ATLANTIC PUFFIN RESPONSE TO CHANGES IN CAPELIN ABUNDANCE IN NEWFOUNDLAND AND LABRADOR: INTER-COLONY AND INTER-DECADE COMPARISON

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ATLANTIC PUFFIN RESPONSE TO CHANGES IN CAPELIN ABUNDANCE IN NEWFOUNDLAND AND LABRADOR:

AN INTER-COLONY AND INTER-DECADE COMPARISON

by

Shauna M. Baillie

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ABSTRACT

I compared Atlantic Puffin chick diet and reproductive performance at the Gannet Islands, Labrador during 1996-98 to that recorded 1) in a similar study undertaken during 1981-1983 at the Gannet Islands prior to a decline in capelin abundance, and 2) at Gull Island, Witless Bay, Newfoundland where capelin were abundant. I hypothesized that chick diet quality and breeding parameters would be dramatically lower at the Gannet Islands in the 1990s. During 1996-1998 at the Gannet Islands, puffin chick diet biomass comprised 3 to 25 % capelin and only in 1996 was breeding success dramatically lower (by 40 %) than any other study colony or year. Chick mass growth rate, and peak and fledging mass were lower in the 1990s than 1980s yet similar to that at Gull Island. Sandlance was the main alternate prey and was significantly higher in lipid, protein and energy density than capelin at both colonies. Atlantic Puffins exhibited behavioural plasticity with respect to foraging and reproduction in a temporally and spatially highly variable environment.

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CHAPTER ONE

GENERAL INTRODUCTION

Behavioural responses of seabirds to environmental change have been found to occur at different temporal and spatial scales for parameters such as population size, clutch size, breeding phenology, chick growth, diet and feeding rates (Schneider and Hunt 1984, Cairns 1987, Montevecchi 1993). Though difficult to predict, changes in measured seabird parameters have allowed researchers to infer causal links between variation in the marine environment and prey base (Ainley and Boekelheide 1983, MacCall 1984, Harris and Hislop 1978, Haney 1991, Montevecchi and Berruti 1991, Cairns 1992, Monaghan 1996), inter-specific and intra-specific competition (Baird 1991, Bryant 1998), predation (Cairns 1985, Craik 1997, Russell and Montevecchi 1996), breeding habitat (Nettleship 1972) and human disturbance (Ollason and Dunnet 1980, Rodway and Montevecchi 1996).

This thesis is concerned with variation in prey base and how that effects breeding seabirds. In broad terms, the optimal foraging theory suggests that foraging animals should not travel further than necessary from the breeding colony to find their food (Cairns 1992). Despite being constrained to a central place during the breeding season, seabirds appear to have considerable capacity to buffer effects of changing food availability (Burger and Piatt 1990). However, as food supply decreases, birds may spend more time and effort foraging (Cairns 1992). Studies on long-lived seabirds lead us to expect that parents which reach the point where free time is exhausted will trade off current for future reproductive success, reproductive performance may detereorate or they may completely abandon breeding attempts because perceived risks to their survival are too great (Monaghan *et al.* 1989a, 1989b; Cairns 1992, Wernham and Bryant 1998). I set out to establish a food supply link to foraging behaviour and reproductive parameters of Atlantic Puffins *Fratercula arctica* in the Northwest Atlantic. My study began after the virtual evacuation of capelin *Mallotus villosus*, the apparent main prey of puffins in the Northwest Atlantic, from the southern Labrador coast (see Page 6). Complete breeding failure under these prey conditions was thought to be eminent, thus I anticipated being able to observe either the threshold where Atlantic Puffin trade off current for future reproductive success or how they buffer the effects of food stress. Originally, I sought to quantify Atlantic Puffin time-activity budget with electronic temperature logging devices (Stowaway Tidbit, Onset Computer Corporation) which produce unique a signature for each activity of flying, diving and resting on the water surface, on the colony slope and inside the nest burrow. Unfortunately, the temperature logging devices proved to have a greater effect on puffin behaviour than the food stress event as the devices were too heavy and bulky.

In recent decades prior to this thesis, puffin diet and reproductive success in Witless Bay, southeastern Newfoundland supposedly was not extremely variable. The proportion of capelin biomass in puffin nestling diet at Great Island, Witless Bay, for six of seven years between 1969 and 1984, ranged from 78 to 94 % capelin, 10 to 15 % sandlance *Ammodytes* spp. and the remainder was immature gadids or miscellaneous items (Nettleship 1972, 1991). Rodway and Montevecchi (1996) also found that Atlantic Puffins at Great Island, Witless Bay fed nestlings a diet of 83 % (by mass) capelin between 1992 and 1994. Alternate prey consisted of mainly sandlance 13 %, and the remainder was immature cod *Gadus* and *Boreogadus* spp. (< 5 %) and miscellaneous items. This low variability in prey harvest at Great Island over decades made it seem that puffins were preferentially selecting capelin and that they employed a nearly fixed foraging strategy. Much of the seabird research in Newfoundland was conducted in Witless Bay and the relationship between capelin and puffins was so strong apparently that Nettleship (1991) hypothesized that the distribution and abundance of capelin was homogeneous throughout the east coast of Newfoundland. However, capelin biomass estimates reported by Carscadden (1984) showed that capelin abundance in Witless Bay (NAFO subarea 3L) were uniquely high. In fact, capelin biomass estimates were higher in Witless Bay than estimates combined for eastern Newfoundland and southern Labrador, area 2J3K. To establish whether Atlantic Puffin diet and the distribution of capelin were homogeneous required further study of puffins and their prey at Newfoundland colonies other than those in Witless Bay.

In 1992-95, Russell (1999) found evidence from breeding Atlantic Puffins that contradicted the hypothesis that diets of piscivorous seabirds are homogeneous throughout eastern Newfoundland. Atlantic Puffin nestling diets at Baccalieu (subarea 3L), Small and Funk Islands (subarea 3K) located on the east coast of insular Newfoundland contained very different proportions of capelin depending on geographic location (Russell 1999). Russell (1999) found that breeding performance was similar in regions of high and low capelin availability because Atlantic Puffins were able to utilize alternate prey. At Small and Funk Islands, 0-group post-larval sandlance and larval 1-group capelin successfully replaced mature capelin as part of a prey suite including juvenile shannies, sculpins, herring, and white hake in addition to several species of small miscellaneous prey (Russell 1999). As was reported in other studies, Russell (1999) found that larval gadids were apparently selected against and had low dietary value (Barrett *et al.* 1987, Russell 1999, this document). Unlike studies in Witless Bay (Nettleship 1972, 1991; Rodway and Montevecchi 1996), Russell (1999) found high inter-annual variability in Atlantic Puffin chick diet as the norm. A study by Birkhead and Nettleship (1983, 1985) at the Gannet Islands, Labrador in the early 1980s showed that puffin chick diet included 17 % by mass capelin in 1981, 74 % in 1982 and 70 % in 1983. At the Gannet Islands, mature sandlance (64 % biomass) replaced capelin in 1981 with no evidence that Atlantic Puffin reproductive performance was inhibited or enhanced. Other prey taxa in the Gannet Islands Atlantic Puffin chick diet included Arctic Cod *Boreogadus saida*, larval sandlance, crustaceans and other unidentified small prey species (Birkhead and Nettleship 1985). Contrary to popular opinion and excepting the Witless Bay area, Atlantic Puffin prey assemblages actually exhibited high interannual variability between and among regions with no instances of breeding failure and puffins used alternate prey to rear young successfully. Atlantic Puffins in the Northwest Atlantic appear to resilient to prey variation with the cost likely expressed in foraging time and adult energy expenditure. There was one documented case in Witless Bay, Newfoundland in which the proportion of capelin fed to Atlantic Puffin chicks at Great Island from decreased from 80 – 100 % (by mass) in previous years to 10 % in 1981 and caused total breeding failure during that one year (Nettleship 1991). However, no concensus has been reached as to whether total breeding failure actually occurred. Extreme cases of breeding failure have been documented for seabird communities around the globe, for example guano birds in Peru (Duffy 1983) and Black Guillemots in the Black Sea (Bergman 1978). However, the only known instance of complete breeding failure of Atlantic Puffins occurred at Røst on the central Norwegian coast. This breeding failure was apparently directly related to a crash in the Atlantic-Scandian herring stocks (Anker-Nilssen and Rostad 1993).

A dramatic change in abundance of capelin before the onset of my study allowed me to test hypotheses on the resilience of puffins to a variable prey environment. Capelin, a small smelt, are known to be a principle prey of seabirds in low-arctic waters of the Northwest Atlantic (Brown and Nettleship 1984). Capelin were the object of a traditional Newfoundland inshore fishery for centuries and in 1971 an international offshore capelin fishery began off Newoundland waters (Nettleship 1991). As a commercially important fish resource, information on biomass, distribution and age class structure of capelin are studied in detail by the Canadian Department of Fisheries and Oceans (DFO). However, relatively little is known of non-commercially important pelagic forage fish such as sandlance. Capelin migrate from offshore banks of Newfoundland and Labrador to inshore coastal waters and beaches each spring to spawn (Nakashima 1992). The spawning aggregations consist of 3-5 year old fish (gravid females, spent females and mature males) mixed with immature or 1-group fish as well as young of the year 0-group fish. In ICNAF/NAFO subarea 3L, capelin from the Avalon stock spawn on beaches of the Avalon Penninsula, Newfoundland in June and July. This spawning aggregation coincides with the chick-rearing period of seabirds at the Witless Bay Ecological Reserve, southeast Newfoundland. Further north in southern Labrador (ICANF/NAFO subarea 2J), Stock A capelin typically migrate north along the beaches of south Labrador in late July and August and are availabile to seabirds provisioning chicks the Gannet Islands Ecological Reserve. Atlantic Puffins at both the southeastern Newfoundland and the south Labrador colonies typically fed chicks 60-80 % (by mass) capelin (Nettleship 1972, 1991; Birkhead and Nettleship 1985, Rodway and Montevecchi 1996). Then a dramatic change occurred in the spawning migration pattern of capelin in Labrador. During the late 1980s, capelin exhibited a population shift offshore and south to the Northeast Newfoundland Shelf (J. Anderson persoanl communication); capelin had ceased to spawn in Labrador in 1992. Thus, as far as we know, for at least five consequetive years at the Gannet Islands prior to my study, puffins were unable to access spawning aggregations of capelin during the breeding season.

To restate, the purpose of my study was to examine Atlantic Puffin breeding response to a depletion in prey source at the Gannet Islands, Labrador and determine whether or not they were able to effectively rear young using alternative prey. I compared Atlantic Puffin chick diet and growth, productivity and adult mass at the Gannet Islands, Labrador during 1996-98 to that in a previous study conducted by Birkhead and Nettleship (1985) in 1981, 1982 and 1983. Additionally, I conducted a simultaneous inter-colony comparison of puffin feeding and breeding parameters at Gull Island, Witless Bay, southeastern Newfoundland and the Gannet Islands, Labrador.

CHAPTER TWO

RESPONSE OF ATLANTIC PUFFINS TO A DECLINE IN CAPELIN ABUNDANCE AT THE GANNET ISLANDS, LABRADOR

Abstract

The chick-rearing period of Atlantic Puffins breeding at the Gannet Islands typically coincided with the occurrence of inshore spawning aggregations of capelin in south and central Labrador, Canada. During the late 1980s, capelin, the main prey of provisioning puffins, exhibited a population shift offshore and south, away from the seabird colonies. At the onset of my study in 1997, capelin apparently had not spawned in Labrador waters since 1992. Information from a previous study of Atlantic Puffin feeding and breeding ecology in 1981-83, made possible my comparison of Atlantic Puffin reproductive parameters before and during this movement of capelin from the Labrador coast.

At the Gannet Islands, Atlantic Puffins delivered 40 - 60 % (by mass) less capelin to their nestlings during 1996-98 than in 1982-83. Virtually no adult capelin appeared in the 1996 chick diet and 0-group and unscaled 1-group capelin did not occur in 1996-98. Capelin increased from 3 to 25 % of diet biomass from 1996 to 1998 partially due to an increasing proportion of larger individual fish. Puffin reproductive parameters were lowest in 1996 and highest in 1997. Adult capelin were smaller and post-larval sandlance

much larger in 1996-98 than in 1981-83. Proximate composition analyses showed that post-larval sandlance delivered to young puffins were higher in lipid content, protein and energy density than capelin. In 1996-98, median chick hatch was four days later and rate of mass gain, peak mass and fledge mass of chicks were significantly lower than those recorded during of the 1980s. During my study Atlantic Puffins did not experience a dramatic reduction in breeding parameters in response to changes in capelin abundance and puffins effectively reared young utilizing alternative prey. My study confirms the suggestion that Atlantic Puffins do not depend on abundant capelin for reproductive success.

