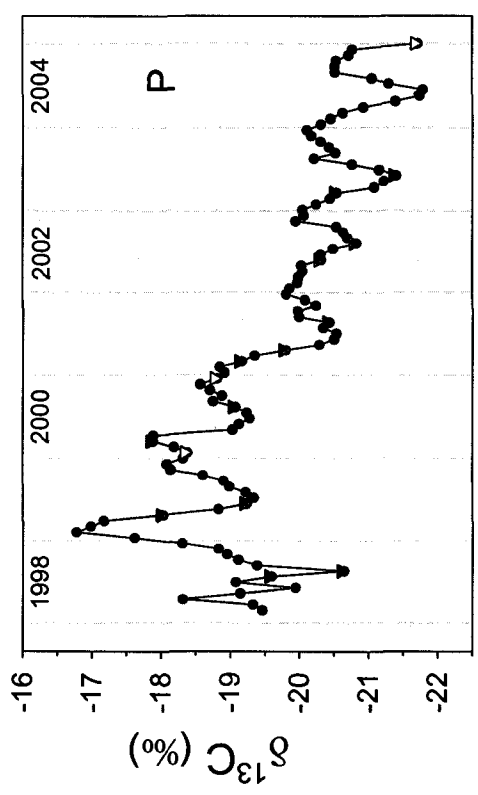
sighting records applied to the data. The year of birth was calculated retroactively given the estimated age of the immature whales and calves, and the structure of their isotope records. The month of December was arbitrarily assigned as the month of birth, based on observations of peak right whale calving in the southeast US.

Eg1004

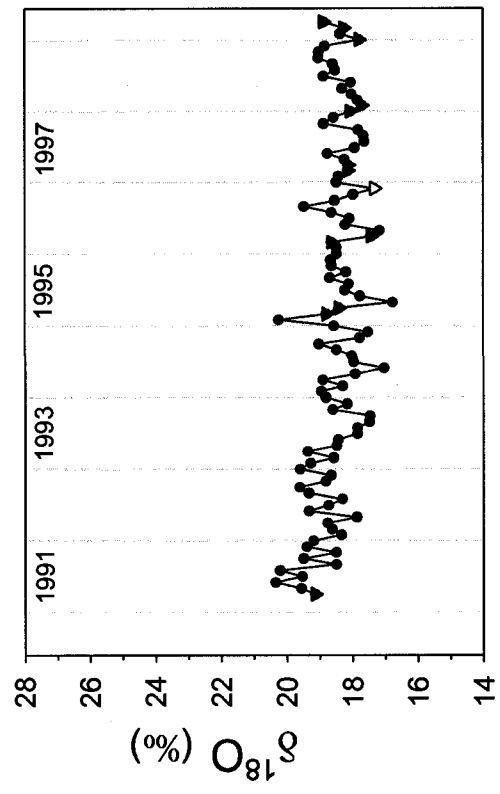
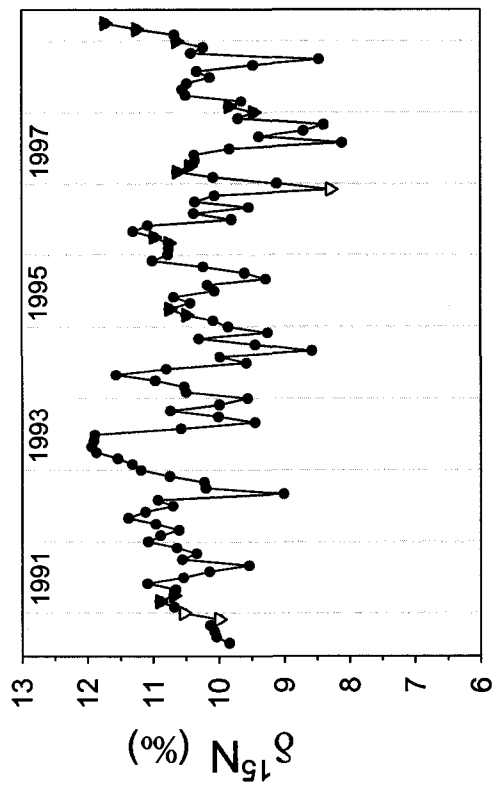
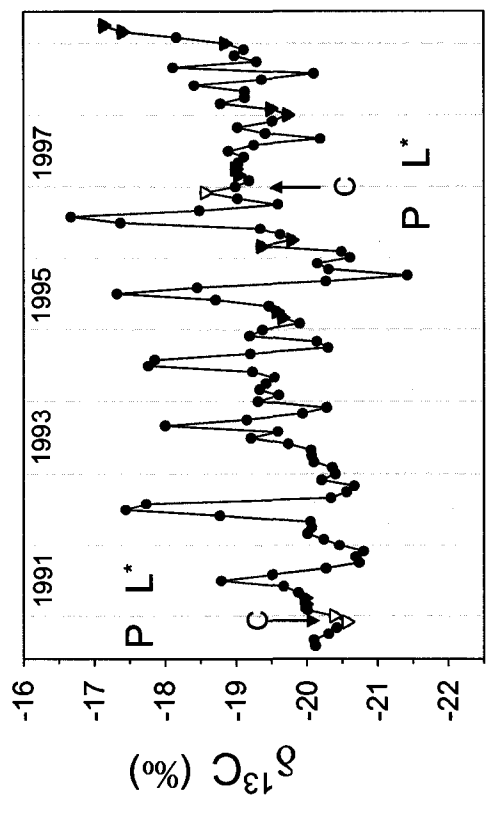




