

Black Guillemots as Indicators of Change in the Near-Shore Arctic Marine
Ecosystem

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Abstract

This study attempted to explain an apparent inverse relationship between pack ice proximity and breeding success of Black Guillemots (*Cepphus grylle*) on Cooper Island, a barrier island in the western Beaufort Sea near Barrow, AK. I elucidated the first linear relationship between energy density and body size for the elusive Arctic Cod (*Boreogadus saida*). I discovered and ground-truthed the existence of previously unknown guillemot foraging habitat on small 50 m² ice floes distant from the pack ice. I developed new daily metrics for quantifying the provisioning to linear (8 d – 18 d) and Post-Linear (19 d – fledge) chicks. I found daily consensus between Linear and Post-Linear chicks about the level of provisioning at the colony. Finally, I explained those daily changes with significant correlations with wind speed and direction.

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Chapter 1: General Introduction

On a broad scale, I am interested in the effects of global warming on the behavior of top vertebrate predators in marine ecosystems; however, the creation of compelling analyses of global climate change's effects requires extensive mechanistic study of populations before causality can be established. I investigated a colony of Black Guillemots (*Cepphus grylle*), a pursuit-diving marine bird, whose numbers and productivity have decreased in the last 15 years during a time of extensive and rapid summer ice retreat (G. Divoky, pers. comm.). The colony is located on Cooper Island (71°41'N, 155°41'W), a barrier island in the western Beaufort Sea in the high Arctic near Barrow, Alaska (Divoky 1998). This Black Guillemot population is the largest colony for that species in the Beaufort Sea. It has been the subject of a long-term study of breeding biology that has found tight correlations between changing conditions of the Arctic climate and changes in the breeding chronology of the birds (Divoky 1998).

Seabirds have become popular as indicators of a wide variety of marine ecosystem changes (Cairns 1987a; Burger and Piatt 1990; Cairns 1992a; Davoren and Montevecchi 2003a; Gaston et al. 2005). This significance runs the gamut from attempting to predict fish stocks for commercial purposes (Montevecchi et al. 1988; Cairns 1992a; Davoren and Montevecchi 2003a) to attempting to show the significance of the impact of environmental factors such as ice extent and ENSO (Ainley et al. 1995; Barbraud and Weimerskirch 2003; Gaston et al. 2005). The close ties between environmental changes and the success of this colony make it an excellent case for advancing this field of study.

There is no commercial fishery in the Arctic to give reliable information on the availability of forage fish species (George et al. 1997). In this thesis I will demonstrate that the establishment of causal links between environmental changes, piscine prey availability, and measurable colony-based metrics would allow bidirectional insights; the future success of the colony may be deduced in a variety of global climate change scenarios, and the state of the marine ecosystem, which remains poorly understood, could be deduced to some degree by changes measured at the guillemot colony.

Theoretical Framework: Central Place Foraging Theory

All foraging animals must make decisions about what species to prey upon and where to find them (Orians and Pearson 1979). Most species that provide parental care, including those of Alcidae who provision semi-precocial chicks, must transport prey from a foraging patch to their dependant and immobile young. The factors influencing the patch location, prey species selected within the patch, and amount of prey to carry to chicks are complex and frequently in flux. A mathematical framework for determining provisioning behavior is Central Place Foraging theory (CPF) (Orians and Pearson 1979).

A Central Place Foraging trip can be considered to have three parts: outbound flight, foraging, and return flight. Although prey are acquired only during foraging, the energy expended during all three must be taken into account when considering the energetic balance of an individual on a foraging trip (Orians and Pearson 1979). Therefore, one would expect more energy-rich prey items to be acquired as the transit time increases. This has been demonstrated experimentally on birds (Hegner 1982).

Morphology provides strong *a priori* influences on what will constitute efficient foraging behavior for a given species in a given season. The bill of Black Guillemots, unlike some other members of Alcidae such as Puffins (genus *Fratercula*), cannot efficiently hold more than one prey item (Bédard 1969). That item is held, often at the gills, crosswise in the guillemot's bill. Given that the bill is the primary instrument of capture, the presumed efficiency of the capture of second and third prey item after the bill is loaded is very low (Bédard 1969). Therefore these birds return a single prey item to their chicks which defines them as “single prey loaders” within the framework of CPF (Orians and Pearson 1979; Lessells and Stephens 1983).

The mathematics of foraging efficiency is comparatively simple for single prey loaders. The transit time to a given prey patch, a measure of expended energy, is defined as T_t and depends on the distance from the central place and possibly weather conditions (Orians and Pearson 1979; Konarzewski and Taylor 1989; Furness and Bryant 1996). For Black Guillemots, prey aggregations are below the surface; therefore, some amount of wing-propelled diving to reach the depth of prey can also be included in T_t .

Some time and energy not dedicated to commuting locomotion are assumed to be expended before prey is captured. This search time is referred to as T_s . For seabirds, this time can be spent flying in search of regions of the ocean's surface that contain prey aggregations beneath them, as well as searching for/pursuing prey while wing-propelled diving (Davoren et al. 2003). Aerial search time can be affected by prey density, the forager's memory, and the presence of conspecifics (Davoren et al. 2003). Successful underwater foraging depends upon the density of prey in the patch as well as a species-specific coefficient that explains how much time each individual requires for pursuit and

capture at a given density. The energetic value (calories) of a given prey item is referred to as C . The model operates under the assumption that foragers know C for encountered prey. Foragers attempt to maximize the equation $\frac{C}{T_t + T_s}$; they want the most caloric “bang” for their energetic “buck” (Orians and Pearson 1979). This means that foragers should select the prey with the highest energy available at a given foraging patch. If equally energy-rich prey are available, foragers should choose the nearer patch to minimize T_t unless prey-densities are so disparate that there is an enormous increase in T_s at the nearer, depauperate patch.

One can add an additional term to the denominator for handling time (T_h) once prey is captured. This addition creates the theoretical cost-benefit calculation $\frac{C}{T_t + T_s + T_h}$.

The ability to conjecture specifically about water-column handling times for members of the Alcidae is extremely limited. Anecdotal evidence exists for increased handling time for capture and ingesting Four-horned Sculpin (*Myoxocephalus quadricornis*) by Black Guillemots (pers. obs.); however, T_h is not readily measured, and is therefore difficult to incorporate into models of foraging behavior

CPF theory dictates the existence and extent of a foraging range. A foraging range is an area within which the cost associated with T_t is small enough as to make the payoff of C worthwhile. By corollary, there is distance that is represented in T_t beyond which it is not energetically efficient to travel to obtain prey with large enough C values. The distance that can be covered in a given time is affected by flight speed that varies according to weather conditions. There are a number of constraints on C values including

available species and ability of the single-prey loader to carry the mass of a prey item that is appropriately energy-rich to warrant the long transit time.

Theoretical Framework: Cairns (1987a)

A second piece of relevant theory relates foraging theory to measurable seabird parameters through prey availability. Cairns (1987a) provided predictions about how different aspects of seabird life history will respond to changes in the availability of prey within their marine foraging range. These hypotheses are borne from a history of attempting to explain seabird reproductive decisions and life history traits as evolutionarily optimized (Lack 1968; Drent and Daan 1980).

David Lack (1968) first theorized that food availability was crucial to the life history decisions made by birds. He believed that birds will attempt to fledge a maximal clutch, but that food limitation to the young and the parent exerted strong pressures on clutch size. Drent and Daan (1980) updated Lack's theories. They rephrased Lack's life history questions about when and whether to attempt to breed by looking at an individual's decisions based on environmental conditions and the state of the parent. Drent and Daan (1980) ultimately hypothesized that energy balance in the parents, as dictated by food supply in the environment, was the main factor driving breeding decisions in birds.

Cairns's (1987a) applied the previous theories to seabirds in particular by establishing that measurable life history parameters such as adult survival, breeding success, chick growth, colony attendance, and time spent foraging will respond to changing prey availability. This framework has been verified experimentally many times

(Burger and Piatt 1990; Uttley et al. 1994; Zador and Piatt 1999). The measurement and analysis of those parameters can, therefore, provide insight into the status of the prey availability. In this way, seabirds can act as indicators of marine ecosystems.

Prey availability is a metric of prey accessibility; can the birds acquire prey in an energetically efficient manner? This accessibility is defined by a series of parameters: how much prey is in the foraging range (abundance), how the prey is distributed across the foraging range (distribution), how dense is the prey within its locales (density), and whether the costs of acquiring prey outweigh the benefits (CPF). Prey availability is the distribution of the prey as viewed through the behavioral filter of the foraging bird. Prey availability is a valuable inferential bioindicator in its own right; however, if we comprehend the behavioral choices of the birds, we can also refine our understanding of the biology and behavior of their prey.

Adult Survival

Cairns (1987a) posited that measurable deviations in different life history parameters indicate different magnitudes of prey availability. The life history parameter theorized to be least sensitive to prey availability is adult survival, which will be decreased noticeably only at the very lowest prey availabilities (Cairns 1987a). Adult survival may not respond negatively to low levels of prey within a foraging range. Low prey abundance causes the parents to abandon the nest and releases the parents from the inefficiencies of CPF foraging that include spatial constraints and extensive transit expenditures (Bergman 1978; Wanless et al. 2005).

Adult Mass

It is tempting to imagine that more subtle gradations at moderate to high prey availability will be discernable using adult mass; however, adult mass is a complex parameter. There is significant variation in adult mass within a species and even a population, and adult mass depends on other variables besides food availability (Coulson 1968). Living alcids exist on a precarious physiological saddle-point. Their wings function both for underwater diving and for flying (Storer 1952). Consequently, they have a very high wing load ($\frac{Bodymass_g}{wingarea_{cm^2}}$) that makes flight energetically expensive and places a premium on weight conservation (Pennycuick 1987). This may explain the adaptive, programmed mass loss that has been observed in adult auks before their egg(s) hatch (Croll et al. 1991a). Breeding birds are constantly engaged in energetically expensive activity as well as intermittent self-feeding; therefore, one expects to see significant natural variability in their mass throughout the day and between days. This breeding strategy, where parents constantly feed themselves during reproduction rather than living off of energy stores, is referred to as “income breeding” (as opposed to “capital breeding”) (Jonsson 1997; Meijer and Drent 1999). Even given these constraints, it remains plausible that parental mass could be an indicator of intermediate-low prey availability if sufficient sample sizes were achieved to counteract natural variability and birds were only measured during the chick-rearing period after the putative programmed loss.

Breeding Success

Cairns (1987a) predicts that intermediate levels of prey availability will be undetectable if one only examines the survival and adult mass of a long-lived parent (Drent and Daan 1980; Cairns 1987a). This prediction is based on a parent-offspring conflict in which parents balance the importance of current and future reproductive output (Drent and Daan 1980). Seabirds are long-lived and some species have more than 20 reproductive opportunities; therefore, they will not, in general, endanger their survival with excessive workloads to feed a chick in any given year when there is not enough food. Instead, they will abandon the chick and save themselves for their many reproductive efforts in the future (Lack 1968; Drent and Daan 1980).

Low-intermediate levels of prey availability will be indicated by observing deviations from the norm in egg and nestling mortality (i.e., breeding success). Parents will have enough food to feed themselves, but they will be unable and/or unwilling to incubate eggs and provision chicks to the normal level as it may reduce their probability of survival. These changes cause increases in chick and egg mortality, which has been documented in Black Guillemots (Bergman 1978).

Chick Mass Gain

Intermediate declines in prey availability will be indicated by changes in the growth rate and fledging mass of chicks. In this scenario, there is enough available prey that parents, based on an internal metric of body condition and food supply, determine it prudent to attempt to successfully rear young; however, their level of prey delivery is suboptimal for the chicks (Drent and Daan 1980; Cairns 1987a; Bertram et al. 1991;

Hario 2001). These metrics are especially tempting as indicators given the ease of access to altricial chicks compared to other parameters previously discussed.

At-nest life history is complex, and fledging weight and growth rate may not accurately reflect prey availability. Chicks with slow growth rate due to prey shortages could be predicted to fledge at a preset mass, but only after longer nestling periods (Ydenberg et al. 1995). These chicks could also simply fledge at lower masses. The ultimate effect of suboptimal growth rate deviations on chick quality and long-term survival is unclear. Other parameters including peak mass are also available as indicators of prey availability; however, peak mass, like other teleological parameters (fledge mass, age at fledge) may be clouded by life history constraints of the chicks (Hipfner and Gaston 1999).

Chick mass gain has been used as an indicator of near-shore prey availability in the surrounding ecosystem. Ricklefs (1984) used the growth of Blue-footed Boobies (*Sula nebouxi*) on different islands in the Galapagos throughout a chick-rearing season to infer prey availability in the near-shore region for each study site and for comparison between the sites.

Assimilation efficiencies and consequent chick mass gain can vary with prey species (Massias and Becker 1990; Brekke and Gabrielsen 1994). Assimilation frequency can be assumed to be constant within a species; therefore, assimilation efficiency can be incorporated into the complex of effects explained by the species of prey brought to chicks (Golet et al. 2000).

Colony Attendance

Cairns (1987a) predicted that colony attendance will be affected by low-intermediate declines in prey availability. If prey is less available, birds will spend more time foraging at sea to provision themselves and their chicks. This prediction assumes an amount of ambient slack time in the time budget of seabirds, which can be converted to foraging time if need be. This theoretical slack time has been validated in the Atlantic Ocean (Burger and Piatt 1990). Low prey availabilities, however, do not dictate decreases in colony attendance in all cases which implies that factors affecting colony attendance vary across taxa (Davoren and Montevecchi 2003a).

Foraging Time

The final portion of Cairns's framework discusses deviations in a metric that cannot be acquired from solely colony-based study. He posits that intermediate-low declines in prey availability can be discriminated by an increase in the amount of time spent foraging by parent birds. It is selectively advantageous for the parent birds to provision young as much as possible without reducing parental lifetime reproductive success; however, the parents will be forced to forage longer at the available level of prey than they would under ideal prey conditions.

The existence of this change in time spent foraging has been well established (Burger and Piatt 1990; Uttley et al. 1994; Bertram et al. 1996; Zador and Piatt 1999; Litzow and Piatt 2003). Measuring this parameter is difficult because foraging and several other activities take place at sea beyond visual range of the colony except in rare cases and even those provide comparatively sparse data (Cairns 1992b; Clowater and Burger 1994). The desire to measure time spent foraging requires a device that can log

the bird's activities at sea by proxy (Cairns et al. 1987a; Cairns et al. 1987b; Wanless et al. 1988; Burger and Piatt 1990; Uttley et al. 1994; Zador and Piatt 1999; Falk et al. 2000; Dall'Antonia et al. 2001; Tremblay et al. 2003; Litzow and Piatt 2003). Unfortunately, with the attachment of a device comes the danger that the device alters behavior (Wanless et al. 1988; Croll et al. 1991b; Hamel et al. 2004).

Black Guillemots

Black Guillemots (*Cephus grylle*) are wing-propelled divers as are all members of the Family Alcidae. They are single-prey loaders that forage near shore, typically within 40 km of the colony, solitarily or in small groups (Butler and Buckley 2002). They feed their chicks a variety of prey, usually demersal fish (Bradstreet and Brown 1985; Cairns 1987b); however, the Cooper Island population delivers primarily Arctic cod (*Boreogadus saida*), which is primarily non-demersal (Bradstreet and Cross 1982; Bradstreet et al. 1986).

Black Guillemots lay two eggs per clutch, which have light blue/grey background and a black speckling pattern. There is normal variation of clutch sizes--approximately 20% of the clutches contain only one egg (Divoky 1998). One-egg clutches are frequently associated with inexperienced breeders (Emms and Verbeek 1991). Three-egg clutches are always the byproduct of multiple females (Divoky 1998). The eggs are on average laid three days apart in small, dark, sheltered cavities, usually on scree slopes or cliffs; however, birds have been found nesting in a variety of habitats including discarded oil drums and other manmade debris (Divoky et al. 1974; Butler and Buckley 2002). The chicks are semi-prococial and remain in the cavity for approximately 28 days during

which time they are provisioned with whole fresh fish by their parents during daylight hours although, due to the long days of the high Arctic summer, there may be some diurnal variation in delivery rate (Cairns 1981; Ewins 1992; Butler and Buckley 2002).

The parent birds fly out to sea to forage, where they search for prey on which to feed. Once prey has been located, the birds most likely feed themselves before they select a prey item to carry back to the chick(s) (Orians and Pearson 1979; Davoren and Burger 1999; Wilson et al. 2004). The prey item is then flown back in the bill to the nest. Parents typically (but not exclusively) alternate delivery of prey items to chicks (pers. obs.).

Black Guillemots have a circumpolar distribution (Kidd and Friesen 1998a; Butler and Buckley 2002). Their range extends south to Newfoundland and even Maine in the Atlantic; however, they remain above the Bering Strait on the Pacific side of North America (Butler and Buckley 2002). There has been much speculation about the variety of races and subspecies (Storer 1952; Kidd and Friesen 1998a). The Cooper Island population is assigned to the subspecies *C. g. mandtii* (Butler and Buckley 2002). Genetic analysis indicates that Black Guillemots diverged from Pigeon Guillemots (*C. columba*) and Spectacled Guillemots (*C. carbo*) coincident with the Bering Land Bridge (Kidd and Friesen 1998a; Kidd and Friesen 1998b). Black Guillemots are not known to breed south of the Bering Strait (U.S Fish and Wildlife 2000). Within Black Guillemots, there have been declarations about subspecific divergence since the 1950s (Storer 1952; Butler and Buckley 2002). Genetics-derived cladistics suggest that the populations are quite isolated and comparatively little gene flow occurs between them (Kidd and Friesen 1998a). *C. g. mandtii* are most closely related to the population in Maine. The populations were most likely separated during recent glacial epochs (Kidd and Friesen 1998a).

Issues Regarding Analysis of Chick Growth

Analyzing chick growth is not an intuitively obvious process. Cairns (1987a) states that chick growth will be affected by moderate declines in prey availability, but chick growth is not static. For most birds, including the Black Guillemot, chick growth is described by a non-linear function (Drent and Daan 1980; Ewins 1992). For *Cepphus*, it has been described as an incomplete parabola and as a roughly sigmoid curve with an increase in variability nearing fledging (Drent and Daan 1980; Cairns 1981; Emms and Verbeek 1991; Ewins 1992). The late-term variability of Ewins's (1992) model frequently manifests as a fledging mass well below the peak mass achieved earlier. Both models contain a loss of mass prior to fledging. This loss is believed to be adaptive rather than indicative of poor prey availability, because it is characteristic of many species of alcid (Hipfner and Gaston 1999). Determination of prey availability using chick growth rate, therefore, tends to exclude this portion of the nestling stage. Within both functions is a region of approximately linear growth ("Linear Growth Phase") (Drent and Daan 1980; Ewins 1992). Ewins (1992) details this phase as extending between Days 8 and 21 after hatch in Black Guillemots.

Cairns assumed that the colony will respond uniformly to different levels of prey availability; he assumes that all adults are equal. This assumption has been repeatedly disproved, and individual variability must be understood for conclusions about at-sea prey availability to be supported (Coulson 1968; Ydenberg et al. 1995; Golet et al. 2000; Hipfner and Gaston 2003). If one uses chick growth as an indicator of prey availability, as Ricklefs (1984) did and Cairns (1987a) theorized, it is important to know what subset

of the colony is being used to assess the colony at large via and what other factors might be affecting chick growth.

