Foraging behaviour of Thick-billed Murres (*Uria lomvia*) in northern Hudson Bay

by

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A Thesis submitted to the Faculty of Graduate Studies of

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THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES
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Abstract

The foraging behaviour of seabirds has been well-studied, but the role of energy costs and prey type in determining foraging behaviour is still poorly known. To investigate how energy costs influence the foraging behaviour of Thick-billed Murres, a generalist seabird, at Coats Island, Nunavut, I attached positively ($n = 9$), negatively (n = 10) and neutrally (n = 9) buoyant handicaps and drag handicaps of cross-sectional area equivalent to three (2.8 cm^2; n = 8) and six (5.6 cm^2; $n = 6$) percent of murre body cross-sectional area. To investigate how murres modify their foraging behaviour for different prey types, I attached time-depth-temperature recorders to chick-rearing murres (n = 23 in 2004; n = 33 in 2005; n = 60 in 2006) and monitored dive behaviour on the dive bout preceding the delivery of prey items observed at the colony. When buoyancy was altered, or drag increased, murres reduced dive depth, dive duration, ascent rates, descent rates and time spent diving. Handicapped murres did not alter surface pause duration, but surface pause duration increased for a given dive duration, agreeing with predictions from foraging theory. Thus, murres altered dive behaviour in response to increasing energy costs. Dive behaviour for the following prey: fish doctor, squid, amphipods, daubed shanny, sand lance and Arctic shanny was discriminated from each other at the 80% or 95% confidence level by minimum convex polygons on a discriminant analysis of dive variables and, therefore, were considered "specialist" prey items. Specifically, amphipods were captured after V-shaped dives near the colony with a slow descent rate, squid were captured after deep V-shaped dives and fish doctor were captured after a long series of U-shaped dives in warm water far from the colony. Dive behaviour for Arctic cod, capelin and sculpin, overlapped both with each other and with the

behaviour associated with other prey items and, therefore, were classified as "generalist" prey items. In general, V-shaped dives preceded deliveries of pelagic prey items and U-shaped dives preceded deliveries of benthic prey items. The relationship between surface pause, dive depth and dive duration also varied with prey type. For example, surface pause duration decreased weakly (but significantly) with prey mass ($R^2 = 0.01$-0.04) and was unrelated to prey type (schooling vs. benthic); dive duration for a given depth increased with prey mass ($R^2 = 0.17$) and was longer for benthic items, presumably because benthic dives involved less energy expenditure. Thus, dive behaviour clearly reflected prey type and, therefore, perceived energy gain. Distance flown for a given prey item and average mass of prey items declined over the season, suggesting that murres depleted prey from waters near the colony. This conclusion was also supported by a tradeoff between depth and distance and a trend towards increasing prey mass with flight distance. Consequently, I concluded that seabird foraging behaviour is influenced by energy costs, prey type and degree of prey depletion. A thorough understanding of these issues is necessary to use seabird foraging behaviour as an indicator for prey abundance or distribution.

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List of symbols and abbreviations

Symbol	Value	Name
A		Surface area exposed
b		Wingspan
C_{Dpar}		Parasite drag coefficient
C_i		Energy value of prey item
CP		Average cost of locomotion at the surface
d		Depth
F_D		Drag force
F_B		Buoyant force
F_g		Gravitational force
g	9.81 m·s^{-2}	Acceleration due to gravity
k		Conductivity of the animal-water boundary
ΔL		Width of the water-body boundary layer
m	1 kg	Mass
η		Metabolic efficiency
ρ	1000 kg·m^{-3}	Density of sea water
P_f		Power expended during flight
P_d		Power expended when diving
P_{mech}		Mechanical power output.
P_{met}		Instantaneous energy expenditure
P_{pro}		Profile power
p_s	101.3 kPa	Atmospheric pressure

RMR	Resting Metabolic Rate
R	Respiration and ventilation factor
S	Body cross-sectional area
t_i	Searching and handling time
T_c	Time spent at the colony
T_d	Time spent diving
T_f	Time spent flying
T_i	Transit time
T_R	Time spent resting
T_w	Time spent on the water
ΔT	Temperature gradient between body and water.
TDR	Time-depth-temperature recorder
U	Forward speed
V_s	Lung and plumage air volume

Introduction

Predator-prey interactions are important ecological processes because they facilitate energy transfer among trophic levels within food webs. Therefore, elucidating predator-prey interactions is key to understanding processes that drive ecosystem-level changes, such as those driven by climate change (Coyle et al. 1992; Tremblay et al. 2005). In the Canadian Arctic, where marine surveys are costly and logistically difficult, seabird diets are often the only long-term data that can be used to monitor shifts in ecosystem-level processes (Gaston and Bradstreet 1993; Gaston and Hipfner 1998; Gaston et al. 2003, 2005). For example, Thick-billed Murres (*Uria lomvia*) revealed changing forage fish community structure in northern Hudson Bay that no other monitoring scheme was able to detect (Gaston et al. 2003, 2005b).

Seabird diet has often been used to determine spatial and temporal changes in forage fish populations (Montevecchi and Myers 1996; Davoren and Montevecchi 2003, 2005; Miller and Sydeman 2004) and for age-specific recruitment in forage fish (Barrett et al. 1990; Barrett 1990; Bertram and Kaiser 1993). Nonetheless, it is often difficult to assess the meaning of these data because they are filtered through complex behavioural processes (Tremblay et al. 2005). For example, seabird foraging behavior can better indicate fish abundance than measures such as body condition indices or feeding rates of offspring, because adults can buffer changes in prey availability through changes in foraging behavior (Cairns 1987, 1992b; Monaghan 1996; Gremillet 1997; Baillie and Jones 2004). The development of miniaturized data recording devices in the last 20 years has enabled researchers to investigate foraging behaviour at sea in relation to behavioural

(e.g., Falk et al. 2000), physiological (Bevan et al. 1997; Green et al. 2003; Froget et al. 2004) and environmental (Watanuki et al.1993) variables.

Seabirds of the family Alcidae (alcids or auks) are breath-hold divers and are therefore constrained by the requirement for access to air to relatively short underwater forays. This requirement limits the dive duration and provides only sporadic and intermittent contact with their prey. Because dive duration scales with body mass (Watanuki and Burger 1999), small-bodied pursuit-diving alcids are particularly time-constrained and, hence, under strong selection for improved underwater performance. Behavioural strategies need to be optimized to take account of these physical and physiological constraints. Existing information on free-roaming individuals addresses largely those species that feed on sessile prey and that therefore know the precise location of prey at the onset of each dive (e.g., Halsey et al. 2003). Many alcids, however, feed upon mobile prey (fish), making each dive outcome relatively unpredictable. Consequently, underwater foraging decisions by these pursuit-diving seabirds are determined by a combination of biomechanics, dive physiology and prey distribution.

I focus my investigation on how pursuit-diving seabirds use behavioural strategies to minimize the energy costs of provisioning chicks, under biomechanical and physiological constraints, during the breeding season in Arctic regions. This is important to predict the influence of changing foraging conditions (i.e., the distribution, density and abundance of important prey species), resulting from climate change, on the foraging behaviour and underlying energetics of breeding seabirds in Arctic regions. This will aid in our ability to predict the population-level impacts of climate change for marine predators.

Central Place Foraging

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A major component of the life history of any organism is the way in which it captures prey items and selects foraging locations, and there is a growing body of literature dealing with this subject (Orians and Pearson 1979; Houston and Carbone 1992; Ydenberg et al. 1994). Many animals must capture their food at one location and bring it to another location, called the "central place" (e.g., nest, cache, lodge; Orians and Pearson 1979). For these animals, foraging time includes transit time, as well as searching and handling time (Orians and Pearson 1979).

Breath-hold divers, such as pursuit-diving seabirds, are a special class of central place forager because they must return to the surface (the central place) periodically to replenish oxygen supplies (Orians and Pearson 1979, Hegner 1982, Houston and Carbone 1992). To maximize underwater foraging time, or bottom time, and the probability that a prey item will be located and captured, breath-hold divers must minimize energy use (oxygen consumption) and/or transit times (Ydenberg and Clark 1989, Thompson and Fedak 2001). Transit distances are dictated largely by prey distribution and decreasing transit time necessitates increasing swim speed and, therefore, energy use (Mori and Boyd 2004, Thompson and Fedak 2001). Thus, diving behaviour for foraging breath-hold divers is a compromise between maximizing energy input (i.e., number and energy content of prey) and minimizing energy output.

Breeding seabirds, whether or not they are also breath-hold divers, are also central place foragers because they must leave the nesting colony (central place) to obtain prey at sea for themselves and their offspring. Breeding seabirds can be divided into two groups depending on the number of prey items they bring back to their offspring at one time (Orians and Pearson 1979). For single-prey loaders, the capture of one prey item

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precludes the capture of another (Houston and McNamara 1985). Alternately, multiple-prey loaders carry multiple prey items at a time. Single-prey loaders have much more constrained foraging behaviour than multiple-prey loaders. For example, central place foraging theory predicts that single-prey loaders will (1) minimize travel time by returning directly from foraging areas to nest sites; (2) have larger loads when provisioning chicks than when self-feeding owing to the higher transit time to the central place; and (3) increase load size with travel distance (Kalcenik 1984; Houston and McNamara 1985; Kalce nik and Cuthill 1990). The reason for the first prediction is merely that once a prey item is caught, no more prey items can be captured and, therefore, there is no reason to continue searching for more prey items until the captured prey item has been delivered to the central place. The reason for the latter two predictions is that the value (*sensu* Orians and Pearson 1979) of a food item i for a central place forager is $\dfrac{C_i}{t_i + T_i}$, where C_i is the energetic value of the prey item, t_i is the searching and handling time and T_i is the transit time. Alternatively, the value of food item i for a non-central place foraging animal is given by $\dfrac{C_i}{t_i}$. The larger the ratio is, the more profitable the prey item. Thus, C_i must be larger for a central place foraging animal than for a non-central place foraging animal for prey item i to be selected, and as T_i increases, C_i must also increase for prey item i to be selected (Orians and Pearson 1979).

Among seabirds, some alcid species are the best examples of single-prey loaders because they only carry a single prey item to their chick at a time. As predicted, Thick-billed Murres return directly to the colony from foraging areas (Benvenuti et al. 1998).

Furthermore, many auks appear to eat smaller prey items than they feed their chicks (Baird 1991, Gaston and Bradstreet 1993, Davoren and Burger 1999, Benvenuti et al. 2002, Wilson et al. 2004). Although many central place foragers increase load size with travel distance (e.g., Carlson and Moreno 1981, Hegner 1982, Krebs and Avery 1985, Bowers and Ellis 1991, Fryxell and Doucet 1991), some do not (e.g., Sodhi 1992, Alonso et al. 1994), and there are little published data for seabirds.

Most published accounts on the foraging behaviour of central place foragers concentrate on energy gain (Carlson and Moreno 1981, Hegner 1982, Krebs and Avery 1985, Bowers and Ellis 1991), whereas few simultaneously examined energy gain and expenditure. Nonetheless, Ydenberg et al. (1994) showed that animals minimizing time spent foraging (e.g., migrants) maximize efficiency (energy intake ÷ energy expended), whereas animals maximizing energy gain (e.g., growing fish) maximize net energy gain (energy intake - energy expended). Chick-rearing alcids are anticipated to fall in the former category because chicks that fledge sooner are more likely to survive and because the provisioning ability of parents is likely a major constraint on the amount of time chicks spend at the colony (Ydenberg 1989).

Energetics of Breeding Seabirds

For breeding seabirds, energy expenditure (*EE*) depends on time spent resting, flying and diving, and power output during each of these activities. Thus,

$$EE = RMR \bullet T_R + P_f \bullet T_f + P_d \bullet T_d \ (1)$$

where *RMR* is Resting Metabolic Rate, P_f is power expended during flight, P_d is power expended when diving and T_R, T_f and T_d are time spent at the colony, flying and diving, respectively. Here, we ignore variation in *RMR* due to diel activity and wakefulness

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patterns, and we assume the animal is within its thermal neutral zone during rest. For pursuit divers, *RMR* at the colony will usually be lower than on the water, due to heat loss via conduction to the water. Thus, equation (1) can be expanded as:

$$RMR \bullet T_R = RMR \bullet T_c + \left[RMR + CP + kA\left(\frac{\Delta T}{\Delta L}\right) \right] T_w \quad (2)$$

where T_c is time spent at the colony, T_w is time spent on the water, *CP* is the average cost of locomotion (paddling) at the surface, *k* is the conductivity of the animal-water boundary, *A* is the surface area exposed, ΔL is the width of the water-body boundary layer and ΔT is the temperature gradient between the body and the water.

For pursuit divers that commute from a central place, the highest instantaneous rate of energy expenditure is during transit, both between the colony and foraging grounds, and between the surface and the depth where prey is located. During locomotion, energy expenditure by an animal, P_{met}, can be modeled as:

$$P_{met} = R(\frac{P_{mech}}{\eta} + RMR) \quad (3)$$

where *R* is a respiration and ventilation factor associated with increased requirements of the lungs and air sacs, η is metabolic efficiency and P_{mech} is mechanical (useful) power output. Note that thermal requirements are subsumed into the value of η; in some cases, working in cold environments will increase η due to thermal substitution of exercise.

During flight, P_{mech} can be modeled as:

$$P_{mech} = \frac{(mg)^2}{\rho\pi b^2 U} + P_{pro} + \frac{1}{2}\rho C_{Dpar}SU^3 \quad (4)$$

where *m* is mass, *p* is density of air, *g* is acceleration due to gravity, *b* is wingspan, *U* is forward speed, P_{pro} is profile power, C_{Dpar} is the parasite drag coefficient and *S* is the

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body cross-sectional area (Pennycuick 1997). The details of the derivation of this model can be found elsewhere (Pennycuick 1997); however, it is important to note that there are two sources of uncertainty in the parameter values for this model (Pennycuick 1997, Rayner 1999). First, C_{Dpar} is difficult to measure in the laboratory, and consequently values in the literature range between 0.05 and 0.50 (Pennycuick 1997, Rayner 1999). Second, P_{pro}, the power required for the drag associated with the motion of the wings, is also difficult to measure in the laboratory, and its relative contribution varies between 2 and 50 % in the literature (Pennycuick 1997, Rayner 1999). Consequently, attempting to quantify flight costs on theoretical grounds is currently fraught with uncertainty.

Biomechanics of Underwater Locomotion

As with other types of locomotion, biomechanics set fundamental constraints under which vertebrate physiology and behavioural strategies must operate during diving. Buoyancy and drag underpin the biomechanics of all marine endotherms during diving. Buoyancy is the primary factor influencing diving behaviour in some species: sea snakes *Pelamis platurus* (Graham et al. 1987), Lesser Scaup *Aythya affinis* (Stephenson 1994), cetaceans (Williams et al. 2000; Nowacek et al. 2001), northern elephant seals *Mirounga angustirostris* (Webb et al. 1998), penguins (Sato et al. 2002; Wilson et al. 2003; Hansen and Ricklefs 2004), Cape Gannets *Morus capensis* (Robert-Coudert et al. 2004). Alternately, drag is the primary factor influencing diving behaviour in other species, including: harbour seals *Phoca vitulina*: (Williams and Kooyman 1985), bottlenose dolphins *Tursiops truncatus* (Williams et al. 1993; Skrovan et al. 1999) and Thick-billed Murres (Lovvorn et al. 2004).

Although drag and buoyancy both clearly influence the biomechanics of swimming in endotherms, precisely how these parameters affect the behavioural strategies used to minimize the energetic costs of locomotion is still poorly understood. For example, buoyancy calculations depend heavily on estimates of air volume trapped within the feathers and respiratory system during diving. Because live birds actively control respiratory and plumage air volumes, estimates derived from dead or restrained individuals may not reflect volumes actually experienced during normal diving behaviour (Lovvorn and Jones 1991, Sato et al. 2002). Estimates for drag have been derived from laboratory experiments on frozen birds (e.g., Lovvorn et al., 1999, 2004), which ignore drag associated with wing motion (profile drag), apparatus effects and behavioural tactics used by living birds to reduce drag. Current thought is that drag coefficients in flying birds are about one-third those obtained on frozen specimens in the laboratory due to reduced flow separation behind living birds (Pennycuick 1997, Rayner 1999, Ward et al. 2001, Tobalske et al. 2003). Conversely, in some marine mammals drag coefficients are lower during active swimming than when measured on gliding or frozen specimens (Williams and Kooyman 1985; Fish 1988, 1993). As buoyancy and drag both influence energy costs of underwater locomotion, they are important parameters to understand underwater decision-making by murres. Specifically, measurements of buoyancy and drag are important to (1) accurately model and calculate underwater energy costs and (2) determine how the choice of dive depth may be mediated by variation in underwater energy costs and prey densities.

Physiology of Underwater Locomotion

Once biomechanical limitations are set, diving animals have two options for maximizing the dive duration and consequently the time spent foraging during a dive: they can increase oxygen stores or reduce the energetic cost of diving (i.e., oxygen consumption). All diving animals increase oxygen stores, through an increase in blood volume, hematocrit and myoglobin concentrations. Dive energetic costs are reduced in penguins (Sato et al. 2002), pinnipeds (Hooker et al. 2004), cetaceans (Nowacek et al. 2001) and reptiles (Graham et al. 1987; Minamikawa et al. 2000) by manipulating air volumes or depth to avoid fighting buoyancy or to use buoyancy to ascend. For example, king penguins *Aptenodytes patagonicus* use buoyancy to passively ascend from depth (Sato et al. 2002), whereas elephant seals descend to a depth of neutral buoyancy and drift. Because physiological costs associated with locomotion in most avian species is roughly 4-5 times higher than the actual biomechanical costs due to low (about 23 %) efficiency (e.g., low power output relative to power input; Rayner 1999, Ward et al. 2001, Tobalske et al. 2003, Taylor et al. 2003), another tactic for minimizing dive costs is to optimize muscle efficiency. Muscle efficiency is poorly known in birds, but recent studies have suggested that it varies greatly among species and within species with contraction frequency (Rayner 1993, 1999; Ward et al. 2001; Tobalske et al. 2003). Lovvorn et al. (2004) argued that murre swim speeds are chosen to optimize muscle contraction efficiency.

Dive costs are also reduced by decreasing blood flow to non-essential tissues. This leads to an increase in peripheral resistance and a drop in heart rate (Andrews et al. 1997; Bevan et al. 1997; Green et al. 2003; Froget et al. 2004). Blood flow to essential tissues (e.g., muscles, eyes) often increases (Kooyman and Ponganis 1998). Because there is a

delay between the onset of a dive and the time for physiological adjustment, instantaneous energetic demands decline over the course of a dive, as circulation to peripheral tissues gradually decreases (Green et al. 2003; Froget et al. 2004). Reducing circulation to non-essential tissues not only directs oxygen towards key tissues but in cold water also reduces the temperature and, therefore, cellular metabolism of these tissues through the Q_{10} effect (Kato et al. 1996, Bevan et al. 1997). Handrich et al. (1997) report a dramatic drop in core temperature of king penguins, suggesting that they may actually adopt "torpor" during deep dives.

For most vertebrates, the aerobic dive limit (ADL), or the longest dive sustainable using aerobic metabolism, sets a theoretical upper bound on dive duration because anaerobic metabolism creates excess lactate, which must then be "burned off" at the surface, reducing the time available for diving (Kooyman and Ponganis 1998; Nagy et al. 2001). The "theoretical" or "calculated" ADL is defined as total oxygen stores divided by oxygen consumption rate (Kooyman and Ponganis 1998). The "physiological" ADL is defined as the dive duration at which blood lactate levels increase above baseline (Kooyman and Ponganis 1998). Theoretical ADLs often diverge from physiological ADLs, suggesting that some of the theoretical assumptions, such as constant metabolic rate, are invalid (Kooyman and Ponganis 1998; Hansen and Ricklefs 2004). Due to the practical difficulty in measuring physiological ADL in free-living animals, the only bird species it has been accomplished for is the Emperor Penguin *Aptenodytes forsteri* (Ponganis et al. 1997; Nagy et al. 2001). Theoretical ADLs have now been calculated for a number of bird species (Kooyman and Ponganis 1998). Unlike mammals, birds routinely exceed their theoretical ADL (Kooyman and Ponganis 1998). A large

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proportion of Emperor Penguin dives exceed their physiological ADL, which suggests that this may not solely be a problem of underestimating theoretical ADL's (Kooyman and Ponganis 1998). Rather than metabolizing lactate after each dive, birds often dive anaerobically and postpone lactate metabolism at the ocean surface after encountering a fish school, presumably to maximize foraging time when an ephemeral prey patch is located (Ydenberg and Clark 1989, Mori et al. 2002). For example, diving Thick-billed Murres likely reduce surface pause duration and increase dive duration when they encounter schools of their preferred food, Arctic cod (*Boreogadus saida*).

This example illustrates that to maximize time available for foraging, diving birds must not only maximize dive duration but must also minimize surface pauses between dives. The relationship between dive duration and subsequent surface pause depends on three factors (Houston and Carbone 1992; Wilson and Quintana 2004). First, it depends on whether the bird has exceeded the ADL and used anaerobic pathways during the dive (Ydenberg and Clark 1989; Mori et al. 2002). Second, the rate at which oxygen is absorbed into body tissues is directly related to the difference in partial pressure between air and body tissues (Houston and Carbone 1992). This leads to a rule of diminishing returns because the longer the bird waits at the surface, the smaller the rate of increase in oxygen stores. Consequently, animals attempting to minimize time at the surface should not dive with body tissues fully-saturated with oxygen, but rather only with that needed for the dive (Wilson and Quintana 2004). Third, diving animals anticipate the length of subsequent dives and, therefore, surface pauses depend partially on anticipated oxygen requirements for the subsequent dive (Wilson and Quintana 2004). Consequently, the

ratio of dive duration to surface pause depends not only oxygen stores but also on expected time required to forage.

Anticipated energy intake therefore clearly plays a role in determining dive behaviour (e.g., surface pauses are reduced when it is anticipated that prey schools are accessible). However, energy intake is not necessarily equivalent to net energy gain because assimilation efficiencies may be different for each prey item. For example, Brekke and Gabrielson (1994) reported that Black-legged Kittiwakes (*Rissa tridactyla*) and Thick-billed Murres have lower assimilation efficiencies for capelin (*Mallotus villosus*) than for Arctic cod. Furthermore, many seabirds are limited by a certain nutrient (e.g., calcium) rather than by energy (Gaston 2004). Although most models do not incorporate assimilation efficiency or nutritional quality, it is important to consider these factors or be aware of the limitations of models that ignore them (Houston and Carbone 1995, Gaston 2004).

Prey Distribution, Abundance and Density

Within the biomechanical and physiological constraints outlined above, the distribution of prey, both horizontally in relation to the colony and vertically in relation to the ocean surface, will influence the energetic costs of foraging and provisioning. In general, the horizontal distribution of prey species is the main factor determining the at-sea distribution of breeding seabirds and, thus, how far a bird must fly from the colony to collect prey (Coyle et al. 1992; Mehlum et al. 1996; Woehler et al. 2003; Davoren et al. 2003; Davoren and Montevecchi 2003; Tremblay et al. 2005). The vertical distribution of prey in the water column will be a primary determinant of dive depth. Diel dive patterns are one example of the influence of vertical prey distribution on foraging behaviour. In

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many cases, dive patterns are known to track the diel vertical migration of krill, copepods and other plankton in basking sharks, *Cetorhinus maximus* (Sims et al. 2005), penguins (Wilson et al. 1993; Putz et al. 1998), and fur seals (Boyd et al. 1991). For example, Rockhopper Penguins *Eudyptes chrysocome* and Baikal seals *Phoca sibirica* switch from fish during the day to plankton at night in response to diel vertical migration of plankton (Schiavini and Rey 2004; Watanabe et al. 2004). In other cases, diel dive patterns appear to be a response to changing light availability and therefore capture success (Croll et al. 1992; Cannell and Cullen 1998; Wanless et al. 1999). At extremely high latitudes, there may be no diel dive pattern at all (Falk et al. 2000, 2002).

One of the consequences of central place foraging is that prey items close to the colony will always be preferred to identical prey items farther from the colony (Orians and Pearson 1979). For pursuit divers, the preference for nearby prey items can lead to the depletion of sedentary benthic fish near the colony (Birt et al. 1987; Lewis et al. 2001; Litzow et al. 2004; Wilson et al. 2005), whereas more mobile pelagic fish are less likely to be depleted (Gaston 2005). This effect, whereby resources close to the colony are depleted, is labeled Ashmole's Halo (Ashmole 1963, 1971). The reduction of resources within the foraging range of a colony can mean that colony size is limited by food resources and provides a mechanism for density dependent population regulation (Cairns 1992a). Population regulation by density-dependent mechanisms acting during the breeding season is often considered to be the cause of "seabird syndrome", the group of life history traits shared by all seabirds (Cairns 1992a; Gaston 2005). These traits include small clutch size, delayed maturity and high adult survivorship, and are typical of K-selected species that experience density-dependence through reproductive limitations

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(Ashmole 1971; Cairns 1992a; Gaston 2005). Nonetheless, there is little evidence that Ashmole's halo actually operates in non-tropical environments (Cairns 1992a; Gaston 2005).

If prey items become depleted near the colony or if prey distribution shifts away from the colony, seabirds must adjust their behaviour to adequately forage for chicks. For example, reductions in food availability near the colony may not translate into reduced provisioning of chicks because adult seabirds can increase time spent foraging during years when food availability is low (Burger and Piatt 1990, Zador and Piatt 1999). During years of high food availability, adults may have no reason to increase energy expenditure, or may choose not to do so to reduce stress and predation risk, thereby increasing survival (Monaghan 1996; Gremillet 1997). Therefore, at moderate-to-high levels of food abundance, adult time budgets may change drastically in response to changes in food availability, but this relationship is likely nonlinear (Cairns 1987). This idea has been called "buffering" (Cairns 1987).

Cairns (1987) expanded on the idea of buffering by hypothesizing that survivorship, reproductive success, chick growth, colony attendance and adult activity budgets, would have different thresholds of prey density because of a variety of buffering mechanisms. Specifically, he hypothesized that adult survivorship would only be reduced at extremely low levels of food availability, whereas chick growth would be affected at moderate levels of food availability and at high levels of food availability only adult time budgets (i.e., time spent at the colony; time spent foraging) would be affected, as adults would buffer any changes in food availability. Thus, by studying the relationships between food

availability and multiple indices, a predictive relationship between seabird behaviour and food availability may be possible over a large range of food levels (Cairns 1987).

