The Cost of Locomotion in North Atlantic Right Whales *Eubalaena glacialis*

by

Anna E. Nousek McGregor

Department of Marine Science and Conservation
of Duke University

Date: ________________

Approved:

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Douglas P. Nowacek, Supervisor

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Frank Fish

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Laurens Howle

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David Johnston

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Mark Sussman

Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Marine Science and Conservation in the Graduate School of Duke University

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Abstract

Locomotion in any environment requires the use of energy to overcome the physical forces inherent in the environment. Most large marine vertebrates have evolved streamlined fusiform body shapes to minimize the resistive force of drag when in a neutral position, but nearly all behaviors result in some increase in that force. Too much energy devoted to locomotion may reduce the available surplus necessary for population-level factors such as reproduction. The population of North Atlantic right whales has not recovered following legal protection due to decreased fecundity, including an increase in the intercalf interval, an increase in the years to first calf and an increase in the number of nulliparous females in the population. This reproductive impairment appears to be related to deficiencies in storing enough energy to meet the costs of reproduction. The goal of this study was to determine whether increases in moving between prey patches at the cost of decreased foraging opportunities could shift these whales into a situation of negative energy gain. The first step is to understand the locomotor costs for this species for the key behaviors of traveling and foraging.

This study investigated the cost of locomotion in right whales by recording the submerged diving behaviors of free-ranging individuals in both their foraging habitat in the Bay of Fundy and their calving grounds in the South Atlantic Bight with a suction-cupped archival tag. The data from the tags were used to quantify the occurrence of different behaviors and their associated swimming behaviors and explore
three behavioral strategies that reduce locomotor costs. First, the influence that changes in blubber thickness has on the buoyancy of these whales was investigated by comparing the descent and ascent glide durations of individual whales with different blubber thicknesses. Next, the depth of surface dives made by animals of different sizes was related to the depth where additional wave drag is generated. Finally, the use of intermittent locomotion during foraging was investigated to understand how much energy is saved by using this gait. The final piece in this study was to determine the drag related to traveling and foraging behaviors from glides recorded by the tags and from two different numerical simulations of flow around whales. One, a custom developed algorithm for multiphase flow, was used to determine the relative drag, while a second commercial package was used to determine the absolute magnitude of the drag force on the simplest model, the traveling animal. The resulting drag estimates were then used in a series of theoretical models that estimated the energetic profit remaining after shifts in the occurrence of traveling and searching behaviors.

The diving behavior of right whales can be classified into three stereotyped behaviors that are characterized by differences in the time spent in different parts of the water column. The time budgets and swimming movements during these behaviors matched those in other species, enabling the dive shapes to be classified as foraging, searching and traveling behaviors. Right whales with thicker blubber layers were found to perform longer ascent glides and shorter descent glides than those with thinner blubber layers, consistent with the hypothesis that positive buoyancy does influence their vertical diving behavior. During horizontal traveling, whales made shallow dives to depths that were slightly deeper than those that would cause additional costs due to wave drag. These dives appear to allow whales to both avoid the costs of diving as well as the costs of swimming near the surface. Next, whales were found to glide for 12% of the bottom phases of their foraging dives, and the
use of ‘stroke-glide’ swimming did not prolong foraging duration from that used by continuous swimmers. Drag coefficients estimated from these glides had an average of 0.014 during foraging dives and 0.0052 during traveling, values which fall in the range of those reported for other marine mammals. One numerical simulation determined drag forces to be comparable, while the other drastically underestimated the drag of all behaviors. Finally, alterations to the behavioral budgets of these animals demonstrated their cost of locomotion constitutes a small portion (8–12%) of the total energy consumed and only extreme increases in traveling time could result in a negative energy balance. In summary, these results show that locomotor costs are no more expensive in this species than those of other cetaceans and that when removed from all the other stressors on this population, these whales are not on an energetic ‘knife edge’.
To my husband Ross and my parents Mary and John
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List of Abbreviations

Abbreviations

- \(a\) peak-to-peak distance traveled by each fluke stroke
- \(A_0\) volume of air-filled tissues at 1 atm
- \(A_g\) area of mouth gape
- \(A_w\) wetted surface area of whale
- ADL aerobic dive limit
- AMR adaptive mesh refinement
- \(B.\) *Balaenoptera*
- BoF Bay of Fundy
- \(c\) slope of a regression of the inverse of velocity over a glide
- cm centimeter
- \(C_d\) drag coefficient
- \(C_{df}\) drag coefficient during foraging
- \(C_{dt}\) drag coefficient during traveling
- \(C_{dv}\) depth-corrected drag coefficient
- CFD computational fluid dynamics
- CLVSOF coupled level-set volume of fluid
- COT cost of transport
- CT x-ray computed tomography
- \(d\) body depth
<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
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<tbody>
<tr>
<td>$D_M$</td>
<td>two-way distance traveled during migration</td>
</tr>
<tr>
<td>DIGITS</td>
<td>Digital Image Gathering and Information Tracking System</td>
</tr>
<tr>
<td>DNS</td>
<td>direct numerical simulation</td>
</tr>
<tr>
<td>Dtag</td>
<td>digital archival tag developed by Woods Hole Oceanographic Institution</td>
</tr>
<tr>
<td>$E_b$</td>
<td>locomotor costs during bottom phases</td>
</tr>
<tr>
<td>$E_d$</td>
<td>locomotor costs during descent phases</td>
</tr>
<tr>
<td>$E_s$</td>
<td>locomotor costs during post-dive surface intervals</td>
</tr>
<tr>
<td>$E_{C5}$</td>
<td>caloric content of one stage 5 <em>Calanus</em> copepod</td>
</tr>
<tr>
<td>$E_G$</td>
<td>total energy gain per dive cycle</td>
</tr>
<tr>
<td>$E_{G1}$</td>
<td>total energy gain for a single Type 1 dive</td>
</tr>
<tr>
<td>$E_{G2}$</td>
<td>total energy gain for a single Type 2 dive</td>
</tr>
<tr>
<td>$E_L$</td>
<td>total locomotor costs per dive cycle</td>
</tr>
<tr>
<td>$E_{L1}$</td>
<td>locomotor costs for a single Type 1 dive</td>
</tr>
<tr>
<td>$E_{L2}$</td>
<td>locomotor costs for a single Type 2 dive</td>
</tr>
<tr>
<td>$E_{L3}$</td>
<td>locomotor costs for a single Type 3 dive</td>
</tr>
<tr>
<td>$E_S$</td>
<td>total energy surplus</td>
</tr>
<tr>
<td>$E_{SM}$</td>
<td>total energy surplus including costs of two-way migration</td>
</tr>
<tr>
<td>EgNo</td>
<td>unique identifying number for every individual whale in the North Atlantic right whale population</td>
</tr>
<tr>
<td>$F_{drag}$</td>
<td>drag force</td>
</tr>
<tr>
<td>$F_f$</td>
<td>drag during foraging</td>
</tr>
<tr>
<td>$F_t$</td>
<td>drag during traveling</td>
</tr>
<tr>
<td>$F_p$</td>
<td>drag while pregnant</td>
</tr>
<tr>
<td>$Fr$</td>
<td>Froude number</td>
</tr>
</tbody>
</table>
$FR$ fineness ratio
$g$ gravitational acceleration constant
GoM Gulf of Maine
GPS Global Positioning System
$h$ submersion depth
$h_{est}$ submersion depth estimated from whale body depth
hr hour
$H$ test statistic for Kruskal-Wallis test
Hz Hertz
$i$ percentage of Type 1 dives made
$I$ prey ingestion rate
$j$ percentage of Type 2 dives made
$J$ joule
$k$ percentage of Type 3 dives made
kg kilogram
kHz kilohertz
kJ kilojoule
km kilometer
$L$ length
$L_m$ length of whale mouth
m meter
min minute
mm millimeter
$M_a$ mass of attached fluid
$M_w$ whale mass
MHz megahertz
<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>no.</td>
<td>number</td>
</tr>
<tr>
<td>N</td>
<td>Newton</td>
</tr>
<tr>
<td>NAO</td>
<td>North Atlantic Oscillation</td>
</tr>
<tr>
<td>NEAq</td>
<td>New England Aquarium</td>
</tr>
<tr>
<td>$p_{sf}$</td>
<td>distance to the seafloor</td>
</tr>
<tr>
<td>$p_w$</td>
<td>depth from surface to tag</td>
</tr>
<tr>
<td>$P$</td>
<td>power</td>
</tr>
<tr>
<td>Re</td>
<td>Reynolds number</td>
</tr>
<tr>
<td>R/V</td>
<td>research vessel</td>
</tr>
<tr>
<td>s</td>
<td>second</td>
</tr>
<tr>
<td>spp.</td>
<td>species</td>
</tr>
<tr>
<td>SAB</td>
<td>South Atlantic Bight</td>
</tr>
<tr>
<td>SAG</td>
<td>surface active group</td>
</tr>
<tr>
<td>SE</td>
<td>standard error</td>
</tr>
<tr>
<td>SEUS</td>
<td>Southeastern United States</td>
</tr>
<tr>
<td>SI</td>
<td>surface interval</td>
</tr>
<tr>
<td>$T_a$</td>
<td>duration of dive ascent phases</td>
</tr>
<tr>
<td>$T_b$</td>
<td>duration of dive bottom phases</td>
</tr>
<tr>
<td>$T_s$</td>
<td>duration of dive surface phases</td>
</tr>
<tr>
<td>$U$</td>
<td>velocity</td>
</tr>
<tr>
<td>$U_a$</td>
<td>velocity of dive ascent phases</td>
</tr>
<tr>
<td>$U_b$</td>
<td>velocity of dive bottom phases</td>
</tr>
<tr>
<td>$U_d$</td>
<td>velocity of dive descent phases</td>
</tr>
<tr>
<td>$U_s$</td>
<td>velocity of dive surface phases</td>
</tr>
<tr>
<td>USA</td>
<td>United States of America</td>
</tr>
<tr>
<td>VHF</td>
<td>Very high frequency</td>
</tr>
</tbody>
</table>
$W$ test statistic for Shapiro-Wilk normality test

$\alpha$ added mass coefficient

$\gamma$ drag augmentation factor

$\theta$ pitch

$\lambda$ increase in drag due to active propulsion

$\rho_{m}$ density of surrounding medium

$\rho_{t}$ density of whale tissue

$\rho_{c}$ average density of *Calanus* prey patch in the Bay of Fundy

$\phi$ intercalf interval
Acknowledgements

Many, many people have assisted me in the completion of this work, both in the form of sharing data, supplying advice and providing encouragement when times got hard. Although I’m sure I will leave someone out, these individuals are those whom I am extremely grateful for their time, effort and patience.

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The other key element in this work was the development of model right whale geometries and the use of numerical methods to solve for the movement of fluids around them. Ross McGregor was indispensable in creating the accurate geometries and has demonstrated unfathomable amounts of patience in spending six months of his life drawing about 450 individual, three-dimensional baleen plates. Joel Bellucci graciously contributed the original three-dimensional geometry, which was then improved for scientific accuracy. Dan Maas and Marc Dantzker assisted with some model development for early models, and the individuals at the Southwest Fisheries Science Center, including Wayne Perryman, Morgan Lynn and Paula Olsen, were
very helpful in allowing us to obtain length and width measurements from their aerial photogrammetry collection. Michael Moore and Bill McClellan provided access to necropsy measurements as well as allowing us to participate in a few necropsies, and Carolyn Miller was very generous in sharing her blubber thickness and pregnancy shape measurements. Finally, I would like to acknowledge the North Atlantic Right Whale Consortium for maintaining an efficient and productive system to share data on this species and allowing us to access both the blubber thickness measurements and the Digital Image Gathering and Information Tracking System (DIGITS).

After the models were developed, the use of numerical methods was critical in determining the dominant hydrodynamics experienced by these animals. In addition to serving on my committee, Mark Sussman devoted many hours of his time to improving and testing his CFD code in order to make it robust for use with a whale, and I am very thankful for his patience both in running simulations, dealing with my requests to add various features to his code and answering many, many questions about the code. The help of his student, Austen Duffy, who animated the geometries that we created, and other colleagues, namely Gordon Erlebacher, in the Florida State University Mathematics and Computer Science Department is also much appreciated. Laurens Howle, who also generously provided his time and advice as part of my committee, was very generous in running models in his flow solver, that allows us to include a second method of determining drag.

I also wish to express my gratitude for the time, patience and advice of the other two members of my committee, Frank Fish and David Johnston. Teaching and research schedules leave very little additional time for serving on committees, and I very much appreciate their willingness to contribute to my work.

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Putland and many other friends should be mentioned, along with my original committee members, David Thistle and Lou St Laurent, and the department chair, Bill Dewar, for their support and help.

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The second to last acknowledgement I want to make is to thank Doug, my advisor. He created the initial idea for my project, secured an initial amount of funding and...
brought me to the wonderful community of the Duke Marine Lab. I appreciate his flexibility in offering me this position, and I thank him for his philosophy of treating each of his students as individuals. Six years is a long time working closely with someone, and I’m glad that I ended up with someone as nice as Doug.

My last thanks goes to the most important individuals in my life, my lovely husband Ross and my parents Mary and John. My parents have always emphasized the importance of both education and determination, and it is their teachings of discipline and pride in my work that gave me the stubbornness to finish and the determination to do it well. He’s been there to discuss any new ideas about my work, listen to my moaning and whining and pick up the mess that is me while writing my thesis. For his determination and love, I am extremely thankful and I am looking forward to the many great adventures that the rest of our lives together will hold.
The ability to move requires that an animal can produce enough energy internally via its muscles to overcome the physical forces inherent in its external environment. Its external morphology directly affects the magnitude of these forces and the type of locomotion that most efficiently overcomes them. Given the amount of movement required for large mammalian predators, strong selection pressure has resulted in morphological adaptations that minimize the use of energy when performing the biologically essential functions of surviving, foraging and reproducing. Additionally, animals must trade off proficiency in one area of locomotor movements for reduced performance in another, resulting in morphological specializations that optimize performance in ways that improve an animal’s survival (Alexander, 2003; Vogel, 1994). Therefore, quantifying the physical forces experienced by an animal and comparing those forces between organisms in different niches of similar environments allows important aspects of an animal’s ecology to be determined.

Energy is needed by warm-blooded individual animals to survive, including basic metabolic processes, thermoregulation, digestion, and growth, while the additional demands of reproduction are necessary to ensure survival of the population (Costa
and estimates of these costs measured in terms of the energy required to move one unit mass over one unit distance, or the cost of transport (COT), have been made for a number of marine mammal species, some that can be maintained in captivity (Rosen & Trites, 2002; Williams, 1999) and other larger, free-ranging ones (Blix & Folkow, 1995; Rodriguez de la Gala-Hernandez et al., 2008; Kshatriya & Blake, 1988; Sumich, 1983; Williams & Noren, 2009). Factors that affect the COT of marine homeotherms include the temperature of the external environment, the animal’s swimming velocity, body shape, body size and activity level (Folkow & Blix, 1992; Hind & Gurney, 1997; Lovvorn, 2007; Costa, 1988; Williams & Yeates, 2004). Most marine species have been shown to use swimming speeds that minimize COT for their most frequently used behaviors (Williams et al., 1993; Watanabe et al., 2010). A minimized COT is extremely beneficial to marine mammals because using less energy while submerged lengthens the time available for foraging while at depth, or an animal’s aerobic dive limit (ADL) (Costa et al., 2004).

1.1 Foraging costs

The costs related to locating, capturing and consuming prey are directly related to feeding methods, which are in turn dictated by the size, shape and speed of an animal as well as the size, speed and density of its prey. A feeding technique prevalent in marine environments, filter feeding can be lower in costs than may other foraging methods. This method relies on the movement of a fluid to carry small organisms into the mouth of a predator, which are then separated from the surrounding fluid by some mesh-like mouth structure that allows the water to pass out of the mouth and keeps the prey in it. Many invertebrates perform truly passive filter-feeding, in which they are fixed to a stationary point and depend on external currents to bring food
through their filtration structures (Vogel, 1974), but in large, mobile vertebrates, active measures are employed to maintain the movement of fluid and prey into their mouths. These techniques have been described as either ‘ram’ or ‘suction’, depending on whether the animal is moving into the fluid or the animal is stationary and drawing the fluid into its mouth, and ‘continuous’ or ‘intermittent’ depending on the duration of the feeding events (Sanderson & Wassersug, 1993). Examples of continuous suction filter-feeders include flamingos (*Phoenicopterus ruber*) and some species of waterfowl (*Anatidae* spp.) that rely on rapid movements of their tongue and hyoid to pump water and prey into their mouth cavity (Jenkins, 1957; Kooloos et al., 1989). Intermittent suction feeding is used by some teleost fishes (Sanderson & Wassersug, 1993), whale sharks (Nelson & Eckert, 2007) and odontocete cetaceans (Bloodworth & Marshall, 2005; Werth, 2006) and has the advantage that larger, more evasive individual prey items can be consumed. This technique relies on the use of external mouthparts to draw water and prey into their mouths at brief and frequent intervals (Wainwright et al., 2007; Westneat, 2005).

Among ram feeders, the continuous method is much more widespread than the intermittent one, although both allow the efficient consumption of huge numbers of prey items for the same amount of foraging time and provide vast resources for plantivorous predators. Continuous ram feeders include several large ray species (Nortarbartolo-di Sciara, 1988), mackerel, anchovies, and herring (Gibson & Ezzi, 1990; Sanderson & Wassersug, 1993), whale and basking sharks (Nelson & Eckert, 2007; Sims, 2008) and bowhead and right whales (Lambertsen, 1983; Lambertsen et al., 2005). In contrast to animals such as black skimmers and nighthawks that move along with open mouths until large, individual prey items are located and captured (Jackson, 2003; Withers & Timko, 1977), ram filter feeders are constantly consuming large quantities of small prey in this way. With abundant resources, large body size becomes a significant asset to the efficiency of continuous ram feed-
ing (Webb & de Buffrénil, 1990), and the largest shark, ray, cetacean and arguably teleost species (extinct species) are all filter feeders (Wilga et al., 2007; Werth, 2000; Friedman et al., 2010). Intermittent ram feeding, in comparison, is not used in elasmobranch or teleost species and only appears in one family of cetaceans (Balaenoptera spp.) (Sanderson & Wassersug, 1993; Lamberti, 1983). This method has the advantage that larger, highly evasive prey (e.g. herring, sandlance) can be captured, but at a relative high cost because of the acceleration forces necessary to draw fluid into the mouth (Lamberti, 1983).

Because ram filter-feeding requires animals to move through the fluid, the costs of this technique are linked to the speed and therefore locomotor capabilities of these animals, unlike the feeding techniques of suction filter-feeding animals (Sanderson & Wassersug, 1993). The more energy lost in moving fluid through a filter results in less energy gained from foraging, so animals have evolved a variety of adaptations to reduce the cost of filter feeding. Most filter-feeding birds and fishes have elongated mouthparts (bills or jaws, respectively) that serve to increase the size of their filter regardless of the type of filter feeding they use (Jenkins, 1957; Kooloo & Zweers, 1991; Sanderson & Wassersug, 1993). Whale and basking sharks have modified gill arches that increase the size of their filters relative to their body, direct water flow out of the mouth and have specialized bristly gill rakers that separate prey items from the water (Sims, 2008; Motta et al., 2010).

Both continuous and intermittent ram filter-feeding are used within mysticete cetaceans, and clear anatomical differences appear between those species that use each technique. The four species of the family Balaenidae use continuous ram feeding, while those of the family Balaenopteridae use the intermittent style, more typically referred to as engulfment lunge feeding. Unlike moving at a constant speed as the balaenids do, these whales accelerate into a prey patch and open their mouths, engulfing a large volume of water and prey. These whales then close their mouths,
letting the water stream out through the baleen and leaving the prey behind in the oral cavity. Adaptations that facilitate this foraging technique include an expandable ventral pouch, which is covered with grooves and ridges that allows the skin to stretch without breaking, short bristly baleen, a small tongue, and a long, streamlined body that reduces pressure drag and therefore can be accelerated faster with less thrust (Lambertsen, 1983; Woodward et al., 2006). In comparison, the mysticetes that feed by ram suspension have large, muscular tongues, relatively larger plates of baleen, and jaws that occupy up to one-third of their total body length, adaptations to maximize the filtration area of their mouths. In addition, the contour of both the racks of the baleen plates and the morphology of the mouth openings appears to generate a reverse pressure differential that pulls water through their mouths, thereby reducing the drag generated when feeding (Werth, 2004; Lambertsen et al., 2005).

1.2 Species background

The four species of right whale, members of the mysticete family Balaenidae, Gray, 1821, are found in all of the world’s north temperate and polar oceans. Bowhead whales Balaena mysticetus occupy the Arctic polar waters, while southern right whales Eubalaena australis inhabit the Southern Ocean, ranging from Antarctica to South Africa, South America and New Zealand (Cummings, 1981). Although historical distributions of the two other right whale species, the North Pacific right whale E. japonica and the North Atlantic right whale E. glacialis included the entire North Pacific and North Atlantic oceans respectively, heavy whaling pressures eliminated the presence of both species on the eastern sides of their respective distributions. All of these species feed in more productive higher latitudes during the boreal spring and summer and then migrate to spend the boreal winter months in either unknown pelagic locations or lower latitudes to give birth.

Despite differences in distribution, all of these species are characterized by sim-
ilarities in morphology, feeding ecology and behavior, which made them excellent targets for over harvesting throughout modern human history. Because these animals spend some of their lives close to shore, swim slowly, and float after death, balaenid whales could be successfully killed and recovered before the advent of sophisticated seagoing and whaling technology. For the North Atlantic species, a lower estimate of 5500 individuals were killed by modern whaling between 1634 and 1951 (Reeves et al., 1999, 2007), and between 25,000–40,000 balaenid whales were killed along the Labrador coast of Canada by Basque whalers from 1530-1610, although the number of bowhead whales may have greatly exceeded that of North Atlantic right whales within this count (Aguilar, 1986; Reeves et al., 2007; Rastogi et al., 2004).

Commercial whaling for North Atlantic right whales ended with international protection for the species granted by the League of Nations in 1935, and the last direct mortalities in this species occurred in the 1960s (Kraus & Rolland, 2007; Reeves et al., 2007). Roughly 400 individuals make up the current population, and the annual growth rate of the population has ranged from about 3.5% in the early 1980s to -2% a decade later (Knowlton et al., 1994; Kraus & Rolland, 2007). This rate of population growth is much lower than that of the southern right whale, for which a 7–8% growth rate in 1997 was reported, evident in the much larger worldwide population size of over 8000 individuals (Best et al., 2001; Cooke et al., 2001), and some estimates predict that the population is too small to maintain enough genetic diversity for recovery (Fujiwara & Caswell, 2001; Caswell et al., 1999). Low population growth in North Atlantic right whales has been clearly attributed to decreased fecundity, through an increase in the number of years between calves (from 3.6 years in 1987 to 5 between 1993 and 1998), a high percentage of nulliparous females within the population, and giving birth to their first calves at a later age (Kraus et al., 2007; Browning et al., 2009; Kraus et al., 2005). In comparison, the mean calving interval of southern right whales has held steady around 3–3.5 years
Such reproductive impairments could be consequences of genetic inbreeding and/or high pollutant or disease levels in their environment (Frasier et al., 2007; Kraus & Rolland, 2007), but the energetic requirement for reproduction in this species is also thought to be very high. Females must store enough fat in their bodies to meet not just their own energetic demands over the course of six months but enough to supply their offspring with energy to grow. A three-year calving interval has been suggested to be the minimum amount of time necessary between subsequent calves because females spend the first year of that period lactating to nourish their previous calf, the second year storing up energy and the third year sustaining a developing fetus (Kraus et al., 2007). The inability to build up sufficient blubber stores to meet the needs of pregnancy and lactation has been suggested as a cause for decrease in fecundity in North Atlantic right whales (Miller Angell, 2006), and increases in calving intervals have been suggested to be related to abortion and neonatal loss of calves, which could happen in females that are unable to energetically support a fetus after migration (Browning et al., 2009). Although a variety of reproductive impairments can be related to nutritional stress in animals (Bronson, 1989; Kauffman et al., 2010; Millon et al., 2010), marine mammals seem to be more sensitive to stress during late gestation and early lactation, as has been observed in decreased fecundity in pinniped populations during years of low food availability (Trillmich & Limberger, 1985; Pitcher et al., 1998; Hadley et al., 2006). Annual variations in the number of right whale births have been connected with patterns in Calanus abundance and the underlying oceanographic processes that influence that abundance, supporting the potential for a link between resource limitations and low population growth in this population (Pendleton et al., 2009; Winn et al., 1986; Greene et al., 2003; Hlista et al., 2009).

Many of the aspects of balaenid biology that have resulted in the preferential
hunting of these species over others relate to their locomotor costs. The slow swimming speeds of these animals suggest that their shape and/or their feeding method may be conducive to generating higher levels of drag, and therefore, they have been thought to have a high cost of locomotion. In addition, many of these whales float after death, which allowed dead right whales to be retrieved and flenced without the need for the carcass to be inflated or floats to be tied on (Reeves & Mitchell, 1986). This anecdotal evidence suggests that balaenids have a clearly different cost of locomotion from their balaenopterid equivalents and therefore the contribution of locomotor costs to their energy budget merits exploration.

Changes in *Calanus* distribution and abundance in the North Atlantic Ocean also appear to be occurring as a consequence both to human disturbance of the area and climatic shifts (Beaugrand & Reid, 2003; Beaugrand et al., 2002; Gislason et al., 2009; Kenney, 2007). Because right whales feed almost exclusively on one stage of this species of zooplankton and require high densities of this prey source, they have few options when changes in this food source arise (Michaud & Taggart, 2007; Kenney et al., 1986; Baumgartner et al., 2007). Some female whales were referred to by whalers as ‘dry skins’ because they either sank when killed or produced very little oil, presumably because they had just returned from their trip to the calving grounds. Such a significant change in the amount of blubber, which have been quantified by Miller Angell (2006), suggests these animals use a considerable amount of stored energy for reproduction and therefore may not have much energy to spare. The aim of this research was to determine the cost of locomotion in right whales through an estimation of the hydrodynamic forces and then explore whether locomotor costs could be a significant element in the overall energetic requirements of this population.
1.3 Project overview

The central goal of this project was to investigate the mechanical locomotor costs of North Atlantic right whales by quantifying the hydrodynamic forces experienced during different behaviors and understand the key behavioral strategies that may reduce these costs. Because movement in different parts of the water column will result in the generation of different hydrodynamic forces and therefore different locomotor costs, the first section of this study quantified the extent to which right whales are present in different regions of the water column. Submerged movements of whales were monitored with an archival tag attached with suction cups to free-ranging right whales in two habitats, which have been identified as being critical to the survival of the species. A clustering algorithm was used to objectively identify the predominant movement patterns, and the dominant behavior of each movement pattern inferred through similarities in swimming kinematics with other marine animals. The goal of this section was then to quantify the differences in swimming kinematics between behaviors so that the effect of those behavior on locomotor cost could be determined.