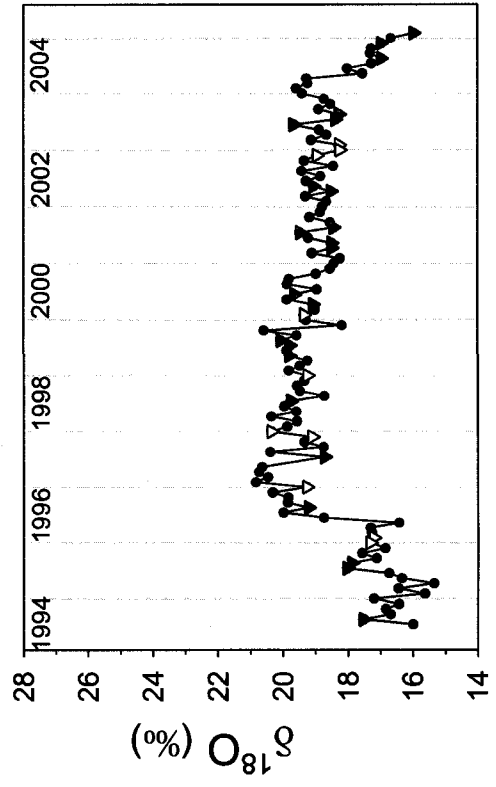
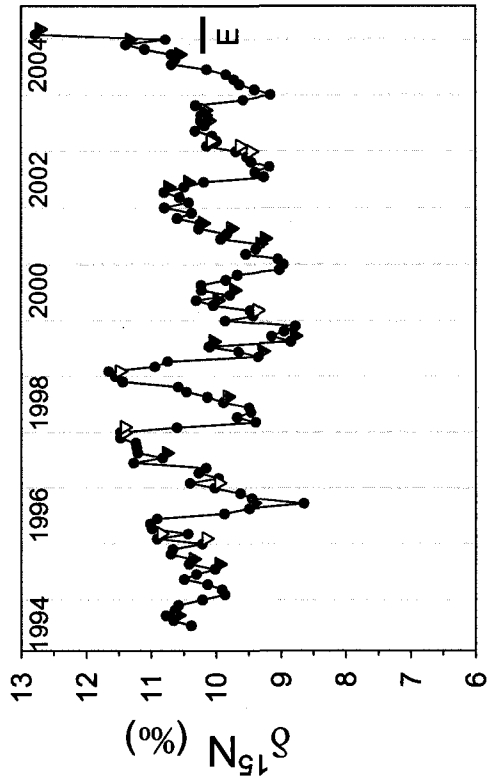
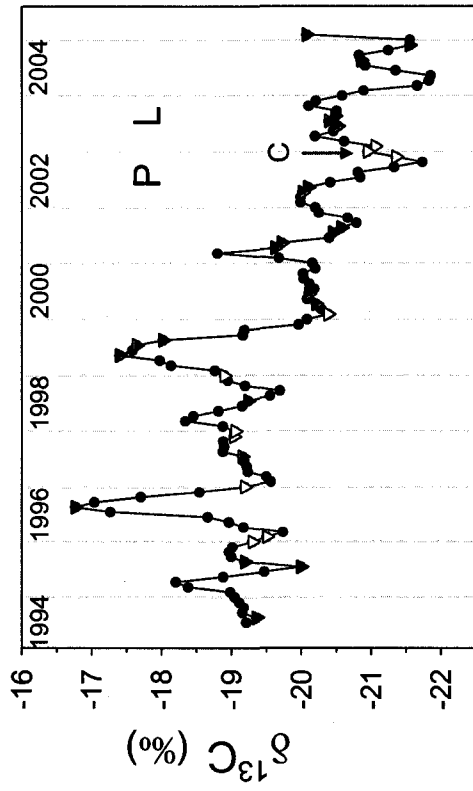
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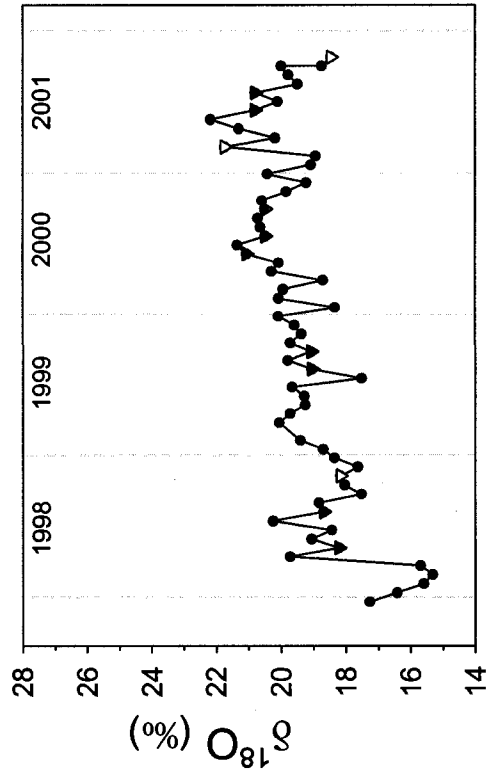
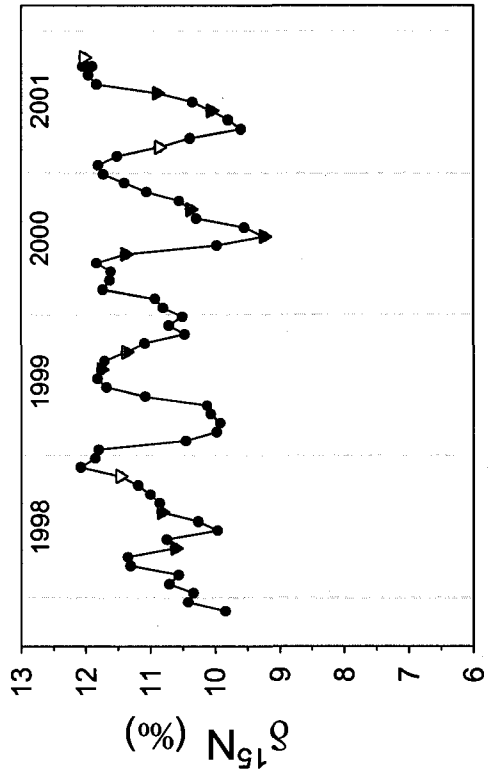
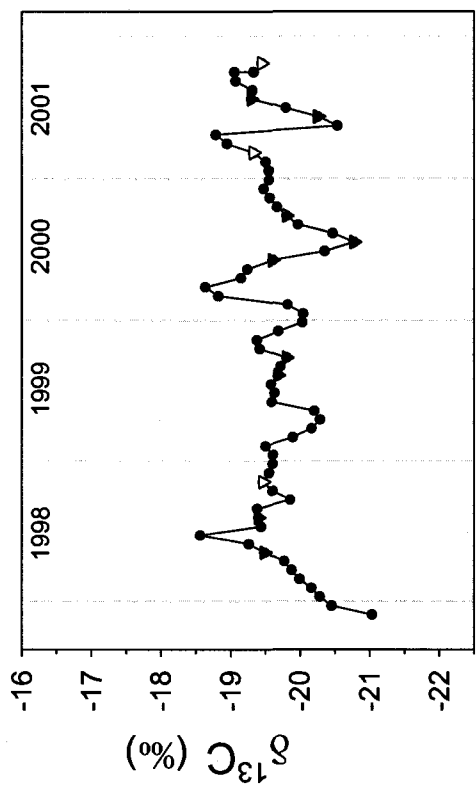
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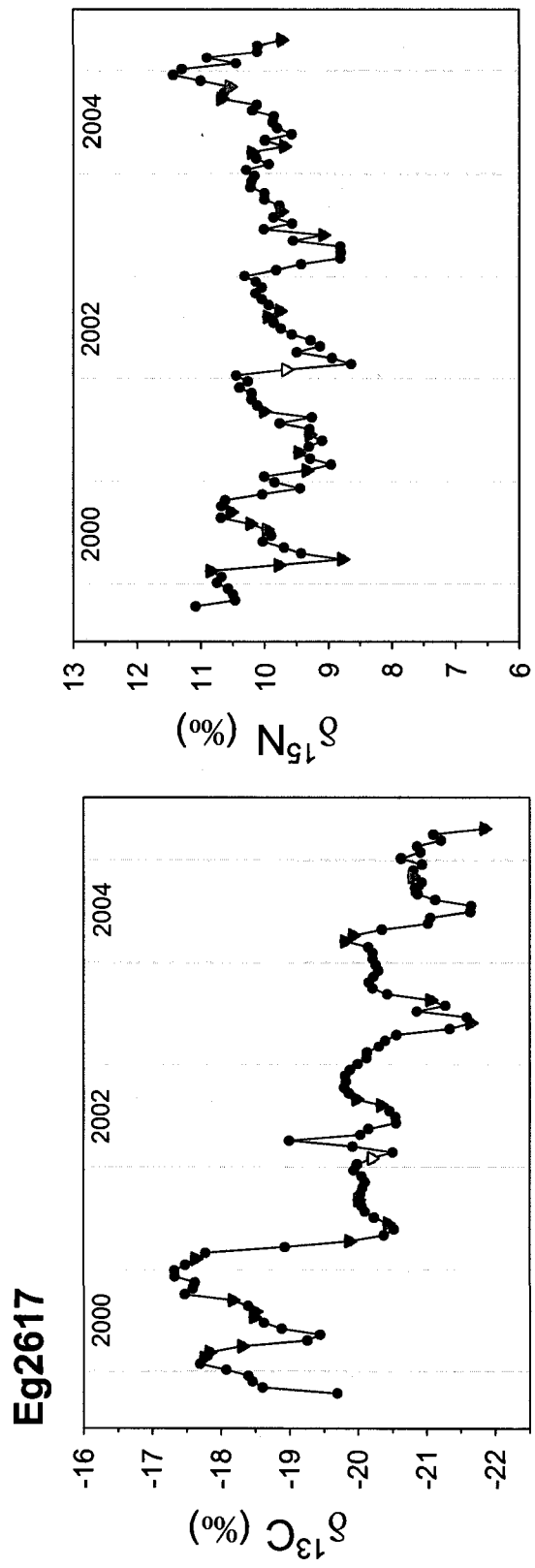