Several studies have now examined some aspects of seabird behaviour in relation to prey distribution, allowing the extraction of functional relationships between seabirds and prey and, thus, tests of some of these hypotheses (Phillips et al. 1996; Furness and Camphuysen 1997; Litzow and Piatt 2003; Davoren and Montevecchi 2003, 2005). In particular, these data have been used in the study of climate change and regime shifts in ecosystems. For example, in an earlier study, Aebischer et al. (1990) revealed a remarkable parallelism in long-term trends across four trophic levels, including phytoplankton, zooplankton, herring and kittiwakes, and the frequency of westerly weather systems in the North Sea.

Thick-billed Murre Foraging Behaviour

Thick-billed Murres are one of the most-studied alcids, primarily because they are extremely abundant and easily observed during the breeding season (Gaston and Nettleship 1981). There are approximately 15-20 million Thick-billed Murres in the world, with about three million nesting in the Canadian Arctic (Gaston and Hipfner 2000). Individuals nesting in the eastern Canadian Arctic winter in the North Atlantic, with large numbers hunted off Newfoundland each winter (Gaston and Hipfner 2000). Globally, Thick-billed Murres are generally associated with cold marine environments below the 8 °C isotherm; their temperate congener, the Common Murre (*Uria aalge*), is found in warmer waters (Gaston and Nettleship 1981). Whereas Common Murres specialize on forage fish (i.e. capelin, sand lance), adult Thick-billed Murres feed primarily on invertebrates, such as euphasiids and amphipods (Gaston and Hipfner 2000).

Nestling diets tend to be fairly catholic, with squid making up most of the diet in the Pacific, Arctic cod in the High Arctic and daubed shanny or capelin in the Low Arctic (Gaston and Hipfner 2000).

Thick-billed Murres nest at colonies varying in size from a few thousand to over a million individuals (Gaston and Hipfner 2000). In Hudson Bay, reproduction is closely tied to ice dynamics, with laying dates generally timed to coincide with the departure of shorefast ice, usually in June or early July (Gaston and Hipfner 2000). Thick-billed Murres lay a single egg on a cliff with no excavation (Gaston and Hipfner 2000). Pairs are socially monogamous although about 15% of offspring result from extrapair fertilizations (Gaston and Hipfner 2000). The incubation period is about 30 days and the chick-rearing period lasts about 20 days (Gaston and Hipfner 2000). The chick grows rapidly during the rearing period, and fledges at about one-quarter of the parents' mass, presumably because adults can no longer provide sufficient food for growth beyond about 200 g (Ydenberg 1989; Gaston and Jones 1998). At this time, the chick cannot fly and is accompanied by the male parent for several months, as they swim to wintering grounds (Gaston and Jones 1998).

Most of what is known about Thick-billed Murres has been gathered by studies at the colony. The recent development of miniaturized recording devices has greatly increased knowledge about foraging behaviour. For example, the use of time-depth recorders (TDRs) has greatly improved the precision of time-activity budgets for free-living murres. Earlier budget estimates were based on time spent at the colony and proportion of birds observed resting, flying or diving (Gaston 1985; Kitaysky et al. 2000). TDRs have allowed for the refinement of individual finer-scale adjustments of time-activity budgets

in response to changing prey abundance (Falk et al. 2000, 2002). At Coats Island, time-activity budgets were similar in 1987, 1988 and 1989 with about half of the day spent on the water (Croll 1990). The energetic costs, consequences and constraints of these activities are still unknown.

The first study to monitor dive behaviour of Thick-billed Murres was undertaken at Coats Island using 35 g back-mounted TDRs (Croll et al. 1992, Croll and McLaren 1993). These studies showed that murres were exceptionally deep divers, diving to depths approximately twice that expected from allometric equations for penguins (Watanuki and Burger 1999). The maximum depth reported by Croll et al. (1992) was 210 m, using a capillary tube, although this measurement is likely erroneous as murres at this location have never subsequently been recorded below 146 m using a much larger sample size of birds equipped with TDRs (KHE, unpublished data). Nonetheless, Croll et al. (1992) observed many diving bouts that included multiple deep dives to > 100 m. They concluded that 48% of dives exceeded the calculated ADL.

Croll et al. (1992) also showed that Thick-billed Murres have a wide variety of adaptations for deep diving in cold water, including high blood volume (relative to penguins), high hemoglobin and hematocrit concentrations (comparable to penguins) and myoglobin concentrations intermediate between penguins and non-diving birds. The latter reflects a compromise between the demand for increased oxygen stores during diving and the demand for increased mitochondrial enzyme concentrations during powered flight (Croll et al. 1992). Laboratory studies by Croll and McLaren (1993) of Coats Island murres reared at Sea World and Scripps Institution of Oceanography showed that they had a high mass-specific metabolic rate with no thermal neutral zone in typical

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environmental conditions (below 20 °C). They also suggested that a high metabolic rate was an adaptation for life as a small animal in cold environments. Thus, the first time-depth recorder study combined at-sea information on foraging behaviour with laboratory studies of energetics.

The next round of studies using recording equipment on Thick-billed Murres occurred in the late 1990s. Benvenuti et al. (1998) used motion detectors to monitor at-sea foraging behaviour from a colony in Iceland. During outbound foraging trips, murres stopped at several locations prior to arriving at the floe edge, apparently sampling the environment (Benvenuti et al. 1998). On the return trip, murres flew directly back to the colony (Benvenuti et al. 1998). Murres either foraged near the colony (<40 km from the colony) or they flew to floe edge (>100 km from the colony; Benvenuti et al. 1998). Mehlum et al. (2001) and Watanuki et al. (2001) used TDTRs (temperature-depth-time recorders) at a Thick-billed Murre colony in Svalbard to monitor the change in water temperature with depth. They determined that, based on variation in water column temperature, most murres foraged within 20 km of the colony (midway up a glacial fjord), although a few foraged beyond 40 km from the colony (outside the fjord or where glacial runoff met the fjord). Mori et al. (2002) used the same data set to model diving behaviour. They concluded that murres reduce subsequent surface pauses relative to dive lengths when they encountered high-quality prey patches (e.g., schools of fish). Time-depth recorders also revealed gender-based stereotyped foraging behaviour, with males foraging during the day and females at night at Gannet Islands, Labrador (Jones et al. 2002) and females foraging during the day and males at night at Coats Island (Woo et al. 1999, Woo 2001). Woo (2001) examined dive behaviour in relation to prey species at Coats Island. Coats

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Island is an ideal location to examine variation in foraging behaviour in response to variation in diet because murres at this location have a particularly diverse diet that spans a hundred-fold difference in prey energetic values (Woo 2001). Woo (2001) found that crustacea were captured at deep depths near the colony, whereas fish were captured at shallower depths farther from the colony. In general, murres flew further to encounter higher-quality prey items, but did not dive deeper (Woo, 2001).

Several investigators have quantified the energetic costs of reproduction in Thick-billed Murres (Gaston 1985; Kitaysky et al. 2000). Earlier researchers used time-activity budgets and estimated the cost of each activity (Gaston 1985). In the late 1980s and early 1990s, researchers measured field metabolic rates using doubly-labelled water. Both Barrett et al. (2002) and Croll (1990) concluded that energetic estimates made using doubly-labelled water were very similar to those made using time-activity budgets and estimating the cost of each activity (Gaston 1985). By measuring energy expenditure by chicks and adults, Barrett et al. (2002) and Croll (1990) estimated tonnage of prey consumed by colonies in Norway and Coats Island, respectively. The estimate for Coats Island was about 14 800 kg day^{-1} which translated to one prey item caught every other dive. Kitaysky et al. (2000) measured Field Metabolic Rates (FMRs) in Alaska and found that energy expenditure during a year of high prey abundance was no higher than during a year of low prey abundance. Chick growth declined during the year of low food availability, suggesting that adults passed on the cost of reduced food availability to their chicks (Kitaysky et al. 2000).

Recently, Watanuki et al. (2003, 2006) and Lovvorn et al. (2004) attached accelerometers to three Thick-billed Murres in Svalbard to provide input parameters for a

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model describing the energetic cost of diving in murres. These instruments measure wingbeat frequency and body angle during dives, contributing to the understanding of biomechanics during diving. As observed in underwater footage at shallow depths (Lovvorn et al. 1999), murres ascend and descend vertically from all depths. Wingbeat frequency and swim speed are relatively constant during descent, although wingbeat frequency decreases slightly and swim speed increases slightly as the bird descends, presumably due to decreased buoyancy (Watanuki et al. 2003; Lovvorn et al. 2004). During ascent, murres gradually reduce wingbeat frequency above 80 m and cease stroking their wings altogether above 40 m, relying solely on buoyancy for passive ascent (Watanuki et al. 2003; Lovvorn et al. 2004). Body angle increases slightly during ascent, and increases from 57° at shallow depths (~27 m) to 70° at deep depths (~120 m; Watanuki et al. 2006). Lovvorn et al. (2004) used these data to develop an energetic model that demonstrates that the energetic cost of drag was much greater than the energetic cost of buoyancy in this species.

Objectives and Chapter Outline

The Thick-billed Murre is one of the best-studied seabirds, and the genus *Uria* has become a model for seabird foraging behaviour. Nonetheless, many questions are still unanswered, including some of the questions that will be addressed in this thesis. The primary goal of my thesis is to investigate how these murres use behavioural strategies to minimize the energy costs of provisioning chicks during the breeding season in Arctic regions. In Chapter 1, I examine how murres alter at-sea foraging behaviour in response to increased energy costs, as simulated through handicapping experiments. In Chapter 2, I examine how murres alter their at-sea foraging behaviour when capturing different prey

items. In Chapter 3, I investigate whether an area of lower prey availability forms around the Coats Island colony during the breeding season, presumably due to predation pressure by murres. Finally, in the Synthesis, I integrate all results to examine how the at-sea foraging behaviour, and underlying energetics, of breeding seabirds in Arctic regions may be modified in relation to varying foraging conditions. This is important to increase our capacity to predict the impacts of climate change at the population level for marine predators.

Chapter 1. Thick-billed Murres alter at-sea foraging behaviour in response to increased energy expenditure during underwater locomotion through handicapping

Breath-hold divers are constrained by their need for access to air during underwater forays. This requirement limits them to brief and intermittent contact with their prey and, thus, lower prey consumption rates relative to other marine organisms that do not require air. To maximize net energy gain during a dive, therefore, breath-hold divers are under strong selection to reduce oxygen consumption while. Adaptations to remain submerged for extended periods may be morphological (e.g., improved hydrodynamics), physiological (e.g., increased oxygen storage capacity), or behavioural (e.g. dive spacing and depth). Behavioural strategies employed by individuals need to be optimized under different foraging conditions to compensate for morphological and physiological constraints, as these constraints secure the energetic costs of diving throughout an individual's lifespan.

Buoyancy and drag underpin the biomechanics of marine endotherms during diving. Buoyancy is the primary factor influencing diving behaviour in some species (e.g., Graham et al. 1987; Skrovan et al. 1999; Beck et al. 2000) and drag in others (e.g., Williams and Kooyman 1985; Williams et al. 1993; Lovvorn et al. 2004). The influence of buoyancy on the energetic costs of diving varies dramatically with dive depth in birds because air volumes in the respiratory system and plumage change with hydrostatic pressure (Wilson et al. 1992; Lovvorn et al. 1999, 2004; Gaston 2004; Enstipp et al. 2006). Penguins, cormorants, sea turtles and whales appear to manipulate their air volumes or dive depths to attain neutral buoyancy to minimize the influence of buoyancy on dive costs (Hustler 1992; Minamikawa et al. 2000; Sato et al. 2002; Wilson et al.

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2003; Hays et al. 2004; Miller et al. 2004). Nonetheless, as the thickness of the insulative layer of air in bird plumage is compressed with increasing depth, heat flux across this layer is expected to increase (Wilson et al. 1992; Grémillet et al. 1998), perhaps creating a conflict between decreased work against buoyancy and increased costs of thermoregulation. The influence of drag on the energetic costs of dives increases dramatically with swim speed and, thus, birds appear to alter swim speeds to minimize increasing energetic costs associated with increased drag (Lovvorn et al. 2004; Tremblay et al. 2005; Heath et al. 2006). An increased layer of insulation may also result in increased cross-sectional area, which may increase drag and buoyancy (volume relative to mass; Hansen and Ricklefs 2004). Overall, as energetic costs per dive increase, more surface time is needed to extract sufficient oxygen for a given dive duration (Kramer 1988; Houston and Carbone 1992). With increased time spent at the surface between dives, marine predators likely experience decreased energy gain as encounter rates with prey during foraging bout are lower.

Although drag and buoyancy both clearly influence the biomechanics of swimming in endotherms, precisely how these parameters affect the energetic costs of underwater locomotion is still poorly understood. For example, energetic costs associated with non-neutral buoyancy depend heavily on estimates of air volume trapped within the feathers and respiratory system during diving. Estimates derived from dead or restrained individuals may not reflect volumes actually experienced during normal diving behaviour (Sato et al. 2002). Furthermore, living animals can manipulate dive depth to achieve neutral buoyancy by choosing depths at which they are neutrally buoyant (Minamikawa et al. 1997). Thus, in response to increased buoyancy animals can increase dive depth

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(and thus decrease buoyancy) and in response to decreased buoyancy animals can decrease dive depth (and thus increase buoyancy). Alternatively, animals can manipulate air stores to achieve neutral buoyancy for a given dive depth (Sato et al. 2002). For instance, pursuit-diving birds appear to increase air stores during longer surface pause durations before a deep dive, presumably to achieve optimal buoyancy during the succeeding dive (e.g., Wilson et al. 2003). Consequently, estimates based on maximal air stores may not be representative of actual energetic costs experienced by free-living animals.

Estimates of the energetic costs associated with drag have been derived from laboratory experiments on frozen birds (e.g., Lovvorn et al. 1999, 2004), which may not completely account for drag associated with wing motion (profile drag), apparatus effects and behavioural tactics (e.g., selecting gaits that reduce flow separation or that induce attached turbulent boundary layers to reduce skin friction) used by living birds and other animals to reduce drag. Drag coefficients and, thus, the energetic costs associated with drag, for birds flying in air are believed to be lower than those obtained on frozen specimens in the laboratory due to reduced flow separation behind living birds (Pennycuick 1997; Rayner 1999, 2001; Park et al. 2001; Ward et al. 2001; Tobalske et al. 2003; Elliott et al. 2004). Conversely, drag coefficients are higher during active swimming in some marine mammals than when measured on gliding or frozen specimens (William and Kooyman 1985; Fish 1988, 1993).

A complete investigation of avian biomechanics is important to understand the energetic costs associated with behavioural strategies of seabirds while foraging, as seabirds modulate foraging behaviour in response to varying energetic costs resulting

from changing prey abundance and distributional patterns (Mehlum et al. 1996; Grémillet and Wilson, 1999; Davoren et al. 2003a,b; Shaffer 2004; Tremblay et al. 2005). Investigating avian biomechanics is also essential for understanding the effect of recording devices on seabird behaviour (Gessaman and Nagy 1988; Obrecht et al. 1988; Bannasch et al. 1994; Culik et al. 1994). For example, recording devices have been found to increase workload without disrupting parental performance (e.g. seals: Boyd et al. 1991; Harcourt et al. 1995; seabirds: Weimerskirch et al. 1995; Kato et al. 2000; Shaffer et al. 2003), but can extend foraging trips (penguins: Croll et al. 1991b; Watanuki et al. 1992; Hull 1997; Ropert-Coudert et al. 2000; Taylor et al. 2001), reduce chick-provisioning rates (murres: Wanless et al. 1988; Watanuki et al. 2001; Hamel et al. 2004; Paredes et al. 2005) and reduce swim speed (Ropert-Coudert et al. 2006). Owing to this, I designed an experimental field study to complement the theoretical, laboratory and observational work on the biomechanics of pursuit-diving seabirds by Wilson et al. (1992), Lovvorn et al. (1999, 2004), Watanuki et al. (2003, 2006), Gaston (2004) and others.

To address the relationship between energetic cost and behaviour, I increased energetic costs of foraging by attaching buoyancy and drag handicaps to parental thick-billed murres during incubation and chick-rearing periods. I monitored the responses in the at-sea foraging behaviour of free-living murres to these handicaps using TDRs. I predicted that when the energetic costs due to drag increased, dive depth, swim speed and duration would decrease to minimize energetic costs but surface pause duration would increase for a given dive duration to allow more time to replenish oxygen reserves. I also predicted that to maintain neutral buoyancy, dive depth would increase when buoyancy

was increased and dive depth would decrease when buoyancy was decreased. In addition, I predicted that birds would increase their air stores as dive depth increased to maintain neutral buoyancy.

Materials and methods

Study Area and Design

Experiments were carried out at the west colony on Coats Island (62°57'N, 82°00'W), Nunavut, Canada (Gaston et al. 2003, 2005) during the incubation and chick-rearing periods in 2005. Past observations indicated variation in time of breeding and site quality, but not feeding rates, across the colony (Hipfner et al. 1997, 2006). Owing to this, I captured individuals at four different sites (Jb, Q, T and Z) for the buoyancy experiment. This experiment was conducted on incubating adults or adults with chicks less than 5 d old. Alternately, the drag experiment was conducted on adults with chicks less than 12 d old. Due to the small number of young chicks remaining by August, only a single site (Z) was used for the drag experiment.

Temperature-Depth Recorders

Thick-billed Murres were caught with a noose pole. All procedures for TDR attachment were approved by the University of Manitoba Animal Care Committee under Protocol Number F04-030. Handling time was always less than 15 min and usually less than 5 min. Lotek 1100LTD TDRs (Lotek Marine Technology, St. John's, Newfoundland, Canada) were secured with duct tape to plastic bands and attached to one legs of each murre during all experiments. Murres do not use their legs for underwater propulsion and, thus, recording devices were thought to have limited impact on diving behaviour (see Chapter 3). These cylindrical devices (mass = 4.5g; diameter = 1 cm;

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length = 3.3 cm) were attached parallel to the leg with the rounded end facing toward the body and the pressure sensor facing toward the foot.

TDRs were programmed to sample temperature and depth every 3 s and were calibrated by the company prior to the field season with accuracy of ± 0.1 m. A SCUBA diving session to 30 m prior to the field season revealed a precision of ± 0.1 m for four of the TDRs. However, drift of ± 1 m was evident in some cases, and error was also present through changes in velocity and acceleration (Bernoulli Effect). Therefore, total absolute error was likely about ± 2 m. The temperature log on the TDRs was used to determine the at-sea time budgets of each parental murre, resulting in estimates of the time spent flying, resting at the colony, resting on the water and diving (see Chapter 2).

Handicap Experimental Design

During the incubation and chick-rearing periods of 2005 (July 15-August 16), I attached three types of buoyancy handicaps to the legs of breeding adult murres. Each buoyancy handicap was constructed from three cylindrical plastic capsules (length = 3.4 cm; diameter = 1.3 cm), each with total volume 15 ± 1 cm^3. The negatively buoyant handicaps (mass = 22.5 ± 0.9 g) were filled with lead shot, and then sealed with a wooden cork, epoxy and duct tape. The positively buoyant handicaps (mass = 7.5 ± 0.2 g) were sealed with a wooden cork, epoxy and duct tape. The neutrally buoyant handicaps were left unsealed and weighed 15.0 ± 0.1 g when filled with water. Thus, the total buoyant force exerted by these handicaps was: 0.075 ± 0.01 N downwards (negatively buoyant), 0.00 ± 0.01 N (neutrally buoyant) and 0.075 ± 0.01 N upwards (positively buoyant). A buoyant force of 0.075 N is roughly 1.5 % of total murre surface buoyancy (4.93 N; Lovvorn et al. 1999, 2004) or 50% of total murre buoyancy at 60 m. Because the plastic

capsules compress little with depth, the buoyancy of the positively buoyant handicaps did not change appreciably over dives.

The buoyancy experiment was completed for ten negatively buoyant, nine neutrally buoyant and nine positively buoyant individuals. To control for individual variation and breeding status, I monitored (with a TDR) each individual for an additional 24 - 48 h prior to attachment of handicaps or after removal of handicaps. In all cases, the entire experiment occurred within a 96-h period. For three positively buoyant, five negatively buoyant and three positively buoyant handicaps, the handicaps were attached for the initial 24-48 h whereas for the remainder the handicaps were attached for the second 24 - 48 h period. I visually inspected all handicaps post-use. Two positively buoyant handicaps showed signs of leakage and were removed from analysis.

For the drag experiment, I attached neutrally buoyant blocks with a cross-sectional area of 2.8 or 5.6 cm^2 (ca. 3 % and 6 % of total body cross-sectional area, respectively) for 24 - 48 h during chick-rearing (August 5-16) in 2005. Each block measured 6.9 cm long, 1.5 cm high, and 3.7 or 1.85 cm wide, and weighed 38.3 or 19.2 g after 30 min submersion in saltwater. The handicaps were made of plywood and, with less than 2 % of the wood appearing above water, were effectively neutrally buoyant after 30 min submersion in saltwater. Grooves 1.4 cm wide and 0.7 cm deep were cut to aid in securing the handicap to the bird. I attached the handicaps to the back feathers of selected murres using cable ties and duct tape. Every effort was made to attach the handicaps parallel to the back and posterior to the wings. Order of attachment (e.g., "control" versus "handicap" period) was randomized by flipping a coin.

Prior to the experiment, I tested negatively ($n = 2$) and neutrally ($n = 2$) buoyant plastic handicaps and 5.6 cm^2 ($n = 2$) wooden handicaps to make sure they did not cause nest abandonment. All initial tests were successful, except for three birds given a third back-mounted wooden handicap (length = 6.9 cm; cross-sectional area = 11 cm^2; mass = 65 g). One of these individuals returned quickly without a handicap, another was not seen for 3 d; the last was never seen again. All three chicks of these individuals fledged (the handicaps were attached to females and the male continued to rear the chick) and in all cases the handicaps were designed to fall off after a few days, as the tape became saturated with water.

Data analyses

All statistical procedures were completed in STATISTICA. Prior to using parametric statistics, I tested for normality (Shapiro-Wilk test) and homogeneity of variance (Levine's test). Means are presented ± SE. To minimize any bias associated with the diel light cycle, all dives between 2200 and 0400 were excluded (Croll et al. 1992). Because I had strong *a priori* expectations, I used one-tailed paired *t*-tests to compare dive depths and durations with and without handicaps.

As ascent and descent rates approximated actual swim speeds (Lovvorn et al., 2004), I estimated ascent and descent rates to whether murres alter swim speeds with increased buoyancy and drag. For each TDR measurement, I calculated ascent and descent rates at a given sampled depth using the formula:

$$U_n = \frac{\dfrac{d_{n+1} - d_n}{3} + \dfrac{d_n - d_{n-1}}{3}}{2} = \frac{d_{n+1} - d_{n-1}}{6}.$$

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where d_{n-1}, d_n and d_{n+1} are the depths at consecutive 3-s sampling intervals and U_n is the vertical speed at sample time n. I binned all dives in 10 m increments according to their maximum depth (e.g. 60-70 m; 70-80 m, etc.; see Fig. 2.1). I only examined ascent and descent rates greater than 10 m above a given bin to avoid including bottom time in my calculations for ascent and descent rates. For instance, for dive depths between 30 and 40 m, I only examined ascent and descent rates above 20 m. I used one-tailed paired t-tests to compare ascent and descent rates when diving to the same 10-m bins of depth. I only included measurements where I had data for at least five individuals for any given maximum depth. To eliminate the possibility that differences in dive depths were due to handicapped individuals reducing or increasing the proportion of non-feeding dives, I completed another set of analyses with dives < 20 m excluded, as murres often do not forage during shallow dives (Croll et al. 1992).

To test the influence of handicaps on surface pause durations, I only used the data from the drag handicaps. I ln-transformed surface pause duration for each of the three treatments (no handicap, 2.8 cm^2 and 5.6 cm^2), then used an ANCOVA to determine whether the relationship between surface pause duration and dive duration was different for each of the three treatments.

To test the influence of handicaps on at-sea time budgets of parental murres, I measured the proportion of time spent flying and diving with and without handicaps. I used a one-tailed t-test to determine whether murres decreased time spent diving or flying when handicapped.

Passive Ascent Model

I developed a simple model for estimating plumage and lung air stores and "optimal" descent rates. Descriptions and values for symbols can be found at the start of the thesis. As the angle between the body and the vertical, θ, increases from 20° during deep dives (~120 m; Lovvorn et al., 2004) to 33° during shallow dives (~27 m; Watanuki et al., 2003, 2006), I modeled ascent assuming both of these values to illustrate the sensitivity of my results to this parameter. Although body angle can change with dive depth, it is usually constant for a given maximum depth, after initial variation during the changeover from the bottom phase to the ascent phase (Lovvorn et al., 2004; Watanuki et al., 2003, 2006). Occasional wingbeats do not greatly impact model accuracy because guillemots approach ±5% of passive ascent speeds within 2 s after each wingbeat (KHE, unpublished data). During ascent, the buoyancy F_B equals drag F_D:

$$F_D = F_B \cos\theta \quad (1)$$

with the horizontal component of buoyancy presumably counteracted by "lift" generated by the almost-vertical wing (Sato et al., 2002); at the steep angles experienced by guillemots during ascent, vertical lift will not be appreciable (Sato et al., 2002). Lovvorn et al., (2004) measured drag on frozen guillemots as a function of swim speed U, giving the relationship $F_D = 1.08 + 2.55U^2 - 1.38U^3 + 0.276U^4$, and I use this expression for F_D. Because studies on flying birds have sometimes shown that body parasite drag measured on frozen specimens in the laboratory is likely lower than the combined body parasite and wing profile drag of living birds (Pennycuick, 1997; Rayner, 1999, 2001; Park et al., 2001; Ward et al., 2001; Tobalske et al., 2003; Elliott et al., 2004), I completed my analyses with drag given by F_D, $0.7F_D$ and $0.3F_D$ to illustrate the sensitivity of my model

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to this parameter. In our case, actual U is determined from ascent rate U_a and angle θ between the bird's body and the vertical:

$$U = \frac{U_a}{\cos\theta} \quad (2)$$

I use the expression for F_B and F_g described in Wilson et al., (1992) with net buoyancy of body tissues given by -0.626 N (Lovvorn et al., 2004). These substitutions provide:

$$1.08 + 2.55U^2 - 1.38U^3 + 0.276U^4 = \left(\frac{\rho g p_s V_s}{p_s + \rho g d} - 0.626\right)\cos\theta \quad (2)$$

where m is mass, g is acceleration due to gravity, p_s is atmospheric pressure, ρ is water density, d is depth and V_s is lung and plumage air volume. Rearranging the equation gives an estimate for V_s:

$$V_s = \left[1.08 + 2.55\left(\frac{U_a}{\cos\theta}\right)^2 - 1.38\left(\frac{U_a}{\cos\theta}\right)^3 + 0.276\left(\frac{U_a}{\cos\theta}\right)^4 + 0.626\cos\theta\right]\frac{p_s + \rho g d}{\rho g p_s \cos\theta} \quad (3)$$

Results

Four out of 14 individuals with 2.8-cm^2 handicaps were not recaptured and, thus, the handicaps were not removed and the data not downloaded from the TDRs. In one case the chick appeared to have fledged prematurely (but apparently successfully) with the adult wearing the handicap. In another case, the chick was depredated and the adult only reappeared at the colony on once. In the other two cases the handicapped parents appeared to have abandoned breeding attempts, and the chick died after 36 - 60 h of intermittent care by the remaining parent. The 5.6-cm^2 handicaps never caused abandonment during 13 attachments, including three without TDRs, two that fell off prior

to 24 h and one for which no control period was obtained due to problems with recapture. One of two birds given large handicaps (11 cm^2) was never observed again at the colony, and presumably abandoned its breeding attempts; the other bird disappeared for three days before reappearing without its handicap. In the latter case, the chick had fledged by the time the bird reappeared, so that particular bird was presumably not involved in chick-rearing after the handicap was attached.