Next, the potential for behavioral strategies to reduce locomotor costs during movement in different parts of the water column was explored. During vertical transits of a positively buoyant animal traveling towards the surface, the force of buoyancy will act in a similar direction to that of the thrust actively produced by an animal, thereby decreasing the thrust required to swim forward (Miller et al., 2004b). When traveling in the opposite direction, additional thrust will be needed to overcome that same force (Sato et al., 2009). In the second section, the effects of buoyancy differences in right whales on vertical diving behavior was explored by quantifying the gliding behavior of whales during vertical diving phases (descents and ascents) and comparing it between animals with different amounts of blubber, which was presumed to be the major source of their positive buoyancy. Data from
archival tags attached to right whales known or estimated to have different amounts of blubber in their bodies, as determined through use of an ultrasound device, and duration of descents and ascents was compared between individuals. The goal of this section was to determine whether animals with thicker blubber layers used longer ascent glides and shorter descent glides than those with thinner blubber layers.

The third section of this project explored behavioral strategies used during horizontal swimming near the water surface. Due to their evolutionary history, whales are tied to the water’s surface because they must obtain oxygen from air. When accessing their food sources at depth is unnecessary, swimming horizontally near the surface would avoid using energy to overcome the effects of vertical diving (drag and buoyancy). However, drag just under the surface can be up to five times that of swimming well submerged (Hertel, 1966), so horizontal movements near the surface would also cause increased locomotor costs. Traveling whales appear to make shallow dives and whether these dives allow them to avoid the costs associated with near-surface swimming was investigated by relating the depth of wave drag to the dive depth of shallow dives made by right whales of different sizes. Marine mammals are limited in their foraging ability by the amount of time they can spend submerged, which is in part determined by their cost of locomotion at depth that can be inferred from the drag forces of passively gliding animals.

The fourth section of this study explored the use of intermittent locomotion in right whales as a means of saving energy. Glides during horizontal ‘bottom phases’ of foraging dives were identified and used to determine whales that were predominantly stroke-glide swimmers and those that were continuous swimmers. Glide duration and a series of stroking behavior parameters were quantified and compared between the two gaits in order to understand the magnitude of savings possible in this species. The influence of stroking parameters on glide duration was then analyzed to confirm how whales were reducing their energy expenditure. Finally, drag coefficients were
determined from the deceleration rates of whales during glides made during foraging dives and those made from whales traveling near the surface in order to determine changes in energetic cost related to those behaviors.

In the final portion of this project, the drag forces related to three different behavioral contexts were modeled in two computational fluid dynamics (CFD) codes and compared to that obtained from the tag records of free-ranging right whales. These forces were then placed in the context of energy requirements of a whale in order to investigate the buffering capacity of these animals to changes in their food source or the amount of time spent searching for it. The drag forces measured from the numerical methods were compared to those estimated from the tag data in the previous section. These drag coefficients were then used in a series of theoretical models to 1) estimate the locomotor costs of different behaviors and 2) explore the effect that shifts in behavior would have on the net energy profit of these animals.
2.1 Introduction

Every mobile animal must use a minimum amount of energy to move their body mass a given distance, but this cost varies considerably within individuals as well as species. In order to compare the energetic requirements between species and locomotor modes, the minimum cost of transport (COT) is usually determined (Schmidt-Nielsen, 1972). Among large marine vertebrates, different behaviors have been shown to have a large effect on the energy needed to move. Foraging in balaenopterid cetaceans drastically increases locomotor costs over the minimum COT because of the lunge-feeding technique used by this group of whales (Acevedo-Gutiérrez et al., 2002; Goldbogen et al., 2007). Conversely, cetaceans have been found to reduce their respiration rate during resting behaviors, indicating that these behaviors require less energy than that used during active foraging and diving (Lyamin et al., 2000; Gnone et al., 2006; Miller et al., 2007). Even within dives of the same individual, different dive phases differ in the amount of energy used. Deep diving marine mammals al-
ternate their foraging at depth with recovery periods at the surface that allow them to recover their oxygen stores for their next deep dive by minimizing the locomotor costs during this recovery phase (Costa & Williams, 1999). The descent phases of positively buoyant species require additional thrust to overcome the upward force of buoyancy, again raising the locomotor costs above those included in the COT, although cetaceans and pinnipeds have behavioral mechanisms and physiological adaptations to reduce those additional costs.

Because subsurface behaviours cannot be observed directly in air-breathing marine vertebrates, reliable evidence must be used to infer behaviour from movement patterns. Hydrophones, stomach temperature sensors and video cameras have all been used in consort with data recorders to link subsurface movements to the confirmed capture of prey items (Lesage et al., 1999; Madden et al., 2008; Miller et al., 2004a; Tyack et al., 2006). Among mysticete cetaceans, the lunge feeding technique used by the blue, fin and minke whales (Balaenoptera musculus, B. physalus, and B. acutorostrata) consists of distinctive movements during prey capture events, allowing foraging to be inferred with high certainty (Croll et al., 2001; Acevedo-Gutiérrez et al., 2002; Goldbogen et al., 2006, 2008). More subtle changes in horizontal swim speed have been used to confirm the occurrence of foraging in the submerged swimming of bowhead whales (Balanena mysticetus) (Simon et al., 2009), which unlike the balaenopterids feed by skimming prey from the water column.

Understanding the submerged diving behavior of North Atlantic right whales (Eubalaena glacialis) has considerable importance because this population is continuing to experience very low recovery rates and high unnatural mortality. Because little is known about its diving behavior, save when it is foraging, the exposure of these whales to sources of mortality is not well understood. Right whale diving behaviour has been recorded, and the resulting time-depth profiles of dives have been visually classified into typical shapes (Murison & Gaskin, 1989; Woodley &
Gaskin, 1996; Baumgartner & Mate, 2003). Foraging was inferred from dives where animals spent the majority of their submerged time at a depth of high prey densities, and nonforaging dives were determined through concurrent surface observations and the lack of dive depths matching prey aggregations (Baumgartner & Mate, 2003). However, visually classifying the time-depth profiles of dives can yield high levels of misclassification when validated with additional methodology (Davis et al., 2003; Madden et al., 2008; Thums et al., 2008), demonstrating that before dive profiles can be used to infer behaviours, the correlation between time-depth profile and behavior should be established. Different behaviors require differences in fine-scale swimming movements, so identifying these swimming movements within reliably classified dive shapes will enable a robust determination of the occurrence of broad-scale behaviors linked to dive shapes.

Based on studies of diving behavior in other large, air-breathing marine species, a series of predictions on the differences in swimming movements between foraging and nonforaging behaviors were developed for use with right whales. Marine vertebrates engaged in foraging dives spend more of their dive cycle in the deepest portion of their dives and less in the descent, ascent and surface phases than during nonforaging dives. Maximizing the amount of time spent in the area of highest prey concentration and minimizing the amount of travel time to that depth, optimizes energy gain (Houston & Carbone, 1992; Mori, 1999). Foraging animals use higher swim speeds during the descent and ascent phases of their dives than during the bottom phase, whereas non-foraging animals use similar swimming speeds throughout the course of their dives (Boyd et al., 1995; Sims, 2000; Simon et al., 2009). Maximum body pitch reached during descent and ascent phases was higher for foraging dives than during non-foraging dives (Goldbogen et al., 2008; Sato et al., 2004), likely because it reduced travel time to foraging depths and thereby help to maximize the available time for foraging. Stroke rates during foraging dives were higher than those used than during
non-foraging dives in the case of predators pursuing their prey (Madden et al., 2008),
or for species that require additional forward force to overcome drag from their open
mouths, as in filter-feeding species (Simon et al., 2009; Sims, 2000). Animals must
be in the same physical space as their prey in order to feed (Madden et al., 2008),
so those that feed on vertically migrating zooplankton should also make dives that
vary in maximum depth, traveling deeper during the day than at night (Baumgartner
et al., 2003). Finally, actively foraging animals are in contact with their prey, so they
do not need to explore new space to locate it. Low rates of change in direction, both
horizontally and vertically, should therefore be related to foraging, while high rates
of change in direction are more likely to be connected with exploratory behaviours
(Mayo & Marx, 1990; Simpkins et al., 2001).

In this study, we expand from previous studies on the foraging behavior of North
Atlantic right whales by quantitatively classifying time-depth profiles to determine
the stereotyped dive patterns used in this species and then comparing fine-scale swim-
ming parameters between those dive patterns to infer behavioral correlates for each.
Suction-cupped digital archival tags were attached to free-ranging North Atlantic
right whales to record their subsurface diving behaviour in two critical habitats,
the Bay of Fundy, Canada, and the South Atlantic Bight, USA, for this species.
Time-depth profiles from the tags were used to identify separate dives, which were
objectively classified with a clustering algorithm into stereotyped shapes. The pre-
dictions listed above were tested between the resulting shapes to determine which
ones were related to foraging or nonforaging behaviors. Next, dive profiles were used
to determine the amount of time that animals encountered different energetic costs
related to behavior and whether those costs varied due to life history stage.
2.2 Methods

2.2.1 Data collection

During July and August 2000, 2001, 2002 and 2005, multi-sensor digital recording tags (Dtags) (Johnson & Tyack, 2003) were temporarily attached to free-swimming North Atlantic right whales in the Bay of Fundy, Canada following the methodology described in Nowacek et al. (2001). Additional field data was gathered in the same way during January 2006 in the coastal waters off the Southeastern USA during January 2006. Tagging locations and tracks of tagged whales are shown in Appendix A. These devices contained a three-axis accelerometer and magnetometer, a pressure sensor and a hydrophone that synchronously recorded three-dimensional whale orientation, depth and acoustic data, respectively. Sensor data were recorded at a sampling rate of 23.5 Hz (2000, 2001, 2002) or 50 Hz (2005, 2006). Decimation and interpolation resulted in a processed sample rate of about 5 Hz. Post-tagging calibrations were made to adjust for any variations in tag position and align the long axis of the tag with the anteroposterior axis of the whale, or in other words, match the x-axis of the tag to that of the whale.

While resting at the surface, whales were approached in a small rigid inflatable boat that had a cantilevered pole system mounted in the bow (Johnson & Tyack, 2003; Nowacek et al., 2001; Moore et al., 2001). Tags were placed on the end of a 15-meter (m) pole and then lowered on to the whale’s dorsal side at the approximate midpoint of the animal’s length and width to be attached with suction cups, which released via a corrosive wire mechanism when the recording memory was full. Positively buoyant foam served to bring the tag to the surface after release, and the emitted VHF signal was used to locate and recover floating tags. High-resolution digital photographs were taken of each whale after a tag was attached, and these photographs were matched to those contained in the New England Aquarium’s (NEAqu)
North Atlantic Right Whale Catalog to obtain the unique EgNo, age and sex of that whale.

The tag’s VHF signal was also tracked with a VHF receiver during attachments when animals were at the surface. For each surfacing, the distance and bearing to the animal from the main tracking vessel, a 40-m long former shrimp boat called the R/V Stellwagen, were recorded with a laser rangefinder. The GPS position of the whale at each surfacing was then determined through georeferencing those measurements from the ship’s position. Whale positions were then plotted onto bathymetric maps of the Bay of Fundy (Roworth & Signell, 1998) and South Atlantic Bight in ArcGIS 9.0 (ESRI, Inc., 2009), and the approximate seafloor depth at each surfacing was extracted. The beginning of each dive recorded on the tags was synchronized with the time of the last GPS position of a whale at the surface, and seafloor depths during dives were determined by averaging the last GPS position of the surfacing before a dive and the first GPS position of the following surfacing.

After collection, sensor data from the tag were calibrated to generate pitch, roll, heading and depth profiles, as described in Johnson & Tyack (2003), and the GPS positions of whales at each surfacing were determined by triangulating the whales distance and bearing from the ships GPS position. All tags that were attached to animals of unknown age and sex or had less than three complete dives were not included in the analysis. Additionally, the first dive of every attachment was removed because the tagging process has been shown to affect an animals behaviour during initial dives.

2.2.2 Winter dive analysis

Time-depth profiles of dives made in the Southeastern US waters were plotted in MATLAB 7.10.0 (The Mathworks Institute, 2010), and dives were separated according to their duration and maximum depth. Dives were considered those portions
of the tag record where the animal reached a minimum depth of two meters and remained away from the surface for at least 10 seconds (s). Any movements that did not satisfy these criteria were considered to be part of the surface interval between dives. After identifying separate dives, dive duration, surface interval (SI) duration, maximum dive depth and distance to the seafloor were measured to understand the basic movements of whales in this area. Finally, two metrics for ship collision risk were determined by calculating the percentage of each dive spent at depths between 2 m and 6.7 m and between 2 m and 15.4 m. These depth ranges were used in order to understand the amount of time whales are below the surface but still within the drafts of the smallest and largest vessel types that frequently occur in right whale habitats (Knowlton et al., 1995, 1998). The distributions of all parameters were found to differ significantly from normal with a Shapiro-Wilk test for normality, so nonparametric Kruskal-Wallis tests were used to determine significance between winter dive groups (Hollander & Wolfe, 1999).

2.2.3 Summer dive classification & time budget analysis

Custom MATLAB software (The Mathworks Institute, 2010) was used to plot the time-depth profile of each tag attachment, and these profiles were used to identify individual dives. All dives exceeding 30 m were standardized to a uniform duration of 100 time points and a uniform depth between 0 and 1, which corresponded to the surface and maximum depth, respectively, so that classification was performed solely on dive shape (Schreer & Testa, 1996; Schreer et al., 1998). Extracted shapes were then classified into one of three categories, subsequently referred to as ‘types’ with a k-means clustering algorithm because this algorithm has been shown to be the most robust for classifying dive shapes (Schreer et al., 1998, 2001). The classification algorithm was repeated using differing numbers of categories, ranging from two to eight, and the number of categories used (three) was selected because it was the
fewest categories that had a low percentage of misclassification (<5%, 14 dives) while still containing enough dives in each category (>2%, 6 dives) (Davis et al., 2003).

Dives were separated into descent, bottom, ascent and surface phases based on their pitch and depth, and all dives with four complete phases, termed a complete dive cycle, were included for analysis. Twenty-three variables that have been shown to differ between foraging and nonforaging dives in other species were selected for comparison and were grouped into three types of parameter. The six duration parameters measured were dive duration, descent duration, bottom duration, ascent duration, pre-dive SI and post-dive SI. Eleven swimming effort parameters were measured: descent velocity, descent maximum pitch, descent stroke rate, descent stroke amplitude, bottom velocity, bottom stroke rate, bottom stroke amplitude, ascent velocity, ascent maximum pitch, ascent stroke rate and ascent stroke amplitude. Finally, six spatial parameters were measured to explore whether different dive types included differing levels of vertical or horizontal movement: rate of heading change during diving, rate of heading change during SI, rate of depth change while at depth, maximum dive depth, distance traveled while at depth and distance traveled during SI.

All phase durations were further expressed as a percentage of the total dive cycle, and pre-dive surface intervals were not included as a portion of the dive cycle to avoid duplication of the surface duration (Tyack et al., 2006; Watwood et al., 2006). Heading was sampled at 10-s intervals to calculate the rates of heading change because this duration would approximate the amount of time necessary for a whale to cover a distance of 10 meters at a typical swimming speed (e.g. 1 ms\(^{-1}\)), a distance which has been shown to be sufficient to detect differences in path linearity relevant to behavioral contexts in right whales (Mayo & Marx, 1990). Rate of depth change, the metric of vertical path linearity, was calculated over 10-s intervals as well.
Velocity was measured for descent and ascent phases by dividing the vertical distance traveled by the sine of the animal’s pitch over 5-s intervals (Aguilar Soto et al., 2008; Tyack et al., 2006). A regression of flow noise and descent velocity for the same 5-s intervals was used to estimate the velocity during bottom phases from the flow noise levels recorded by the Dtag hydrophone to improve the estimation of velocity for segments where the animal is at a low pitch angle (Simon et al., 2009). Stroke rate and maximum pitch angle were measured directly from the Dtags pitch record, pitch was corrected for the location of the tag on the animal’s body, and amplitude was corrected for tag position based on a sine wave (Nowacek et al., 2001). Stroke rate, amplitude and velocity were not calculated for the bottom phase of Type 3 dives because of the short duration of this phase for this dive type.

The duration parameters were compared between dive types and between life history classes within each type to understand whether body size and composition had an influence on dive budgets with Kruskal-Wallis tests. Stroke rate and velocity were compared between phases within each dive type with Kruskal-Wallis tests, and stroke amplitude and maximum pitch were compared with circular median tests to account for the circular nature of their units (Fisher, 1996). Finally, spatial parameters were compared between dive types with a Kruskal-Wallis test to support the connection between dive types and potential behaviors. Linear statistics were calculated in JMP 8.0.2 (SAS Institute, Inc., 2009), circular statistics in MATLAB 7.10.0 with the CircStat toolbox (Berens, 2009). All test statistics were determined to be significant at the 95% confidence level.

2.2.4 Mortality risk assessment

Four more parameters were compared between dive types to assess the relative risk of interaction between right whales and their most frequent causes of unnatural mortality, ship strike and entanglement in fishing gear, caused by each of the three
behaviors (Knowlton & Kraus, 2001). Because ship collision can only occur approximately where the ship’s hull extends below the water line, the amount of time that whales spent at depths less than the draft of the largest vessels found in right whale habitat (15 m) was measured (Knowlton et al., 1995, 1998). Right whales are most often found entangled in fixed fishing gear such as lobster traps, and the entanglement could occur in the portion of the line that is fixed horizontally to the seafloor, the ‘groundline’ section, or the two lengths of line that extend from the seafloor to the surface to allow the traps to be recovered, the ‘endline’ section (Johnson et al., 2005). The risk of entanglement in groundlines was assessed by determining 2) the amount of time spent within 30 m of the seafloor and 3) the distance from the deepest depth of each dive to the seafloor. Thirty meters was chosen as the critical value for groundline entanglements to include whales possibly foraging on copepods aggregated above the bottom mixed layer (Baumgartner & Mate, 2003) and account for any gear that had been damaged or shifted along the seafloor. Finally, the relative risk of entanglement in the endlines of fishing gear was determined by comparing 4) the amount of time spent moving through the water column, which was determined by the sum of descent and ascent phase durations. The above mortality risk parameters were compared between dive types with Kruskal-Wallis tests similar to those used for the swimming parameters.

2.3 Results

2.3.1 Winter dive analysis

Six right whales, consisting of one juvenile female, one juvenile male, one adult female and two unidentified animals, were tagged off Jacksonville, Florida on their calving grounds in the Southeastern US, and a total of approximately 24 hours of data were recorded. One tag failed to record, four of the attachments were brief, each less than 2 hours in duration, and one highly successful tag remained on the animal for
eighteen hours. In total, 271 dives were recorded from these animals, 234 of which were from the long attachment. Three of the tagged whales were identified from the NEAq Catalog and found to be a three-year old male (Eg3323), a two-year old female (Eg3430) and an adult female (Eg1151) that was sighted with a calf three days later, indicating that this animal was heavily pregnant when tagged. Two animals spent most of their tag attachments away from the surface, while the other three remained primarily at the surface (Fig. 2.1).

Table 2.1: Average (± SE) swimming parameters for winter dives made by right whales in their calving grounds in the Southeastern US and results of nonparametric \( \chi^2 \) tests comparing dives between depth categories. All parameters were found to be significantly different, suggesting that each dive group is connected with a different behavior. See text for details of dive parameter extraction.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Shallow (&lt;10 m)</th>
<th>Deep (&gt;10 m)</th>
<th>H</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>174</td>
<td>95</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>dive (min)</td>
<td>1.83 (0.14)</td>
<td>6.58 (0.28)</td>
<td>133.45</td>
<td>1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>surface interval (min)</td>
<td>0.91 (0.12)</td>
<td>2.44 (0.23)</td>
<td>26.81</td>
<td>1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>seafloor distance (m)</td>
<td>13.31 (0.31)</td>
<td>3.46 (0.31)</td>
<td>145.69</td>
<td>1</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

The mean depth of these dives was 7.96m (±0.33 SE), which represents a distance of approximately 9.80m (±0.37 SE) above the seafloor. These dives were highly variable in shape, so no classification algorithm could be used to identify behaviors. Instead, the bimodal distribution of maximum depths showed that dives fell into two categories (Fig. 2.2), presumably related to two broad-scale behavioral states. After grouping dives based on their maximum depth, the other swimming parameters measured from these dives were found to be significantly different, (Table 2.1), suggesting these categories are valid. Shallow dives were significantly shorter in duration, had shorter post-dive surface intervals and were much further from the seafloor than deep dives (Table 2.1).
Figure 2.1: Distribution of time spent at different depths by individual whales (A) and all whales (B), shown in 2m bins. Two individuals (hatched) spent time at depths deeper than the draft of most ships, while the other three (solid) remained near the surface (<8m) for the duration of the tag attachment.

2.3.2 Summer dive analysis

Twenty-five tag attachments recorded at least three complete dives and were made to individuals of known age and sex classes, which qualified them as sufficient for analysis. These attachments were made in the Bay of Fundy during the summers of 2000 (2 attachments), 2001 (2), 2002 (8) and 2005 (13). Approximately 120 hours of recording time were obtained from 19 different individuals and resulted in a total
Figure 2.2: Example dive profiles from right whales in the SEUS calving grounds showing the depth (———) of the whales in relation to the seafloor (— —). Seafloor depths were measured along the track of the whale directly (———) or estimated from seafloor depths during a previous part of the tag attachment (— —). Whales either spend the majority of the attachments making short, irregular dives near the surface (A) or deep regular dives that were closer to the seafloor (B).

Out of 276 dives for analysis. Eleven females were tagged, including four known to be adults (nine years or older) and seven to be juveniles (eight years or younger), and eight animals were identified as male, consisting of five adults and three juveniles. Out of the 276 dives, the clustering algorithm placed 237 (85.87%) dives in the first category, which will be assigned the category title of ‘Type 1 dives’, 24 (8.70%) in the second, as ‘Type 2’ dives, and 15 (5.43%) in the third, as ‘Type 3’ dives. Averaged profiles generated by the clustering algorithm matched the dive shapes appearing in the tag data reasonably well (Fig. 2.3).

The duration of descent, bottom, ascent, post-dive surface interval and pre-dive surface interval phases differed significantly between types (Table 2.2, Fig. 2.4). The
dive cycle of Type 1 dives was dominated by the bottom phase (56.33% of the dive cycle), with descent (10.82%), ascent (10.03%) and surface (22.80%) phases that were shorter than those in the other dive types. Compared to Type 1 dives, animals in Type 2 dives spent less time in the bottom phase (23.66%), more in traveling phases (descents: 16.62%, ascents: 17.34%), and the most in the surface phase (42.38%). Type 3 dives had the shortest bottom phases (0.40%), the longest ascent phases (23.38%) and the longest surface (65.26%) phases of the three types, and descent (11.05%) phases that were similar to those of Type 1 dives (Fig. 2.4).

Neither the dive heading change nor the surface heading change differed significantly between types, but the rate of depth change did (Table 2.2). Type 2 dives had a higher rate of depth change than Type 1 dives (not measured for Type 3 dives). No differences in dive distance, surface distance or maximum dive depth between dive
types were observed (Table 2.2), and whales traveled throughout the water column during all three dive types (Fig. 2.6). The long bottom phases and differences in maximum depth of Type 1 dives produced a wide distribution of time at the deeper depths for this dive type, while the short bottom phase duration was reflected in the lack of time spent at deep depths for this dive type. All three dive types included some time at the surface during which the whales were recovering their oxygen stores, but the distribution of time in the shallowest depth bin shows that whales spent much more time at the surface during Type 2 and 3 dives (Fig. 2.6).

All three dive types were recorded from individuals of the four life history classes, and dive type frequency was relatively even across classes (Fig. 2.7). Juvenile males
Phase durations differed significantly between life history classes only in Type 1 dives, but overall dive duration did not (Table 2.3). For descent phases of Type 1 dives, males had shorter descents than both females and juveniles, while the ascent phases of juveniles were longer than either adult classes (Fig. 2.5). Within this dive type, the bottom phases of dives made by juvenile animals were shorter in duration than those of adults (Fig. 2.5). In addition, descent and ascent phase durations were similar between males and juveniles but not in females (Fig. 2.5). Differences in
**Figure 2.6:** Distribution of time spent by right whales at different depths during Type 1 (■), Type 2 (■) and Type 3 (■) dives in the Bay of Fundy. Depths are grouped into 10m depth bins. Typical water depth in the Bay of Fundy is 150–200m. Error bars show one standard error.

**Figure 2.7:** Percentage of Type 1 (A), Type 2 (B) and Type 3 (C) dives performed by each life history class: adult males (■), adult females (■), juvenile males (□) and juvenile females (■). All classes performed at least one dive of each type.
Table 2.2: Mean (± SE) duration and spatial parameters and results of Kruskal-Wallis tests used to compare parameters between dive types. All duration parameters are reported in minutes. See text for explanation of parameter extraction.

<table>
<thead>
<tr>
<th></th>
<th>Type 1</th>
<th>Type 2</th>
<th>Type 3</th>
<th>H</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N=237</td>
<td>N=24</td>
<td>N=15</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>duration parameters</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>dive cycle</td>
<td>16.42 (0.16)</td>
<td>18.79 (2.08)</td>
<td>40.82 (12.64)</td>
<td>6.26</td>
<td>2</td>
<td>0.04</td>
</tr>
<tr>
<td>dive</td>
<td>12.56 (0.09)</td>
<td>9.26 (0.38)</td>
<td>8.00 (0.42)</td>
<td>78.84</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>descent</td>
<td>1.77 (0.03)</td>
<td>2.66 (0.20)</td>
<td>2.45 (0.19)</td>
<td>29.41</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>bottom</td>
<td>9.17 (0.10)</td>
<td>3.87 (0.53)</td>
<td>0.06 (0.03)</td>
<td>88.93</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>ascent</td>
<td>1.63 (0.03)</td>
<td>2.73 (0.24)</td>
<td>5.50 (0.35)</td>
<td>68.87</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>post SI</td>
<td>3.85 (0.13)</td>
<td>9.53 (2.03)</td>
<td>35.54 (12.43)</td>
<td>23.03</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>pre SI</td>
<td>4.34 (0.34)</td>
<td>24.14 (8.65)</td>
<td>22.00 (5.35)</td>
<td>19.43</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>spatial parameters</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>dive heading (°10s⁻¹)</td>
<td>10.39 (0.40)</td>
<td>11.53 (2.11)</td>
<td>13.08 (2.59)</td>
<td>0.33</td>
<td>2</td>
<td>0.85</td>
</tr>
<tr>
<td>dive distance (km)</td>
<td>0.84 (0.06)</td>
<td>0.87 (0.16)</td>
<td>0.89 (0.42)</td>
<td>0.45</td>
<td>2</td>
<td>0.80</td>
</tr>
<tr>
<td>depth change (m 10s⁻¹)</td>
<td>1.17 (0.04)</td>
<td>2.42 (0.24)</td>
<td>–</td>
<td>31.73</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>maximum depth (m)</td>
<td>129.58 (2.36)</td>
<td>127.65 (5.81)</td>
<td>115.39 (8.45)</td>
<td>3.53</td>
<td>2</td>
<td>0.17</td>
</tr>
<tr>
<td>surface distance (km)</td>
<td>0.51 (0.06)</td>
<td>0.74 (0.36)</td>
<td>3.07 (2.35)</td>
<td>1.36</td>
<td>2</td>
<td>0.51</td>
</tr>
<tr>
<td>surface heading (°10s⁻¹)</td>
<td>7.98 (0.42)</td>
<td>8.21 (1.81)</td>
<td>9.74 (2.98)</td>
<td>3.69</td>
<td>2</td>
<td>0.16</td>
</tr>
</tbody>
</table>

descent phase duration due to life history class approached significance for Type 3 dives, suggesting that the descent phases of males making Type 1 dives may have biological significance (Table 2.3).