2.1 Introduction

Avian marine predators prey on invertebrates and fish on their breeding (Cairns 1992, Montevecchi 1993) and over-wintering grounds (Elliot *et al.* 1990, Rowe *et al. in press*). During the summer months, foraging activity of breeding Atlantic Puffins *Fratercula arctica* in the Northwest Atlantic is constrained to areas within 100 km of their colonies. Breeding adults experience increased energetic demands as a consequence of the physiological stress of reproduction, elevated inter- and intra-specific competition, and the requirement to provision young as well as themselves (Erikstad *et al.* 1997). Therefore Atlantic Puffins must optimize energetic return to first, avoid placing themselves at risk of mortality and second, provide an adequate level of care to their young (Cairns 1992). Puffins provisioning chicks appear to specialize on prey of high lipid and energy content such as capelin *Mallotus villosus*, sandeel *Ammodytes marinus*, sprat *Sprattus sprattus* or herring *Clupea harengus* (Harris and Hislop 1978, Barrett and Furness 1990, Hislop *et al.* 1991, Harris and Bailey 1992, K. Amey pers. comm.). Nevertheless, nestlings often receive lesser quality miscellaneous prey such as larval gadids, squid or crustaceans in smaller proportions (Anker-Nilssen 1987, Gaston and Jones 1998). In the Northwest Atlantic, puffin breeding performance varies depending on prey and oceanographic conditions yet the conditions under which puffins decide it is no longer energetically feasible to rear young are not clearly delineated. Instances of complete breeding failure in Atlantic Puffins are extremely rare but on Rost, Norway, a contiguous period of reproductive failure over 22 years has been attributed to low spawning yields of preferred prey, herring, and the absence of suitable alternative prey (Anker-Nilssen 1987, Barrett *et al.* 1987, Barrett and Rikardsen 1992). In Witless Bay, Newfoundland the reproductive failure of puffins in 1981 was attributed to a large scale international capelin fishery (Nettleship 1991), however, no consensus on this hypothesis has been reached. Puffins in North Norway actually increased their intake of capelin after a decrease in the Barents Sea capelin stock by utilizing a separate capelin spawning stock (Barrett and Furness 1990, Barrett and Krasnov 1996). Capelin, a schooling migratory smelt, has been considered the preferred prey of chick-rearing puffins (Brown and Nettleship 1984, Gaston and Jones 1998) and central to food web energetics models in the Northwest Atlantic (Carscadden 1984). Brown and Nettleship (1984) opined that there is no alternative prey to capelin for marine predators as specialized as seabirds, and that up to a point their populations can remain stable but without capelin, breeding failure and adult mortality is inevitable. However, Russell (1999) showed that at several colonies in insular Newfoundland, puffins successfully reared nestlings on diets with a highly variable contribution of capelin.

Historically, a large component of Atlantic Puffin nestling diet at the Gannet Islands, Labrador consisted of capelin (Birkhead and Nettleship 1983, 1985). After an alleged cold water event in the late 1980s (J. Anderson pers. comm.), the capelin population shifted south and offshore beyond the summer foraging range of Atlantic

Puffins (Miller and Lilly 1991, Mann and Drinkwater 1994). This population shift was coincident with delayed arrival of spawning aggregations and then in 1992 capelin ceased to spawn off the south and central coast of Labrador (G. Rowes pers. comm.).

In order to investigate responses to changes in food supply, I quantified Atlantic Puffin chick diet, prey nutrient value, adult body mass, phenology, productivity and chick growth at the Gannet Islands in 1997 and 1998, and incorporated data collected from this colony by my colleagues in 1996. I had the opportunity to compare my results to those of a previous study at the same site conducted by T.R. Birkhead and D.N. Nettleship in 1981, 1982 and 1983 when capelin were plentiful (Birkhead and Nettleship 1985). This revisit to the Gannet Islands has permitted further investigation of the relationship between capelin and breeding puffins and provided insights about the role of alternative prey for this seabird species in Labrador. Based on, first, the magnitude of the decrease in capelin abundance and initial observations in 1996 when virtually no capelin occurred in Atlantic Puffin diets, and second, current hypotheses about this seabird species' capelin dependence, I predicted that Atlantic Puffins at the Gannet Islands would experience an extreme decrease in reproductive success or breeding failure.

2.2 Methods

2.2.1 Study site

The Gannet Islands, Labrador (53°56'N, 56°32'W) comprise a group of seven islands, five of which are located within 500 m of each other, GC1 - GC5 (Figure 2.1). The archipelago lies 35 km offshore from Cartwright, Labrador, Canada. My study was conducted on GC2 which is 16 hectares in area, a relatively steep-sloped island with a maximum elevation of 40 m covered with low cropped ericaceous and herbaceous vegetation and exposed bedrock. Summer (July - August) temperatures average 10 °C and extensive sea ice is normally present between December and early June (Birkhead and Nettleship 1995).

Several species of marine birds breed on these islands including Common Murres (*Uria aalgae*) and Thick-billed Murres (*U. lomvia*), Razorbills (*Alca tordo*), Black-legged Kittiwakes (*Rissa tridactyla*), Black Guillemots (*Cepphus grylle*), Northern Fulmars (*Fulmatus glacialis*), Herring Gulls (*Larus argentatus*) and Greater Black-backed Gulls (*Larus marinus*). The Gannet Islands support the largest and most diverse alcid breeding colony in Labrador. The Atlantic Puffin population was estimated to be 41,300 pairs when last censused in the early 1980s (Birkhead and Nettleship 1995) and is believed to have remained relatively stable if not increased slightly in recent years (G. Robertson, unpubl. data). On the islet, GC2, approximately 10,000 pairs of puffins breed and have a median hatch date between 30 July - 10 August (Birkhead and Nettleship 1995). Median fledge date at the Gannet Islands is in mid to late September (Birkhead and Nettleship 1985).

2.2.2 Nestling diet

I collected bill-loads from adult puffins using a 3 m net pole and a large 12 x 24 m nylon monofilament barrier net with 5 cm mesh during August and September of 1996-98 (Table 2.1). Prey samples were placed in plastic bags and either measured immediately or frozen. Upon capture, puffins were marked with numbered stainless steel leg bands to ensure that bill-loads were recorded from each individual only once. In 1997 and 1998, the total length of each fish was recorded to the nearest 0.1 mm. Prey items, including invertebrates, were individually weighed to the nearest 0.1 g using an Acculab electronic balance.

In 1996, Ian Jones (during August), Mark Hipfner and Tony Roberts (during early September) collected puffin chick diet samples. They measured larger prey items immediately and preserved bill-loads containing smaller items in 70 % isopropyl alcohol. In 1998, I re-measured the bill-loads that were collected in 1996. Because specimens stored in alcohol weighed less and were shorter than when fresh, I devised a conversion factor for each species and size class from fish with known fresh weights and lengths.

Methods for feeding rates were similar to those of Birkhead and Nettleship 1983,1985) however method of bill-load collection was different. Birkhead and

Nettleship (1985) state that Atlantic Puffin prey items were collected from the vicinity of the burrow (puffins were encouraged to drop their chick meals). They did not use nets. Of the fish they collected, they obtained a mean mass for each prey item in certain size classes and used visual records of bill-loads being delivered to chicks to calculate bill-load mass (Birkhead and Nettleship 1985).

2.2.3 Proximate composition and energy density of prey items

Relative proportions of water, fat, ash and protein were determined by proximate composition analysis for 12 species of fish and invertebrates of various size classes commonly delivered to puffin nestlings at the Gannet Islands in 1997. First, I air dried fish in the field, then I oven dried fish to a constant weight at 80 °C (Kerr *et al.* 1982) to obtain water content (percent water content = 100 x (tissue wet weight - tissue dry weight)/ wet weight). Small items were cut into pieces less than 5 mm diameter, larger items were made into a homogenate using an electric coffee grinder. These samples were sent to the University of Western Ontario, where technician Sarah Lee, extracted fat using petroleum ether (Dobush *et al.* 1985) in a modified Soxholet apparatus. Lean samples were then placed in a muffle furnace overnight at 550 °C to burn the protein from the tissue and the remaining ash was weighed. Total protein (grams) in each sample was calculated by subtracting weight of water, lipid and ash from the original sample wet weight.

I estimated calorific value, or energy density ED, using two common energy equivalents (A: 38.0 for lipid $kJ \cdot g^{-1}$ and 20.0 $kJ \cdot g^{-1}$ for protein, and B: 39.54 $kJ \cdot g^{-1}$ for lipid and 23.64 $kJ \cdot g^{-1}$ for protein) which were multiplied by the weight of fat and protein in each sample (Hislop *et al.* 1991, Lawson *et al.* 1998, Russell 1999).

2.2.4 Adult mass

Adult Atlantic Puffins were captured in a 12 x 24 m nylon barrier net with 5 cm mesh size set close to their breeding sites. This method of capture was unselective and successful breeders, unsuccessful breeders and non-breeders were obtained. To quantify adult mass, I excluded juvenile non-breeders (puffins with less than two bill grooves) from analysis. Each bird was marked with a stainless steel leg band and recaptured individuals were eliminated from statistical analyses. Puffins were held briefly in cloth bags and weighed with a 1000 g Pesola spring scale to the nearest 1 g. Wing length was measured to the nearest 1 mm and culmen and bill depth were measured to the nearest 0.1 mm as part of a concurrent Atlantic Puffin demography study (Veitch 1998). Adult morphometrics were obtained using very similar methods to those of Birkhead and Nettleship (1983, 1985).

2.2.5 Timing of breeding

I did not directly quantify laying dates for all burrows in 1996-98 because, to reduce disturbance, burrows were not examined until adult puffins were first observed flying with bill-loads (at this time some burrows still had eggs). For burrows in which hatch date was unknown, I used an estimate for Atlantic Puffin incubation period of 37 days (Birkhead and Nettleship 1983). After the onset of chick provisioning, a sample of 60 - 120 burrows were checked every three days and their contents recorded as 'egg', 'chick' or 'empty'. I determined median hatch date for individual chicks to within two days of age by calculating the midpoint between burrow visits when an 'egg' and 'chick' was recorded (Birkhead and Nettleship 1983). Similarly, I estimated median fledge date as the midpoint between burrow visits when contents were recorded as 'chick' and 'empty'.

Age of chicks with unknown hatch dates was approximated using the relationship between mass and wing of known age chicks. To estimate fledge date for chicks that reached peak mass before I left the colony (and thus fledged after I left the colony), I used the relationship between peak mass and fledge date for known age chicks.

2.2.6 Productivity

During 1996-98, marked puffin burrows were visited every three days once adult puffins were first observed delivering first bill-loads to burrows to obtain hatch and fledge success estimates. Hatch success was determined as the percentage of chicks that hatched from eggs. Fledge success was estimated as the percentage of chicks that reached over 30 days of age. When a chick was not reachable for more than three checks (9 d) and the burrow appeared inactive (e.g. with no excrement at burrow entrance), the chick was presumed dead or fledged. All burrows were re-examined at end of each field season for signs of activity.

In 1998, I decided to examine investigator disturbance at the nest during incubation and chick-rearing. Marked puffin burrows were visited every three days during incubation for two reasons: 1) to measure egg mass change (adult puffins and/or eggs were taken out of burrow; this was part of a concurrent study at the Gannet Islands which was independent of my research) or 2) to obtain hatch date only (reached hand in briefly to verify egg presence). I divided the burrows into these two handling categories to examine success (see * in Table 2.8). I also examined two measures of fledging success in each year to determine whether fledging success differed between burrows that were disturbed during incubation ($\%_{CB}$) and those that not disturbed during incubation ($\%_{ED}$) (see Table 2.8 and 3.7). After hatch, nestlings in all burrows were handled in the same manner.

In the early 1980s, Birkhead and Nettleship reported a 55 % reduction in breeding success between burrows frequently visited (as described above) and those only checked twice (check dates: 11 - 12 July and 04 - 05 September; Birkhead and Nettleship 1985).

Atlantic Puffin breeding success at the Gannet Islands in 1982 (35 %) and 1983 (36 %) averaged 35.5 % in plots where chicks were visited every three days for morphological measurements and 78.5 % in plots where chicks were only checked twice (Birkhead and Nettleship 1985). Thus I used a conversion factor (breeding $\text{success}_{\text{TRUE}}$ = breeding $\text{success}_{\text{DISTURBED}}$ x 78.5/35.5) derived from their study to extrapolate my breeding success estimates in plots where chicks where frequently visited.

2.2.7 Chick growth

I used the methods similar to those of Birkhead and Nettleship (1985) to determine chick morphology and growth. A sample of 60 - 120 burrows were marked and visited every three days (see above). To lessen disturbance, the chick was not measured if an adult was present unless it had not been measured in three visits (except in 1996 when burrows were checked regardless of adult presence). In order to monitor the disturbance effect of frequent visitation, I collected a separate sample of 25 chicks (which were measured only one time) when most chicks reached 140 mm wing length and compared their masses to chicks which were frequently visited. Body mass was measured to the nearest gram with a 300 g or 600 g Pesola spring scale. Flattened wing chord was measured to the nearest millimetre, excluding downy feathers and including the emerging feather shaft.

Growth patterns of puffin chicks in all study years did not consistently fit conventional growth equations such as logistic curve or Gompertz equation. As an alternative method, I determined linear growth rate (the rate at which mass and wing length gain was linearly dependent on time) by inspecting residuals of linear regressions on pooled growth measurements against age for each study year. I proceeded to eliminate data from the upper and lower ages of the curve until residuals first became linear. In all study years, linear growth occurred between chick age 13 and 25 days. Then I performed a linear regression on growth and age for each chick to obtain the mathematical slope of the linear equation and averaged the slopes for all the chicks measured to obtain growth rate representative of the population. In order to assess the entire growth curve meaningfully, I arranged data on mass and wing length at discrete intervals of the chick growth curve in the following age categories chick 1 - 3 d, 9 - 12 d, 37 - 40 d, peak mass and fledge mass.

2.2.8 Maximum dive depth

Originally, I wanted to assess time-activity-budget and energy expenditure of Atlantic Puffins at the Gannet Islands in 1997 and 1998. Dive depth data would have been useful to test whether or not puffins expend more energy on deeper dives. Thus, I captured 15 puffins and attached capillary depth tubes (maximum depth tube MDG) to record maximum puffin dive depths. The depth gauges were attached to each birds' stainless steel leg band with dental floss and retrieved within 48 hours of deployment. The MDGs were constructed from 10 cm lengths of Tygon tubing and the inside surface laced with icing sugar (Burger and Wilson 1988). As the MDG is submerged the icing sugar dissolves inside the tube at a length proportional to the depth of water. The equation used to calculate maximum dive depth was:

$d = 10.08 (L_s/L_d - 1)$ (from Burger and Wilson 1988)

Where d is maximum dive depth, L_s is the length of tubing coated with icing sugar before being submerged, and L_d is the length of tubing with icing sugar remaining after submergence.