At-sea Foraging Behaviour

For non-handicapped birds, descent rates increased with depth to about 70 - 100 m ($F_{20,241}$ = 12.54, P < 0.001, Fig. 1.1), but were independent of maximum dive depth ($F_{30,247}$ = 0.49, P = 0.97). Ascent rates during a given dive were generally uniform between 80 - 140 m in depth and then increased steeply at shallower depths (Fig. 1.1). Ascent rates also increased with maximum depth. The passive ascent model revealed that estimated equivalent surface air and plumage volumes increased with maximum depth to about 90 m (Fig. 1.2) but decreased as the murre surfaced over the final 20 m (Fig. 1.3).

Handicapped murres did not dive as deep, or for as long, and descended more slowly, whenever drag or buoyancy was altered, but showed no difference when neutrally buoyant handicaps were attached to the leg (Table 1.1). Murres ascended slower when buoyancy was decreased or drag increased, but showed no difference when neutrally or positively buoyant handicaps were attached to the leg (Table 1.1).

Comparisons between handicapped and non-handicapped birds revealed that when drag was increased, there was no difference in surface pause duration (5.6 cm^2 = 14 ± 22 m; paired t = 0.64; df = 5; P = 0.56; 2.8 cm^2 = -22 ± 74 m; paired t = -0.74; df = 7; P = 0.50). This occurred because handicapped individuals paused longer at the surface for a

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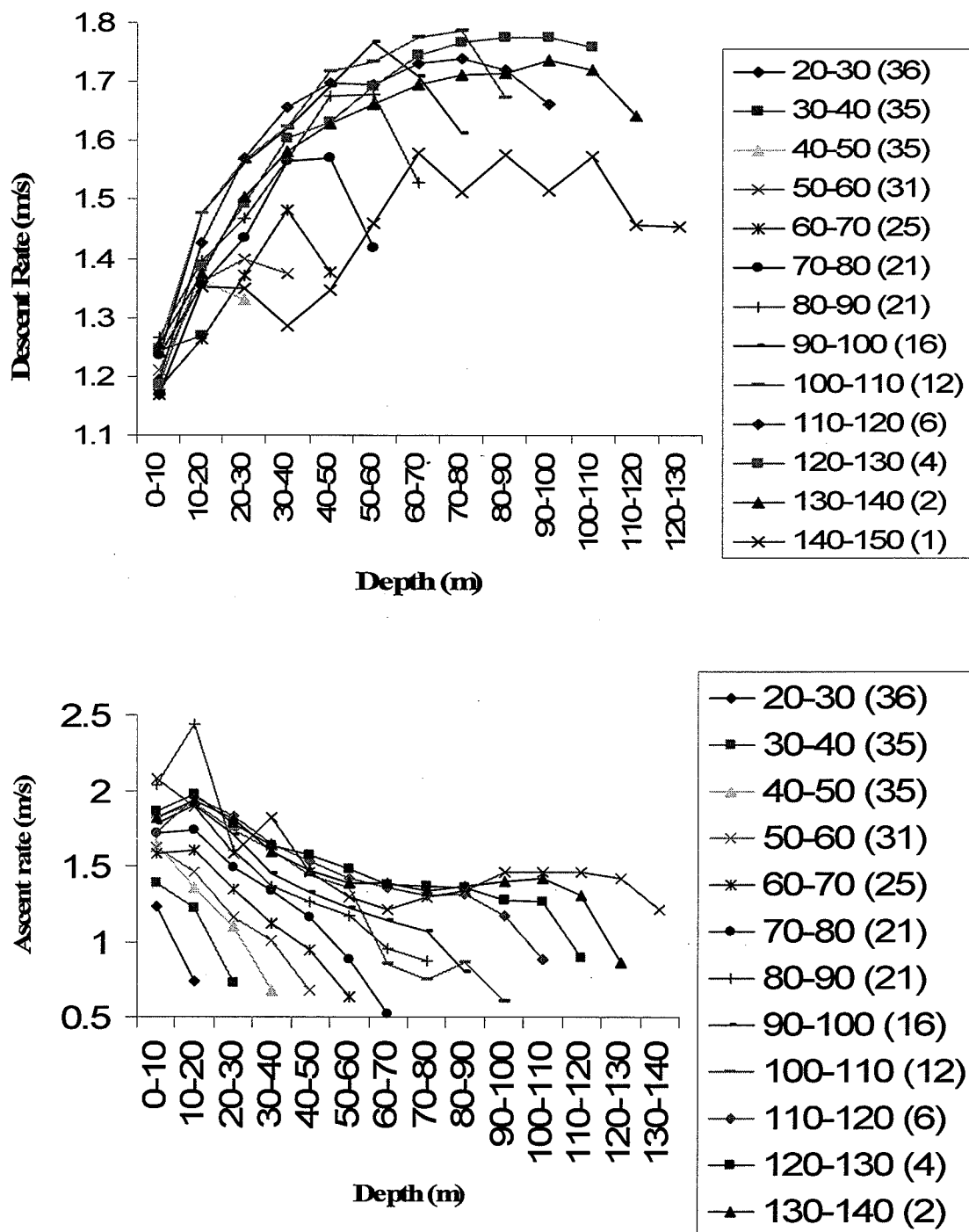
Figure 1.1. (a) Descent rates (m/s) relative to dive depth for dives with different maximum depths. (b) Ascent rates (m/s) relative to dive depth for dives with different maximum depths. Symbols denote mean values for non-handicapped Thick-billed Murres diving to different maximum dive depths within each 10-m bin (number of individuals in parentheses).
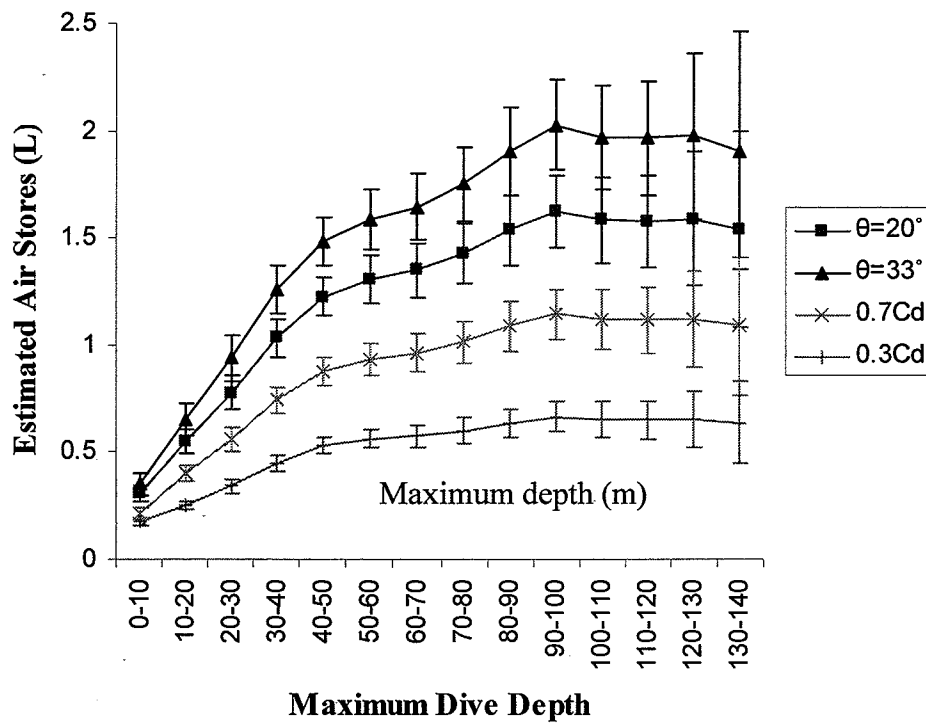
Figure 1.2. Estimated equivalent surface respiratory and plumage air volume versus maximum depth for non-handicapped Thick-billed Murres (n = 20), assuming θ = 20° and θ = 33°, where θ is the angle between the body and the vertical. Body angles for Thick-billed Murres increases from θ = 20° at deep depths (~120 m; Lovvorn et al., 2004) to θ = 33° at shallow depths (~27 m; Watanuki et al, 2003, 2006). The sensitivity of the model to drag estimates is illustrated by multiplying the values given in Lovvorn et al., (1999, 2004) by 0.7 (0.7Cd) and 0.3 (0.3Cd). Values for each individual are averaged over all dive depths >40 m, or 5 m above the beginning of ascent (for dives shallower than 40 m), to avoid including active portions of ascent. Error bars refer to SE.
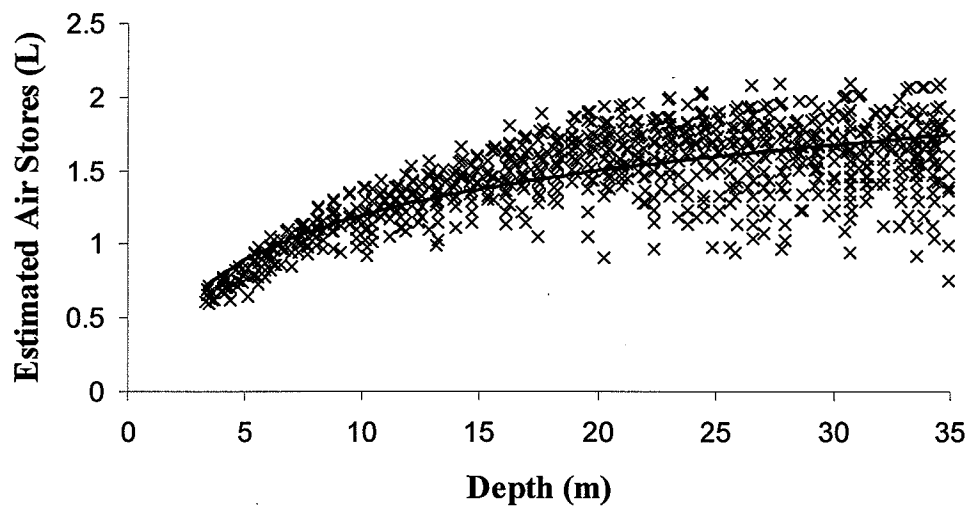
Figure 1.3. Estimated equivalent surface lung and plumage air volume versus depth during ascent for non-handicapped Thick-billed Murres (n = 20), assuming the angle between the body and the vertical is 20°. Only dives with maximum depth > 90 m are included to avoid confounding the relationship between estimated air volumes and maximum depth.

Table 1.1. Mean ± SE decrease in dive depth, duration, ascent rate, and descent rate between handicapped and non-handicapped Thick-billed Murres at Coats Island, Nunavut, Canada.

	B+ (10)	B- (11)	B0 (9)	2.8 cm^2 (8)	5.6 cm^2 (6)
Depth (m)	19 ± 9*	7.9 ± 3.0*	4.4 ± 8.8	12 ± 5*	27 ± 11*
Duration (s)	26 ± 11*	21 ± 7*	-0.6 ± 12.0	9.1 ± 6.8	46 ± 14*
Ascent rate (m·s^{-1})	0.06 ± 0.05	0.13 ± 0.05*	0.06 ± 0.05	0.13 ± 0.06*	0.16 ± 0.04†
Descent rate (m·s^{-1})	0.12 ± 0.06*	0.17 ± 0.05†	0.01 ± 0.02	0.13 ± 0.05*	0.32 ± 0.02†

B+, increased buoyancy; B-, decreased buoyancy; B0, neutral buoyancy; 2.8cm^2, 2.8cm^2 cross-section neutral buoyancy; 5.6çm^2, 5.6cm^2 cross-section neutral buoyancy.
* and † denote significant differences from non-handicapped murres at $P<0.05$ and $P<0.01$, respectively (paired t-test).

given dive depth and duration (Fig. 1.4). Murres with drag handicaps spent significantly less time diving (5.6 cm^2: 67 ± 45 mins·d^{-1}, unhandicapped: 196 ± 65 mins·d^{-1}; one-tailed paired t_5 = 4.56, P = 0.0001; 2.8 cm^2: 129 ± 69 mins·d^{-1}, unhandicapped: 257 ± 89 mins·d^{-1}; one-tailed paired t_7 = 3.66, P = 0.003;), but showed no difference in time spent flying (5.6 cm^2: 44 ± 52 mins·d^{-1}, unhandicapped: 79 ± 65 mins·d^{-1}; one-tailed paired t_5 = 1.92, P = 0.07; 2.8 cm^2: 54 ± 49 mins·d^{-1}, unhandicapped: 77 ± 49 mins·d^{-1}; one-tailed paired t_7 = 1.57, P = 0.10;).

Murres with negatively buoyant handicaps spent significantly less time diving (handicapped: 117 ± 69 mins·d^{-1}, unhandicapped: 201 ± 78 mins·d^{-1}; one-tailed paired t_{10} = 3.25, P = 0.004), but showed no difference in time spent flying (handicapped: 80 ± 47 mins·d^{-1}, unhandicapped: 94 ± 30 mins·d^{-1}; t_{10} = 0.78, P = 0.23), whereas murres with neutrally buoyant handicaps showed no difference in time spent diving (handicapped: 191 ± 255 mins·d^{-1}, unhandicapped: 139 ± 54 mins·d^{-1}; t_8 = 0.69, P = 0.25) or flying (handicapped: 84 ± 122 mins·d^{-1}, unhandicapped: 69 ± 54 mins·d^{-1}; t_8 = 0.38, P = 0.32). Murres with positively buoyant handicaps also spent significantly less time diving (handicapped: 135 ± 71 mins·d^{-1}, unhandicapped: 212 ± 70 mins·d^{-1}; one-tailed paired t_9 = 2.54, P = 0.02) and showed no difference in time spent flying (handicapped: 99 ± 41 mins·d^{-1}, unhandicapped: 91 ± 50 mins·d^{-1}; t_9 = 1.18, P = 0.16).

Discussion

The results of this study suggests that attachment of devices that increase drag or alter buoyancy alters foraging behaviour, including dive depth, duration, swim speeds, at-sea time budgets, and the relationship between surface pause duration and dive duration. The

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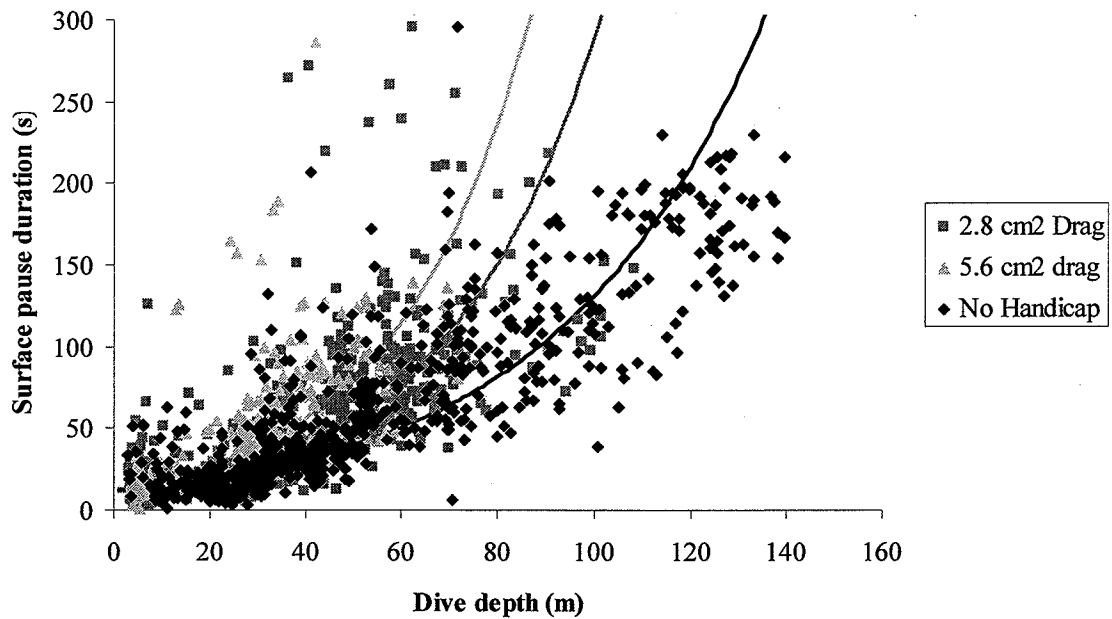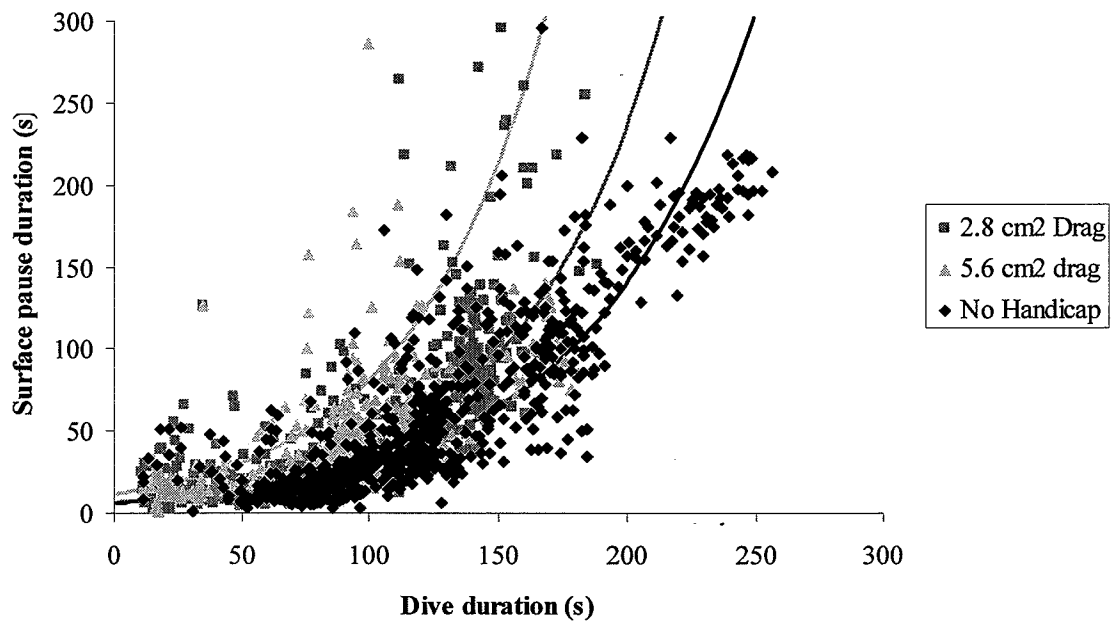
Figure 1.4. Subsequent surface pause duration of handicapped individuals relative to (a) dive duration and (b) dive depth. Equations shown are: (a) 5.6 cm^2: $11.7e^{0.019\text{Duration}}$ ($R^2 = 0.48$); 2.8 cm^2: $6.48e^{0.018\text{Duration}}$ ($R^2 = 0.69$); No Handicap: $6.22e^{0.016\text{Duration}}$ ($R^2 = 0.65$); (b) 5.6 cm^2: $13.0e^{0.036\text{Duration}}$ ($R^2 = 0.50$); 2.8 cm^2: $10.9e^{0.033\text{Duration}}$ ($R^2 = 0.63$); No Handicap: $12.2e^{0.024\text{Duration}}$ ($R^2 = 0.68$).

decreasing size of data-logging devices used on murres from the 32 g back-mounted TDRs used by Croll et al. (1992) to the 4.5-g leg-mounted TDRs used in this study likely explains why maximum dive depth and dive duration reported for murres have steadily increased since Croll et al.'s (1992) original study (Table 1.2), assuming data from a few anomalously deep dives determined from capillary tubes are false (Croll et al. 1992). The leg-mounted TDRs used in this study showed no effect on provisioning rate or adult mass loss, in comparison to individuals without TDRs (see Chapter 3), in contrast to all previous studies of murres in which these parameters have been quantified (Wanless et al. 1988; Croll et al. 1993; Watanuki et al. 2001; Hamel et al. 2004; Paredes et al. 2005). Small ventral or internal attachments, which have successfully overcome these difficulties in other species (cf. Ballard et al. 2001), affect behaviour of murres and other alcids (Meyers et al. 1998; Hatch et al. 2000; Tremblay et al. 2003). Furthermore, neutrally buoyant handicaps attached to the legs had no measurable impact on dive parameters, whereas neutrally buoyant devices attached to the backs did. Consequently, the leg-attachment method appears to be the best available device position for murres.

Influence of Buoyancy and Drag Handicaps on Dive Parameters

When buoyancy was altered or drag increased murres reduced both dive depth and duration. This suggests that murres do not manipulate dive depth solely to obtain neutral buoyancy. Rather, murres likely choose dive depths based on expected energy gain relative to energy expenditure (Gaston 2004). Increasing energy expenditure by increasing drag or altering buoyancy likely leads to more rapid depletion of oxygen stores and thus reduced duration. Northern elephant seals (*Mirounga angustirostris*) similarly decreased depth and duration in response to alterations in buoyancy (Webb et al. 1998).

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Table 1.2. Mean dive parameters of chick-rearing Thick-billed Murres from studies with TDRs of different sizes and masses.

TDR Mass (g)	Area (mm^2)	N[1]	Depth (m)	Maximum depth (m)[2]	Dura-tion (s)	Maximum duration (s)[3]	Source
4.5	75	17	79	88 (140)	68	153 (246)	This study[4]
12	254	2	29	76 (77)	78	132 (136)	Woo 2001[6]
14	177	9	48	114 (136)	105	175 (196)	Mori et al. 2002
19.2	280	8	36	86 (112)	82	156 (177)	This study[5]
17	450	17			98	187 (240)	Jones et al. 2002
28.5	417	25			100	187 (249)	Woo 2001[6]
28.5	414	14				123 (240)	Falk et al. 2000
28.5	417	3			105		Benvenuti et al. 2002
35	375	8	18	74 (107)	55	156 (224)	Croll et al. 1992
38.3	560	8	26	61 (74)	68	132 (171)	This study[5]

[1]Number of birds per study; [2]Maximum dive depth over all individuals in parentheses; [3]Maximum dive duration over all individuals in parentheses; [4]Unhandicapped individuals sampled during chick-rearing period; [5]Individuals handicapped with drag handicaps (larger sample size due to individuals for which no control period was obtained); [6]Parameters derived from raw data obtained using Star-Oddi and Benvenuti TDRs for Woo (2001)

My results, in this respect, are remarkably similar to those of elephant seals, although seal results were not significant, possibly due to low sample sizes.

I hypothesize that dive depths in most species are determined by prey depth and energetic costs rather than by a need for achieving neutral buoyancy, except under unusual circumstances, such as non-feeding loggerhead turtles (*Caretta caretta*) at shallow depths where drag is minimal as the turtles are not moving (Minamikawa et al. 2000). Several murres handicapped with 5.6-cm^2 handicaps switched from bouts primarily consisting of deep dives with lots of bottom time to bouts consisting of shallow dives with little bottom time. The latter individuals often delivered amphipods to their chicks, whereas most deliveries were of fish 10-100 times heavier than amphipods (see Chapter 2). Hence, this handicap may have caused individuals to switch to a prey species that costs less to capture but provided chicks with less energy (Gaston et al. 2003, 2005).

Rather than manipulating depths to achieve neutral buoyancy, murres appeared to control pre-dive air volumes to achieve neutral buoyancy for a given depth because ascent rate increased with maximum dive depth (Fig. 1.1b). The increase in ascent rate with maximum depth partially represents a change in dive angle, as murres reduce dive angle during ascent from ~70° during deep dives to ~57° during shallow dives (Watanuki et al. 2006). Nonetheless, to account for a change in ascent rate from 1.3 to 1.8 m·s^{-1} at 10 m (Fig. 1.1b), an increase in dive angle from ~35° to 70° would be necessary. This is well beyond that shown in Lovvorn et al. (2004) and Watanuki et al. (2006) or for shallow-diving birds observed from atop the colony or during underwater video footage. It is unlikely that this relationship represents differences in wingbeat frequency or initial ascent speed as murres usually do not beat their wings during ascent and they quickly

achieve passive ascent speed during ascent (Lovvorn et al. 1999, 2004). Beyond 70 - 90 m, pre-dive air volumes appeared to be maximal (Fig. 1.2).

The ability to adjust buoyancy, with the exception of negative buoyancy beyond the point where pre-dive air stores were maximized, may also explain why I saw a reduction in ascent rates for negatively buoyant handicaps but no change in the rate for positively buoyant handicaps. Sato et al. (2002), using passive ascent models and accelerometer data, concluded that penguins control air volumes to regulate buoyancy. Wilson (2003) and Wilson et al. (2003), using air flow loggers attached to the mouth, showed that spheniscid penguins actively control inhaled air volume depending on the depth of the subsequent dive. Metabolic rate depends heavily on dive depth in benthic-feeding cormorants and they may also control inhaled air volumes (Enstipp et al. 2006).

No avian study has yet been able to separate increased air volume for neutral buoyancy at depth from increased air intake for increased dive duration at depth. For murres, air stores increased approximately linearly with dive depth < 60 m (Fig. 1.2) and surface pause duration increases linearly with dive duration for short dives (Croll et al. 1992; Mori et al. 2002), suggesting that air stores may track dive duration, which increases linearly with depth, rather than buoyancy, which increases non-linearly with depth. I concluded that air stores were likely manipulated to achieve a compromise between sufficient oxygen stores for a given dive depth and minimal costs associated with buoyancy. Turtles, which dive for long periods to shallow depths, control air volumes to achieve neutral buoyancy rather than extending dive duration (Milsom 1975; Minamikawa et al. 1997). Estimated air stores decreased in the top 20 m during deep dives (Fig. 1.3; Gaston 2004), suggesting that murres reduce air stores near the surface,

presumably to reduce the risk of decompression sickness (Croll et al. 1992). Other deep-diving vertebrates also exhibit shallow water slow-down, including penguins (Kooyman et al. 1971; Sato et al. 2002) and Antarctic fur seals (*Arctocephalus gazelle*; Hooker et al. 2005).