During Type 1 and Type 2 dives, animals used a significantly slower swimming velocity during bottom phases than during descent or ascent phases (Table 2.4). Type 3 dives had significantly higher velocities during ascents than descents. Stroke rate differed significantly between phases in Type 1 and Type 3 dives only, with ascents having a higher stroke rate than descent or bottom phases (Fig. 2.8). Stroke amplitude differed significantly between phases in Type 1 and Type 2 dives, but not in Type 3 dives.

The duration of the dive cycle spent in the top 15 m of the water column differed significantly between dive types (Table 2.5, Fig. 2.6). Type 3 dives had the highest duration in surface waters, Type 2 less and Type 1 the lowest, which represented 67.67%, 53.07%, and 26.53% of the dive cycle respectively. Regarding entanglement risk in groundlines, whales were close to the seafloor during slightly more of Type 3...
Table 2.3: Mean (± SE) duration parameters of each dive type grouped by life history class and results of Kruskal-Wallis test used to compare dive phase durations between life history class. Bold values indicate parameters that were significantly different between life history classes.

<table>
<thead>
<tr>
<th></th>
<th>male</th>
<th>female</th>
<th>juvenile</th>
<th>H</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>dive</td>
<td>12.60 (0.20)</td>
<td>12.76 (0.22)</td>
<td>12.49 (0.11)</td>
<td>1.25</td>
<td>2</td>
<td>0.54</td>
</tr>
<tr>
<td>descent</td>
<td>1.38 (0.06)</td>
<td>1.85 (0.06)</td>
<td>1.88 (0.04)</td>
<td>1.25</td>
<td>2</td>
<td>0.54</td>
</tr>
<tr>
<td>bottom</td>
<td>9.84 (0.19)</td>
<td>9.47 (0.24)</td>
<td>8.84 (0.12)</td>
<td>23.38</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>ascent</td>
<td>1.37 (0.06)</td>
<td>1.44 (0.04)</td>
<td>1.77 (0.03)</td>
<td>51.69</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>post SI</td>
<td>3.62 (0.30)</td>
<td>4.01 (0.27)</td>
<td>3.89 (0.17)</td>
<td>5.00</td>
<td>2</td>
<td>0.08</td>
</tr>
<tr>
<td>Type 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>dive</td>
<td>9.34 (1.92)</td>
<td>7.68 (1.05)</td>
<td>9.51 (0.37)</td>
<td>3.61</td>
<td>2</td>
<td>0.16</td>
</tr>
<tr>
<td>descent</td>
<td>1.92 (0.14)</td>
<td>2.22 (0.42)</td>
<td>2.85 (0.24)</td>
<td>3.17</td>
<td>2</td>
<td>0.21</td>
</tr>
<tr>
<td>bottom</td>
<td>5.45 (2.10)</td>
<td>2.70 (0.28)</td>
<td>3.80 (0.62)</td>
<td>1.22</td>
<td>2</td>
<td>0.54</td>
</tr>
<tr>
<td>ascent</td>
<td>1.97 (0.32)</td>
<td>2.76 (0.59)</td>
<td>2.85 (0.29)</td>
<td>1.61</td>
<td>2</td>
<td>0.45</td>
</tr>
<tr>
<td>post SI</td>
<td>16.01 (12.63)</td>
<td>10.76 (4.89)</td>
<td>8.24 (1.82)</td>
<td>0.32</td>
<td>2</td>
<td>0.85</td>
</tr>
<tr>
<td>Type 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>dive</td>
<td>6.68 (0.94)</td>
<td>8.18 (0.64)</td>
<td>8.38 (0.57)</td>
<td>1.69</td>
<td>2</td>
<td>0.43</td>
</tr>
<tr>
<td>descent</td>
<td>1.55 (0.04)</td>
<td>2.93 (0.22)</td>
<td>2.59 (0.24)</td>
<td>5.69</td>
<td>2</td>
<td>0.06</td>
</tr>
<tr>
<td>bottom</td>
<td>0.08 (0.04)</td>
<td>0.008 (0.005)</td>
<td>0.07 (0.06)</td>
<td>1.04</td>
<td>2</td>
<td>0.59</td>
</tr>
<tr>
<td>ascent</td>
<td>5.06 (0.96)</td>
<td>5.25 (0.48)</td>
<td>5.73 (0.49)</td>
<td>0.69</td>
<td>2</td>
<td>0.71</td>
</tr>
<tr>
<td>post SI</td>
<td>38.78 (8.02)</td>
<td>83.58 (57.62)</td>
<td>18.45 (6.00)</td>
<td>3.59</td>
<td>2</td>
<td>0.17</td>
</tr>
</tbody>
</table>

and Type 1 dives than during Type 2 dives (4.40%, 2.91%, 1.91%, respectively), but within the dives that were close to the seafloor, Type 1 dives included a significantly larger portion of the dive cycle close to the seafloor (Table 2.5). The portion of the dive cycle during which whales could encounter the endlines of fishing gear was largest for Type 3 dives (40.12%), followed by Type 2 (33.96%) and Type 1 (20.85%) dives in that order. The average amount of time close to the seafloor suggested that whales were close to the seafloor for the longest during Type 3 dives, less during Type 2 and the least during Type 1 dives (Table 2.5). However, the deviation from the mean value was very high during Type 1 dives, with the amount of time ranging from 7.10% to 60.13% of their dive cycle.
Table 2.4: Mean (±SE) swimming effort parameters by dive phase within types and results of Kruskal-Wallis tests (or *circular median test) for between phase comparisons. Bold font shows parameters for which there was a significant difference between phases.

<table>
<thead>
<tr>
<th>Type</th>
<th>descent</th>
<th>bottom</th>
<th>ascent</th>
<th>H</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stroke rate (Hz)</td>
<td>0.15 (0.005)</td>
<td>0.15 (0.003)</td>
<td>0.17 (0.002)</td>
<td><strong>114.78</strong></td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>velocity (ms(^{-1}))</td>
<td>1.96 (0.33)</td>
<td>1.05 (0.02)</td>
<td>1.70 (0.03)</td>
<td><strong>222.26</strong></td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>amplitude (°)</td>
<td>14.89 (0.36)</td>
<td>16.72 (0.53)</td>
<td>17.51 (0.42)</td>
<td>2.78*</td>
<td>2*</td>
<td>0.25*</td>
</tr>
<tr>
<td>pitch (°)</td>
<td>65.57 (0.97)</td>
<td>–</td>
<td>56.23 (1.31)</td>
<td>0.009*</td>
<td>1*</td>
<td>0.93*</td>
</tr>
<tr>
<td>Type 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stroke rate</td>
<td>0.15 (0.01)</td>
<td>0.15 (0.008)</td>
<td>0.16 (0.006)</td>
<td><strong>6.35</strong></td>
<td>2</td>
<td>0.04</td>
</tr>
<tr>
<td>velocity</td>
<td>1.84 (0.21)</td>
<td>0.94 (0.06)</td>
<td>1.90 (0.10)</td>
<td><strong>33.67</strong></td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>amplitude (°)</td>
<td>13.76 (1.34)</td>
<td>16.03 (1.38)</td>
<td>16.97 (1.22)</td>
<td>5.45*</td>
<td>2*</td>
<td>0.07*</td>
</tr>
<tr>
<td>pitch (°)</td>
<td>63.41 (4.74)</td>
<td>–</td>
<td>47.32 (5.08)</td>
<td>0.11*</td>
<td>1*</td>
<td>0.75*</td>
</tr>
<tr>
<td>Type 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stroke rate</td>
<td>0.15 (0.02)</td>
<td>–</td>
<td>0.17 (0.007)</td>
<td>2.42</td>
<td>1</td>
<td>0.12</td>
</tr>
<tr>
<td>velocity</td>
<td>1.60 (0.06)</td>
<td>–</td>
<td>2.68 (0.33)</td>
<td><strong>19.15</strong></td>
<td>1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>amplitude (°)</td>
<td>14.92 (1.36)</td>
<td>–</td>
<td>17.73 (2.05)</td>
<td><strong>3.97</strong></td>
<td>1*</td>
<td>0.05*</td>
</tr>
<tr>
<td>pitch (°)</td>
<td>55.70 (5.33)</td>
<td>–</td>
<td>43.33 (6.08)</td>
<td>0.54*</td>
<td>1*</td>
<td>0.46*</td>
</tr>
</tbody>
</table>

Table 2.5: Mean (±SE) risk assessment parameters for which whales are at risk of interaction with significant sources of mortality according to dive type. Ship interactions could occur within top 15m of water column, groundline interactions within 30m of the seafloor, and endline interactions throughout transiting phases (descent, ascent).

<table>
<thead>
<tr>
<th>Type</th>
<th>Type 1</th>
<th>Type 2</th>
<th>Type 3</th>
<th>H</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>ship strike duration (min)</td>
<td>4.45 (0.13)</td>
<td>10.98 (2.04)</td>
<td>35.89 (13.33)</td>
<td><strong>33.01</strong></td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>groundline duration (min)</td>
<td>0.46 (0.14)</td>
<td>0.37 (0.19)</td>
<td>0.73 (0.31)</td>
<td><strong>9.92</strong></td>
<td>2</td>
<td>0.007</td>
</tr>
<tr>
<td>endline duration (min)</td>
<td>3.39 (0.05)</td>
<td>5.39 (0.37)</td>
<td>7.95 (0.43)</td>
<td><strong>72.08</strong></td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>seafloor distance (m)</td>
<td>52.14 (1.64)</td>
<td>45.50 (9.36)</td>
<td>26.15 (6.58)</td>
<td><strong>9.82</strong></td>
<td>2</td>
<td>0.007</td>
</tr>
</tbody>
</table>

2.4 Discussion

2.4.1 Winter dive behavior

These initial tag records show that right whale diving behavior in their calving grounds off the southeastern US is dramatically different from that in their foraging grounds off eastern Canada (Figs 2.2, 2.3), most clearly due to the considerable difference in water depth. Understanding the importance of the Southeastern US habitat
to right whales is relatively recent, with its discovery in the mid-1980’s (Brown et al., 2006; Kraus et al., 1986), and their submerged behavior in this area remained relatively unexplored. The high degree of variability in dive profiles and the bimodal distribution in maximum dive depth provides preliminary evidence that these whales are engaged in two broad behaviors, which supports surface observations in this area. The use of longer deep dives that bring the animals close to the seafloor suggest some degree of horizontal movement, or traveling, and the much shallower and shorter second category could be related to surface social activities. Field observations made at the time of tagging report one whale (Eg3430) to be traveling for the duration of the tag attachment. The tag from another whale (Eg1151) was recovered nearly 50 miles from the location of attachment, which lasted 18 hours in duration, indicating that
she had traveled for much of the attachment. Many more deep dives were recorded from these two animals, which indicates that this dive pattern could be related to traveling contexts in this habitat. Because the long attachment lasted through the overnight hours, no GPS positions were taken, and the period of traveling could not be directly synchronized with the tag record to estimate the distance traveled or the speed used. The other three tags (Eg3323, rw06_024b, rw06_024c) were attached to whales that were part of a small group, and the close proximity of other whales caused the tag to be rubbed off prematurely, indicating a social context during those attachments.

Finally, these results indicate the vulnerability of right whales to ship strike in the SEUS habitat. All individuals used the upper half of the water column (<10m) during some portion of their tag attachment, and only two animals spent the majority of their time outside of the draft of most large ships (>15m) (Figs. 2.2, 2.1). The shallow water depth and subsequent shallow diving behavior of right whales in this areas results in whales being submerged but within the draft of most large ships for an average of 67% and 97% of their dives, depending on the type of ship. The broad, shallow continental shelf in this region gives these whales almost no vertical space in which to avoid ships, making all types of ship is cause for concern in this area. In addition, the ship draft values used here are conservative thresholds for the zone of interaction because they do not account for any hydrodynamic effects caused by vessels underway. In both computer simulation and flow tank studies, whales outside the draft of a ship but still within a certain proximity were pulled into the path of the ship (Knowlton et al., 1995, 1998; Silber et al., 2010).

2.4.2 Behavioral correlates of dive type

These results show that the differences in stereotyped dive patterns of right whales are quantifiable, and these differences are likely correlated with different behavioural
contexts because considerable variation in swimming behavior, not just the time spent at different depths exist. The results of this study match those from other studies. Type 1 dives have characteristics of foraging dives that support the prediction that animals will minimize the amount of time reaching a foraging patch in order to maximize their time in the patch. A similar dive pattern (referred to as ‘U-shaped’) has been found to be well correlated with the depth of the highest zooplankton density in this area (Baumgartner et al., 2003). The average maximum depth, bottom phase duration and dive duration reported in that study (121.2m, 9.39min, 12.17 min, respectively) match those here, which allow Type 1 dives to be reliably considered to indicate foraging. Descent and ascent pitch angles were the highest of the three dive types and the duration of these phases was lower, suggesting a direct transit to depth. Stroke rate and velocity differed significantly between dive phases, differences caused by a higher stroke rate during ascents and a lower velocity during bottom phases. Increased stroking during ascents may relate to shifting from horizontal to vertical swimming. Swimming speeds at depth were lower than those used to reach depth, a pattern that has been observed in other large marine vertebrates that feed by ram-filtration, suggesting that animals are speed-limited by the filtration capacity of their baleen and/or the drag created by the filtering apparatus (Mayo et al., 2001; Costa & Williams, 1999; Sims, 2000; Simon et al., 2009; Motta et al., 2010, this study).

Variation within dive types due to life history class only occurred within the Type 1 foraging dive pattern. However, the dive duration, which did not include the surface phase, did not vary significantly, suggesting that differences in aerobic capacity related to breath-holding ability are not driving the observed differences. Aerobic dive limit, or the maximum amount of time a diving animal can stay away from the surface without beginning to use anaerobic metabolism, generally scales with body size and age (Costa & Williams, 1999). Body size may also influence
vertical diving ability, as juveniles spent more of their dive cycle in transiting phases at a reduction in bottom phase duration, possibly due to lower buoyancy and higher energy expenditure in overcoming the effects of their buoyancy. As bottom phase duration can be inferred as foraging time, these results also indicate that juveniles have less time to forage for the same amount of energy needed to dive. Previous work found that calves (animals under one year of age) were physiologically limited by their aerobic capacity, consequently reducing the dive durations of their mothers behaviorally (Baumgartner & Mate, 2003), although because animals at this age would not be foraging, dive duration would not be related to energetic gain. In this study, the female life history class showed a clear difference in the duration of descent and ascent phases, unlike the other two life history categories, a difference which also may be related to the buoyancy of individual animals. In order to sustain the energetic requirements of reproduction, females build up significant blubber layers over the period of three to five years, creating a ‘physiological timeline’ (Miller Angell, 2006) that is not present in males or juveniles. This increase in buoyancy may be enough to exceed the force that is possible through behavioral strategies such as body and/or flipper angle (Chapter 3), so whales must rely on active propulsion, increasing their energy usage for locomotion and decreasing their net energy gain from foraging. Female right whales with energy stores are large enough to support offspring may therefore experience changes in their dive budget such as descents, during which they are using energy against their buoyancy, that are longer than their ascents.

Type 2 dives, classified as ‘other’ dives in previous studies (Baumgartner & Mate, 2003) contained some characteristics of foraging dives, but they did not appear to maximize the amount of time spent at depth. Descent and ascent durations were longer than those of Type 1 foraging dives. Maximum pitch during these dives was slightly shallower than Type 1 dives, suggesting that whales were not minimizing
their travel time to depth, and these dives had a significantly higher rate of change in depth while at the bottom phase, indicating that whales are covering a larger three-dimensional volume of water while at depth. However, the decrease in velocity during bottom phases provides evidence that whales are still foraging. In other species, shortened bottom phase durations have been reliably linked to temporary foraging in low quality prey patches, where brief periods of foraging occur before that area is abandoned to locate a better one (Charrassin et al., 2002; Sparling et al., 2007; Thompson & Fedak, 2001). The prey densities of these patches are too low to make foraging efficient, so searching for higher quality patches is more efficient than remaining in a low quality one. Right whales require very high density prey patches in order to satisfy their energetic requirements (Michaud & Taggart, 2007; Baumgartner et al., 2007; Kenney et al., 1986), so foraging decisions that maximize prey intake are critical.

In contrast, Type 3 dives do not contain any of the typical characteristics of a foraging dive and consist of a completely different dive cycle. Animals spent very little time at the depths known to contain their prey and much more time traveling through the water column or resting at the surface, reflecting the ‘V-shaped’ dive description in Baumgartner & Mate (2003). Animals descended more slowly than they ascended, possibly allowing for more searching of the water column and a faster transit away once an area has been determined to be low quality foraging. This dive pattern may also allow right whales to take advantage of their positive buoyancy while traveling over long distance, similar to the drift dives performed by elephant seals (Crocker et al., 1997; Biuw et al., 2003). Maximum pitches while traveling are shallower than those of the other dive types, suggesting a less direct transit to depth, and these dives had a greater rate of change in horizontal path, allowing a larger volume of water to be covered in the same amount of time. No evidence that foraging occurs during transit phases in this dive type exist, and the high speeds
reached during descents and ascents suggest that it is unlikely. The occurrence of these dives in response to controlled exposure experiments suggests the primary function of this dive type is to cover horizontal distances (Nowacek et al., 2004), and the excursions from the surface are due to animals occasionally exploring deeper into the water column for high-quality prey patches. The extended portion of the dive cycle spent at the surface could also indicate the occurrence of social behaviors between deep dives, and the lack of a consistently large distance at the surface could be related to the mixture of these two potential behaviors. Other marine vertebrates perform dives that only consist of descent, ascent and surface phases, and a similar function has been inferred for most species (Schreer et al., 2001). In species that consume individual prey items such as penguins and pinnipeds, this dive type has been shown to allow predators to make deeper dives to reach single prey items that are higher in quality than their normal foraging dives can reach (Schreer et al., 2001), but the lack of a difference in maximum depth between dive types and the general foraging ecology of this species suggests this function is unlikely. Type 3 dives are often found in sequence with Type 2 dives, both in this study and Baumgartner & Mate (2003), and such a pattern across dives could be related to the alternation between changing physical location to detect new patches (Type 3 dives) and more intensively testing the quality of a prey patch after detection (Type 2 dives).

2.4.3 Conservation implications

The amount of time that whales spend at different depths alters the potential threats that right whales could interact with, and since these results provide an understanding of submerged diving behavior in this species, their vulnerability to those specific threats can be assessed. In the Bay of Fundy, right whales are mostly performing Type 1 foraging dives, during which they only spend a small amount of time near the surface, where they are vulnerable to collisions with ships. During Type 3 ex-
ploratory dives, the same whales are at a much higher risk of ship strike because they are spending nearly 36% of their time within the draft of a large ship. The variation in time spent at the surface was very high as well, and during these surface phases, whales repeatedly made shallow dives of 5-10m in depth (Chapter 4) during which they were not visible at the surface but still would be within the draft of a large ship. In addition, the threshold for ship collision concern used in this study did not compensate for the hydrodynamic effect caused by the boundary layer of a moving ship. Other studies have found that the area of interaction between a ship and a whale could extend to up to three times the ship's actual draft (Hertel, 1966; Knowlton et al., 1995; Silber et al., 2010), which would extend the zone of possible collision to include a portion of the whale's transiting phases. Because these phases appear in all three dive types and whales are not lingering at these intermediate depths, the hydrodynamic interaction zone was not included in this initial analysis.

Type 3 traveling dives were also the highest risk behavior for fishing gear interactions because whales spent the most time in areas with high entanglement potential. Whales were closer to the seafloor and spent more of their dive cycle near the seafloor and traveling to it than during the other dive types. However, whales may or may not have their mouths open during this dive type, and many entanglements of right whales include some portion of the gear wrapped through the mouth cavity (Johnson et al., 2005). The infrequency of this dive type also suggests that even though this behavior appears to pose the highest risk of hazardous encounters, other behaviors also contain some amount of risk. Whales making Type 1 foraging dives spend the largest portion of their dives in the bottom phase (56%) and in certain individuals up to 60% of their dives were close enough to the seafloor to cause concern. During these dives, whales are swimming with their mouths open in some range of the seafloor, and because the depth at which they choose to forage is entirely dependent on the location and abundance of their prey, whales will exploit these patches regardless of
how close they are to the seafloor. Evidence exists that whales may even swim in an upside-down orientation to enable them to consume prey that would otherwise be inaccessible because of its depth distribution, creating a high degree of entanglement risk should they come across deployed fishing gear (Woodward, 2006; Maresh, 2005; Baumgartner & Mate, 2003). The searching nature of Type 2 dives could cause some potential risk in all four parameters measured here, and this behavior also probably includes prolonged swimming with an open mouth. Therefore, whales may be more likely to encounter hazards during this dive type than during Type 1 dives and be more likely to become entangled than during Type 3 dives.

Despite spending different portions of their dive cycle in different parts of the water column, all dive types included some period of time at the surface and traveling to depth. Spending time resting and/or traveling at the surface and foraging near the seafloor are unavoidable aspects of survival for these whales, so some degree of interaction between these whales, ships and fishing gear is inevitable regardless of the whales’ behavior. However, understanding the frequency and duration of these interactions will allow the development of new methods that could reduce the potential of such interactions to lead to mortality, demonstrating the importance of studying behavior when the conservation of a species is a high priority.

2.4.4 Effects of behavior on cost of locomotion

Moving through the water requires energy to overcome the resistance of the external environment, and these forces change based on the angle, speed and depth of the animal. Differences in dive types therefore influence the relative amount of energy required by each behavior. During transiting phases, animals encounter buoyancy effects, so a portion of their energy is expended in overcoming this upward force, which is highest at the surface and decreases with increasing depth (Alexander, 2003). Animals moving at or near the surface would be affected by surface wave drag, which
is caused by the animal’s wake deforming the water surface and causes constructive interference of waves around the object (Hertel, 1966). Higher speeds would increase the resistance to forward motion by the animal, described as its drag, increasing the relative cost of movement within each of those behaviors (Vogel, 1994). All of these situations present an increase from the resistance encountered by a well submerged animal swimming horizontally. In this situation, all of the animal’s locomotor forces are used to overcome its drag and present a minimum requirement for its cost of locomotion.

Right whales have been found to be positively buoyant (Nowacek et al., 2001), so energy would be needed above the minimum cost to overcome the up-thrust due to the positive buoyancy during descent phases. Although these phases occur in all three dive types, they are significantly shorter in duration during Type 1 dives than in the other two. On the other hand, the same force would be acting to accelerate the animal, reducing the energy it needs to generate. The longer ascent duration of Type 3 dives may enable animals to save more energy than was used on descent as well as cover distance without active propulsion as they move through the water column, a horizontal ‘shortcut’. Drag on an animal moving near the surface can be between 2.5 and 5 times the drag of the same object when submerged (Hertel, 1966). The long surface duration of Type 3 dives therefore would result in surface phases with a higher cost than those of other dive types, especially since most whales are virtually stationary during surface phases of Type 1 dives (Nowacek, pers. comm.).

Despite understanding how diving behaviors increase the cost of locomotion from its minimal level during submerged forward movement, the magnitude of the increase in cost has not been included and in order to determine which behaviors are more or less costly, the forces involved must be measured. In addition, whales are feeding during the bottom phases of Type 1 and Type 2 dives, and the effect that foraging has on the cost of locomotion is not well understood. Ram filtration has been suggested
to increase drag and subsequent swimming costs due to the increased surface area of
the intra-oral cavity (Simon et al., 2009; Motta et al., 2010). Because drag increases
with the square of velocity, swimming speeds during foraging (i.e. bottom phases)
are under energetic constraints and therefore are consistently lower than descent and
ascent phases in several species of ram filter feeders (Sims, 2000; Simon et al., 2009;
Motta et al., 2010). However, evidence also exists that the drag inherent in filter
feeding could be less than expected due to the morphology of the head and baleen
(Werth, 2004; Lambertsen et al., 2005), and whether these adaptations lower the
animals’ overall drag or merely reduce the increase has not been determined. More
work is necessary to fully understand the relative costs involved with swimming in
this species before a complete model of their locomotor costs can be developed.

This discussion of relative energy requirements has been based entirely on move-
ment patterns in this species. As the following chapters will explore, animals can use
many different behavioral and anatomical strategies to reduce the cost of locomo-
ton, and this initial analysis has been simplified to generate a first approximation
of variations in energy use due to behavior. Additionally, because this work is con-
cerned with understanding the energetic requirements of locomotion, only the loss
of energy has been discussed here. Dive types will also have differences in net en-
ergy gain due to the amount of prey consumed, and, assuming that prey densities
are constant and foraging only occurs at depth, the longer bottom phase duration
of Type 1 dives suggests that energy intake is highest during this dive type, and
these dives would probably have an overwhelming positive energy balance because
animals are able to maintain their metabolism and even store energy for migration
and reproduction. Type 2 dives would also be positive in their energy gain, while
Type 3 dives constitute only energy loss. Bottom phase duration has been shown
to be a reliable indicator of prey patch quality (Sparling et al., 2007), making the
occurrence of Type 2 dives a potential indicator of periods of lower relative energy
gain than during Type 1 dives. Complete bioenergetic models should take other such factors that influence the overall energy balance into account.

The dive shape categories determined with this classification method were similar to those proposed in other studies on air-breathing marine species (Davis et al., 2003; Madden et al., 2008; Schreer et al., 2001), and the behavioural correlates suggested for those species were comparable. Further empirical work is necessary to confirm these hypotheses in the field with simultaneous video recorders and data-loggers or novel technologies to confirm the occurrence of different behaviours, as well as to identify finer-scale patterns in diving behaviour that would serve to separate other behaviours from the broad groups used here. However, this work demonstrates the need to incorporate behavioral data into understanding the cost of locomotion of a large, mobile organism. As with any tagging study, these data were influenced by variations in the behaviour of individuals as well the tag attachment process, but, in spite of those limitations, all of the parameters measured were more consistent within dive shapes than between them, suggesting that dive profiles are indicative of broad behavioural categories. The presence of a long-standing study of individuals within the North Atlantic right whale population has allowed these findings to be placed within the context of the species life history. Therefore, they can be robustly applied to the whole population, providing a critical step in improving our understanding of the ecology of this critically endangered species and developing better methods to reduce human-induced mortality.
North Atlantic right whales change their behaviour in response to their buoyancy

3.1 Introduction

Blubber is a critical element in the adaptation of marine mammals to their environment because it addresses many of the challenges inherent in an aquatic lifestyle. This thick, subdermal layer allows animals to store energy and acts as a thermal insulator, reducing the amount of heat convected away from a warm-blooded animal living in cold water (Fish, 2000). Blubber may also increase hydrodynamic efficiency by forming a streamlined exterior (Pabst, 1996; Fish, 2006). Because of its low density, this tissue acts as a positively buoyant float for animals that are surfacing from dives, and some deep-diving marine mammal species appear to rely on this positive buoyancy to save energy by reducing the amount of active propulsion (Nowacek et al., 2001; Williams, 2001; Miller et al., 2004b).

The mobilization of blubber as an energy reserve has been shown to reduce its effectiveness in other functions. During their fasting periods, grey (Halichoerus grypus) and harbor (Phoca vitulina) seals increase their metabolic heat production to
compensate for reduced thermal insulation as blubber reserves are depleted (Worthy, 1991). As southern elephant seals (*Mirounga leonina*) metabolize their blubber layer, the gliding portion of their dive descents becomes shorter, indicating that the amount of blubber on their bodies has a direct effect on their buoyancy (Biuw *et al.*, 2003). Experimental manipulations of northern elephant seal (*Mirounga angustirostris*) buoyancy also demonstrated that buoyancy was negatively correlated with descent drift rate (Webb *et al.*, 1998).