2.3 Results

2.3.1 Diet Composition

2.3.1.1 Inter-annual variation Gannet Islands 1996-98

Twenty taxa of prey items were brought to nestlings by provisioning Atlantic Puffins, consisting mainly of small forage fishes (92 % by mass, 90 % by frequency) and several benthic and pelagic invertebrates including squid, polychaetes, pterapods and crustaceans (Table 2.2). Across years combinations of adult sandlance, capelin and arctic cod (length over 90 mm) consistently comprised the majority of food items, though variation in proportions was high. Twelve taxa of larval and juvenile fish (20 to 89 mm) constituted 44 % of the fish biomass fed to young puffins in 1996-98. In 1998, two loads of a single adult daubed shanny, the major item in murre chick diet at the Gannet Islands during 1996-98 (Bryant *et al.* 1999), were observed in puffin bills. Annual diet composition during 1996-98 was expressed as percent biomass, frequency and occurrence in bill-loads for each year and varied significantly (by mass; $\chi^2 = 65.0$, df = 9, $p < 0.0001$; Figure 2.2).

The predominant prey assemblage by biomass in 1996 was adult sandlance, gadids, polychaetes and crustaceans with capelin being the least used prey taxon (Table 2.2). In 1997, sandlance, capelin and cottids were prevalent, with gadids and blenniids least prevalent. In 1998 capelin ranked highest followed by a tie between sandlance and blenniids, then cottids with gadids delivered in the lowest frequency.

Capelin was virtually absent from nestling diet in 1996 at the Gannet Islands. Although the proportion of capelin as a percent of diet biomass increased each year and was highest in 1998, the numerical frequency and occurrence of capelin in bill-loads was lower in 1998 than in 1997 (Table 2.2). The higher percent biomass of capelin in 1998 resulted from a greater proportion of larger individual fish than in 1997. Capelin delivered to puffin chicks in 1996-98 consisted mainly of immature fish or spent females. In all years almost no male, gravid or 0-group capelin were observed in puffin bill-loads.

Proportions of post-larval sandlance by percent mass, frequency and occurrence were highest in 1997 though very similar between 1997 and 1996 (Table 2.2). Percent diet biomass of post-larval sandlance decreased dramatically from near 50 % in 1996 and 1997 to less than 20 % in 1998. Percent occurrence in bill-loads of post-larval sandlance was approximately 65 % lower in 1998 than in 1996 and 1997. Proportions by percent mass, frequency and occurrence of larval sandlance were similar in 1996 and 1997 then increased in percent mass in 1998 by 46 %.

The highest proportions of smaller fish and invertebrates by percent mass, frequency and occurrence in bill-loads occurred in 1998 when they exceeded the combined contribution of adult capelin and sandlance (Table 2.2). In 1996, larval gadids predominated the miscellaneous prey assemblage in percent mass, frequency and occurrence. Sculpins and squid were the most important miscellaneous prey items by percent biomass in 1997. In 1998, sculpins and blennies were delivered in similar proportions and squid were less important. Contribution to chick diet from crustaceans was highest in 1996 at 3.5 % but were virtually absent from bill-loads in 1997 and 1998.

Puffins often brought more than one prey taxon to nestlings in a single load. Load mass ranged from 0.3 - 41.8 g in 1996, 0.8 - 45.6 g in 1997, and 0.8 - 34.4 g in 1998 and number of prey per load ranged from 1 - 45 in 1996, 1 - 38 in 1996 and 1 - 32 in 1998. Annual mean bill-load mass meals brought to puffin chicks in 1997 (11.1 ± 8.1 g, N = 104) were significantly greater than in 1996 (8.1 ± 7.3 g, N = 101) and 1998 (6.9 ± 5.8 g, N = 120) ($F_{2,322}$= 10.7, $p < 0.0001$; see Appendix A for Fisher's PLSD post hoc examination). Mean number of items per bill-load 10.5 ± 10.9 (N = 105), 9.4 ± 8.0 (N = 107) and 12.5 ± 7.5 (N = 120) in 1996, 1997 and 1998, respectively, varied statistically ($F_{2,329}$ = 3.4, $p = 0.03$). Bill-loads in 1998 contained a statistically higher number of prey items than in 1997 but not in 1996 (Appendix A). Load mass and numbers in study years 1996 and 1998 were similar despite representing very different prey assemblages. The relationship between number of items per load and load mass was: $Y = 8.7 - 0.06x$, r^2 = 0.008 in 1996 ; $Y = 9.3 - 0.2x$, $r^2 = 0.006$ in 1997; and $14.2 - 0.3x$, $r^2 = 0.009$ in 1998; where Y = number of items per bill-load and x = bill-load mass (Figure 2.3). The majority of bill-loads with 10 to 40 prey items weighed less than 10 g. However, 1 - 2 fish loads were the heaviest thus meal mass generally decreased with increasing number of small prey items (Figure 2.3). In 1996, percent occurrence of adult fish in loads delivered to chicks (35 %; mainly sandlance) was slightly higher than in 1998 (30 %; similar proportions of sandlance and capelin). In 1997, 51 % of bill-loads comprised adult fish and 69 % of those contained sandlance.

2.3.1.2 Intra-annual variation Gannet Islands, Labrador 1996-98

The taxonomic composition of puffin chick diet at the Gannet Islands was highly variable among the four bi-weekly periods of chick-rearing: early (1 - 15 August), mid

(16 - 31 August), late (1 - 15 September) and end (after 16 September) (Figure 2.4 and Appendix B).

The contribution of immature or spent capelin by percent mass, frequency and occurrence in bill-loads was highest during mid-chick-rearing (15 - 31 August in 1996, 1997 and 1998). No 1-group unscaled capelin appeared in bill-loads before 15 August in any study year and, thereafter, they occurred sporadically until the end of the season.

The seasonal trend of occurrence of post-larval sandlance in chick diets was similar to that for immature or spent capelin, except in 1998 when percent occurrence in bill-loads continued to increase through the season corresponding with the gradual decline in capelin. In 1996, post-larval sandlance did not occur during early chick-rearing but constituted 49 % of chick diet biomass throughout the middle and late chick-rearing periods. In 1997, post-larval sandlance predominated the prey assemblage in early chick-rearing at 30 % biomass, increased to 54 % then experienced declined to 44 % biomass. In 1998, capelin actually exceeded the contribution of sandlance in percent biomass in early and middle chick-rearing.

In 1996, larval gadids and crustaceans increased through the season while cottids and blenniids decreased. During this study year the proportion and diversity of small miscellaneous prey was lowest in early chick-rearing and highest in late chick-rearing. In 1997, larval gadids increased through the season as in 1996 and other small prey items decreased with cottids completely absent in late chick-rearing. In 1998, the study year with the highest contribution from small miscellaneous prey, larval gadids were virtually absent from the diet, cottids increased through the season, and the lowest proportions and diversity of small prey taxa occurred during early chick-rearing.

Load mass through the season did not vary significantly in 1996, 1997 or 1998 ($F_{3,97} = 0.2$, $p = 0.9$; $F_{4,98} = 1.7$, $p = 0.1$; and $F_{4,115} = 1.9$, $p = 0.1$ respectively). There was a slight seasonal increase in load mass except in 1996 where load mass decreased sharply from middle to late chick-rearing corresponding with a sharp increase in number of items per load (Figure 2.5). The trend in number of items per bill-load in 1996-98 was highly variable. In 1996 and 1998, the number of items per load declined from early to middle period, then increased from middle to late period. However, in 1997, number of items per bill-load gradually decreased throughout the season.

2.3.1.3 Inter-annual comparison early 1980s and late 1990s

Atlantic Puffin chick diet was highly variable in both decades (Figure 2.6). Fifty-four percent, 54 %, of the puffin diet biomass in 1981-83 comprised capelin, which was much higher than the mean biomass of 14 % recorded for the 1990s chick diet. The contribution from capelin in chick diet and was higher in 1982 and 1983 than other study years (Figure 2.6). However, the proportion of capelin in 1981 was similar to that in 1997 and 32 % lower than in 1998.

As reported above, in 1996-97 post-larval sandlance constituted almost 50 % of diet biomass, lower than the proportion of post-larval sandlance in 1981 chick diets. In 1983, sandlance was replaced by small miscellaneous prey items. This decrease in the proportion of sandlance corresponded to an increased the proportion of capelin in chick diet.

A greater amount and bewildering diversity of small miscellaneous prey taxa was delivered to puffin nestlings in the late 1990s compared to the early 1980s. Relative percent biomass of items other than adult capelin and post-larval sandlance in 1981, 1982 and 1983 was 19 %, 11 % and 27 %, respectively. Relative percent biomass of items other than adult capelin and post-larval sandlance in 1996, 1997 and 1998 was 48 %, 39 % and 57 %, respectively.

Of all six study years, bill-load mass was the lowest in 1998 when larval fish contributed the greatest proportions to chick diet. Mean bill-load mass brought to puffin nestlings was 15.3 ± 8.1 g (N=56) in 1981, 15.9 ± 8.3 g (N=100) in 1982, and 17.9 ± 7.2 (N=181) in 1983 (Birkhead and Nettleship 1985). Birkhead and Nettleship (1985) reported that meal sizes by mass did not differ significantly throughout the season from one 5-day interval to the next. A seasonal trend common among the early 1980s and late 1990s was that bill-load mass was highest during middle chick-rearing.

2.3.2 Size distribution of prey

Length and mass of fish prey items in bill-loads delivered in 1996-98 ranged from a 15 mm blenny to a 212 mm sandlance and 0.1 g crustaceans to a 15.8 g capelin respectively (Appendix C(i)). Crustaceans, pterapods, polychaetes, and squid had approximate modal lengths of 30, 25, 60, and 80 mm, respectively. Masses of invertebrate taxa ranged from 0.2 g in crustaceans to 14 g in squid.

2.3.2.1 Inter-annual variation Gannet Islands 1996-98

Body size of immature or spent capelin fed to young puffins increased from 1996 to 1998 (Table 2.3). Total length of adult capelin ranged from 95 - 128 mm, 75 - 154 mm and 125 - 160 mm and individual body mass from 0.7 - 8.8 g, 0.8 - 15.8 g and 0.3 - 15.6 g in 1996, 1997 and 1998, respectively. Overall mean mass of adult capelin for 1996-98 was 9.0 ± 4.3 g (N = 42) with mean length of 129.0 ± 24.8 mm (N = 42). Fish lengths displayed a unimodal trend predominated by 125 - 160 mm capelin in 1998, a bimodal trend in 1997 with greater frequency of 80 - 100 mm capelin and again no 0-group fish (Figure 2.7).

Post-larval sandlance (with non-translucent skin > 79 mm in total length) body mass and length were similar in chick diets in 1996 and 1997 yet were considerably smaller in 1998 (Table 2.3). Mean length of adult sandlance in 1996-98 was 136.3 ± 26.4 mm (N = 240) and ranged from 80 - 175 mm in 1996, 80 - 174 mm in 1997, and 84 - 212 mm in 1998. In 1996 adult sandlance mass ranged from 1.0 - 2.9 g, 1.1 - 29.6 g in 1997 and 1.1 - 14.6 g in 1998 with a mean of 4.2 ± 0.3 g (N = 225). In 1998 over 50 % of sandlance brought to chicks were larval or juvenile while in 1996 and 1997, a greater frequency of 100 – 160 mm fish were brought to the colony by puffins (Figure 2.8).

2.3.2.2 Inter-annual comparison Gannet Islands 1980s and 1990s

Total fish length of prey items collected in 1983 ranged from 28 mm larval fish to a 195 mm capelin and body mass ranged from 0.1 g crustaceans to a 38.8 g male capelin. Mature capelin were statistically smaller in the 1990s than in the 1983 dataset (one-way ANOVAs by year 1983, 1996, 1997, 1998 for body mass) ($F_{3,250} = 11.0$, $p < 0.0001$) and length ($F_{3,250} = 11.3$, $p < 0.0001$) (Tables 2.3). Capelin were significantly smallest in 1996, significantly smaller capelin were harvested in 1996 and 1997 than in 1983 and 1998, and capelin size was statistically similar between 1983 and 1998 (Appendix D). The most frequently occurring size classes of capelin (relative percent in parentheses) in 1996, 1997, and 1998 were 120 - 140 mm (40 %), 140 - 160 mm (36 %), and 140 - 160 mm (60 %), respectively (Figure 2.7). In contrast, Birkhead and Nettleship (1985) reported that smaller capelin were used more frequently in 1981 (21 - 60 mm) and 1982 (1 - 120 mm) than in 1983 (121 - 160 mm).

Measurements of sandlance collected from puffins in 1983, 1996, 1997 and 1998 did not vary statistically (length: $F_{3,197} = 0.8$, $p = 0.5$; mass: $F_{3,211} = 1.4$, $p = 0.5$) (Table

2.3; Figure 2.8). Since most larval sandlance were not individually measured in 1983, the relative frequency histogram for fish length is unnaturally skewed toward larger fish (Figure 2.8d).

2.3.3 Proximate composition and energy density of chick diet

Several size classes of juvenile and adult capelin, sandlance and arctic cod were analyzed for proximate composition as were juvenile cottids, daubed shannies, blennies, alligatorfish, snailfish and three types of invertebrates polychaetes, pterapods and squid (Table 2.4). Two samples, larval sandlance (50 - 75 mm) and gadids (120 mm) were excluded from analysis because I suspected they had become dehydrated.

Water content

The lowest value for water content (72 %) was in a sample of post-larval sandlance (50 - 75 mm length) and the highest (88 %) was in arctic cod (110 - 120 mm). Adult fish samples had a water content 9 % lower than those of juvenile fish and 6 % lower than invertebrates. Juvenile fish including cottids, blenniids and other species had a higher overall water content (86 %) than adult fish (78 %) and invertebrates (84 %).