Changes in Surface Pause Duration in Relation to Handicaps

As predicted by Carbone and Houston (1992), dive duration decreased when energetic costs of diving were increased, whereas surface pause duration did not change. This occurred because increased drag resulted in surface pause duration increasing for a given dive duration or depth (Fig. 1.4). Similar results have been found for ducks (Carbone and Houston 1994; Halsey et al. 2002), sea lions (Cornick and Horning 2003) and elephant seals (Webb et al. 1998). These studies provide support for optimal foraging models proposed by Carbone and Houston (1992), and suggest a strong link between energetic costs of underwater locomotion and the relationship between surface pause duration and dive duration. As energetic costs increase, surface pause duration becomes an increasing portion of the dive cycle (Monaghan et al. 1996). Eventually, dive duration, and, therefore, bottom time, will be a small proportion of the dive cycle. Thus, as energetic costs increase, the amount of time available for energy intake (bottom time) decreases. At some point, energetic costs will be so high that energy intake will no longer be able to balance energetic costs, and the animal will be in a negative energy balance (Mori 1999).

Conclusions

Increased energetic costs resulted in pronounced effects on the at-sea foraging behaviour of this pursuit-diving species. These results suggest that interpretations of dive behaviour must take into consideration the likely effect of devices on behaviour. The

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results also show that murres appear to manipulate pre-dive air stores to obtain optimal buoyancy for a given depth. This is important, because it suggests that murres select depth for prey availability and not to obtain optimal buoyancy. Thus, depth presumably reflects a tradeoff between energy and time costs of transit and variation in prey density. My results also show that as energetic costs increase, time spent foraging (percent of time diving, percent of the dive cycle spent underwater) decreases. Eventually, energetic costs would likely become so high that it is no longer profitable to forage. At this point, the birds may cease foraging and wait for conditions to improve. Over a short time scale, this may reflect reduced time spent underwater. Over a large time scale, this may reflect postponing breeding until the following season. The latter case may explain why several birds, when handicapped with large drag handicaps, abandoned breeding altogether. Alternatively, birds may switch to a more profitable prey patch, where prey can be captured with reduced energy expenditure. This may explain why several birds with drag handicaps returned with amphipods. A more detailed examination of the role of prey quality influencing at-sea foraging behaviour is the subject of the next chapter.

Chapter 2: The influence of prey type on the at-sea foraging behaviour of Thick-billed Murres

Early theoretical formulations of foraging ecology characterized animals as naïve foragers, randomly encountering prey items while foraging (Macarthur and Pianka 1966; Ward and Zahavi 1973; Orians and Pearson 1979). Recent empirical results, however, have shown that predators specializing on specific prey types ("specialists") actively return to locations known to have high abundance aggregations of that specific prey (Davoren et al. 2003; Wilson et al. 2005). Nonetheless, it is unclear whether predators that prey on a variety of prey types ("generalists") also actively change their behaviour to search for and capture specific prey items, or whether they move randomly through a habitat and consume prey items as they are encountered (Barrett 2002; Woehler et al. 2003; Tremblay et al. 2005). Therefore, it is unclear whether the proportions of prey items in the diet reflect the relative abundance in the environment (Barrett 2002), the selection of more energetically profitable items (Gaston 2004), or the relative abundance of individuals specializing on specific prey types within a population (Bolnick et al. 2002; 2003).

Seabirds with a generalist diet are potentially ideal indicators of changes in the marine ecosystem because they are conspicuous predators that are easily monitored and that provide simultaneous information on several prey items and potentially several trophic levels (Barrett and Krasnov 1996; Montevecchi and Myers 1996; Furness and Camphuysen 1997). In arctic environments, the use of seabirds to monitor environmental change is especially important because conventional marine sampling techniques are prohibitively expensive. Many arctic seabirds are generalists (Gaston et al. 2003; Gaston

2004) and because the foraging behaviour of generalist predators is poorly understood, it is unclear whether dietary shifts reflect changes in prey abundance or changes in predator behaviour (Bryant et al. 1999; Gaston 2004). Therefore, generalist seabirds are not frequently used as indicators (Montevecchi and Myers 1996; Bryant et al. 1999; Gaston et al. 2003), whereas specialist seabirds are frequently used as indicators of changes in spatial and temporal changes in fish populations (Aebischer et al. 1990; Watanuki et al. 1993; Monaghan 1996; Davoren and Montevecchi 2003, 2005; Miller and Sydeman 2004) and age-specific recruitment in fish (Barrett et al. 1990; Barrett 1990; Bertram and Kaiser 1993).

The at-sea foraging behavior of seabirds is thought to be a better indicator of prey abundance than colony measures, such as chick growth or breeding success, because adults can buffer changes in prey availability through changes in provisioning behavior (Cairns 1987, 1992; Monaghan 1996; Grémillet 1997; Baillie and Jones 2004; Jodice et al. 2006). With the invention of miniaturized bird-borne devices, seabird biologists have been able to examine many aspects of foraging behavior at sea that were formerly difficult or impossible to observe (e.g., Wilson et al. 1992, 1995; Putz et al. 1998; Charrassin et al. 2001; Charrassin and Bost 2001; Catry et al. 2003; Takahashi et al. 2004).

Dive parameters, including duration, depth and shape have been touted as potential tools for inferring the vertical distribution of prey as well as foraging locations, although the interpretation of dive shape is complex (Schreer et al. 2001). Dive depth and duration are known to be directly correlated and generally indicative of bathymetry where benthic species are captured, but indicative of the vertical distribution of pelagic prey. Jodice and

Collopy (1999) compared correlation coefficients among different predators, and concluded that dive depth and duration were correlated for benthic predators but not for pelagic predators. They argued that this occurred because benthic prey types occur at a fixed dive depth, whereas pelagic prey types may be distributed throughout the water column. Mori et al. (2002) argued that if prey are distributed in patches, then dive duration will be shorter, for a given dive depth, in patches of high prey density than patches of low prey density because reducing bottom time relative to transit time will only be profitable if prey densities are high.

Surface pause duration is also expected to change with prey type and has been used as an indicator of prey abundance (Monaghan 1996). Surface pause duration is closely correlated with both dive depth and duration, either because divers anticipating a deep dive remain at the surface longer to obtain sufficient oxygen stores or because divers surfacing from a deep dive remain at the surface to remove lactate and carbon dioxide from the blood (Carbone and Houston 1996, Costa et al. 2001, Wilson et al. 2003). Surface pause duration increases rapidly once oxygen stores are depleted due to the slow rate of lactate metabolism (Carbone and Houston 1996, Kooyman and Ponganis 1998, Butler 2006). Therefore, to maximize time spent foraging during a dive, breath-hold divers are anticipated to dive within their ADL, which is the maximum time a diver can remain submerged without resorting solely to anaerobic respiration (Costa et al. 2001, Kooyman and Ponganis 1998, Butler 2006). Nonetheless, it may be beneficial to increase bottom time by exceeding ADL once prey items are encountered (Ydenberg and Clark 1988; Croll et al. 1992). Anaerobosis can be cost-effective if (1) high prey density generally of schooling fish resulting in high capture rates, outweighs the cost of lower

encounter rates with prey as surface durations increase, or (2) the probability of losing contact with an ephemeral prey source during transit to the surface is high, especially if locating a new prey source is time/energy consuming (Ydenberg and Clark 1988; Jodice and Collopy 1999). Increasing bottom time to maximize time spent pursuing ephemeral, schooling fish has been the dominant explanation for understanding why some deep-diving birds routinely exceed their ADL (Ponganis et al. 1997; Kooyman and Ponganis 1998; Nagy et al. 2001).

Thick-billed Murres in the sub-arctic are particularly well-suited for investigating how at-sea foraging behaviour changes when capturing different prey types. First, these murres usually return to the colony with a single prey item ("single prey loaders", *sensu* Orians and Pearson 1979) and are sufficiently large that recording equipment can be deployed with limited impact on dive behavior (Jones et al. 2002; Mori et al. 2002; Paredes et al. 2006). Second, these murres have an especially diverse diet (Gaston 1980; Gaston and Bradstreet 1993), which partly reflects specialization by individual parents on different prey taxa. For instance, many parents breeding on Coats Island, Hudson Bay, are known to specialize on certain prey types both within a given breeding season and from year to year because they consistently provision their chicks with rare prey items (Woo 2001). Alternately, many other parents provision their chicks with a diversity of different prey types (Woo 2001). Thus, some parents specialize on certain prey types, whereas others readily switch between prey types.

To determine whether the foraging strategies of parental thick-billed murres, specifically dive behaviour and location (i.e. distance from the colony), differ when searching for and capturing different prey types, I quantified the species composition of

parental prey deliveries to chicks at the colony and integrated this with the at-sea foraging behavior from TDRs attached to parents during the chick-rearing season. I assumed that the last dive made by parents prior to returning to the colony represented the dive during which prey was captured for the chick (Houston 2000) and that dive parameters during the last dive bout represented foraging behaviour typical for searching for that species. I categorized the variety of prey types delivered to murre chicks based on ecological characters likely to influence foraging strategies, including prey mass (large, medium and small), density (solitary versus schooling), depth (benthic versus pelagic) and persistence in a location (stationary versus ephemeral; see Table 2.1).

Using this information, I made a number of predictions. First, I predicted that surface pauses will be longer, for a given dive depth or duration, during bouts preceding delivery of small, or low quality, prey types (e.g., amphipods, ~0.4 g) relative to large, or high quality prey types (e.g., large fish, ~10 g) and during bouts preceding delivery of stationary, benthic relative to ephemeral, schooling fish. For similar reasons, I predicted that dives will be longer, for a given dive depth, during bouts preceding delivery of large, or high quality prey types (e.g., large fish, ~10 g) relative to small, or low quality, prey types and during bouts preceding delivery of stationary, benthic relative to ephemeral, schooling fish. Second, I predicted that dive depths would represent the depth ranges generally utilized by a particular prey type. Third, I predicted that pelagic, schooling prey items would be obtained during V-shaped dives, where prey density is high and limited pursuit is required, whereas benthic prey items would be obtained during U-shaped dives, where prey are often solitary and pursuit is required to capture individual prey items.

Table 3.1. A summary of the ecological information for prey taxa delivered to chicks of Thick-billed Murres at Coats Island (1984-2004). Information are compiled from Brown and Green (1976), Kristensen (1984), Robins and Ray (1986), Scott and Scott (1988), Atkinson and Percy (1992), Borga et al. (2002). Age refers to the modal age, based on fork lengths observed. Depth refers to preferred depth (Shallow is < 60 m; Deep is > 90 m). Substrate refers to preferred substrate. Spawning period refers to average spawning period at closest reported location. Size refers to average size delivered to chicks (Small = < 5 g; Medium = 5-10 g; Small = > 10 g).

Latin name	Size	Depth	Persistence	Substrate	Spawning
Ammodytes hexapterus	Medium	Shallow	Ephemeral	Sandy	Winter
Boreogadus saida	Large	Variable	Ephemeral	Ice	Winter
Cottidae					
Myoxocephalus scorpius	Medium	Shallow	Stationary	Sandy, Kelp	Winter
Myoxocephalus aenaeus	Medium	Shallow	Stationary	Sandy	Winter
Icelus spatula	Medium	Variable	Stationary	Sandy	Fall
Triglops pingeli	Medium	Variable	Stationary	-	Winter
Triglops murrayi	Medium	Variable	Stationary	Sandy	Summer?
Gymnocanthus tricuspis	Medium	Deep	Stationary	Sandy, rocky	Winter
Eumesogrammus praecisus	Medium	Shallow	Stationary	Rocky	Fall
Gymnelus spp.	Large	Shallow	Stationary	All, kelp	Fall
Leptoclinus maculates	Medium	Deep	Stationary	Sandy, rocky	Winter
Mallotus villosus	Medium	Variable	Ephemeral	-	Summer
Stichaeus punctatus	Medium	Shallow	Stationary	Rocky	Winter
Lebbeus groenlandicus	Small	Variable		Rocky	Summer
Gonatus fabricii	Medium	Deep		Pelagic	Fall?
Parathemisto libellula	Small	Deep		Pelagic	?

Finally, following Jodice and Collopy (1999), I predict that dive duration and depth will be strongly correlated for benthic prey types but not for pelagic prey types.

Materials and methods

My study was conducted at the west colony on Coats Island (62°57'N, 82°00'W), Nunavut, Canada (Gaston et al. 2003, 2005a,b) during the breeding season in 2004 and 2005. To determine the species composition of prey deliveries to chicks by parental murres at the colony, continuous observational watches of nest sites ('feeding watches') were carried out. All observations were made from blinds situated on the study plots, within 6 m of the birds. A range of 40 – 100 nest sites were watched at one time, with a specific focus on nest sites of murres with attached data logging devices. Three 24 or 48 h continuous feeding watches were conducted during 2004 (Q-Plot: 30 July; 8 August; 14 August) and 2005 (Q-Plot: 24-26 July; 2-3 August; 7-8 August), as well as two shorter feeding watches (T-Plot: 14:00-19:00 28 July 2005; Z-Plot: 12:00-17:00 10 August 2005). I did not conduct feeding watches when it was too dark to see deliveries (roughly 01:00-02:00 local time in late July; 23:00-0:400 in mid August) because nestlings are rarely fed at this time (Gaston et al. 2003). During these observation sessions, prey items delivered to chicks at the colony were identified whenever possible and the arrival and departure times of parental birds at the colony were recorded. Fish length was estimated by reference to the white streak on the upper mandible of the adult birds' bill (~5 cm). These were then converted to mass using taxon-specific length-mass relationships (KHE, unpublished data).

Data Logging Device Attachment and Data Processing

To attach data logging devices, parental murres were caught at nest sites with a noose pole (2004: n = 23; 2005: n = 33). All TDR procedures followed those outlined in Chapter 1. I used temperature from the TDRs to determine whether the bird was sitting on the water, flying in the air, or sitting at the colony (Tremblay et al. 2003, see Chapter 3). Water temperature was always < 6 °C and air temperature was always > 6 °C. Because I also knew when the bird arrived at the colony from the feeding watches, I was able to determine the duration of the return flight to the colony after the last dive bout. I converted flight time into distance assuming 75 km·h^{-1} flight speed, ignoring variation in flight speed with wind speed, load and other factors (KHE, unpublished data). This calculation assumed that murres returned in a straight line from their foraging destination, as predicted from theoretical considerations for single-prey loaders (Orians and Pearson 1979, Houston 2000) and shown for murres at other colonies (Benvenuti et al. 1998; Falk et al. 2000, 2002). Because I assumed that the last dive made by a parent prior to returning to the colony represented the dive during which prey was captured for the chick, I assumed that the maximum depth of the last dive prior to returning to the colony represented the depth at which the prey item was collected. I obtained dive depths, durations and surface pause durations for all dives during the final dive bout preceding each prey delivery using a custom-built MS Excel macro that corrected for device drift and determined bouts based on sequential differences (Mori et al. 2001; difference criterion = 37.4 m or 63.4 s).

The shape of each dive was visually classified into 5 categories using the dive profile (Lescroël and Bost 2005; Fig. 2.1). W dives were approximately symmetrical with pronounced ragged bottom. V dives were symmetrical dives with no bottom phase. U1
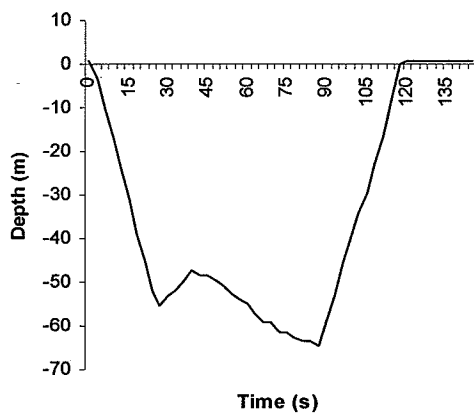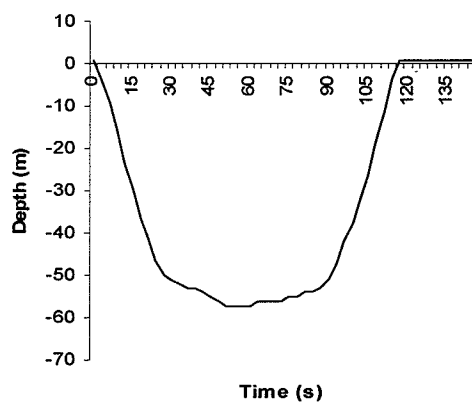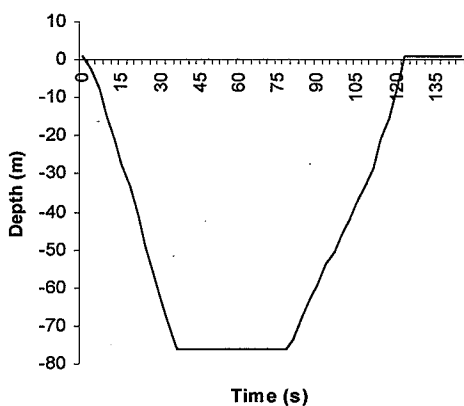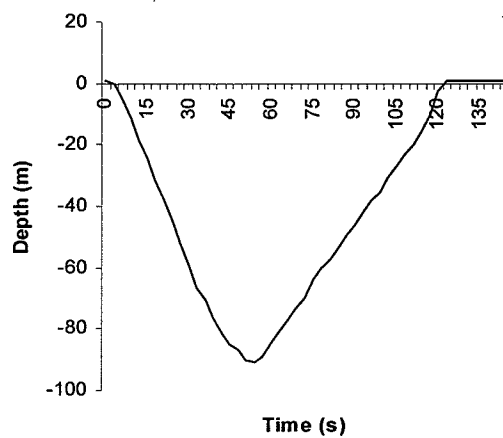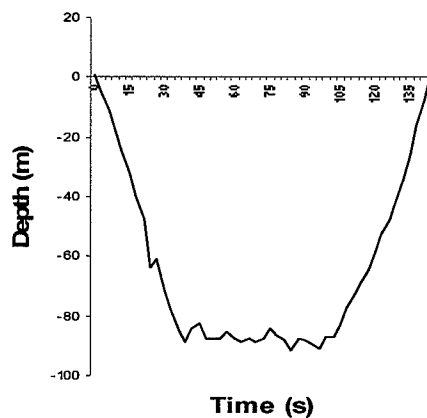
Figure 2.1. Dive shape classes: (a) W-shaped; (b) U2-shaped; (c) U1-shaped; (d) V-shaped (e) Irregular (I)-shaped. All profiles are from the same individual on August 13, 2004.

dives had > 3 consecutive identical measurements during the bottom phase, whereas U2 dives had a well-defined bottom phase with ≤ 3 consecutive identical measurements. I (irregular) dives were all others, such as those that repeatedly increased and decreased depth.

Water temperature

To determine whether prey types were collected at different locations with specific temperature regimes, I analysed surface temperature, depth-temperature profile, and temperature-at-maximum-depth, for the final dive for each prey type. Surface temperature was obtained immediately prior to the return flight to the colony. An index of the depth-temperature profile ("water temperature index") and temperature at maximum depth were obtained using a custom-built macro that calculated actual ambient temperature. Because the measured temperature was not the actual ambient temperature (due to device transience; Watanuki et al. 2001), I developed a formula that determined actual ambient temperature based on change in temperature between successive measurements. To do this, I placed all TDRs in water of known temperature and determined a time constant of 0.036 ± 0.005 s^{-1} for the TDR thermistor. Using Newton's Law of Cooling, I estimated ambient temperature, T_a, at time t, based on the average of the temperature difference between consecutive measurements:

$$T_a = 0.5 \cdot \left(\frac{T_{t-3}e^{-0.09} - T_t}{e^{-0.09} - 1} + \frac{T_{t-6}e^{-0.18} - T_t}{e^{-0.18} - 1} \right)$$

The results from this method are comparable to those described by Watanuki et al. (2001) and Mehlum et al. (2001), although mine tended to be less smooth. Because the averaging method employed by these authors would not work for V-shaped dives near maximum depth, I used the Newton's Law method for the entire data set. As T_a changed

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nonlinearly with depth, I used Akaike's Information Criterion (AIC) to determine the best polynomial approximation to the T_a-depth function across all deliveries (ΔAIC 5th order: 0.0; ΔAIC 6th order: 2.2; ΔAIC 4th order: 42.5). To calculate a water temperature index on the final dive prior to prey delivery, I averaged the difference between measured T_a and that predicted by the 5th order best fit function.

Descent rate

To determine whether the descent rates of parental murres differed among prey types, I calculated descent rate at a given sampled depth for each dive using the formula developed in Chapter 1. Because murres hold their bodies nearly vertical during descent, descent rate is very close to actual swim speed (Lovvorn et al. 1999, 2004). I only examined descent rates greater than 10 m above where depth stopped increasing monotonically to avoid including bottom time or deceleration in calculations for descent rate. As descent rate changes nonlinearly with depth (Watanuki et al. 2003, 2006, Gaston 2004; Fig. 2.2), I used AIC to determine the best polynomial approximation to the average descent rate-depth function across all prey deliveries (ΔAIC 5th order: 0.0; ΔAIC 6th order: 5.9; ΔAIC 4th order: 10.2). To calculate a descent rate index on the final dive prior to prey delivery, I averaged the difference between measured descent rate and that predicted by the 5th order best fit function.

Modeling Foraging Locations

To estimate the potential capture locations of benthic prey items and pelagic prey items possibly caught near the seabed (i.e. on U-shaped dives), I integrated information on bathymetry, dive depth and flight distance, as described in Chapter 3. These data were used to test the hypothesis that birds used stereotyped behaviour to return to the same
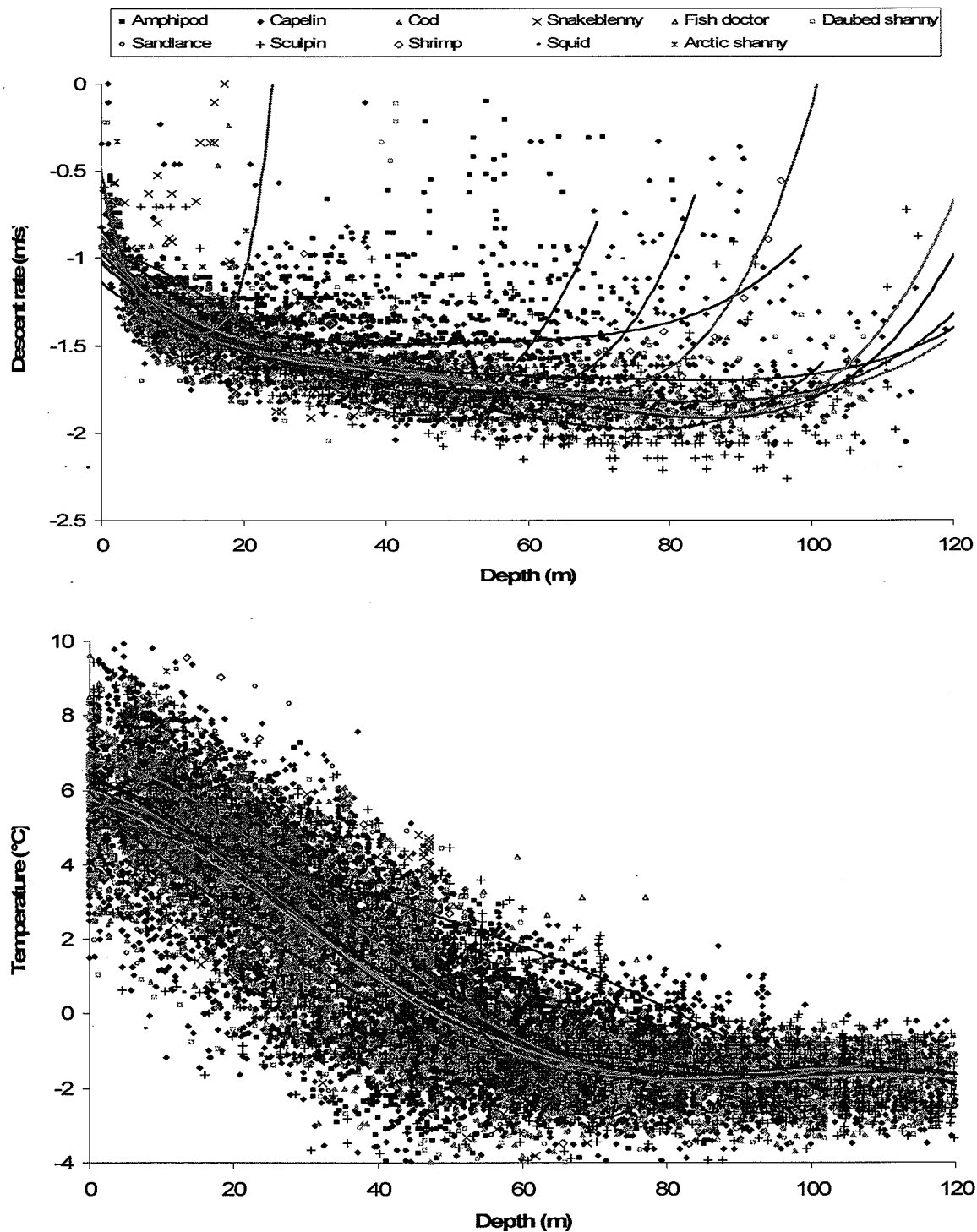
Figure 2.2. (a) Descent rate and (b) water temperature as a function of depth on the final dive preceding the delivery of different prey types. The best fit functions represent fourth order polynomial approximations. The upswing in (a) presumably represents a reduction in descent rate associated with searching near the bottom of each dive. Depths within 10 m of maximum depth during each dive were excluded from descent rate analyses.

general area during subsequent trips to collect similar prey types. The bathymetric maps were combined with return flight distances that ended in the delivery of a benthic prey type to estimate the locations of prey capture. The prey capture index relative to distance from the colony for pelagic prey types was calculated by dividing the number of prey items collected within each 10-km horizontal bin by the amount (km^2) of ocean surface available within that distance range to the west of the colony. The prey capture index relative to distance from the colony for benthic prey items was calculated from the ocean area available with depth < 140 m (maximum dive depth for murres; Chapter 1). The prey capture index relative to depth was only calculated for benthic prey items by dividing the number of prey items collected within each 20-m bin by the amount (km^2) of ocean floor available within that 20-m bin within 60 km to the west of the colony. The values for all indices were then normalized so that the sum of all values, for each prey item, added to one.