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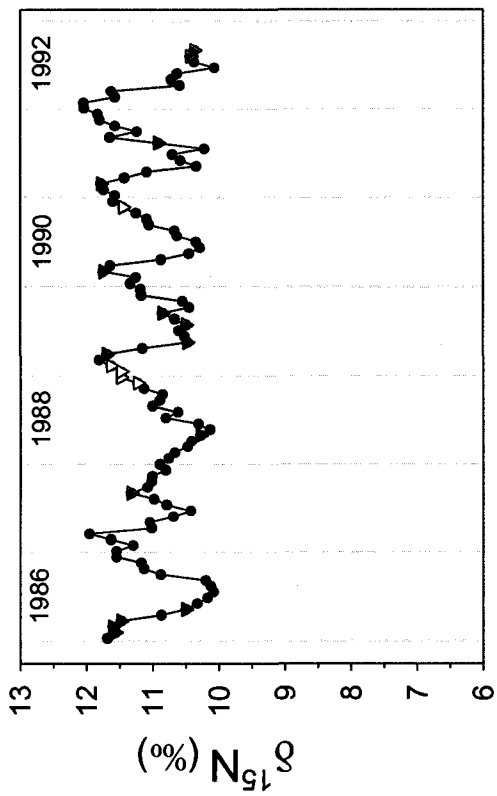
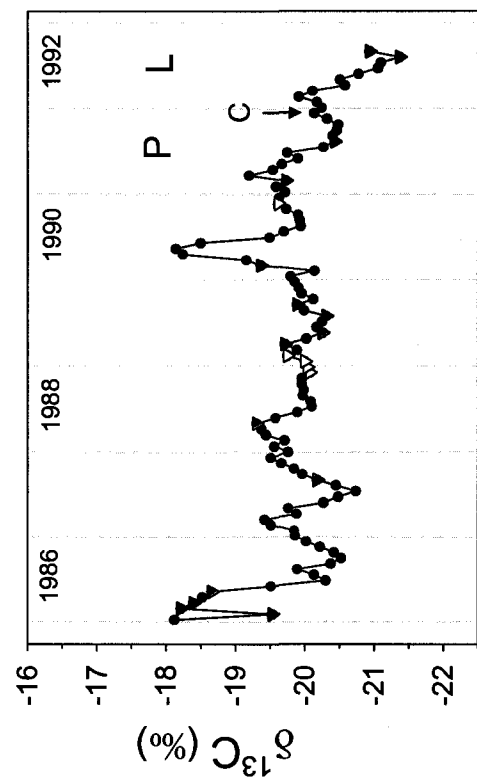


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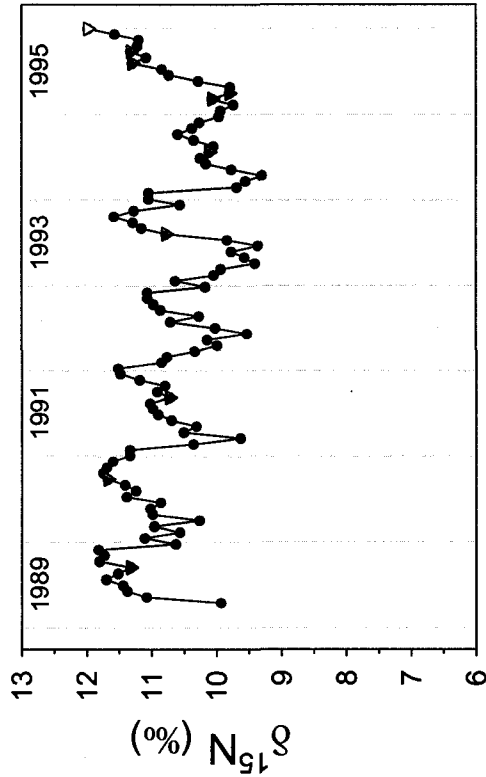
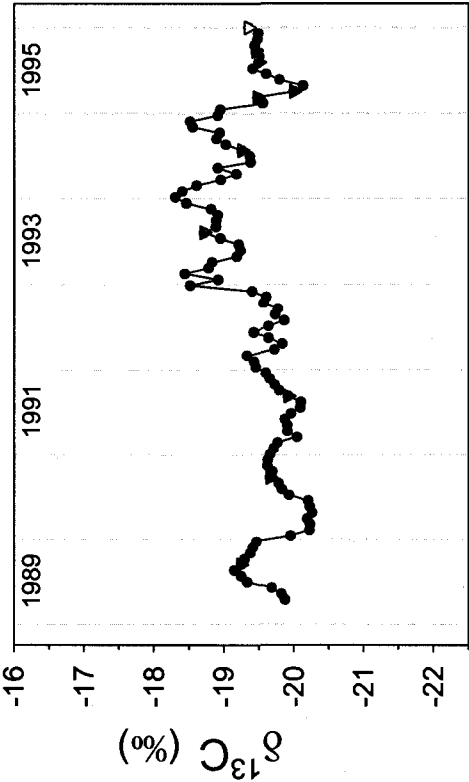