For free-ranging marine animals, changes in body composition are inevitable because energetic demands vary considerably throughout their lives. Moulting, pregnancy and lactation all consume more energy than basal metabolic processes, and seasonal variations in prey availability force animals to rely on their blubber stores. Some species have been shown to use changes in behaviour to compensate for reduced swimming efficiency during periods of reduced blubber and buoyancy. During dive descents and ascents, Baikal seals (*Phoca sibirica*) swam at a higher speeds with steeper pitches and stroked more frequently when their buoyancy was temporarily reduced (Watanabe *et al.*, 2006). Diving Weddell seals (*Leptonychotes weddellii*) with thicker blubber layers alternate between active swimming and passive gliding, instead of using continuous glides as seals with thinner blubber layers did (Weihs, 1974; Sato *et al.*, 2003).

Increased buoyancy has been shown to limit the amount of blubber that bottlenose dolphins (*Tursiops truncatus*) can store for thermal insulation during the winter (Noren & Wells, 2009), but the extent to which large cetaceans are affected by changes in blubber and subsequently modify their behaviour to offset those effects is difficult to determine. However, large cetaceans likely undergo significant changes in the amount of blubber they have. North Atlantic right whales feed in colder northern waters during the spring and summer, storing blubber to supply their energetic requirements for the winter (Winn *et al.*, 1995; Kenney *et al.*, 2001).
Once fall arrives, these whales are generally thought to leave the productive waters off New England and eastern Canada and travel to either the calving grounds off the southeastern US or unknown destinations for the winter (Malik et al., 1999), journeys during which they are thought not to feed. Parturition and some amount of lactation occurs during this fasting period (Kraus et al., 1986), so the blubber stores of migrating pregnant females must provide enough energy for not only their own needs but also those of delivering an offspring and transferring energy for its growth. These increased energetic demands directly affect the amount of adipose tissue of right whales, as is shown by the significant reduction in blubber stores during lactation (Miller Angell, 2006).

Right whales have much larger blubber stores, as evidenced by thicker blubber layers, than most other cetacean species including the balaenopterid mysticetes. The average blubber thickness of adult Antarctic minke whales (*Balaenoptera bonaerensis*) has been measured to range from 3.56 cm (males) to 4.02 cm (pregnant females) (Konishi et al., 2008), and the typical thicknesses of the same life history classes in fin whales (*Balaenoptera physalus*) were about 6cm and 7.5cm, respectively (Lockyer, 1986). These measurements are much lower than those of North Atlantic right whales, which can range from about 13 cm (adult males) to nearly 17 cm (pregnant females) (Miller Angell, 2006). These thicker blubber layers appear to cause overall positive buoyancy, unlike those in balaenopterids, and whales appear to use this force when surfacing from deep foraging dives (Nowacek et al., 2001). However, the extent to which such significant changes in the thickness of their blubber layers may influence swimming efficiency has not been determined. Improvements in remote data-logging devices have allowed the underwater movements of right whales to be recorded continuously (Johnson & Tyack, 2003), and novel ultrasonic techniques have been developed that enable the body condition of free-ranging whales to be measured (Moore et al., 2001). In this study, we investigated the influence of changes in
blubber thickness on the buoyancy of North Atlantic right whales by comparing the swimming behaviour of individual whales with different blubber thicknesses.

3.2 Methods

The blubber thickness of free-ranging right whales was measured in a similar manner as to the tag attachment procedure described in Chapter 2. A small boat with a bow-mounted cantilevered pole was used to approach surfacing individual right whales in the Bay of Fundy during August 2000–2002. Attached to the outboard end of the pole was a 0.5-MHz transducer, controlled with a handle on the inboard end of the pole. Changes in the echo strength recorded by the transducer indicated the transition from blubber tissue to muscle, which determined the thickness of the blubber layer (Miller Angell, 2006; Moore et al., 2001). Suction-cupped digital archival tags (Dtags) were attached to whales following a similar method during late summer 2000, 2001, 2002 and 2005 (Johnson & Tyack, 2003; Nowacek et al., 2001) [see Chapter 2 for a complete description of the tagging and calibration procedures]. Tagging locations and tracks of tagged whales are shown in Appendix A. Variations in the position of attachment were accounted for with post-attachment calibrations, and the raw accelerometer and magnetometer data were used to determine motion around one of the three axes of motion, which will be referred to as pitch, roll and heading (Fig. 3.1). Pitch was defined as rotation around the animal’s lateral (y) axis, which causes changes in the vertical direction. Roll consisted of rotation around the longitudinal (x) axis of the animal, and heading was defined as rotation around the animal’s vertical (z) axis, which would result in changes in the horizontal direction. Each successfully tagged or measured whale was photographed, and the resulting photographs were compared with those in the North Atlantic Right Whale Catalogue (Hamilton & Martin, 1999; Kraus et al., 1986) to obtain the individual’s catalogue number, age and sex.

Pitch and depth profiles recorded by the tags were used to identify descent and
Figure 3.1: Three dimensions of movement recorded on the tag. Pitch (---) was defined as movements around the lateral axis, which resulted in changes in the vertical direction of the tag, roll (----) was rotation around the animal’s longitudinal axis, which caused changes in the side-to-side direction of the tag, and heading (-----) was rotation around the animal’s vertical axis, which caused changes in the horizontal direction of the tag.

ascent phases of deep dives and their constituent gliding and active swimming, or ‘stroking’ phases. Descents were characterized by high negative pitch (> 30°) and increasing depth, while ascents had a high positive pitch and constant rate of decreasing depth. The duration of each phase spent gliding, the ratio of ascent to descent rate and the ratio of ascent to descent maximum pitch were measured as indicators of positive buoyancy (Nowacek et al., 2001). The frequency and amplitude of fluke strokes, determined from pitch oscillations, and the glide start depth were measured as indices of swimming effort.

Each parameter was determined by individual and compared according to the
Figure 3.2: Example pitch (A,B) and depth (C,D) profiles from Dtag records showing stroking (—) periods where animals were actively fluking and gliding (—) periods where animals stopped fluking to passively move during descent (A,C) and ascent (B,D) dive phases of deep foraging dives made in the Bay of Fundy.

life history class of the individual. Four separate comparisons were performed, each between categories of different blubber thickness: 1) individuals, 2) juveniles (younger/older) and 3) nonfemales (younger juvenile/adult male) and 4) females (lactating/nonlactating) (Table 3.1).

Individual comparisons included whales for which blubber thickness measurements and Dtag attachments were made in the same year from the same whale. The other three comparisons included whales that were not directly measured but were from life history categories found to have significantly different blubber thicknesses (Miller Angell, 2006). Juvenile comparisons were made between younger juveniles between ages 1 and 4, which had thinner blubber layers, and older juveniles between ages 5 and 8 that had thicker blubber layers. Nonfemale comparisons were made between younger juveniles (thinner) and adult males (thicker), and female comparisons were made between lactating females (thinner), females that had given birth during the preceding winter, and nonlactating females (thicker), which had not given birth
Table 3.1: Life history information for each individual right whale included in this analysis, including the comparison(s) that individuals were used in. Individual whales are listed by their unique identifier (EgNo), which was obtained from the North Atlantic Right Whale Catalogue.

<table>
<thead>
<tr>
<th>whale (EgNo)</th>
<th>age</th>
<th>sex</th>
<th>year tagged</th>
<th>body length(m)</th>
<th>no. dives</th>
<th>life history category</th>
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<td>11.90</td>
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<tr>
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<td>2005</td>
<td>12.46</td>
<td>4</td>
<td>male</td>
</tr>
</tbody>
</table>

for at least two years (Table 3.1). Body lengths and maximum widths of individuals were obtained (W. Perryman, unpublished) and compared to ensure that differences in measured blubber thickness were representative of differences in the overall amount of blubber, not artifacts of size differences. Interspecies comparisons have shown that stroke frequency and amplitude are influenced by body size (Fish, 1998; Sato et al., 2003), so the influence of body length on stroke frequency or amplitude was tested with Spearman’s correlation coefficient (Hollander & Wolfe, 1999). No significant correlation was found (descents: $r = -0.49, p = 0.18$; ascents: $r = 0.20, p = 0.60$), likely because the range of body lengths for these animals was relatively small, so all parameters were not corrected for body size.

The portion of each phase spent gliding was transformed with an arcsine trans-
formation, and ratios were log transformed before statistical comparisons were made. Glide percentages and the depth at which gliding begin were compared between life history categories within each comparison for descent and ascent phases separately. The ratio of ascent rate to descent rate was determined and compared between life history categories within each comparison, as was the ratio of ascent pitch to descent pitch. Finally, the difference between stroke rate and stroke amplitude during descent and ascent phases was determined and compared with Kruskal-Wallis tests to determine whether differences in swimming effort could cause differences in gliding behavior. All tests were performed in JMP 8.0.2 (SAS Institute, Inc., 2009) and evaluated for significance at $p < 0.05$.

### 3.3 Results

Individual comparison included 56 dives of three whales, whose blubber thicknesses were 9.69, 12.81 and 14.09 cm (Table 3.1). The juvenile comparison consisted of 116 dives from eight whales (seven younger, one older), the female comparison had 45 dives from four whales (three lactating, one nonlactating) and the nonfemale comparison had 140 dives from 11 whales (seven younger juveniles, four adult males) (Table 3.1).

Whales with thicker blubber layers spent less time gliding during descent and more time gliding during ascent than those with thinner blubber layers (Fig. 3.3), although the difference was significant for both phases in individual comparisons only (Table 3.2). Nonfemale and female comparisons were close to significance for both phases, while the juvenile comparison had significantly different percents spent gliding in the descent phase only.

Animals of thicker blubber layer categories had higher ascent to descent pitch ratios (Fig. 3.4) and lower ascent to descent rate ratios (Fig. 3.5) than those with thinner layers for all four sets of comparisons. Differences in pitch ratio were signifi-
Figure 3.3: Mean (±SE) percent of time spent gliding during descent (■) and ascent (□) phases for whales of each blubber thickness category, listed in order from left to right of increasing thickness, for the following comparisons: (a) individuals (n=3), (b) juveniles (seven younger, one older), (c) nonfemales (seven younger juveniles, four adult males), and (d) females (three lactating, one nonlactating).

cant in the individual and nonfemale comparisons, while those in the rate ratio were significant only for the individual comparisons (Table 3.3).

The stroke rate, stroke amplitude and glide start depth were significantly different during both descent and ascent phases for individual comparisons. The only other significant difference in swimming parameters was found for the stroke amplitude of ascent phases of the nonfemale comparison (Table 3.4).

3.4 Discussion

This study has shown that animals with thicker blubber layers spent significantly more time gliding during ascents and less time gliding during descents than animals
Table 3.2: Results of Kruskal Wallis tests that compared indicators of buoyancy between right whale life history categories known to have differences in blubber thickness. Descent and ascent phases comparisons performed independently. Categories are listed in order of increasing blubber thickness. Significant differences between categories are shown in bold.

<table>
<thead>
<tr>
<th>comparison category</th>
<th>descent glide start depth (m)</th>
<th>H</th>
<th>df</th>
<th>p</th>
<th>ascent glide start depth (m)</th>
<th>H</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
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<td>9.69</td>
<td>74.55 (1.78)</td>
<td>21.38</td>
<td>2</td>
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<td>19.55 (1.29)</td>
<td>31.92</td>
</tr>
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<td></td>
<td>12.81</td>
<td>58.73 (4.80)</td>
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<tr>
<td></td>
<td>14.09</td>
<td>61.82 (2.16)</td>
<td>36.12</td>
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</tr>
<tr>
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<td>31.28 (2.15)</td>
<td>28.72</td>
<td>0.78</td>
<td></td>
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<tr>
<td></td>
<td>older</td>
<td>9.53 (3.47)</td>
<td>30.96</td>
<td>5.21</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>nonfemales younger</td>
<td></td>
<td>31.28 (2.15)</td>
<td>28.72</td>
<td>0.78</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>males</td>
<td>22.29 (2.18)</td>
<td>30.81</td>
<td>1.59</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>females lactating</td>
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<td>21.69 (2.29)</td>
<td>28.14</td>
<td>0.71</td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>resting</td>
<td>11.07 (2.43)</td>
<td>34.98</td>
<td>2.76</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>26.42 (2.91)</td>
<td>19.04</td>
<td>2</td>
<td>&lt;0.0001</td>
<td>23.95 (1.53)</td>
<td>35.56</td>
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</tr>
<tr>
<td></td>
<td>12.81</td>
<td>48.40 (6.11)</td>
<td>47.39</td>
<td>0.96</td>
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<tr>
<td></td>
<td>14.09</td>
<td>37.06 (2.38)</td>
<td>46.07</td>
<td>3.44</td>
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</tr>
<tr>
<td>juveniles younger</td>
<td></td>
<td>66.99 (4.10)</td>
<td>35.41</td>
<td>1.42</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>older</td>
<td>100.39 (15.69)</td>
<td>38.03</td>
<td>7.04</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>nonfemales younger</td>
<td></td>
<td>66.99 (4.10)</td>
<td>35.41</td>
<td>1.42</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>males</td>
<td>34.55 (2.88)</td>
<td>23.29</td>
<td>1.34</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>females lactating</td>
<td></td>
<td>73.59 (5.57)</td>
<td>28.92</td>
<td>1.55</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>resting</td>
<td>45.63 (5.28)</td>
<td>31.42</td>
<td>2.53</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

with thinner blubber layers. This result is consistent with the hypothesis that positive buoyancy in right whales decreases as animals mobilize their blubber layers. Therefore, both the health of individuals, the reproductive state of females and the age of juveniles must be taken into consideration when studying the energy consumption and/or diving effort of this species. As blubber layer thickness decreased, whales increased their pitch angle during descents and decreased it for ascents. These patterns in glide duration and pitch angle were present for all of the comparisons. Few differences in swimming behavior between life history categories with different blubber thicknesses were observed, suggesting that differences in glide length are not caused by swimming effort. Moreover, those differences that were observed did not follow a consistent trend with difference in blubber thickness.

Controlling buoyancy with a static mechanism such as blubber requires that whatever savings gained from a longer passive ascent would need to be spent on overcoming that same force during descent (Taylor, 1994). Coupling this mecha-
Table 3.3: Results of Kruskal Wallis tests that compared ratio of ascent to descent rate during glides and ascent to descent pitch angle between right whale life history categories known to have differences in blubber thickness. Categories are listed from in order of increasing blubber thickness. Significant differences between categories are shown in bold.

<table>
<thead>
<tr>
<th>comparison category</th>
<th>descent glide rate (ms(^{-1}))</th>
<th>ascent glide rate (ms(^{-1}))</th>
<th>H</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>individual</td>
<td>62.87 (3.64)</td>
<td>62.09 (2.75)</td>
<td>18.59</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>12.81</td>
<td>79.28 (0.43)</td>
<td>65.41 (1.32)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14.09</td>
<td>65.92 (2.15)</td>
<td>36.74 (3.10)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>juveniles</td>
<td>1.45 (0.03)</td>
<td>1.19 (0.03)</td>
<td>0.006</td>
<td>1</td>
<td>0.94</td>
</tr>
<tr>
<td>younger</td>
<td>0.76 (0.23)</td>
<td>1.12 (0.07)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>older</td>
<td>1.45 (0.03)</td>
<td>1.19 (0.03)</td>
<td>1.36</td>
<td>1</td>
<td>0.24</td>
</tr>
<tr>
<td>nonfemales</td>
<td>1.34 (0.07)</td>
<td>1.05 (0.04)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>younger</td>
<td>1.25 (0.05)</td>
<td>1.17 (0.03)</td>
<td>0.94</td>
<td>1</td>
<td>0.33</td>
</tr>
<tr>
<td>males</td>
<td>1.29 (0.05)</td>
<td>1.03 (0.09)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>females</td>
<td>1.29 (0.05)</td>
<td>1.03 (0.09)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>lactating</td>
<td>1.29 (0.05)</td>
<td>1.03 (0.09)</td>
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<td></td>
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</tr>
<tr>
<td>resting</td>
<td>1.29 (0.05)</td>
<td>1.03 (0.09)</td>
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</table>

<table>
<thead>
<tr>
<th>comparison category</th>
<th>descent pitch (°)</th>
<th>ascent pitch (°)</th>
<th>H</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>individual</td>
<td>62.97 (3.20)</td>
<td>60.49 (2.58)</td>
<td>18.43</td>
<td>2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>12.81</td>
<td>79.14 (0.37)</td>
<td>65.05 (1.14)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14.09</td>
<td>63.91 (2.29)</td>
<td>40.16 (3.04)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>juveniles</td>
<td>72.70 (0.88)</td>
<td>67.84 (0.88)</td>
<td>0.002</td>
<td>1</td>
<td>0.96</td>
</tr>
<tr>
<td>younger</td>
<td>73.05 (4.91)</td>
<td>60.24 (3.68)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>older</td>
<td>72.70 (0.88)</td>
<td>67.84 (0.88)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>nonfemales</td>
<td>78.89 (0.75)</td>
<td>59.28 (1.77)</td>
<td>26.45</td>
<td>1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>younger</td>
<td>78.89 (0.75)</td>
<td>59.28 (1.77)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>males</td>
<td>78.89 (0.75)</td>
<td>59.28 (1.77)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>females</td>
<td>69.89 (1.34)</td>
<td>66.76 (1.58)</td>
<td>0.66</td>
<td>1</td>
<td>0.42</td>
</tr>
<tr>
<td>lactating</td>
<td>75.92 (1.95)</td>
<td>60.89 (4.64)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>resting</td>
<td>75.92 (1.95)</td>
<td>60.89 (4.64)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

A behavioral mechanism with an additional behavioral one would allow whales to compensate for their buoyancy without increasing the energetic output. Increases in negative pitch may serve to increase the magnitude of downward directed lift generated by flow over the pectoral fins and, possibly, the body (Weihs, 1993), which has been shown to occur in several other marine species (Wilga & Lauder, 2000; Webb, 2002; Ribak et al., 2004). Whales with less blubber have less upward force to overcome when descending, which would require less lift to overcome and, therefore, allow them to use a less negative pitch on descent, as observed in the thinner animals in this study.

Buoyancy differences between individual right whales were reported by whalers, who observed that some right whales sank after death while the majority floated.
Table 3.4: Results of Kruskal Wallis tests that compared stroke rate and amplitude during ascent and descent phases between right whale life history categories known to have differences in blubber thickness. Categories are listed from in order of increasing blubber thickness. Significant differences between categories are shown in bold.

<table>
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<th>descent stroke rate (Hz)</th>
<th>ascent stroke rate (Hz)</th>
<th>H</th>
<th>df</th>
<th>p</th>
</tr>
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<td>0.20</td>
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<tr>
<td></td>
<td>12.81</td>
<td>0.16 (0.006)</td>
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<td>1</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>14.09</td>
<td>0.17 (0.003)</td>
<td></td>
<td>1</td>
<td>0.001</td>
</tr>
<tr>
<td>juveniles younger</td>
<td>0.16 (0.004)</td>
<td>0.17 (0.002)</td>
<td>3.84</td>
<td>1</td>
<td>0.05</td>
</tr>
<tr>
<td>older</td>
<td>0.15 (0.03)</td>
<td>0.20 (0.01)</td>
<td></td>
<td>1</td>
<td>0.066</td>
</tr>
<tr>
<td>nonfemales younger</td>
<td>0.16 (0.004)</td>
<td>0.17 (0.002)</td>
<td>0.19</td>
<td>1</td>
<td>0.66</td>
</tr>
<tr>
<td>male</td>
<td>0.14 (0.003)</td>
<td>0.17 (0.003)</td>
<td></td>
<td>1</td>
<td>0.66</td>
</tr>
<tr>
<td>females lactating</td>
<td>0.14 (0.009)</td>
<td>0.19 (0.003)</td>
<td>13.12</td>
<td>1</td>
<td>0.0003</td>
</tr>
<tr>
<td>resting</td>
<td>0.16 (0.005)</td>
<td>0.18 (0.002)</td>
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<table>
<thead>
<tr>
<th>individual</th>
<th>stroke amplitude (m)</th>
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<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>9.69</td>
<td>0.79 (0.08)</td>
<td>0.65 (0.03)</td>
<td>15.78</td>
</tr>
<tr>
<td></td>
<td>12.81</td>
<td>1.50 (0.07)</td>
<td>0.59 (0.06)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>14.09</td>
<td>1.38 (0.13)</td>
<td>0.67 (0.02)</td>
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</tr>
<tr>
<td>juveniles younger</td>
<td>1.37 (0.04)</td>
<td>1.82 (0.05)</td>
<td>7.17</td>
<td>1</td>
</tr>
<tr>
<td>older</td>
<td>1.59 (0.07)</td>
<td>1.36 (0.23)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>nonfemales younger</td>
<td>1.37 (0.04)</td>
<td>1.82 (0.05)</td>
<td>33.23</td>
<td>1</td>
</tr>
<tr>
<td>male</td>
<td>1.66 (0.10)</td>
<td>3.17 (0.15)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>females lactating</td>
<td>0.86 (0.05)</td>
<td>1.70 (0.08)</td>
<td>0.11</td>
<td>1</td>
</tr>
<tr>
<td>resting</td>
<td>1.59 (0.15)</td>
<td>2.38 (0.24)</td>
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<td></td>
</tr>
</tbody>
</table>

(Reeves & Mitchell, 1986). The negative buoyancy of those ‘dry skins’ may have been caused by a reduced body condition from lactation or lack of food, while the ‘floaters’ were whales in a health body condition. Buoyancy measurements made from blubber samples of two stranded adult female right whales with the methodology of Fish et al. (2002) showed that blubber had a mean buoyant force of 1.73 N, supporting the hypothesis that blubber is positively buoyancy. However, in order for an animal to float, all of the positively buoyant tissues must provide a greater force than all of the negatively buoyant tissues, so estimates of buoyancy for all right whale tissues are necessary before the net buoyancy of these whales can be determined. Lockyer (1976) described the right whale has having a high proportion of blubber relative to other internal tissues, providing evidence that the positively buoyant tissues in this species
would provide a greater upward force than those that provide a downward one, and right whales use higher stroke rates on descent than ascent at depths below that at which lung collapse occurs, presumably to actively work against their positive buoyancy (Nowacek et al., 2001; Woodward, 2006). Preliminary work has shown that right whale mandibles have a density that is low in comparison to most other mammalian bone (Campbell-Malone, pers. comm.), suggesting a strong adaptation for positive buoyancy.

In this study we assumed that the only difference in body composition of these whales was a difference in the amount of positively buoyant tissue, assumed to be
Figure 3.5: Mean (±SE) ratio of ascent to descent rate for each of four comparisons between animals with different blubber thicknesses, increasing from thin (■) to intermediate (■) to thick (■) layers: (A) individuals (N=3), (B) juveniles (N=8), (C) nonfemales (N=11) and (D) females (N=4).

Blubber. However, these assumptions should be tested with models to explore the densities of different tissues, measure their contributions to total buoyancy and estimate the lift forces possible from both the body and control surfaces (flukes and flippers) of a right whale. Such studies would help to understand and compensate for variations in diving behavior in this species. Some of the comparisons here included measurements from single individuals within life history categories, and these individuals could be not be representative of others in the same life history category. Three of the four comparisons used an assumed difference in blubber thickness based on the individual’s life history, not the thickness measured from individual
whales. Avoiding these assumptions would require blubber thickness measurements and simultaneous tag attachments to be made from the same individuals at different times of the year. However, the comparisons that did not have significant results demonstrated a trend that matched and supported those of the comparison that did demonstrate significant results. Regardless, this study uses a novel combination of techniques that could be applied to many other marine vertebrates. The consistent trends observed here provide strong initial evidence that reduced buoyancy may be related to the mobilization of lipids from the blubber in North Atlantic right whales.
The effect of wave drag on submersion depth for traveling North Atlantic right whales

4.1 Introduction

Many types of marine organisms regularly interact with the interface between water and air for fundamental biological purposes, such as foraging, breathing and swimming. Marine mammals must frequently surface to breathe and may remain at the water’s surface to recover depleted oxygen stores after a long dive (Costa & Williams, 1999). However, few marine animals spend prolonged amounts of time moving along this boundary (Vogel, 1994). Studies on both ship hydrodynamics and animal movement at the surface have shown that objects moving along this interface encounter a more complex hydrodynamic regime than that found at depth, which causes an increased drag force because of an additional source of drag known as wave drag (Lighthill, 1978).

Wave drag is caused by the interaction of two different wave systems generated by an object moving at the water’s surface and the deformation of this interface. Diverging waves move laterally away from the object’s direction of motion in a V
shaped pattern, while transverse waves move opposite to the object’s direction of travel (Crawford, 1984; Blake, 2009). Because each set of waves consists of both peaks and troughs, the combination of the two wave systems causes areas of either increased peaks or trough where the waves add together or complete lack of waves where the waves cancel each other. These peaks and troughs are further complicated by the presence of the object, because the bow wave at the anterior end of the object and, to a lesser extent, the stern wave at the posterior end of the object create more peaks at the end of the object and troughs along its sides. The interaction of these wave is directly related to the speed and length of an object, known as the Froude number, and the more the waves become additive (i.e. the larger the peak), the larger the resistive drag force of the fluid becomes until a point where the object reaches a high enough speed that the wave amplitude decreases and the resistive force also decreases accordingly (Hoerner, 1965). The peak in wave drag resistance has been found to occur at a Froude number of about 0.5, above which the resistance gradually reduces to zero (Hoerner, 1965).

Fully submerged objects in close proximity to the surface will incur higher drag due to wave drag because their wave systems are still interacting with the surface. As an object moves further away from the surface, wave drag gradually decreases, becoming negligible at a submersion depth that is greater than three times the maximum diameter of the body (Hertel, 1966). In addition to submersion depth, the magnitude by which the drag on a fully submerged object drag is increased by wave drag, known as the drag augmentation factor, is also affected by both the Reynolds number and the Froude number (Goldman, 2001; Blake, 2009). Empirical evidence from objects towed at different speeds and depths predicts that drag will be between 2.5 and 5 times higher when at the surface than when fully submerged because of wave drag and that this additional drag component can contribute more than 50% of the overall total drag force (Goldman, 2001; Vennell et al., 2006; Blake, 2009).
The addition of wave drag translates into increased energetic effort for animals that swim at or near the surface. As drag increases exponentially with velocity, the increase is more significant for large animals that can swim at high speeds (Blake, 2009). For animals that swim just below the surface, wave drag can have a significant effect on their energy usage because they operate at lower Froude numbers because of their larger size and maximum obtainable speed (Fish et al., 1991; Denny, 1995). Fin whales feeding at the surface had a significantly shorter interval between breaths than those feeding below the surface, suggesting that they had a higher level of oxygen consumption and therefore were using more energy (Kopelman & Sadove, 1995).

Across species of fish, those that swim near the surface use slightly more energy than those that are completely submerged (Videler & Nolet, 1990). The consequences of increased drag from sub-surface swimming include a decrease in the maximum speed that an animal can reach and/or a decrease in duration that those top speeds can be maintained. In response, some species use behavioral adaptations to reduce the amount of time spent near the surface. Because they must travel at the surface to be able to breathe, small cetaceans swimming at high speeds will repeatedly leap out of the water, a behavior known as porpoising, in order to avoid the effects of surface wave drag while performing high speed swimming (Blake, 1983; Williams et al., 1992).