Dive bout measurements

I compiled the following parameters for the dive bout prior to each prey delivery where available: (1) average and standard deviation of depth, (2) average and standard deviation of duration, (3) average and standard deviation of surface pause duration, (4) average and standard deviation of the ratio of surface pause to dive duration, (5) number of dives and (6) proportion of V-shaped dives. I also compiled the following parameters for the last dive of this final bout prior to each prey delivery: (1) depth, (2) duration, (3) shape, (4) temperature index, (5) temperature at maximum depth, (6) average surface temperature and (7) descent rate index. As many of these parameters are highly

correlated, I show separate multigroup discriminant analyses with all axes included and only with non-redundant axes included.

Statistical analyses

All statistical analyses were completed in R 3.2.1. Prior to using parametric statistics, I tested for normality (Shapiro-Wilk test) and homogeneity of variance (Bartlett's test). Proportions were arcsine-transformed and variables that were not normally distributed were log-transformed prior to analyses. Means are presented ± SE.

To determine whether foraging trips that resulted in the same prey type clustered together, I completed a multigroup discriminant analysis (MDA) on all variables but dive shape using SYNTAX (SYNTAX 2000). Rare prey types were grouped together so that each group had a minimum of seven data points. I used minimum convex polygon algorithms to cluster foraging parameters associated with the same prey type. I completed two different MDAs. The first MDA included those variables measured for most dive bouts in all years, to maximize the number of deliveries included. The second MDA only included those variables that were found to be significant by the ANOVA and were not redundant. To determine whether dive parameters differed with prey type or year, I used a two-way ANOVA with year and prey type as model effects and dive parameters as dependent variables. To account for individual specialization in dive behaviour (Golet et al. 2000, Bolnick et al. 2002, 2003, Bearhop et al. 2006), I randomly selected a single dive for each prey item-individual combination, and I performed the ANOVA on the reduced data set.

RESULTS

Average water temperature and water temperature at maximum depth both differed significantly among prey types (Table 2.2) although there was no difference in descent rate anomaly (F = 1.29, df = 7,121 p = 0.39) and surface temperature (F = 2.02, df = 7, 121, p = 0.06). The only effect of year was that surface temperatures in 2004 were higher than in 2005 (F = 31.6, df = 1, 121, p < 0.0001). A GLM with dive depth and prey species as independent variables showed significant relationships among prey species and both descent rate and water temperature (Fig. 2.2). A post-hoc t-test showed that murres returning with amphipods descended significantly slower during dives preceding delivery than murres returning with any other prey item and that amphipods and fish doctors were caught during dives with significantly higher temperature readings across all depths, whereas all other groupings of prey types were caught at similar temperature (Fig. 2.2).

There was no significant difference among prey types in the number of dives per bout ($F_{8,227}$ = 1.09, p = 0.38), average surface interval in the preceding bout ($F_{8,118}$ = 1.26, p = 0.27) or surface pause to dive duration ratio ($F_{8,118}$ = 1.49, p = 0.16) or among years (dives per bout: $F_{3,227}$ = 0.75, p = 0.52; surface pause: $F_{3,118}$ = 0.93, p = 0.43; surface pause:dive duration: $F_{3,118}$ = 2.06, p = 0.11). There was also no relationship among prey types in standard deviation of dive depth ($F_{8,118}$ = 0.28, p = 0.97), dive duration ($F_{8,118}$ = 0.62, p = 0.66), surface pause duration ($F_{8,118}$ = 0.32, p = 0.96) or surface pause to dive duration ratio ($F_{8,118}$ = 0.26, p = 0.98) or among years (sd of depth: $F_{3,118}$ = 1.89, p = 0.14; sd of duration: $F_{3,118}$ = 1.64, p = 0.20; sd of surface pause: $F_{3,118}$ = 0.80, p = 0.50; sd of pause:duration: $F_{3,118}$ = 0.16, p = 0.92).

Depth and duration of dives varied among prey species, and varied generally in the same manner, with squid obtained on long, deep dives, fish doctor and sand lance on

Table 2.2. Temperature anomaly and temperature at maximum depth for the final dive preceding delivery of a prey type. Parameters are averaged ± SE over all prey deliveries. Superscripts represent homogenous subsets ($\alpha = 0.05$). Because there was no significant effect of year, we pooled the values for each prey type across years (2004-06). Groups that were not included in the ANOVA (either because they were not independent or had small sample sizes) are included below "Amphipods". The second column represents sample size for each prey type and degrees of freedom for each statistical test. Post-hoc tests were not completed on prey items with small sample sizes, which are shown in the last four rows prior to statistical tests

Prey	n/df	Temperature Anomaly (°C)	Minimum Temperature (°C)
Sandlance	4	$-0.7 \pm 1.2^{*}$	$2.5 \pm 1.6^{*}$
Arctic cod	18	$0.2 \pm 0.3^{**}$	$1.0 \pm 0.5^{**}$
Sculpin	20	$-0.1 \pm 0.2^{**}$	$-0.7 \pm 0.4^{**}$
Fish doctor	4	$0.9 \pm 0.2^{**}$	$4.5 \pm 0.2^{*}$
Daubed shanny	18	$-0.2 \pm 0.2^{*}$	$-0.5 \pm 0.4^{**}$
Capelin	88	$-0.2 \pm 0.1^{**}$	$-0.2 \pm 0.2^{**}$
Squid	6	$-0.4 \pm 0.3^{*}$	$-1.8 \pm 0.2^{**}$
Amphipods	19	$0.7 \pm 0.2^{**}$	$-0.3 \pm 0.3^{**}$
Snakeblenny	1	0.2	2.1
Arctic shanny	1	-0.8	2.3
Myoxocephalus	2	0.6 ± 0.8	-0.0 ± 1.7
Triglops	2	0.3 ± 0.6	-0.3 ± 1.3
F		2.42 ± 0.01	2.09 ± 0.03
F (year)	1	1.31 ± 0.26	0.40 ± 0.53
F (prey)	7	2.44 ± 0.03	3.05 ± 0.008
F (year*prey)	5	3.23 ± 0.01	0.70 ± 0.62
r^2		0.19	0.15
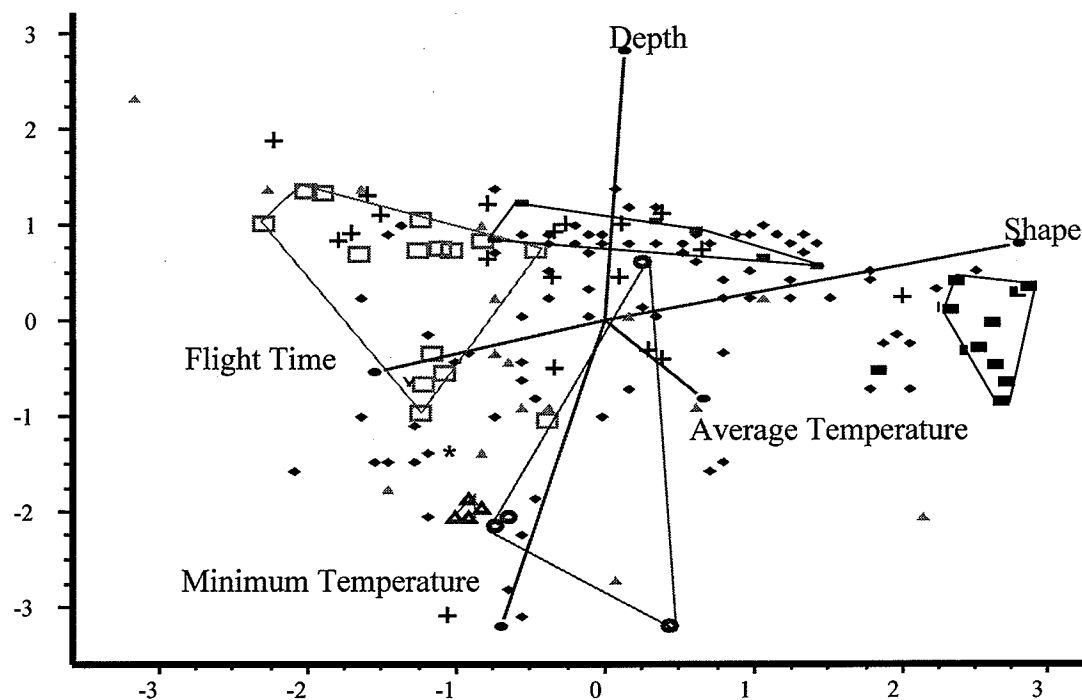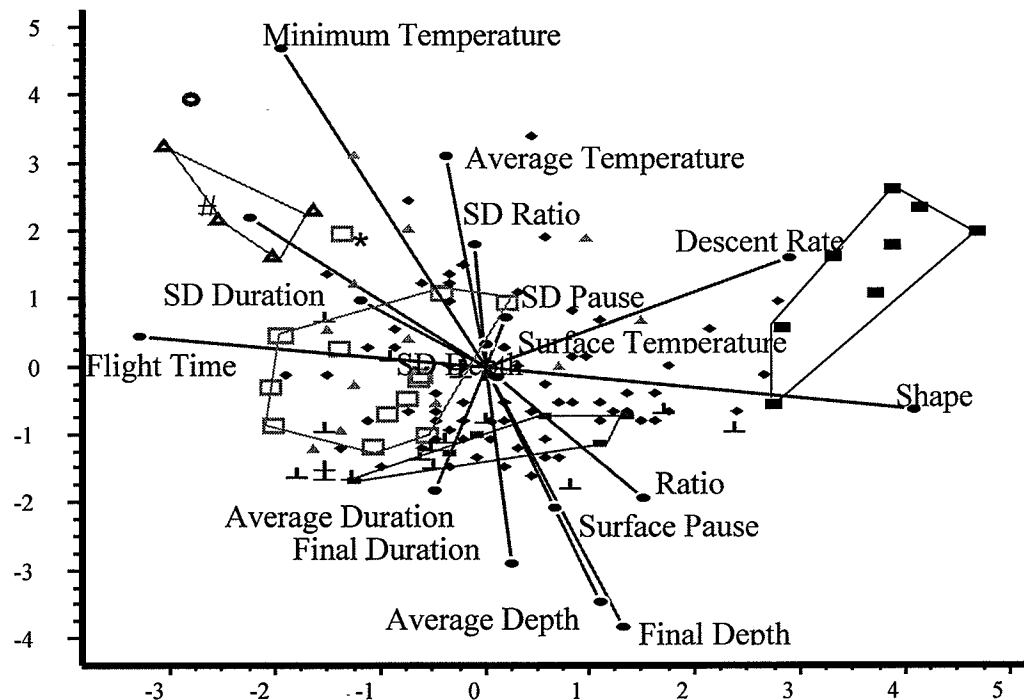
Figure 2.3. Multigroup discriminant analyses for Thick-billed Murre prey items delivered 2004-2006. Prey groups were: amphipod (■); rare benthics (Arctic shanny: *; snakeblenny: x; fish doctor Δ; sand lance O); sculpin (+); daubed shanny (□); capelin (♦); Arctic cod (▲). Polygons represent 95% minimum convex polygons. (a) including all variables and (b) including just significant (ANOVA) variables

short, shallow dives and the remaining prey items at a wide variety of depths and dive durations (Table 2.3). Flight time generally increased with mass of the prey type, as amphipods and squid were captured prior to short return flights, whereas fish doctor, snakeblenny, daubed shanny and Arctic cod were captured prior to long return flights (Table 2.4). Similar trends were seen in dive shape, where amphipods and squid were primarily captured after V-shaped dives, whereas sand lance, Arctic cod, snakeblenny, fish doctor and daubed shanny were caught after flat-bottomed dives; capelin and sculpin showed a wide variety of both dive types (Table 2.4).

The MDAs reflected many of these similar trends, with capelin, sculpin and Arctic cod poorly distinguished and the remaining species well-separated (Fig. 2.3). The MDA including all three years distinguished amphipods and fish doctor with 95 % accuracy and sand lance and squid with 80 % accuracy (Fig. 2.3). Daubed shanny and snakeblenny were also distinguishable from the other groups with 80 % accuracy, but the daubed shanny polygon contained the snakeblenny polygon completely (Fig. 2.3). The MDA including all 17 variables distinguished amphipods, fish doctor, daubed shanny and squid with 95 % accuracy (Fig. 2.3a). The MDA including only the non-redundant, significant group of variables, distinguished amphipods, fish doctor, daubed shanny, squid and sand lance with 95 % accuracy (Fig. 2.3b).

The model results of potential prey capture locations showed definite groupings of prey types (Fig. 2.4). Sculpin captures were clustered along the narrow shelf east of Bencas Island, whereas fish doctor captures were clustered on the shallow bench west of Bencas Island. Snakeblenny and Arctic shanny were taken on the bench both east and west of Bencas Island. Other prey types were more generally clustered. After accounting

Table 2.3. Depth and duration of final dives preceding prey deliveries and average depth and duration of dives during dive bout preceding prey deliveries, organized by prey. Superscripts represent homogenous subsets ($\alpha = 0.05$). Because there was no significant effect of year, I pooled all years (2004-06). The second column represents sample size for each prey item and degrees of freedom for each statistical test. Post-hoc tests were not completed on prey items with small sample sizes, which are shown in the last four rows prior to statistical tests. SE or p-values are in parentheses.

Prey	n/df	Depth of Final Dive (m)	Duration of Final Dive (s)	Mean Dive Depth of Final Bout (m)	Mean Dive Duration of Final Bout (s)
Amphipods	25	66.9 ± 2.3^{1}	$121 \pm 4^{*}$	$60.0 \pm 4.0^{*}$	$125 \pm 7^{*}$
Squid	6	96.8 ± 8.1^{2}	$148 \pm 8^{*}$	$94.2 \pm 5.2^{*}$	$175 \pm 6^{*}$
Sandlance	15	29.5 ± 6.2^{3}	$79 \pm 13^{**}$	$36.4 \pm 6.8^{**}$	$104 \pm 14^{**}$
Capelin	120	61.4 ± 3.1^{1}	$116 \pm 4^{*}$	$57.7 \pm 2.9^{*}$	$129 \pm 5^{*}$
Arctic cod	47	49.2 ± 4.2^{1}	$112 \pm 6^{*}$	$45.0 \pm 3.3^{*}$	$135 \pm 5^{*}$
Sculpin	28	71.9 ± 5.7^{1}	$137 \pm 8^{*}$	$71.4 \pm 5.7^{*}$	$164 \pm 8^{*}$
Daubed shanny	27	74.2 ± 5.7^{1}	$153 \pm 8^{*}$	$71.3 \pm 6.0^{*}$	$169 \pm 9^{*}$
Snakeblenny	6	55.1 ± 6.3^{1}	$131 \pm 13^{*}$	$55.4 \pm 7.0^{*}$	$154 \pm 15^{*}$
Fish doctor	7	24.8 ± 4.2^{3}	$72 \pm 11^{2**}$	$24.9 \pm 4.7^{**}$	$109 \pm 11^{*}$
Arctic shanny	2	41.4 ± 19.6	133 ± 25	39.6 ± 5.2	157 ± 11
Shrimp	1	76	212	76	222
Myoxocephalus	2	79.5 ± 25.0	173 ± 14	98	172
Triglops	6	55.6 ± 9.3	127 ± 19	71.3 ± 7.0	141 ± 12
F (model)	28	2.13 ± 0.005	1.50 ± 0.07	2.31 ± 0.002	1.77 ± 0.02
F (year)	3	1.92 ± 0.13	1.91 ± 0.13	1.86 ± 0.14	0.81 ± 0.43
F (prey)	8	3.02 ± 0.004	2.26 ± 0.03	2.56 ± 0.01	2.10 ± 0.04
F (year*prey)	17	1.07 ± 0.39	0.60 ± 0.89	1.65 ± 0.07	1.29 ± 0.22
r^2		0.19	0.09	0.22	0.10
χ^2 (random)	28	53.2 ± 0.002		42.6 ± 0.04	
χ^2 (year)	3	4.4 ± 0.22		4.1 ± 0.25	
χ^2 (year*prey)	8	22.1 ± 0.005		19.1 ± 0.02	
χ^2 (year*prey)	17	10.1 ± 0.90		25.1 ± 0.10	

Table 2.4. Flight time from the colony, average shape of dive bout and proportion of V-shaped final dives preceding delivery of prey items. Average shape was calculated by assigning 1 for V-shaped dives and 0 for all others; analyses were completed on arcsin-transformed data. Parameters are averaged over all prey deliveries. Superscripts represent homogenous subsets ($\alpha = 0.05$). Because there was no significant effect of year, we pooled all years (2004-06). The second column represents sample size for each prey item and degrees of freedom for each statistical test. Post-hoc tests were not completed on prey items with small sample sizes, which are shown in the last four rows prior to statistical tests. SE (for averages) or p-values (for statistical tests) are in parentheses

Prey	n/df	Mean shape of final dive bout	Return flight time (min)	Shape of final dive
Sandlance	15	0.17 ± 0.19^{1}	23.5 ± 4.7^{1}	0.08
Arctic cod	46	0.08 ± 0.06^{1}	34.9 ± 2.6^{1}	0.14
Sculpin	29	$0.22 \pm 0.10^{1,2}$	22.3 ± 2.4^{1}	0.22
Snakeblenny	5	0.0 ± 0.0^{1}	35.8 ± 3.1^{1}	0.00
Fish doctor	7	0.01 ± 0.04^{1}	37.2 ± 4.6^{1}	0.00
Daubed shanny	23	0.06 ± 0.07^{1}	27.3 ± 2.9^{1}	0.03
Capelin	113	0.40 ± 0.06^{1}	22.0 ± 1.3^{1}	0.50
Squid	6	0.65 ± 0.23^{2}	14.3 ± 3.9^{1}	1.00
Amphipods	25	0.96 ± 0.06^{3}	5.9 ± 0.7^{2}	0.96
Arctic shanny	2	0.0 ± 0.0	25.0 ± 2.0	
Shrimp	1	0.0 ± 0.0	11.9	
Myoxocephalus	1	0.31 ± 0.46	18.7 ± 2.7	
Triglops	5	0.03 ± 0.08	37.8 ± 6.7	
F	27	3.37 ± 0.00001	2.83 ± 0.00006	
F (year)	3	5.05 ± 0.003	4.94 ± 0.003	
F (prey)	8	3.74 ± 0.001	4.08 ± 0.0003	
F (year*prey)	16	1.02 ± 0.45	1.10 ± 0.36	
r^{2}		0.33	0.28	
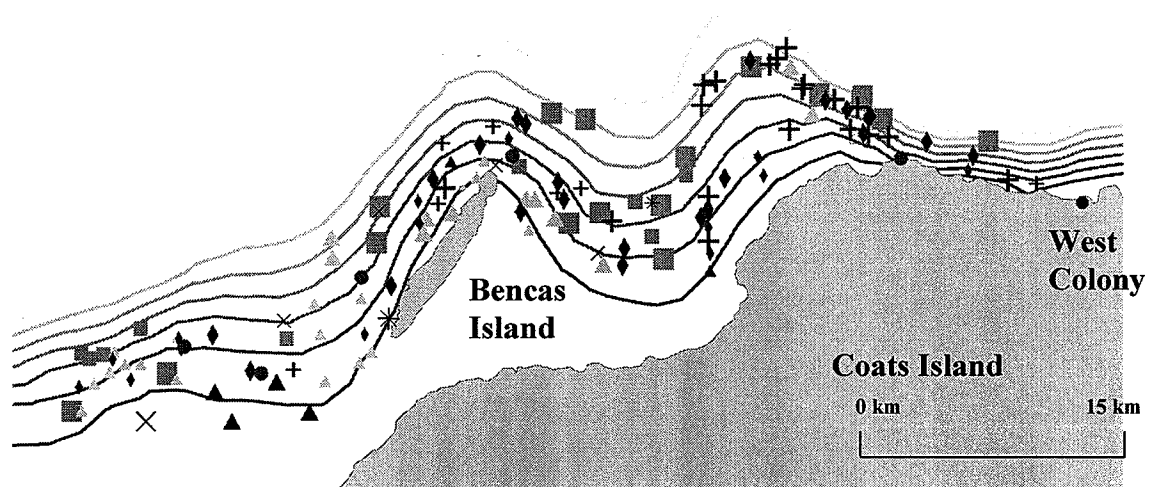
Figure 2.4. Estimated locations where prey items were taken by Thick-billed Murres in the vicinity of the Coats Island, Nunavut colony. Depth contours are in 20 m intervals between 20 and 140 m. Symbols represent daubed shanny (■),snakeblenny (×), Arctic shanny (*), fish doctor (▲), sculpin (+), capelin (◊), cod (▲) and sand lance (●).

for the proportion of depths available within 60 km of the colony, a univariate analysis of dive depth relative to available depths, for benthic species, showed that depths were chosen non-randomly, with fish doctor and snakeblenny captured at shallower depths than other species (Fig. 2.5). A similar analysis of flight distance, relative to ocean surface available, showed that flight distances were chosen non-randomly for both benthic and pelagic species, with amphipods, daubed shanny and capelin taken closer to the colony and snakeblenny taken farther from the colony (Fig. 2.6).

Surface pause duration increased exponentially with dive duration for all prey types and the pattern was similar except for amphipods (Fig. 2.7). Surface pause duration also increased exponentially with dive depth for all prey items, with considerable variation among prey items (Fig. 2.7). Surface pause duration decreased with prey mass (Fig. 2.7), although these trends were weak. Dive duration was a decelerating power function of dive depth (Fig. 2.7). For a given depth, dive duration increased with prey mass (Fig. 2.7). For a given depth and prey mass, dive duration was greater for benthic than schooling prey items (schooling residual = -2.8 ± 3.3; benthic residual = 11.0 ± 1.8; t = 3.51, df = 60, P = 0.0008). There was no difference in surface pause duration in response to dive duration (schooling residual = 0.49 ± 4.3; benthic residual = -9.6 ± 3.8; t = 1.48, df = 60, P = 0.14) or depth (schooling residual = 5.3 ± 3.3; benthic residual = 12.6 ± 1.8; t = 1.62, df = 60, P = 0.11).

DISCUSSION

The search and capture strategies of Thick-billed Murres varied significantly among most prey types, but especially for fish doctor and amphipods (Table 2.2-2.4; Fig. 2.3). For example, there was no overlap between six different prey types (squid, snakeblenny,

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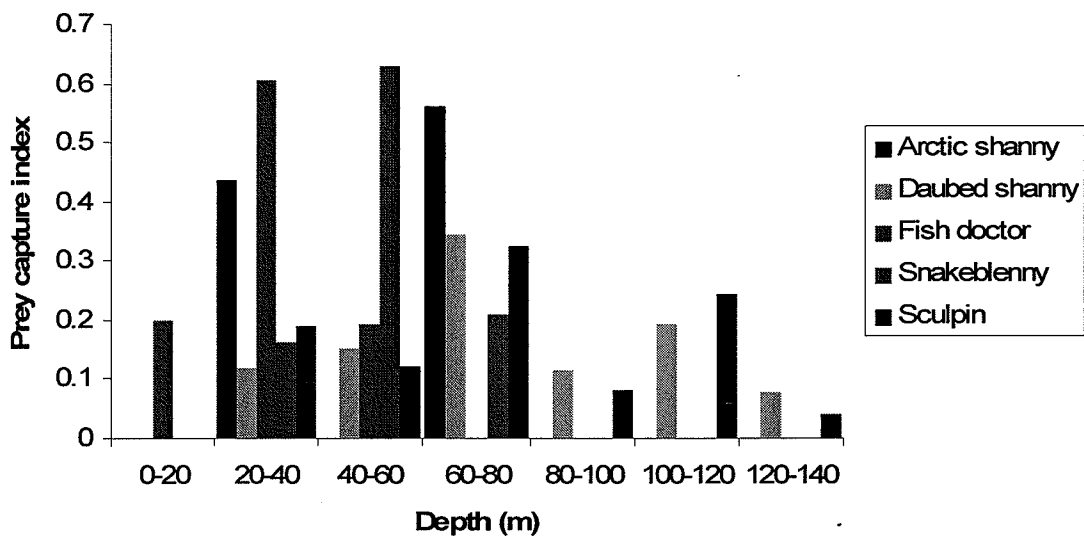
Figure 2.5. Proportion of benthic prey taxa taken at each depth, as a function of the amount of available seafloor at that depth within 60 km of the colony. The index was calculated by dividing the number of prey items collected within each 20-m bin by the amount (km^2) of ocean floor available within that depth range within 60 km to the west of the colony. This value was then normalized so that the sum of all values, for each prey item, adds to one.
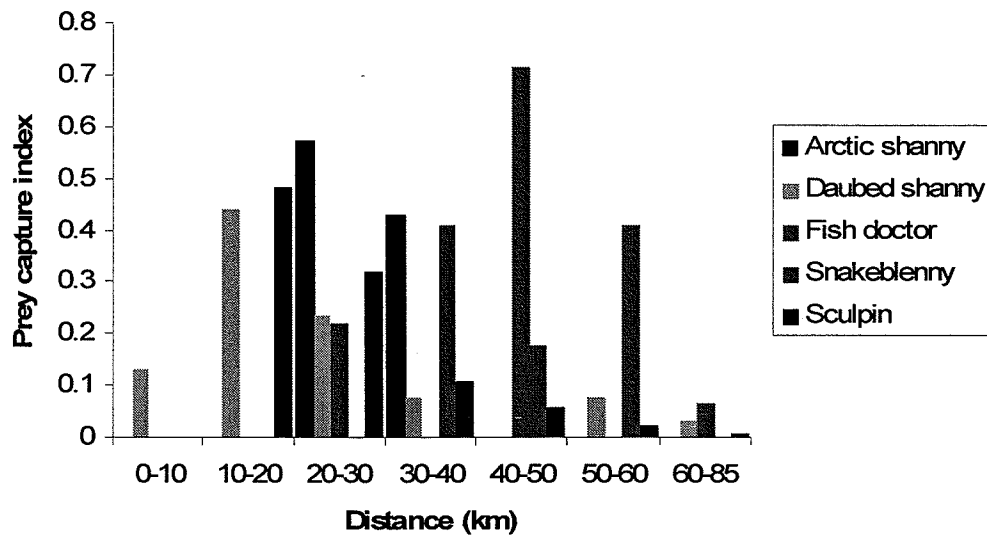
(a)
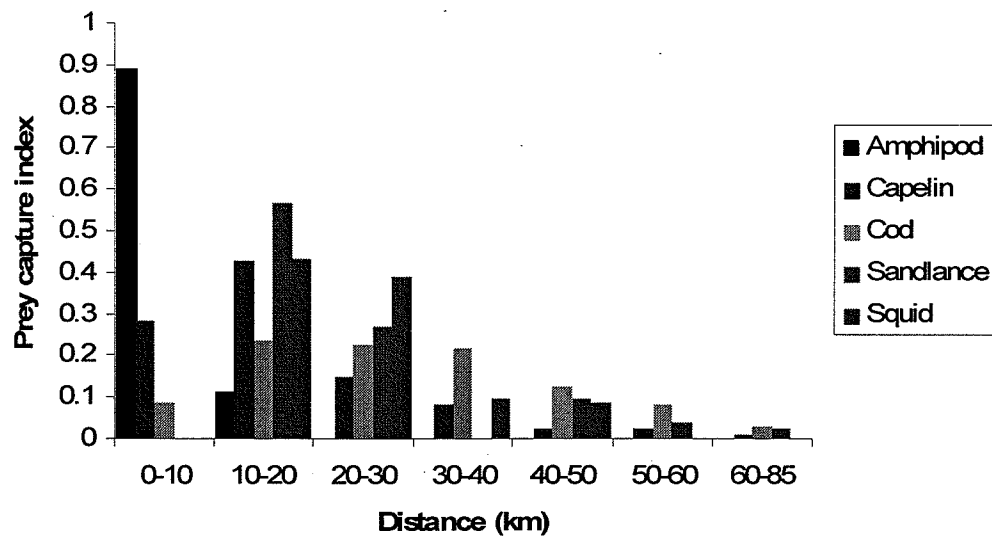
(b)