Due to asynchronous clutch initiation, only a subset of the colony is at a given breeding stage on a given day. Egg laying does not occur uniformly at a colony, and parent birds are not all the same age as experienced. Older, more experienced birds tend to lay earlier (Morbey and Ydenberg 1997; Hipfner and Gaston 2002). Chicks reared earlier in the season are, therefore, typically being reared by a more experienced subset of the population. Seabird chicks often fledge at lower masses later in the breeding season (Ydenberg et al. 1995; Hipfner and Gaston 1999). It is disputed, however, whether chicks that fledge earlier and heavier are byproducts of higher prey availability, parents that are more adept at provisioning, or an ecological adaptation to the length of appropriate conditions for being nidicolous (Coulson 1968; Ydenberg et al. 1995; Morbey and Ydenberg 1997; Hipfner and Gaston 2002).

Chick growth rate can be affected by many factors. Provisioning rate (kJ / h) is the most obvious proximate cause. There is a body of work dedicated to how provisioning rates influence chick growth (Montevecchi et al. 1984; Massias and Becker 1990; Hatchwell 1991; Hamer et al. 1991; Bertram et al. 1991; Brekke and Gabrielsen 1994; Golet et al. 2000). The primary conclusion is that provisioning rate (kJ / h) is strongly correlated with chick growth. Provisioning rate is affected by the energy density (kJ / g) of the prey as well as the delivery rate of prey.

The amount of energy the chick consumes can be affected by conditions in the nest and at sea. While the parents are at sea, delivery rates (feeds / hr) can be reduced by poor weather, increased search time for prey, and increased kleptoparasitism (Orians and

Pearson 1979; Birt and Cairns 1987; Furness and Bryant 1996; Litzow et al. 2002). The energetic stress of foraging is eased by high winds for Procellariiformes; however, foraging energy expenditure by parents is increased for Dovekies (*Alle alle*), a confamilial of Black Guillemots (Konarzewski and Taylor 1989; Gabrielsen et al. 1991). All of these conditions in addition to prey availability in the ecosystem may affect the species and size of prey returned to the chick.

In the nest growth can be effected by the assimilation efficiency of digestion and the rejection of prey too difficult to swallow (Brekke and Gabrielsen 1994; Golet et al. 2000). Guillemot chicks have some difficulty swallowing Four-horned Sculpin (*Myoxocephalus quadricornis*) (pers. obs.). There were two probable choking deaths in 2005, and as many as 12 rejected sculpin accumulated, unconsumed, in some nests. Other chicks consumed all prey taxa presented (including sculpin anecdotally) without recorded incident. Foraging energy spent on rejected prey could be a significant factor in the overall metric of provisioning as could the exposure to a probability of chick mortality for certain prey taxa.

Sibling competition within the nest can alter how delivered prey is consumed. Black Guillemots have been identified as facultative sibling aggressors in times of low provisioning (Cook et al. 2000). External blockage of the nest entrance by snow can also cause interruptions in prey delivery (G. Divoky pers. comm.). Thermal conditions within the nest could affect metabolism, homeostasis, and survival, but anecdotal evidence suggests it does not (G. Divoky pers. comm.).

External stresses including human disturbance can also affect chick growth. Several investigators have examined the effects of handling and disturbance by humans

on the growth of seabird chicks (Cairns 1980; Hatchwell 1989). The extent of the effect has been variable; however, it is agreed that human disturbance and handling have negative effects on chick growth. Growth rate and fledging mass were shown to decrease slightly with increased handling in Black Guillemots at other colonies (Cairns 1980). Fledging masses at the Cooper Island colony in 2005 were on average higher than those in Cairns's undisturbed control group. All chicks on Cooper Island are handled an equal amount; therefore, one can assume any depressions in growth due to disturbance are distributed equally and are for my purposes negligible.

Arctic Cod

Arctic Cod (*Boreogadu saida*) is an understudied species and the traditional prey of the Cooper Island population of Black Guillemots (Bradstreet et al. 1986; Divoky 1998). Arctic Cod is often singled out as an important trophic link between small producers and top vertebrate consumers such as whales, seals, and marine birds in the comparatively unproductive Arctic ecosystem (Bradstreet 1982; Bradstreet et al. 1986; Hobson and Welch 1992; Welch et al. 1993; Hoekstra et al. 2002). The list of Arctic Cod consumers includes Ringed Seal (*Phoca hispida*), Bearded Seals (*Erignathus barbatus*), Harp Seals (*Phoca groenlandicus*), and Beluga Whale (*Dephinapterus leucas*), as well as Thick-billed and Common Murres (*Uria lomvia* and *Uria aalge*), Black-legged Kittiwakes (*Rissa tridactyla*), Northern Fulmars (*Fulmarus glacialis*), Glaucous Gulls (*Larus hyperboreus*), Ivory and Ross's Gulls (*Pagophila eburnean* and *Rhodostethia rosea*), Arctic Terns (*Sterna paradisaea*), in addition to Black Guillemots (Bradstreet

1979; Boekelheide 1980; Lowry and Frost 1981; Divoky 1981; Bradstreet 1982; Divoky 1984; Bradstreet et al. 1986).

Arctic Cod is a comparatively fast-growing and short-lived fish never exceeding seven years of age (Bradstreet et al. 1986). They reach sexual maturity at 2-3 years (Craig et al. 1982). They rarely exceed 200 mm in length and spawn in midwinter (Bradstreet et al. 1986). The eggs develop into planktonic larvae and young-of-the-year (YOY) cod by the ice-free period of summer (Bradstreet et al. 1986; Cannon et al. 1991). Juvenile and adult cod appear to tolerate a wide variety of temperatures and salinities, but prefer colder marine water (Lowry and Frost 1981; Bradstreet et al. 1986; Moulton and Tarbox 1987; Cannon et al. 1991; Jarvela and Thorsteinson 1999). There have been reports of on-shore “pre-spawning” migrations of cod in August; however, no reports have ever been recorded near Cooper Island (Bradstreet et al. 1986).

Arctic Cod are traditionally regarded as an ice-associated species that is found near the edge of the pack ice, as well as in large schools near isolated ice floes (Lowry and Frost 1981; Craig et al. 1982; Bradstreet et al. 1986; Moulton and Tarbox 1987; Welch et al. 1993; Gradinger and Bluhm 2004). They have been found in open marine waters of the near-shore Beaufort Sea, occasionally associated with temperature and salinity windows (Lowry and Frost 1981; Jarvela and Thorsteinson 1999). Arctic Cod have also been found in the warm brackish lagoon waters southeast of the western Beaufort barrier island chain (Craig 1984). Most cod found in open waters vary between years zero (YOY) and three (Jarvela and Thorsteinson 1999; Thedinga and Johnson 2006), whereas those near the ice-edge range from year one to the maximum life span of age seven (Lowry and Frost 1981; Bradstreet et al. 1986).

Although surveying near-shore Arctic waters is an imperfect science due to variations in sampling methods and available open water, a variety of other species, both benthic and pelagic, have been detected in the oceanic environments of the near shore Beaufort Sea including areas north and east of Cooper Island. These include Four-horned Sculpin, Capelin (*Mallotus villosus*), Sandlance (*Ammodytes hexapterus*), and flatfish of disputed taxonomy (Welch et al. 1993; Jarvela and Thorsteinson 1999; Thedinga and Johnson 2006). In the sheltered, brackish waters of Elson Lagoon, the chain of barrier islands of which Cooper Island is a part, a preponderance of *M. quadricornis* exists and a notable population of Least Cisco (*Coregonus sardinella*) (George et al. 1997). Saffron Cod (*Eleginus gracilis*), which are visually similar to Arctic Cod (*Boreogadus saida*), are also found in the lagoon in low densities in what appear to be small schools (Cannon et al. 1991; George et al. 1997).

Due to the difficulties associated with acquiring knowledge about Arctic Cod, Bradstreet et al. (1986) proposed the use of animals adapted to capture cod as sampling devices. His original proposition relies on otolith examination, as otoliths are often retained in the stomachs of predators. Whole otoliths can be aged with equivalent accuracy to sectioned otoliths and with much greater accuracy than fish scales (Bradstreet et al. 1986).

Bradstreet et al. (1986) only examined the stomach contents of birds shot at sea and found their otoliths were low in number and frequently broken in comparison to larger marine mammals. Colony-based studies, however, can easily capture whole fresh fish delivered by parents to chicks. Using prey returned to chicks to sample prey within the foraging range; however, has limitations as CPF theory predicts that birds forage non-

randomly (Orians and Pearson 1979). This non-random sampling is exacerbated by the small size of recently hatched chicks, which precludes them from consuming larger size/age classes of cod. Parents tend to provision chicks with size-appropriate prey (Cairns 1987b). Nonetheless, the sample returned to chicks at the colony can provide important information on the ecology of nearby fish species about which little is known.

A series of ice-edge tows were performed in the western Beaufort Sea that established growth rates, age class structure, and stomach contents for western Beaufort Arctic Cod (Lowry and Frost 1981). Growth rates are spatially variable across the North American range of Arctic Cod (Lowry and Frost 1981; Bradstreet et al. 1986). Overall, Black Guillemot prey analysis can significantly increase the understanding of guillemot foraging while providing information of the ecology of Arctic Cod.

Previous Research

Cooper Island is primarily composed of sand and gravel; however, there is a small patch of tundra on the eastern end of the island. The maximum elevation is approximately three m (Divoky 1998). Black Guillemots were first discovered nesting there in man-made debris in 1972 (Divoky et al. 1974; Boekelheide 1980). The colony grew precipitously during the 1980s to a peak of more than 200 breeding pairs in 1987 (Divoky 1998). The growth was in large part due to the construction of artificial nest sites by Dr. Divoky (Divoky 1998). The colony size contracted in the 1990s to approximately 115 breeding pairs in 1998 and 1999 (Divoky 1998). It increased to approximately 150 pairs in the 21st century and continues to be the largest known colony in the Beaufort Sea (Divoky 1998).

A long-term monitoring project has been taking place on Cooper Island since 1975. Of the adult population on the island, > 85% of breeding adults are color-banded (Divoky 1998). This study has yielded significant knowledge about the age, experience, breeding locations, and breeding history of nearly all the birds in the colony (Divoky 1998). This study also has established a link between the time of disappearance of snow in the spring and clutch initiation (Divoky 1998). Egg formation cannot begin until females have access to a darkened cavity and the ground-level nests on Cooper make guillemots sensitive to climatic conditions (Sealy 1975; Divoky 1998). Hatching success has shown no annual trend during the study but fledging success has declined since a phase change in the Arctic Oscillation in 1989 (G. Divoky pers. comm.).

Fledging success at the colony has been correlated inversely with the proximity of ice in the middle of the nestling period throughout the course of the study (G. Divoky pers. comm.). This change is associated with a shift in the species of prey that adults bring to their chicks. Early in the chick-rearing period, parents bring almost exclusively (>95%) lipid-rich, energy-dense Arctic Cod to their chicks (“early cod phase”). In the late summer, coincident with the observed retreat of the Arctic pack ice, a variety of demersal prey, primarily Four-horned Sculpin and various eelpouts (*Lycodes* spp.), are brought to the chicks (“open water prey phase”) (G. Divoky pers. comm.). This open water prey is of lower energy density (Van Pelt et al. 1997b; Møller 2001; Woo 2001). Decreases in chick growth and fledging success have been associated with this prey shift (G. Divoky, pers. comm.).

Previous work has documented the diet of Black Guillemots in other parts of the world (Cairns 1981; Cairns 1987c; Ewins 1990; Hario 2001). These studies have

generally found the birds feeding on demersal fishes and have focused on how the prey species composition and/or provisioning rate varied between breeding seasons (Cairns 1987c; Ewins 1990; Ewins 1992). Golet et al. (2000) observed the effects of prey species composition on the congeneric Pigeon Guillemot. They found that prey item mass and energy density of prey (kJ / g) were both significant predictors of the number of chicks fledged (Golet et al. 2000).

Climatic changes and their relationships to organisms in Arctic regions have been prominent in the scientific literature recently (Smith 1994; Smith et al. 1999; Hughes 2000; Gaston et al. 2005). Attempts have been made to correlate spring ice conditions with breeding success. In the Canadian Arctic, Gaston et al. focused on Thick-Billed Murres (*Uria lomvia*), also an alcid (Gaston et al. 2005). The murre study focused on the inhibitory properties of ice as an increaser of foraging distances from the colony. A previous Cooper Island study demonstrated the benefits of ice to sea birds. Arctic Terns on Cooper Island appear to struggle with the acquisition of Arctic Cod for their chicks in the absence of ice (Boekelheide 1980). In the Antarctic, increased ice extent positively affected breeding success but negatively affected adult survival of Emperor Penguins (*Aptenodytes forsteri*) (Barbraud and Weimerskirch 2001).

Chapter Outlines

I investigated the Arctic ecosystem and its relationships to Black Guillemot breeding. One previous study correlated chick mass changes with weather variables (Konarzewski and Taylor 1989). It showed that daily deviations from colony-wide mean mass versus age curves had a significant inverse relationship with wind speed. It has also

been shown that the feeding rate of Common Murres is inversely proportional to wind speed (Birkhead 1976). Similar studies have been performed on Arctic Terns and found similar results (Dunn 1975; Taylor 1983).

In Chapter 2, I analyze the energy density (ED) of Arctic Cod acquired at the colony from Black Guillemots. I quantify the first linear relationships between fork length and ED for Arctic Cod. This relationship will permit more accurate and simple estimates of the energy consumption of the many predators on Arctic Cod. I also survey the sparse Arctic Cod energetic literature to discern regional differences in size, water content, and energy density within the species.

In Chapter 3, I explore the existence of small pieces ($< 50 \text{ m}^2$) of ice and the possibility that they represent significant foraging habitat. I a combination of satellite images and boat trips to actual pieces to establish methods others might use for exploring this habitat.

In Chapter 4, I develop methods for analyzing provisioning effort on a fine temporal scale (daily) using anomalies in the mass of all guillemot chicks at the Cooper Island colony throughout their nestling phase. This required generating predictive curves for both the well-established Linear Growth Phase (LGP) (8 - 18 d) of chick growth as well as the poorly understood Post-Linear Growth Phase (PLGP) (19 d - fledge) so that anomalies could be analyzed.

In Chapter 5, I use these daily chick mass anomalies throughout chick-rearing and attempt to explain trends in the anomalies using environmental conditions. I have measured a variety of environmental parameters including wind speed and direction, temperature, and ice conditions.

There are lots of opportunities for new research on the Arctic ecosystem. The difficulties of gathering data in these regions mean that there is room for descriptive as well as theoretical inquiries. As is the case with much ecological science, retesting results on other organisms and in new environs can aid in extending or establishing the boundaries of the application of theoretical frameworks.

Chapter 2: Analysis the energy density (ED) of Arctic Cod (*Boreogradus saida*) acquired at the colony from Black Guillemots.

2.1 Introduction:

Arctic Cod are often singled out as an important trophic link between small producers and top vertebrate consumers such as whales, seals, and marine birds in Arctic marine ecosystems (Boekelheide 1980; Lowry and Frost 1981; Bradstreet 1982; Bradstreet et al. 1986; Hobson and Welch 1992; Welch et al. 1993; Hoekstra et al. 2002). Despite this crucial role, there is a dearth of basic knowledge about Arctic Cod, likely due to the logistical constraints (i.e., collections restricted to ice-free periods) and expense (i.e., collections requiring costly ship-based research) in conducting marine fish research in the Arctic.

The relative proximate composition (energy density, lipid, ash, and water content) of forage fish species in northern temperate ocean regions has been analyzed (Van Pelt et al. 1997; Lawson et al. 1998; Payne et al. 1999; Ball et al. 2007). There is a distinct paucity, however, of work investigating the value of Arctic Cod as a food source, despite its clear importance to a wide variety of marine top predators. Although some previous investigations report single values for the energy density of Arctic Cod, none has had a sufficient sample size to investigate the intraspecies relationships among size, moisture, and energy density. Additionally, no studies have investigated this species in the Arctic Ocean in general and the Beaufort Sea in particular (Van Pelt et al. 1997; Lawson et al. 1998; Payne et al. 1999), with the exception of a small study in the eastern Canadian Arctic, where Black Guillemots were used as samplers (Cairns 1984).

Due to the difficulties associated with acquiring knowledge about Arctic Cod, Bradstreet et al. (1986) proposed the use of animals adapted to capture Arctic Cod as sampling devices. Unlike some seabirds which carry partially digested prey in a gular sac back to feed their chicks, Black Guillemots return whole fresh carried crosswise in the bill to their chicks. This makes them ideal prey samplers as prey are pristine and can be easily sampled at the colony.

Using seabirds as samplers of Arctic Cod has some drawbacks. Fisheries studies tend to analyze fish in terms of kJ / g of wet mass (Montevecchi and Piatt 1987; Van Pelt et al. 1997; Lawson et al. 1998). Fish that are collected at the colony have been flown from the foraging ground by the parent bird, which exposes the prey to dehydration. Fortunately, a correction for dehydration during flight has been developed using seabirds and small clupeids (Montevecchi and Piatt 1987).

In this chapter, I investigate the intraspecific relationships among energy density, fish size (fork length), and water content for Arctic Cod captured by Black Guillemots over two years in the western Beaufort Sea.

2.2 Methods:

Arctic Cod were collected at the Black Guillemot colony on Cooper Island, Alaska (71°41'N, 155°41'W), which is a barrier island in the western Beaufort Sea in the high Arctic near Barrow, Alaska (Divoky 1998). Fish were collected opportunistically during August, 2005 and throughout the chick-rearing period (July and August) in 2006. One method of collection involved “rushing the nest” shortly after I observed a prey

delivery. I also collected fish immediately after they were dropped during kleptoparasitic events before the kleptoparasite (usually a Parasitic Jaeger (*Stercorarius parasiticus*)) could acquire them. Fish were identified using an unfinished manual authored by J. Craig George and comparison to voucher specimens caught at Cooper Island by a Auk Bay Laboratory crew led by John Thedinga. Fish were then weighed on an electronic scale (nearest 0.1 g) and fork length (mm) was measured. Each fish was placed into a plastic bag, labeled with the mass, fork length, date, location of collection, and then frozen.

In the laboratory, each frozen fish was freeze-dried for 36 h in a Labconco freeze drier. The freeze-dried cod were weighed prior to being homogenized using a blade coffee grinder. I prepared pellets ranging from 0.3 - 0.6 g using a Parr pellet press. If the fish was large enough, 2 - 3 pellets were made to ensure accurate energy density values for the fish by averaging the pellet values to correct for any errors that possibly stemmed from pellets whose contents did not accurately reflect that of the whole fish. The pellets were dried at 55 °C for 24 h and weighed to the nearest 0.0001 g. The pellets were combusted in a Parr adiabatic calorimeter, which I calibrated using a benzoic acid standard.

I performed the standard corrections for residual acid and fuse wire burning. Fuse wire combustion generates heat not derived from the pellet. The amount of heat is proportional to the length of wire burned; therefore, the length of burned wire was multiplied by a coefficient and subtracted from the joule total. A small amount of the pellet remains uncombusted and is converted to acid. The quantity of acid was determined using HNO₃ titration and added these results to the joule total to create a more accurate joule measure for the pellet. The corrections accounted for 1 – 2 % of the

total joules in the pellet. Given that the final measure of the pellets was in kJ with two significant digits, these calculations were almost certainly rendered moot. These procedures, including the strength of the titrating base and the multiplicative coefficients, are specifically outlined in the Parr Operating Instructions.