Fat content

Percent fat content of wet mass ranged from a low of 0.5 % in juvenile sculpins and daubed shannies to a high of 4.6 % in adult capelin. Adult fish had a mean fat content of approximately 4 % which is 43 and 41 % higher than juvenile fish and invertebrates. Fat content (4 - 5 %) and length of capelin were positively correlated with the exception of two samples in which the fat content was uncharacteristically low. Sandlance in length classes of 30 - 75, 100 - 155 and 155 - 175 mm correlated positively with percent fat content of 1, 3 and 6 % respectively. Fat content in arctic cod decreased with increasing length. Pterapods had a fat content in the median range of most fish.

Percent protein

Percent protein of wet body mass was lowest in adult arctic cod (7 %) and highest in adult sandlance (20 %) in the 120 - 140 mm size range. Post-larval sandlance had the highest protein content of the adult fish: mean for sandlance was 19 % (N = 8) and 15 % (N = 5) for capelin, and 11 % (N=3) for arctic cod. Juvenile fish and invertebrates had overall protein contents of 14 and 13 %, respectively. Juvenile fish in puffin chick diet, in ranked order from highest to lowest protein content, were blennies 18 %, sandlance 18 %, cottids 16 %, daubed shannies 16 %, capelin 16 % and arctic cod 14 %. Snailfish had the lowest protein value for juvenile fish. Alligatorfish had the highest proportion of inorganic material (5 %).

Energy density

Wet energy density determined using conversion factors A and B (Lawson *et al.* 1998) ranged from 2.5 and 2.8 kJ·g $^{-1}$, respectively, in a sample of to a high of 6.2 and 7.0 kJ·g $^{-1}$ in sandlance 155 - 170 mm. Overall energy densities of adult sandlance (5.3 and 6.0 kJ·g $^{-1}$) were 20 % higher than those for adult capelin (4.2 and 4.8) while arctic cod had the lowest at 3.4 and 3.9 kJ·g $^{-1}$. Highest mean energy densities were in adult fish and lowest in invertebrates. Of the larval fish and invertebrates, capelin (70 - 75 mm), blennies (25 - 35 mm), sandlance (30 - 49 mm), gadids (40 - 67 mm), then cottids (20 - 50 mm) had the highest energy densities.

2.3.4 Adult mass

Mean adult puffin body mass in 1996, 1997 and 1998 was 481.4 ± 36.8 g (N = 543), 474.3 ± 37.9 g (N = 356), and 488.7 ± 41.2 (N = 65), respectively. Adult body mass from pre-laying, incubation and chick-rearing periods (see section 2.3.5.1) was compared within and between each year of study during 1981-83 (Birkhead and Nettleship 1985) and 1996-98 (Table 2.5). A two-way ANOVA for adult puffin mass, 1996-98, by period and year showed no significant difference between years ($F_{2,955} = 0.6$, $p = 0.8$), and a significant difference within breeding season ($F_{2,955} = 3.2$, $p = 0.004$). However, annual adult mass was statistically lower in 1997 than in 1996 and 1998 (Appendix E). Adult puffins did not lose mass between pre-laying and incubation and lost a significant amount of mass from incubation to the chick-rearing period during each study year.

The pooled mean mass of adult puffins from 1996-98 (479.0 ± 37.5 g, N = 923) was similar to that reported by Birkhead and Nettleship (1985) in 1981-83 (482.6 ± 32.4 g, N = 318). I was given privy to one year, 1983, of the raw data for adult puffin mass collected by Birkhead and Nettleship. Mean adult puffin mass sampled between 12 June and 17 September in 1983 was 468.0 ± 38.6 (N = 169). There was no statistical difference in puffin mass between the 1990s and 1980s ($t_{1127} = -1.9$, $p = 0.06$). The pooled data for adult mass in the 1990s was lower during incubation yet higher during chick-rearing than in the 1980s (Table 2.5). Percent mass loss from incubation to chick-rearing was 3.0, 5.4 and 2.1 % in 1996, 1997, and 1998 respectively. Mass loss from incubation to chick rearing by 8.0 and 8.9 % in 1982 and 1983, respectively, was more than double that of the 1990s.

2.3.5 Timing of breeding

There was no significant difference in median hatch dates among study years within the late 1990s (test of medians: $\chi^2 = 2.8$; df = 2, $p = 0.2$) (Table 2.6). Frequency distributions of hatch date were similar between study years 1996, 1997 and 1998 at the Gannet Islands and 59, 62 and 62 % of chicks hatched between 04 and 09 August in each year, respectively. Mean fledging age was 44.8 ± 2.2 d (N = 10) and the chick-rearing period ranged from 41 to 48 days. Chicks that hatched after late August either died or were in poor condition. The mean duration of the incubation period in 1981-83 was 37 d (Birkhead and Nettleship 1983; Table 2.6). Median hatch date of chicks was four to five days later in 1996-98 than in 1981 and 1983, yet median hatch date of chicks was three to four days earlier in 1996-98 than in 1982. Median fledge date of chicks in 1996-98 was similar to that in 1982 though chicks fledged five to 11 days later in 1996-98 than in 1981 and 1983. Puffin chicks fledged 1.4 d older in the 1990s than the 1980s (mean 43.4 ± 2.7 d, N = 28 from Birkhead and Nettleship 1985).

2.3.6 Productivity

My mean estimate for overall breeding success during 1996-98 was 27 % for Atlantic Puffins; 60 % of the eggs hatched and 46 % of the chicks fledged (Table 2.7). Overall breeding success was highest in 1997 and lowest in 1996 for both estimates A and B. Among study years 1996, 1997 ad 1998 there was a significant difference in breeding success in estimate A, nests initially observed with eggs ($\chi^2 = 6.7$, df = 2, p = 0.03), and no significant difference in estimate B which incorporated all nests in the study ($\chi^2 = 5.1$, df = 2, p = 0.08). Hatching success differed significantly among the three study years yet fledging success did not (hatch: $\chi^2 = 12.1$, df = 2, p = 0.002; fledge: $\chi^2 = 1.5$, df = 2, p = 0.5). Hatching success was highest in 1997 and very similar in 1996 and 1998. Fledging success increased slightly from 1996 through to 1998.

Extrapolated overall breeding success estimates were 38 % in 1996, 82 % in 1997 and 67 % in 1998 (from breeding success estimate A in Table 2.7). These estimates were calculated using the conversion factor described in my methods section to represent and compare values obtained from burrows not regularly visited. The mean overall breeding success estimate in 1997-98 (75 %) was similar to that during in 1982-83 (78 %) (Birkhead and Nettleship 1985).

Fledging success was moderately lower, by 10 %, in burrows with chicks that were disturbed as eggs but this difference was not significant ($\chi^2 = 0.2$, df = 1, $p = 0.7$). Hatching success was also 10% lower, but not significantly, in burrows with eggs that were regularly handled ($\chi^2 = 0.1$, df = 1, $p = 0.8$) (Table 2.7). Fledging success in burrows where eggs were handled was 19 % lower, but not significantly, than those in which eggs were merely touched ($\chi^2 = 0.2$, df = 1, $p = 0.7$). Breeding success was compared and overall breeding success was 24 % lower, but not significantly, in burrows from which eggs were regularly removed for weighing ($\chi^2 = 0.3$, df = 1, $p = 0.6$). Overall, this indicated that productivity was not notably affected by frequent visitation of burrows.

2.3.7 Chick growth

2.3.7.1 Inter-annual variation Gannet Islands 1996-98

The linear phase of Atlantic Puffin chick growth at the Gannet Islands occurred from age 13 to 25 d in 1996-98 (Figure 2.9). Mean growth rate during the linear phase for mass and wing length was 8.3 ± 2.6 g (N = 93) and 4.0 ± 0.8 mm (N = 89), respectively. The rate of mass gain in 1996 was much lower than in other years yet there was little difference between 1997 and 1998 (Table 2.8). Linear growth rate for wing in 1996 could not be compared to other years due to different measuring techniques.

In 1996-98, mean mass and wing length of chicks at age 1 - 3 d was 53.2 ± 9.3 g (N = 118) and 23.5 ± 3.4 mm (N = 118) and age 10 – 12 d was 127.6 ± 24.8 g (N = 94) for mass and 36.1 ± 6.3 mm (N = 94) for wing length. Mean nestling mass and mean wing length at age 37 - 40 d was 309.2 ± 54.8 g (N = 78) and 127.5 ± 11.1 mm (N = 78), respectively during 1996-98. In 1996, mass and wing length of chicks at age 37 - 40 d were again lower than in 1997, by 25 % and 8 %, and 1998, by 20 % and 10 %, respectively. Mean peak mass in the late 1990s was 333.2 ± 46.6 g (N = 90). Mean wing length and age at peak mass was 125.9 ± 14.8 mm (N = 90) and 36.7 ± 8.4 d (N = 79), respectively. In the late 1990s, means for peak mass and wing length were greatest in 1997 and lowest in 1996. Puffin nestlings reached peak mass at a significantly younger age in 1998 (see next section). Nestlings attained a mean fledge mass of 340.5 ± 26.1 g (N = 21) and wing length of 141.6 ± 4.3 mm (N = 21) at age 43.5 ± 2.2 d (N = 16).

Fledge mass was similar between 1997 and 1998 but almost 55 g lower in 1996. Fledge wing length was highest in 1996 though the greatest mean difference was only 1.1 mm between study years. Chicks fledged at the youngest age in 1998 and oldest in 1996 (by three days).

Mean mass loss from peak mass age to fledge mass was 22.6 ± 12.2 g (N = 12) during the late 1990s. However, in 1996 and 1998, the chick population did not exhibit a true peak mass, most chicks continually gained mass until they fledged. Chicks lost 8 % body mass in 1997, yet gained 2 and 1 % body mass in 1996 and 1998, respectively from peak mass age to fledge mass. Puffin chicks fledged at 69 % of adult body mass (calculated from pooled chick-rearing period measurements). Fledge mass as a percentage of adult body mass was much lower in 1996 (63 %) than that in 1997 (71 %) and 1998 (73 %). Chicks that were visited frequently weighed 5, 2 and 13 % less than chicks measured only once in 1996, 1997 and 1998, respectively (Table 2.9).

2.3.7.2 Inter-annual comparison Gannet Islands 1980s and 1990s

The linear growth rate for nestling mass in 1983 was significantly higher than 1996-98 by a mean of 31 % ($F_{3,118} = 21.1$, $p < 0.0001$) (see Appendix F for post hoc examinations of ANOVAs). Conversely, rate of wing length gain was not statistically different between years ($F_{3,114} = 0.3$, $p = 0.9$).

In 1983, nestlings aged 1 - 3 d (mass: $F_{3,154} = 7.4$, $p = 0.0001$; wing length: $F_{3,157} = 2.8$, $p = 0.04$) and 10 - 12 d (mass: $F_{3,124} = 13.1$, $p = 0.0001$) were significantly smaller than similar aged chicks in 1996-98. Post-hoc examination showed no statistical difference between 1983 and 1996 (Appendix F). Nestlings older than 12 d in 1983 grew faster and were larger, especially by mass, than nestlings of the late 1990s. At age 37 - 40 d, chick mass was significantly greater in 1983 than in 1996-98 ($F_{3,105} = 58.2$, $p < 0.0001$), but wing length was significantly lower than 1983 only in 1996 ($F_{3,105} = 13.0$, $p < 0.0001$) (Appendix F).

Peak mass was statistically greater in 1983 than in 1996-98 chicks ($F_{3,121} = 60.0$, $p < 0.0001$) (Appendix F). Wing length of chicks was highest in 1998 and wings were significantly smaller only in 1996 than in 1983 ($F_{3,119} = 4.3$, $p = 0.007$). Age at which chicks reached peak mass was similar in all study years with the exception of 1998, when chicks reached peak mass approximately 4.5 d younger than those in 1983, 1996 and 1997 ($F_{3,106} = 174.9$, $p = 0.02$). Mean fledge mass for study year ranked from highest to lowest was 1983, 1998, 1997 and 1996 with only 1996 statistically different ($F_{3,51} = 3.8$, $p = 0.02$). Chicks that fledged in 1996 weighed 67.2 g (23 %) less than chicks in 1983. There was no difference in fledging wing length in any study year ($F_{3,49} = 0.2$, $p = 0.9$). In 1983, chicks lost more weight (11 % body mass loss) between peak and fledge mass than those in 1996-98.

2.3.8 Feeding rates and daily food intake

Atlantic Puffins delivered meals to their young at a higher rate during 1998 than in 1997 (Table 2.10). Feeding rate was positively correlated with the numerical frequency of miscellaneous larval prey items in bill-loads. Daily food intake values (grams per day, $g \cdot d^{-1}$) were higher in 1997 than in 1998 during late chick-rearing. Meals delivered in 1982-83 had higher daily food intake values than in 1997-98. Values for feeding rate in 1982-83 are very similar to those I collected in 1997-98. Though feeding rates and intake values for 1982 and 1997 were strikingly similar, the proportion of capelin delivered to nestlings was 60 % higher in 1982.

2.3.9 Maximum dive depth

Mean maximum diving depth recorded by capillary tubes attached to the legs of Atlantic Puffins for 48 hour periods at the Gannet Islands in 1997 was 38.1 ± 4.1 m (N = 4) and ranged from 32.3 m to 40.9 m in depth.