Figure 2.6. Proportion of (a) benthic and (b) pelagic prey types taken at each distance interval, as a function of the amount of ocean area available. The index was calculated by dividing the number of prey items collected within each 10-km bin by the amount (km^2) of ocean surface available within that distance range to the west of the colony. The distance indices for benthic prey items were calculated from the ocean surface area available with depth < 140 m. These values were then normalized so that the sum of all values, for each prey item, adds to one.
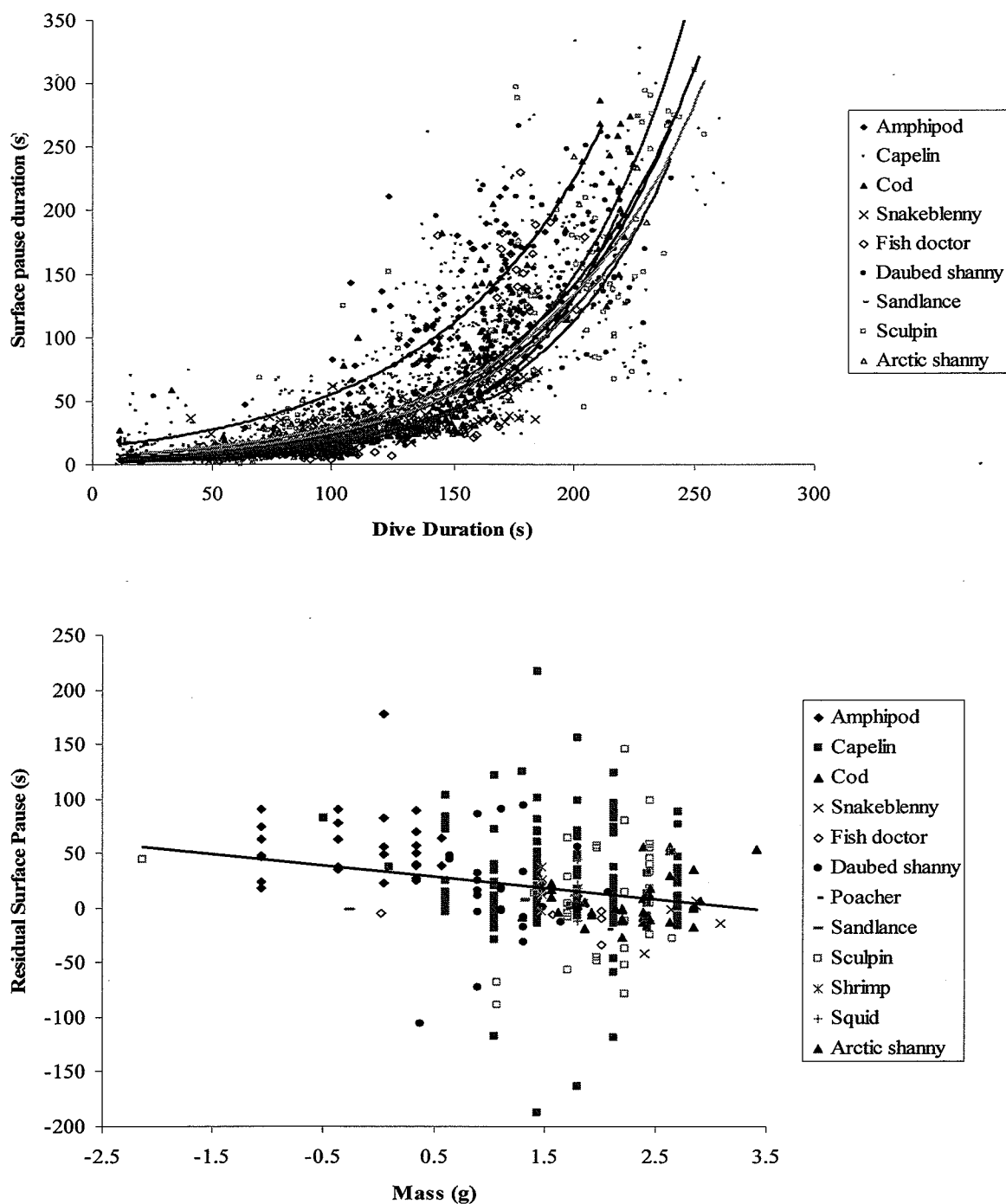
Figure 2.7. (a) Subsequent surface pause duration (s) increases exponentially with dive duration (s) for all prey types. (b) Residual surface pause duration decreases with prey type mass. The data represents the average residual for each prey delivery (n = 327). Residuals are calculated as deviation from the relationship when all prey items are pooled. Prey mass is shown on a natural logarithmic scale. Res*(Pause)* = (-6.08 ± 2.85)Ln(*Mass*) + 5.06 ± 5.10 (t = -2.14; df = 326; P = 0.03; R^2 = 0.014).
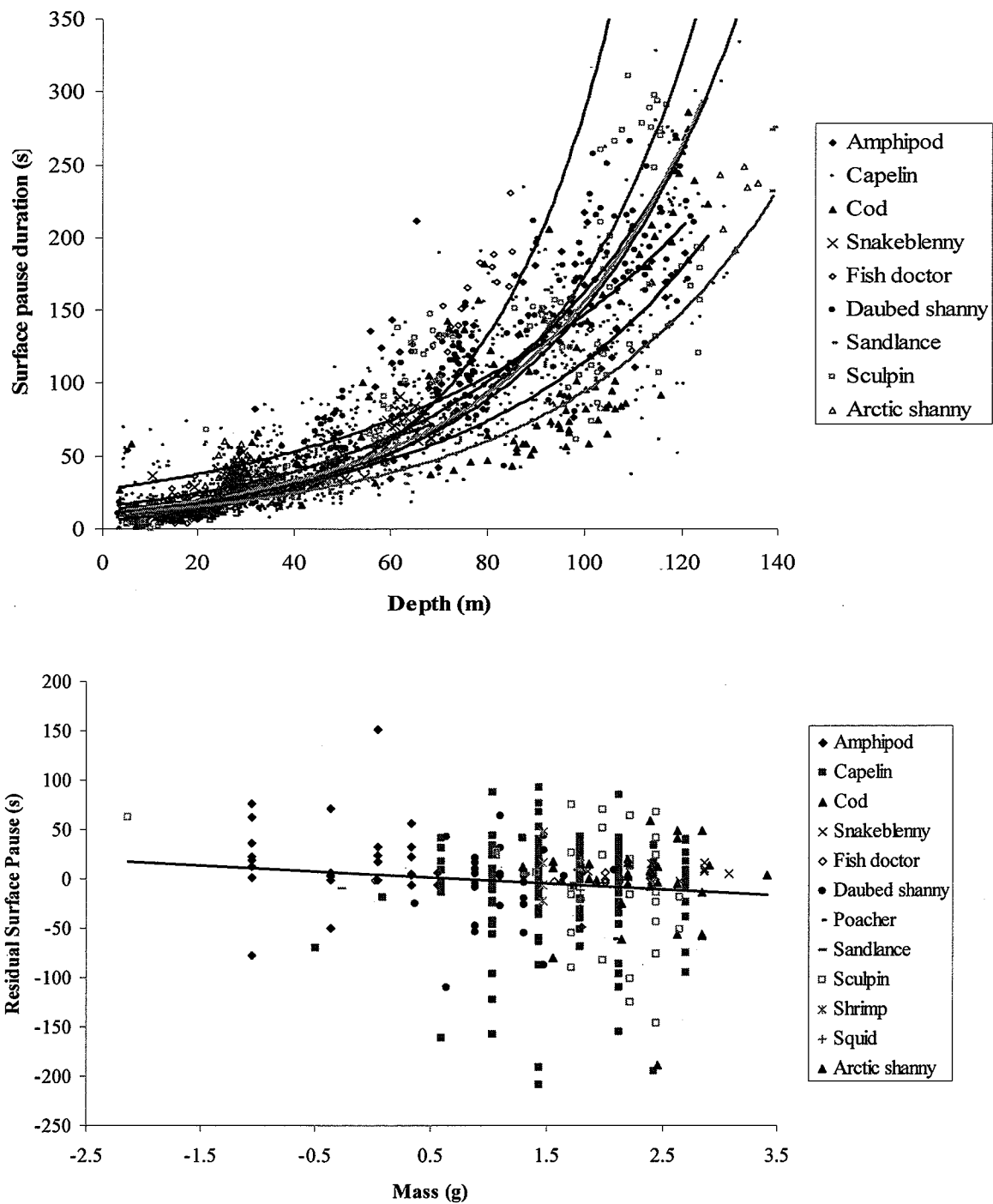
Figure 2.7. (c) Surface pause duration (s) is an exponential function of dive depth (m) for all prey types. (d) Residual surface pause duration decreases with prey item mass. The data represents the average residual for each prey delivery (n = 500). Residuals are calculated as deviation from the relationship calculated when all prey items are pooled. Prey mass is shown on a natural logarithmic scale. Res*(Duration)* = (9.6 ± 0.9)Ln(*Mass*) − 23.6 ± 1.6 (t = 10.21; df = 499; P < 0.00001; R^2 = 0.173).
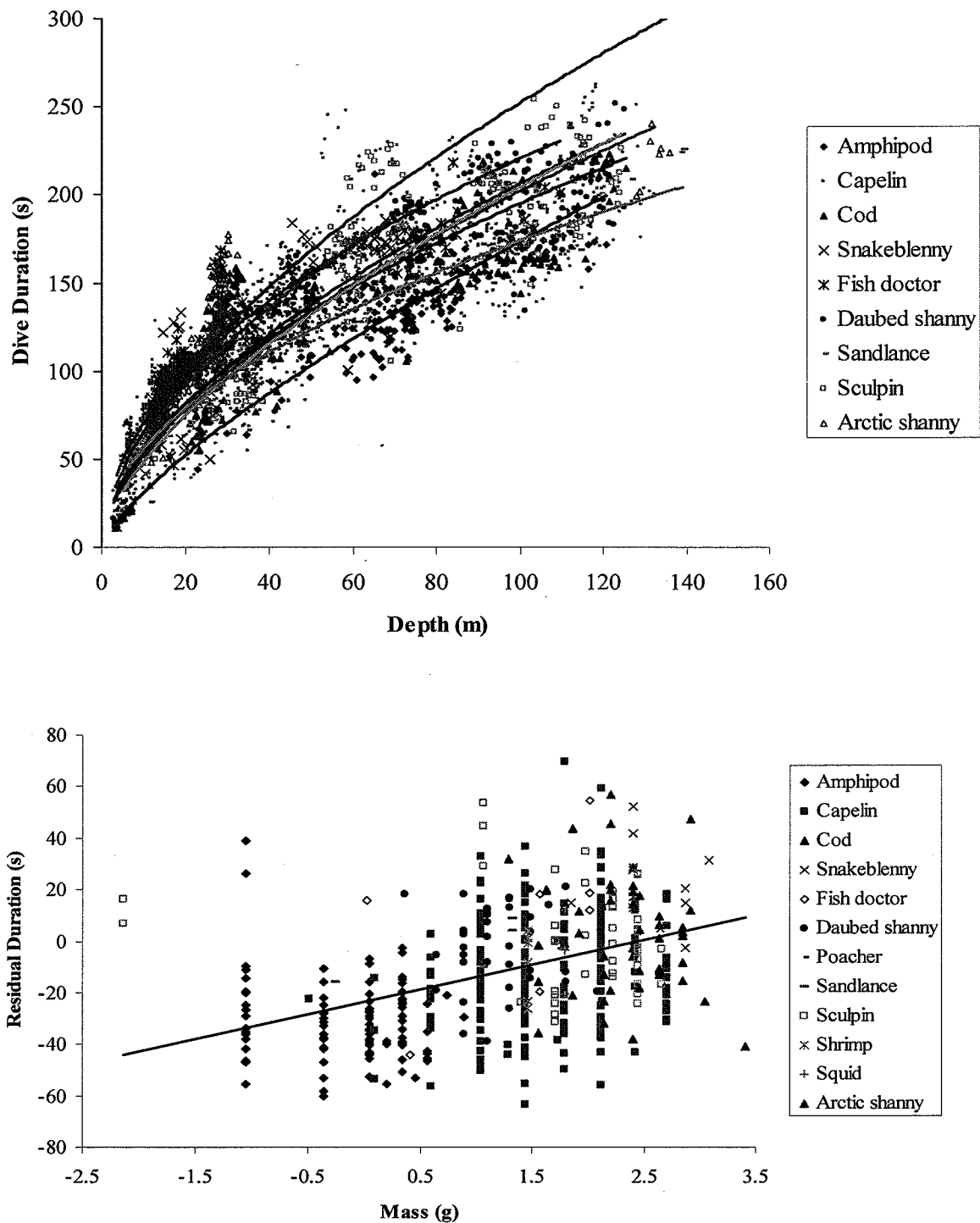
Figure 2.7. (e) Dive duration (s) is an increasing power function of dive depth (m) for all prey items. (f) Residual dive duration increases with prey item mass. The data represents the average residual for each prey delivery (n = 500). Residuals are calculated as deviation from the relationship calculated when all prey items are pooled. Prey mass is shown on a natural logarithmic scale. Res*(Duration)* = (9.6 ± 0.9)Ln(*Mass*) − 23.6 ± 1.6 (t = 10.21; df = 499; P < 0.00001; R^2 = 0.173).

amphipods, Arctic shanny, fish doctor and amphipods) and very limited overlap between daubed shanny and these prey types (Fig. 2.3). Other prey types, such as capelin, Arctic cod and sculpin, were captured using a variety of different foraging strategies (Fig. 2.3). It must be kept in mind that some of the extreme data points may actually represent visual misidentifications of prey types during feeding watches.

Coats Island is known to have many adult murres that are considered to specialize on certain prey types both within a given breeding season and from year to year because they consistently provision their chicks with rare prey items (Woo 2001). This observation, coupled with my results, suggest that adults specialize on certain prey types by altering foraging strategies, including dive behaviour and locations, so that they are tailored for capturing a given prey type, as dive profiles are usually remarkably similar throughout a given provisioning trip. For example, adults provisioning with amphipods invariably return visibly wet from a foraging trip lasting less than 30 min with a single, deep dive. Adults provisioning with fish doctors return with a fish that is very dried and the TDR traces invariably show a long series of shallow dives to identical depths followed by a lengthy return flight time. These birds apparently do not sample their environment but instead use past experience to forage at a specific location (Davoren et al. 2003), presumably where amphipods or fish doctors are known to be accessible. Although individuals may rely on past experience of successful dive locations or behaviour and by assessing current environmental conditions, murres sometimes used dive behaviour at the beginning of foraging bouts that is significantly different from the last dive. This suggests that they also assess current environmental conditions and prey

locations, at least at the fine-scale level, prior to actively searching for prey (Woo 2001, Davoren et al. 2003).

Dive behaviour varied in approximately three different major axes, as observed by the approximate co-linearity of these variables on the multigroup discriminant analyses (Fig. 2.3): (1) depth (duration, surface pause interval, minimum temperature), (2) flight time (number of dives) and (3) shape, although only a few of these variables showed significant variation (Tables 2.1-2.3). The depth axis likely reflects the depth range at which the prey types are accessible to murres, the flight time axis correlates with prey mass (see Chapter 3) and dive shape partially represented benthic versus pelagic foraging, with pelagic prey items caught on primarily V-shaped dives and benthic prey items caught primarily on U1-shaped dives, as predicted.

The V-pelagic and U-benthic dichotomy had been deduced previously because epipelagic foragers generally have V-shaped dives (Schreer et al. 2001, Kato et al. 2003, Kuroki et al. 2003, Benvenuti et al. 2001), whereas benthic foragers generally have U-shaped dives (Croll et al. 1992, Schreer et al. 2001, Gazo et al. 2006). Whether birds display U versus V shaped dives, likely depends on the amount of time pursuing each prey item upon encounter at depth. Therefore, species with strongly stratified epipelagic prey also show U-shaped dive patterns (Chappell et al. 1993), and some species show both dive patterns when foraging. For example, gannets display U-shaped dives when capturing multiple, small fish from a school during a dive and V-shaped dives when capturing single, large fish near the ocean surface (Garthe et al. 2000). As U-shaped dives sometimes preceded deliveries of squid, capelin and amphipods, it is likely that these dives also represented pursuit of schools at a specific depth (Garthe et al. 2000, Mori et

al. 2002). Other researchers have used other classifications of dive shape, including left or right-skewed dives (Schreer and Testa 1996), or the number of wiggles per "W" dives (Schreer et al. 2001, Simeone and Wilson 2003). Simeone and Wilson (2003) show that each wiggle represents a prey capture by Magellanic Penguins (*Spheniscus magellanicus*). Thus, additional analysis of dive shape, especially if coupled with bird-borne camera equipment (Takahashi et al. 2004), stomach temperature loggers (Simeone and Wilson 2003) or satellite transmitters (Rodary et al. 2000), will provide greater information on murre foraging strategies.

The relationship between surface pause duration, dive duration and dive depth varied among prey types (Fig. 2.7). As expected, for a given depth, duration increased with anticipated gain (prey mass; Fig. 2.7). Surface pause duration increased with smaller prey types as predicted, although these relationships were very weak (Fig. 2.7). The clearest relationship, and the one primarily responsible for the relationship between surface pause residual and prey mass, was that surface pauses tended to be longer, for a given dive duration, when birds were preying on amphipods (Fig. 2.7). These small invertebrates weigh only about 0.35 g and are presumably unable to migrate out of the area in the time scale of a murre dive bout. As the relationship appeared to be anticipatory (Chapter 1), I suggest that the birds were reducing effort (increasing surface pause duration) in anticipation a low-value, non-ephemeral prey item, rather than reacting to high energy costs associated with searching and capturing these small items in the water column.

Conversely, I found no support that surface pause duration differed between ephemeral and stationary fish. In contrast to my initial expectations, birds dived longer for stationary fish than ephemeral fish. This may reflect high dive costs when foraging

for ephemeral prey types; foraging for stationary prey items appears to be a "sit-and-wait" strategy (S. Benvenuti, pers. comm.). Dive duration and depth were strongly correlated for all prey types, including pelagic prey types (Fig. 2.7); I found no support that this correlation was weaker when capturing pelagic prey types relative benthic prey types (Jodice and Collopy 1999).

Although foraging strategies could be categorized generally for pelagic versus benthic prey types, strategies differed among species within these categories. I highlight these differences below.

Pelagic prey types. Dives preceding deliveries of pelagic prey items were usually V-shaped and with relatively slow descent rate. The trend towards a slower descent rate, however, was only present for amphipods. Presumably, this reflected searching for amphipods in the water column starting at about 40 m in depth. Pelagic prey types also appeared to be captured following particularly deep dives (squid, amphipods). Dive duration was particularly short for a given dive depth for Arctic cod (Fig 2.7e), suggesting that this type may be particularly energetically costly to capture or particularly easy to capture. Accelerometer traces suggest unusually high number of wingbeats during dives preceding deliveries of Arctic cod (S. Benvenuti, pers. comm.). Were cod particularly energetically costly to capture, then one would expect that oxygen stores would be used up quickly and dives would be terminated quickly. Alternatively, cod may have been particularly easy to capture, and therefore not necessitated extensive bottom time, resulting in short dive durations.

Benthic prey types. Dives preceding deliveries of benthic prey items were usually U1-shaped and were often relatively warm. The trend towards warmer water temperature,

however, was only found for fish doctor and Arctic shanny. This may have reflected the warm water over shallow shelf waters, in comparison to cold, deep pelagic waters. Benthic prey items also appeared to be captured following rather shallow dives (snakeblenny, fish doctor, Arctic shanny). Prey-capture locations for these prey items appeared to be along the shelf around Bencas Island, highlighting the importance of this shelf for these prey items. Sculpin and daubed shanny were more uniformly distributed along the entire coastline. Dive bouts for benthic prey items often had many dives, suggesting that numerous dives were necessary to locate and capture a benthic prey item.

Benthic and pelagic prey types. Capelin were caught after a wide variety of different dive behaviour (Fig. 2.3), possibly because they occupy a wider variety of habitats than most prey types (Davoren et al. 2006). Alternatively, capelin may have been caught as a secondary option when a foraging bout did not encounter a higher quality prey item. In support, capelin were usually caught relatively close to the colony (Table 2.3; Fig. 2.6) and individuals that tended to specialize on other prey types, such as fish doctor and daubed shanny, sometimes returned with capelin (KHE, unpublished data). Additionally, the dive bout preceding the delivery of capelin looked visually identical to the dive bout preceding delivery of these specialist prey types, suggesting that perhaps the specialist was searching for these items, but captured capelin instead (KHE, unpublished data).

Conclusion

On the one hand, these results show that murres are not merely naïve, random predators and, therefore, that the proportion of a given prey type in diets does not equate to its encounter rates. Clearly, the underlying principles of at-sea decision-making and searching by murres must be better understood before diet and time budgets can be

translated into at-sea prey abundance. On the other hand, these results suggest that these generalist predators may be excellent indicators of the horizontal and vertical distribution of their prey, as at-sea behavioural patterns appeared to indicate only two or three possible prey types for most measurements.

Overall, these results strongly suggest that generalist marine predators, Thick-billed Murres, use stereotyped behavioural strategies to select specific prey types. This behaviour may partially reflect individual specialization, with individuals specializing on a given prey type utilizing behaviour that maximizes encounter rate with that prey type. Nonetheless, as many individuals switch prey types between years and within a year, these differences must also reflect behavioural decisions made by adult murres in response to perceived changes in prey abundance. Thus, the use of TDRs allows researchers to monitor temporal trends in seabird behavior and how they change for specific prey types, which presumably reflect changes in the biology and behaviour of forage fish species. Nonetheless, not only do ecology of different prey types influence the behaviour of murres, but murres, as predators, also affect the behaviour of these prey types. This is the subject of the next chapter.

Chapter 3: Central-place foraging in an arctic seabird lends evidence for Ashmole's halo.

Many marine animals, including lactating seals and breeding seabirds, must return to a central location after each foraging bout. For these central place foragers, foraging time includes transit time to and from the central place, as well as searching and handling time (Orians and Pearson 1979, Robert-Coudert et al. 2004, Wilson et al. 2005). To maximize foraging efficiency, central place foragers are expected to minimize transit time by selecting nearby foraging patches and traveling along the most direct path between the foraging patch and the central place (Orians and Pearson 1979, Ydenberg et al. 1994, Saunders and Ydenberg 1995). Distant foraging patches, however, may be accessed if larger prey items are located in patches farther from the central place, and if the net energy gain of these larger prey items is higher than the value of smaller prey items captured at closer patches (Houston and McNamara 1985, Cuthill and Kacelnik 1990, Waite and Ydenberg 1996). As predicted, the size of prey captured increases with the distance to the patch for many central place foragers (e.g. Wanless et al. 1993b). There are examples, however, where this trend was not observed (e.g., Jenkins 1980, Sodhi 1992, Alonso et al. 1994, Frey et al. 1995), and there is little information available for marine animals. Due to the three-dimensional nature of marine environments, other factors (e.g., bathymetry) may be more important than distance for increasing the foraging efficiency of marine central place foragers (Haney and Schauer 1994, Sjoberg and Ball 2000, Rodary et al. 2000).

Central place foraging implies that food items are more valuable at some distance from the central place than at the central place; if this were not so, there would be no

reason to leave the central place. In the context of seabird colonies, foraging away from the immediate vicinity of the central place can occur for three reasons. First, there may be unsuitable habitat for nesting near prey patches. For example, Common Murre (*Uria aalge*) foraging patches, which are capelin (*Mallotus villosus*) spawning grounds in coastal Newfoundland, occur up to 100 km from the only island distant enough from human habitation to sustain a colony into the 20th Century (Davoren et al. 2003a). Second, intraspecific competition at prey patches close to the colony may decrease foraging efficiency at nearby patches (Davoren et al. 2003b). Lastly, prey may be distributed uniformly, but may become depleted close to the colony due to preferential selection of prey items near the colony early in the breeding season. This can occur either through the removal of benthic species (Birt et al. 1987) or predator avoidance and, thus, movement away from the colony by mobile pelagic species (Lewis et al. 2001, Litzow et al. 2004).