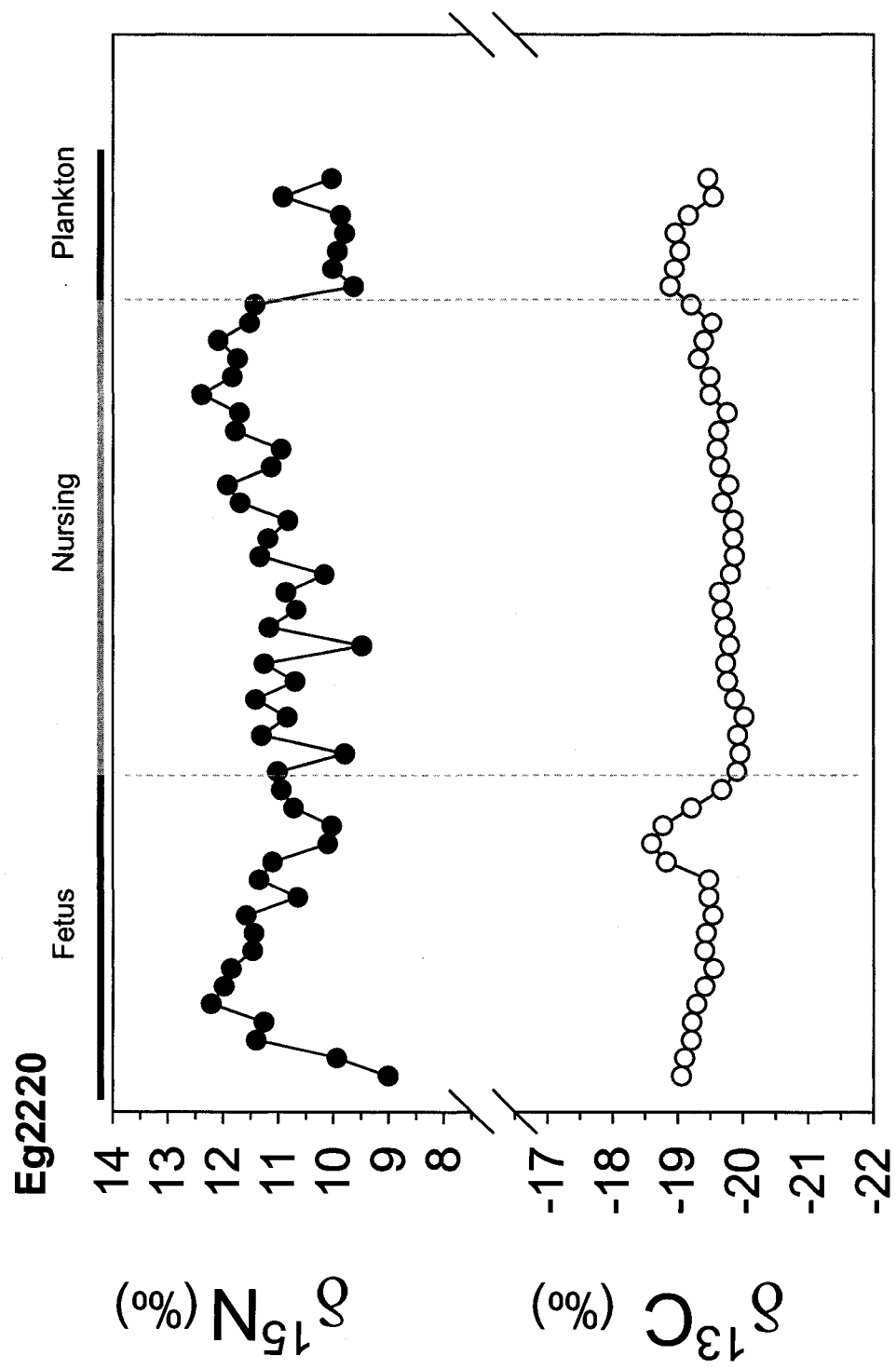


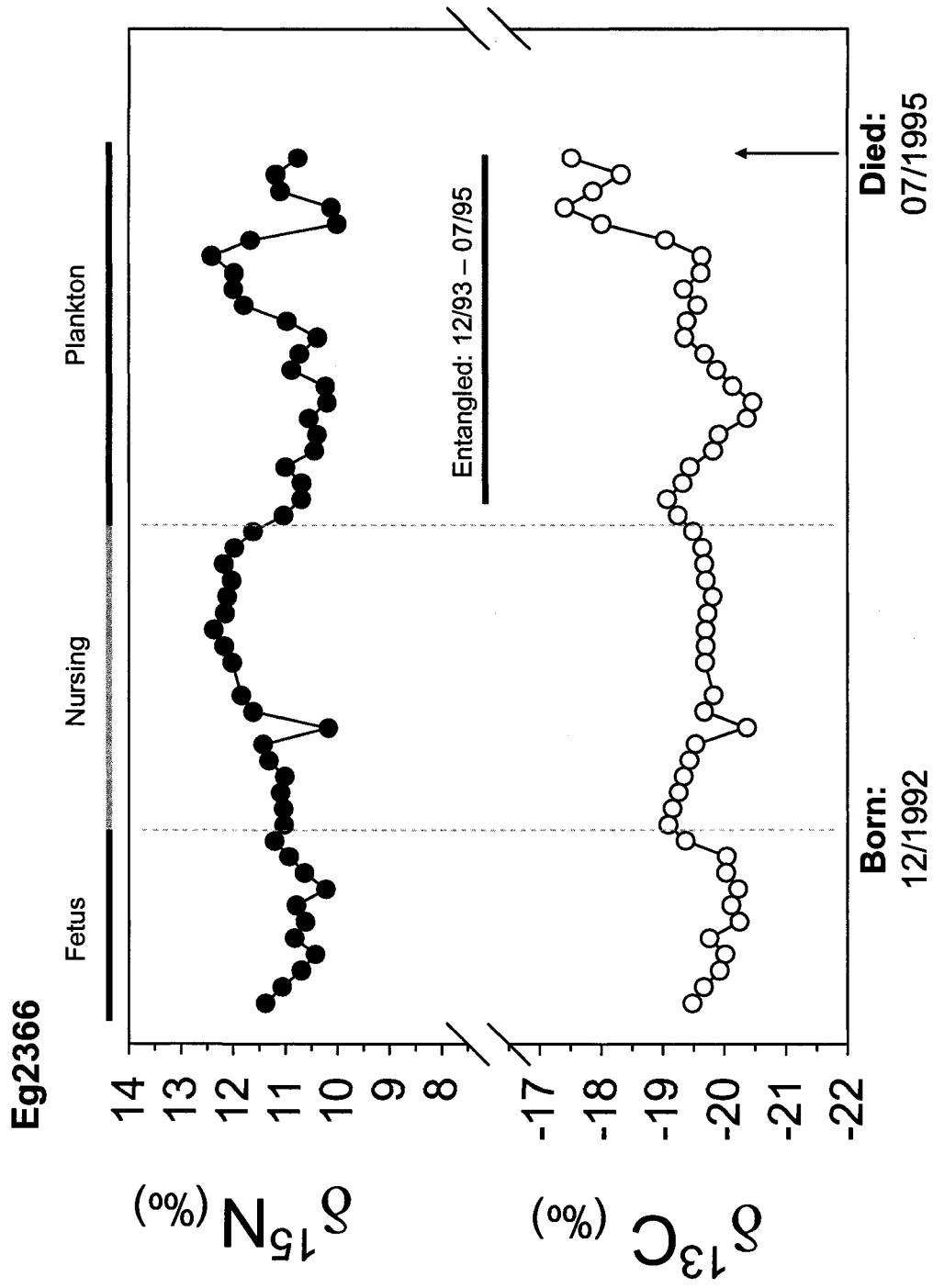
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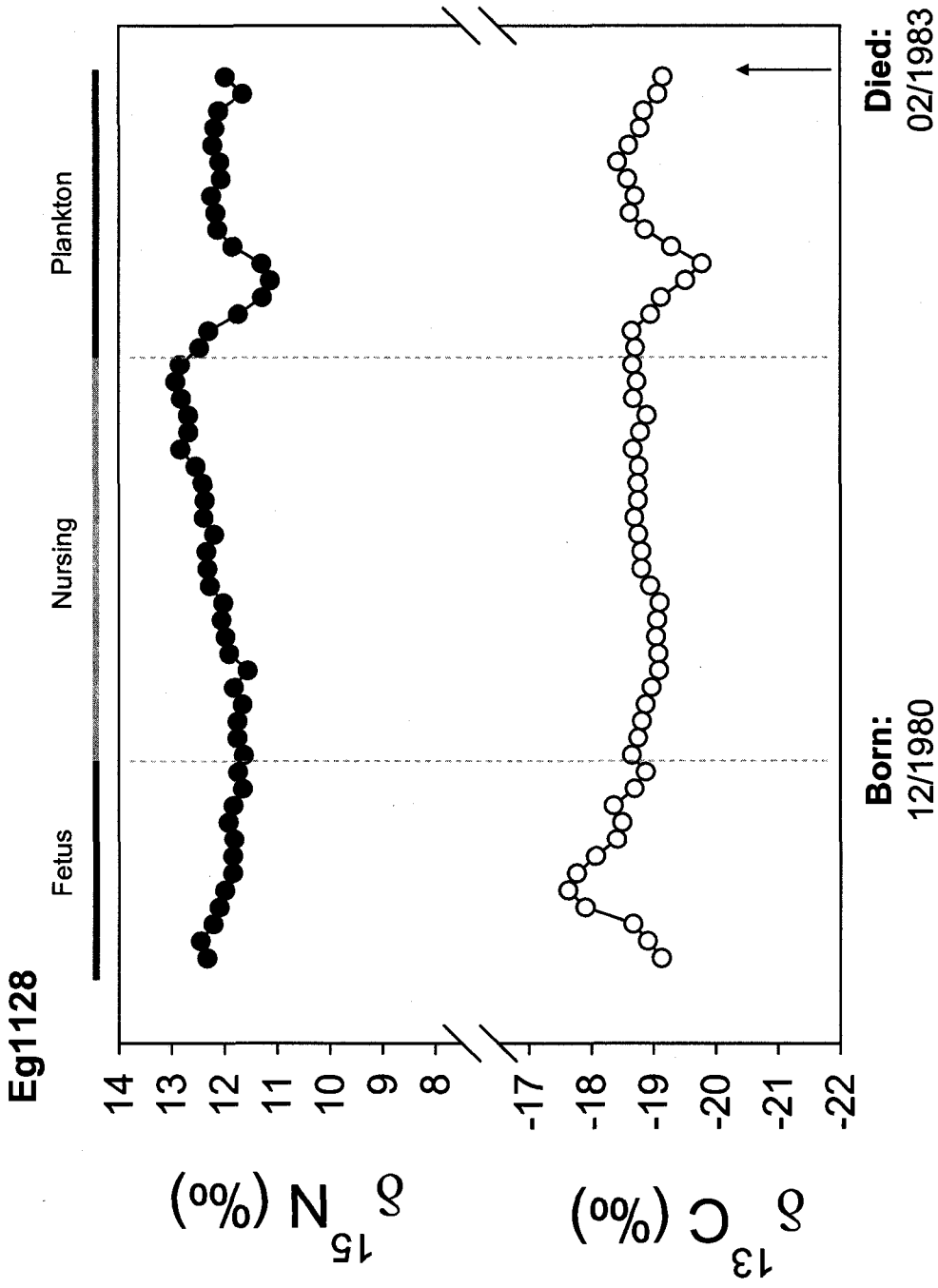