Marine mammals capable of making sustained deep dives have the ability to avoid prolonged movements at the surface by diving to depths unaffected by surface drag. However, performing such dives requires the use of energy to overcome the buoyancy of their bodies and, regardless of how long and deep they can dive, they must travel back to the surface to breathe. In cetaceans, the migration of the nasal passages and nostrils from the front of the skull to the top of the head has improved efficiency in breathing at the water’s surface, but this adaptation requires the animal’s body to be located directly below the surface, a position where the wave drag component
maximized, should the animal choose to move horizontally (Hertel, 1966). Tagging studies have shown that many deep-diving pinniped and cetacean species perform extended bouts of shallow dives interspersed between their deep dives (Le Boeuf et al., 1988; Schreer & Testa, 1996; Tyack et al., 2006; Watwood et al., 2006). This dive pattern was hypothesized to be performed by traveling animals that are leaving the surface to avoid wave drag, but no evidence relating their dive depth to the layer of wave drag exists.

The North Atlantic right whale, *Eubalaena glacialis*, is an ideal species to explore whether making shallow dives could be an energy-saving behavior because it avoids the region of wave drag. While these whales dive to depths of 150-200m to forage in one habitat, earlier in the year they skim-feed at the surface in another (Baumgartner et al., 2007). Tagging studies have shown that right whales use dive patterns that consist of a series of shallow dives to depths less than 30m alternated with deep dives (Baumgartner et al., 2003, Nowacek, unpublished). Moreover, these whales perform migrations along the Atlantic coast of North America, a journey from their northern foraging grounds to their southern calving grounds during which they are thought to live off energy stored in their blubber (Kraus et al., 1986). The ability to reduce the cost of locomotion while making this migration should increase the margin of their survival if food resources are low upon their return. This study explores whether North Atlantic right whales dive to depths below the influence of wave drag when they are traveling horizontally by estimating the traveling depths of right whales of different sizes.

4.2 Methods

4.2.1 Data collection

Digital archival tags (Johnson & Tyack, 2003, Dtags) were attached to free-ranging North Atlantic right whales in the Bay of Fundy (BoF) and the South Atlantic Bight.
(SAB) following the procedure described in Chapter 3. Tagging locations and tracks of tagged whales are shown in Appendix A. In addition to the tagging protocol detailed previously, tagged whales were tracked with a VHF signal produced by the tag during daylight hours, and a laser rangefinder was used to take the whale’s position relative to the ship at each surfacing. These positions were georeferenced onto a bathymetric map of the area for each surfacing by triangulating the range and bearing measurements from the ship’s GPS position.

4.2.2 Dive extraction & analysis

Surface dives were identified from the time-depth profile of the Dtag and defined as dives that were greater than two meters but less than 30m in maximum depth. Dives that exceeded 30m were considered to be foraging-type deep dives during which animals chose to leave the surface in search of prey (Baumgartner et al., 2003) and therefore were excluded because they represented behaviors other than traveling. Short duration dives (<30s) were also excluded because they are typically caused by the fluke strokes of animals resting at the surface, often in preparation for a deep dive, and therefore do not represent animals moving horizontally. Traveling behaviors were then separated from non-traveling surface activities such as social behaviors. For tag attachments in the BoF, surface dives made in response to controlled exposures of ship alarm signals were considered to be traveling dives because whales have been shown to prematurely abandon deep foraging dives and move away from the area in response to these signals (Nowacek et al., 2004). Because none of these experiments were performed in the SAB, surface dives that occurred during periods of constant heading were considered to be traveling because a low rate of heading change has been shown to indicate this behavior (Mayo & Marx, 1990). This definition was supported by observations during data collection of one whale (Eg3430) traveling, and the considerable distance that a second whale (Eg1151) covered during the overnight
hours. All other surface dives in either region were considered to be non-traveling.

4.2.3 Determination of submersion depth

During the tagging process, photographs of tagged whales were taken and then compared with those contained in the North Atlantic Right Whale Catalogue, which contains age and sex information for most of the entire population (Hamilton & Martin, 1999). Right whales are individually identified by patterns in their scars and callosities, the rough white patches of keratinized skin on their heads (Kraus et al., 1986). Matching photographs of individual whales to the catalogue allowed life history information on most individuals of the population to be determined. Tagged animals were grouped into categories that have noticeable differences in body depth: 1) juveniles, whales between one and four years old, 2) adults, those eight years old and older, and 3) pregnant (Miller Angell, 2006). The first two categories were determined according to ages with similar body sizes, not necessarily their level of sexual maturity. Eight-year old right whales are typically considered juveniles because they are not yet reproductively mature (Hamilton et al., 1998), but because they are closer to adult body size than the rest of the juvenile whales that were tagged and no whales between the ages of five and seven were tagged, they were considered to be adults for this study. Pregnant whales were those that were observed with a calf less than six months after the tagging season.

The maximum submersion depth \((h)\) for which a body incurs the effects of wave drag area approximately three times the depth of the animals body \((d)\) (Hertel, 1966, Fig. 4.1). Because body size measurements were not obtained during tagging and body depths are difficult to measure accurately from either live or dead whales, whales were assumed to be circular in cross-section and body width was used as a proxy for body depth. Body width measurements were obtained from necropsy reports of stranded animals (Moore et al., 2004) as well as aerial photogrammetric measurements.
measurements of live whales at sea (Miller Angell, 2006; Perryman & Lynn, 2002). Widths were averaged according to the three age categories (juvenile, adult and pregnant) and used for all tagged individuals of that category. The dive depths recorded on the Dtags were adjusted to submersion depth by adding one-half of the body depth for that animal’s category in order to account for the difference between the tag’s location and the animal’s central axis (Fig. 4.1).

Figure 4.1: Schematic showing the submersion depths ($h$) where wave drag (blue gradient) will have an effect on objects of body depth ($d$). Wave drag is maximal for whales just below the surface (A) and becomes negligible at a submersion depth of three times their body depth (B, —). Submersion depth (—) is measured from the surface to the central axis of the whale (—), while body depth is measured at the animal’s largest width between the dorsal and ventral sides (—). Tags were positioned (■) at roughly one-half body depth above the animal’s central axis. Adapted from Hertel (1966).

Swimming near the seafloor could cause additional ground effects (Vogel, 1994), so the shortest distance between whales and the seafloor was measured to determine
whether the presence of the seafloor could affect them when in the shallow waters of the SEUS where whales were tagged in 10–40m of water. Traveling dives made by individuals of each age group were compared between habitats to determine whether proximity to the seafloor had any influence on diving depth. The distance between whales and the seafloor was determined for whales in the SEUS by plotting the whales’ GPS positions over a 10m resolution bathymetry in ArcGIS 9.3.1 (ESRI, Inc., 2009) and extracting seafloor depth from that bathymetry for each surfacing. Because surface positions were only available for a limited number of the dives and seafloor depth is relatively consistent over the ranges used by these animals, seafloor depths were averaged across all surface positions for a particular whale.

Submersion depths were averaged by behavior and compared between habitats to determine whether differences in diving behavior exist between the geographic regions with a Kruskal-Wallis test. Because these results were significant at p<0.05, all subsequent comparisons were performed separately between the two habitats. First, comparisons of submersion depths were made between behavioral states for each age category. Non-traveling dives were predicted to have significantly lower submersion depths than traveling dives, because whales are not moving horizontally during those dives. Second, within each behavioral state, submersion depths were compared across age categories. Finally, distance to the seafloor was compared between behaviors to test whether whales were closer to the seafloor when traveling. This comparison was only made for the SEUS whales because the BoF whales were in water depths between 150–200m. All comparisons were found to have distributions that differed significantly from normal, so nonparametric Wilcoxon tests were used to determine significance at a level of p<0.05 (Hollander & Wolfe, 1999).
4.3 Results

Tag attachments to 23 whales were made to individuals of known age that performed some surface dives, allowing body depth to be determined. These animals made a total of 617 surface dives that were divided into 247 traveling and 370 non-traveling dives. The average body depths of the 13 juvenile whales, nine adults and one pregnant individual were 2.65m, 3.15m and 3.50m, which resulted in expected submersion depths of 7.95m, 9.45m and 10.50m, respectively, (Table 4.1).

Table 4.1: Mean (±) submersion depth (h) and distance to seafloor (p_{sf}) of tagged right whales of three age categories during traveling (upper box) and non-traveling (lower box) dives in each of two habitats, the waters off the Southeastern US (SEUS) and the Bay of Fundy, Canada (BoF). Body depths (d) for each age were averaged from body width measurements of live and dead right whales and used to estimate the submersion depth (h_{est}) at which wave drag would no longer affect them.

<table>
<thead>
<tr>
<th>Age</th>
<th>SEUS</th>
<th>BoF</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>travel</td>
<td>non-travel</td>
</tr>
<tr>
<td></td>
<td>d (m)</td>
<td>n</td>
</tr>
<tr>
<td>juvenile</td>
<td>2.65</td>
<td>8</td>
</tr>
<tr>
<td>adult</td>
<td>3.15</td>
<td>-</td>
</tr>
<tr>
<td>pregnant</td>
<td>3.50</td>
<td>85</td>
</tr>
<tr>
<td>juvenile</td>
<td>27</td>
<td>152</td>
</tr>
<tr>
<td>adult</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>pregnant</td>
<td>133</td>
<td>10.76(0.45)</td>
</tr>
</tbody>
</table>

Whales in the SEUS made significantly deeper dives than those in the BoF during traveling ($H_{1,247} = 17.24, p < 0.0001$) and non-traveling dives ($H_{1,370} = 8.59, p = 0.003$). Traveling dives had significantly deeper submersion depths than non-traveling dives within all age categories for both habitats (Table 4.2, Fig. 4.2–4.3).
Non-traveling dives did not differ significantly in submersion depth when compared between ages (SEUS : $H_{1,162} = 2.25, p = 0.13$; BoF : $H_{1,210} = 2.04, p = 0.15$). In the SEUS, whales of all age categories were significantly closer to the seafloor during traveling behaviors than non-traveling behaviors (juveniles : $H_{1,35} = 22.00, p < 0.0001$; pregnant : $H_{1,218} = 151.23, p < 0.0001$) (Fig. 4.2). During traveling, this distance equated to approximately less than two body depths from the seafloor (Table 4.1).

**Table 4.2:** Difference in submersion depth between traveling and non-traveling dives for whales of three age categories in the waters of the Southeastern US (SEUS) and the Bay of Fundy, Canada (BoF).

<table>
<thead>
<tr>
<th>Age</th>
<th>SEUS</th>
<th>BoF</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$H$ df p</td>
<td>$H$ df p</td>
</tr>
<tr>
<td>juvenile</td>
<td>12.78 1 0.0004</td>
<td>6.17 1 0.013</td>
</tr>
<tr>
<td>adult</td>
<td>— 33.68 1 &lt;0.0001</td>
<td>—</td>
</tr>
<tr>
<td>pregnant</td>
<td>17.29 1 &lt;0.0001</td>
<td>—</td>
</tr>
</tbody>
</table>

Whales of ages with larger body depths used deeper submersion depths than those with smaller body depth during traveling dives in the BoF ($H_{1,154} = 11.27, p = 0.0008$) but whales with smaller body depths used deeper submersion depths in the SEUS ($H_{1,93} = 4.57, p = 0.03$) (Fig. 4.2–4.3). Non-traveling dives did not differ significantly in submersion depth when compared between ages (SEUS : $H_{1,160} = 2.25, p = 0.13$; BoF : $H_{1,210} = 2.04, p = 0.15$) (Fig. 4.2–4.3). Whales of all age categories were significantly closer to the seafloor during traveling than non-traveling behaviors (juveniles : $H_{1,35} = 12.78, p < 0.0001$; pregnant : $H_{1,218} = 17.29, p < 0.0001$) (Fig. 4.2). Traveling dives were less than two body depths above the seafloor (Table 4.1).
4.4 Discussion

For both habitats, each age group used significantly deeper dives during traveling behaviors than during non-traveling ones, which supports the hypothesis that traveling animals avoid surface wave drag. These results also show that the average depths reached by traveling animals were slightly deeper than the depth where they would be affected by wave drag, while the average depths of non-traveling animals were not, for all age groups in the BoF (Fig. 4.3). Larger animals dived deeper than smaller ones when traveling but not during other behaviors, which also supports the hypothesis that these animals are selecting depths to minimize wave drag. The link between body size and submersion depth suggests that these whales have some mechanism to detect fine-scale changes in the water flow around their bodies.
Figure 4.3: Mean submersion depth of traveling (■) and non-traveling (□) dives made by right whales of two age categories (juvenile, adult) in their foraging habitat in the Bay of Fundy (BoF). Traveling dives had significantly deeper submersion depths than non-traveling dives for both age categories. Submersion depths were significantly different between ages for dives but not non-traveling dives. Traveling dives matched the minimum depth at which wave drag effects were negligible (— ), as estimated from the average body depth of animals from that category, but non-traveling dives were considerably shallower. Error bars show one standard error.

While pinnipeds have been shown to have a highly sensitive vibrissal system capable of detecting hydrodynamic trails of fish and possibly aid in navigation (Hyvärinen, 1989; Wieskotten et al., 2010), the sensory capabilities of cetaceans are not well understood. Right whales have retained a small number of highly innervated hairs on their rostrum (Ling, 1977; Reeb et al., 2007), which have been suggested to function in detecting the presence or density of their copepod prey (Baumgartner et al., 2007; Kenney et al., 2001). Should these hairs function in this way, they may also allow right whales to sense the depth of the wave drag layer, possibly through changes
in their swim speed connected with the effect of increased drag. Surface dives have been observed in several pinniped species (Le Boeuf et al., 1988; Schreer & Testa, 1996; Lesage et al., 1999), which also may use a similar sensory mechanism to detect the depth at which horizontal travel is most efficient.

The two age categories that were tagged in the SEUS, juveniles and pregnant animals, had similar submersion depths even though these animals have very different body sizes, suggesting that wave drag avoidance may not be the primary force behind traveling dive behavior in this habitat. The average depth of the area where whales were tagged was between 10–30m, so these waters would have a very different hydrodynamic regime than those in the Bay of Fundy. Friction between the seafloor and water moving over it cause a reduction in flow velocity near it, known as the bottom boundary layer (Vogel, 1994), and the bottom boundary layer and the surface boundary layer meet (Schwing et al., 1983), causing reduced velocities throughout the water column. Although this effect could be a part of the reason why right whales migrate to this region to calve, it probably does not have an effect on their diving behavior. Instead, traveling whales appeared to be diving very close to the seafloor (Fig. 4.2).

Animals have been shown to exploit ground effects to reduce the power needed to move by traveling close to a boundary, either above the water’s surface for flyers such as black skimmers, shearwaters, and pelicans (Withers & Timko, 1977; Hainsworth, 1988; Rosén & Hedenström, 2001) or above the seafloor for swimmers such as mandarin fish and poachers (Blake, 1979, 1983; Nowroozi et al., 2009). In addition to reduced drag, swimming along a solid surface also may aid in lift generation and reduce the cost of swimming (Weis-Fogh, 1973; Cooter & Baker, 1977). Moving near the seafloor accelerates the fluid between the animal and the solid surface, and several different species of cetacean have been documented to move close to the seafloor, typically in a dorso-ventral orientation (Dietz et al., 2007; Woodward & Winn, 2006;
Herald et al., 1969). Both whales that were predominantly traveling were less than two body depths from the seafloor, as measured from the animal’s central axis, so the animal’s ventral side would be about one body depth away from the seafloor. In addition, seafloor depths were averaged across the GPS coordinates of each whale’s position, reducing the precision at which seafloor depth could be determined. The speed at which whales in this area were moving is also unknown. Surface dives in the BoF appear to be connected with high-speed swimming, while whales tagged in the SEUS appeared to be traveling slowly. Should SEUS whales have been responding to the same stimuli as those in the BoF, they may have used a shallower mode of swimming both due to the need to breathe and reach higher speed while avoiding wave drag.

However, surface dives were also observed in the Bay of Fundy where water depths are greater than 150m and wave drag is likely to be the only additional source of drag for whales near the surface. In this habitat, the submersion depths used by traveling whales matched the depth of negligible wave drag very well (Fig. 4.3). Moving below the surface will end the interaction between the waves generated by an animal’s movement and the water’s surface, decreasing the drag augmentation related to that interaction. Surface swimming can increase the drag experienced by an animal by five to ten times the force when fully submerged (Hertel, 1966; Williams, 1983). This increase in drag translates into a considerable increase in the cost of locomotion and a significant limitation in the maximum speeds obtainable at the surface (Prange & Schmidt-Nielsen, 1970; Hui, 1988; Videler & Nolet, 1990). Avoiding this depth would allow fully submerged animals to either save energy or reach higher speeds for the same amount of energy. However, for any air-breathing marine animal, diving away from the surface requires an increase in locomotor costs, both because of the physiological demands of breath-holding and the forces involved in diving. For an animal such as a right whale that may be positively buoyant, the costs related to
diving may be higher than other cetaceans and/or marine air-breathers, as buoyancy can contribute up to 60% of the costs of descent. Minimizing the amount of time spent diving against that force therefore likely saves considerable amounts of energy.

The pregnant whale in the SEUS followed a pattern similar to those of the BoF animals, where its average submersion depth was just deeper than the depth of negligible wave drag, but the juvenile group did not fit this trend. Despite having a smaller body size, juveniles used much deeper submersion depths when traveling, although their non-traveling submersion depths were similar to that of the pregnant animal. No juveniles in the SEUS performed both traveling and non-traveling dives, and the individual that traveled was associated with another right whale of unknown age and sex. Therefore, its behavior could have been influenced by that of its conspecific, possibly using other behavioral strategies such as drafting to save energy. The short duration of the attachment to the traveling juvenile (<2 hours) in comparison to the extremely long attachment to the pregnant animal also affected the average submersion depth. The pregnant whale did perform dives to depths of 20–23 m, which were greater than any made by the juvenile. Finally, the behavior of the pregnant animal could not be observed during much of the tag attachment, and dives were assigned to traveling and non-traveling states based on the linearity of the animal’s path. Brief changes in the animal’s behavior during the period classified as ‘traveling’ could have resulted in the misclassification of behaviors and a lowered average submersion depth for this animal. More long tag attachments and direct surface observations are necessary to determine the variability in submersion depths used by individual whales.

These results also clearly show that habitat had a considerable effect on diving behavior (Figs. 4.2–4.3). Whales were tagged in the SEUS in waters 10–30m in depth, so the hydrodynamic regime of this region will be different from that of the BoF. Friction at the seafloor will reduce the velocity of water near it, causing a bottom
boundary layer to exist (Vogel, 1994). In the SEUS the bottom boundary layer and the surface boundary layer meet (Schwing et al., 1983), causing reduced velocities throughout the water column. Although this effect could be a part of the reason why right whales migrate to this region to calve, it may therefore reduce the advantage gained by avoiding wave drag. The proximity of traveling whales to the seafloor in this region means they may experience and could exploit other hydrodynamic phenomena. The practice of swimming close to a solid surface may help to decrease induced drag, known as the ground effect. Animals have been shown to exploit ground effects to reduce the power needed to move by traveling close to a boundary, either above the water’s surface for flyers such as black skimmers, shearwaters, and pelicans (Withers & Timko, 1977; Hainsworth, 1988; Rosén & Hedenström, 2001) or above the seafloor for swimmers such as mandarin fish and poachers (Blake, 1979, 1983; Nowroozi et al., 2009). More precise measurements, such as the distance from the whale to the seafloor and the speed of the whale, would help to determine whether this behavior has any hydrodynamic advantage for a large cetacean.

The observed difference in shallow diving behavior between habitats could reflect the seasonal behavioral patterns of these whales. Surface traveling dives in the BoF were directly connected with high-speed swimming because they were made in response to a direct stimulus (a controlled exposure experiment of high frequency noise), while the traveling SEUS whales were not exhibited strongly directed movements. Surface swimming is a response used by some species of baleen whale when pursued by a predator. Saving energy in this situation would be especially beneficial and therefore strongly selected for as it would allow an animal to travel farther or longer, increasing its ability to successfully evade predator. Staying close to the surface could also allow whales to increase their breathing rate and devote more of their aerobic capacity to propulsion than during deep breath-hold dives, but the associated hydrodynamic costs would suggest a disadvantage to high-speed surface swimming.
Five species of the genus Balaenopteridae (common minke whale *B. acutorostrata*, Bryde’s whale *B. edeni brydei*, sei whale *B. borealis*, fin whale *B. physalus* and blue whale *B. musculus*) have been observed on multiple occasions to make rectilinear high-speed (20–40 kmh$^{-1}$) surface dives when pursued by killer whales (*Orcinus orca*) (Ford & Reeves, 2008). Playbacks of killer whale calls to grey whales, *Eschrichtius robustus*, resulted in a similar response where whales switched to directed travel at high speed (Cummings & Thompson, 1971). Right whales have also been found to abandon foraging dives, return to the surface and begin making shallow surface dives in response to alarm signals (Nowacek et al., 2004), although high speed swimming in right whales is more commonly observed in males of the species approaching potential mating situations (Kraus & Hatch, 2001; Parks, 2003). In order to reach their highest speed, large baleen whales will perform a behavior known as ‘race-diving’. This behavior consists of animals traveling in a straight line, arching their bodies partially out of the water, taking a single breath and raising their fluke at a 45° angle at each surfacing (Parks, 2003; Ford & Reeves, 2008). The high angle of the flukes suggests these ‘race dives’ are to depths below those affected by wave drag, not just submerging their bodies, and therefore, race-diving may be the optimal balance between access to air at the surface and moving at high speeds without substantial wave drag.

Wave drag causes an upper limit to swimming speed, known as hull speed, that few animals exceed (Vogel, 1994; Fish, 2000). The dimensionless Froude number ($Fr$) shows the wave pattern predicted for a certain size and speed,

\[ Fr = \frac{U^2}{gL} \]  \hspace{1cm} (4.1)

where $U$ is the object’s velocity, $g$ gravitational acceleration and $L$ the object’s length at the waterline, and can be used to predict the speed of peak resistance and,
therefore, hull speed for a particular object moving at the water’s surface. Hull speed occurs at about \( Fr = 0.45 \) (Hoerner, 1965), and the maximum speeds reached by most surface swimming animals are close to but do not exceed the hull speeds predicted by their Froude number (Prange & Schmidt-Nielsen, 1970; Fish, 1984; Vogel, 1994; Fish & Baudinette, 1999; Blake & Chan, 2007). However, some animals are able to exceed hull speed by additional measures, such as hydroplaning in ducklings (Aigeldinger & Fish, 1995), synchronous kicking in frogs (Johansson & Lauder, 2004) and porpoising in small cetaceans (Weihs, 2002). Race-diving may be an equivalent measure to avoid the speed-limiting effects of high-speed surface swimming.

Right whales present a special case when investigating the study of surface locomotion because these whales spend extended periods not just moving but feeding at the ocean’s surface. Right whale foraging behavior is directly related to the water depth where aggregations of a particular life history stage of their primary food source, *Calanus finmarchicus*, are the most dense (Baumgartner et al., 2003). In the late winter and early spring, this stage stays in the upper water column to feed on phytoplankton that are limited to the surface waters, but once these copepods enter their diapause phase, they will descend away from the surface to depths of approximately 150–200m. Following their prey, right whales will skim-feed near the surface during the early spring, where they would certainly be exposed to wave drag effects, and then switch to submerged feeding later in the year (Baumgartner et al., 2007). Several morphological adaptations that reduce drag by inducing water flow through the mouth, such as Venturi and Bernoulli effects caused by the curvature of the baleen racks and the arrangement and size of openings in the baleen, have been shown for bowhead whales (Werth, 2004; Lambertsen et al., 2005), and are most likely also present in right whales. Additional features of the head and mouth may also allow these whales to reduce the enhanced bow wave created by swimming at the surface and consequently decrease the resulting wave drag. A bow wave would
be especially counterproductive for large ram filter feeding animals because in addition to the costs of increased drag, it would push some portion of their prey up and out of their mouths instead of into them. Right whales have two large patches of keratinized skin on either side of the tip of their lower jaw that may act as a ‘bulbous bow’, lowering the wave drag resistance and reducing or eliminating the bow wave in front of the animal (Hoerner, 1965). Water flowing over the bulbous bow creates a wave in front of the bow wave and a trough that should coincide with the bow wave itself, acting to partly or entirely cancel it out (Taylor, 1933). Of the three species of large shark that feed on zooplankton (basking shark *Cetorhinus maximus*, whale shark *Rhincodon typus*, and megamouth shark *Megachasma pelagios*) only the basking shark truly feeds by ram filtration (Diamond, 1985; Clark & Nelson, 1997). The anterior end of this shark’s upper jaw forms a slightly upturned rounded shape that protrudes well in front of its mouth and lower jaw that may serve a ‘bulbous bow’-type purpose similar to that of the front lower jaw callosities in right whales, generating destructive interference to dampen bow waves created when feeding near the surface. This structure is not found on either of the two shark species that are not exclusive ram filter feeders.

The shape of the baleen racks and lower jaw of balaenid whales, thinner anteriorly and thicker posteriorly, may also reduce the profile of the mouth exposed to the flow, further inhibiting the creation of a bow wave. Using a slow swimming speed also reduces the bow wave, and North Atlantic right whales can do so because their prey is too small to evade them. High speeds when feeding at the surface are possible, however, although an exceedingly large wake is produced when doing so. A southern right whale (*Eubalaena australis*) feeding on Antarctic krill at the surface had to reach a speed of 4–4.5 ms$^{-1}$ to feed on this prey (Hamner et al., 1988), which suggests that the right whale body shape and feeding apparatus can achieve speeds close to hull speed, but the behavior and body size of their prey do not require their use.
Because these data were obtained from two different habitats and only a limited number of animals, more records of surface behaviors should be collected to confirm these findings. Further work on the forces that could be generated by a large animal swimming close to a boundary should be completed to support a hydrodynamic cause for this behavior and rule out other possibilities such as protection. More precise measurements of the water depth in relation to the whale’s depth are needed to determine the relative forces involved before conclusions can be made as to which effect(s) are the predominant causes behind this behavior. Measurements of speed and distance would also help to confirm the occurrence of traveling behaviors on a more specific temporal scale. However, these findings provide solid initial evidence that right whales make shallow dives to avoid the costs associated with swimming near the surface, potentially helping them achieve higher speeds in some cases. They may also be employing other hydrodynamic phenomena when in shallow water that help to reduce their swimming cost. Finally, they appear to have several morphological adaptations that inhibit a bow wave from forming when they do need to move near the surface, but whether these adaptations function only when whales are feeding has not been determined. Further work is necessary to understand the mechanisms and flow kinematics behind these adaptations and explore the overall hydrodynamics involved with both surface feeding and bottom swimming, but this study provides an initial exploration of surface swimming behaviors and wave drag in North Atlantic right whales.
Kinematics of stroke & glide swimming in North Atlantic right whales: tricks to save energy

5.1 Introduction

Intermittent locomotion is performed by many different groups of mobile organisms but the advantages towards performance vary considerably depending on the environment and the animal. In all cases, this behavior consists of alternating between periods of active locomotion and pauses. In the terrestrial environment where animals produce force by moving against a solid object, pauses in locomotion increase the distance that animals can travel before muscular exhaustion by allowing some metabolic and muscular recovery while still moving, as well as improving their ability to detect and evade predators and locate prey, but at a cost of time and energy (Weinstein, 2001; McAdam & Kramer, 1998). For animals that move by accelerating the fluid around them, forward motion does not cease immediately when propulsion stops, and therefore intermittent locomotion can save energy for animals that fly or swim (Kramer & McLaughlin, 2001; Rayner, 2001). This pattern of movement is characterized by periods of acceleration when the animal is using energy to move,
known as the stroke phase, followed by shorter periods of deceleration, known as 
glides when the animal stops stroking and relies on its existing movement to main-
tain forward progress (Videler & Weihs, 1982).