2.4 Discussion

2.4.1 Prey harvest

The diet of Atlantic Puffins varied markedly over six years, apparently without significant variation in breeding success. Immature or spent capelin dominated the diet of 1982 and 1983 but post-larval sandlance comprised the majority of chick diet in 1996, 1997 and 1981. Unlike the other study years, in 1998, chick diet was not dominated by capelin or post-larval sandlance but by small larval fish and invertebrates. Though meal masses were smallest in 1998, productivity and chick growth parameters were better in 1998 than in 1996. Breeding performance was highest in 1997. The high nutritional quality in 1997 appears to be mainly attributable to post-larval sandlance delivered to young puffins in 1997. Looking back at the 1980s, capelin and sandlance appear to play interchangeable roles in Atlantic Puffin chick diet at the Gannet Islands. However, in the 1990s, small miscellaneous prey were more prevalent, rendering the relationship between capelin, sandlance and Atlantic Puffin reproductive success less clear. In an investigation on alternative prey to capelin, Russell (1999) predicted that sandlance was the best food in the Northwest Atlantic. On the other side of the Atlantic Ocean, in the Barents Sea, it was also recognized that the seabirds relied heavily on sandlance (Barrett and Furness 1990). Additionally, at times when schooling migratory pelagic fish like sprat, herring, sandlance and capelin were not reliably available, puffins in the Barents Sea were able to prey switch and use smaller fish like sculpins, blennies, hake, whiting and rockling (Barrett and Furness 1990). This ability for provisioning puffins to prey switch to smaller prey items and raise chicks successfully is what was exhibited at the Gannet Islands in the late 1990s.

The proportion of diet biomass of mature capelin delivered to young puffins in increased from 3 % in 1996, 14 % in 1997, and 25% in 1998. The number of capelin brought to chicks did not differ between 1997 and 1998, thus the increase in biomass between 1997 and 1998 was a function of an increase in mass/size of individual capelin. In Scotland, Hislop and Harris (1985) found that the variable puffin diets appear to reflect local variability in distribution of prey populations. Perhaps the increase in the size of capelin delivered to nestlings is an early indication of an increase in the health or recovery of the Labrador capelin stocks. Indeed, there were reports from local fishermen that capelin may have spawned off the south Labrador coast in 1998 though no gravid capelin were reported delivered to seabird chicks. Also, it is implied by 1998 seabird diets that the alleged spawning aggregations of capelin were either not as large, not as dense, or occurred farther away from the breeding colonies than in the previous decade. In the early 1980s, Birkhead and Nettleship (1985) reported puffins and murres returning from sea to feed chicks meals of gravid capelin in addition to 0-group and unscaled 1-group capelin. These age classes were completely absent from puffin chick diets in the late 1990s. In 1982 and 1983, prior to the capelin population shift, puffin diet comprised mainly capelin but in 1981 the diet was more similar to that in 1996 and 1997. The trend in the data showed that capelin delivered to young puffins were smaller, and sandlance and gadids were larger in the 1990s than in the 1980s. A more detailed look showed that capelin length in 1983 and 1998 was similar but individual body mass was lower in 1998 than 1983.

If there truly were more capelin off the Labrador coast in 1998, then puffins did not bring more capelin to nestlings than the previous year. Murres at the Gannet Islands did the unexpected and switched prey to daubed shannies a benthic fish (Bryant 1998, Byrant and Jones 1999). It is possible that capelin aggregations were still too far away or had densities below a threshold in which puffins could avoid high foraging energy expenditure. If prey density determines the frequency at which birds return from foraging grounds carrying fish (Harris and Hislop 1978), then my results indicate that puffins taking cues from other puffins carrying prey were not encountering large schools of capelin. Instead puffins, exploited the readily accessible supply of larval and juvenile fish in abundance around their colony at the Gannet Islands. The size of loads carried by Atlantic Puffins may reflect the distance traveled to foraging grounds and back, the smaller the load, the closer the fish were obtained (Birkhead and Nettleship, 1983 Granadeiro *et al.* 1998). There is a large difference in load sizes of puffins breeding on both sides of the North Atlantic and puffins in eastern Canada generally carry larger loads (Harris and Hislop 1978, Barrett *et al.* 1987, Rodway *et al.* 1998). The 1981-1983 mean load mass estimates were heavier than bill-loads reported in other studies in Northwest Atlantic (Nettleship 1991, Rodway and Montevecchi 1996, Russell 1999, Baillie this text) and Northeast Atlantic (Harris 1984, Anker-Nilssen 1987, Ashcroft 1979, Barrett and Rikardsen 1992). Birkhead and Nettleship (1985) state that these values were "biased upwards because birds with heavier loads were easier to catch" using their methodology (as describe in Section 2.2.2 of this thesis).

Generally, the highest fat and protein content is present in adult fish. Sandlance brought to chicks had higher fat and a 20 % higher energy density than capelin, a result also reported by Russell (1999). Sculpins and blennies were relatively low in fat content but high in protein. It is necessary for puffin nestlings to lay down fat reserves in order to survive both burrow and post-fledge conditions. It is possible that essential amino acids may limit growth (Harris and Hislop 1978) and chicks may benefit greatly from an adequate amount of protein from sculpins and small blennies. However, it would seem that puffins fed entirely on small miscellaneous somewhat lipid deficient fish may have to utilize protein to supply energy for metabolic processes (Harris and Hislop 1978) and thus require a diet supplemented with a yet undefined threshold quantity of post-larval sandlance or capelin.

2.4.2 Adult mass

Adult puffins did not lose mass between pre-laying and incubation but lost a significant and similar amount of mass between incubation and chick-rearing during the late 1990s at the Gannet Islands. Despite this, adults did not weigh less in the 1990s than in the 1980s during chick-rearing. Thus I found no evidence that adult body mass responded to the changes in capelin distribution. Puffin adult body mass during chick-rearing at the Gannet Islands 1996-98 was lowest in 1997 and highest in 1998. The data show, however, that inter-year variation in mass correlated negatively with the proportion of adult fish in bill-loads. Similarly adult puffin mass was highest when chick diet comprised mostly larval fish and invertebrates. A possible explanation for this is that puffins expended more energy reserves when searching or acquiring adult sized fish and expended more energy diving at or traveling to higher quality prey patches. Energy expenditure may well be reduced when puffins forage on juvenile sculpins and blennies in shallow waters close to the colony.

Compared with the 1980s, seasonal mass loss was not as great in 1996-98 likely due to differential sampling methods. Birkhead and Nettleship in 1981-83 collected measurements from breeding puffins taken from active burrows (Birkhead and Nettleship 1985). In contrast, my vertical barrier nets did not discriminate between breeders, unsuccessful breeders and non-breeders. However, it is also likely that successful and unsuccessful breeders had mass differences related to reproductive and foraging effort which may lead to underestimation of mass early in the season and overestimation late in the season.

2.4.3 Timing of breeding

Onset of breeding for Atlantic Puffins at the Gannet Islands, Labrador was later in the 1990s compared to the 1980s but there was no conclusive evidence of environmentally induced variation during my study. Notably, all breeding seabirds at the Gannet Islands began laying eggs later in the 1990s than in the 1980s. Atlantic Puffins had the least pronounced difference in hatch dates between decades while murres and kittiwakes were a full week later in the 1990s than the 1980s (Bryant 1998, Hipfer *et al.In press*). I believe these timing delays of a few days in hatch dates for example are unlikely result of food availability considering the high inter-year variability of prey movements under normal conditions. However, on a broader temporal scale, the chick-rearing period could be timed with optimal food abundance in order to maximize the number of young produced (Lack 1968). Seabirds necessarily breed later with increasing latitude because low temperatures, frozen ground and sea ice constrain the physical ability of puffins to breed on islands. Along this line of reasoning, seabirds in Labrador may be breeding later due to oceanographic change associated with a cold ocean event which began in the late 1980s (Drinkwater 1996, J. Anderson pers. comm.). Also, the presence of predators, such as Arctic Fox, may have delayed breeding in certain years but predation may be more likely to prevent or spoil breeding rather than delay laying (Cairns 1985, Craik 1997).

2.4.4 Productivity

One of the most striking results of my study was the observation that puffins at the Gannet Islands fledged chicks in the absence of their supposedly preferred prey. The lowest hatching and fledging success occurred in 1996. The absolute reason behind the low breeding success in 1996 is unclear but was likely exacerbated by poor capelin conditions. Several theories have been put forth to explain this phenomenon, such as, late land fast ice and the presence of arctic fox during pre-laying and incubation in 1996 at the Gannet Islands may also have been a factor affecting egg-laying and hatching (Birkhead and Nettleship 1985). Though hatching success was much lower in 1998 than 1997, chances of chick survival after hatching were similar, suggesting that factors occurring before chick-rearing were most important in determining breeding success in 1997-98. The influence of both avian predators and parasite loading were considered negligible at the Gannet Islands, Labrador. As in other studies, a seasonal decline in breeding success was detected at the Gannet Islands puffin colony (Gaston and Nettleship 1981).

The temporal and spatial availability of fish has been shown to influence the breeding performance of puffins (Hatch and Hatch 1989a, 1989b). Other studies on Atlantic Puffins report negative responses to deleterious prey conditions but these are cases of extreme breeding failure (e.g. Anker-Nilssen 1987). Nettleship (1991) showed a significant decrease in puffin breeding success at Great Island, Witless bay in 1981 as a result of decrease in capelin population but these birds exist in an entirely different ecosystem with a different array of stress and constraints than in the Northeast Atlantic or in Norway. The breeding success of seabirds at the Gannet Islands 1996-98 varied from species to species. Black-legged Kittiwakes experienced total breeding failure in 1997 at the Gannet Islands, Labrador and fledged few young in 1998 due to low food availability early in the season (Hipfner *et al .in press*). On the other hand, Common and Thick-billed Murres showed no reduction in productivity between 1981-83 and 1996-97 (Bryant *et al.*1999). Evidently, surface feeders like the kittiwakes are more sensitive to changes in capelin supply because their foraging strategy is limited to the first few centimetres of the water column. In the absence of schooling capelin, it is advantageous that seabirds are able to exploit other food resources through diving.

Investigating Atlantic Puffin burrows during incubation may have a negative effect on breeding performance (Anker-Nilssen 1987, Harris 1984, Rodway *et al.*1996, 1998; Rodway 1997, Baillie this text), thus my breeding success estimates may be somewhat reduced compared to the natural population. Mortality of regularly visited chicks during 1996-98 was most likely a result of parental neglect, an indirect effect of disturbance at the burrow. Despite the negative investigator effect, I can confidently report that my results show no evidence for breeding failure in 1996-98.

2.4.5 Chick growth

The rate of mass gain of Atlantic Puffin chicks was higher in 1983 than in 1996-98. However, the singular dataset I acquired, 1983, was not necessarily representative of chicks in 1981 and 1982. Birkhead and Nettleship (1985) reported mass growth rates from 1981 and 1982 that were very similar to those in 1997 and 1998. Furthermore, there was no difference in wing-length growth between study years on the 1980s and 1990s which leads me to conclude that wing growth did not respond to the decline of capelin in chick diet. The Atlantic Puffin has semi-precocial chick development in which the chick leaves the nest in complete juvenile plumage after 38 to 75 plus days (Ydenberg 1989). Puffins generally fledge at 60 - 80 % of adult mass (Ydenberg 1989, Oyan and Anker-Nilssen 1996) and rate of mass gain of puffin nestlings is determined by food intake (Hislop and Harris 1978). Rate of linear growth and other parameters were uncharacteristically low in 1996 but it was difficult to make a direct causal link between this and diet composition because chick diet was very similar in 1996 and 1997 at the Gannet Islands. It is possible that 1996 was the anomaly in chick growth due to a nutritional deficit caused by delayed and limited availability of larger fish (Ricklefs 1983). If food stress was the only constraint, puffin chicks should have faired better instead of worse in 1996 than in 1998. I say this because chicks consumed a greater proportion of large adult fish in 1996. These fish were mainly sandlance, a fish of equal or greater nutritional value than capelin. In study year 1998, the chicks grew equally as well as those in 1997 despite a diet of mainly small miscellaneous prey. The high proportion of larval gadids in the diet during 1996 may be evidence that sculpins and blenniids, which are of greater nutritional value than gadids, were not as plentiful in near colony waters as in 1998.

2.4.6 Conclusions

Among the three years of my study of Atlantic Puffins at the Gannet Islands in the late 1990s, 1996 appeared to have anomalous low breeding performance. If feeding conditions were good in 1981-83, it would seem that feeding conditions were poor in 1996 and moderate in 1997 and 1998. Poor food supply in 1996 can be defined by a virtual absence of capelin and a reduced adequate alternative prey source, i.e. post-larval sandlance. The breeding parameters that appeared to respond to poor food supply were fledging success, chick mass at age 37 - 40 d and peak mass. Chick wing growth remained unchanged.

The results of my study 1996-98 do not support the hypothesis that Atlantic Puffins experience breeding failure or dramatically reduced breeding success during periods of absence of capelin. Atlantic Puffins in this study made use of alternate prey, which suggests that individuals at minimal energetic cost to themselves were able to supply their chicks with a level of nutrition sufficient for them to grow and fledge successfully. Puffins apparently survived and raised young for at least five years in the virtual absence of spawning aggregations of capelin in southern Labrador. Post-larval sandlance appear to be a superior alternative to capelin. Post-larval sandlance brought to puffin nestlings was equivalent or greater in lipid, protein and energy density than immature or spent capelin (Russell 1999, Baillie this text). It is apparent that the role of sandlance in puffin diets of the Northwest Atlantic has been understated as even in the early 1980s post-larval sandlance comprised up to 65 % biomass of puffin chick diet.

Table 2.1 Summary of Atlantic Puffin bill-loads collected at the Gannet Islands, Labrador during 1996-98.