The energy density of each fish was calculated as the mean kJ/g value of all pellets successfully bombed from that fish. Corrections for dehydration were calculated according to $massloss_g = -0.037(time_m)$ in Montevecchi and Piatt (1987). Transit times between the foraging site and the colony were assumed to be 25 min based on a 50-min mean foraging trip length for guillemot parents at Cooper Island (B. Harter unpubl. data).

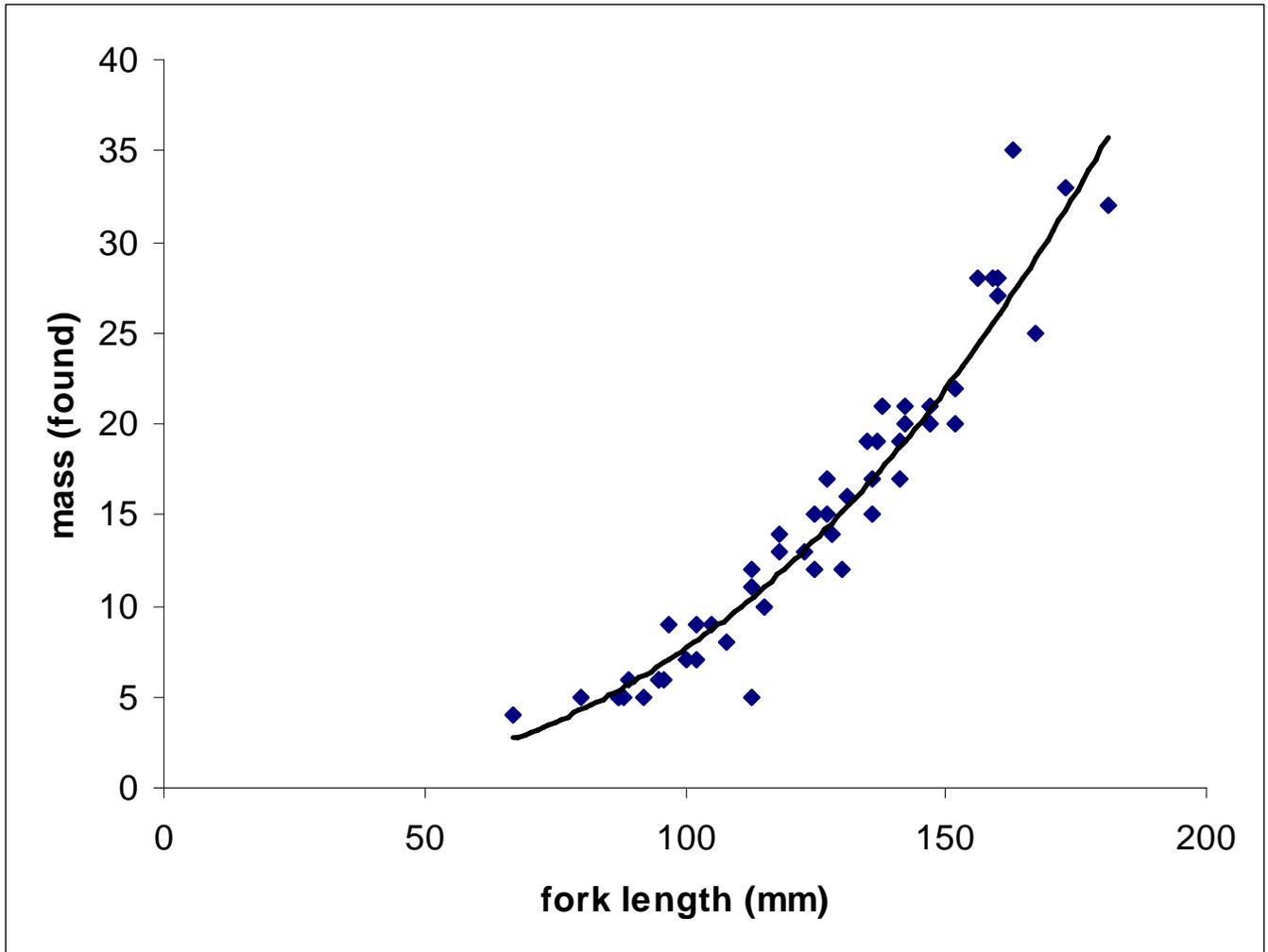
2.3 Results:

Fifty fish were collected and the procedures outlined above were conducted on 16 fish selected to cover the size/mass range of those collected. Two fish were removed from calculation after showing abnormally low ED values, most likely due to dehydration from extended periods in the nest prior to collection. The fish span the length range of Arctic Cod (see Bradstreet *et al.* (1986)) (Table 2.1). The mean dry energy density for the Arctic Cod in my study was $22.24 \text{ kJ/g} \pm 0.46$ (SE) and the calculated moisture content and wet energy density was $82.6 \pm 0.83 \%$ and $3.92 \pm 0.25 \text{ kJ/g}$, respectively (Table 2.1). As expected, there was a strong positive relationship between fork length and mass at collection ($foundmass_g = 0.00005forklength_{mm}^{2.6001}$; power function regression: $r^2 = 0.92$, $df = 50$, $F = 608.65$, $p < 0.0001$; Figure 2.1). The duration of transit for fish is unknown

Table 2.1. A comparison between mean \pm SE energy densities and percent body moisture of Arctic Cod found in this and previous studies. Asterisk denotes unavailable data.

mean values (SD)	Western Beaufort	Labrador	Nuvuk Island	Eastern Bering
N	12	52	2	1
Range of fork length	87-165 mm	*	*	*
Range of wet body mass (inferred)	5.925 – 33.925 g	*	*	*
Range of body mass at collection	5 - 33 g			
dry kJ/g	22.24 \pm 1.67	*	29.16	16.6
wet kJ/g (found)	3.93 \pm 0.89			
wet kJ/g (25m flight)	3.66 \pm 0.98	4.4 \pm 0.11	*	1.2
% body moisture at sea (inferred)	82.6 \pm 3.1			
% body moisture after 25 min of flight	83.9 \pm 3.4	77.9 \pm 0.3		84.4
Source	This study	Lawson 1998	Cairns 1984	Ball 2007

Figure 2.1. The relationship between fork length and body mass at time of collection in 2006 ($\text{foundmass}_g = 0.00005\text{forklength}_{\text{mm}}^{2.6001}$; $r^2 = 0.9246$ $n = 50$ $p < 0.0001$).



and thus must be assumed in order to generate at-sea wet weights. Parameters based on wet weight are fairly robust to possible variations in duration of transit. The difference between minimum and maximum estimates for percent body water was small (mean = 1.8 %, maximum = 3.3 %, minimum = 0.9 %, n = 12 SE = 0.2 %), whereas wet ED were more noticeably affected (mean = 0.41 kJ / g, maximum = 0.75 kJ / g, minimum = 0.21 kJ / g, n = 12, SE = 0.04 kJ / g), with an average weight energy density change of 10.9 % between the at-sea estimate and the at-colony value.

The dry ED of fish did not differ significantly between collection years (Independent sample t-test, $t = 0.531$, $df = 11$, $p > 0.25$) or between July and August when years were combined (Independent sample t-test, $t = -1.487$, $df = 11$, $p > 0.165$). Owing to this, all fish collections were pooled for subsequent analyses.

There was a high degree of regularity and interrelationship between a number of parameters, suggesting that linear equations can be used to estimate energy density from simple measures of fish that are more easily measured than calorimetry. Specifically, fork length was a very good predictor of energy density. Assuming a constant 25 min transit duration, fork length had a strong positive linear relationship with wet energy density ($r^2 = 0.848$, $n = 11$, $p < 0.0001$; Figure 2.2) as well as calculated dry energy density ($r^2 = 0.736$, $n = 12$, $p < 0.0001$; Fig. 2.3). The highly robust parameter of percent body water also had a strong positive linear relationship with dry energy density using the mass at collection to generate the percent body water ($r^2 = 0.808$, $n = 12$, $p < 0.0001$) and using the calculated wet mass at sea ($r^2 = 0.807$, $n = 12$, $p < 0.0001$).

2.4 Discussion:

Figure 2.2. The relationship between fork length and wet energy density (kJ/g) for Arctic Cod based on a 25-min flight time

($\text{WetED}_{\text{kJ/g}} = 0.0304\text{Forklength}_{\text{mm}} - 0.1638$ $r^2 = 0.848$, $n = 11$, $p < 0.0001$).

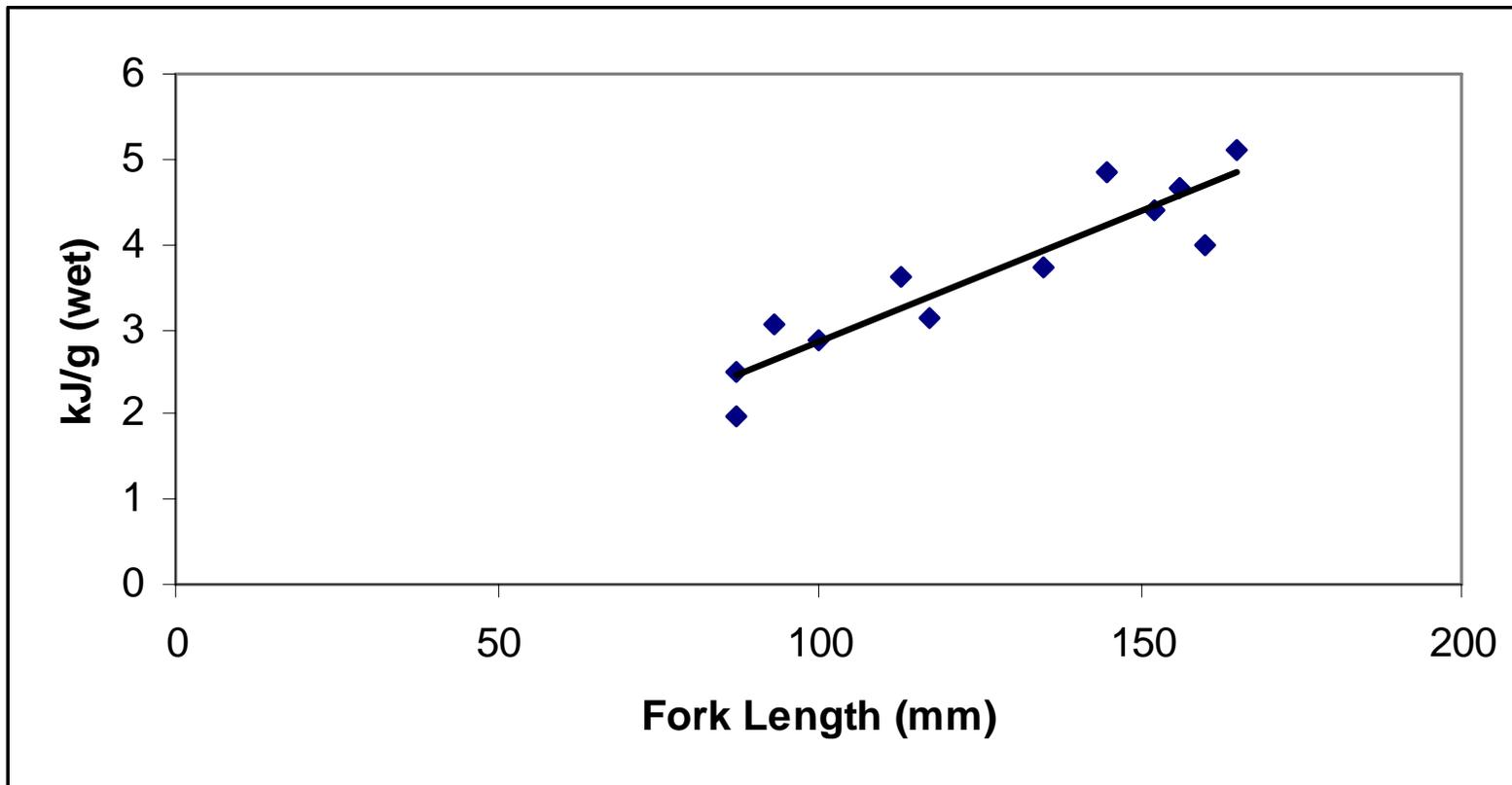
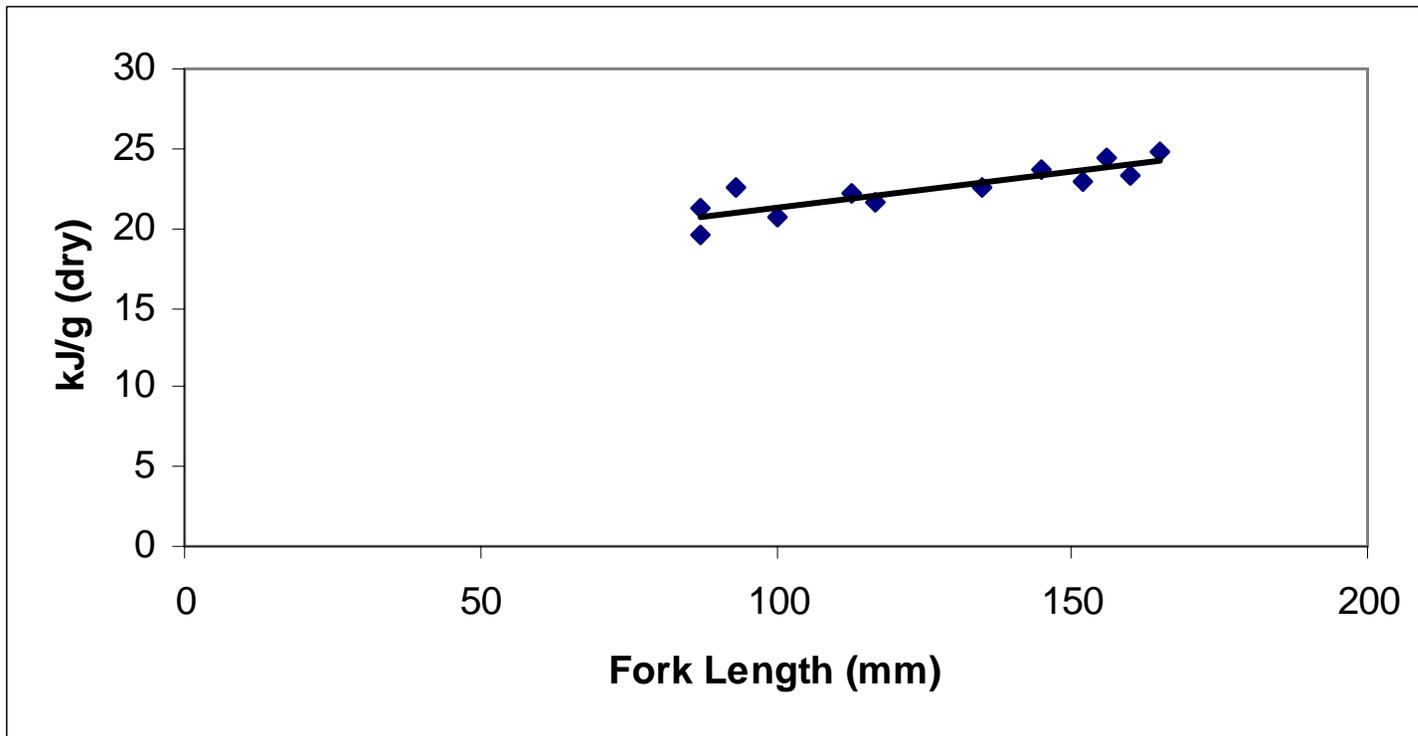


Figure 2.3. The relationship between fork length and dry energy density for Arctic Cod ($r^2=0.736$, $n = 12$, $p<0.0001$). $\text{DryED}_{\text{kJ/g}} = 0.044(\text{forklength}_{\text{mm}}) + 16.933$



Arctic Cod are an important prey to many marine mammals and are difficult for scientists to collect. Some seabirds can be a viable cost-effective method for acquiring samples of their marine prey. My analysis yielded significant relationships between fork length and energy density and wet mass, which suggest that researchers can gain valuable information about this crucial prey item using only a ruler. Specifically, the strong positive linear relationships among fork length, wet and dry energy density and percent body moisture of Arctic Cod from the western Beaufort Sea, suggest the possibility of estimates of energy density from field-based measures of fish length and mass. This eliminates the difficulty and expense of freezing and transporting samples as well as the time-consuming laboratory processing techniques using expensive infrastructure.

Many fish species show a relationship between fork length and energy density (Lawson et al. 1998; Ball et al. 2007). I generated the first such relationship for Arctic Cod. This is advantageous, because of the notorious difficulty of acquiring Arctic Cod as well as its importance to the Arctic ecosystem. Arctic Cod otoliths are frequently sampled from the stomachs of a variety of marine mammals (Bradstreet et al. 1986). The establishment of relationships between otolith size and fork length could allow for insights into the foraging ecology and energetics of a variety of animals using my energetic relationship.

Intra- and interspecific Comparisons

There are limited existing data for Arctic Cod as a prey source (see Table 2.1) and, thus, patterns are difficult to discern. My samples in the western Beaufort Sea suggest that energy densities of cod are notably lower than those collected from the eastern Nuvuk Islands and the eastern Bering Sea, although the sample sizes from both

studies are notably small and no size information is given (Cairns 1984; Ball et al. 2007). The larger sample size from Labrador allows the determination of a significantly lower body water content for those fish than my western Beaufort samples (t-test, $t = 7.803$, $df = 64$, $p < 0.005$). This is somewhat counterintuitive given the tendency of more northern fish to have more fat than other fish (Tocher 2003; Garvey and Marschall 2003). Given that the Labrador values were from fish collected at sea, further study is needed to determine whether this regional result is robust or an artifact of my adaptation of the dehydration correction. These findings should help increase sample sizes for Arctic Cod research and hopefully be a building block for regional energetic comparisons.

There are no published studies of piscine prey EDs in the Beaufort Sea. This paucity makes concrete insights into the energetic tradeoffs of top predator foraging choices difficult. The most similar study for comparison is Van Pelt et al. (1997) from the north Pacific, water that shares some piscifauna with the western Beaufort. Western Beaufort Arctic Cod have a higher dry energy density than all but one of the sampled forage fish species in the north Pacific. The exception was myctophids (Lanternfish), which were not observed as prey on Cooper Island in 2005 or 2006. Western Beaufort Arctic Cod have higher EDs than Pacific Sandlance from the north Pacific (Van Pelt et al. 1997). Sandlance comprised a small percentage (<15%) of the prey fed to chicks on Cooper Island in 2005 and 2006. Counter intuitively, the inferred wet ED of my cod is lower than 63% of species sampled in the north Pacific (Van Pelt et al. 1997). This may also undermine the strength of the wet weight inferences. The proximity of the north Pacific to the western Beaufort makes it the most accurate for comparison; however, the higher sea-surface temperature (SST) of the north Pacific, as well as its different species

composition, makes it an imperfect corollary. Myoxocephalids in the eastern Canadian Arctic, which are returned to chicks by Cooper Island Black Guillemots, have lower energy density than Western Beaufort Arctic Cod (Cairns 1984). The inability to find comparable research in my study area speaks to the dearth of Arctic research on marine fish in general.

The inverse linear relationship between percent body water and energy density may imply that fish are replacing water with lipid and vice versa to achieve some internal standard. The relationship is similar to the results from similar analyses on other fishes (Payne et al. 1999).