Stoke-glide gaits are even more efficient than continuous locomotion for those 
animals that move underwater and therefore have been observed in a wide variety of 
submerged swimmers, such as fish, diving birds and marine mammals. Cormorants, 
penguins and alcids all perform some variation on stroke-glide swimming, providing 
savings of up to 32% over continuous wing-propelled forward movement (Ribak 
et al., 2005). These pauses in active stroking appear to reduce the energy needed 
to swim by reducing drag inherent in oscillating hydrofoils and still may experience 
some lift production, such as that created by fluid flow over the body and any fixed 
appendages, although these advantages are related to the mass and speed of the fish, 
so that larger fish that can reach higher speeds obtain larger benefits (Weihs, 1974; 
McHenry & Lauder, 2005; Swanson et al., 1998).

Saving energy when diving is especially crucial for air-breathing marine animals 
because these animals have access to a limited amount of oxygen during their dives. 
The slower they consume their available oxygen stores, the more time they have for 
locating and capturing prey at depth. The stroke-glide gait is frequently used by 
marine mammals during periods of vertical travel from deep dives. Northern ele-
phant seals Mirounga angustirostris, New Zealand fur seals Arctocephalus forsteri, 
bottlenose dolphins Tursiops truncatus, sperm whales Physeter macrocephalus and 
blue whales Balaenoptera musculus all spend some portion of their dive ascents al-
tering stroking periods with glides (Williams, 2001; Davis et al., 2001; Skrovan et al., 
1999; Miller et al., 2004b). Individual variation in the use of this gait within a species 
occurs, suggesting that it can be used as a strategy to compensate behaviourally for 
physiological changes, such as increases in buoyancy related to fat storage. Fatter 
Weddell seals Leptonychotes weddelli used a stroke-glide gait when descending from
dives, presumably because they needed to overcome more positive buoyancy, than thinner seals (Sato et al., 2004). Baikal seals Pusa sibirica demonstrated prolonged glides during vertical diving when their buoyancy was experimentally decreased by the attachment of a lead weight but switched to stroke-glide swimming when the weight was released and their buoyancy increased (Watanabe et al., 2006). Therefore, the stroke-glide gait may be a behavioral strategy used to reduce the added costs of buoyancy causes during vertical travel.

Intermittent locomotion during vertical dive phases allows animals to take advantage of the force of their buoyancy to propel themselves through the water column, either towards the surface or away from it (Miller et al., 2004b; Skrovan et al., 1999; Watanabe et al., 2010). During horizontal swimming, the advantages of intermittent locomotion are related to reducing drag while still moving forward and have been estimated to reduce energy expenditure by between 50-80% (Weihs, 1973; Wu et al., 2007). The act of thunniform locomotion increases the drag on an actively swimming animal by approximately three to five times that of the same animal when gliding, a difference caused by increases in pressure drag, separation of the boundary layer and drag due to the generation of thrust (Webb, 1975; Fish, 1998), so by spending portions of horizontal swimming in a passive glide, the overall energetic cost of horizontal movement is less than that of continuous active propulsion (Videler & Weihs, 1982). Similar to aerial locomotion, speed appears to have an influence on the effectiveness of this gait; fish used stroke-and-glide swimming either at low speeds or at high speeds close to their optimal cruising speed, but not at intermediate speeds or for small body sizes (Videler & Weihs, 1982; Videler, 1981; Chung, 2009; Videler, 1993). Body shape also limits the efficiency of this gait, and those groups of fish that have fineness ratios between 4.5 and 6 perform intermittent locomotion while species with fineness ratios outside of this range do not (Blake, 1983, 2004).

Most species of marine mammal have fineness ratios that fall within this range,
suggesting that the use of stroke-glide swimming will also be energetically advantageous. However, the majority of work on this gait has been done only on the vertical portions of dives. The goals of this study were to quantify the differences between stroke-glide swimming and continuous swimming in North Atlantic right whales through a fine-scale analysis of their swimming kinematics and then determine the drag experienced by these animals when foraging. Stroke-glide swimming has been observed from bowhead whales *Balaena mysticetus* during the bottoms of their foraging dives and has been suggested to offset the high costs of filter-feeding (Simon *et al.*, 2009), but whether increases in drag occur when feeding has not been determined. A high-resolution suction-cup tag was attached to free-ranging North Atlantic right whales at their foraging grounds in the Bay of Fundy to record their three-dimensional movements. Vertical oscillations in the Dtag record were used to identify the occurrence of glides, and a series of kinematic parameters were measured from both stroke and glide sequences of animals that performed regular stroke-glide swimming and those that swam continuously throughout the bottom of their foraging dives. Finally, drag coefficients were determined from the rate of deceleration during glides from the bottom of foraging dives and from shallow dives made near the water’s surface.

5.2 Methods

Digital archival tags known as Dtags (Johnson & Tyack, 2003) were attached to free-ranging North Atlantic right whales (*Eubalaena glacialis*) in the Bay of Fundy during August and September 2000, 2001, 2002 and 2005, and details of the tag attachment procedure are outlined in Chapter 3. The three-axis accelerometers and magnetometers were used to determine motion around one of the three axes of motion, which will be referred to as pitch, roll and heading (Chapter 3). These tags also contained a hydrophone that allowed the acoustic environment of the animals to be

5.2.1 Kinematic analysis

Pitch and depth profiles recorded with the Dtags and analyzed in MATLAB 7.10.0 (The Mathworks Institute, 2010) were used to separate dives and locate the four dive phases (descent, bottom, ascent and surface) within each dive. Descents were defined as periods of high negative pitch (< −5°) and rapidly increasing depth, indicating that animals were moving from the surface to depths typical of foraging. Ascents were determined by high positive pitch (> 5°) and rapidly decreasing depth, indicating that whales had presumably terminated foraging and were returning to the surface to breathe. Bottom phases were the periods between descents and ascents when animals remained approximately horizontal in pitch and at a relatively constant depth. Surface periods were defined as the time between the end of one ascent and the beginning of the following descent, when animals were resting at the surface, recovering their oxygen stores.

Direct measurements of speed during periods of low body pitch, such as the bottom phases of most foraging dives, are complicated by the whale’s body oscillations, so low-frequency flow noise recorded by the tag’s hydrophone was used to determine animal speed during bottom phases, following the methods described in Goldbogen et al. (2006) and Simon et al. (2009). During portions of descent phases with high pitch (> 30°), vertical velocity ($U$) was determined over five-second intervals by dividing the mean change in depth ($p_w$) by the sine of the animal’s pitch ($\theta$),

$$U = \frac{\Delta p_w}{\sin(\theta)}$$  \hspace{1cm} (5.1)

The flow noise at 500 Hz was filtered with a two-pole Butterworth filter, and the
root-mean-squared noise level at this frequency was measured over five-second time
blocks. These levels were then plotted against vertical velocity for corresponding
time blocks, and a linear regression was then fitted for all descents made by each
whale (Simon et al., 2009; Goldbogen et al., 2006), excluding those that occurred
directly after tagging, during playback experiments as described in Nowacek et al.
(2004) or during periods of extremely high or variable background noise (e.g. vessels
passing nearby). Noise levels at 500 Hz were then measured for the bottom phases
of dives of that animal, and the linear function generated by the descent regression
used to determine animal speed throughout the bottom phase.

Each bottom phase was then divided into periods of active and passive loco-
motion, called ‘stroking’ and ‘gliding’ periods, respectively, based on the vertical
oscillations in the pitch record (Fig. 5.1). Glides were identified following the proce-
dure outlined in Woodward (2006). The frequency spectrum of the discrete Fourier
transform of pitch for the bottom phase only was windowed with a 100-point Han-
ing window to identify two spectral peaks, the higher of which was connected with
fluke stroke oscillation and the lower more general changes in pitch (Woodward,
2006). The dominant stroke frequency was determined by bandpass filtering around
the higher spectral peak, using the spectral peak as the center frequency of the filter
and the minima between the two peaks as the bandwidth. Durations of zero pitch
in the filtered record were classified as glides, following Woodward (2006) (Fig. 5.1B).
Whales were then classified as either ‘continuous’ swimmers, those that performed
few, irregularly spaced glides or ‘stroke-glide’ swimmers, those that performed glides
at regular intervals during the bottom phase of foraging dives.

The percentage of the bottom phase spent gliding, number of strokes, number of
glides, bottom phase duration, and maximum depth of each dive were determined
for each dive, averaged and compared between the two locomotor gaits with a lin-
ear mixed model that included individuals as a random effect in order to compare
energetic output necessary for each gaits. In addition, stroke rate, peak-to-peak fluke amplitude, and speed were also measured, averaged and compared to assess whether any considerable difference in swimming behavior was present between the two swimming gaits. Finally, the body lengths and body conditions of the whales were compared between the two gaits in order to determine if body size had any influence on whether whales swam continuously or used the intermittent gait. Stroke rate was determined as the inverse of the amount of time between consecutive upstroke peaks, and amplitude was measured as the peak-to-peak distance between upstrokes and downstrokes. Fluke amplitude was adjusted from the angular displacement from the horizontal that is measured by the tag to the distance traveled by the flukes with the following equation,
\[ a = \theta \frac{\pi}{180} \left( \frac{2}{3} L \right) \]  

where \( \theta \) is the pitch angle in degrees recorded by the tag, \( L \) body length, and \( a \) the distance traveled during the fluke stroke. Two-thirds of the total body length was used to measure from the whale’s center of mass, which is at about 40% body length (Fish, 2002), to the leading edge of the flukes. Amplitude was not measured to the fluke’s trailing edge in order to avoid any influence of fluke cambering on the resulting amplitude measurement (Fish et al., 2006). Body lengths were obtained through aerial photogrammetry measurements (Perryman & Lynn, 2002) if available or from the average length of stranded individuals of the same age (Moore et al., 2004).

In addition to those measured for all whales, a series of additional parameters based on theoretical predictions about stroke-glide swimming were measure for both continuous and stroke-glide swimmers (Videler & Weihs, 1982; Weihs, 1974). Wilcoxon signed rank tests were used to compare speed between the start and end of each stroking period and the mean speed of the glide with that of the stroking period (Hollander & Wolfe, 1999). Mathematical models as well as empirical studies have shown that deceleration occurs during the glide period, which would result in a lower mean glide speed than mean stroke speed, and that animals must return to a maximum speed threshold before performing the next glide in order to remain in a positive energy balance (Weihs, 1974). Eight parameters were measured for each stroking period (time from start of dive, stroke duration, number of strokes, mean stroke rate, mean stroke amplitude, amplitude of last fluke stroke, mean stroke speed, and speed at end of stroking period), and their influence on glide duration was tested with a Kruskal-Wallis test in order to account for their non-normal distribution (Hollander & Wolfe, 1999).
5.2.2 Measurement of drag coefficient

Drag coefficients were then determined from those animals that 1) had strongly correlated flow noise regressions ($R^2 > 0.50$), 2) had low background noise levels, 3) used predominantly ‘stroke-glide’ swimming and 4) performed Type 3 as well as Type 1 dives during some section of their tag attachment. The high correlation coefficient and low background noise levels were used as selection criteria to ensure that speed measurements from the tag data were accurate. The deceleration rate of whales during gliding periods was determined from a regression of the inverse of the speed against time over the course of the glide (Bilo & Nachtigall, 1980; Stelle et al., 2000), and the slope of this regression was used to determine a drag coefficient ($C_d$),

$$C_d = \frac{2c(M_w + M_a)}{A_w \rho_m}$$  \hspace{1cm} (5.3)

where $c$ is the slope of the regression, $M_w$ the mass of the animal, $M_a$ the additional mass of fluid attached to the animal, $A_w$ the area of the animal and $\rho_m$ the density of the fluid (1025 kg m$^{-3}$). Whale mass ($M_w$, kg) was estimated from body length ($L$, m) with the following relationship (Lockyer, 1976),

$$M_w = 0.0132L^{3.06}$$  \hspace{1cm} (5.4)

Wetted surface area ($A_w$, m$^2$) was used as the reference area in computing drag coefficients because it has been used to determine drag coefficients in several other species of marine mammal (Miller et al., 2004b; Stelle et al., 2000; Fish, 1998) and can be predicted from the above body mass estimation using the following equation (Woodward, 2006; Fish, 1993),

$$A_w = 0.08M_w^{0.65}$$  \hspace{1cm} (5.5)
Because the surface area of foraging whales increases due to their exposed baleen, the surface area of the baleen was estimated and added to the surface area predicted with Equation 5.3. A linear relationship \( R^2 = 0.67 \) between body length and mouth length \( (L_m) \) was generated from published morphometric measurements (Moore et al., 2004), and this function was used to estimate mouth length for the individuals in this study. These lengths were then used to scale the baleen surface area that was measured from a 10-m whale \( (8.70\text{m}^2) \) (Mayo et al., 2001) to the baleen surface area of larger whales.

\[
L_m = 0.303482L - 1.07283 \tag{5.6}
\]

The added mass of fluid attached to the whale \( (M_a, \text{m}^2) \) was determined as the product of the added mass coefficient \( (\alpha) \), the density of the fluid and the whale’s volume, which was approximated from body mass and the density of the surrounding water. Assuming that whales are neutrally buoyant (Bose et al., 1990; Woodward et al., 2006), the added mass is the product of the added mass coefficient and the whale mass. Although this may underestimate the body volume of this species because of their positive buoyancy (Nowacek et al., 2001, Chapter 3), right whales should be neutrally buoyant at some part of the water column, making this assumption reasonable. The added mass coefficient \( (0.06, \alpha) \) was determined by using that of a prolate ellipsoid of the same length to width ratio oriented parallel to the flow (Lamb, 1932; Vogel, 1994; Stelle et al., 2000; McHenry & Lauder, 2005).

\[
M_a = \alpha M_w \tag{5.7}
\]

Pitch was measured at one-second intervals and averaged over the glide period, and any glides with average pitches that exceeded the angular motion caused by the fluke strokes \( (\pm 10^\circ) \) were removed from the analysis. Drag coefficients were
determined from two contexts, both when animals were swimming horizontally: 1) the bottom phases of foraging dives and 2) the shallow dives made during the surface intervals of traveling dives. The ascents and descents of shallow surface dives were typically characterized by pitches greater than 15°, so they were also excluded from the analysis. Although the shallow dives made by right whales typically reach maximum depths greater than the depth where surface wave drag would act on the animal, a depth-corrected drag coefficient was determined \((C_{d_v})\) by applying a drag augmentation factor \((\gamma)\) to the drag coefficients measured from shallow dives (Fish, 1998).

\[
C_{d_v} = \frac{C_d}{\gamma}
\]  

(5.8)

The drag augmentation factor was determined from the average submersion depth \((h)\) of the whale during the glide and the body depth of the whale (Hertel, 1966). Whale body depth was determined by dividing the individual’s body length \((L)\) by the fineness ratio of a right whale \((FR = 4.5)\) (Woodward et al., 2006). Dive depths measured on the tag were corrected to the centerline of the animal’s body by adding one-half body depth to the tag’s depth measurement. For submersion depths where wave drag was no longer acting on the animal \(\left(\frac{h}{d} > 3\right)\), a drag augmentation factor of 1 was used.

\[
\gamma = 2.8136 \times \frac{h}{4.5L}^{0.89940}
\]  

(5.9)

Drag coefficients from deep foraging dives and shallow traveling dives were compared for each individual as well as all of the individuals with a nonparametric Kruskal-Wallis test because the results of a Shapiro-Wilks test showed drag coefficients differed significantly from a normal distribution \((W = 0.78, p < 0.0001)\)
Finally, the drag force \( F_{\text{drag}} \) experienced by each whale was determined from the following equation (Vogel, 1994; Alexander, 2003),

\[
F_{\text{drag}} = \frac{1}{2} \rho m A_w U^2 C_d
\]  

(5.10)

Whale speed \( U \) was determined from the average speed of the glide and the average drag coefficient for each animal, and the reference area for foraging whales was increased by the estimated surface area of baleen (Eq. 5.3).

5.3 Results

Twenty tag attachments were long enough in duration to record at least two complete dives, and of these attachments, six whales performed continuous stroking while 14 animals used a stroke-glide gait. A total of 106 dives were made by the continuous swimmers, which included 401 glides, and 186 dives with 1476 glides were made by the stroke-glide animals, demonstrating that the stroke-glide included nearly twice as many glides per dives.

5.3.1 Gait comparison

Stroke-glide swimmers performed significantly more glides per dive \( (H_{1,288} = 43.72, p < 0.0001) \) and spent a significantly lower percentage of their bottom phase actively stroking \( (H_{1,288} = 11.51, p = 0.0035) \) than continuous swimmers did (Fig. 5.2).

The number of strokes per dive, stroke amplitude, stroke rate, speed and phase duration were not significantly different between the two gaits, but stroke-glide whales used significantly deeper maximum dive depths (Table 5.1). Body length did not differ significantly between the two gaits \( (H_{1,17} = 1.89, p = 0.17) \).

The speed at the end of the stroking period was significantly greater than that at its start for stroke-glide swimmers \( (H_{1,1657} = 12.32, p < 0.0001) \) but not for
Figure 5.2: Mean percentage of dive bottom spent stroking for continuous (■) and stroke-glide (■) swimmers.

Table 5.1: Mean (SE) of parameters for continuous and stroke-glide swimmers and results of Kruskal-Wallis tests comparing stroke-glide parameters between the two locomotor gaits.

<table>
<thead>
<tr>
<th></th>
<th>continuous</th>
<th>stroke-glide</th>
<th>H</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>no. glides</td>
<td>3.76 (0.51)</td>
<td>7.99 (0.38)</td>
<td>43.72</td>
<td>1</td>
<td>0.0001</td>
</tr>
<tr>
<td>% glide</td>
<td>6.10 (0.59)</td>
<td>11.82 (0.37)</td>
<td>11.51</td>
<td>1</td>
<td>0.0035</td>
</tr>
<tr>
<td>no. strokes</td>
<td>71.27 (6.05)</td>
<td>78.03 (4.44)</td>
<td>0.81</td>
<td>1</td>
<td>0.38</td>
</tr>
<tr>
<td>stroke rate (Hz)</td>
<td>0.16 (0.0055)</td>
<td>0.16 (0.0040)</td>
<td>0.35</td>
<td>1</td>
<td>0.56</td>
</tr>
<tr>
<td>stroke amplitude (m)</td>
<td>1.85 (0.28)</td>
<td>1.97 (0.21)</td>
<td>0.13</td>
<td>1</td>
<td>0.72</td>
</tr>
<tr>
<td>stroke speed (m/s)</td>
<td>1.01 (0.11)</td>
<td>1.12 (0.08)</td>
<td>0.62</td>
<td>1</td>
<td>0.44</td>
</tr>
<tr>
<td>bottom duration (s)</td>
<td>481.13 (32.5)</td>
<td>531.29 (23.87)</td>
<td>1.55</td>
<td>1</td>
<td>0.23</td>
</tr>
<tr>
<td>maximum depth (m)</td>
<td>121.16 (7.72)</td>
<td>143.56 (5.67)</td>
<td>5.47</td>
<td>1</td>
<td>0.03</td>
</tr>
</tbody>
</table>
continuous swimmers \((H_{1,506} = -0.26, p = 0.79)\). Mean stroke speed was significantly greater than mean glide speed for both gaits \((\text{continuous} : H_{1,506} = 5.79, p < 0.0001; \text{stroke} - \text{glide} : H_{1,1496} = 29.60, p < 0.0001)\). Glide duration was significantly positively correlated with time from dive start, stroke duration, stroke end speed and the number of strokes for stroke-glide swimmers (Table 5.2). The single stroke parameter that influenced glide duration in continuous swimmers was mean stroke rate (Table 5.2).

Table 5.2: Results of Spearmans’ correlations to investigate the effect of stroking parameters on glide duration. Correlations were performed between glides and the average parameter for the preceding stroking section.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>continuous</th>
<th>stroke-glide</th>
</tr>
</thead>
<tbody>
<tr>
<td>time from dive start</td>
<td>0.81</td>
<td>19.27</td>
</tr>
<tr>
<td>stroke duration</td>
<td>0.17</td>
<td>9.89</td>
</tr>
<tr>
<td>stroke speed, mean</td>
<td>0.04</td>
<td>0.49</td>
</tr>
<tr>
<td>stroke speed, end</td>
<td>0.82</td>
<td>9.22</td>
</tr>
<tr>
<td>no. strokes</td>
<td>0.25</td>
<td>10.22</td>
</tr>
<tr>
<td>stroke rate</td>
<td>0.63</td>
<td>0.63</td>
</tr>
<tr>
<td>stroke amplitude, mean</td>
<td>0.065</td>
<td>0.39</td>
</tr>
<tr>
<td>stroke amplitude, last</td>
<td>0.092</td>
<td>1.40</td>
</tr>
</tbody>
</table>

5.3.2 Drag coefficients

Four right whales met the criteria for determining drag coefficients, and from these animals, 630 glides (316 foraging, 314 traveling) were included for analysis. Foraging dives had significantly higher drag coefficients than traveling dives despite having a significantly slower mean speed (Table 5.3). Drag coefficients differed significantly between individuals for foraging dives \((H_{3,315} = 72.90, p < 0.0001)\) but did not for traveling ones \((H_{3,313} = 7.15, p = 0.07)\). Within all four individuals, drag coefficients and the resulting drag force were significantly higher during foraging dives than during traveling ones even though whales were using similar speeds (Table 5.3). The mean drag augmentation factor used on the traveling dives was 1.48 \((\pm 0.025 \text{ SE}),\)
Table 5.3: Mean drag coefficients (±SE) for individual right whales determined from
whales during foraging and traveling behaviors. Whales are identified by their unique EgNo, which was used to obtain age and estimate length. Drag coefficients are
referenced to wetted surface area, which was determined from the mass of individual
whales and accounts for the increase in surface area due to exposed baleen. Drag coefficients from traveling whales were corrected for depth to account for any increased
drag due to wave drag effects.

<table>
<thead>
<tr>
<th>whale</th>
<th>age(years)</th>
<th>length(m)</th>
<th>n</th>
<th>( C_d )</th>
<th>( U(\text{m} \cdot \text{s}^{-1}) )</th>
<th>( F_{\text{drag}}(N) )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>foraging</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2753</td>
<td>8</td>
<td>13</td>
<td>33</td>
<td>0.0099 (0.0007)</td>
<td>0.95 (0.02)</td>
<td>292.92 (7.05)</td>
</tr>
<tr>
<td>3142</td>
<td>4</td>
<td>11.5</td>
<td>99</td>
<td>0.012 (0.0009)</td>
<td>1.02 (0.014)</td>
<td>436.50 (120.06)</td>
</tr>
<tr>
<td>3208</td>
<td>3</td>
<td>11</td>
<td>89</td>
<td>0.024 (0.001)</td>
<td>0.91 (0.02)</td>
<td>624.27 (23.46)</td>
</tr>
<tr>
<td>3323</td>
<td>2</td>
<td>10</td>
<td>95</td>
<td>0.0091 (0.0006)</td>
<td>1.06 (0.02)</td>
<td>268.98 (8.53)</td>
</tr>
<tr>
<td>all</td>
<td>–</td>
<td>–</td>
<td>316</td>
<td>0.014 (0.0006)</td>
<td>0.99 (0.009)</td>
<td>424.03 (11.37)</td>
</tr>
<tr>
<td></td>
<td>traveling</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2753</td>
<td>8</td>
<td>13</td>
<td>43</td>
<td>0.0036 (0.0003)</td>
<td>1.00 (0.03)</td>
<td>135.70 (8.38)</td>
</tr>
<tr>
<td>3142</td>
<td>4</td>
<td>11.5</td>
<td>12</td>
<td>0.0038 (0.0004)</td>
<td>1.07 (0.10)</td>
<td>134.79 (23.89)</td>
</tr>
<tr>
<td>3208</td>
<td>3</td>
<td>11</td>
<td>94</td>
<td>0.0049 (0.0004)</td>
<td>1.08 (0.04)</td>
<td>165.75 (13.06)</td>
</tr>
<tr>
<td>3323</td>
<td>2</td>
<td>10</td>
<td>165</td>
<td>0.0059 (0.0004)</td>
<td>0.90 (0.02)</td>
<td>111.25 (5.00)</td>
</tr>
<tr>
<td>all</td>
<td>–</td>
<td>–</td>
<td>314</td>
<td>0.0052 (0.0003)</td>
<td>0.97 (0.018)</td>
<td>131.81 (5.09)</td>
</tr>
</tbody>
</table>

suggesting that the majority of traveling dives encountered very little additional drag
due to wave drag near the surface (see Chapter 4).

5.4 Discussion

Individual variation appears to exist in the locomotor gaits of right whales, similar
to studies of bowhead whales, bottlenose dolphins, elephant seals and Baikal seals.
Energetic savings from stroke-glide swimming do not appear to be used to prolong
the amount of time available for foraging at depth, as animals that used intermittent
swimming did not have longer bottom phase durations than those that fluked continu-
ously. The stroke-glide gait in this species doubled the amount of time spent gliding
during the bottom phases of foraging dives, which would yield even higher advan-
tages for the high drag context of filter feeding. Active locomotion causes a threefold
increase in drag from a gliding or towed animal (Fish et al., 1988; Lighthill, 1971;
Table 5.4: Results of Kruskal-Wallis tests used to compare drag parameters between behaviors within individual right whales. Whales are identified by their unique EgNo, which was used to obtain age and estimate length.

<table>
<thead>
<tr>
<th></th>
<th>Cd</th>
<th></th>
<th>U</th>
<th></th>
<th>F_{drag}</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>H</td>
<td>df</td>
<td>p</td>
<td>H</td>
<td>df</td>
<td>p</td>
</tr>
<tr>
<td>2753</td>
<td>37.14</td>
<td>1</td>
<td>&lt;0.0001</td>
<td>2.55</td>
<td>1</td>
<td>0.11</td>
</tr>
<tr>
<td>3142</td>
<td>13.58</td>
<td>1</td>
<td>&lt;0.0001</td>
<td>0.004</td>
<td>1</td>
<td>0.95</td>
</tr>
<tr>
<td>3208</td>
<td>107.82</td>
<td>1</td>
<td>&lt;0.0001</td>
<td>2.84</td>
<td>1</td>
<td>0.09</td>
</tr>
<tr>
<td>3323</td>
<td>23.12</td>
<td>1</td>
<td>&lt;0.0001</td>
<td>25.49</td>
<td>1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>all</td>
<td>173.86</td>
<td>1</td>
<td>&lt;0.0001</td>
<td>9.00</td>
<td>1</td>
<td>0.003</td>
</tr>
</tbody>
</table>

Ribak et al., 2005; Williams & Kooyman, 1985), so the combination of increased drag from the filter-feeding apparatus with the drag related to active locomotion would drastically increase the drag on filter-feeding cetaceans such as right and bowhead whales. By gliding, these animals limit the increase in drag to only that related to foraging, which these whales likely also have anatomical adaptations to reduce (Werth, 2004; Lambertsen et al., 2005). Because right whales must consume large amounts of their prey to meet their projected energy requirements and, ideally, exceed them to store energy for migration and reproduction (Baumgartner et al., 2007; Kenney et al., 1986), any methods of spending less energy while still consuming prey should be advantageous. In addition, the difference in maximum depth between stroke-glide and continuous swimming (Table 5.1) suggests that those whales that save energy on bottom phase swimming may use it on accessing deeper regions of the water column, where their prey may be aggregated by the bottom mixed layer (Baumgartner & Mate, 2003).