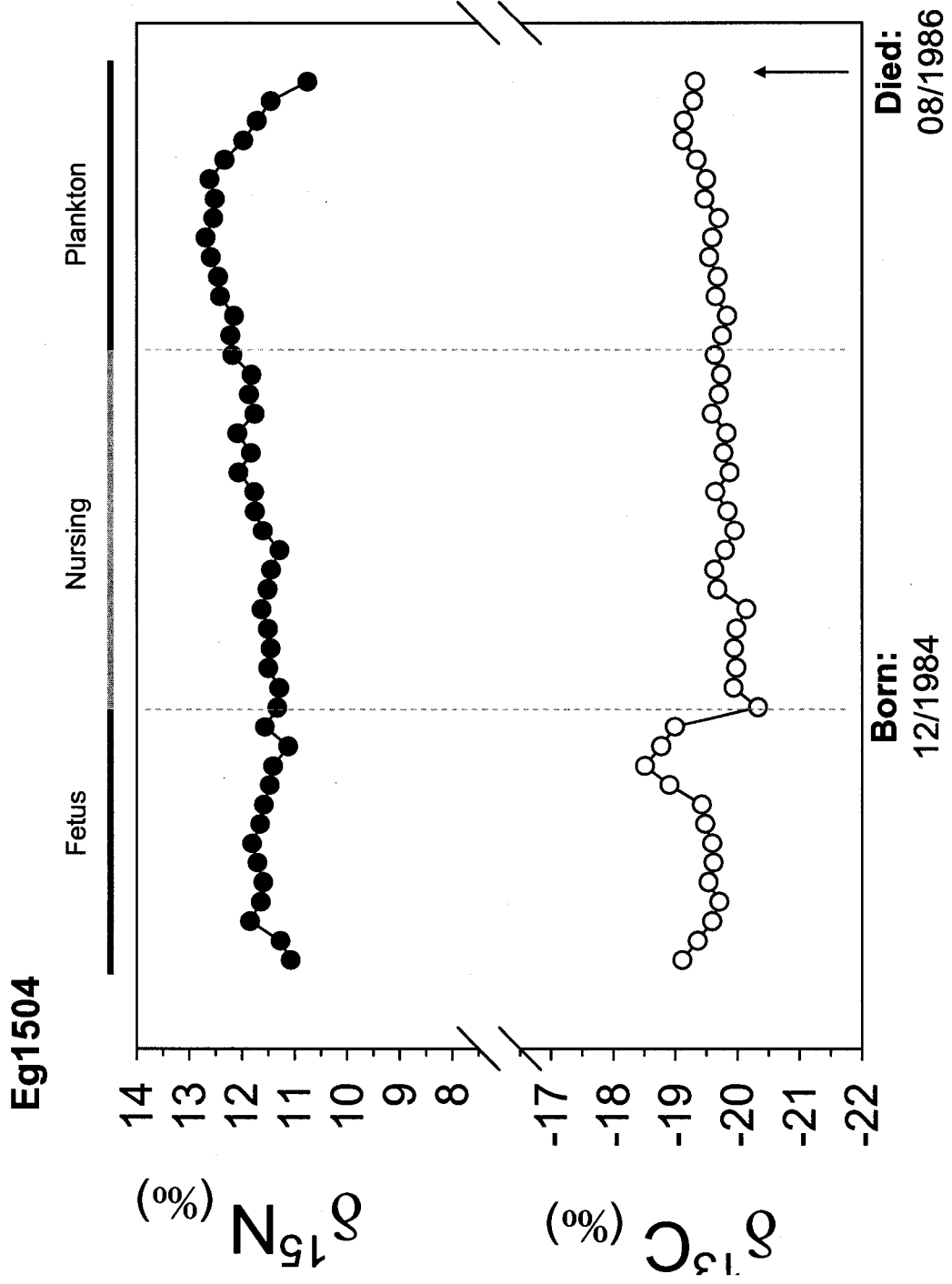
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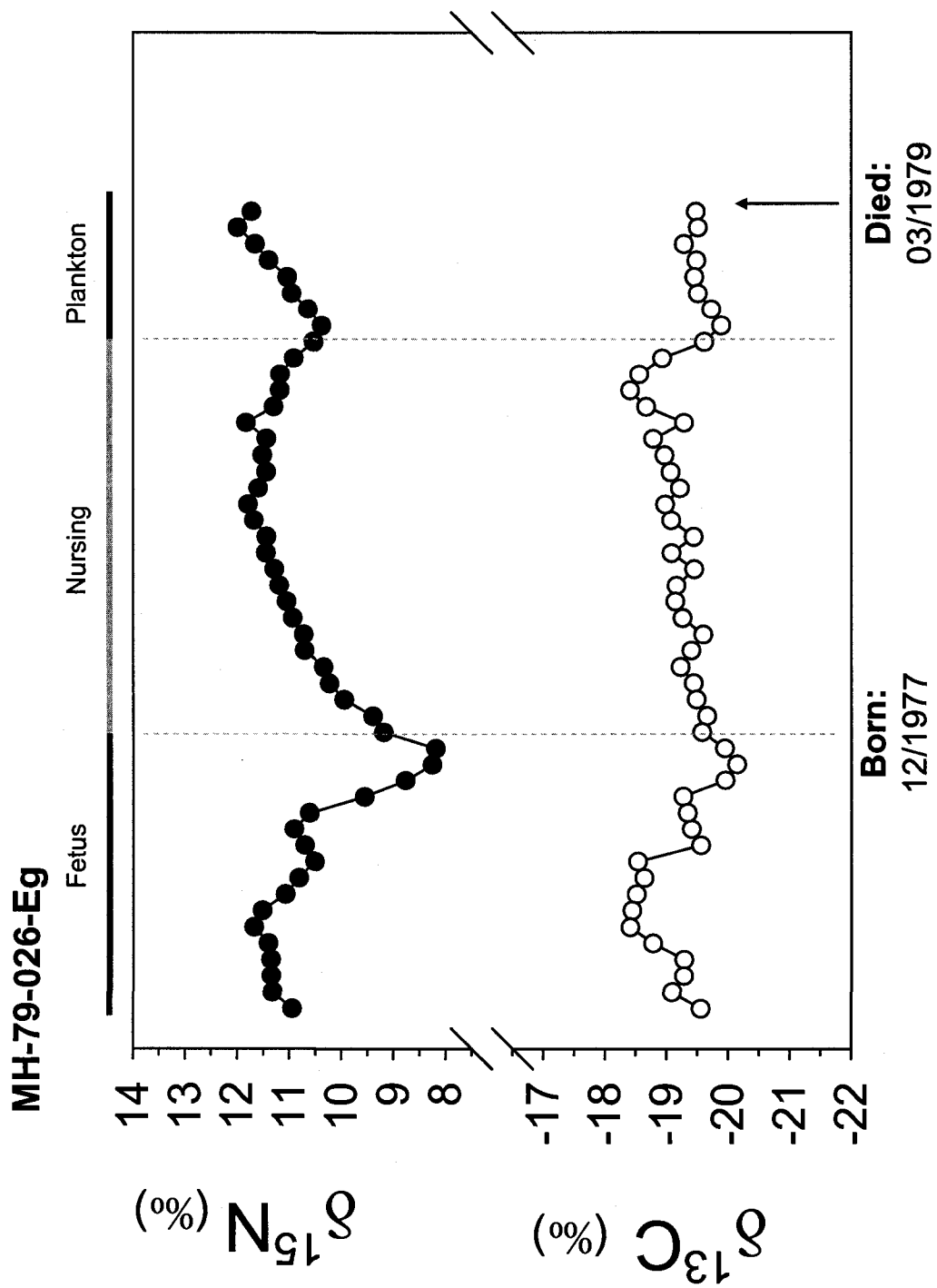