Arctic Cod as Prey

Arctic Cod has been identified as the primary link between lower trophic levels and marine predators. My findings imply that the ability to find large cod constitutes a “double bonus” for marine predators. Not only do they receive exponentially increasing mass of food from larger fish, but larger fish are also more energy-rich than smaller individuals (Figure 2.2). This is particularly noteworthy because younger, smaller cod are more frequently associated with brackish, open water habitats, whereas older, larger cod are almost always associated with ice (Lowry and Frost 1981; Bradstreet et al. 1986; Jarvela and Thorsteinson 1999; Thedinga and Johnson 2006). This may cause Arctic pack ice retreat to have a particularly strong influence on the foraging efficiency of Black Guillemots and other marine predators with foraging ranges determined by central place foraging tenets associated with stationary chicks (Orians and Pearson 1979; Lessells and Stephens 1983). My work also highlights the use of seabirds as samplers of forage fish,

which over the long-term may indicate temporal changes in proximate composition and body condition, where other sampling techniques are logistically difficult (e.g., Davoren and Montevecchi 2003a).

Chapter 3: Determining the existence and biological relevance of small pieces of ice in the western Beaufort Sea

3.1 Introduction:

Between the expanses of solid sea ice and open ocean in the polar regions is a shifting band of ice and water known as the ice edge. The ice edge is essential habitat for a wide variety of marine predators (and obviously their prey) including at least 12 species of seabirds and seven species of marine mammals such as whales and seals (Siniff et al. 1970; Bradstreet 1979; Divoky 1979; Divoky 1981; Bradstreet 1982; Murase et al. 2002; Simpkins et al. 2003). The waters at the ice edge are uniquely productive among polar marine waters and support a rich foraging environment for predators (El-Sayed 1970; Divoky 1981; Smith and Nelson 1986). Therefore, the ice edge zone offers air-breathing predators access to the comparatively rich ice-associated fauna as well as protection from comparative hydrophobic predators such as polar bears (Mauritzen et al. 2003).

Arctic Cod is the primary forage fish species in the Arctic Ocean and is the primary food link between secondary producers and top carnivores (Hobson and Welch 1992), presumably due to its high energy densities relative to other forage species (Hobson and Welch 1992; Van Pelt et al. 1997). Due to an absence of a commercial fishery in the Arctic, however, the distribution and life history of Arctic Cod are poorly understood. This species is associated with ice and feeds on under-ice amphipods (Lowry and Frost 1981; Welch et al. 1993; Gradinger and Bluhm 2004). In primarily open waters with <5% ice cover, Arctic Cod have been found in small dense schools underneath the ice floes; however, these schools disperse when the ice disappears (Welch et al. 1993;

Crawford and Jorgenson 1993). These open water ice floes provide significant microhabitat for the fish and, thus, could be a key foraging habitat for predators.

There are documented cases of cod predators preferring ice edge habitats with comparatively little ice cover. In Canada's Barrow Strait, Thick-billed Murres associated significantly more frequently with areas which had < 25 % (as low as 1 %) ice cover than with other ice-water interface zones (Bradstreet 1979). Consequently, the ability to detect this low ice environment may be critical to locate and identify key areas where high abundances of animals congregate to feed ('biological hotspots') (Davoren 2007).

Traditional studies of the ice edge as animal habitat have involved visual at-sea surveys on boats or ice breakers. Due to the expense of these vessels, the studies often use aggregates of data collected incidentally on shipping vessels or on vessels engaged in environmental surveys for the petroleum extraction industry (Divoky 1979; Divoky 1981; Divoky 1984). If ice density is quantified at all, it is normally estimated visually using a system of "octas" or 1/8ths ice cover (Siniff *et al.* 1970).

Remotely sensed data provide new tools for locating low-density ice habitat. The satellite coverage over the Arctic is poor because of frequent cloud cover in the region, the loss of resolution suffered by cloud-penetrating remote sensing methods, and the comparative lack of commercially valuable areas. The finest-scale daily product is the Moderate Resolution Spectroradiometer (MODIS) that has a resolution of only 250 m² - 500 m² depending on the number of bands. The occurrence of a cover type on a spatial scale smaller than the pixel size of remote sensing devices is known as partial cover or subpixel cover. Numerous methods have been developed for identifying and quantifying subpixel phenomena, one of which is linear unmixing (Chase and Holyer 1990; Sohn and

Mccooy 1997; Braswell et al. 2003; Hedley et al. 2004; Wolbers and Stahel 2005). This technique is based on the theoretical assumption that the proportion of the pixel's spectral signature that is explained by the endmember's spectral signature is proportional to the percent of the pixel footprint covered by that endmember. Endmembers are theoretical pixels composed purely of a single cover type such as "ice" or "cloud" or "shallow water" that are used for 'training' the classifier such that weighted average endmember mixtures can be identified for each pixel within the image. Therefore, it assumes there is no spectral interaction between the endmember types (Sohn and Mccooy 1997). It also assumes that pixels are composed of composites of pure endmembers; there are no intermediate cover types (Hedley et al. 2004).

Band ratioing is another simple technique used to extract additional information from multispectral images. Band ratio images are grey-scale images whose digital number (DN) at a given pixel is the quotient of the DNs for that pixel from two of the bands of the image (Ryerson et al. 1998). The mathematical process of division allows for the small spectral differences between cover types to be amplified. Ratioing is traditionally used to reduce topographic effects, observe vegetation differences, or resolve subtle differences between rock and soil types (Richards 1986). The disparate albedos of ice and water indicate that pixels with a mixture of ice (albeit slight) and water, and those of pure water ought to have distinct spectral signatures whose differences would be amplified by band ratioing.

The breeding colony of Black Guillemots allows for an in-depth case study of the relevance of ice edge conditions to a marine top predator (Divoky 1998). Black Guillemots rear two chicks in one season, whereas most other alcids only rear one.

Central Place Foraging (CPF) Theory predicts that energy-dense prey (kJ / g) will be preferred for delivery to chicks. Therefore, guillemots are predicted to prefer Arctic Cod for delivery to their chicks on Cooper Island. Black Guillemots generally forage near to shore within 15 - 20 km of the colony and certainly within 40 km (Cairns 1987c; Clowater and Burger 1994). The summer retreat of the pack ice beyond the foraging range has been tightly correlated with decreases in Arctic Cod delivered to chicks and consequent high levels of chick mortality (G. Divoky pers. comm.).

During the summer months (July - September), the region around Cooper Island is part of the ice-edge zone — a mixture of ice and open water that varies in composition. Initial examinations of daily MODIS true-color composites for this region during the summer showed the ice edge to be beyond guillemot foraging ranges; however, pieces of ice were detected visually by researchers at the colony. This disparity indicated the possibility of subpixel ice within the foraging range that went undetected by traditional remote sensing methods. Here, I develop a protocol to produce information on low-density ice-covered habitat at a biologically relevant spatial scale from easily accessed, remotely sensed images. Specifically, I employ spectral mixture analysis and band ratioing to probe the information hidden within the digital numbers of these at-sensor radiance images.

3.2 Methods:

MODIS images of the Barrow region including Cooper Island during July and August of 2005 and 2006 were previewed from a database of daily composites to select image files from comparatively cloud free days. MODIS L1B calibrated radiance image

files were acquired from the Earth Observing System (EOS) Data Gateway interface. (These images have recently been moved to the Level 1 and Atmospheric Archive and Distribution System (LAADS)). Images were acquired from MODIS Aqua. MODIS Aqua senses in the following spectra: Band 1 (620-670 nm), Band 2 (841-876 nm), Band 3 (459-479 nm), Band 4 (545-565 nm), Band 5 (1230-1250 nm), and Band 7 (2105-2155 nm) (Masuoka et al. 1998).

I acquired images files of two types: MOD02QKM (two band) as well as MOD02HKM (seven band). Both types of images are calibrated and geolocated radiances for MODIS. Two band images are composed of spectral bands one and two at 250 m² resolution while seven band images contain spectral bands one through seven (visible to thermal) at 500 m² resolution (Masuoka et al. 1998). All operations requiring the integrity of the pixel format as transmitted from the satellite (such as georeferencing, image transformation, stacking, and masking) in this analysis were performed using ENVI 4.2 (Research Systems Inc. 2005). MODIS L1B images cover hundreds of square miles. To improve the speed of computing, images were cropped to the identical region of interest (ROI) of approximately 80 km surrounding Cooper Island. Images were simultaneously georeferenced and bowtie corrected to improve ease of navigation and interpretation using ENVI's MODIS tool.

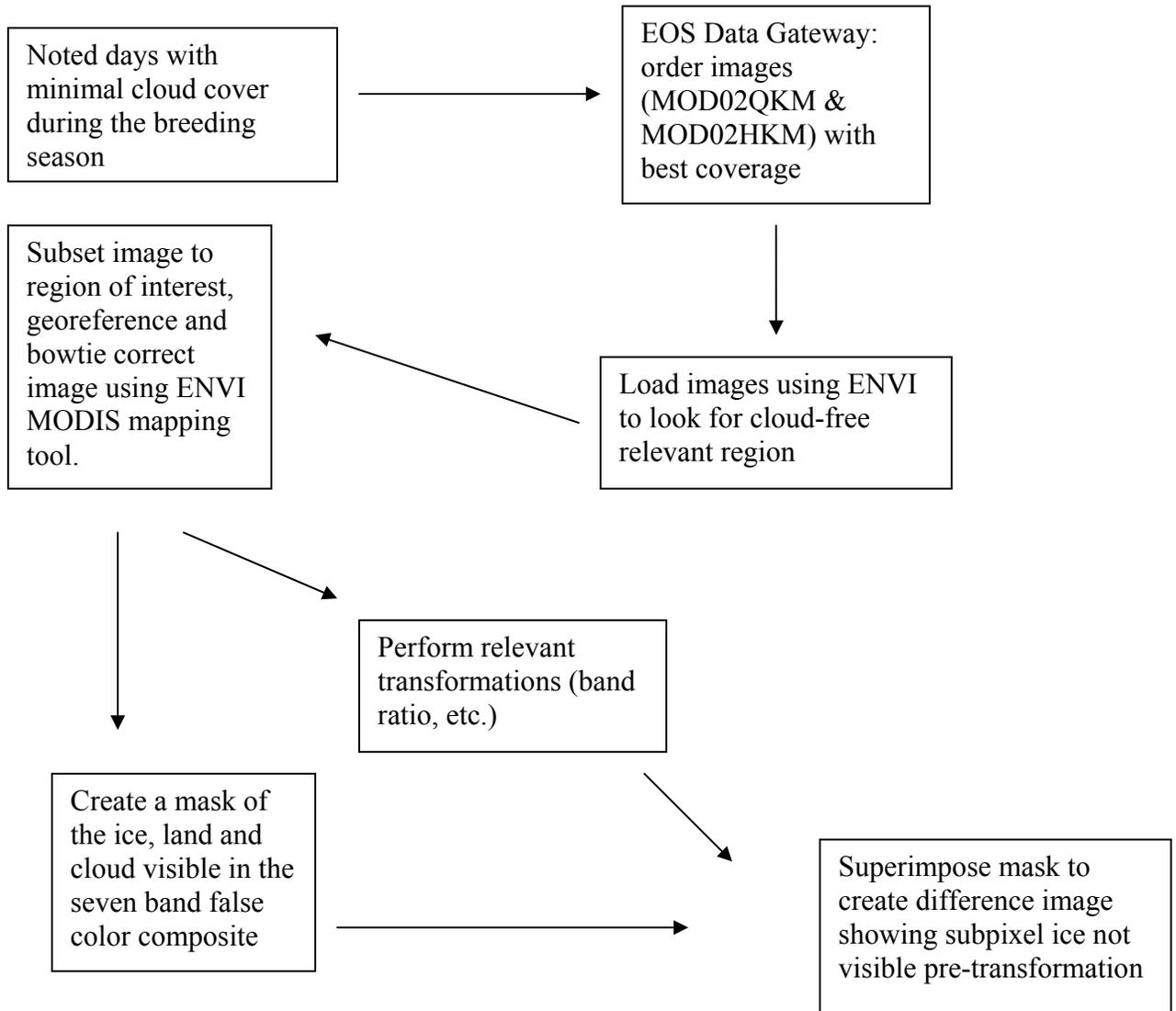
MODIS is a side scanner. It swings its sensing mirror from side to side as the satellite moves forward. The geometry of the changing angle of observation creates a field of view for the sensor that is wide at the most distant points observed and narrow just below the sensor. This forms the shape of a bowtie. This alteration creates blurry original images in which some parts are repeated. Georeferencing with bowtie correction

turns the raw, sensed image onto a more traditionally legible map projection such as Universal Transverse Mercator (UTM). Seven band images were also resampled to the same pixel size as 2 band images (250 m²) and cropped again to fit the ROI. This pre-analysis work is summarized in Figure 3. 1.

Band ratioing was performed on the MOD02QKM images. Linear unmixing protocols which require more than two bands were performed on MOD02HKM images. Band ratioing was foregone on these images because it would have utilized Bands 1 and 2 which are the same bands present in the MOD02QKM files. Endmembers for linear unmixing analyses were collected from within the image itself using the endmember collection protocol in ENVI 4.2's linear unmixing module. Endmembers were taken for deep water, shallow water, cloud, land, and ice.

The ability to identify ice that is visible in a transformed image (such as a band ratio), which is hidden in the original true-color composites, is essential to this work. To understand this subtlety, one must understand the way satellite images are turned into pictures. Unlike photographs, which only absorb in the visible spectrum, MODIS absorbs light in a variety spectra that the eye cannot perceive. In order to make this intelligible to the eye, the different bands (typically bands 1, 3, and 5) are designated with a basic color (red, green, and blue (RGB), respectively). The strength of absorption in the chosen bands in each pixel dictates the strength of the color in that pixel. An entire image projected this way is referred to as a "false-color composite" because the colors in the image do not correspond to the colors that a human eye would see from the satellite. The National Snow and Ice Data Center (NSIDC) created an algorithm that creates false color

Figure 3.1. Flow chart detailing the processing steps from raw images to the detection of subpixel ice.



composites that closely mimic the coloration of a photograph of the same region. These are available for free on a daily basis for our ROI and are referred to as “true-color composites”.

Once the files were resampled and cropped to the ROI, I generated a mask from the seven band georeferenced image. A mask is a device used in mapping where some pixels are opaque (black) while others are translucent (white). When the mask is applied to a new image, the parts of the new image which correspond to the black pixels in the mask appear black while the pixels in the new image that correspond to the white pixels of the mask appear as they would in an unmasked image.

Ice, land, and cloud have different spectral signatures across the seven bands which made creating a single mask that encompasses all three cover types tricky. I utilized the fact that all three of those cover types have a reflectance higher than water. I used minimum threshold reflectance to create the mask which blacked out all ice visible in the untransformed images as well as all land and cloud. I then applied the mask to the band ratioed image to show unambiguously the new cover type from the region that appeared as water in the true-color composite.

To ground-truth the relevance of subpixel ice floes as habitat for Arctic Cod and other marine predators, a boat trip was taken to two subpixel ice floes on 6 August 2006. The boat was docked on one floe, which measured less than 50 m² and bird activity (presence on the ice or in nearby waters, attendance numbers, dive durations, and species composition of prey captured and brought to the surface) was recorded for 30 min. All arrivals and departures of birds were noted, and focal individuals were followed to quantify dive behaviour. These observations were followed by two circumnavigatory

surface tows (0 - 2 m) with a plankton net (5 mm² mesh) to quantify the presence/absence of various zooplankton species, along with size ranges and biomass estimates. Each catch was placed into a plastic bag and analyzed immediately following the tows. The species composition and biomass of these tows were compared with a similar surface tow in the open water of the Beaufort Sea < 3000 m from the location of the ice tow but > 500 m from any piece of ice. Methodology and gear were identical in all zooplankton tows.

3.3 Results:

Band ratioing detected a class of pixels that is most likely subpixel ice. That being said, the methodology is time-consuming, because of the large number of processing steps. From the image files ordered on days that were believed to be relatively cloud-free, a comparatively small percentage (n = 17, 58 %) were clear enough so that the ROI could be located and was visible in 2005. Of those clear enough to proceed with analysis, only three images showed qualitative evidence of subpixel ice and only one showed strong evidence. I continued with the analysis (focusing on Aug 23, 2006—the most obviously subpixel-bearing image I encountered) in the interest of honing the methodologies and strengthening my conjecture that subpixel ice can be sensed on a daily basis from single, raw MODIS images.

The 1, 3, 5 RGB false-color composite on the image with the highest success of investigation (Aug 23, 2006) is presented in Figure 3.2. The mask created to cover the features that are visible in the original false-color composite is presented in Figure 3.3. This mask leaves only the region that appears as open water to be visible. When the

Figure 3.2. The false-color composite of the untransformed file for Aug 23, 2006 after georeferencing.



Figure 3.3. The mask that blocks out land, ice, and cloud from the image.