Year	Collection period	Date	Number of sampling days	Number of loads N (% loads)	Mean no. of items per load x (SD)	load mass (g) x (SD)
	1	01 - 15 Aug	4	15 (12)	11.4 (8.9)	5.2 (4.6)
1996	2	16 - 31 Aug	4	10 (8)	6.4 (9.4)	5.7 (3.8)
	3	01 - 15 Sep	14	98 (80)	10.7 (10.9)	8.2 (9.3)
	4	16 -31 Sep	–	–	–	–
	1	01 - 15 Aug	–	–	–	–
1997	2	16 - 31 Aug	7	22 (21)	11.3 (11.3)	8.0 (8.6)
	3	01 - 15 Sep	10	58 (54)	9.0 (6.8)	11.6 (6.9)
	4	16 -31 Sep	9	27 (25)	8.9 (6.3)	8.9 (6.3)
	1	01 - 15 Aug	2	21 (18)	12.6 (6.5)	4.3 (7.0)
1998	2	16 - 31 Aug	7	62 (52)	11.2 (7.8)	7.3 (6.4)
	3	01 - 15 Sep	5	37 (31)	14.4 (7.5)	7.4 (4.7)
	4	16 - 31 Sep	–	–	–	–

Table 2.2 Relative percent biomass of Atlantic Puffin chick diet taxa at the Gannet Islands, Labrador during 1996-98.

	1996 % (n)	1997 % (n)	1998 % (n)
capelin (larval)	0.2 (2)	0.3 (3)	< 0.1 (1)
capelin (immature/female)	2.2 (3)	13.5 (19)	25.3 (19)
capelin (gravid female)	–	–	–
capelin (male)	–	–	–
overall capelin	2.4 (5)	13.9 (22)	25.3 (20)
sandlance (larval)	5.6 (93)	7.9 (230)	13.6 (372)
sandlance (adult)	49.2 (63)	46.7 (93)	18.3 (26)
overall sandlance	54.8 (156)	54.6 (323)	31.9 (398)
arctic cod (larval)	10.1 (269)	1.4 (33)	1.5 (33)
arctic cod (adult)	5.5 (6)	4.8 (9)	2.1 (2)
overall arctic cod	15.6 (275)	6.1 (42)	3.6 (35)
blenny	1.6 (115)	0.8 (65)	15.8 (558)
sculpin	7.5 (165)	13.2 (339)	15.7 (375)
alligatorfish	0.3 (15)	0.2 (10)	0.4 (23)
white hake	–	–	–
brown hake	–	–	–
daubed shanny	5.7 (201)	3.0 (120)	2.4 (65)
flatfish	–	–	0.1 (2)
lumpfish	< 0.1 (1)	0.2 (5)	0.1 (1)
snailfish	0.2 (10)	< 0.1 (3)	0.4 (13)
squid	1.8 (7)	6.9 (45)	3.0 (8)
pterapod	0.7 (14)	< 0.1 (1)	0.3 (4)
polychaete	5.9 (116)	0.7 (17)	0.5 (12)
crustacean	3.5 (112)	0.3 (29)	0.4 (13)
unknown	< 0.1 (4)	< 0.1 (3)	–
Number of bill-loads	106	107	120

Table 2.3 Comparison of mean mass and length of larger prey taxa collected from Atlantic Puffins provisioning chicks at the Gannet Islands, Labrador in the early 1980s and late 1990s.

Prey type	Year	Mass (g)			Length (mm)		
		x	SD	(N)	x	SD	(N)
capelin							
immature or spent	1981*	10.4	7.5	(86)	–	–	–
	1982*	9.9	2.0	(117)	128	2.1	(117)
	1983*	14.5	6.1	(227)	149	23.3	(227)
	1996	5.6	4.9	(6)	106.7	29.9	(6)
	1997	8.4	4.2	(19)	126.4	24.5	(19)
	1998	11.4	2.6	(19)	143.1	11.0	(17)
sandlance							
post-larval	1981*	7.4	1.9	(5)	–	–	–
	1982*	4.6	3.6	(63)	111	35.0	(63)
	1983*	5.5	2.6	(33)	126	19.1	(33)
	1996	5.2	3.4	(98)	118.1	27.0	(97)
	1997	5.2	3.0	(108)	118.1	24.2	(106)
	1998	2.4	3.1	(71)	84.1	31.0	(79)

* from Birkhead and Nettleship 1985 (unpublished CWS report)

Table 2.4 Proximate composition of water, fat, ash and protein (PN) in Atlantic Puffin prey taxa at the Gannet Islands, Labrador in 1997, with two estimates of calculated energy density (ED). See text for explanation of variables.

Species	No. fish	Length (mm) x (SD)	N	% Water x (SD)	% Fat x (SD)	% Ash x (SD)	% PN x (SD)	ED (A) $kJ \cdot g^{-1}$ x (SD)	ED (B) $kJ \cdot g^{-1}$ x (SD)
0-group capelin	1	75.0	1	77.9	3.6	2.9	15.7	4.5	5.1
spent female or immature capelin	3	91 (1.7)	1	78.1	4.6	1.6	15.7	4.9	5.5
	3	136.7 (2.5)	2	81.7 (1.2)	1.7 (1.3)	2.0 (0.3)	14.6 (0.2)	3.6 (0.5)	4.1 (0.6)
	2	147.0 (2.8)	1	81.0	5.1	1.6	12.3	4.4	4.9
	3	151-153	1	79.7	1.8	2.5	16.0	3.9	4.5
larval sandlance	129	30 - 49	2	78.2 (3.2)	1.5	2.4 (0.3)	17.9 (1.4)	4.1 (0.9)	4.8 (0.9)
	44	50 - 75	1	66.4	1.0	3.6	29.0	6.2	7.2
post-larval sandlance	32	100 - 120	3	75.3 (1.7)	4.1 (1.6)	2.4 (0.1)	18.3 (0.1)	5.2 (0.6)	5.9 (0.6)
	12	120 - 140	2	75.4 (0.1)	2.6 (0.9)	2.3 (0.1)	19.7 (0.9)	4.9 (0.2)	5.7 (0.1)
	4	140 - 155	1	79.2	2.2	2.2	17.0	4.0	4.6
	2	155 - 170	1	72.6	6.5	2.2	18.6	6.2	7.0
	1	174.0	1	71.8	5.7	2.2	20.3	6.2	7.0
gadids	15	40 - 50	1	82.8	1.7	1.8	13.8	3.4	3.9
	1	67.0	1	80.7	4.0	0.7	14.7	4.5	5.0
	2	111.0 (5.7)	1	88.1	3.9	0.9	7.1	2.9	3.2
	1	120.0	1	62.3	10.0	3.7	24.0	8.6	9.6
	1	124.0	1	80.2	2.9	2.7	14.1	3.9	4.5
cottids	70	20 - 30	1	80.5	0.5	2.5	16.4	3.5	4.1
	119	35 - 50	3	79.4 (1.1)	1.8 (0.6)	2.9 (0.3)	15.9 (0.5)	3.9 (0.3)	4.5 (0.3)
daubed shanny	72	30 - 50	2	83.2 (1.8)	1.3 (0.3)	0.9 (1.2)	14.6 (0.2)	3.4 (0.2)	4.0 (0.2)
	59	50 - 70	1	80.2	0.5	2.1	17.3	3.6	4.3
blenny	28	25 - 35	1	78.0	1.5	2.4	18.0	4.2	4.9
alligatorfish	3	42.0 (0.0)	1	80.0	5.0	5.0	10.0	3.9	4.3
snailfish	7	20 - 40	1	86.8	2.3	2.7	8.2	2.5	2.8
polychaete	14	50 - 75	1	85.5	0.8	1.8	11.9	2.7	3.1
pterapod	1		1	83.3	3.3	1.1	12.2	3.7	4.2
squid	15	large	1	82.1	2.8	1.6	13.5	3.8	4.3
	11	small	1	83.4	2.0	1.8	12.8	3.3	3.8

Table 2.5 Change in mean body mass of adult Atlantic Puffins through the breeding season at the Gannet Islands, Labrador during 1981-83 and 1996-98.

Year	Pre-laying			Incubation			Chick-rearing		
	x (g)	SD	(N)	x (g)	SD	(N)	x (g)	SD	(N)
1981*	–	–	–	–	–	–	484.4	29.7	(24)
1982*	–	–	–	498.3	31.2	(44)	458.4	30.0	(77)
1983**	507.0	38.5	(37)	499.2	37.0	(30)	457.6	30.8	(130)
1981-83		–		498.7	0.6	(74)	466.8	15.2	(231)
1996	494.8	32.6	(28)	484.6	37.2	(374)	470.2	34.1	(141)
1997	473.3	28.9	(3)	493.4	37.2	(101)	466.7	35.6	(252)
1998	489.5	40.2	(20)	490.3	43.6	(37)	479.8	37.6	(8)
1996-98	491.5	35.4	(51)	486.7	37.8	(512)	468.2	35.1	(401)

* from Birkhead and Nettleship unpublished CWS report 1985

** re-analyzed data from Birkhead and Nettleship

Table 2.6 Comparison of Atlantic Puffin breeding phenology at the Gannet Islands, Labrador between the early 1980s and the late 1990s.

Year	First eggs	Median laying	First chicks	Median hatching	First fledging	Median fledging
1981 *	08 Jun	23 Jun	17 Jul	01 Aug	25 Aug	09 Sep
1982 *	22 Jun	30 Jun	01 Aug	09 Aug	09 Sep	18 Sep
1983 *	18 Jun	30 Jun	25 Jul	02 Aug	05 Sep	12 Sep
1996	_	26 Jun †	03 Aug	05 Aug	15 Sep	20 Sep
1997	_	27 Jun †	01 Aug	06 Aug	18 Sep	21 Sep
1998	_	26 Jun †	28 Jul	05 Aug	12 Sep	17 Sep

* from Birkhead and Nettleship 1985 (unpublished CWS report)

† median laying dates were back-calculated by subtracting 40 days from median hatch date (Harris 1984).

Table 2.7 Summary of Atlantic Puffin breeding success at the Gannet Islands during 1996, 1997 and 1998.

Year	1996	1997	1998*		
Was there visitation disturbance 'throughout' the incubation period?	YES	NO	Combined YES/NO 1998 sample	YES	NO
No. eggs$_{A}$	82	38	75	35	40
No. chicks (initially found as eggs)$_{B}$	42	32	43	19	24
Hatching success (%)$_{B/A}$	(51.2)	(84.2)	(57.0)	(54.0)	(60.0)
No. fledged$_{C}$	14	14	23	9	14
Fledging success A (%)$_{C B}$	(33.3)	(43.8)	(53.5)	(47.4)	(58.3)
No. chicks (initially found as chick)$_{D}$	70	10	42		
No. fledged$_{E}$	33	5	20		
Fledging success B (%)$_{E D}$	(47.0)	(50.0)	(47.6)		
Total nests in study$_{A-D}$	152	48	117		
Total nests with chicks N(%)$_{B-D}$	112 (73.7)	42 (87.5)	85 (72.6)		
Total no. chicks that fledged$_{C-E}$	47	19	43		
Fledging success C (%)$_{F=(C-E)(B-D)}$	(42.0)	(45.0)	(51.0)		
Breeding success A: (%$_{B A}$ x %$_{C B}$)	17%	37%	31%	26%	34%
B: (%$_{B A}$ x %$_{F}$)	22%	38%	29%	_	_

* Data for 1998 split into two groups: burrows which were regularly extracted for egg mass measurements and burrows with eggs that were left relatively undisturbed until the chicks hatched.

Table 2.8 Summary of Atlantic Puffin chick growth parameters at the Gannet Islands, Labrador 1996-98 and 1983 (re-analyzed raw data collected by Birkhead and Nettleshipin 1983).

Growth Parameter	Units	1996			1997			1998			1983		
		x	SD	N	x	SD	N	x	SD	N	x	SD	N
Linear Phase Growth Rate	mass increase (g d^{-1})	7.1	2.8	(40)	9.0	1.8	(18)	9.4	2.2	(35)	12.1	3.1	(29)
	wing increase (mm d^{-1})				3.9	0.3	(18)	4.1	0.4	(35)	4.0	0.7	(29)
Age 1 - 3 d	mass (g)	51.1	8.0	(60)	59.6	12.0	(12)	54.2	9.3	(46)	48.6	4.3	(40)
	wing (mm)	23.0	4.1	(60)	22.7	1.1	(12)	24.4	2.6	(46)	22.8	1.7	(40)
Age 10 - 12 d	mass (g)	116.7	24.8	(46)	126.9	16.9	(7)	139.9	20.0	(41)	110.1	21.3	(34)
	wing (mm)	32.1	4.2	(46)	38.7	7.7	(7)	40.2	5.1	(41)	32.3	4.1	(34)
Age 37 - 40 d	mass (g)	268.7	41.6	(37)	355.8	31.3	(18)	337.7	39.2	(23)	380.7	29.9	(31)
	wing (mm)	121.2	11.8	(37)	131.8	4.9	(18)	134.2	7.6	(23)	130.6	7.2	(31)
Peak Mass	mass (g)	290.4	34.6	(29)	370.3	24.8	(20)	345.5	39.1	(41)	400.3	28.9	(35)
	wing (mm)	120.0	21.8	(29)	133.1	7.1	(20)	126.6	9.1	(41)	128.4	9.7	(33)
	age (d)	38.9	12.7	(29)	38.8	3.0	(17)	33.8	3.5	(33)	37.9	3.6	(31)
Fledge	mass (g)	295.5	5.0	(2)	344.3	25.0	(14)	348.0	15.2	(5)	362.3	34.4	(34)
	wing (mm)	142.5	2.1	(2)	141.4	4.5	(14)	141.8	4.9	(5)	142.6	5.0	(30)
	age (d)	45.0	0.0	(2)	43.9	2.3	(10)	41.7	1.5	(3)	44.9	2.1	

Table 2.9 Mean mass comparison of frequently weighed Atlantic Puffin chicks and those weighed only once at the Gannet Islands, Labrador during 1996, 1997 and 1998.