Since the amount of a bottom phase that animals spent gliding instead of stroking should increase the net energetic gain from each dive, the ability to glide for longer should be beneficial. Glide duration was related to the number of strokes in the preceding stroke period, the stroke rate, the stroke end speed and the time from the start of the dive, suggesting that an increase in the swimming effort does result
Figure 5.3: Mean $C_d$ for traveling (■) and foraging (□) animals estimated from horizontal glides recorded on the tags in longer glides. The balance between extra effort before a glide and the energetic savings during a glide suggests that the energetic savings during the glide outweigh the additional effort, resulting in a net positive savings. The occurrence of longer glides towards the end of a foraging dive suggests that whales may be reaching their dive limit and decreasing their energy usage in order to continue foraging before they need to surface. The lack of any relationship between swimming effort and glide duration in the continuously stroking animals suggests that such glides are used opportunistically and do not necessarily contribute an energetic advantage.

Finally, these results provide the first direct evidence that filter-feeding increases the cost of locomotion in right whales despite their anatomical adaptations to reduce drag during feeding. The drag coefficients measured from animals traveling near the surface were less than those measured from the same individuals during the bottom phases of foraging dives, when whales are thought to be foraging. Because traveling
animals make shallow dives to depth below the wave drag layer at the surface, this increase in drag is not due to a difference in where the whales are in the water column, results which were supported by the low drag augmentation factor (Chapter 4). Some variation in drag coefficient between individuals occurred, but only in the coefficient for foraging dives. As visual confirmation of foraging behaviors was impossible, some traveling while at depth could be possible, which would influence the resulting average drag coefficient for assumed foraging behaviors.

The drag coefficients measured for traveling right whales are comparable with those determined for other cetacean species, which range from 0.0026 for killer whales to 0.012 in belugas (Fish, 1998). Amongst the large whales, right whales had average drag coefficients that were lower than that of gray whales and similar to that of sperm whales (Miller et al., 2004b; Sumich, 1983), which match the predictions for swimming efficiency based on body shape and ecological niche. Right whales perform deeper dives and have a higher fineness ratios (ratio of body length to width) in comparison with gray whales (Woodward, 2006; Woodward et al., 2006), which would suggest a stronger selection pressure for a lower drag form. In comparison to other species with a similar fineness ratio, the drag coefficients from these whales are similar and are roughly similar to turbulent flow over a flat plate at an equivalent Reynolds number (Vogel, 1994; Stelle et al., 2000; Miller et al., 2004b).

The cost of locomotion and foraging in the two families of mysticete cetacean has been hypothesized to be drastically different based on the differences in body shape and prey type between the two. Species in the family Balaenopteridae have higher fineness ratio bodies, have higher maximum swim speeds and feed on larger, more mobile prey than those of the Balaenidae (Woodward et al., 2006; Ford & Reeves, 2008; Harper & Blake, 1988). The drag coefficients found for Balaenopterid species during traveling behaviors are lower than those determined here but higher during foraging. Because drag is a major component in expanding the buccal cavity of these
whales during lunge-feeding and the animal’s shape is no longer streamlined during
the lunge events, a higher drag coefficient occurs (Goldbogen et al., 2007, 2006).
These results support the prior predictions that despite the higher minimum cost of
locomotion for balaenid whales, the lunge-feeding technique used by balaenopterids is
more expensive than the ram suspension feeding one used by balaenids. This relative
cost also reflects the duration of foraging activities in the two families; balaenid
whales spend a large proportion of their time foraging, while active prey capture
occurs in discrete lunge events for the rorqual whales. The relative difference in prey
quality must account for both the difference in the amount of prey captured and the
amount of time spent capturing prey. In addition, this relative difference in foraging
costs supports the difference in dive time between the two major types of mysticete.
Balaenopterid whales use significantly shorter dive times than expected for their body
size, while bowhead whales were found to use dive times that were much closer to the
duration expected for their mass, although still below what is expected according to
the allometric relationship (Schreer & Kovacs, 1997). Therefore, filter feeding does
increase the cost of locomotion for these whales.

These initial measurements of drag from North Atlantic right whales refute the
historical notion that right whales are inherently slow swimmers and have a high
cost of locomotion. In order to improve these results, better measurements of speed
are necessary. These drag coefficients are based on swimming speeds measured from
flow noise recorded on the Dtag’s hydrophone, and the acoustic environment that
North Atlantic right whales live in is both noisy and variable. In addition, the
animal’s fluke strokes also produced noticeable variation in the speed measurements,
introducing some variation into the speeds measured during active swimming. Speed
regressions are only possible from animals that make highly pitched descents during
some portion of their tag attachment, limiting this analysis to animals making deep
foraging dives in the Bay of Fundy. Right whales in other habitats such as Cape
Cod Bay, their springtime foraging ground, and the nearshore waters of the South Atlantic Bight, their winter calving ground, seldomly exceed a pitch of 20°, so speed measurements and the resulting drag coefficients must be determined with a different method or technology.

Finally, drag coefficients were only obtained from juvenile animals within this dataset. Validation of the occurrence of foraging would also help to improve these results. For this study, stereotyped dive shapes were used to identify when whales were foraging, but behaviors can occur at a higher resolution than can be sampled with this method (Simpkins et al., 2001). Therefore, additional methodology to document the occurrence of foraging synchronized with orientation or movement parameters would improve these results. Regardless, these results provide strong initial evidence for both the cost of foraging and swimming in this species of ram filter-feeding cetacean.
6.1 Introduction

Animals use energy to accomplish a variety of biological processes, including thermoregulation, metabolism, digestion and reproduction, and therefore must consume enough energy in the form of food to at least meet these costs. In order to grow and reproduce, their energy consumption must exceed those costs, leaving an energy surplus. For mobile, carnivorous predators that feed on mobile prey, some energy must also be devoted to pursuing and capturing their prey. However, the amount of energy needed to consume prey is not solely controlled by the locomotor costs of the predator. The prey’s spatial distribution influences the cost of searching for prey, and these costs present a complete energy deficit because no energy gain occurs when moving between prey patches. Because the spatial aggregations of planktonic prey are highly variable due to their dependence on both small- and large-scale oceanographic processes (Würsig et al., 1984; Baumgartner et al., 2003; Johnston et al., 2005), predators should have an energetic buffer to allow for increases in searching
behaviors. Should prey abundance decrease enough to exceed this buffer, the energy available for other processes such as maintaining body heat and reproducing may then be affected (Wallace et al., 2006). In order to estimate the extent of this buffer for a certain species, the overall locomotor costs must be established, specifically in relation to key biological needs that likely change those costs such as consuming prey and reproducing.

Filter feeding is a strategy that relies on a large difference in size between predator and prey to maximize the amount of prey consumed for the same foraging effort and minimize the prey’s ability to escape the predator (Webb & de Buffrénil, 1990; Harper & Blake, 1988). Large marine filter feeders such as mysticete cetaceans and whale and basking sharks have evolved considerable morphological adaptations to filter feed. Within mysticetes, two styles of ram filtration are used, each requiring specific morphological and behavioral adaptations. Balaenopterid whales use an intermittent ram filtration method, where animals make frequent yet brief lunges to engulf volumes of water. This family has evolved a massive, expandable oral cavity that, in consort with active forward accelerations or ‘lunges’, allow a larger volume of water to be pulled into the mouth, yielding the consumption of higher quality, larger prey (e.g. herring, sandlance, krill) at a higher cost of movement (Goldbogen et al., 2007; Lambertsen, 1983). The other method, ram filter feeding, passively draws water and prey through a static mouth structure by the animal’s forward motion and is found in balaenid whales and basking sharks (Werth, 2004; Sims, 2008). Interestingly, whale sharks appear to use both ram filter feeding and suction filter feeding, possibly to allow them to exploit different habitat-specific prey aggregations (Nelson & Eckert, 2007; Motta et al., 2010).

Continuous ram filter feeding in balaenid whales has been thought to be less costly than the lunge-feeding method of balaenopterid whales due to the rapid accelerations and high drag forces inherent in expansion of the ventral pouch (Acevedo-
Gutiérrez et al., 2002; Goldbogen et al., 2007). The anatomical adaptations of balaenid cetaceans suggest increased cost is related to the increase in surface area caused by the filtration appuratus, and the low aspect ratio shape of the flukes (i.e. their propulsive hydrofoils) strongly suggests that these whales require considerable amounts of thrust when swimming, presumably to compensate for additional drag when feeding (Woodward et al., 2006). Differences in dive duration also suggest that the balaenopterid mysticetes consume their oxygen stores more quickly that their balaenid counterparts (Acevedo-Gutiérrez et al., 2002; Croll et al., 2001). The larger number of balaenopterid species (10 species) in comparison with the four balaenids has been suggested to indicate that the lunge-feeding strategy is more evolutionarily successful; while it costs more, the energetic gain from lunge-feeding is higher and therefore these whales have been able to access more ecological niches (Goldbogen et al., 2007). However, quantitative comparisons between the forces involved in both locomotion and the cost of the two foraging techniques have not been made.

In addition to the costs of foraging, migration can constitute a major portion of the energy requirements of animals. Both otariid pinnipeds and mysticete cetaceans forage for a portion of the year in highly productive areas of the ocean, storing up energy in the form of blubber, and then migrate to different areas while fasting to give birth and nourish their offspring. For diving animals, increased fat storage increases positive buoyancy, which then requires more energy to overcome when diving (Biuw et al., 2003). Factors other than additional fat storage also affect the cost of migration. Andogenous fishes migrate upstream against the river’s current to spawn, which can require 60-70% of their energy reserves prior to migration (Jonsson et al., 1997). Abdominal distension in female grey whales during migration decreases their fineness ratio and appears to increase their drag during migrations (Perryman & Lynn, 2002). Therefore, in order to understand the locomotor costs necessary for population-level survival, the additional locomotor costs related to migration should
also be estimated.

Estimating the cost of locomotion can be accomplished by quantifying the drag forces acting on an animal, because motion at a constant speed requires forward thrust to be equal to the resistive drag (Vogel, 1994; Alexander, 2003). Estimates of the drag of marine mammals have been obtained from dataloggers attached to gliding animals (Miller et al., 2004b; Biuw et al., 2003) or from trained animals (Stelle et al., 2000; Fish, 1998; Lang & Pryor, 1966), but these methods do not allow the drag of specific behaviors to be estimated. Dive profiles can help to infer behaviors (Chapter 2), but many behaviors occur on shorter timescales than that of entire dives (Simpkins et al., 2001). Therefore, the use of a method such as computational fluid dynamics (CFD) to examine the effects of artificial manipulations of shape and orientation on the hydrodynamic forces is necessary. CFD has allowed many theoretical and applied aspects of biological locomotion to be investigated. Adding the body undulations of one type of fish to the morphology of another allowed the effect of these normally inseparable aspects of fish locomotion to be explored independently (Tytell et al., 2010). Similarly, the effect that dorsal fin position has on swimming ability in one species of fish was explored with this method by positioning the fin in different places on a model geometry of a fish and observing the change in propulsive forces in the resultant flow (Tian-jiang et al., 2006). Other interesting theoretical applications of CFD modeling to biology have been determining whether giraffes can swim and whether pterosaurs were skimfeeders (Henderson & Naish, 2010; Humphries et al., 2007). Practical applications of this technique have included investigating the size, shape and attachment location of dataloggers on marine mammals, as well as differences in the lift and drag forces caused by different cetacean flipper shapes (Pavlov et al., 2007; Hazekamp et al., 2009; Weber et al., 2009).

In this study, the drag forces related to the body shape and kinematics of North Atlantic right whales were explored via two CFD approaches to understand the
relative cost of locomotion during three different behaviors in this species. Morphologically accurate whale geometries were developed by combining measurements of right whales from three sources: 1) necropsy reports of stranded animals, 2) aerial photogrammetry and 3) digital photographs of individually identified live animals at sea. Three model geometries were developed: 1) a traveling whale to estimate the minimum amount of drag experienced, 2) a foraging whale to estimate the drag related to ram suspension feeding in this species and 3) a pregnant whale. Two different numerical methods were used to estimate the movement of fluids around these geometries, and the drag forces and corresponding drag coefficients were calculated from the solutions of those methods. Finally, the drag forces estimated from these methods and those determined from tags attached to free-ranging animals were used in a series of scenarios to relate changes in behavior to changes in the energetic profits of foraging.

6.2 Methods

6.2.1 Development of whale geometries

Three-dimensional right whale geometry was constructed in LightWave 3D (NewTek, Inc., 2010) by Bellucci Designs (Bellucci, 2007) and modified according to measurements of right whales to form a morphometrically accurate, three-dimensional computer representation of a North Atlantic right whale. Several additional geometries were created by adapting that basic whale in Blender 2.49 (Blender Foundation, 2010) to represent additional behavioral stages that could influence drag. Three-dimensional laser scanners and computed tomography (CT) scans have been used to create accurate geometries for CFD studies (Weber et al., 2009; Tsukrov et al., 2009; Field et al., 2010), but this technique can not be used with completely submerged animals. Considerable distortion of body shape due to gravity occurs to whales after stranding, and the difficulties in manipulating carcasses for scanning limit quantita-
tive measurements of the geometric proportions of right whales to two-dimensional measurements. Measurements were obtained from necropsy reports of dead whales in the North Atlantic Right Whale database (Right Whale Consortium, 2007c; Moore et al., 2004), aerial photogrammetry (Perryman & Lynn, 2002) and high-resolution digital photographs from the North Atlantic Right Whale Catalogue (Right Whale Consortium, 2007b). All measurements were applied to the initial whale geometry to create an accurate, static three-dimensional right whale geometry of a whale in a neutral gliding position (Fig. 6.1A–6.2A).

This geometry was then modified to create two additional whale geometries representative of behavioral states that may influence on locomotor cost in this species. First, an open mouth geometry was created to represent the morphological changes associated with ram filtration foraging (R. McGregor, pers. comm.). Baleen plates were shaped individually and then arranged in the upper jaw of the basic geometry according to previously published measurements and photographs of stranded animals (Lambertsen et al., 2005; Werth, 2004; Omura et al., 1969). The sides of the anterior end of the lower jaw were flexed outward to create the large scoop shape of the mouth opening (Baumgartner et al., 2007), and a tongue was constructed from a combination of Lambertsen et al. (2005)’s measurements of bowhead whales with digital photographs of right whale mouth cavities and added to the lower jaw (McGregor, unpublished data). Next, the basic whale was modified according to the body shape changes experienced during pregnancy (R. McGregor, pers. comm.). Pregnant females undergo significant increases in body width from 30-70% of their total body length, and sufficient alterations to the basic geometry were made with aerial photogrammetric measurements and blubber thickness data of whales in their foraging ground six months prior to parturition (Miller Angell, 2006; Right Whale Consortium, 2007a).
Figure 6.1: Lateral view of right whale model geometries developed for use in a CFD algorithm to investigate the locomotor costs of whales during three behaviors: traveling (A), foraging (B), and pregnant (C). The traveling model was modified to account for swimming with an open mouth in the foraging whale and abdominal distension to reflect pregnancy in the migrating whale.
Figure 6.2: Anterodorsal view of right whale model geometries developed for use in a CFD algorithm to investigate locomotor costs of whales during three behaviors: traveling (A), foraging (B), and pregnant (C). The traveling model was modified to account for swimming with an open mouth in the foraging whale and abdominal distension to reflect pregnancy in the migrating whale. Apparent larger size of foraging model is related to the open mouth causing the head area to seem larger, and the differences in shading in the peduncle region are an artifact of lighting in the mouth cavity.

6.2.2 Fluid dynamic modeling

Two finite volume CFD approaches were used to model the flow of water around these geometries and determine the overall drag force of each geometry. The first, a coupled level-set volume of fluid (CLSVOF) method, used a Cartesian mesh that incorporated adaptive mesh refinement (AMR) techniques to increase the resolution of the flow solver in complex regions of the geometries (Sussman, 2005; Sussman et al., 2007), such as the intraoral cavity of the foraging whale. Although this flow solver allows for two-phase flow, all models were run in a completely submerged stage to simulate whales moving at depth. A no-slip boundary condition was used, along with direct numerical simulation (DNS). No turbulence models were used. The grid
resolution was tested for convergence, and a computational domain of \(1024 \times 256 \times 512\) cells was used as the relative drag between models no longer was affected by grid resolution. This grid size allowed for the solution of flow down to Reynolds numbers of 1000, which enabled the viscous drag component as well as the overall pressure drag to be solved. In order to avoid the inclusion of the effects of differences in the two codes, this code was used to compare the relative drag between models, not the absolute forces involved.

Because the grid resolution of the first code was not predicted by Kolmorgov’s turbulence theory (Kolmogorov, 1941, 1962) to be fine enough to fully resolve turbulence in the range of high Reynolds numbers encountered by a whale, a second commercial CFD package that incorporated a turbulence model was used to determine an absolute value of the drag on the traveling whale geometry. This code was run in Solidworks (Dassault Systèmes SolidWorks Corporation, 2009) and included a k-\(\varepsilon\) turbulence model and computational domain of \(20 \times 50 \times 20\) meters. Only the traveling model was run in this code due to the complexity of the open mouth geometry. However, this code was used to determine an absolute value for the drag forces generated by whales during this behavior.

The resultant forces in the y-dimension were scaled by the wetted surface area and velocity of the fluid used in the models to form the dimensionless drag coefficient \((C_d)\) with the following equation,

\[
C_d = \frac{F}{0.5\rho U^2 A}
\]  

(6.1)

where \(F\) represents the drag force, \(\rho_m\) the density of the surrounding fluid, \(U\) the animal’s speed and \(A\) the animal’s wetted surface area as estimated from body length. The surface area of the models was changed according to the model. For foraging models, the surface area was increased by 15.43m\(^2\), which is the area of the
baleen (Mayo et al., 2001), and for pregnant models, the surface area was increased by 5% of the surface area of a traveling whale (R. McGregor, unpublished data). The drag for each model was determined for speeds from 0–15 ms\(^{-1}\) with the following equation (Vogel, 1994),

\[ F = \frac{1}{2} C_d \rho AU^2 \]  

(6.2)

Since the thrust required to move should be equal to the drag for an object moving at constant speed, the power \((P)\) needed to swim for each of the models for speeds of 0–15 ms\(^{-1}\) should be

\[ P = FU = \frac{1}{2} C_d \rho U^3 A \]  

(6.3)

### 6.2.3 Energy profit models

Right whales in the Bay of Fundy perform three stereotypical dive patterns, each of which appears to be related to a different behavior (Baumgartner & Mate, 2003, Chapter 2). The overall behavioral pattern used by whales in this habitat will trade off three variables: 1) energy used to move, 2) energy gained by foraging and 3) distance covered. A simple model was developed to explore the effects of different behavioral budgets on these three factors. This model was then adjusted to determine the effects of reduced energy densities over the course of a season that could potentially be caused by reductions in the abundance of their prey.

Locomotor costs, or energy loss \((E_L, J)\), for each dive type were determined by summing the costs of the four dive phases,

\[ E_L = E_b + E_a + E_s + E_d \]  

(6.4)

where costs of bottom \((E_b)\), ascent \((E_a)\) and surface \((E_s)\) phases were estimated
by multiplying the drag (N) of the predominant behavior (foraging $F_f$; traveling $F_t$, Table 5.3) by the average duration (s) and speed ($U$, ms$^{-1}$) of that phase for that dive type (bottom $T_b, U_b$; ascent $T_a, U_a$; SI $T_s, U_s$, Tables 2.2, 2.4).

$$E_b = F_f \times T_b \times U_b$$  
(6.5)

$$E_a = F_t \times T_a \times U_a$$  
(6.6)

$$E_s = F_t \times T_s \times U_s$$  
(6.7)

The cost of ascent was estimated to be equal to the cost of horizontal swimming, assuming no savings from the effects of positive buoyancy because this force varies between individual whales. Although movement near the surface can increase the drag experienced by an animal, right whales appear to avoid the region of the water column where this phenomenon exists (Chapter 4). Therefore, no additional correction for surface wave drag was included in the term relating to the drag force during surface intervals. No correction for stroke-and-glide swimming was included because the factors that influence the occurrence of this behavior are not well understood (Chapter 5). Descent costs ($E_d$) were determined from Equation 2.10 in Sato et al. (2009) in order to account for the costs of overcoming buoyancy on descent,

$$E_d = 10A_0\rho_m g \left(\ln \frac{p_w}{10} + 1\right) + \left\{ \left(\frac{\rho_m}{\rho_t} - 1\right) M_w g - \frac{\rho_m \lambda C_d A_w U^2}{2 \sin \theta} \right\} p_w$$  
(6.8)

where $A_0$ represents the volume of air-filled tissues at 1 atm (5.26 m$^3$), $\rho_m$ the density of seawater (1026 kg m$^{-3}$), $g$ the gravitational acceleration constant (9.81 ms$^{-2}$), $\rho_t$ the density of the whale’s tissues (1030 kg m$^{-3}$), $M_w$ the animal’s mass (52,049 kg, Eq. 5.4), $\lambda$ the increase in drag related to active locomotion (3), $C_d$ the
drag coefficient \((0.0052, \text{Table } 5.3)\), \(A_w\) the animal’s wetted surface area \((93.48 \text{ m}^2, \text{Eq. 5.5})\), \(U_d\) the average descent speed (Chapter 2), \(\theta\) the average pitch angle during descents (Table 2.4), and \(p_w\) the average vertical distance traveled during descents (Table 2.2). Tissue buoyancy was estimated using that determined for a sperm whale (Miller et al., 2004b), and the volume of air-filled tissues from an allometric relationship based on animal mass (Piscitelli et al., 2010; Kooyman, 1973). Animal body mass and surface area were estimated for a 15-m right whale (Chapter 5). Speed, pitch angle and distance traveled were averaged within each dive type.

Energy gain per dive \((E_G, J)\) was determined for each dive type by multiplying the average speed and duration of whales during bottom phases of their dives (Tables 2.2, 2.4) by the average prey ingestion rate \((I, W)\) for whales in the Bay of Fundy,

\[
E_G = U_b \times T_b \times I
\]  

(6.9)

Prey ingestion rate was determined from Equation 1 in (Baumgartner & Mate, 2003),

\[
I = A_g U_b T_b E_{CS5} \rho_C
\]  

(6.10)

where \(A_g\) is the area of the mouth gape \((1.21 \text{ m}^2)\) (Mayo et al., 2001), \(E_{CS5}\) the caloric content of a single stage 5 \textit{Calanus} copepod \((6.78 \text{ J copepod}^{-1})\) (Comita et al., 1966), and \(\rho_C\) the average prey density of \textit{Calanus} in this habitat \((6618 \text{ copepods m}^{-1})\) (Baumgartner & Mate, 2003). Energy surplus \((E_S, J)\) was then determined to be the difference between energy loss and gain,

\[
E_S = E_G - E_L
\]  

(6.11)

This equation was then used in four behavioral scenarios and two prey availability
ones that explored the effects of behavioral changes on energy surplus. For all of these scenarios, the total number of dives made by right whales over the course of a four-month foraging season in the Bay of Fundy was held constant at 10,000 dives and the proportion of those dives of each dive type varied,

\[ E_S = 10000((iE_{G1} + jE_{G2}) - (iE_{L1} + jE_{L2} + kE_{L3})) \]  \hspace{1cm} (6.12)

where \( E_L \) and \( E_G \) show the energy losses and gains for each dive type (Type 1–3) and \( i, j \) and \( k \) are the percentage of dives of each type. The percentage of Type 1 foraging dives \( (i, \text{ Chapter 2}) \) was decreased at a constant rate of 10% intervals, while the increase in the percentage of Type 2 searching \( (j) \) and Type 3 traveling dives \( (k) \) varied according to the scenario. The first ‘even’ scenario consisted of an equal increase in the percentage of searching and traveling dives \( (j = k) \). Next, an ‘increased searching’ scenario was performed following the assumption that as high quality foraging opportunities disappear, whales will begin to forage on lower quality patches and increase their searching-type dives, resulting in a disproportionate increase in the amount of searching dives. Once again, the foraging dive frequency was decreased by 10% per iteration, but the percentage of searching dives was increased by four times the increase in traveling \( (j = 4k) \). The third scenario, ‘increased traveling’, modeled the effects of a disproportionate increase in the amount of traveling dives for each 10% reduction in foraging dives \( (4j = k) \). This scenario would reflect whales still accessing high quality prey patches even though they are much more distant. Finally, a fourth scenario was similar to the even scenario with the exception of an additional term to account for the costs of migration.

\[ E_{SM} = 10000 \left( (iE_{G1} + jE_{G2}) - \left( iE_{L1} + jE_{L2} + kE_{L3} + \frac{D_M \lambda F_\phi}{\phi} \right) \right) \]  \hspace{1cm} (6.13)
This additional term multiplies the approximate two-way distance of migration ($D_M$, 4500 km) (Winn et al., 1986), the drag experienced by a pregnant whale ($F_p$, Chapter 5) and the increase in drag due to active propulsion (Webb, 1975) and divides the result by the number of years between calves ($\phi$, 3) (Kraus et al., 2001), assuming that whales only migrate in years that they give birth.

Two prey abundance scenarios were then performed to place the effects of the above behavioral shifts in the context of the effects of changes in prey density. In these scenarios, the energy losses in the ‘even’ scenario were held constant at those in the ‘even’ scenario and the gains term adjusted. For the first scenario, the prey ingestion rate was decreased by 1% intervals and 2% intervals in the second scenario.

6.3 Results

6.3.1 Drag estimates

The drag coefficient of the traveling whale measured in the SolidWorks algorithm was very close to that measured from the tag during foraging but higher than that during traveling (Table 6.1). Between models, the CLVSOF algorithm found the pressure drag to be highest for the foraging whale, and less for the pregnant and traveling animals which were very similar (Fig. 6.3). Additionally, the viscous drag was highest for the pregnant model, intermediate for the foraging model and lowest for the traveling one (Fig. 6.4). Assuming that the viscous drag contributes 25% of the overall drag, the increase in drag related to pregnancy would be approximately 3–4%.

According to the drag coefficients determined with tag data, the drag experienced by whales during foraging and traveling was reasonably similar for speeds between 0 and 2m$^{-1}$ (Fig. 6.7). At speeds above approximately 2m$^{-1}$, the drag of the two behaviors diverged considerably. The drag predictions for pregnant whales showed very little difference in drag from the traveling models. However, the power required
to move remained similar between foraging and traveling animals until a speed of about 5ms\(^{-1}\) (Fig. 6.8). Similar to the drag forces, the difference in power between pregnant and traveling animals was similar across all speeds.

Table 6.1: Absolute drag forces measured for the traveling right whale geometry in the Solidworks code and the drag predicted from the drag coefficients determined with the tags. Resulting drag coefficients were referenced to wetted surface area.