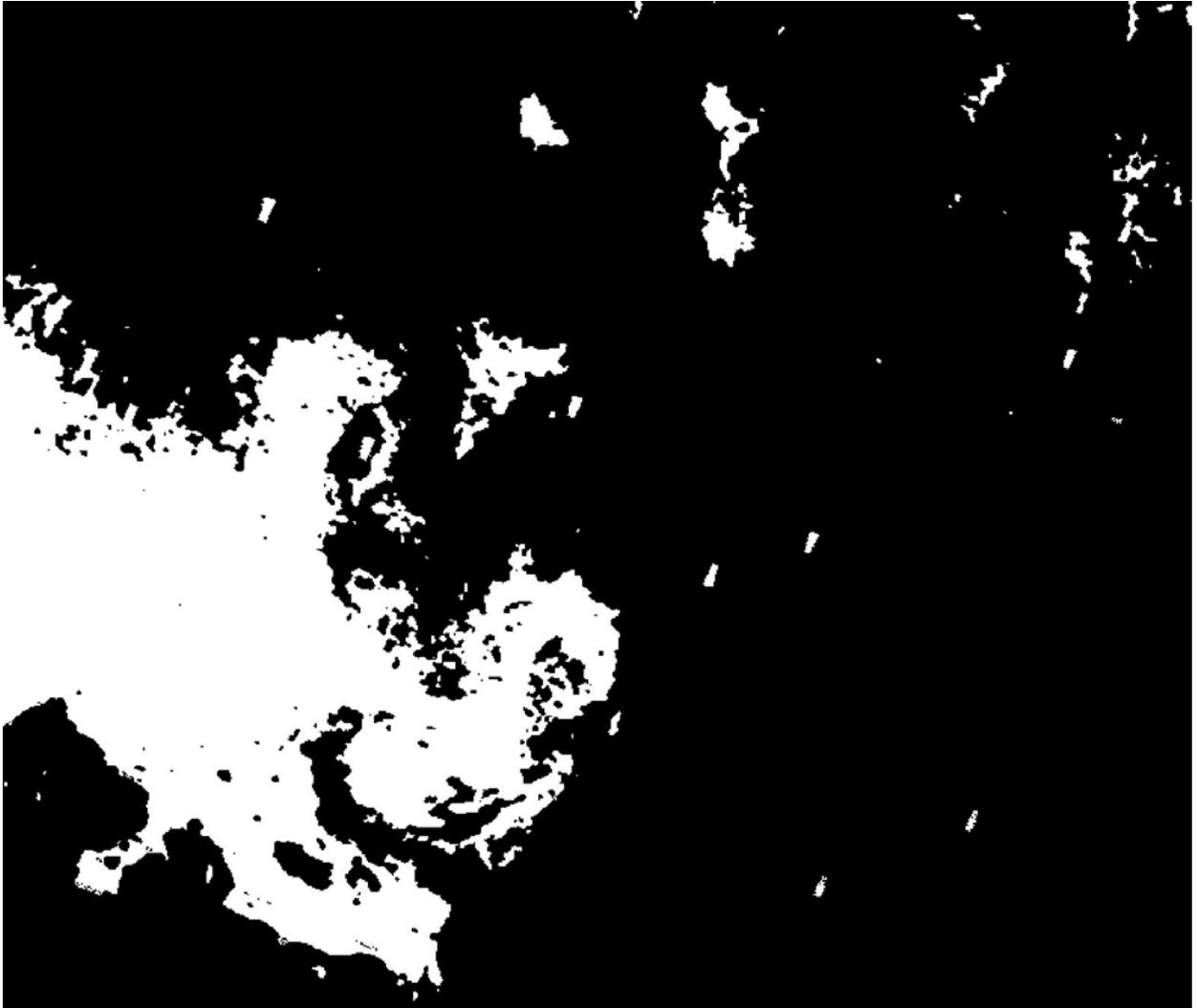
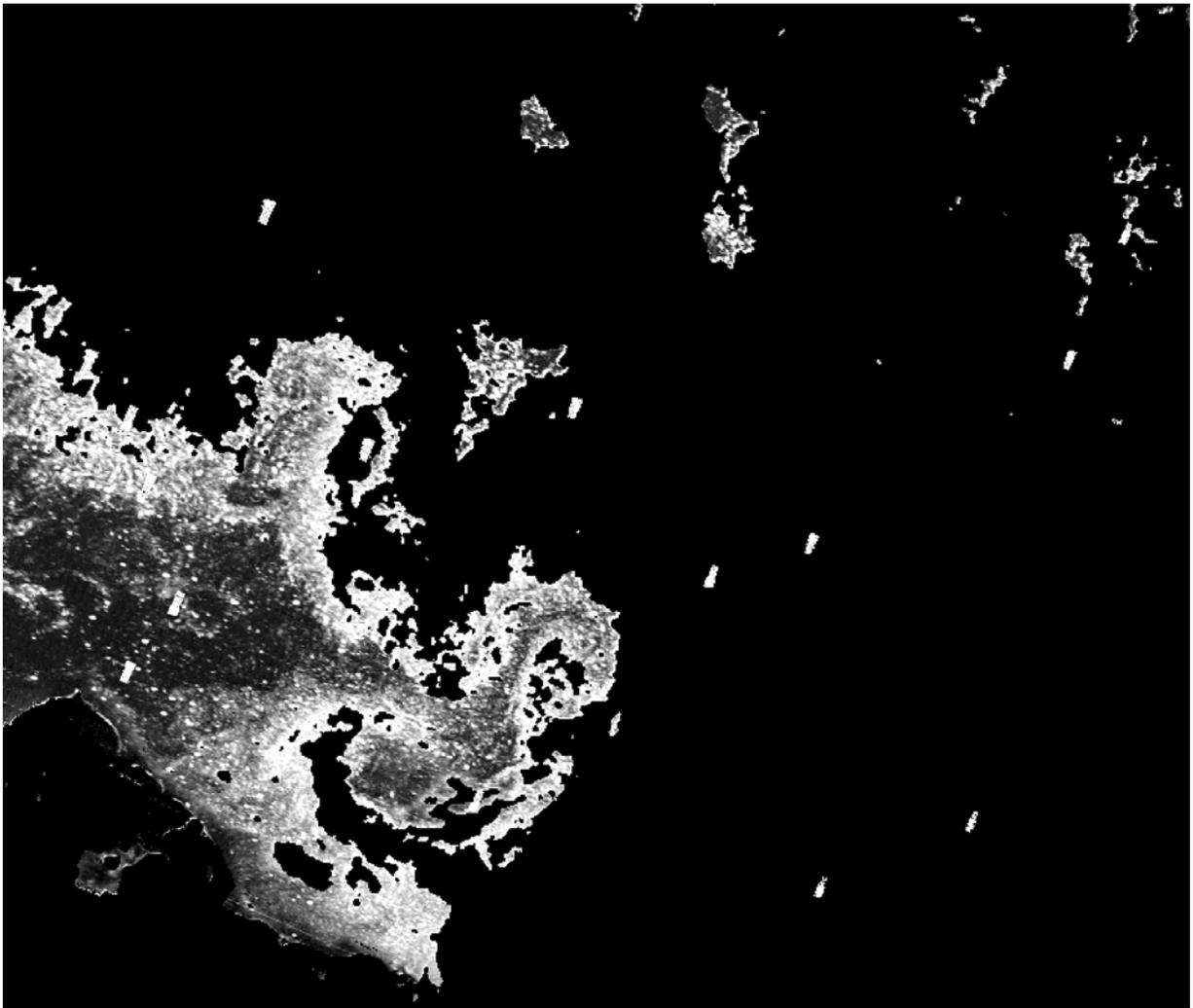


Figure 3.4. The band ratioed image of Aug 23, 2006 with the mask applied. A high density of non-pure-water pixels can be seen in the unmasked region which represents open water in the false-color composite. The density of these pixels increases near the region occupied by known ice indicating that these non-pure-water pixels are subpixel ice.



mask is applied to the band ratioed image (Figure 3.4), the evidence for subpixel ice in the habitat previously classified as open water becomes obvious. The class of pixels visible in the band ratioed image but not in the original image is most densely clustered near to an established area of visible ice. The density of these pixels declines proportionally to distance from the previously visible ice. The pattern of distribution of this new class of mixed pixels is consistent with the density pattern of ice floes near the ice edge (Divoky 1981).

Band ratio images were not able to distinguish cloud from ice. The band ratios did create three clear cover types of land, water, and cloud/ice. The extent of cloud is detectable by their distinctive shape and pattern in addition to being visible in the false color composite.

Linear unmixing also proved successful, although no subpixel ice was detected. Linear mixture models were able to detect thin layers of clouds, where they were not immediately obvious in the false color composite, and they were able to separate cloud from ice in all cases ($n = 2$). The technique was able to extract ice from beneath a cloud mask (albeit a thin one) in one image (Figure 3.5). The selection of the five endmembers appeared to explain the variation in the image quite well as shown by the Root Mean Square (RMS) error image which consists largely of speckle pixels (Figure 3.6). The at-ice observations revealed that Black Guillemots ($n = 1 - 7$) were present at subpixel ice floes. Most of the birds (57 %) observed at the ice floe were diving. Dive duration ranged from 38 - 47 s, which are generally regarded as feeding dives (Cairns 1992c). Out of the eight dives observed, guillemots surfaced twice with Arctic Cod. This

Figure 3.5. Linear unmixing isolates relatively sparse clouds well as is visible in the comparison between the cloud endmember unmix of a UTM-projected bowtie corrected image (left) and the false-color composite (right) of the same image.

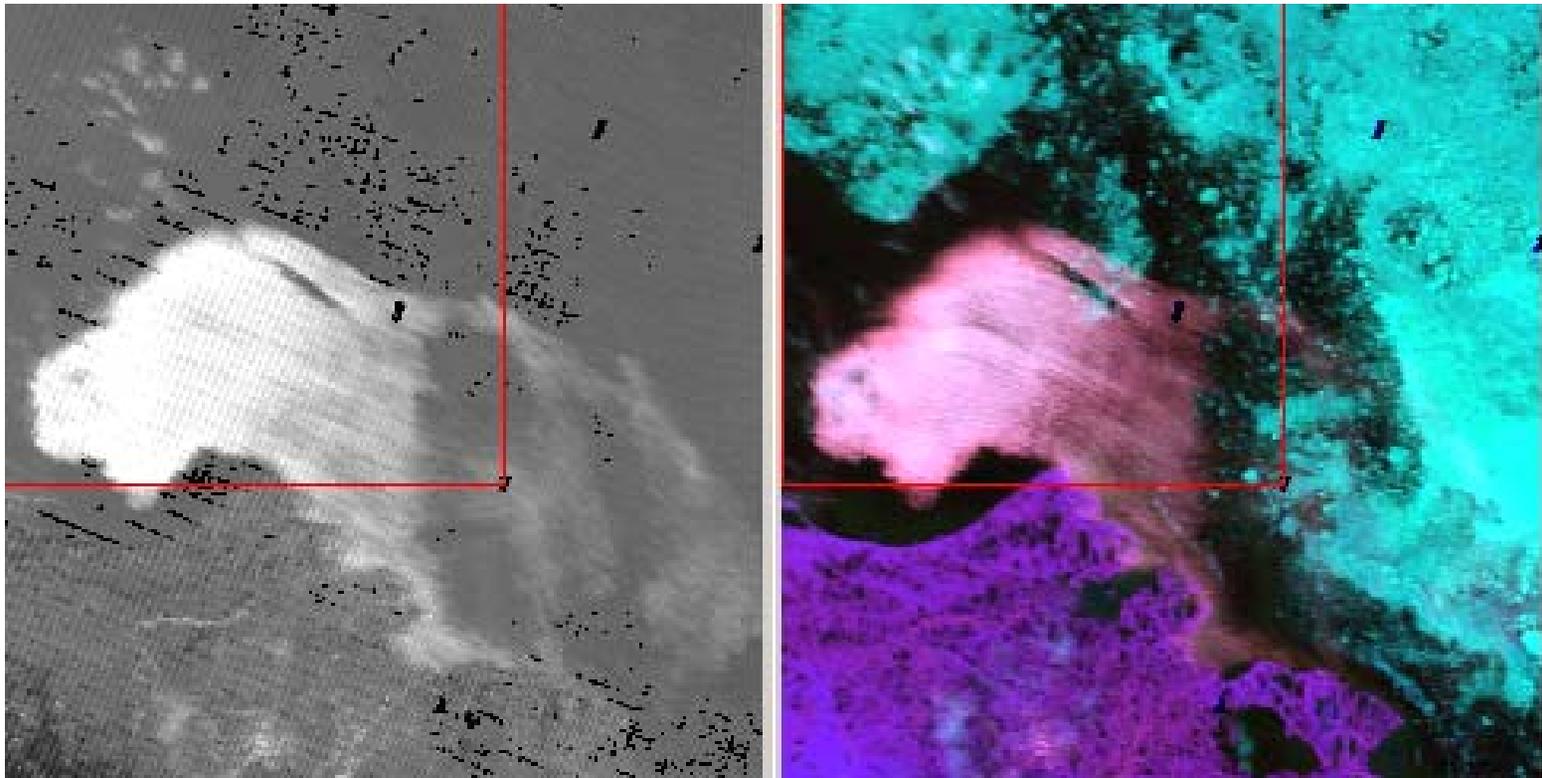


Figure 3.6. The RMS error image for the UTM projected linear unmix (left) and the false color composite (7,4,2) (right). Regions of error seem to be limited to speckle pixels and a second cloud endmember.

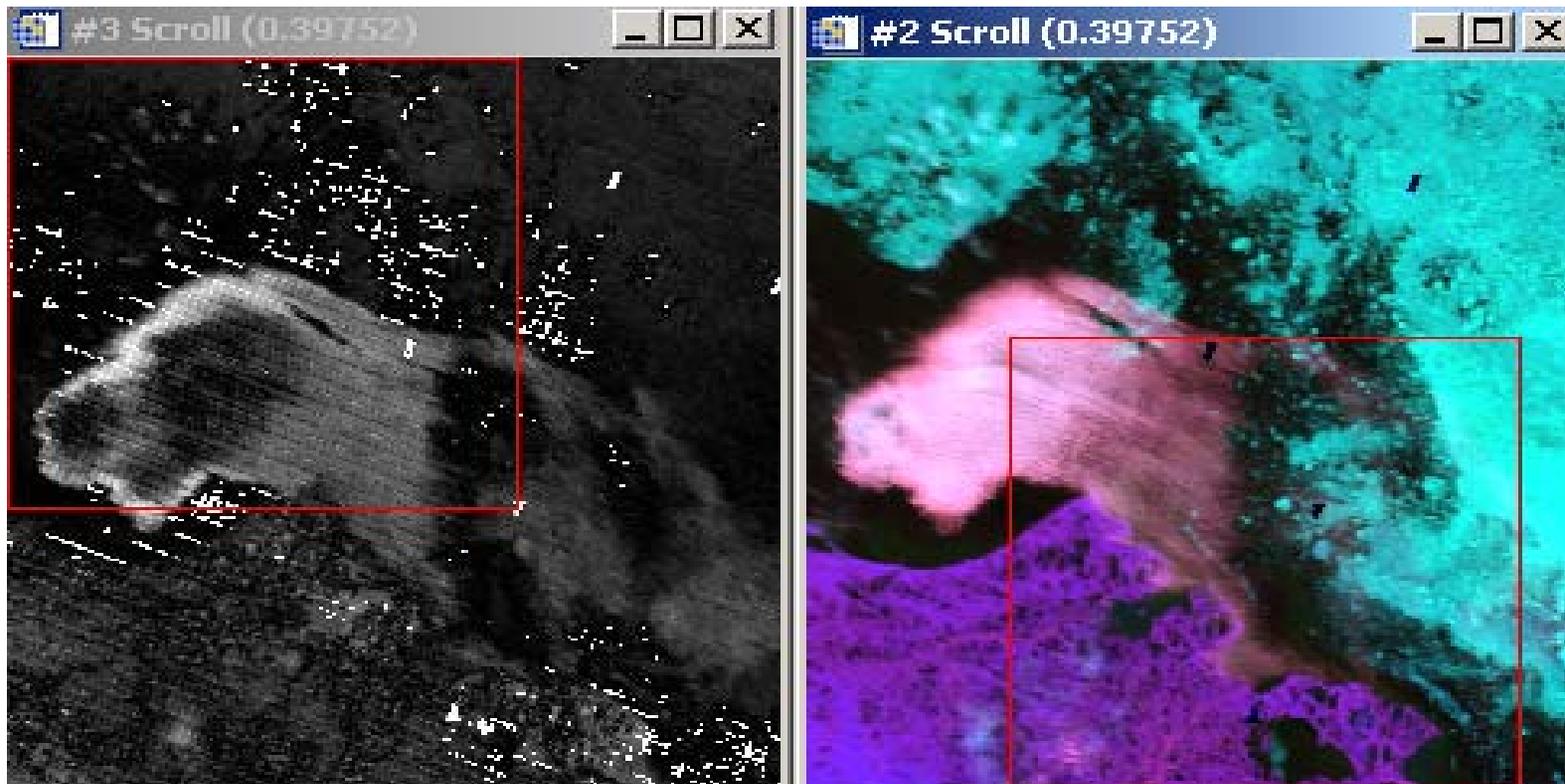


Table 3.1. The identified fauna from two surface plankton tows taken at subpixel ice floes and in open water

Subpixel Ice Floe	Open Water
Larval Fish	Amphipod
Cnidaria	Cnidaria
Copepod	
Amphipod	

was the only fish species observed to be captured by guillemots. Analysis of plankton tows indicated that zooplankton were generally larger and more dense at the ice cod at ice floes compared to open water (Table 3.1).

3.4 Discussion:

My masked band ratio technique revealed the presence of daily fine-scale ice where it was not detected using standard visualization techniques such as NSIDC true-color composites. The detection of small ($< 250 \text{ m}^2$) ice floes extending away from the edge of the pack ice toward the shore is important as it reveals important habitat for ice edge animals that would be overlooked using only true-color composites.

Band Ratioing

Band ratioing was the most effective method at detecting subpixel ice. It consistently generated images that depicted a larger area or higher density of ice than was visible in the true-color composite. The mask is not necessary to using band rationing to search for qualitative increases in subpixel ice. It simply makes subpixel ice easier to see and the debate about its existence less qualitative. Band ratioing is also a fairly simple method compared to linear unmixing. It requires less computing power and can be used on the higher-resolution (250 m^2) two band images. In contrast, linear unmixing requires a larger number of bands than endmembers, so it can only be used with the 7 band (500 m^2) images. These can be resampled to 250 m^2 pixels, but that should theoretically reduce the information content which is at a premium in subpixel analyses.

Linear Unmixing

The assumptions associated with linear unmixing do not accurately represent reality for most terrestrial habitats, and more complicated mixture modeling methods have been developed (Braswell et al. 2003; Chang et al. 2004; Wolbers and Stahel 2005). These tend to require dedicated satellite time and/or prior knowledge/manipulations of the remotely sensed region (Braswell et al. 2003; Hedley et al. 2004; Carter et al. 2005). Linear unmixing has been attempted on sea ice, but never with MODIS data (Chase and Holyer 1990).

Discounting interference by clouds, I observed a largely binary and mutually exclusive cover system of ice and water or, at its most complicated, a three endmember system (shallow water, deep water, ice); therefore the assumptions about pure subpixel endmembers appear to be valid (Settle and Drake 1993). If anything, sea ice, with its high albedo and irregular surface may actually over-represent itself from interactions between surfaces and illumination angles (Mather 2005).

Within the regions of broken ice extending out from the solid pack, linear unmixing did not detect an appreciable qualitative increase in the frequency of ice when compared with the false color composite nor did it detect ice where none was visible in the true-color composite. The subtlety with which linear unmixing is able to distinguish among cover types makes it a strong candidate for subpixel ice detection, but I was unable to generate tangible results in any of my analyses.

Importance of Subpixel Ice Detection

My ground truthing reinforced that these small floes are important foraging habitat for marine top predators that inhabit ice edges. Ground truth visits to small (~50 m²) widely spaced floes in the near-shore Beaufort in 2006 confirmed the presence of guillemots feeding on Arctic Cod at these floes. Plankton tows suggested a richer planktonfauna than the surrounding open ocean (Table 3.1). These facts underscore the biological importance of subpixel ice floes to marine top predators, such as guillemots.

The presence of Arctic Cod within the rich microhabitats of subpixel floes has direct effects on the success of the birds. In 2005 and 2006, when the ice was visible to observers at the colony, > 95 % of prey delivered by guillemots to chicks at Cooper Island was Arctic Cod. In 2005, the seasonal ice retreat resulted in the pack ice being situated beyond the 40-km foraging range; however, guillemots continued to deliver Arctic Cod to chicks, quite possibly acquired from subpixel floes. The percentage of cod in chick diets was lower (10 - 70 %) than when the pack ice was visible within foraging range in the true-color composites earlier in the season (> 95 %); however, this continuing source of cod without pack ice may have been vital to chick success. Fledging success was 63 %, whereas in 2004 when only sculpins were observed at nest sites late in the breeding season, the fledging success was 13 % (Divoky unpublished.; Divoky and Harter Unpublished).

Conclusion

The results of this study attest to the value and extent of free data available promptly upon request from NASA. The study also indicates promising methodological leads in the search for ecological explanations of variations in Black Guillemot breeding

success and chick growth. An extensive survey of available images using band ratioing and linear unmixing for all available MOD02QKM and MOD02HKM images may well yield a pattern of subpixel ice consistent with colony-based observations of visible ice within foraging ranges and percentage of Arctic cod in the diet of this marine predator. That being said, the amount of pre-processing required at the current stage is time-consuming, and MODIS images are useless on days of heavy cloud cover. An interface tool that links remotely sensed data to biologists would increase the possibilities for biological application markedly.

Chapter 4: New Methods for Using Chick Mass as an Indicator of Provisioning

4.1 Introduction:

Whether seabirds can be used to monitor changes in the marine environment has been a long-standing debate in the scientific literature (Cairns 1987a; Cairns 1992a; Davoren and Montevecchi 2003a). Colony-based studies are the simplest way in which seabird ecology can be studied, and chick mass is the easiest and cheapest colony-based measure. Chick mass is preferable to adult mass, because nidiculous chicks are a fairly simple system with regard to disturbance and energetics compared to parents who, among other complications, may have programmed mass loss unrelated to foraging conditions (Croll et al. 1991a).