Wing length class (mm)	Year	Weighed once (g)			Frequently weighed (g)			t-test results			
		x	SD	N	x	SD	N	Mean Diff.	df	t	p
	1996	261.5	46.0	2	262.8	19.6	5				
110-119	1997	310.8	25.0	6	330.0	_	1				
	1998	296.5	31.8	2	253.0	37.6	5				
	1996	283.0	41.0	13	272.7	45.2	15	8.8	43	1	0.5
120-129	1997	350.0	42.5	9	352.5	36.2	2	-2.5	13	-0	0.9
	1998	331.0	28.3	2	310.6	40.3	8	20.4	8	1	0.5
	1996	290.1	45.6	14	282.4	22.0	10	4.3	28	0	0.7
130-139	1997	362.1	44.2	12	345.0	27.4	4	17.1	14	1	0.5
	1998	385.4	44.1	5	327.3	29.4	16	58.1	19	3	0.003
	1996	320.0	28.1	6	305.3	11.8	4	15	11	1	0.2
140-149	1997	358.9	39.8	9	335.0	24.2	5	23.9	12	1	0.3
	1998	376.4	29.3	14	346.7	29.8	14	30	26	3	0.01
	1996	_	_	0	_	_	0				
150-159	1997	_	_	0	355.0	_	1				
	1998	431.5	27.6	2	_	_	0				
	1996	291.0	42.3	35	277.9	34.7	34	11.3	86	1	0.2
110-159	1997	349.7	42.6	36	344.4	27.7	17	12.8	43	1	0.3
	1998	372.8	43.1	25	324.0	41.5	41	43.5	57	5	<.0001

Table 2.10 Feeding rates reported for Atlantic Puffins in Newfoundland and Labrador during chick-rearing.

Colony	Year	Bill-load mass (g)			Feeding rate (meals·d^{-1})			Daily food intake (gd^{-1})		
		x	SD	N	x	SD	N	x	SD	N
Gannet Islands	1996	8.1	7.3	(101)	–	–	–	–	–	–
	1997	11.1	8.1	(104)	3.2	0.4	(3)	35	–	–
	1998	6.9	5.8	(120)	4.7	0.8	(2)	32	–	–
	1981*	15.3	8.1	(56)	–	–	–	–	–	–
	1982*	12.4	–	(100)	3.1	0.2	(2)	38	–	–
	1983*	14.8	–	(181)	4.0	0.8	(2)	59	–	–
Great Island	1967-69**	12	6.4	174	3.6	1.1	(17)	44	–	–
	1981**	–	–	–	–	–	–	45	–	–
	1982-83**	14	6.6	180	3.8	1.1	(60)	51	–	–

* From Birkhead and Nettleship 1985

** From Nettleship 1991

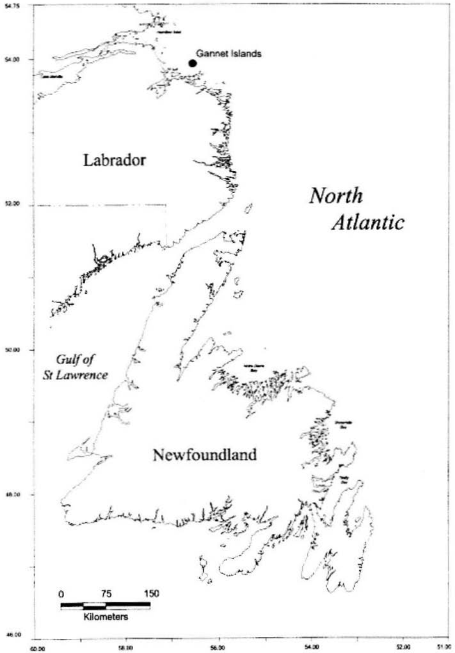

Figure 2.1 Map showing the position of the Gannet Islands Ecological Reserve.

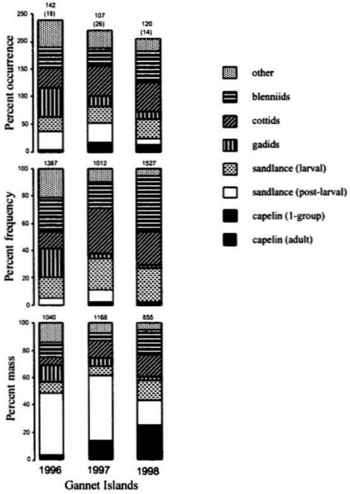

Figure 2.2 Annual proportions of prey delivered to Atlantic Puffin chicks at the Gannet Islands 1996-98. Number of bill-loads (number of sampling days in parentheses), number of prey items and total mass (g) of prey are displayed above each bar of the percent occurrence, percent frequency and percent mass graphs, respectively.

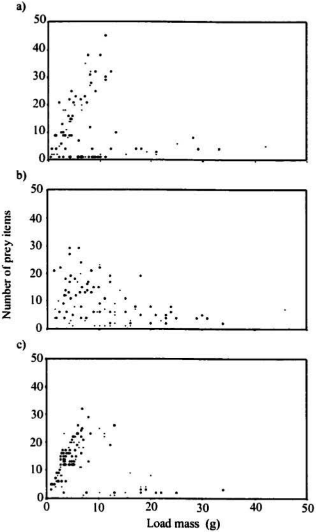

Figure 2.3 Scatterplots display the relationship between food load mass and number of items per load brought to puffin nestlings at the Gannet Islands, Labrador in 1996 (a), 1997 (b) and 1998 (c).

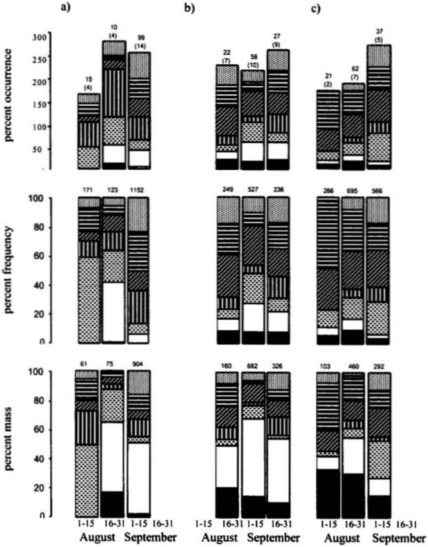

Figure 2.4 Seasonal change in proportions of prey delivered to Atlantic Puffin chicks at the Gannet Islands in 1996 (a), 1997 (b) and 1998 (c). Legend and explanation of numbers over bars are in Figure 2.2.

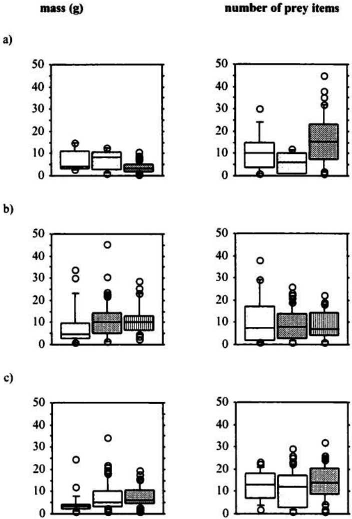

Figure 2.5 Seasonal change of bill-load mass and number of items per bill-load fed to young puffins at the Gannet Islands in 1996 (a), 1997 (b) and 1998 (c). Early, middle, late, and end chick-rearing period are represented by, white, stippled, horizontally- and vertically-striped boxes. Upper and lower boundaries of box (25th to 75th quartiles) contain 50 % of the values, whiskers extend to higher and lower values and empty circles represent outliers.

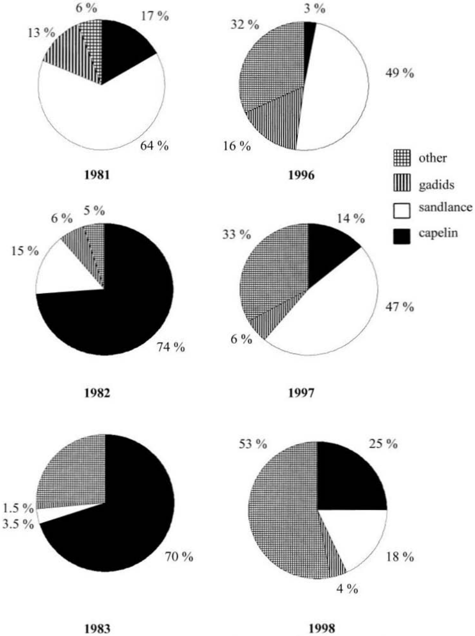

Figure 2.6 Comparison of relative percent biomass of prey items delivered to young Atlantic Puffins at the Gannet Islands in the early 1980s and late 1990s.

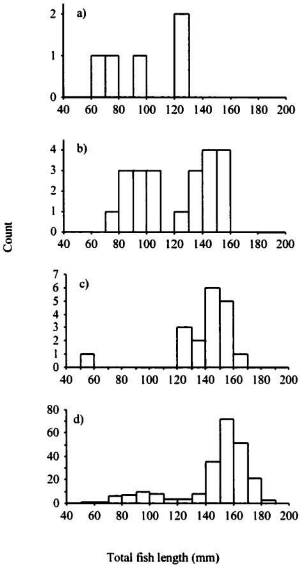

Figure 2.7 Length frequency distribution of capelin collected from Atlantic Puffins provisioning chicks at the Gannet Islands in 1996 (a), 1997 (b), 1998 (c) and 1983 (d).

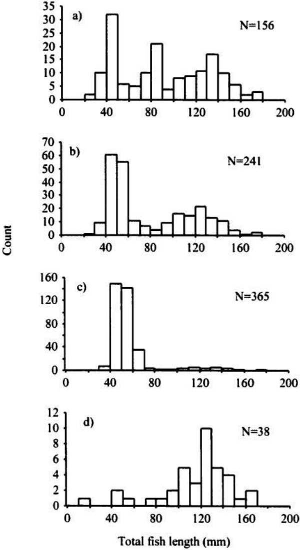

Figure 2.8 Length frequency distribution of sandlance collected from Atlantic Puffins provisioning chicks at the Gannet Islands in 1996 (a), 1997 (b), 1998 (c) and 1983 (d).

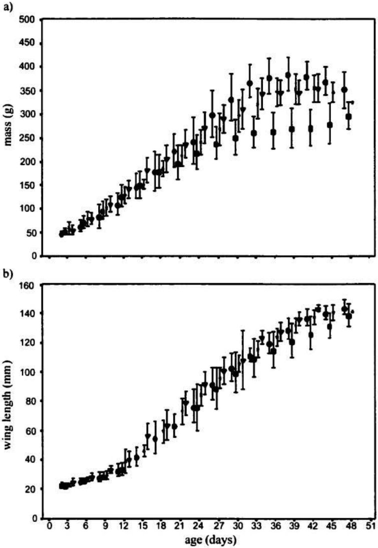

Figure 2.9 Growth curves of Atlantic Puffin chick mass (a) and wing length (b) at the Gannet Islands. Solid dots represent study year 1983, solid squares for 1996, asterisk for 1997 and solid triangle for 1998.

CHAPTER THREE

INTER-COLONY COMPARISON OF ATLANTIC PUFFIN NESTLING DIET AND REPRODUCTIVE PARAMETERS: GULL ISLAND, WITLESS BAY, NEWFOUNDLAND AND THE GANNET ISLANDS, LABRADOR

Abstract

I compared nestling diet and growth, breeding phenology, breeding success and adult mass of Atlantic Puffins between two seabird colonies with presumed high and low capelin availability. Puffins at their Gull Island, Witless Bay breeding colony were expected to exhibit better reproductive performance than puffins under apparent food stress at the Gannet Islands, Labrador. Puffin chick diet at Gull Island 1997-98 consisted of approximately 60 to 70 % (by mass) capelin, supplemented by larval sandlance in 1997 (16 %), and post-larval sandlance in 1998 (21 %). The proportion of capelin in chick diet at Gull Island consistently exceeded that at the Gannet Islands by 35 to 67 %. Gravid and 1-group capelin, predominant in early chick-rearing at Gull Island, were completely absent from chick diet at the Gannet Islands. Alternate prey (by percent mass) at the Gannet Islands were post-larval sandlance in 1996 (46 %) and 1997 (48 %), and smaller miscellaneous prey (55 %) in 1998. There was no inter-colony difference in the nutritional value of capelin or sandlance. Inter-species lipid, protein and energy density was significantly higher in post-larval sandlance than in both adult and immature

capelin at both colonies. Puffins at the Gannet Islands colony experienced low breeding success in 1996. Peak and fledge mass of chicks was consistently lower at Gull Island even when expressed as a percent of adult mass. The high inter-year variability in chick diet at both colonies and the low variation in breeding parameters during my study leads me to suggest that puffins at the Labrador colony are resilient to large scale but perhaps not extreme prey base changes.

3.1 Introduction

In the Northwest Atlantic, capelin *Mallotus villosus*, a small migratory pelagic smelt, is considered to be the preferred prey for Alcids during the breeding season. The diet of nestling Atlantic Puffins *Fratercula arctica* consists almost entirely of small fish and to a lesser extent invertebrate species (Anker-Nilssen 1987; Barrett *et al.*1985, 1987; Anker-Nilssen and Rostad 1993; Russell 1999). Atlantic Puffins are multiple prey-loaders which means they can capture and carry several prey types in one foraging trip (Harris and Hislop 1978). Despite widely documented variability in puffin diets (Ashcroft 1979, Barrett and Furness 1990, Barrett and Krasnov 1996, Rodway and Montevecchi 1996, Russell 1999), some researchers have suggested that puffins in the Northwest Atlantic are specialist feeders and unable to cope with large scale prey base variation (Brown and Nettleship 1984). This assumption was made, in part, because puffins provisioning chicks in Witless Bay, Newfoundland consistently utilized capelin during the capelin spawning season and experienced breeding failure in one year of low capelin abundance (Nettleship 1991, Rodway and Montevecchi 1996, Baillie this text). In the early 1980s at a more northern colony in Labrador, puffin chick diets comprised mainly capelin in two years during a three year study (Birkhead and Nettleship 1985). Russell (1999) recently reported that capelin consistently dominated puffin diets at Baccalieu Island, but showed that at several other breeding colonies of insular Newfoundland, percentage of capelin received by nestlings was more variable and much lower (to 0 % at times) with no apparent negative repercussions for Atlantic Puffin reproductive success. This contradicted the previously held assumption that there was no suitable alternative prey to spawning capelin (Brown and Nettleship 1984). It was also predicted that in the prolonged absence of capelin, seabird productivity and survivorship would suffer (Brown and Nettleship 1984). For at least five breeding seasons prior to my study, puffins were likely unable to access spawning aggregations of capelin at the Gannet Islands, Labrador.