The last alternative implies that an annulus forms around the colony ("Ashmole's halo") where prey items become absent or in low abundance (Ashmole 1963, Gaston 2004). The size of Ashmole's halo is predicted to increase with the number of seabirds at the colony (Cairns 1989). Seabird foraging success, and, therefore, reproductive success, decreases with the size of the halo (Cairns 1989). This relationship is believed to lead to food-limited, density-dependent population regulation, which may be the ultimate cause for K-selected life history strategies in seabirds, including delayed maturity, low fecundity and high adult survival (Gaston 2004). Despite the potential importance of Ashmole's halo for understanding seabird population ecology, it has only been directly tested once. Fewer benthic fish were counted on SCUBA transects near a cormorant

colony than on those farther away (Birt et al. 1987). Indirect evidence for prey depletion, however, has been deduced from positive correlations between colony size and (1) reduced chick physiological condition (Tella et al. 2001, Davoren and Montevecchi 2003), growth (Gaston et al. 1983, Kitaysky et al. 2000) and meal size (Ainley et al. 2004) or quality (Forero et al. 2002), (2) reduced adult body condition (Gaston and Hipfner 2006) or increased adult metabolic rate (Kitaysky et al. 2000), (3) reduced neighboring colony size (Furness and Birkhead 1984, Ainley et al. 1995, 2003, 2004, Lewis et al. 2001, Forero et al. 2002), and (4) increased trip duration (Lewis et al. 2001, Ainley et al. 2003, 2004, Davoren and Montevecchi 2003). Nonetheless, these correlations are not always observed (e.g. Frederikson et al. 2005, Peterson et al. 2006), or only in some years (Ainley et al. 2004). Cairns et al. (1990) suggested that a reduction in dive time with increasing travel distance from a Common Murre colony may represent a response to prey depletion in the vicinity of this colony because birds choose to capture more accessible, shallow water prey at more distant locations rather than capturing less accessible, deep prey close to the colony. Furthermore, these correlations may occur because of interference competition rather than exploitative competition (Ainley et al. 2003, Davoren et al. 2003b).

With the invention of miniaturized bird-borne devices, seabird biologists have been able to examine many aspects of foraging behavior that were formerly difficult or impossible to observe (e.g., Wilson et al. 1992, 1995, 2002, Putz et al. 1998, Charrassin et al. 2001, Catry et al. 2003). Because most seabirds make relatively long foraging trips and return with many prey items, however, it is difficult to link specific dive bouts to specific prey species or size (Simeone and Wilson 2005; Tremblay et al. 2005, Wilson et

al. 2005). Thick-billed Murres provide an opportunity for overcoming this difficulty because they are single-prey loaders, usually returning with a single, readily identifiable prey item and they are sufficiently large and robust to accommodate data logging devices with limited impact on behavior (Croll et al. 1992, Benvenuti et al. 2002, Jones et al. 2002, Mori et al. 2002). These same traits are thought to make murres useful indicators of prey distribution and abundance, especially at locations where measuring these prey parameters directly is extremely expensive (Gaston and Hipfner 1998, Gaston et al. 2003, 2005a,b). To effectively use these birds, and other central place foragers, as indicators of such prey parameters, however, it is important to quantify the biases (e.g., prey selectivity) associated with the way in which they sample the marine environment (Houston 2000; Sjoberg and Ball 2000; Weimerkirch et al. 2005).

I combined information on prey deliveries to chicks with at-sea foraging behavior obtained from temperature-depth recorders (TDRs) attached to Thick-billed Murre parents at a subarctic colony during chick-rearing. I assumed that the last dive represented the dive during which prey destined for the chick was captured and that individuals returned directly to the colony after the last dive bout, as predicted from theoretical considerations for single prey loaders (Orians and Pearson 1979; Houston 1987, 2000) and has been shown in other studies (Benvenuti et al. 1998; Falk et al. 2000, 2002). Based on theoretical considerations, I predicted that: (1) prey size would increase with distance to a foraging patch; (2) dive depth would decrease with distance to a foraging patch, possibly due to the depletion of easily accessible shallow water prey in the vicinity of the colony; (3) distance to a foraging patch would increase with date during each breeding season, because of depletion of prey items in the vicinity of the

colony, and (4) for similar reasons, the proportion of large prey items would decrease as the breeding season progressed.

Based on estimated densities of Arctic cod in arctic regions (eg., Lancaster Sound:2 200 fish·km^{-2}; Welch et al. 1992, 1993; cf. Crawford and Jorgensen 1996) and population densities of Thick-billed Murres near colonies during the breeding season, I expect that murres likely exert a significant predation pressure on fish stocks surrounding arctic breeding colonies (~ 8 % of Arctic cod predation while breeding in Lancaster Sound; Welch et al. 1992, 1993). In support, Croll (1990) measured energy expenditure using doubly-labeled water and estimated that individual adult murres at Coats Island need approximately 286 g·d^{-1}. Thus, 30 000 murres feeding in a foraging radius of ~ 40 km remove 8 kg·d^{-1}·km^{-2} or 96 000 fish·km^{-2} over the entire breeding season (Croll 1990). Additionally, the relative scarcity of seals and belugas in the vicinity of Coats Island, once the floe edge leaves (Gaston and Ouellet 1997), suggests that this area may not be very productive during the summer.

Materials and Methods

This study was conducted at the west colony on Coats Island (62°57'N, 82°00'W), Nunavut, Canada (Gaston et al. 2003, 2005a,b) during 1999, 2004 and 2005. Data collected prior to 2004 were made available by Environment Canada (A.J. Gaston) for analysis within my thesis.

TDR Attachment

Murres were caught with a noose pole for device attachment over the three years of this study (n = 24 in 1999; n = 23 in 2004; n = 33 in 2005). During 1999, I used TDRs identical to those described by Falk et al. (2000, 2002) and Benvenuti et al. (1998, 2002).

The "Benvenuti" TDRs were 80 mm in length, with a width varying from 23 mm (tip) to 30 mm (base) and a depth of 13-18.5 mm. The casing housed a pressure sensor and two motion recorders. The motion recorders sampled every 8 s and distinguished flying, swimming and resting (Benvenuti et al. 1998). The pressure sensors sampled every 4 s and recorded depths up to 76 m. The Benvenuti TDRs were fitted to feathers along the midline of the lower back using tape to minimize drag (Bannasch et al. 1994). During 2004 and 2005, the TDR procedures followed those outlined in Chapters 2 and 3.

Back-mounted TDRs are known to influence murre provisioning rates, trip duration and body mass (Croll et al. 1992, Falk et al. 2000, 2002, Watanuki et al. 2001, Tremblay et al. 2003, Hamel et al. 2004, Paredes et al. 2005). To determine whether my devices significantly impacted provisioning rates, I compared provisioning rates of individuals with TDRs to their partners without TDRs and chick feeding rates of the same individuals with and without TDRs. Because the Benvenuti TDRs were larger than the Lotek TDRs, birds with these TDRs likely decreased dive depth, duration and flight speed relative to birds with Lotek TDRs (Paredes et al. 2005, Chapter 1). Therefore, analyses were only completed within each year to avoid device effects. Because only 7% of the dives (1999: 7/81; 2004: 3/50; 2005: 9/129) were within the period when murre dive depth is reduced due to decreased light availability (2100-0400; Croll et al. 1992), I ignored time of day as a factor in our analysis. Time-of-day effects were further reduced by analyzing some of the data by species; for example, sandlance (*Ammodytes* spp.) were delivered after 35 % of the dives within the 2100-0400 time period, so.

Nest Observations ('Feeding Watches')

During the deployment of TDRs, continuous observational watches of 61 Thick-billed Murre nest sites were carried out (feeding watches). All observations were made from blinds situated on the study plots, within 6 m of the birds. Three 24- or 48-h continuous feeding watches were conducted during 1999 (Q and Jb sub-colonies: 28-30 July; 7-9 August; 12-14 August), 2004 (Q subcolony: 30 July; 8 August; 14 August) and 2005 (Q subcolony: 24-26 July; 2-3 August; 7-8 August), as well as two shorter feeding watches (T subcolony: 14:00-19:00 28 July 2005; Z subcolony: 12:00-17:00 10 August 2005). Observers watched for 3-4 h bouts. I also obtained information from feeding watches (three 24-h continuous feeding watches at Q subcolony) in years when TDRs were not deployed (1994-2005), with feeding watches spaced approximately five to seven days apart, starting when about 50 % of nestlings were hatched (Gaston et al. 2003). Feeding watches were not conducted when it was too dark to see prey deliveries to chicks (roughly 01:00-02:00 in late July; 23:00-0:400 in mid August) because nestlings are rarely fed at this time (Gaston et al. 2003).

During these observation sessions, prey items delivered to chicks were visually identified to species (where possible). Fish length was estimated by reference to the white streak on the upper mandible of the adult's bill (~5 cm). Length was then converted into fish mass using mass-length relationships (KHE, unpublished data). Because of their similarity in life history and difficulty in identification in the field, we pooled all zoarcoids (fish doctor, daubed shanny, Arctic shanny and snakeblenny; Chapter 2) and all crustaceans (shrimp, amphipods; Chapter 2) into single categories to increase power for some analyses.

Modeling Foraging Locations

As bathymetry may play an important role in determining dive depths of murres for benthic species, I investigated its role in determining the relationship between dive depth and flight distance. To do this, I estimated the capture locations of benthic prey using bathymetric data. I obtained bathymetric data from the General Bathymetric Chart of the Oceans (GEBCO) at one-minute resolution through the Canadian Department of Fisheries and Oceans. I then used ArcGIS 9.0 Geostatistical Wizard to determine the best model for interpolating depths between those provided by GEBCO. I created a training data set comprising 90 % of the points (108845 points) and a test data set comprising the remaining 10 % (12094 points), and I used the Root Mean Square of the deviations in the test data set from the predicted to determine the best method of interpolation. I compared Inverse Distance Weighting (IDW) with fixed second order polynomial (RMS = 8.69), Ordinary Kriging (RMS = 11.41), Simple Kriging (RMS = 8.55) and IDW with Optimized Power Value (RMS = 7.92; Optimized Power = 3.27) and, therefore, selected the IDW method with power value of 3.27.

Using the ArcGIS 9.0 Geostatistical Wizard, I then created a layer measuring cost-weighted distance from the colony (62°57'N, 82°00'W), with cost of traveling over land set at 10 000 times the cost of traveling over water to effectively exclude overland travel. I assumed that all birds flew west of the colony (KHE, unpublished data). I manually selected the unique combination of depth and cost-weighted distance for each benthic prey delivery by zooming in to an accuracy of 200 m x 200 m and assuming that maximum dive depth for these deliveries was equal to the ocean depth. I also assumed that birds returned via the shortest route possible that did not pass over land and that they flew at 75 km·hr^{-1} (KHE, unpublished data). I qualitatively compared the capture

locations of benthic prey items with the proportion of depths available between 40 - 140 m at all distances from the colony.

<p style="text-align:center">Statistical analyses</p>

All statistical analyses were performed in STATISTICA. Prior to using parametric statistics, I tested for normality (Shapiro-Wilk test) and homogeneity of variance (Levine's test). Prey mass, distance from the colony and dive depth were log-normally distributed (Shapiro-Wilk test after transformation) and, therefore, I ln-transformed these data prior to analysis. I only analysed dives with maximum depth >3 m. I used linear regression to compare prey mass and dive depth with distance from the colony. I completed least squares regressions on four two-parameter models (ae^{bx}, $ax+b$, ax^b $a\log x+b$) and one three-parameter model (ax^2+bx+c) for each relationship (mass and distance; depth and distance), to determine whether a nonlinear relationship improved fit. I used the highest r^2 to select the best model.

Because the Benvenuti TDRs recorded a maximum depth of 76 m and depth was therefore not normally or log-normally distributed, I used a *t*-test on ln-transformed data to compare distance traveled for prey items collected above or below 76 m. I also used *t*-tests to determine whether the same prey items were collected farther from the colony during August than during July.

I calculated the proportion of fish that were (1) benthic zoarcoids, (2) Arctic cod and (3) capelin during each feeding watch from 1994-2005 and the proportion of total deliveries that were (4) crustaceans during each feeding watch (see Chapter 2 for ecological descriptions). I used paired *t*-tests (paired by year) to determine whether the arcsine-transformed proportion of each of the four prey classes differed between August

and July. I also used a Z-test to determine whether the slope of the least squares regression (calculated for each year) on the arcsine-transformed proportion of each of the four prey classes against date (days since June 1) was significantly different from zero.

Results

There was no significant difference in feeding rates of birds with Lotek TDRs (6.2 ± 3.4 feeds per watch) compared with their mates with no devices (5.0 ± 4.0 feeds per day; paired $t = 0.58$, df = 24, p = 0.72) or compared with themselves with no devices at a prior or later date (TDR birds: 3.9 ± 2.3 feeds per day; no TDR birds: 3.1 ± 2.6 feeds per day; paired $t = 1.85$, df = 24, p = 0.96). Birds with Benvenuti TDRs (2.1 ± 1.1 feeds per day) had significantly fewer feeds than their mates (3.6 ± 2.8 feeds per day; paired $t = 2.35$, df = 20, p = 0.01). I could not compare observations of the same individuals with and without Benvenuti TDRs, as there were very few observations.

When all prey species were pooled, prey mass increased with distance from the colony in all three years and this remained true when invertebrates were excluded (Table 3.1). Capelin (2005) and sculpins (1999) were the only taxa that showed significant relationships when prey types were analyzed separately, with mass increasing with distance from the colony for both taxa (Table 3.1). The relationship was nonlinear, with the strongest increases in mass with distance occurring within the first 20 km (Fig. 3.1).

Dive depth decreased with distance from the colony in 2004 and 2005 for all species combined (Fig. 3.2; Table 3.2). There was a strong negative relationship between depth and distance for capelin (2004 and 2005) and benthic zoarcoids prey (2005; only three were reported in 2004). This was not due solely to bathymetry, as the proportion of

Table 3.1. Relationship between prey mass and return flight distance for each prey type and all prey types combined delivered by thick-billed murre parents to their chick during 1999, 2004 and 2005 at Coats Island. All parameters refer to linear regressions on ln transformed data. Only taxa with > 5 observations in a given year are included. The final column shows analyses with invertebrates excluded (no invertebrates were observed in 2004).

Year		Capelin	Amphipod	Arctic cod	Daubed shanny	Sculpin	Total	Total - inverts
1999	Slope	0.38		0.167	-0.04	3.41	0.51	0.62
	Intercept	-0.78		1.51	1.11	-10.74	-0.64	-1.03
	r^2	0.09		0.01	0.002	0.80	0.13	0.13
	df	24		23	7	5	78	73
	t	1.81		0.51	-0.11	4.65	3.44	3.35
	p	0.08		0.62	0.91	0.01	0.0009	0.001
2004	Slope	0.24		1.89		0.24	0.41	0.41
	Intercept	-0.34		-0.04		0.57	-0.45	-0.45
	r^2	0.009		0.002		0.01	0.09	0.09
	df	26		6		5	46	46
	t	1.12		-0.1		0.3	2.33	2.33
	p	0.28		0.93		0.78	0.02	0.02
2005	Slope	0.37	0.02	-0.03	0.22	0.37	0.31	0.21
	Intercept	0.03	2.14	2.01	0.15	0.48	2.76	2.06
	r^2	0.083	0.0008	0.0017	0.087	0.15	0.10	0.10
	df	54	18	9	14	11	121	102
	t	2.43	0.11	-0.12	1.11	1.37	3.59	3.01
	p	0.02	0.91	0.91	0.29	0.2	0.0005	0.003

Capelin ◆ Amphipods ■ Arctic cod ▲ Snakeblenny × Fish doctor △
Daubed shanny □ Sandlance ◇ Sculpin + Squid - Arctic shanny ✕

Mass (g)

Mass (g)

Mass (g)
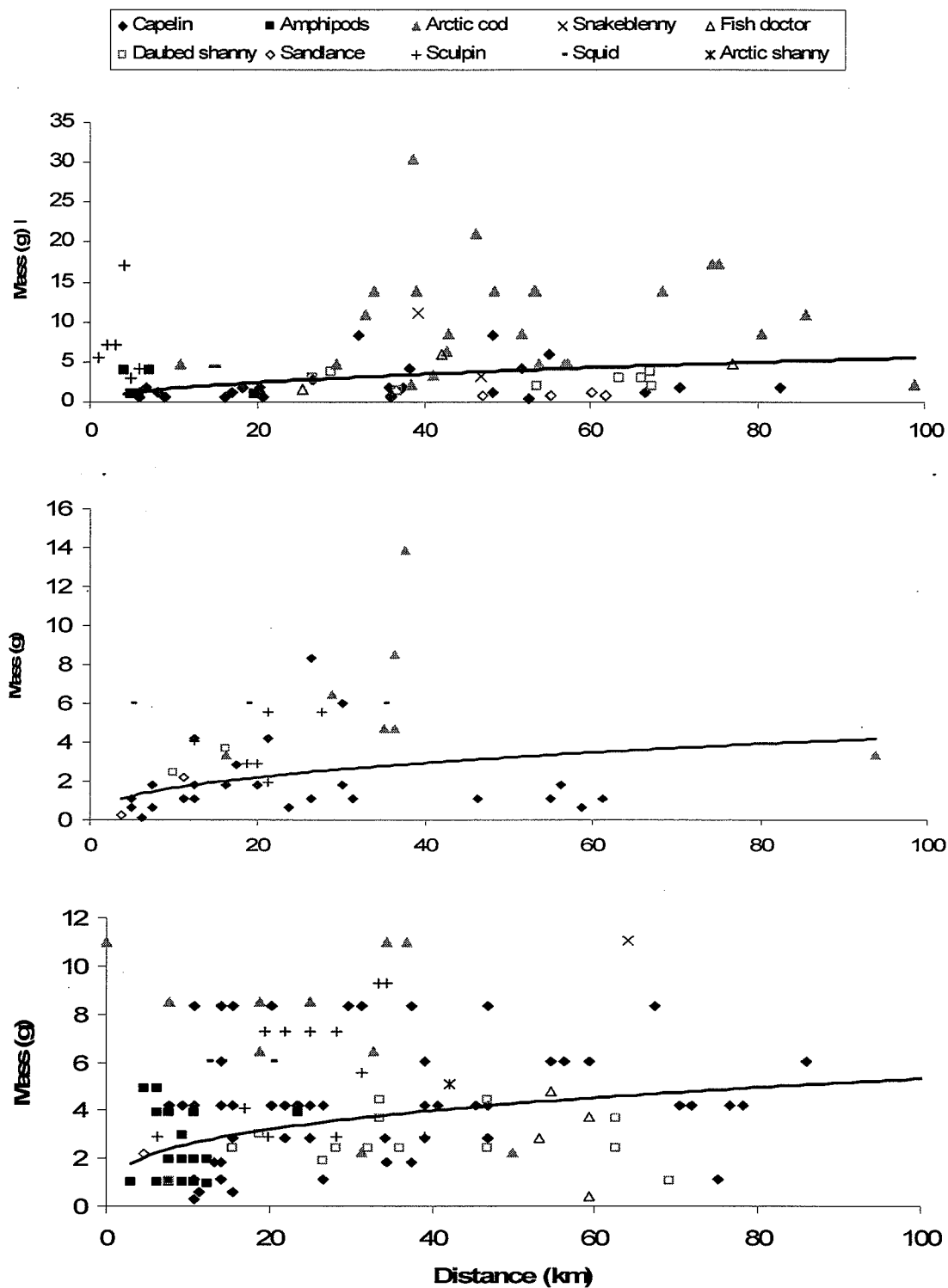
Distance (km)

Figure 3.1. Relationship between prey mass and return flight distance for all prey types combined delivered by thick-billed murres parents to their chick at Coats Island in (a) 1999 (Mass = 1.25 Distance$^{0.31}$; r^2 = 0.10); (b) 2004 (Mass = 0.64 Distance$^{0.41}$, r^2 = 0.11); and (c) 2005 (Mass = 0.52 Distance$^{0.51}$, r^2 = 0.13).
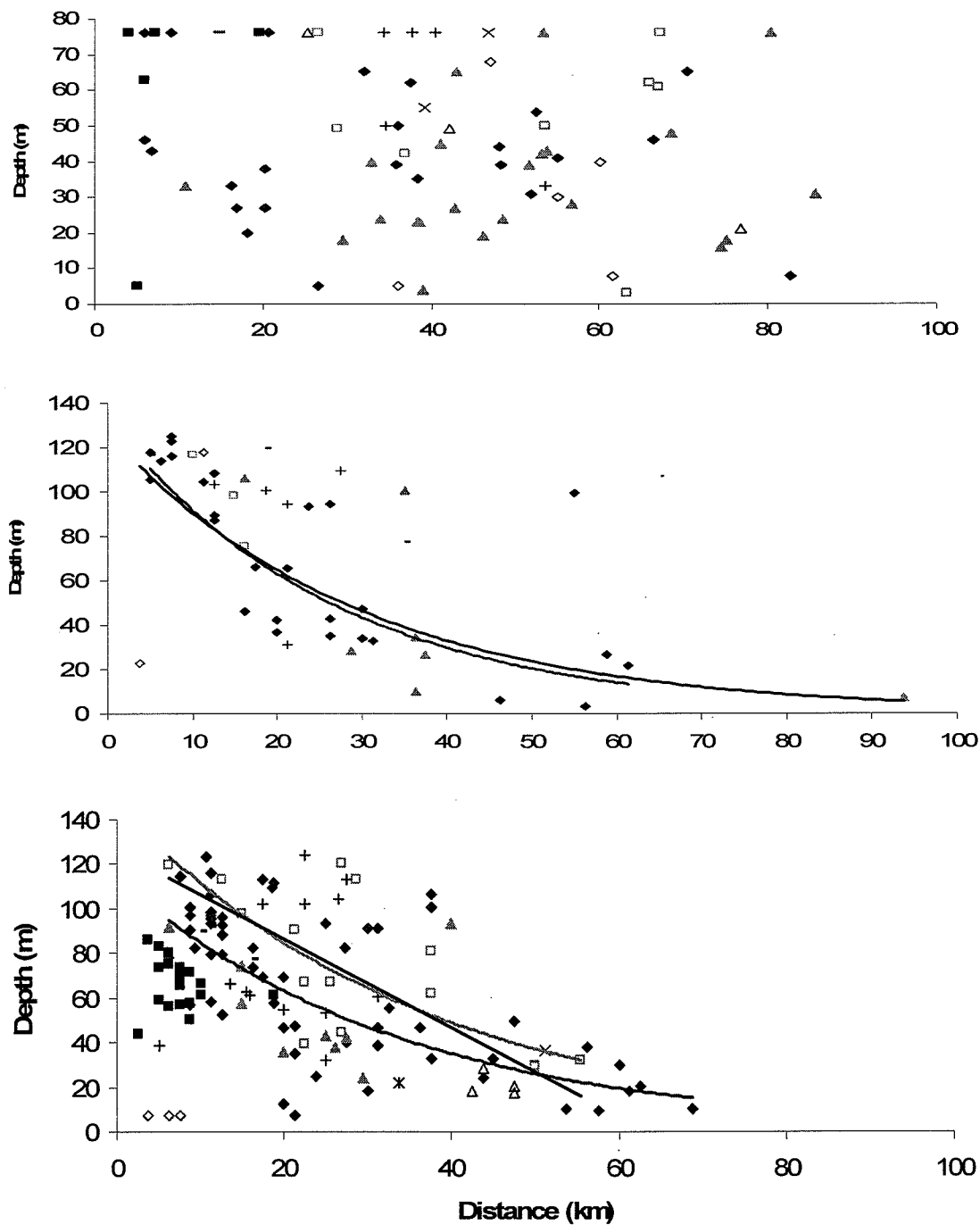
Figure 3.2. Relationship between depth and return flight distance for all prey types combined delivered by thick-billed murres parents to their chick at Coats Island in (a) 1999 (Ln(Depth) = -0.13 Ln(Distance) + 3.92; r^2 = 0.01); (b) 2004 (Depth = 127 $e^{-0.034 \, Depth}$; r^2 = 0.48; capelin: Depth = 134 $e^{-0.038 \, Depth}$; r^2 = 0.53); and (c) 2005 (capelin: Depth = 114 $e^{-0.029 \, Distance}$; r^2 = 0.44; daubed shanny: Depth = 147 $e^{-0.027 \, Distance}$; r^2 = 0.47; all zoarcoids: Depth = -2.00 Distance + 12; r^2 = 0.59). Legend same as previous figure.

Table 3.2. Relationship between depth of last dive preceding delivery of a prey item and return flight distance for prey items delivered by thick-billed murre parents to their chick during 2004 and 2005 at Coats Island. All parameters refer to linear regressions on ln transformed data. Only taxa with > 5 observations in a given year are included. The final column shows analyses with invertebrates excluded (no invertebrates were observed in 2004). Because Benvenuti TDRs did not measure depths > 76 m in 1999, this analysis was not completed for that year

Year		Capelin	Amphi pod	Arctic cod	Daubed shanny	Sculpin	Total	Total without Inverts
2004	Slope	-0.85		-1.48		-0.24	-0.72	-0.72
	Intcpt.	6.49		8.71		5.14	6.17	6.17
	r^2	0.51		0.56		0.02	0.37	0.37
	df	26		6		4	46	46
	t	-5.15		2.50		-0.23	-5.17	-5.17
	p	0.00003		0.06		0.84	<0.001	<0.001
2005	Slope	-0.73	4.17	-0.04	-0.63	0.20	-0.27	-0.32
	Intcpt.	6.22	0.01	4.10	6.22	3.62	4.77	4.92
	r^2	0.41	0.02	0.01	0.48	0.09	0.08	0.08
	df	57	17	9	14	13	127	109
	t	-6.23	0.11	-0.19	-3.47	1.09	-4.55	-3.15
	p	0.00001	0.91	0.86	0.004	0.30	0.002	0.002

depths available between 40 - 140 m was roughly similar at all distances from the colony (Fig. 3.3). In 1999, murres returned with prey from significantly greater distances (t = 1.77, df = 22, p = 0.04) when they had final dives > 76 m than when they had final dives < 76 m. There was no relationship between the dive depth and prey mass in any year (1999: t = -0.30, df = 78, p = 0.76, r^2 = 0.001; 2004: t = -0.21, df = 45, p = 0.83, r^2 = 0.001; 2005: t = -0.57, df = 124, p = 0.52, r^2 = 0.003).

In general, prey were captured farther from the colony in August than in July in 1999, 2004 and 2005. In 1999, Arctic cod were captured farther from the colony in August (66.9 ± 5.8 km) than in July (42.5 ± 3.9 km; t = -3.47, df = 20, p = 0.001). No analysis was possible in 2004 or 2005 due to two or fewer observations during either July or August. In 1999, capelin were captured at roughly the same distance during July and August (Table 3.3). This was due to very short distances traveled during the third feeding watch, at which time capelin were significantly smaller than those collected during other feeding watches (t = 2.72, df = 24, p = 0.006). When the third feeding watch was excluded, capelin were captured farther from the colony in August than in July (Table 3.3). Capelin were captured farther during August than during July in 2004 and 2005 (Table 3.3). Comparisons were not made for any of the other prey items because none of them had > 5 observations in both July and August during any of the three years.