The life history strategy of seabirds is generally characterized by long life and low fecundity (Lack 1968; Drent and Daan 1980). The strategy for maximizing lifetime reproductive success within these parameters is one in which the parent provisions itself first and provisions its chicks only if internal energy balance is above some threshold level (Drent and Daan 1980). Therefore, alterations in the ease of prey acquisition and delivery to chicks will first be seen in changes to time spent foraging (Cairns 1987a; Burger and Piatt 1990; Zador and Piatt 1999; Litzow and Piatt 2003). Only after parent birds have comfortably allotted more time to foraging and continue to suffer an unfavorable energy balance will they begin to shift time and energy allotment away from provisioning chicks toward even more time and effort spent self-feeding (Cairns 1987a; Burger and Piatt 1990; Zador and Piatt 1999; Litzow and Piatt 2003). Therefore, deviations in chick provisioning and consequently in chick mass represent noteworthy

changes in the ease of foraging and changes in chick mass are positioned a saddle-point of foraging conditions.

There has been a constant need for a simple method for comparing the growth rates of offspring among individuals of a given population or species (Walford 1946; Ricklefs 1967). Within the growth curve of many animals including humans, amphibians, and a wide variety of birds, at least one phase of linear mass gain (Linear Growth Phase, LGP) can be identified (Walford 1946; Morton 1973; Werner 1986; Ewins 1992; Nisbet et al. 1998; Hautvast et al. 2000). Young animals gain approximately the same amount of mass each day throughout this phase. Within the bird literature, this phase is regarded as purely descriptive; however, endocrinology indicates that the phase is internally mediated in humans (Merimee et al. 1991; Hautvast et al. 2000). The slope of the LGP has been the preferred method to monitor seasonal provisioning for all bird species and particularly seabirds, because the slope is the mean daily gain of the linear period (Cairns 1980; Ricklefs et al. 1984; Piatt et al. 1990; Hautvast et al. 2000; Hamel et al. 2004a). This parameter, however, only indicates changes in provisioning at a low temporal resolution.

After chicks leave the LGP, they enter a part of the growth curve that is highly variable, during which most seabird chicks lose some mass before they fledge (Ricklefs 1968; Sealy 1973; Simons 1981; Sealy 1981). This pre-fledging weight recession is adaptive for increased efficiency of flying, diving, or both, and is mediated primarily through dehydration of body tissues (Ricklefs 1968; Sealy 1973). This type of mass loss is independent of provisioning and, thus, has been one of the major impediments to using older chicks to monitor foraging conditions of parents. Therefore, there have been very few attempts in the seabird literature to use the “Post-Linear Growth Phase (PLGP)” in its

entirety to monitor provisioning (Konarzewski and Taylor 1989). Konarzewski and Taylor's (1989) work involved complex curve-fitting. Most researchers use peak weight (the highest recorded mass) and/or fledge weight (the last recorded mass) as proxies for provisioning (Sealy 1981; Hatchwell 1989; Golet et al. 2000; Hipfner and Gaston 2002). The ability to determine provisioning levels from the PLGP in a simple, regular manner that is relatable to the LGP provisioning would be extremely useful, because the PLGP for many seabirds is much longer than the LGP.

In this chapter, I generate a fine-scale (daily) parameter to assess changes in provisioning throughout the LGP and PLGP for Black Guillemots. The LGP phase of Black Guillemots lasts from approximately 8 to 18 d of age (Ewins 1992), followed by the PLGP that lasts from 19 d to fledge (~ 14 days). Due to a comparatively synchronous hatching of colonial seabirds in general and Black Guillemots in particular, most of the colony is in the same phase of growth at any given point in time (Divoky 1998). Using chick mass gain/loss during the LGP and PLGP, I generate predictive curves based on chick age and compare the daily anomalies from these curves to quantify the relative strength of daily provisioning at the colony. The predictive curves are based on the amount of mass change to be expected of guillemot chicks at a given age. This, rather than using anomalies from a predicated mass, helps to correct for individual variation based on parental quality, nest location, date of hatch, or provisioning on previous days (Coulson 1968; Coulson and Horobin 1976; Morbey et al. 1999). The ability to use chicks during the PLGP as monitors of provisioning effort creates a vehicle to monitor a period of time that was previously unknown.

4.2 Methods:

During the breeding season (June-September) of 2005-2006, I measured the mass of each chick at every nest (136 nests) within the Black Guillemot colony on Cooper Island under the auspices of Dr. G.J. Divoky (Divoky *et al.* 1974). Dr. Divoky offered the chick mass measurements from 2004 for inclusion in the analysis to include a year of poor provisioning (Divoky pers. comm.).

Near hatching, all nests were checked daily and dates of hatch were recorded, which resulted in accurate chick ages. The second egg generally hatched 1-3 days after the first. Hatch day was called Day 1, because hatch could have occurred any time in the intervening 24 h. Chicks were weighed at approximately the same time of day once brooding stopped (6 d) using 100-g, 300-g, or 500-g Pesola spring scales. Scales were standardized daily against a digital scale and observer techniques were standardized weekly by collective measurement of the same chick.

The mass of each chick measured daily was entered into a spreadsheet along with the date and chick age. As an attempt to control for the changing make-up of chicks (particularly during times of food shortage) on a given date, only chicks that fledged were included in analyses. Subtracting the previous day's mass from the current mass yielded daily measurements of mass change for each day. If there were not measurements for both the previous and current day, this metric was left blank. I divided the nidiculous phase of each chick into LGP (8 – 18 d) and PLGP (19 d – fledge) subsets. I discarded all measurements taken before day 8, because they show a high degree of regularity in all conditions. Mass loss associated with handling birds was controlled for by the uniform

handling of all birds and because analyses were based on daily changes rather than absolute masses.

I calculated the seasonal mean mass gain during the linear growth phase, similar to previous studies (Ewins 1992). This was defined as the mean of all LGP daily mass changes of all chicks in a given year. I then began work on the fine-scale metric. I determined my metric to be the average difference between the expected daily mass change and actual observed mass change. Expected average mass change happens to be the same each day due to linearity of growth.

The daily mass changes were then sorted by date of measurement. I calculated the mean of all LGP mass changes for each date. I then subtracted the seasonal mean from this daily mean. The difference between these two numbers represented the mean daily mass change anomaly (hereafter referred to as ‘provisioning index’). Each date was associated with a mean provisioning index value and SE. After visual analysis of the provisioning index to look for fine-scale anomalies that may have affected the seasonal daily mean, such as wind speed and direction (see Chapter 5), post-hoc analyses of the abridged versions of the 2005 seasonal mean LGP were performed excluding brief periods of poor growth for comparison with overall seasonal means.

I then attempted to generate a regular, simple metric for assessing provisioning in the PLGP. I did this by creating a theoretically identical metric as I did to the LGP provisioning index for a slightly more complicated data set. The PLGP provisioning index is the average difference between the expected daily mass change and actual observed mass change. In the case of the PLGP (as opposed to LGP), the expected mass change varied with age, unlike the LGP.

For all the PLGP chick measurements in a given year, I calculated the mean mass change for each chick age (19 d, 20 d, 21 d, etc.). I then fitted a regression to the plotted data, resulting in a predictive curve for the mass change behavior of all PLGP chicks. The regression for the daily mass change was linear and significant with a high r^2 for all three years. I then calculated the anomaly for each individual measurement as the difference between the observed daily mass change and the one predicted by the season-wide curve based on chick age. I generated daily PLGP provisioning index values by taking all of the PLGP individual anomalies for a given date and calculating the mean and SE.

I related the provisioning indices of the LGP and the PLGP by performing regression between the metrics. I plotted the daily values of both indices (i.e., x-axis LGP, y-axis PLGP). Therefore, a single data point represented the same day's LGP and PLGP provisioning index values. I then fitted a regression to each year of the data to investigate the regularity of the relationship between the LGP and PLGP provisioning indices and its robustness to different years. When the LGP chicks indicated that provisioning was poor on a given day, did the PLGP chicks concur? Does this relationship happen in some years, or all years?

The provisioning indices daily values are mathematical means. Statistically, sample mean values are only reliable approximations of idealized population means with an appropriately large sample size. To investigate the effect of daily sample size on the robustness of the relationship between the LGP and PLGP provisioning indices and attempt to establish guidelines for other users of my methods, I performed the same LGP/PLGP regression analysis method from the previous paragraph, but this time I

performed regression on different subsets of the data within a single year (2005). I varied the minimum threshold values (>10, >15, >20, >25) for the number of chicks in both phases, and I only included data points from days that contained appropriately large sample sizes of both LGP and PLGP chicks in the regression. For example, a day with 11 LGP data points and 42 PLGP data points would be included in the analysis for the “>10” regression, but none of the others.

4.3 Results:

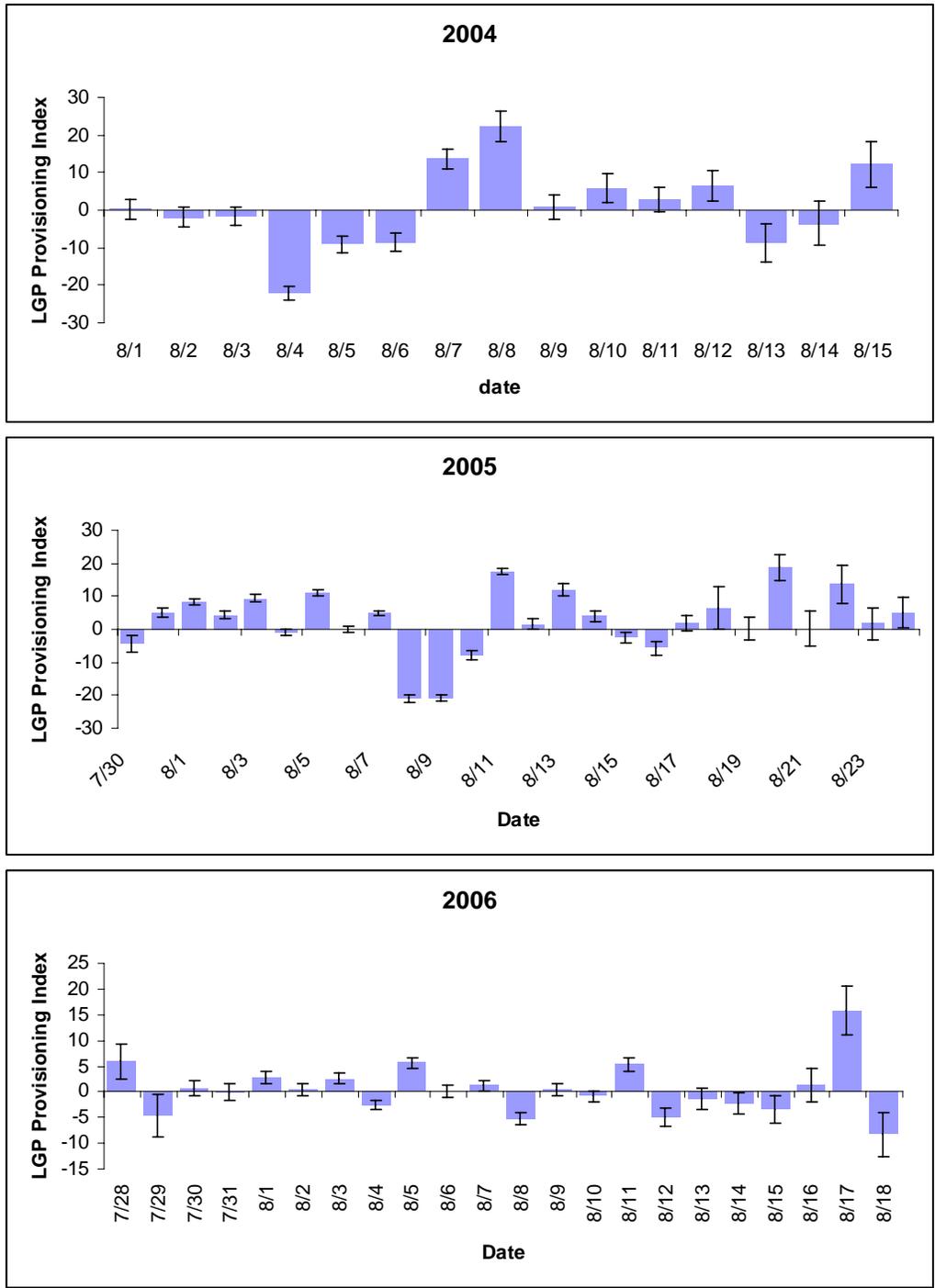
The seasonal daily mean mass gain of LGP chicks was significantly different among the years (ANOVA $df = 2$, $F = 30.888$, $p < 0.0001$). It was lower in 2005 (11.1 ± 0.4 g/d) relative to 2006 (15.1 ± 0.3 g/d; t-test: $df = 3672$, $t = -15.658$, $p = 7.630 \times 10^{-54}$); however, the exclusion of 3 d of poor growth from 2005 made the seasonal means identical (15.1 ± 0.4 g/d) (t-test $df = 3023$, $t = 0.018$, $p = 0.4930$). The overall seasonal mean in 2004 was 11.1 ± 0.8 g / d, which is similar to the 2005 seasonal mean; however, the seasonal mean of chicks that fledged in 2004 was 14.7 ± 1.1 g/d which is not significantly different from the seasonal mean of 2006 or the abridged 2005 mean according to the previously mentioned ANOVA. There was no relationship between seasonal LGP daily mean mass gain and fledging success (regression: $df = 1$, $F = 1.337$, $p = 0.4539$). This suggests that using a seasonal daily mean of LGP chicks to compare levels of provisioning among years may be problematic due to the disproportionate effects of a few high- or low-level days on seasonal means. It also shows the surprising recurrence of growth rates associated with poor fledging success (~ 11 g/d) and good

fledging success (~15 g/d) for Cooper Island Black Guillemots although these occur in subsets of the data that require more subtlety than the traditional seasonal LGP mass gain.

The absolute value of the LGP provisioning index was greater than the standard error (except for 2006), which suggests that daily values are sufficiently varied to imply external driver (Figure 4.1). This provides evidence for the validity of using fine-scale parameters to measure provisioning (see Chapter 5). In 2006, the daily provisioning indices were extremely consistent and with the standard error many of the daily values were indistinguishable. The alternating pattern of values slightly above and below the seasonal mean suggests small corrections around an ideal daily mass gain. This suggests that colony-wide provisioning was not affected by any short-term, transitory external factors in 2006. High fledging success (87 %; G. Divoky pers. comm.), a traditional measure of colony success (Montevecchi and Wells 1984), corroborates the high provisioning throughout 2006.

During 2005, high provisioning indices were observed throughout most of the breeding season with a notable exception of three days (August 8 - 10). Immediately following the days of notably poor provisioning, the provisioning index values were unusually high, and then returned to more regular levels. Overall, there appears to be a disproportionate number of good days, because the seasonal mean of 11.3 g/d was used as the basis for the anomaly instead of the 15.1 g/d, which was the seasonal mean without the anomalous bad days in August. The decision of where to center the anomaly makes days that may in fact be normal provisioning days appear better. The generally high provisioning index in 2005 punctuated by a very brief, precipitous decline is corroborated by lower fledging success (63 %) relative to 2006.

Figure 4.1. Mean (\pm SE) daily provisioning indices for Linear Growth Phase (8-18 d) chicks for 2004-2006. Provisioning Indices are daily mass change for LGP chicks in that year with the seasonal mean subtracted to create a seasonal anomaly. The seasonal LGP means were 2004: 11.1 g/d; 2005 11.1 g/d; 2006: 15.1 g/d.



During 2004, there was a dearth of days for which the provisioning index could be calculated, due to 13 % fledging success which severely reduced the number of available chicks for measurement on any given day and frequently made further analyses impossible (Table 4.1). The provisioning index was not calculated for < 5 chicks after exploratory work proved such small numbers to be highly variable and unreliable. This year was characterized by a similar pattern to 2005, with days with very poor provisioning index values followed by a spike in the provisioning index. The phenomenon of high provisioning index values after several days of low values will be referred to as the “post-low-value bounce”

There was chick mortality associated with both the 2004 and 2006 periods of poor provisioning (G. Divoky pers. comm.) and it is tempting to assume that these post-low-value bounces in the provisioning index are simply a factor of brood reduction. Although only chicks that fledged were used in the analyses, the provisioning index would still be sensitive to the death of a sibling, because the numerator of “calories entering the nest” would be divided by one mouth instead of two after brood reduction. Brood reduction was not the cause of the post-low-value bounce. Mass changes on the day a sibling was found dead and the day after when mass changes might be more visible were not significantly different from the overall seasonal LGP mean mass gain for the whole colony and after a sibling died yielded no significant differences in mass change (Day after sibling died: 10.2 ± 3.4 g/d; day sibling died: 15.4 g/d ± 5.2 ; overall seasonal mean: 11.1 g/d ± 0.8) (ANOVA $df = 2$, $F = 0.456$, $p = 0.633$). This suggests that that the

increased provisioning indices after these depauperate bouts were an attempt at recovering from poor days.

Mean daily PLGP provisioning indices were highly correlated with daily LGP anomalies on days when both parameters were calculated for all years tested (2006: $r^2 = 0.88$, $p < 0.002$; 2005: $r^2 = 0.94$ $p < 3 \times 10^{-9}$; 2004: $r^2 = 0.57$ $p < 0.02$; Figure 4.2, Table 4.1). The persistence of this correlation underscores the robust nature of the provisioning index both for LGP and PLGP chicks. The fact that both indices move significantly in tandem implies that they are indicative of an external factor which effects the provisioning of chicks regardless of age. When all the data from all years were pooled, there is also a significant relationship between LGP and PLGP ($r^2 = 0.81$, $p < 0.001$). This indicates that the slopes of the lines that relate PLGP to LGP in each year are not very different from one another. This was confirmed by an ANCOVA that showed no difference between the slopes that relate LGP and PLGP for the three years tested ($df = 2$, $F = 0.971$, $p < 0.3930$). The regression was weakest in 2006. This is likely attributable to absence of strong external factors to affect provisioning as discussed above.