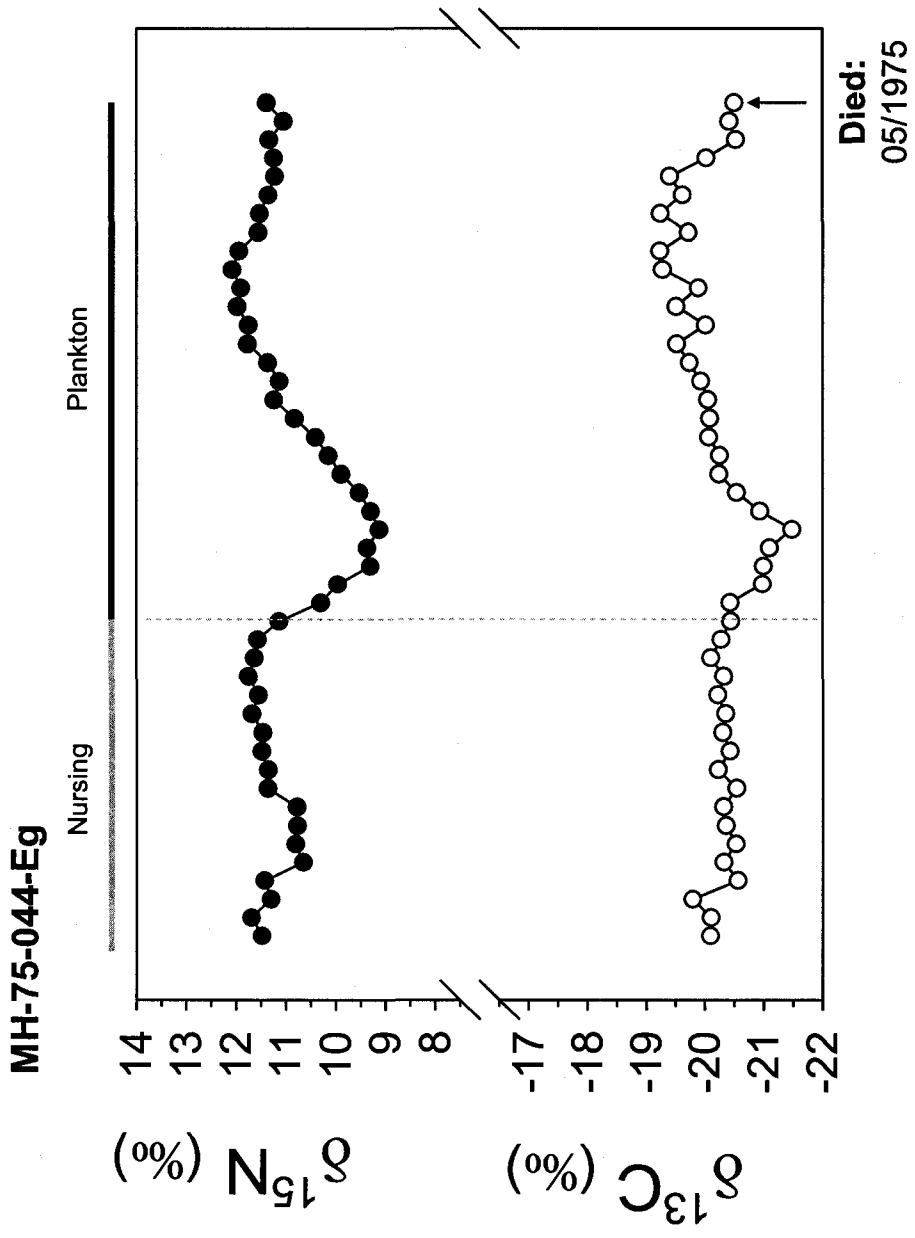


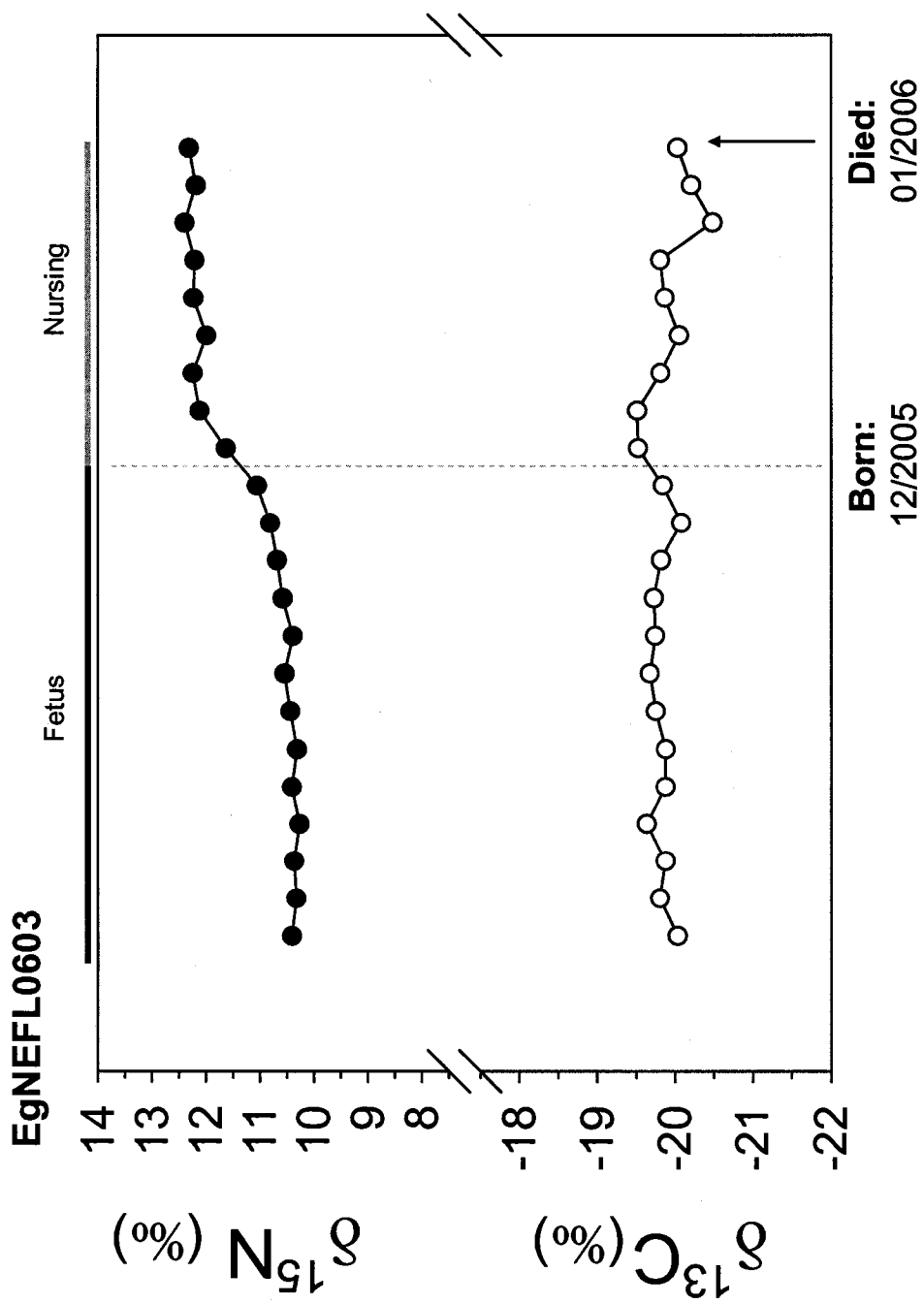


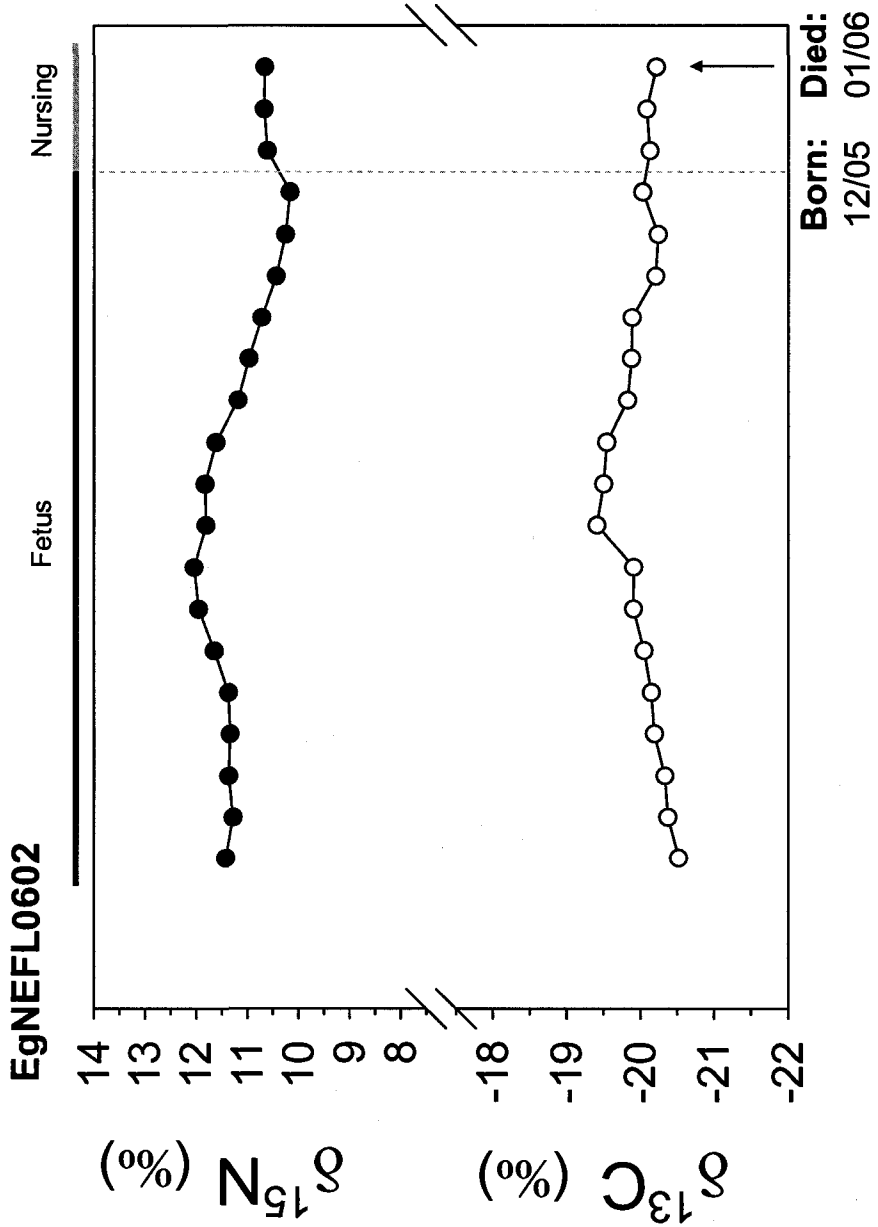


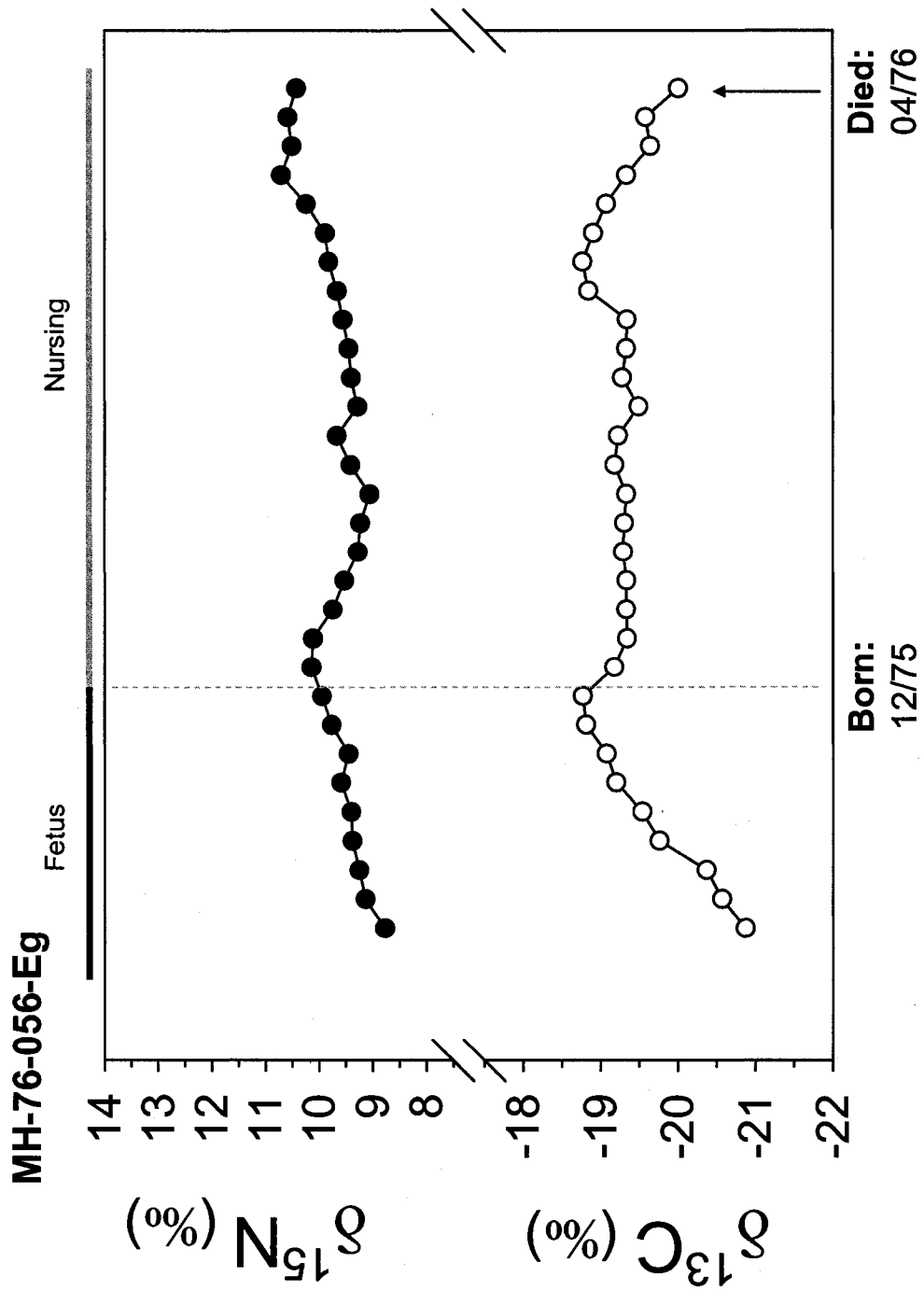












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CURRICULUM VITAE

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EDUCATION

Ph.D. (January 2009)

Boston University, Boston, MA, USA
Biology, Marine Program

M.A. (May 2007)

Boston University, Boston, MA, USA
Biology, Marine Program

B.A. *Cum Laude* (June 2003)

Gustavus Adolphus College, St. Peter, MN, USA
Biology and History with Honors

ADDITIONAL STUDIES

Massachusetts Institute of Technology/Woods Hole Oceanographic Institution Joint Program, Woods Hole, MA, USA

Graduate course audits: Applied Statistics (2004) and Scientific Programming (2008)

University of Utah, Salt Lake City, UT, USA

Graduate course audit: Stable Isotope Ecology (2004)

University of Queensland, Brisbane, Australia

Undergraduate semester abroad, emphasis in Marine Science (2002)

RESEARCH EXPERIENCE

Graduate Research Assistant, 2003 – 2008.

Woods Hole Oceanographic Institution, 2005 – 2008.