Across all years where feeding watches were conducted (1994-2005), the proportion of different prey types delivered to chicks differed in August relative to July. The proportion of large prey types, Arctic cod and benthic zoarcoids, was lower in August, whereas the proportion of smaller prey types, capelin and invertebrates, was higher in August than July (Table 3.4). Furthermore, the proportion of these larger prey types
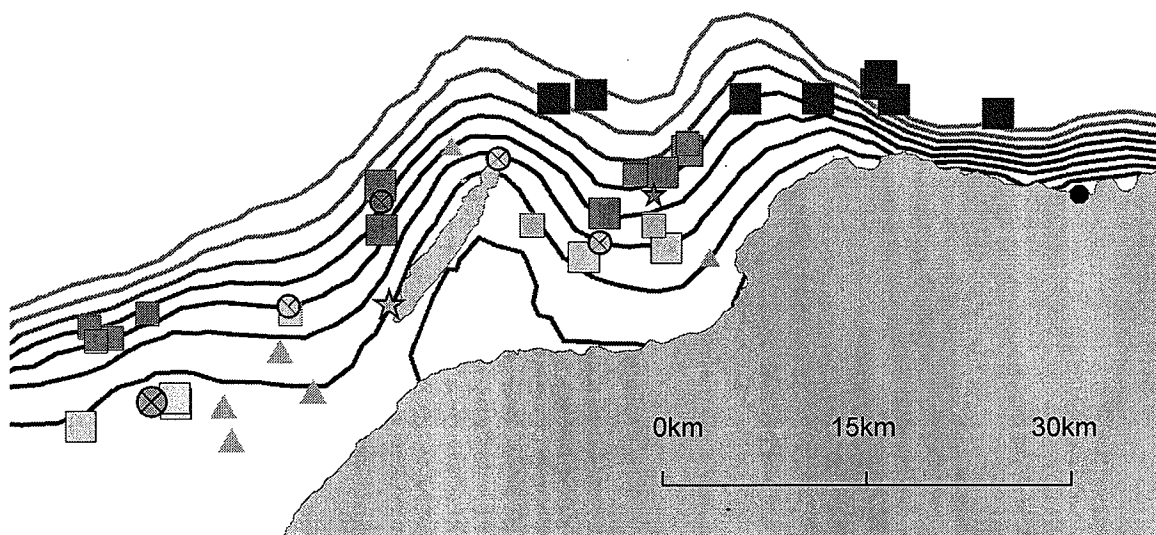
Figure 3.3. Locations where benthic prey items were taken by Thick-billed Murre parents in the vicinity of the Coats Island, Nunavut colony, in relation to depth. Depth contours are in 20 m intervals between 0 and 140 m. Squares represent daubed shanny, circles snakeblenny, stars Arctic shanny and triangles fish doctor. Small symbols show 1999-2000 values; large symbols show 2004-2005 values. Light grey represent prey items taken below 60 m, medium grey those prey items taken between 60 and 90 m (including three values from 1999-2000 that read >76 m) and dark grey represent those prey items taken below 90 m.

Table 4.3. Mean distance (in km ± SD) from the Coats Island colony that capelin were collected by Thick-billed murre parents during 1999, 2004 and 2005. Values for 1999 are shown with and without Feeding Watch 3 (FW3). During FW3 a large number of exceptionally small capelin were delivered

Year	August	July	t	df	P
1999 (with FW3)	34.6 ± 7.5	39.9 ± 3.2	-0.15	21	0.95
1999 (without FW3)	56.2 ± 8.3	39.9 ± 3.2	1.78	12	0.04
2004	26.5 ± 4.1	16.3 ± 2.0	2.22	25	0.02
2005	30.3 ± 6.6	14.5 ± 1.4	3.62	34	0.0006

Table 4.4. Mean ± SD percentages of Thick-billed Murre nestling deliveries that were of each prey type at Coats Island during July and August 1994-2005. Paired t-tests (df = 11) were completed on arcsin-transformed proportions of each fish (zoarcoids, capelin, Arctic cod) or invertebrate prey type. Slope represents rate of change in proportions of total fish (zoarcoids, capelin, Arctic cod) or total deliveries (crustacean) per day (linear regression) averaged across years, with p-values representing Z-test on slopes from arcsin-transformed proportions across years

	July	August	t	P	Slope $(\cdot 10^{-3})$	P
Zoarcoids	14.3 ± 6.7	7.3 ± 2.3	4.18	0.0008	-6.62 ± 1.39	0.00001
Capelin	28.1 ± 11.6	37.7 ± 13.9	2.09	0.03	15.56 ± 3.51	0.001
Arctic cod	26.4 ± 19.2	19.4 ± 12.8	2.55	0.01	-9.36 ± 2.73	0.0003
Invertebrates	0.36 ± 0.41	7.1 ± 10.1	3.36	0.003	7.49 ± 3.21	0.00001

decreased with date, whereas the proportion of these smaller prey types increased with date (Table 4.4).

Discussion

Prey size increased with distance from the colony in all three years of this study, although distance explained only a small portion of the variation in prey size ($r^2 \sim 0.1$; Fig. 3.1). Factors other than distance likely also determine the location where murres can forage most efficiently. Even in relatively simple terrestrial systems, the explained variation (r^2) for size-distance relationships are generally low (Carlson and Moreno 1981, Hegner 1982, Carlson 1983, Kacelnik 1984, Kacelnik and Cuthill 1990). In marine systems, physical factors, such as time of day, tide, weather and bathymetry, influence both prey density and distribution and, thus, the energetic costs of foraging in marine predators, which may obscure size-distance relationships (e.g., Sjoberg and Ball 2000). Furthermore, error associated with species identification and estimates of fish length and mass-length relationships also obscure these relationships.

The distance-mass relationship was largely driven by differences in the composition of prey species rather than mass within species. Murres brought back larger prey types, such as Arctic cod and zoarcoids, when foraging farther from the colony and brought back smaller prey species, such as amphipods and capelin, when foraging close to the colony. The relationship was nonlinear, with most of the increase in prey mass occurring within roughly 20 km of the colony (Fig. 3.1). Because parents do not increase the mass of prey delivered to their chicks after the first three days post-hatch (Paredes et al. 2005), it is unlikely that this merely reflects seasonal changes in prey selectivity by parents. Instead, it suggests that larger prey species are less available near the colony; otherwise, there

would be no reason for murres to commute longer distances to collect them. Additionally, if the mass-distance relationship was mainly due to a tradeoff between chick energy gain (prey mass) and adult energy expenditure (flight time), then one would predict that mass would be directly proportional to travel distance (e.g., Mass $\propto$ Distance). The best-fit relationship, however, approximated Mass $\propto$ Distance$^{0.5}$ (Fig. 3.1), suggesting that seabird foraging pressure may have been directly responsible for prey mass distribution. As suggested by Lewis et al. (2001), randomly distributed foragers from a central place would distribute foraging pressure according to an inverse-square law. If these foragers were depleting prey items in a manner proportional to the predators' abundance (Ashmole's halo), this would then lead to prey distributions following an inverse-square law.

The conclusion that some prey items were less abundant in the vicinity of the colony was supported by the tradeoff between distance and depth (cf. Cairns et al. 1990). Prey items collected at shallower depths were collected at greater distances from the colony (Fig. 3.2, 3.3). This trend could be due to seabird behaviour (e.g., a tradeoff between energy expenditure during diving and flying), or it may reflect habitat features, such as areas of shallow bathymetric relief, where prey persistently aggregate some distance from the colony. It is likely that murres expended similar amounts of energy diving farther away because the number of dives per bout increased with flight time (KHE, unpublished data). Furthermore, this trend occurred much more strongly within certain prey species than when all prey species were combined, suggesting that this relationship reflects prey distribution rather than predator behaviour. Specifically, it appeared that capelin occupied less accessible, deep water close to the colony or more accessible, shallow water farther

from the colony, creating a three-dimensional zone around the colony where either capelin was absent or sparse, or where murres chose not to obtain them. Furthermore, this relationship was relatively continuous (Fig. 3.2) and did not show abrupt changes that might reflect shallow benthic spawning grounds.

Bathymetry may play an important role in determining dive depths of murres for benthic species. Parental murres captured benthic zoarcoids at shallower depths as flight distance increased in 2005, the only year when significant numbers were observed in the diet. At distances less than 20 km, murres captured zoarcoids from depths below 90 m, which is deeper than the average murre dive depth (18 m; Croll et al. 1992). At distances greater than 20 km, murres took zoarcoids at shallower depths (20-40 m). Thus, it appeared that murres depleted zoarcoids from the nearshore shelf, either in the incubation or early chick-rearing period, as obtaining this prey type meant either traveling 20 km or more to a shallow bench or diving deep close to the colony (Fig. 3.3). It did not appear that the negative relationship between depth and distance for zoarcoids merely reflected the distribution of suitable habitat for zoarcoids because rocky outcrops, the favoured habitat for most zoarcoids including daubed shanny, are abundant at shallow depths in the vicinity of the colony, although it is possible that zoarcoids were responding to finer-scale variation in habitat.

For both capelin and zoarcoids, the depth-distance relationship was nonlinear, with depth decreasing sharply beyond 20 km (Fig. 3.2). Although the distance-depth tradeoff was only significant for two taxa, sample sizes were small and distances were less variable for the remaining taxa, making it difficult to detect trends. In the case of sculpins, trends may have also been obscured because different species were involved;

large *Myoxocephalus scorpius* sculpins, a shallow water species, were captured by local Inuit immediately next to the colony, whereas the few deeper-water *Triglops* spp. sculpins that were identified during feeding watches were preceded by relatively long flights. Adults brought back fewer sculpins when other prey sources were present, suggesting that murres avoided sculpins, possibly because they are lipid-poor or because they have opercular spines that may impede swallowing.

Some of the variation in the relationship between prey mass and distance may also be due to variation in mass-length relationships or energy density. I chose to analyze mass, rather than energy density, because energy density values for some prey items were unavailable in the literature. Energy densities varied between 17 - 27 kJ/g dry weight among the species of known energy density (Cairns 1984), whereas mass varied from < 0.5 g to > 15 g, so that most of the variation in prey energy value was due to mass rather than energy density. Furthermore, energy density increased with mass at nearby Digges Island (Cairns 1984). For example, invertebrates had the lowest energy density, sculpins had higher energy densities, benthic zoarcoids (*Eumesogrammus*, *Gymnelus*, *Leptoclinus* and *Stichaeus*) had still higher energy densities, and Arctic cod had the highest energy densities (Cairns 1984). Therefore, relationships between mass and distance from the colony would have been accentuated had I been able to estimate energetic quality rather than mass, leading to the potential for Type II errors.

Possible evidence for prey depletion also was provided by the increase in flight distance for the two species with largest sample sizes, capelin and Arctic cod (Table 3.3), and the reduction in the proportion of large prey types, Arctic cod and zoarcoids, captured (Table 3.4), as the season progressed. While it is possible that these changes

represent migrations of prey towards or from spawning grounds or other seasonal movements (Rose 2005; Davoren et al. 2006), they are also consistent with murre predation pressure causing local prey depletion. Murres feed themselves with small invertebrates, primarily amphipods, during incubation, but switch to larger fish during chick-rearing (Gaston and Bradstreet 1993). Presumably, mobile prey species may be able to respond to this switch by moving farther away from the colony, whereas benthic species that require specific habitat features may become reduced in number. As the chick-rearing period progresses, murres appeared to fly farther to capture schooling fish and benthic species. By the end of the chick-rearing period, profitable prey items appeared to have been depleted to such an extent that they were effectively no longer present within foraging ranges, and adults were left to exploit less profitable (smaller) taxa, such as amphipods, capelin or sculpins.

I have presented four pieces of evidence in favour of the hypothesis that Thick-billed Murres deplete local stocks of prey around Coats Island: (1) murres flew farther for a given prey type later in the breeding season; (2) murres switched to lower quality (lower mass) prey items later in the breeding season; (3) dive depth decreased with flight distance; and (4) prey mass increased with flight distance according to an inverse-square law. Although alternative explanations exist, the most parsimonious explanation for the data, based on previous studies (Birt et al. 1987; Cairns et al. 1990), is that large prey items are depleted from near the colony and from shallow depths near the colony as the breeding season progresses. Nonetheless, it can be argued that because I did not measure prey abundance independently, these relationships merely reflect consequences of murre behaviour and do not reflect prey abundance. This issue could be overcome by direct

measurements of prey abundance at varying distances from the colony throughout the breeding season.

Regardless, I believe that it may not be necessary to know whether the number of individual fish (or any other index of prey abundance) actually changes with distance, depth or time. From the murres' perspective, what matters is prey *availability*. Predators may alter prey availability without altering prey abundance by altering prey behaviour (Hamilton 1971; Cartar and Abrahams 2000; Ydenberg et al. 2004). In the context of Thick-billed Murres at Coats Island, this could occur if (1) mobile fish, such as capelin, move away from the colony or deeper in response to predation pressure; (2) schooling fish, such as capelin, became less aggregated near the colony in response to predation pressure; or (3) benthic fish stayed nearer to potential refuges (e.g., reefs) or otherwise altered their predator-avoidance behaviour in response to predation pressure. In the hypothetical situation where there is an equal number of fish at all distances from the colony, but they are less available, for whatever reason, near the colony, then, from the murres' perspective an Ashmole halo is still in effect—provided the predators are causing the dispersion. Thus, studying Ashmole's halo from the predator's perspective is warranted, provided conclusions are only made relative to the predator. Presumably, seabird behaviour is a better index of prey availability than prey abundance.

It can also be argued that correlations between prey abundance and various indices do not necessarily reflect cause and effect. To demonstrate a cause-and-effect relationship—in other words to conclusively demonstrate an Ashmole halo effect—it would be necessary to manipulate colony size at different colonies and monitor changes in prey abundance. In practice, this is unethical and impractical. Nonetheless, variation in

hunting pressure may allow such an experiment in the future and it would, therefore, be useful to measure prey abundance in the area around several colonies currently to have a baseline for future comparisons.

Indirect evidence for Ashmole's halo in the vicinity of Coats Island supports the hypothesis that the sizes of Thick-billed Murre colonies in the Canadian Arctic are partially regulated by prey availability during the breeding season. Indirect evidence for exploitative competition has been deduced from increased foraging radius (Gaston 1983) and reduced adult and chick mass (Gaston et al. 1983, Gaston and Hipfner 2006) at larger colonies although similar relationships among Common Murre colonies in Newfoundland may be driven by interference competition at the foraging patch (Davoren and Montevecchi 2003). Therefore, my evidence that intraspecific competition may be driven by prey distribution and abundance is among the first positive results for Ashmole's hypothesis (Birt et al. 1987, Gaston 2004).

Synthesis

Predator-prey interactions are important ecological processes because they allow energy transfer among trophic levels within food webs. Therefore, elucidating predator-prey interactions is key to understanding ecological processes that drive ecosystem-level changes, such as those observed in polar regions in response to climate change (Croxall 1992; Loeb et al. 1997; Stirling et al. 1999, Barbaud and Weimerskirch 2001). In the Canadian Arctic, where marine surveys are costly and logistically difficult, seabird diets are often the only long-term data that can be used to monitor shifts in ecosystem-level processes. The parental prey deliveries to chicks of Thick-billed Murres at colonies in Hudson Bay have been studied for over two decades and form one of the only long-term data sets available for the region (Gaston et al. 2003). As the most rapid and dramatic changes in climate are predicted to occur in Arctic regions, these data sets are currently invaluable to retroactively investigate the biological impacts of climate change. Over this period, the dietary composition of murre chicks has switched from Arctic cod (an Arctic forage fish) to capelin (a temperate forage fish) concurrent with a decrease in the annual ice coverage (Gaston et al. 2003), a widely cited example of the impact of climate change within Arctic regions. The question remains whether this indicates an ecosystem-level shift in abundance and distributional patterns of these fish species and, thus, the fish species composition in the region, or simply a shift in dietary preferences of this bird.

Although it is clear that Thick-billed Murres at Coats Island have switched from provisioning their chicks primarily with Arctic cod to primarily with capelin, the causes and implications of this switch are less clear. On the one hand, this dietary switch may have been caused by the movement of capelin into northern Hudson Bay and, thus, an

increase in capelin abundance. On the other hand, this switch may reflect a change in the distributional patterns of cod and, thus a decrease in cod abundance in northern Hudson Bay, leaving capelin as the numerically dominant prey type. Alternately, this switch may reflect a change in Thick-billed Murre prey preferences, likely resulting from a combination of the above factors integrated with changes in prey behaviour. It is also unclear whether the switch will have an impact on Thick-billed Murres at a population-level. My thesis provides a background for addressing these issues.

Net Energy Gain in Relation to Changing Prey Availability

Changes in the availability of preferred prey types may lead to increased energy costs for marine predators, including Thick-billed Murres. Reduced net energy gain through increased foraging effort could result from increased average burst speeds of prey, increased depth of prey, decreased density of prey within patches, increased distance of patches relative to the colony, or decreased prey abundance. In Chapter 2, I showed that increases in energy costs have large impacts on the foraging behaviour of murres. As energy costs increased, birds either: (1) ceased foraging and waited for conditions to improve, or (2) switched to a more profitable prey type. The former response may explain why birds abandon reproduction altogether when energy costs increase greatly. Were climate change to lead to an increase in energy costs through changes in the availability of high quality prey, then this would have major negative implications for murre reproductive success at Coats Island over the long-term. The latter response may explain why murres have switched from cod to capelin, if energy costs for finding and capturing Arctic cod have increased.

Changes in the availability of prey also may lead to higher energy costs for colonial marine predators, if prey items are located farther from colony during the breeding season. In Chapter 4, I argued that Thick-billed Murres at Coats Island depleted the abundance of prey in waters near the colony and, thus, parents had to fly farther and began delivering lower quality prey types as the breeding season progressed. Although I did not quantify the impact of this presumably lower prey availability close to the colony on breeding success, this has been suggested to be one of the major causes of reduced breeding success for parents breeding later in the season (Hipfner and Gaston 2002; Gaston et al. 2005; Hipfner et al. 2005). In fact, this has been suggested as a primary reason for the K-selected life history strategies displayed by seabirds. Overall, this illustrates the potential for murre reproductive success to be impacted by changes in prey abundance. If prey depletion is a mechanism for population regulation, then changes in prey abundance may have a very pronounced effect on predator population size.

Changes in the availability of prey also may lead to reduced energy gain for marine predators, if prey items of lower energy value are replaced with prey items of higher energy value. As shown in Chapter 3, murres use different foraging tactics for different prey items, and these differences partially reflect differences in net energy gain. Thus, there is the potential for monitoring changes in prey abundance or distribution through changes in the at-sea foraging behaviour of murres.

More Capelin or Fewer Cod?

The absence of independent ship-based measures of fish biomass makes a definite answer to this question impossible. Nonetheless, some insights were provided by the data presented within my thesis.

Capelin at Coats Island are much smaller than Arctic cod (KHE, unpublished data), with capelin averaging about half the average mass of Arctic cod. In Chapter 4, I demonstrated that Thick-billed Murres obeyed the basic predictions of the Central Place Foraging model, including the prediction that parents will deliver larger prey items as distance from the colony increases. Applying this to the capelin-cod dichotomy, it would appear that murres would only switch to a lower-mass prey item (capelin) if it were present closer to the colony. Thus, were Arctic cod disappearing from the region, one would expect that seabirds would need to fly increasingly far as local stocks were depleted (Chapter 4). Eventually, it would be more profitable to switch to a closer, less profitable prey item (e.g. capelin). It is worth noting that during 1988 and 1989, dive behaviour at Coats Island involved shallow, U-shaped dives (Croll et al. 1992). Although the shallow depths (~18 m) suggest some impacts of the larger devices (Chapter 2, 4), they are also more similar in profile to those involved in capture of Arctic cod relative to capelin (Chapter 3).

A reduction in flight distance has indeed been recently observed, suggesting that a reduction in the abundance of Arctic cod has played a role in the dietary switch. During the late 1990s, average return flight distances were about 40 km (Woo 2001), whereas in 2004-2006, mean flight distances were about 25 km (Chapter 3). As device size had little impact on percent of time flying (Chapter 2), it appears that murres fed closer to the colony in 2004-2006 than during the late 1990s. This may reflect a reduction in the size of 'Ashmole's halo' near Coats Island (Chapter 4), and suggests the distribution of new prey types near the colony. A likely explanation is that capelin populations increased near the colony between these two periods.

Evidence that capelin are recent arrivals near Coats Island was further provided by evidence for capelin spawning found during the 2006 field season. During July of 2006, for the first time since monitoring began in 1981, gravid female capelin (n = 8) were collected from ledges at Coats Island. This suggests capelin are now spawning near Coats Island or have shifted their spawning season to coincide with the breeding season of murres. Capelin reproduction in Newfoundland has also changed considerably in recent years; many traditional beach-spawning locations have apparently switched to demersal-spawning locations, possibly due to warming of beaches linked to climate change (Davoren et al. 2006). Furthermore, during the first feeding watch in 2006 (the only one conducted in July), return flight times preceding deliveries of capelin were very short (<5 km), suggesting that the spawning grounds may have been very close to the colony. Finally, the tradeoff between depth and distance (Chapter 4), which was very pronounced for capelin during 2004 and 2005, was absent in 2006, suggesting that (1) this tradeoff in earlier years was not driven by the existence of distant, shallow spawning locations; and (2) the "halo" that existed in 2004 and 2005 was decoupled in 2006 by the presence of an abundant source of prey (capelin spawning ground).

Woo (2001) reported that many individual murres specialize on rare prey items at Coats Island, illustrating the potential for a dietary switch to represent merely a change in the proportion of specialists within the population. In Chapter 3, I showed that murres do not forage randomly, tailoring there foraging strategies for specific prey items, further implicating a change in specialization as a potential route for a dietary switch. Nonetheless, Davidson (2005) found that older birds were no less likely to obtain Arctic

cod than younger birds, suggesting that although some birds may specialize on a given prey item, there is flexibility to respond to changes in prey abundance or distribution.

Consequently, I conclude that it is likely that the dietary switch represents both an increase in capelin abundance and a decline in Arctic cod abundance near the Coats Island colony. Future monitoring through hydro-acoustic surveys, especially near more northerly murre colonies where murres have yet to undergo this dietary switch (i.e. Prince Leopold Island, Lancaster Sound), would be key to confirming this conclusion.

Implications for Thick-billed Murre Populations?

The switch from Arctic cod to capelin with climate change is unlikely to lead to a reduction in reproductive success through reduced food availability for Thick-billed Murre chicks at Coats Island. First, it is unclear that capelin are a less profitable prey item than Arctic cod. Although they are smaller, they are apparently present in very high densities, are readily captured close to the colony and are captured using a wide variety of foraging strategies (Chapters 3 and 4). This suggests that they are relatively easy to capture, and that the dietary switch may have therefore increased chick energy intake. Second, Thick-billed Murre nestlings already do very well at Coats Island, receiving more food and fledging at nearly twice the weight of those at other colonies (Gaston and Hipfner 2006). Thus, it appears that reproductive success and population size at Coats Island are regulated by mechanisms other than food availability at the chick stage. Consequently, even a substantial reduction in food availability would be unlikely to severely affect Thick-billed Murres at Coats Island at the population level.

While the dietary switch may not influence reproductive success through differences in food availability, it may lead to the colonization of other seabird species into Arctic

regions and, consequently, interspecific competition. During 1998-2002, sand lance made up over 10 % of Thick-billed Murre diet at Coats Island, suggesting that sand lance may have been particularly abundant during those years. These were particularly warm years in northern Hudson Bay. Those years also coincided with peaks in the number of post-breeding Razorbills at Coats Island (A. Gaston, pers. Comm.). Razorbills are a north temperate species which primarily breed in the Gulf of Saint Lawrence and feed primarily on sand lance. Razorbills are not known to breed at Coats Island, but many would appear on loafing sites for several weeks in July and August. This observation suggests the potential for competing seabird species to colonize Coats Island as prey species composition is altered near the colony, potentially in response to climate change.

Common Murres are a closely related seabird species that tends to specializes on capelin in the Northwest Atlantic. At locations where Common and Thick-billed Murres exist in sympatry (e.g. Gannet Islands in Labrador), Common Murres feed on capelin and Thick-billed Murres feed on benthic prey items (Jones et al. 2002), whereas at locations at similar latitudes where Thick-billed Murres exist in allopatry (e.g. Coats Island), Thick-billed Murres feed on capelin. This suggests that Common Murres may be more competitively dominant than Thick-billed Murres for capelin. Thus, the arrival of capelin at Coats Island may signal a future range extension of Common Murres, like Razorbills, into Hudson Bay. Thick-billed Murres may then be unable to compete with Common Murres for capelin and may show reduced reproductive success.

A final argument illustrating the potential for northward range expansion is shown by the thermal ecophysiology of murres. Bird ranges often coincide closely with temperature isotherms (Root 1988), suggesting that avian physiology is optimized within a narrow

range of temperatures. For Thick-billed Murres, this occurs at the 8°C isotherm (Gaston and Hipfner 2000), meaning that they breed and winter in regions where surface water temperature is below 8°C. Arctic waters are predicted to increase by 2 - 6°C over the next century (IPCC 2001), and, as this happens, the region where murre physiology is adapted to will presumably migrate northwards.

This observation is supported by the arguments put forth by Gaston et al. (2005). They showed that timing of breeding for Thick-billed Murres was positively correlated with both summer ice cover and spring temperatures. At Coats Island, near the southern limit of Thick-billed Murre breeding ranges, the date of egg-laying has advanced and lower chick growth rates and lower adult body mass are correlated with decreased ice cover. At Prince Leopold Island, near the northern limit of Thick-billed Murre breeding ranges, the date of egg-laying has not advanced and reproductive success increases in years of decreased ice cover. Thus, it appears that as climate change progresses, conditions will deteriorate near the southern limit of the range and improve near the northern limit of the range, producing a northward migration of the species. The close connection between marine predators and their prey (Chapter 4) suggests that this migration will be linked to a northward migration of the entire marine ecosystem.

Conclusion

It appears that the increase in capelin and decrease in Arctic cod in Thick-billed Murre diet reflects both an increase in capelin abundance and decrease in Arctic cod abundance near Coats Island. Indeed, it appears that capelin are now spawning in close proximity to the colony. This is unlikely to lead directly to reduced food availability for nestling Thick-billed Murres. Rather, this is likely to lead to an increase in competing seabirds

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(e.g. Common Murres) and, consequently, a reduction in food availability. As has been predicted on theoretical grounds, it is likely that the centre of distribution of both Thick-billed Murres and Common Murres will move northward as the centre of distribution of their prey moves northward. Eventually, the centre of distribution will be so far north that there will be no breeding grounds and the species will presumably become extinct, although this is unlikely to happen for many years.

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