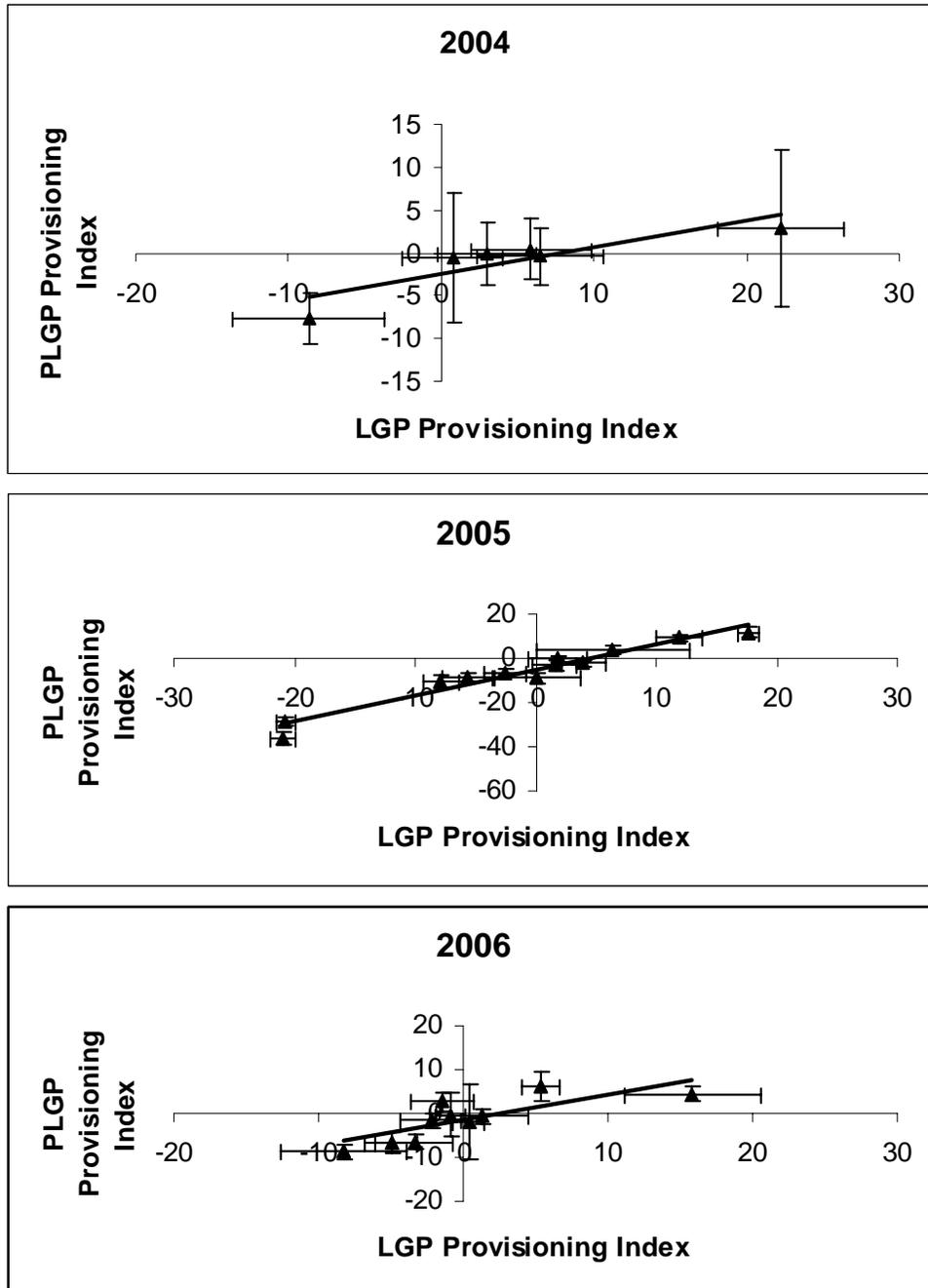
Being mean values, the PLGP and LGP provisioning indices have associated standard errors. I attempted to correct for this potential error by performing weighted least squares regression which gives more credence to data points with smaller SE. The r^2 value for the regression using weighted least squares regression ($r^2 = 0.820$) was similar to that of standard linear regression ($r^2 = 0.814$), suggesting that the associated SE had only a small influence on this relationship.

To determine the minimum number of chicks needed for suitable comparisons

Table 4.1. The relationship between PLGP and LGP provisioning indices using a different minimum number of chicks. All regressions with > 3 data points were significant ($p < 0.02$) with $r^2 > 0.57$. Asterisks indicates regressions with too few data points to generate values.

	All years	2004	2005	2006
Min. 10 chicks				
r^2	0.81	0.88	0.95	0.57
N	28	5	12	11
P	<0.001	<0.017	<0.001	<0.007
15 chicks				
r^2	0.85	0	0.95	0.63
N	25	25	10	12
P	<0.001	<0.986	<0.001	<0.01
20 chicks				
r^2	0.847	*	0.978	0.54
N	18	2	8	8
P	<0.001	*	<0.001	<0.038
25 chicks				
r^2	0.63	*	0.981	0.742
N	19	1	7	7
P	0.001	*	<0.001	<0.013

Figure 4.2. The daily mean Post Linear Growth Phase and Linear Growth Phase provisioning indices (\pm SE) on the same day in 2004-2006. Days with <10 chicks were excluded from the analysis. The regression equations and statistics (2004 PLGP = $0.3103LGP - 2.4904$, $r^2 = 0.88$, $p < 0.017$; 2005: $PLGP = 1.1713LGP - 5.2595$, $r^2 = 0.95$, $p < 0.001$; 2006: $PLGP = 0.5841LGP - 1.3815$, $r^2 = 0.57$, $p < 0.007$).



in both the PLGP and LGP, I performed the same regressions with a different minimum number of chicks with consecutive measurements in both the LGP and PLGP for a given day (Table 4.1). The desire for maximal sample size must be balanced by the fact that low sample sizes are often the only available data. For instance, hatching is fairly synchronous at Cooper Island; therefore the number of chicks at different ages (i.e. LGP vs. PLGP) is comparatively small. My results support the theoretical dictates of the accuracy advantage of larger sample sizes. With larger minimum numbers of chicks, a tighter relationship between mass changes in the PLGP and the LGP were observed (Table 4.1). Overall, the increasing strength of the regression with increasing specificity of the data points supports the hypothesis that changes in mass for PLGP and LGP chicks are driven by a common factor.

When data points from all years were pooled, the relationship between the PLGP versus LGP provisioning indices was significant at each minimum number of chicks, but the strength of the regression did not increase (Table 4.1). The significant relationship for aggregated years exists because each year's relationship is linear with a slope relatively close to one and an intercept close to zero (Figure 4.2). The declining r^2 values with higher minimum numbers of chicks (Table 4.1) indicate that there are intrinsically different equations describing the LGP versus PLGP relationship in different years even if the equations are somewhat similar.

4.4 Discussion:

Through a thorough investigation of the existing methods of measuring provisioning, I have exposed some shortcomings in the prevailing LGP model.

Specifically, the mean seasonal provisioning index in both the LGP and PLGP was susceptible to short-term deviations. Therefore, measurements taken on one or a few dates may not be representative of the season. The daily instability, however, suggests that chick mass is a useful indicator of short-term variation in provisioning quality. This newly developed method could be easily and inexpensively performed to measure fine-scale changes in chick-provisioning. For instance, the daily variation could be used to quantify the impact of a number of external factors that effect provisioning including environmental conditions, the presence of kleptoparasites and/or predators, and intensive/prolonged human disturbance (see Chapter 5). In addition, given the highly correlated relationship of LGP and PLGP provisioning indices on the same days in all years of this study, the previously ignored Post-Linear Growth Phase of nestling growth appears to be viable for monitoring provisioning quality, using the developed methodology herein. It also appears that a minimum sample of 10 chicks is required to use the developed methodology; however, larger sample sizes would be preferable if available.

My results also hint at the possibility of an ideal LGP growth rate for Black Guillemots in Arctic regions. The similarity between the 2006 and the abridged 2005 seasonal LGP means implies the possibility that ~15 g/d may be close to the ideal growth rate for a colony with environmental constraints similar to those on Cooper Island (~70 °N). This is supported by data from other Black Guillemot chick studies. Black Guillemots on Mousa in the Shetland Islands (~60 °N) grew at a rate of 15.7 g/d in 1983 and 18.0 g/d in 1984 according to the somewhat less exact method of fitting a tangent to the linear curve by eye (Ricklefs 1967; Ewins 1992). My application of this technique to

Cairns's southern Quebec (~50 °N) data in 1977 yielded a LGP growth rate of ~15 g/d (Cairns 1981). The repetition of the 15 g/d figure may indicate its intrinsic strength.

Minimum number of chicks

The method outlined in this chapter is robust to changes in the threshold number of chicks in the PLGP and LGP on the same date required to be included in the regression. Unsurprisingly, when the minimum number of chicks in both the LGP and PLGP is high (e.g. 25), some years have only one or two data points which makes regression analysis impossible (Table 1). This trend is counterbalanced by the logical conclusion that larger threshold values create more accurate mean values. Consequently, when there are sufficient days with large threshold chick numbers, the r^2 values tend to increase because the data points are less affected by stochasticity. When trying to calculate the linear relationship for a given year, it seems that choosing the highest threshold chick number with sufficient data points will yield the most accurate relationship. Pooling the data from all years in an attempt to form a universal linear relationship produced significant relationships but is not necessarily a productive venture. The slopes of the individual year regressions are quite similar, but the overall regression will be affected by differences in sample size between years. Years with more data points will have more effect.

Post-Linear Growth Phase

At a basic theoretical level, my findings demonstrate that there is regularity to the PLGP growth curve when the colony is viewed as an aggregate. My findings also

demonstrate the utility of fine-scale (daily) chick mass measurements as indicators of some factor common to chicks (most likely provisioning).

How to quantify chick growth has been an area of much debate (Walford 1946; Ricklefs 1967; Konarzewski and Taylor 1989). There was a study that fitted Richards growth curves to the majority of the curve and a nearly linear polynomial function to the final mass recession of Dovekies (Konarzewski and Taylor 1989). They calculated an anomaly by subtracting the mass from the colony-wide average mass at a given age. Both of these metrics had significant relationships with wind speed, which indicates some form of regularity in older chicks; however, there was no suggestion of correlating the two metrics. I attempted to use prescriptive mass instead of mass change early in my work with guillemots and found no regularity between prescriptive-mass-derived LGP and PLGP anomalies.

Given the widespread use of the seasonal daily mean of the Linear Growth Phase as an indicator of provisioning, these findings may have applications beyond the immediate field of seabird biology. The linear nature of the relationship between LGP and PLGP provisioning indices allowed PLGP anomalies to be converted to the same scale as LGP anomalies. This created as much as 150 % more days that are monitored by a reliably large sample of chicks in a given breeding season. Therefore, comparisons are possible within and among breeding seasons to measure seasonal alterations in the level of provisioning during parts of the breeding season which were previously eliminated from analysis due to a few late breeders. This technique has exciting possible applications for monitoring using a wide spectrum of future and archived chick mass data.

The significant relationship between LGP and PLGP provisioning indices in all three years indicates a consistent response using daily PLGP mass changes which has never before been documented. It also indicates a persistent, non-random relationship between the mass change of LGP and PLGP chicks on any given date. This finding extends the utility of chick mass as a viable method for measuring provisioning effort.

It is worth noting theoretically, that the predictive curve for both the LGP and PLGP curve are based on the daily mass change which mathematically is the instantaneous rate of change of the mass curve, also known as the first derivative. In the LGP, our predictive curve is the first derivative of a straight line, hence a common value. The PLGP mass curve is an approximate parabola and, consequently, the predictive mass change curve is a straight line with a slope (which was confirmed experimentally in these analyses). This theoretical relationship indicates the possibility of a mathematical unity between the PLGP and the LGP. This makes sense intuitively because of the unlikelihood of there being a biologically programmed LGP which lasts an exact number of days. The observed linear growth is more likely a byproduct of internal controls which may be applied for varying lengths of time depending on conditions. Ultimately it may be possible to integrate the entire growth curve as a higher order function and use deviations from that derivative to indicate daily provisioning rather than having to generate two separate curves, link them by regression and then convert them using the regression slope.

In conclusion, the discovery of mathematical regularity within the PLGP and the high degree of daily correlation between mass changes in LGP and PLGP are exciting theoretical breakthroughs with far-ranging applications. The regularity of the PLGP

greatly increases the window for using seabirds to monitor parental provisioning of chicks and, thus, potential changes in the marine ecosystem. The tight correlation between the provisioning indices of the PLGP and LGP implies common forcing factors for these changes, such as changes in prey availability. The establishment of this relationship allows for the use of fine-scale (daily) mass changes of easily-accessed chicks as monitors for the foraging conditions of parents without the potentially behavior-altering effects of loggers. This is critical, as quantifying the quality of foraging conditions has been one of the most persistent problems in seabird biology and further suggests that these birds may be useful indicators of the marine environment during the breeding season.

Chapter 5: The Effect of Weather on Provisioning

5.1 Introduction:

What seabirds do at sea has been a topic of great interest and comparatively little insight (Sealy 1990). The window for studying them at the colony is small and it is nearly impossible to follow them out to sea. The traditional method for using seabirds to indicate the marine environment is to record colony-based measures, such as chick mass (Ricklefs et al. 1984; Cairns 1987a; Bertram et al. 2002). Chick mass is not a direct measure of provisioning effort/prey availability; therefore, many researchers have begun to employ other new techniques in an attempt to quantify adult interactions with their environment more accurately. A number of technologically advanced techniques have surfaced recently. Doubly-labeled water, bird-borne data loggers, and radio transmitters have generated insights into where and how the birds spend their time at sea (Falk et al. 2000; Dall'Antonia et al. 2001; Tremblay et al. 2003; Litzow and Piatt 2003; Litzow et al. 2004; Jodice et al. 2006). These techniques, however, are expensive and can suffer from alterations from natural behaviour (Wanless et al. 1988; Croll et al. 1991b; Zador and Piatt 1999; Davoren 2000; Litzow and Piatt 2003; Hamel et al. 2004).

Despite being a coarse and somewhat old-fashioned method, chick mass retains some definite advantages. The invasiveness of chick-mass-based studies on the parents is fundamentally nil, and the disturbance window for the chicks is less than 5 min/d. Chick mass studies are significantly cheaper than logger-based data. Colony-based methods also allow for a comparatively large sample size relative to logger-based methods which allows for a more global colonial picture and eliminate skewed conclusions that might

arise from small, non-representative samples (Coulson 1968; Coulson and Horobin 1976; Golet et al. 2000).

In this study, I revisit chick mass with the hope of generating insights fine time-scale. I attacked this problem theoretically in Chapter 4 by devising a chick-mass-derived metric with fine-scale resolution for determining daily differences in parental provisioning effort, defined as the provisioning index (PI). I deploy the PI in this investigation to understand the effect of external environmental factors, including wind speed and ambient temperature, on the foraging and provisioning effort of Black Guillemot parents and, consequently, on the daily weight gain of chicks.

This investigation is important as the body of work on the effects of fine-scale environmental variation on seabirds is slim. For instance, there appears to be only one study which employs doubly-labeled water to determine that higher winds force alcid to work harder in flight (Furness and Bryant 1996). There is a body work correlating environmental factors like wind speed and temperature with different measures of provisioning (Dunn 1975; Birkhead 1976; Taylor 1983; Konarzewski and Taylor 1989). Only a pair concentrate on Auks (Birkhead 1976; Konarzewski and Taylor 1989). Of those neither looks at daily effects on chicks.

In addition, it is difficult to generate rules about the effect of temperature on chicks. Changes in ambient temperature may alter the energetic requirements and/or growth of nestlings (Murphy 1985; Jorgensen and Blix 1985; Konarzewski and Taylor 1989; Weathers and Sullivan 1991; Hodum and Weathers 2003). At northern latitudes, cooler temperatures harm the growth of some birds such as Willow Ptarmigans (*Lagopus l. lagopus*) (Jorgensen and Blix 1985) while temperature has no effect on other species,

such as the Dovekie (*Alle alle*) (Konarzewski and Taylor 1989). Among temperate altricial chicks, the effect is unclear. Cooler temperatures benefit Eastern Kingbird (*Tyrannus tyrannus*) chicks; however, warmer temperatures benefit Yellow-eyed Juncos (*Junco phaeonotus*) (Weathers and Sullivan 1991).

5.2 Methods:

Chick mass and age data for Black Guillemots were collected at the Cooper Island colony in 2004, 2005 and 2006, as outlined in Chapter 4. The daily Linear Growth Phase (LGP) and Post-Linear Growth Phase (PLGP) provisioning indices (PIs) were also calculated following the previously outlined protocols. I created a seasonal PI from the LGP and PLGP indices by converting daily PLGP indices to LGP-scale values by using the linear regression equation between daily LGP and PLGP indices with >10 chicks. On days when PIs existed for both the LGP and PLGP, I selected the index derived from the larger sample size as the value in the seasonal PI. Using the LGP and PLGP in concert to indicate changes in provisioning was discussed in Chapter 4 as one of the primary benefits of the strong correlation between daily LGP and PLGP PI values.

Daily environmental data were extracted from local climatological datasheets for Barrow, Alaska. These data are available for free to IP addresses in the USA from the National Climatic Data Center (NCDC). As it is important to avoid “fishing” when looking for explanatory variables, I narrowed down the available variables *a priori* to those that I had reason to believe might influence prey availability and, thus, provisioning. During 2005, there was a decline in provisioning as well as a shift in prey species coincident with strong winds from the southwest. In addition, previous research

indicates that strong winds make foraging difficult for other pursuit-diving birds (Furness and Bryant 1996). Therefore, I examined the influence of wind speed and direction on provisioning. Daily anomalies were calculated by adding or subtracting the daily mean from the mean of all days in which there was a provisioning index. I created a negative wind speed anomaly ('wind speed anomaly') which subtracts the daily mean wind speed from the seasonal mean. This creates negative values for days with strong winds. I did this to minimize confusion and changes of sign because I anticipated provisioning declines to be associated with wind speed increases (Furness and Bryant 1996). Adding or subtracting a constant (as I have done to create the wind speed anomaly) will not affect the overall significance of any correlations. To avoid redundancy, I tested the relationship between two pairs of variables: maximum wind speed versus mean wind speed and maximum temperature versus mean temperature.

I also examined the influence of ambient temperature on the PI, owing to the influence of nest temperature on chick metabolism. To do this, I examined the relationship between the temperature of a given day and chick mass change on that same day or the next one (as seen through the PI).

As PIs are derived from measurements of chick mass (see Chapter 4), it is important to control the time of chick measurement on the accuracy of the PI's representation of that day. I repeated my environmental correlate tests with the independent variables offset one day from the dependant ones to determine if the wind speed on one day affects the PI on the next day. This would reveal whether environmental variation had a time-lagged influence on chick mass changes.

I performed single variable linear modeling for my chosen variables by combining data from 2004, 2005, and 2006. I performed these statistical manipulations using R 2.4.1. To avoid type I errors, I used a Bonferroni correction to lower my α -value appropriately ($n_{\text{tests}} = 6$, $\alpha = 0.05$, $p < 0.0083$). I performed the same tests on the data subsetted *post hoc* by year to investigate the role of individual years in shaping the relationships as well as the universality of the results. I eliminated one variable “mean temperature plus one day” from the seasonal tests because there was no evidence in the tests when all years were pooled that it had any effect on provisioning ($n_{\text{tests}} = 5$, $\alpha = 0.05$, $p < 0.01$).

5.3 Results:

Interannual Relationships

There were strong correlations within categories of wind speed and temperature when all years were pooled. Daily maximum wind speed and daily mean wind speed were significantly correlated ($n = 112$, $r^2 = 0.7804$, $t = 19.948$, $p < 0.0001$). Mean daily temperature was also significantly correlated with maximum daily temperature ($n = 114$, $r^2 = 0.9398$, $t = 42.186$, $p < 0.0001$).

When all the data for 2004, 2005, and 2006 were pooled, several environmental factors had a significant relationship with provisioning, with wind speed being the most pronounced (Table 5.1). Wind speed regardless of direction (as expressed through the “mean wind anomaly”) was associated with lower PIs on the same day according to the PLGP and seasonal PIs (Table 5.1).

Table 5.1. The linear model results for the relationship between a series of environmental variables and provisioning index for 2004, 2005 and 2006 combined. Bolded P-values are significant with the Bonferroni correction $P < 0.0083$.