Supervisor: Dr. Michael Moore, Marine Mammal Forensics Laboratory

Boston University Marine Program, 2003 – 2006.

Supervisor: Dr. Ivan Valiela, Marine Ecology Laboratory, 2004 – 2006.

Supervisor: Dr. Gabrielle Gerlach, Molecular Ecology Laboratory, 2003.

Marine Mammal Observer, 2004 – 2008.

Woods Hole Oceanographic Institution. 2005 – 2008.

Supervisor: Dr. Mark Baumgartner, Biology Department

NOAA Fisheries, Northeast Fisheries Science Center, 2004 – 2007.

Supervisor: Fred Wenzel, Protected Species Branch

Undergraduate Research Assistant, 2001 – 2002.

Gustavus Adolphus College. 2001 – 2002.

Supervisor: Dr. Nancy Butler, Aquatic Ecology Laboratory

SEA DUTY

2008

Marine Mammal Observer and Oceanographer, Pacific Right Whale Evaluation Study (PRIEST) Cruise: Southeast Bering Sea, *F/V Ocean Olympic*. August 2 – 15.

2007

Marine Mammal Observer, Humpback Whale Tagging & Bioacoustics Cruise: Stellwagen Bank National Marine Sanctuary, *R/V Tioga*. July 18 – 20.

Marine Mammal Observer, North Atlantic Right Whale Foraging Ecology Cruise IV: Great South Channel, *NOAA Ship Albatross IV*. May 7 – June 10.