<table>
<thead>
<tr>
<th></th>
<th>SolidWorks</th>
<th>Tag data</th>
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<tbody>
<tr>
<td></td>
<td>F</td>
<td>U</td>
</tr>
<tr>
<td>normal</td>
<td>114.67</td>
<td>0.514</td>
</tr>
<tr>
<td>open mouth</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>pregnant</td>
<td>—</td>
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</tr>
</tbody>
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6.3.2 Model scenarios

The cost of Type 3 dives was the highest of the three dive types with no energy profit because no foraging occurs during this type. Type 2 dives had the lowest cost of the three types and had less energetic gain than Type 1 dives (Fig. 6.6). Type 1 dives had higher costs than Type 2 dives but also had larger gains, resulting in the highest profit. For Type 1 dives, 8.8% of the energy consumed was spent on locomotor costs, while for Type 2 dives, 13.6% of the energy consumed went to locomotor costs. Extrapolating these costs and gains to the course of a foraging season and assuming the behavioral frequencies recorded on the tag are representative of the entire season produced an overall energy loss of 3.56 \(\times\) 10\(^7\) kJ and an energy gain of 3.64 \(\times\) 10\(^8\) kJ, which constituted approximately 9.78% of the energy gained over the time period. Regardless of behavior, horizontal swimming constituted the largest portion of locomotor costs of each dive, while the costs related to descending were the next largest (Fig. 6.5). The ascent phase had the lowest costs of any dive phase.

Increases in the time spent traveling resulted in lower energy surplus but a larger distance covered for the same decrease in time spent foraging (Fig. 6.9). A higher increase in searching behaviors resulted in higher surplus but less distance covered.
for the same decrease in time spent foraging. The ratio of searching to traveling behaviors recorded on the tag resulted in the highest surplus and the most distance traveled. Finally, the only behavioral patterns that resulted in negative surpluses were those with > 92% decrease in foraging and > 83% increase in traveling.

6.4 Discussion

6.4.1 Drag and costs

These results suggest that the costs of foraging are higher than those of traveling, even though these whales possess morphological adaptations that reduce drag during
Figure 6.4: Relative viscous drag component for traveling (---), foraging (-----) and pregnant (---) whale geometries run at two finest levels of grid resolution (fine ---, coarse --). Truncated lines indicate abbreviated simulation runs. Courtesy M. Sussman.

Figure 6.5: Percentage of total locomotor costs contributed by descent (■), ascent (■) and horizontal (■) dive phases for each Type 1 (A), Type 2 (B) and Type 3 (C) dive.
Figure 6.6: Estimates of total locomotor costs (■), energetic gains (■) and the difference between the losses and gains (surplus) (■) for a single dive of each dive type. Costs were determined from tag drag coefficients for a 15-m right whale moving at the average speed for each dive type, and gains were determined from an average prey density in the Bay of Fundy (6618 copepods m\(^{-1}\)).

Filter feeding (Lambertsen et al., 2005; Werth, 2004). A high cost to ram suspension feeding would also match the observations that these whales are extremely powerful and have evolved large propulsors, as they must rely on their muscular effort to overcome drag forces inherent in their feeding method (Woodward et al., 2006; Johnson et al., 2007). Even though ram feeding still increases the drag experienced by a right whale, these forces are still less than those required in engulfment feeding (Goldbogen et al., 2007). Referenced to wetted surface area using the conversion method in Vogel (1994), the maximum drag coefficient of a foraging fin whale measured mid-lunge was approximately 0.19 (Goldbogen et al., 2007). Drag during the lunge has been predicted to be an order of magnitude higher than that during steady state...
swimming, which was estimated at 0.012 and 0.006 in two different studies (Goldbogen et al., 2007; Bose & Lien, 1989). In comparison, ram filter feeding appears to only double the drag (Table 6.1).

The relative increase in drag and power across different speeds also demonstrates the effects of cost increases related to different behaviors. Whales typically feed at speeds between 0.8 and 1.5 ms$^{-1}$, and the increase in drag over that of swimming is not very large at these speeds (Mayo & Marx, 1990; Winn et al., 1995; Baumgartner & Mate, 2003; Baumgartner et al., 2007). Once speeds exceed this range, foraging becomes exponentially more expensive. The power required to move also matches
Figure 6.8: Estimated power requirements as determined from drag coefficients for right whales during traveling (---), foraging (-----) and pregnant (----) contexts. Power was estimated for traveling animals with both CFD modeling (----) and archival tags (-----), while power for foraging animals was only determined from the tags. Power for pregnant animals was determined from the drag coefficients of traveling animals and an increased wetted surface area.

The speeds observed in free-ranging animals. The highest speed observed from a foraging whale was between 4 and 4.5 ms\(^{-1}\) (Hamner et al., 1988), at which point the difference in power required by foraging and traveling increases considerably.

Pregnancy does appear to increase locomotor costs in this species, resulting in a potential 3–4% increase in drag due to pregnancy. This increase is entirely related to an increase in the viscous drag, with negligible differences in pressure drag. Body shape changes can be observed in whales at the foraging grounds six months prior to parturition when females are still foraging (Miller Angell, 2006). Increases in drag related to abdominal distension would compound the increased drag of foraging and
Figure 6.9: Effects of decreased foraging and prey declines on energy profits after locomotor costs were subtracted from energy consumed. Decreased foraging was compensated for with four models of behavioral shifts, an even increase in the number of searching and traveling dives (---), a substantial increase in the number of searching dives (---), a substantial increase in the number of traveling dives (---) or an even increase in the number of searching to traveling dives including the locomotor costs of migration (---). Two additional models of prey decline were applied to the even increase model, a 1% decrease in prey density (---) and a 2% decrease in prey density (---).

fluking and therefore could present 24-fold increase in the overall drag measured from a gliding traveling animal. The consequences of losing energy to drag at this point in their physiological timelines may be high enough to exert selection pressure to make morphological changes that do not alter drag, such as abdominal distension that does not alter fineness ratio.

The similarity between the drag predicted by the SolidWorks algorithm for the
Figure 6.10: Effects of behavioral shifts on distance travelled for three model scenarios in response to decreases in foraging opportunities. Decreased foraging was shifted into an even increase in the number of searching and traveling dives ( ), a substantial increase in the number of searching dives ( ), a substantial increase in the number of traveling dives ( ) or an even increase in the number of searching to traveling dives including the locomotor costs of migration ( ). All other models plotted in Fig. 6.9 represented additional iterations of the ‘even’ behavioral shift so were not included here because no changes in distance would occur.

traveling whale and that measured from the tag data suggests that the assumption that whales are foraging continuously throughout the bottom of their foraging dives may not be correct. While the use of glides during foraging activities may allow these animals to save energy, they may also be saving energy by closing their mouths while gliding. Other explanations include the use of stroke-glide swimming when foraging in low quality prey patches. Closing their mouths while gliding would decrease the drag experienced, while the loss in the amount of prey consumed would be lower due
Table 6.2: Comparison of morphological adaptations and foraging parameters between the two major families of mysticete cetacean.

<table>
<thead>
<tr>
<th></th>
<th>Balaenoptera</th>
<th>Balaenidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>filtration technique</td>
<td>intermittent engulfment&lt;sup&gt;a&lt;/sup&gt;</td>
<td>continuous ram&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>no. species</td>
<td>10&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>baleen type</td>
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<td>long, fine&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>prey types</td>
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<td>Calanus spp.&lt;sup&gt;a,b&lt;/sup&gt;</td>
</tr>
<tr>
<td>predator niche</td>
<td>generalist</td>
<td>specialist</td>
</tr>
<tr>
<td>prey size (cm)</td>
<td>3–20&lt;sup&gt;a,c&lt;/sup&gt;</td>
<td>0.05–1&lt;sup&gt;d,e&lt;/sup&gt;</td>
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<tr>
<td>body length to width ratio</td>
<td>5–6&lt;sup&gt;f&lt;/sup&gt;</td>
<td>4.5&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>maximum speed, foraging (ms&lt;sup&gt;−1&lt;/sup&gt;)</td>
<td>3.0&lt;sup&gt;g&lt;/sup&gt;</td>
<td>1.35&lt;sup&gt;b,d,j&lt;/sup&gt;</td>
</tr>
<tr>
<td>maximum speed, sprinting (ms&lt;sup&gt;−1&lt;/sup&gt;)</td>
<td>5.5–8.3&lt;sup&gt;h&lt;/sup&gt;</td>
<td>4–5&lt;sup&gt;h&lt;/sup&gt;</td>
</tr>
<tr>
<td>maximum projected mouth area (m&lt;sup&gt;2&lt;/sup&gt;)&lt;sup&gt;*&lt;/sup&gt;</td>
<td>8.5&lt;sup&gt;g&lt;/sup&gt;</td>
<td>1.21&lt;sup&gt;d&lt;/sup&gt;</td>
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<tr>
<td>feeding volume (m&lt;sup&gt;3&lt;/sup&gt; s&lt;sup&gt;−1&lt;/sup&gt;)&lt;sup&gt;*&lt;/sup&gt;</td>
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<td>1.63&lt;sup&gt;d,e,j&lt;/sup&gt;</td>
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<tr>
<td>filtration rate (m&lt;sup&gt;3&lt;/sup&gt; s&lt;sup&gt;−1&lt;/sup&gt;)&lt;sup&gt;*&lt;/sup&gt;</td>
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<td>1.74&lt;sup&gt;d,e&lt;/sup&gt;</td>
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<td>0.014&lt;sup&gt;j&lt;/sup&gt;</td>
</tr>
<tr>
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<td>0.006–0.012&lt;sup&gt;g,j&lt;/sup&gt;</td>
<td>0.0052&lt;sup&gt;j&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup>Wells et al. 1999, <sup>b</sup>Watkins & Schevill 1976, <sup>c</sup>Dzik & Jazdzewski 1978, <sup>d</sup>Mayo et al. 2001, <sup>e</sup>Baumgartner & Mate 2003, <sup>f</sup>Woodward et al. 2006, <sup>g</sup>Goldbogen et al. 2007, <sup>h</sup>Ford & Reeves 2008, <sup>i</sup>Bose & Lien 1989, <sup>j</sup>this study

*foraging parameters determined for an average adult whale from a representative species: for Balaenoptera, a 20-m long, 50000 kg fin whale (Balaenoptera physalus) was used and for Balaenidae, a 15-m, 40000 kg North Atlantic right whale (Eubalaena glacialis) was used.

† referenced to wetted surface area

to lower prey densities. In this case, the difference in drag that was found between behaviors for the tag data could be related to measuring speed through flow noise. Refraction of noise from the surface and surface water movements could add to the low-frequency noise levels measured from whales close to the surface and would not be present for submerged animals, although those factors would likely result in a higher noise levels and therefore overestimates of speed.

Differences between CFD results and those from tag data also could be related to anatomical flow control strategies in these animals that can not be accounted. Early work on the hydrodynamics of swimming bottlenose dolphins found that these animals were able to achieve higher speeds than those predicted to be possible based on the forces produced by their muscles (Gray, 1936). A series of drag-reduction strate-
gies were suggested to explain how these animals were able to do this, including mucus coatings, heating of the boundary layer, compliant skin and dermal ridges. Although most of these strategies have been debunked since they were suggested and the measurements made by Gray that established his ‘paradox’ were flawed, the presence of a turbulent boundary layer appears to be a key factor in reducing drag in cetaceans (Fish, 2006). The rough dermal patches known as callosities on the head and rostrum of right whales could help to initiate turbulence as flow first encounters the animal, ensuring the onset of turbulence at the anterior end of the animal even when moving at low speeds. A small right whale (10m) moving at 1ms$^{-1}$ in 20$^\circ$ seawater would have a Reynolds number around 5.7$\times$10$^6$, and an adult right whale (13m) moving at the same speed in colder water would be moving at Re=7.4$\times$10$^6$, which falls within the transitional range (5 $\times$ 10$^5$–1 $\times$ 10$^7$) (Vogel, 1994; Hoerner, 1965). Behavioral modifications such as increased swim speed have been suggested to have similar function in marine birds because these birds are close to the transition between the two regimes because of their small size (Watanabe et al., 2010). Work on the size of these patches in relation to the thickness of the boundary layer, their roughness and the distance between patches would help to determine whether these patches could cause additional drag (as fouling on ship hulls does), induce vortices that aid in prey capture or decrease drag through reducing skin friction (as shark skin and biomimetic shark-skin swimming suits do) (Dean & Bhushan, 2010; Bechert et al., 1997). In addition, the numerical models used in this study measured the resistance of a static whale geometry. Numerical simulations investigating the forces and flow around undulating bodies demonstrated that body and caudal fin oscillations act to pump fluid behind the body, which keeps the boundary layer attached to the animal and therefore lowers the pressure drag of the body (Borazjani & Sotiropoulos, 2009). Such effects were not included in the static simulations performed here and likely caused some differences in the resulting drag estimate.
6.4.2 Energy balance - lack of food or cost of getting there?

The model scenarios demonstrate that alternating searching and traveling behaviors provides the best trade off between energy profit and distance. Should foraging opportunities decrease, this behavioral pattern still allows more energetic gain while covering more distance. Using a higher amount of traveling behaviors covers more distance but less energy is ingested for the same decrease in foraging. Similarly, a larger increase in searching maintains more energy intake but at a cost of less distance being covered, which would have the potential drawback of limiting animals from locating better prey patches. These results also show that whales would have to spend most of their time moving between prey patches and not foraging at all to reach the point of having a negative energy balance, suggesting that changes in prey density are more likely to cause decreased reproduction in these animals. A better strategy for animals in years of low prey availability would be to move to areas of high density, instead of foraging on less dense prey in their typical foraging areas.

In order to survive despite variations in their environment, many animals can devote less energy to maintaining certain aspects of their life history during periods of poor environmental quality, which allows them to reduce their overall energetic needs so that they may survive and reproduce when conditions improve. One key life history parameter that is often used in physiological response to periods of low food availability is reproduction. The demands of reproduction in females of all taxa are typically very high, especially in k-selected species such as mammals and birds that produce relatively few offspring and devote more energy to ensuring each survives to adulthood (MacArthur & Wilson, 1967). Small passerines will reduce their clutch size in response to low food availability in order to ensure the female reserves enough energy to survive to reproduce again. Larger animals that only produce a single offspring do not have the option of reducing the number of offspring per reproductive
cycle and therefore are limited to increasing the amount of time between offspring. In comparison to their terrestrial counterparts, large pelagic seabirds only produce a single chick each year so when food is less abundant, the only life history trade off they can make is to skip reproduction for a year (Cubaynes et al., 2010; Weimerskirch et al., 2001, 2005). Declines in the reproductive success of several seal populations have been linked to El Niño events that result in decreases in prey availability, and as in whales, the single-offspring nature of these species requires that females skip reproducing for a season (Rosen & Trites, 2002; Trites & Donnelly, 2003; Le Boeuf & Crocker, 2005; Reid & Forcada, 2005; Hadley et al., 2006). Because right whales produce a single offspring every three years, they may not skip a reproductive cycle entirely, but instead delay it until a period of improved environmental quality. The high variability in right whale reproduction and close connection between right whale births, primary production and the North Atlantic Oscillation (NAO) all support the occurrence of such a life history trade offs occurring in this species (Greene et al., 2003; Baumgartner et al., 2007).

The parameters used for the unaltered scenario represent the foraging behavior and current densities of *Calanus* in this habitat and are likely not representative of the ecosystem a few hundred years ago when right whales were abundant in this area. The present state of the Gulf of Maine ecosystem is considerably altered from the ecosystem that right whales evolved to exploit. The severe decrease in top predator abundance, including cetaceans, seabirds and large predatory fish, and increases in pollutants and nitrogen-rich run-off from cities in the Northeastern US have been accompanied by altered trophic interactions throughout the Gulf of Maine food web (Lotze & Milewski, 2004). Even though coastal New Brunswick is relatively undeveloped, the Bay of Fundy is tied into the physical processes of the broader Gulf of Maine system, which is surrounded by one of the most populated parts of North America (Bigelow, 1927; Brooks, 1994). Finally, variations in climate will also have
affected this ecosystem, although these changes will probably have a more significant effect in upcoming years (Mueter et al., 2009; Pershing et al., 2005; Beaugrand & Reid, 2003).

Finally, these estimates of energy use relative to energy gain do not account for any of the other minimum energy requirements for this species. Other demands on the energy exist, including those to maintain their metabolism, produce heat in a cold environment, digest ingested food will also reduce the amount of energy that animals can store. These costs vary depending on the life history stage of a right whale and are affected by both ontogeny and reproduction. Although the locomotor costs for animals that are pregnant or lactating may not subtract from the energy profits significantly, the other costs of survival may, resulting in a much smaller energy profit than shown here.

6.4.3 Differences from other habitats

The annual cycle of right whale behavior includes seasonal changes in behavior and distribution that are related to their habitat and the life cycle of their prey. The late summer foraging grounds for some of the population, the destination and behavior of non-calving animals during the winter, and the changes in cost related to feeding near the surface, or ‘skim-feeding’ are all unknown factors. First, some degree of foraging site fidelity has been shown in right whales, as the genetic diversity of right whales detected in the Bay of Fundy foraging does not account for the entire North Atlantic population. About one-third of female right whales do not bring their calves into the Bay of Fundy for the summer, and because where they do go is not known, the effects that these movement patterns have on locomotor costs is entirely uncertain (Schaeff et al., 1993; Malik et al., 1999). Next, only a portion of the North Atlantic right whale population consisting of pregnant females and some juveniles performs winter migrations to the waters of the South Atlantic Bight. The remainder of the
population moves to an unknown location somewhere in the Atlantic Ocean. One right whale was documented to travel from Cape Cod to Norway in a period of six months during the winter, and the historical distribution of these animals included most of the North Atlantic, with right whale sighting and killings stretching from Iceland and Norway to Spain (Jacobsen et al., 2004; Kraus & Rolland, 2007). Studies on the few sightings of animals in Iceland and Norway suggest that these animals are from a single population, and the effect of such long-distance movements on the cost of locomotion, the amount of energy gained or the duration of winter foraging activities can not be included in this model because so little data about them are available.

Finally, when whales return to the coastal foraging grounds off New England, their first destination is areas such as Cape Cod Bay and the Great South Channel, where they will begin feeding. Because their main Calanus prey has not descended into the water column to initiate diapause, whales feed on them at or near the surface in addition to small amounts of other zooplankton species such as Pseudocalanus (Baumgartner et al., 2007; Mayo & Marx, 1990). While this behavior would eliminate the costs of making deep foraging dives, the cost of foraging would be increased as animals frequently forage at depths just beneath the surface or with upper jaws protruding through the surface, which would cause additional drag components such as wave and spray drag (Hertel, 1966; Hoerner, 1965). While clear anatomical adaptations exist to reduce the cost of foraging at the surface, some increase in drag is probable. In addition, their prey is earlier in its life cycle so it generally has smaller lipid reserves, and the less-preferred Pseudocalanus also has less lipid content than stage five Calanus copepods (Durbin et al., 1995; Michaud & Taggart, 2007; Pepin & Head, 2009). A similar amount of foraging on these zooplankton would likely yield less energetic gain for the same duration of foraging. Behavioral studies of whales in these areas and work on understanding differences in caloric value and/or copepod
abundance are necessary to further improve an overall annual energetic cycle of these animals.

In addition to improving these models to account for all aspects of the life history of this species, additional modeling work would also improve these results. Better estimates of the costs of foraging from the CFD models are necessary. The open-mouth geometry was too complicated for easy use in different CFD codes and decreasing the resolution of this geometry may allow a better first-approximation of the results. A more complete exploration of the drag of each geometry at different speeds would help to understand the locomotor costs in these animals. Finally, improved technology used in conjunction with datalogging tags, such as video devices to detect the occurrence of foraging while at depth or propellers to record speeds precisely, would also improve the drag measurements made from free-ranging animals. However, these results represent the first attempt to estimate the costs of filter feeding in a large vertebrate and demonstrate the need for further work on understanding this species.
Over the last forty years, several teams of dedicated researchers have devoted their work into understanding the few remaining individuals of the species *Eubalaena glacialis*. In addition to improving the scientific understanding of the biology of these animals, these efforts have helped to implement measures to reduce the indirect mortality rates and improve the potential for this population to recover, especially through the designation of critical habitat areas, speed restrictions on vessels in those areas and seasonal closures of fishing grounds. However, despite all such efforts to decrease the number of whales killed each year, the survival of the population depends on the number of whales born, something that management efforts can not change at all. These whales live in relatively urban environment and face an alarming number of environmental stressors merely by their geographic location. This study has attempted to explore one potential factor in the current predicament of these animals and in doing so improve the understanding of one key area in their biology.

The major findings of this work include determining that the filter feeding strategy of these animals does have an increased cost, but because of the vast quantities of individual prey items that it allows a whale to consume, that cost is a relatively
minimal factor. Changes in prey density, which affects the number of prey items consumed for the same cost of movement, have a much larger affect on the energy surplus than changes in behavior. In addition, the continuous feeding strategy used by balaenid whales only increases drag forces by a factor of two, a small increase in comparison to the order of magnitude increase documented in balaenopterid whales. Although more work is necessary to understand individual variation and the effects of ontogeny on these estimates, they provide initial evidence that supports hypotheses about the relative costs and energetic strategies of continuous and intermittent filter feeding strategies.

In addition to the morphological adaptations that these whales have evolved to reduce the costs of foraging, several behavioral strategies are used to reduce the energy spent on movement in different parts of the water column. Previous work on the hydrodynamics of cetaceans has shown that the solution to ‘Gray’s Paradox’ and the secret of cost-efficient submerged locomotion lies in a turbulent boundary layer and behavioral strategies to reduce drag. This study is the first to document several of these strategies in a large mysticete cetacean. These whales rely on their positive buoyancy to passively assist their ascents from deep dives and change their body pitch to offset those costs on descent. When traveling horizontally, these whales are able to exploit an energetic window of opportunity by making shallow dives to depths of approximately 10 m below the surface. Diving to these depths avoids the increased drag caused by the interaction of the whale’s boundary layer with the water surface but also enables them to spend the least amount of energy on overcoming the forces such as buoyancy that are inherent in diving. Finally, some whales use intermittent locomotion while foraging at depth, a strategy that reduces energy expenditure by reducing induced drag caused by lift generation, avoiding boundary layer thinning related to body oscillations and stopping the use of energy by the muscles.

In combination these strategies allow right whales to save energy in all three
crucial areas of movement for a diving animal, during foraging at depth, traveling at
the surface and diving through the water column. While these strategies have been
documented in other marine vertebrates across a variety of taxa, including marine
mammals, reptiles and birds, this study is the first to put together a comprehensive
study of locomotion across all three contexts. Further work that is necessary in order
to improve these estimates would be studies on the metabolic rates of these animals,
especially in terms of different behaviors, and on changes in body composition and
behavior with ontogeny. However, this study provides the foundations for more
detailed explorations of behavior, cost of locomotion and energetic budgets in the
future. This investigation into the relative costs of locomotion and strategies used
to reduce them provides an initial link between individual behavior and population
survival, which is the key to understanding how the health of individual whales can
affect population recovery.
Appendix A: Tagging locations

North Atlantic right whales were tagged in two areas of the western North Atlantic Ocean that represent two key habitats for this species (Fig. 8.1). The Bay of Fundy, Canada, (Fig. 8.2) is a high-quality foraging ground for these whales, while the South Atlantic Bight (Fig. 8.3) is a location where female right whales have been observed giving birth to their calves. These tracks were plotted by locating tagged whales during surfacings between dives by the VHF signal of the Dtag. The range and bearing from the tracking vessel (R/V Stellwagen) to the whale was measured with a laser rangefinder, and then the GPS log of the vessel was used to dead-reckon the GPS position of the whale. These surface positions were then interpolated using the XTools module of ArcGIS (ESRI, Inc., 2009) to create a line for the whale’s course of movement over the portion of tag attachment for which visual observations of whales at the surface were possible, which typically consisted of daylight hours. Therefore, in some cases, these tracks do not cover the entire duration of tag attachment.
Figure 8.1: Whales spend late summer and fall (July through October) in northern foraging grounds (—) such as the Bay of Fundy where they are feeding on diapauing late stage *Calanus finmarchicus*. During late fall, all whales leave these coastal areas. Pregnant females and some juveniles travel to the calving grounds (—) in the South Atlantic Bight off the Southeastern US, while the rest of the population travels to unknown locations, presumably in the pelagic North Atlantic.
Figure 8.2: Tracks of 25 individual right whales during tag attachments in the Bay of Fundy during August and September 2000, 2001, 2002 and 2005. All whales were tagged within approximately 30km off the eastern coast of Grand Manan Island in the area of Grand Manan Basin. The occurrence of right whales in this area, along with other cetaceans and seabirds, has been linked to the tidally-driven aggregations of plankton caused by the island’s wake (Johnston et al., 2005). The island appears on the lower left side, and the mainland coast of New Brunswick is visible along the top edge. Contours show 10m depth intervals ranging from white at 0m to dark blue at 250m, and water depths in the area used by the whales were between 150 and 200m.
Figure 8.3: Tracks of six right whales tagged during January 2006 in their calving ground in the nearshore waters of the South Atlantic Bight off the coast of northern Florida. Five out of six whales were tagged within the designated critical habitat (---) for the species, and all whales were tagged within approximately 30 km of the shoreline (----). Water depths in this area were between 10 and 20m.
Appendix B: Tag dataset

The following tables summarize the individual right whales included for analysis. Body length was obtained from age data for whales in the SEUS, so both catalogued whales and non-catalogued ones were included for this habitat (Table 9.1). Age and sex information was required for animals tagged in the Bay of Fundy in order to obtain animal body length, so only tag records from whales that had been catalogued were used for this habitat (Table 9.2).

Table 9.1: Summary of life history information and tagging results from individual North Atlantic right whales tagged in the South Atlantic Bight off Northern Florida in January 2006. Whales that were not matched to individuals in the New England Aquarium’s catalogue are identified by their temporary Dtag attachment number instead of their unique EgNo. Adults are considered to be animals over nine years of age.

<table>
<thead>
<tr>
<th>EgNo</th>
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<td>1151</td>
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<td>A</td>
<td>18:00</td>
<td>640</td>
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</table>
Table 9.2: Summary of life history information and tagging records from North Atlantic right whales tagged in the Bay of Fundy in August and September 2000, 2001, 2002 and 2005. Life history information and unique EgNo were obtained from the New England Aquarium’s North Atlantic Right Whale Catalogue, and body lengths were obtained from aerial photogrammetry, when possible or estimated from the animal’s age (*).

<table>
<thead>
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<th>EgNo</th>
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<th>year tagged</th>
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Appendix C: CFD model parameters

Table 10.1: Input parameters used in two CFD algorithms to solve for flow around right whales. Results from the commercial package (Dassault Systèmes SolidWorks Corporation, 2009) were used to determine an absolute value of the resistance experienced by a whale, while the custom package (Sussman, 2005; Sussman et al., 2007) was used to determine the relative drag of three different geometries, each representative of whales during different behaviors.

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References


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Blender Foundation (2010). *Blender 2.49*.


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Parks, S.E. (2003). Response of North Atlantic right whales (Eubalaena glacialis) to playback of calls recorded from surface active groups in both the North and South Atlantic. Marine Mammal Science, 19, 563–580.


SAS Institute, Inc. (2009). *JMP 8.0.2*.


Biography

ANNA ELIZABETH NOUSEK MCGREGOR

Birthplace and date: State College, Pennsylvania, USA - October 01, 1981

EDUCATION


PhD, Duke University, Marine Science and Conservation, Beaufort, NC, USA, current. Supervisor: Douglas P. Nowacek.

SELECTED PUBLICATIONS


SELECTED AWARDS and APPOINTMENTS

Best Student Poster, Society for Integrative and Comparative Biology Annual Meeting, Division of Vertebrate Morphology, 2010.


Marine Bioacoustics Workshop, University of Washington Friday Harbor Laboratories, August 2005.