Dependant Var.	Independent Variable	Estimate	df	T	p	r²
LGP	mean wind speed anomaly	0.7372	55	2.327	0.0238	0.09112
	mean temperature	0.2106	55	0.82	0.415	
	mean wind speed anomaly (southwest only)	1.5574	14	1.876	0.0833	
	mean wind speed anomaly +1d	1.4397	55	5.103	4.45E-06	0.3253
	mean wind speed anomaly (southwest only) +1d	2.5621	14	4.239	0.000966	0.5803
	mean temperature +1d	0.0498	55	0.312	0.757	
PLGP	mean wind speed anomaly	1.2345	76	3.216	0.00192	0.1212
	mean temperature	0.0897	76	0.446	0.657	
	mean wind speed anomaly (southwest only)	2.234	15	2.205	0.0447	0.1992
	mean wind speed anomaly +1d	0.4814	76	1.184	0.24	
	mean wind speed anomaly (southwest only) +1d	2.6146	17	4.106	0.000827	0.513
	mean temperature +1d	-0.0528	75	-0.277	0.782	
Seasonal (LGP/PLGP)	mean wind speed anomaly	0.9097	103	3.261	0.00151	0.08444
	mean temperature	0.3055	103	2.022	0.0458	0.03905
	mean wind speed anomaly (southwest only)	1.3182	20	1.903	0.0723	0.1601
	mean wind speed anomaly +1d	0.6828	103	2.321	0.0223	0.07305
	mean wind speed anomaly (southwest only) +1d	2.315	20	4.178	0.00051	0.4789
	mean temperature +1d	0.1218	102	0.817	0.416	

The wind speed on one day also had an impact on the PI on the next day (“...+1d”). When the wind was stronger, provisioning was diminished, as seen by the significant positive relationship between the mean wind anomaly plus 1 day and the LGP PI (Table 5.1).

In addition to the general speed of the wind, winds blowing from southwest (SW) (from Continental Alaska out into the Beaufort Sea) had a particularly strong impact on provisioning; when there were SW winds, provisioning was negatively influenced. Increased SW wind speed resulted in a decrease in PI for PLGP chicks (Table 5.1). Provisioning also decreased the day after strong SW winds, as shown by significant relationships between the LGP, PLGP and seasonal PI on the days following SW winds (Table 5.1). The strength of the previous day’s winds when from the SW had by far the strongest power to explain the variation in the provisioning index (~50% for LGP, PLGP, and seasonal). For the seasonal PI, SW wind speed had an order of magnitude more explanatory power than any other variable tested. The difference is less stark between SW wind speeds and other environmental variables for LPG and PLGP due to higher r^2 values of other environmental variables like overall wind speed (Table 5.1).

Mean temperature had no significant effect on the PI overall. There was also no effect of temperature on the following day’s chick mass changes.

Seasonal Relationships

The intra-annual relationships between provisioning and environmental variables reveal that the majority of the correlations when years were pooled were largely influenced by very strong relationships in 2005.

In 2004, there were no significant relationships between PIs and wind speed or direction. Temperature had a significant positive effect on the PI of LGP chicks; however, temperature had no effect on older chicks (Table 5.2).

In 2005, I saw the strongest evidence of PI variation explained by environmental variables. The strength of the previous day's wind was associated with a significant decrease in all three PIs (Table 5.3). A similarly significant inverse relationship existed between the wind speed on days with SW winds and all three PIs. The speed of SW winds had a stronger effect on provisioning than general wind speed (Table 5.3). Depending on the PI used, the amount of variation explained by the SW linear model was 150 - 500 % more than the previous day's general wind speed anomaly. There does appear to be some relationship between wind speed and provisioning on the same day, but none of my metrics showed same-day wind speed to have a significant effect on provisioning (Table 5.3).

In 2006, there was a complete absence of significant correlations between provisioning and the environmental variables analyzed (Table 5.4). During this year, there was also a dearth of days with southwest winds ($n = 2$), 400 % less than 2004 or 2005.

5.4 Discussion:

Wind speed appeared to have the highest influence on provisioning in Black Guillemots. High wind speeds primarily were associated with decreased provisioning on the following day, although high wind speed was also associated with declines in provisioning on the same day. Relationships were particularly strong when only winds

Table 5.2. The linear model results for the relationship between a series of environmental variables and provisioning for 2004. Bolded P-values are significant with the Bonferroni correction $P < 0.01$.

Dependant Var.	Independent Variable	Estimate	df	t	p	r²
LGP	mean wind speed anomaly	1.4345	12	2.181	0.0518	0.4779
	mean temperature	1.0491	12	3.173	0.00887	
	mean wind speed anomaly (southwest only)	2.003	5	1.737	0.157	
	mean wind speed anomaly +1d	0.9513	12	1.322	0.21	
	mean wind speed anomaly (southwest only) +1d	0.5732	5	0.407	0.705	
PLGP	mean wind speed anomaly	2.0103	22	2.47	0.0222	0.2251
	mean temperature	-0.01627	22	-0.028	0.978	
	mean wind speed anomaly (southwest only)	1.319	6	0.793	0.464	
	mean wind speed anomaly +1d	0.1909	22	0.209	0.837	
	mean wind speed anomaly (southwest only) +1d	1.0073	7	0.671	0.527	
Seasonal (LGP/PLGP)	mean wind speed anomaly	1.5132	29	2.603	0.0146	0.1948
	mean temperature	0.522	29	1.32	0.198	
	mean wind speed anomaly (southwest only)	1.504	8	1.176	0.2782	
	mean wind speed anomaly +1d	0.8699	29	1.388	0.176	
	mean wind speed anomaly (southwest only) +1d	0.9918	8	0.666	0.527	

Table 5.3. The linear model results for the relationship between a series of environmental variables and provisioning for 2005. Bolded P-values are significant with the Bonferroni correction $P < 0.01$.

Dependant Var.	Independent Variable	Estimate	df	t	p	r²
LGP	mean wind speed anomaly	1.0244	20	1.749	0.0964	
	mean temperature	-0.004968	20	-0.017	0.987	
	mean wind speed anomaly (southwest only)	1.203	6	0.952	0.385	
	mean wind speed anomaly +1d	2.1801	20	5.351	3.65E-05	0.6012
	mean wind speed anomaly (southwest only) +1d	3.2354	6	8.983	0.000285	0.9417
PLGP	mean wind speed anomaly	1.2599	28	2.394	0.0239	0.1751
	mean temperature	-0.2929	28	-1.065	0.296	
	mean wind speed anomaly (southwest only)	2.311	8	1.895	0.107	
	mean wind speed anomaly +1d	1.361	28	2.816	0.00897	0.227
	mean wind speed anomaly (southwest only) +1d	3.3451	8	7.975	9.30E-05	0.9009
Seasonal (LGP/PLGP)	mean wind speed anomaly	0.8109	36	2.105	0.0425	0.1124
	mean temperature	-0.1333	36	-0.646	0.522	
	mean wind speed anomaly (southwest only)	0.9072	9	0.991	0.351	
	mean wind speed anomaly +1d	1.1421	36	3.136	0.00346	0.2194
	mean wind speed anomaly (southwest only) +1d	2.8787	9	8.143	3.84E-05	0.8923

Table 5.4. The linear model results for the relationship between a series of environmental variables and provisioning for 2006. Bolded P-values are significant with the Bonferroni correction $P < 0.01$.

Dependant Var.	Independent Variable	Estimate	df	t	p	r²
LGP	mean wind speed anomaly	0.1025	21	0.253	0.803	
	mean temperature	-0.2641	21	-0.984	0.337	
	mean wind speed anomaly (southwest only)	0.3649	2	0.216	0.864	
	mean wind speed anomaly +1d	0.422	21	0.998	0.33	
	mean wind speed anomaly (southwest only) +1d	-1.3201	2	-1.857	0.314	
PLGP	mean wind speed anomaly	-0.6985	25	-1.339	0.19314	
	mean temperature	0.396	25	0.949	0.352	
	mean wind speed anomaly (southwest only)	NA	0	NA	NA	
	mean wind speed anomaly +1d	-0.4124	25	-0.776	0.4454	
	mean wind speed anomaly (southwest only) +1d	NA	0	NA	NA	
Seasonal (LGP/PLGP)	mean wind speed anomaly	-0.1797	35	-0.442	0.6614	
	mean temperature	0.502	35	1.791	0.0822	
	mean wind speed anomaly (southwest only)	0.3649	2	0.216	0.864	
	mean wind speed anomaly +1d	0.06264	35	0.152	0.8804	
	mean wind speed anomaly (southwest only) +1d	-1.3201	2	-1.857	0.314	

from the southwest were included, primarily owing to the particularly strong correlation between southwest winds and provisioning in 2005. In addition, there was slight evidence that chicks gained more mass when daily temperature was higher; however, this relationship was not strong nor observed in every year. It is also important to note that the strong correlations within categories of environmental variables (e.g., wind speed) supported the testing of only one derivative of these variables as an explanatory variable for variation in PI. Redundant testing of cross-correlated variables makes the Bonferroni correction too conservative.

Influence of Wind Speed and Direction on Provisioning

This work is among the first clear demonstrations of the effect of wind speed on daily chick growth of piscivorous auks and the first to explore the impact of wind direction. An initial study claimed that sea roughness, but not wind speed affected delivery rate by parents of the piscivorous, pursuit diving Common Murres (*Uria aalge*) (Birkhead 1976). The planktivorous Dovekie with longer foraging trips had lower chick growth rates and higher adult FMR associated with higher wind speeds (Konarzewski and Taylor 1989). My suite of results indicates that wind affects parental provisioning for inshore feeders as well. It takes the Furness & Bryant (1996) relationship between wind speed and alcid FMR a step further by showing that the wind also affects the mass of chicks who are dependent on those parents for provisioning. This result suggests the effect is quite strong, otherwise the parents would compensate for the reduced efficiency with extended chick provisioning (Cairns 1987a; Burger and Piatt 1990; Litzow and Piatt 2003).

This general relationship between wind speed and provisioning seems logical. Alcids are not unusually strong fliers due to their high wing load (Cody 1973). This causes high winds to make them work harder (Furness and Bryant 1996). This alone may be enough to alter parental behavior, such as changes in foraging strategies or reduced foraging effort. It is also possible that the Black Guillemot's method of prey loading (crosswise in the bill) increases drag at the front end of the bird during flight where it has a disproportionate effect (Obrecht et al. 1998).

The sharing of the effects of wind speed on provisioning between the day of the wind and the following day is likely an artifact of the time of measurement and changes in the circadian patterns of the birds. Colony attendance and provisioning patterns vary depending on the light regime (G. Divoky & B. Harter unpublished data). The time when feeding begins on any given day varies depending upon a number of factors, primarily changes in the daylight regime (G. Divoky unpublished data). The time of measurement also takes place over several hours (0800-1600). This probably allowed the majority of chicks to be measured before the effects of that day's weather on provisioning could be determined using chick mass, whereas the masses of those measured late in the day were influenced by environmentally-mediated changes in provisioning. For wind, which may affect prey delivery and potentially prey capture, the difference between same-day and previous-day effects is probably illusory. The sharing out of the effect between the PIs of two days may generate some type II error.

The high explanatory power of southwest winds on provisioning makes them a tempting topic for explanation. The mainland and barrier islands of the North Slope of Alaska are oriented from northwest to southeast at Cooper Island. Therefore, a

northeasterly departure from the colony would be the most efficient route to the deepening waters of the continental shelf. Birds returning with prey have been observed coming primarily from the northeast (B. Harter & G. Divoky unpublished data). Southwest winds may have a disproportionate effect based on this foraging direction. Black Guillemot parents will experience more drag when returning loaded with cumbersome prey than while flying out to forage. A loaded return directly into a strong wind may create multiplicative inefficiencies which reduce parental provisioning.

Another possible explanation exists for the disproportionate effect of SW winds on provisioning. In 2005, it was the strongest year for an environmental effect on provisioning particularly SW winds. The SW wind event in 2005 was accompanied by the disappearance of visible ice from the colony and a shift in prey species delivered. Continuous observation of nest sites during the wind event revealed no feeds at any of five nests watched for two hours. This is far below the mean of 0.42 ± 0.02 feeds/h/chick of the comparable 2006. Observations during the wind event showed parent birds returning Four-horned Sculpin and decapods as opposed to the > 95 % Arctic Cod fed previously. It is possible that the strong winds moved the ice and concomitantly the dense source of cod farther from the colony (Welch et al. 1993; Gradinger and Bluhm 2004). This may have caused the birds to shift to other, poorer-quality prey (Cairns 1984; Van Pelt et al. 1997; Lawson et al. 1998) (see Arctic Cod Chapter). The high wind/drag hypothesis also may explain the prey shift if cod was found farther from the colony, penalizing longer commutes between the colony and foraging grounds.

The movement of ice away from the colony could not be confirmed in this analysis. MODIS true-color composites were only available sporadically due to cloud

cover and no appropriately sensitive daily ice metric was available. This was the impetus for the investigation in Chapter 2. This work does not rule out the possibility of ice being a strong driver of provisioning within this system particularly on catastrophic provisioning days, but it does not appear to be the only one or to be driving most of the fine-scale daily variation seen in the PIs.

Influence of Temperature on Chick Mass Gain

Ambient temperature appears to affect the Black Guillemot chicks on Cooper Island during certain periods but not others. Chick mass gain was only significantly higher for LGP chicks on warmer days in 2004. The wind relationships (SW and general) showed a pattern of sharing the effect between the day of and day after; however, no such pattern was evident for temperature. This seems to imply that the temperature is not sensitive to changes in the light and consequently the feeding regime. This could imply that it is ambient nest temperature that influences chick metabolism which is manifesting itself through chick mass as a change in provisioning.

Cooper Island guillemot chicks exist in a harsh environment far below their body temperature. They are covered only with down before they develop feathers. This shift during the chick period from down to feathers may explain the positive effect of temperature on younger chicks but not older ones. The significant effect of temperature in 2004 alone may be explained by comparing the temperatures of different years. The mean temperature for the chick rearing period of 2004 was 6.8° which was a + 3.1 °C departure from the 30-year norm. In 2005, it was only + 1.8 °C above the 30-year mean, and 2006 was characterized by a - 1.3 °C deviation. My analysis of chick mass changes during

short term (1-4 hr) natural starvation in 2006 yielded no significant relationship between ambient temperature and rate of mass loss ($n = 106$, $t = 1.37961$, $p = 0.170665$); however, there was no relationship between PI and ambient temperature in 2006 either. If one regards the temperature results as robust (as opposed to spurious), the result undermines the validity of the PI as an analytical tool (see Chapter 4). Nest temperature would constitute a non-provisioning-based factor which affected the PI. The results are not robust enough to prove this conclusively; however, it does warrant further investigation.

The temperature results are as thoroughly inconclusive as the extant literature. It is plausible to see my results in light of Jorgensen and Blix (1985), which would imply that warmer temperatures aid birds in cold climates. It is also plausible to see my results as corroborating Konarzewski & Taylor's (1989) findings that ambient temperature had no effect on Dovekie chick growth. If ambient temperature does have an effect, it is a very slight one as the low r^2 values attest. It may only be noticeable in remarkable anomalous temperature years if at all.

In conclusion, a strong wind speed has a significant negative influence on chick mass gain. This appears to be the first demonstration of tangible effects of ambient wind speed on chick mass. In 2005, there were particularly strong inverse relationships between the speed of the wind and the mass gain of chicks. These discoveries could be attributable to aerodynamic effects to a time lag from shifting search image. The ability to find significant correlations between the derived provisioning indices and environmental factors strengthens the validity of this metric as a measuring tool and shows its utility simultaneously.

Chapter 6: General Conclusion

This study functions as a lesson in the complexity of ecological systems. At the core of the scientific method is the conceptual belief that if you hold all variables except one constant, then you can understand the changes of that one variable. Ecology is more complicated than that, because ecologists are not blessed with laboratories. Our systems involve a web of interacting variables. To determine real changes, ecologists must somehow treat all of the variables other than the ones of interest as behaving with some form of regularity rather than as fixed. The complexity of this assumption varies depending on current knowledge and the specificity necessary to understand the prescribed goal. Whether in the case of actual mathematical modeling in which variables must be assigned properties to simulate their actual effect on the outcome of interest, or something as simple as trying to calculate the daily caloric consumption of a Black Guillemot chick, ecologists need to know a lot about the systems they study. This is difficult in the field and particularly in the Arctic.

I have added notably to the conceptual methodologies, pragmatic tools, general understanding of the near-shore marine Arctic ecosystem, particularly the top predator seabirds. This thesis performed one of the first comprehensive laboratory analyses of Arctic Cod. I enumerated the specific linear relationship between body size and energy density. This will allow for more efficient estimates of the energetic consumption of a variety of marine top predators that rely on Arctic Cod. I also synthesized the existing body of knowledge about the energetics of Arctic Cod as a prey item to building basic science and in the hope of verifying or refuting the existence of region differences within

the species. My work with Arctic Cod should be a building block for other Arctic biologists.

My work with small pieces of ice in the near-shore Beaufort Sea and their biological significance as foraging habitat should allow for refined understanding of the foraging of top predators in the marine ecosystem. I developed the idea that such small pieces were in the ocean despite an inability to detect them using traditional satellite methods. I established the existence of these small (subpixel) pieces of ice using band ratioing of remotely sensed images. A ground-truthing boat trip to a small piece of ice verified that the guillemots were using it as foraging habitat and that it supported a rich planktofauna. The further investigation of this habitat could yield significant increases in understanding about the biology of Arctic Cod, and the assemblage of top predators and fish in time and space ('biological hotspots').

The development of a regular metric for sensing daily changes in provisioning for both the Linear Growth Phase and Post-Linear Growth Phase is an exciting development both theoretically and practically. At a theoretical level, finding regularity within the highly irregular Post-Linear Growth Phase was exciting. The close, persistent linkage in scale and time between changes in the provisioning index values of both phases supported the contention that my predictive curve anomaly methodology was effectively isolating changes in provisioning from the other, stochastic factors that effect daily individual mass. Ultimately, that linkage also opens the door to a higher-order function from which to generate anomalies rather than needing two functions.

At a practical level, the method allows for the establishment of fine-scale monitoring of the effect of external factors such as weather conditions, predators, and

human disturbance using the simple and easily acquired parameter of chick mass. The inclusion of the Post-Linear Growth Phase extends the window for monitoring 150 % compared to simple Linear Growth Phase work. This methodology is simple, and can be used on new or archival data. It presents an exciting opportunity to discover more about the interactions of birds and their environment.

The application of these techniques to available weather data allowed me to gain insight into the effects of wind speed, wind direction, and ambient temperature on chick growth. Wind speed was a significant predictor of provisioning which corroborates previous findings. Wind direction was also very important for this colony. These findings may allow insights towards determining the relative importance of different foraging constraints (such as flight in high winds or prey-loaded flight). Ambient temperature work yielded some curious results that warrant further investigation into understanding how Arctic animals experience the Arctic.

Climate change has placed a sense of immediacy into our ability to predict future ecosystem change (particularly the Arctic) where some environmental parameters are changing. This is impossible without an in-depth understanding of all the factors involved: the biology of the relevant species, the power (and shortcomings) of our current observational tools, as well as our best understanding of the top predators which are so often of interest.

Seabird biologists continually struggle to justify our existence. As with much macrobiology, seabird biology is squeezed between an endangered species rock, and a theoretical hard place. It is difficult to answer basic ecological questions about seabirds because we have access to them for such a short period of their annual cycle during the

breeding season. At the same time, within the myriad species of our planet, many are under severe population pressures that would seem to move them to the front of the descriptive biology queue. Therefore, unless we are gaining insight into the habits of endangered seabirds, other work can be classified as tangential, glorified naturalism.

Using seabirds as indicators of marine ecosystems allows a unique window into the ocean environments that are so difficult to study and comprehend. This in my view is a valuable way out of the trap I have previously described. Although not currently threatened, and not as easily manipulated as the *Drosophila* or the zebrafish, seabirds can provide a rough guide to the status of ocean ecosystems easily and cheaply compared to dedicated, at-sea work.

Appendix I: Literature Cited

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