2006

Marine Mammal Observer, North Atlantic Right Whale Tagging & Habitat Modeling Cruise: Jeffrey's Ledge, *R/V Tioga*. December 4 – 6.

Marine Mammal Observer, North Atlantic Right Whale Foraging Ecology Cruise III: Great South Channel, *NOAA Ship Albatross IV*. May 1 – May 26.

Marine Mammal Observer, North Atlantic Right Whale Tagging & Habitat Modeling Cruise: Cape Cod Bay, *R/V Tioga*. March 13.

2005

Oceanographer, Large Whale Foraging Ecology Cruise: Northern Gulf of Maine, *NOAA Ship Delaware II*. July 27 – August 19.

Marine Mammal Observer, North Atlantic Right Whale Tagging & Habitat Modeling Cruise: Great South Channel, *R/V Tioga*. July 15.

Marine Mammal Observer, North Atlantic Right Whale Foraging Ecology Cruise II: Great South Channel, *NOAA Ship Albatross IV*. April 28 – May 20.

2004

Marine Mammal Observer, North Atlantic Right Whale Foraging Ecology Cruise I: Great South Channel, *NOAA Ship Albatross IV*. April 26 – May 21.

TEACHING EXPERIENCE

Research Mentor – Marine Biological Laboratory, Woods Hole, Summer 2007.

Advised an undergraduate intern for the NSF Research Experiences for Undergraduates (REU) Program.

Guest Lecturer, Massachusetts Marine Educators Annual High School Marine Science Symposia, March 2007 and 2008. “North Atlantic Right Whales: Can We Save Them?”

Teaching Assistant & Guest Lecturer, Boston University Marine Program. Fall Semester 2005 & 2006.

Course: Global Coastal Change. Instructor: Dr. Ivan Valiela.

Teaching Assistant, Gustavus Adolphus College. Fall Semester 2002.

Course: Invertebrate Zoology. Instructor: Dr. Shannon Fisher.

AWARD AND HONORS

American [Dissertation] Fellowship, American Association of University Women. 2007. Fellowship in support of dissertation completion, awarded for scholarly excellence and an active commitment to helping women through service in one’s community, profession, or field of research.

Graduate Research Abroad Fellowship, Boston University. 2006. Fellowship in support of novel research conducted at museums in Scandinavia and the United Kingdom.

SEASPACE Scholarship, Houston Underwater Club. 2006. Awarded for academic excellence in the study of marine sciences.

Rainer Voight Memorial Award (First Place), Boston University Marine Program. 2005. Scholarship in support of the pursuit of innovative research at the master’s level: *Developing Multi-Isotope Tracers to Determine North Atlantic Right Whale Habitat Use*

DeNault Award, Gustavus Adolphus College. 2002. Awarded for outstanding writing in history.

Barry M. Goldwater Scholarship, Barry M. Goldwater Foundation. 2002. Awarded for academic excellence and continuing undergraduate science research.

Charles C. Hamrum Scholarship, Gustavus Adolphus College. 2002 & 2003. Awarded for excellence in academics and independent research.

Dean's List, Gustavus Adolphus College. 2001

MANUSCRIPTS IN PREPARATION

McMahon, K. W., **N.S. Lysiak**, L.D. Brin, K. Buckman, J. Kneeland, F. Gibbons, and S.R. Thorrold. Ocean ecogeochemistry applied to connectivity analyses in marine populations. *Estuarine, Coastal, and Shelf Science*.

PEER-REVIEWED PUBLICATIONS

Gerlach, G. and **N. S. Lysiak**. 2006. Kin recognition and inbreeding avoidance in zebrafish, *Danio rerio*, is based on phenotype matching. *Animal Behaviour* **71**:1371-1377.

PUBLISHED ABSTRACTS

Lysiak, N.S., M.J. Moore, and A.R. Knowlton. 2008. Interpreting a Long-Term Stable Isotope Record Derived from North Atlantic Right Whale Baleen (poster). ISOSCAPES 2008 Meeting, Santa Barbara, CA.

Lysiak, N.S., M.J. Moore, A.R. Knowlton, and I. Valiela. 2008. Interpreting a Long-Term Stable Isotope Record Derived from North Atlantic Right Whale Baleen: Implications for Ecosystem-Level Changes in the Gulf of Maine? (poster). American Society of Limnology & Oceanography Ocean Sciences Meeting, Orlando, FL.

Lysiak, N.S., M.J. Moore, A.R. Knowlton, A.R. Solow. 2007. Deciphering Stable Isotope Records in Right Whale Baleen. 17th Biennial Conference on the Biology of Marine Mammals, Cape Town, South Africa.

Lysiak, N.S., M.J. Moore, B.A. McLeod, T.R. Frasier, C.R. Hammerschmidt, A.P. McNichol, and R. Löchen. 2007. Biogeochemical analysis of baleen fragments

discovered within Viking Era ships. North Atlantic Right Whale Consortium Annual Meeting, New Bedford, MA.

Lysiak, N.S., M.J. Moore, I. Valiela, A.R. Knowlton, and C.W. Potter. 2007. Tracking the Migration Patterns and Habitat Use of North Atlantic Right Whales with Stable Isotopes. American Society of Limnology & Oceanography Aquatic Sciences Meeting, Santa Fe, NM.

Lysiak, N.S., M.J. Moore, I. Valiela, A.R. Knowlton, and C.W. Potter. 2006. Biogeochemistry of Baleen: Creating Long-Term Records of Right Whale Movement Patterns With Stable Isotope Analysis. North Atlantic Right Whale Consortium Annual Meeting, New Bedford, MA.

Hammerschmidt, C., N.S. Lysiak, M. Saito, and M.J. Moore. 2006. Northern Right Whale Foraging and Metabolism Inferred from Stable Isotope and Methylmercury Analysis of Baleen (poster). 8th International Conference on Mercury as a Global Pollutant, Madison, WI.

Lysiak, N.S., M.J. Moore, I. Valiela, and A.R. Knowlton. 2006. Seasonal Movement and Trophic Status of Right Whales in the Northwest Atlantic Assessed with Stable Isotope Analysis of Baleen and Zooplankton. 86th American Society of Mammalogists Annual Meeting, Amherst, MA.

Lysiak, N.S., M.J. Moore, I. Valiela, and A.R. Knowlton. 2005. Stable Isotopes Analysis Utilized to Create Multi-annual Records of Right Whale Migration Patterns. 16th Biennial Conference on the Biology of Marine Mammals, San Diego, CA.

Lysiak, N. S., M. J. Moore, I. Valiela, and A. R. Knowlton. 2005. Stable Isotopes of North Atlantic Right Whale Baleen as Indicators of Foraging and Migration Patterns. North Atlantic Right Whale Consortium Annual Meeting, New Bedford, MA.

Lysiak, N. S., M. J. Moore, I. Valiela, and A. R. Knowlton. 2005. Stable Isotopes of North Atlantic Right Whale Baleen as Indicators of Foraging and Migration Patterns. American Society of Limnology & Oceanography Summer Meeting, Santiago de Compostela, Spain.

Lysiak, N.S., A.A. Hamp, and N.M. Butler. 2002. The Phototactic Behavior of Marine and Freshwater Zooplankton as Influenced by Habitat and Light Quality. American Society of Limnology & Oceanography Ocean Sciences Meeting, Honolulu, HI.

Hamp, A.A., N.S. Lysiak, and N.M. Butler. 2002. Investigations into the Phototactic Behaviors of Marine and Freshwater Mysids. American Society of Limnology & Oceanography Ocean Sciences Meeting, Honolulu, HI.

Ortenblad, M., K.N. Howe, N.S. Lysiak, and N.M. Butler. 2001. Field and Laboratory Investigations of the Phototactic Behaviors of *Diatomus* and *Daphnia* in Response to Four Wavelengths of Light. National Conference on Undergraduate Research, Louisville, KY.

COMMUNITY SERVICE

Marine Mammal Stranding Responder/Necropsy Participant. Cape Cod Stranding Network. Yarmouth, MA. 2005 – present.

Volunteer Aquarist. NOAA Woods Hole Aquarium, Woods Hole, MA. 2004 – 2007.

PROFESSIONAL AFFILIATION

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