I compared Atlantic Puffin parental prey harvest and breeding parameters between the Gannet Islands, Labrador and Gull Island, Witless Bay, southeastern Newfoundland. The objectives of my study were to assess the degree to which puffin reproductive parameters were affected by the dramatic decline in capelin abundance in Labrador and to contrast these reproductive parameters with a Newfoundland colony near which capelin were plentiful. I hypothesized that puffins in a region of low capelin abundance would experience lower reproductive success and chick growth parameters than puffins in Witless Bay, southeastern Newfoundland.

3.2 Methods

3.2.1 Study sites

Seventy-five percent of Atlantic Puffins in the Northwest Atlantic breed within the Witless Bay Ecological Reserve on the Avalon Peninsula, Newfoundland (Rodway *et* *al.* 1998) (Figure 3.1). The first of my two study colonies, Gull Island, Witless Bay (47° 15.8'N, 52° 46.3'W) is the second largest puffin breeding colony within this reserve (Cairns *et al.* 1989). Gull Island lies less than 5 km from land and 50 - 74 m cliffs surround the island which supports an over-mature coniferous forest bordered by tussocky grass and areas of bare rock and soil. Summer temperatures average 20 °C and land fast ice in nearby bays dissipates by late April (Birkhead and Nettleship 1995). The Gannet Islands archipelago (53° 56'N, 56° 32'W) Labrador (Figure 3.1), are home to approximately 100,000 pairs of auks including 39,300 pairs of puffins (Lock *et al.* 1994). The islet known as GC2 where I conducted my research within the archipelago, is predominantly used by burrow and crevice nesters such as puffins and Razorbills. Summer temperature averages 10 °C with extensive sea ice between December and mid-June (Birkhead and Nettleship 1995).

Atlantic Puffins at Gull Island, Witless Bay arrive at the colony in April and begin laying in May, four to five weeks earlier than those at the Gannet Islands (Birkhead and Nettleship 1985, Nettleship 1991). Median hatch and fledge dates for Atlantic Puffins at Gull Island are late June and mid-August (Cairns *et al.* 1989). At the Gannet Islands median hatching date for Atlantic Puffins is 30 July - 10 August (Birkhead and Nettleship 1995) and median fledging date is late September (Birkhead 1985). The nestling populations finish fledging at roughly the same time by calendar date at both colonies. I conducted fieldwork on Gull Island from early June to late July and the Gannet Islands in early August to mid - late September during both study years. In 1998, a field assistant remained at Gull Island after my departure to continue data collection through to mid-August.

In addition to location, climate and differential prey regimes, other important differences exist between study colonies. Entirely absent at the Gannet Islands, seabird- and whale-based tourism is a heavy source of human traffic around Gull Island and though landings at the island are restricted, at least 20 boat trips pass the island at close proximity each day. Levels of Herring Gull kleptoparasitism were high at Gull Island and virtually non-existent at the Gannet Islands (personal observation). Great Black-backed Gull populations and potential for predation appeared to be higher at Gull Island, especially before the spawning aggregations of capelin arrive (pers. obs.).

3.2.2 Field methodology and data analyses

Data collection and treatment of diet composition, prey size, proximate composition analyses, adult mass, phenology, productivity and chick growth were conducted as described in Section 2.2 (pp. 12-18). Puffin chick diet was collected at Gull Island in 1997 only during mid chick-rearing, therefore inter-annual statistical analyses were limited to this period. I did not procure laying dates as Atlantic Puffins typically exhibit a negative breeding response to investigator disturbance at burrows early in the breeding season (Birkhead and Nettleship 1983, Harris 1984, Rodway and Montevecchi

1996). Atlantic Puffin burrows on Gull Island were inspected regularly in 1998, however only date of first hatching chicks was observed in 1997. I estimated median hatch date for 1997 by adding the time interval between first chicks and median hatch (12 days), observed in 1998, to the date of first chicks in 1997. Median laying dates for both study years were based on previously reported estimates for incubation period in Witless Bay of 42 days (Nettleship 1972). Though chicks were not regularly measured in 1997, haphazard samples of once-measured chicks were collected on 20 - 24 August 1997 (N = 131) and 12 - 13 September 1997 (N = 117). A sample of once-measured chicks was also obtained in 1998 (N = 25) on 13 - 14 August 1998. I grouped chicks into 1 cm wing length classes to compare chick condition as a function of mass.

Statistical methodology is outlined in Results 3.3 where necessary. All statistical analyses were conducted in SPSS 6.0 and Statview 4.0 for Macintosh. Wherever Chi-square 2 x 2 contingency tables exist, I used Yates correction equation (Zar 1984). In 1998, chicks of known age were measured regularly through early July to the middle of August (Figure 3.11). I determined the time period in which the rate of mass and wing gain was linearly dependent on time by inspecting residuals of linear regressions on pooled data of growth parameters through time. I proceeded to eliminate data from the upper and lower ages of the curve until residuals first became linear which was between chick age 13 - 25 days. Then I performed a linear regression on growth and age for each chick to obtain the mathematical slope of the linear equation and averaged the slopes to obtain growth rates representative of the population. For the inter-colony comparison of chick growth, I considered two modes of comparison for puffin chicks between the Gull Island, Witless Bay 1997-98 and Gannet Islands 1996-98 breeding colonies. First, I assessed the inter-colony morphological size difference between chick populations by comparing chick mass within 1-cm wing length classes. Wing length in 1996 at the Gannet Islands was measured differently than in other colony-years between the ages of 10 days and 25 days. This is the period between when the feather shaft began to develop (30 - 50 mm) and before the feather emerged from the shaft (80 - 100 mm). Chicks with wing lengths over 110 mm were used in the inter - colony comparison of mass at 1-cm wing lengths but 1996 nestling measurements were not included in analyses for wing growth rate. Second, I compared the mass, wing length and tarsus length of known age chicks at discrete age classes (i.e. 1 - 3 d, 10 - 12 d, 37 - 40 d, peak mass, fledge mass) and chick growth rates between colonies. Chick mass was expressed as a percent of adult mass to account for geographic differences in morphology and the resultant percentage data were arcsine transformed for statistical analyses to meet assumptions of residual normality.

3.3 Results

3.3.1 Diet composition

Atlantic Puffins breeding at Gull Island, Witless Bay 1997-98 delivered 15 taxa of small pelagic fish and invertebrates to their young. In 1997, forage fish constituted 96 % (by mass) and 98 % (by numbers) of chick diet. In 1998, forage fish comprised 98 % (by mass) and 89 % (by numbers) of chick diet. The majority of these fish comprised immature or spent capelin with mean seasonal biomass of 53 % in 1998, the only year in which sampling occurred from early to late nestling periods (Figure 3.2a). In 1998, the second most abundant food item in young puffin diets was post-larval sandlance at 34 % biomass. Invertebrate species consisted of hyperiid and gammarid amphipods, euphausiids and one species of squid, *Illex illecebrosus*.

3.3.1.1 Inter-annual variation Gull Island 1997-98

Annual variation was apparent in both the presence and proportions of various prey species or groups of species. I limited inter-annual comparison of puffin chick diet to the middle chick-rearing period (the second bi-weekly period after median chick hatch) because this was the only period in which diet was sampled in 1997 (Figure 3.2b; Appendix B for numerical representation of proportions). For initial perusal of inter-annual variation in diet, I categorized species into eight groups: adult capelin (post 1-group), 1-group capelin, post-larval sandlance, larval sandlance, cottids, blenniids, hake and other. In a 2 x 8 contingency table, significant variation in diet composition was apparent during middle chick-rearing between study years 1997 and 1998 by biomass ($\chi^2 = 192.4$, df = 7, $p < 0.0001$) and by numbers ($\chi^2 = 190.7$, df = 7, $p < 0.0001$). Inspection for high local χ^2 statistics within the contingency table suggested that variation was largely due to differences in proportions of 1-group capelin, larval sandlance and post-larval sandlance between years. This is evident from inspection of the data alone (Appendix B). There were decidedly higher proportions of 1-group capelin and larval sandlance and lower proportions of post-larval sandlance at Gull Island in 1997 than in 1998.

At Gull Island, adult capelin comprised 70 and 67 % of diet biomass in 1997 and 1998 during middle chick-rearing ($\chi^2 = 1.9$, df = 1, $p = 0.2$). The numerical frequency of adult capelin in 1997, at 34 %, was lower than 42 % recorded in 1998. Relative proportions of gravid, male, and immature or spent female capelin biomass did not vary from year to year during middle chick-rearing period ($\chi^2 = 5.7$, df = 2, $p = 0.06$).

At Gull Island in 1998, the proportion of post-larval sandlance by biomass, frequency and occurrence in bill-loads was ten times greater compared to the same phase of the nestling period during 1997. The difference in annual post-larval sandlance biomass was significant ($\chi^2 = 89.5$, df = 1, $p < 0.0001$). In 1997, post-larval fish comprised only 11 % of total sandlance intake, whereas in 1998, post-larval sandlance made up 86 % of total sandlance biomass delivered to nestlings.

Despite this, overall proportion of smaller fish and invertebrates, prey other than adult capelin and sandlance, was higher in 1997 than 1998 at Gull Island. The difference in percent biomass between 1997, 27 %, and 1998, 13 %, was significant ($\chi^2 = 34.8$, df = 1, $p < 0.0001$) which corresponded to a decline in numerical frequency of miscellaneous prey from 87 % in 1997 to 71 % in 1998 ($\chi^2 = 20.5$, df = 1, $p < 0.0001$). Squid was collected in 1998 and not in 1997 though puffins were seen carrying squid to young in the latter mentioned year.

Mean bill-load mass during chick-rearing in 1997 (9.9 ± 6.3 g, N = 66) was not statistically different from that in 1998 (9.3 ± 6.5 g, N = 59; $t_{123} = 0.5$, $p = 0.6$). The statistical variance for number of items per bill-load was over twice as large as the mean so these data were logarithmically transformed to meet assumptions of normality (Fowler and Cohen 1992). Original mean for items per bill-load in 1997 (7.1 ± 7.9, N = 67) was significantly higher than in 1998 (3.3 ± 4.5, N = 59; $t_{124} = 3.2$, $p = 0.002$). Puffins provisioned nestlings with meals containing twice as many items per bill-load in 1997 than in 1998, yet there was a greater proportion of one fish bill-loads in 1997 (48 %) than in 1998 (27 %).

3.3.1.2 Intra-annual variation Gull Island 1998

Diet biomass of adult capelin at Gull Island increased markedly from 37 % in early chick-rearing, to 67 % in middle season, then declined slightly in late chick-rearing to 57 %. Despite the late season decline in biomass, numbers of adult capelin brought to nestlings doubled from 22 % to 42 % in the first two bi-weekly periods then increased the third to 52 % diet frequency.

The relative proportion of gravid, male, and immature or spent capelin biomass delivered to puffin nestlings varied statistically from early to middle to late chick-rearing ($\chi^2 = 246.2$, df = 4, $p < 0.0001$). Seventy-nine percent by mass (N = 14) of gravid female capelin collected in 1998 were delivered during the first bi-weekly period of chick-rearing. In early chick-rearing, gravid females comprised 44 % of adult capelin biomass which decreased to 8 % in middle chick-rearing and were completely absent from diet in late chick-rearing after 29 July 1998. Immature or spent capelin comprised 49, 74 and 87 % of total adult capelin mass in early, middle and late chick-rearing. Immature or spent female capelin were the sole prey items present in over half of all bill-loads delivered to puffin chicks in middle and late chick-rearing. The proportion of male capelin was consistently lower than gravid and immature or spent individuals reaching a peak in the middle chick-rearing during late July. Biomass, numerical frequency and occurrence in bill-loads of 1-group capelin was relatively high early in the season then diminished in the third week after median hatch date. After 20 July 1998, 1-group capelin were completely absent from chick diet.

The contribution of post-larval sandlance to nestling diet at Gull Island was relatively high throughout the season. Post-larval sandlance temporarily declined in diet by percent biomass and occurrence during the second bi-weekly period after chick hatch and then reached original proportions by late season (Appendix B). In contrast, a minute increase in the numerical frequency of sandlance from early and middle chick-rearing preceeded a four-fold numerical frequency increase from middle to late chick-rearing. The differences for percent mass, frequency and occurrence in bill-loads between periods differed significantly ($\chi^2 = 77.1$, df = 2, $p < 0.0001$; $\chi^2 = 25.5$, df = 2, $p < 0.0001$; $\chi^2 = 9.2$, df = 2, $p = 0.01$, respectively).

Analysis of smaller fish and invertebrate prey items revealed a distinct seasonal decline at Gull Island from 100 % occurrence in bill-loads early in the season to 18.8 % in late chick-rearing. Percent biomass of small fish and invertebrates declined from 19 to 13 to 3 % through early, middle and late chick-rearing. Percent frequency of these tiny prey decreased from 90 % to 73 % early in the summer and dropped markedly to 28 % of prey items in late chick-rearing. The decreases in percent biomass, frequency, and occurrence of adult fish were significant ($\chi^2 = 69.9$, df = 2, $p < 0.0001$; $\chi^2 = 160.7$, df = 2, $p < 0.0001$; $\chi^2 = 10.7$, df = 2, $p = 0.005$, respectively).

Bill-load size means did not vary significantly in mass from early (10.2 ± 6.7 g, N = 60) to middle (9.3 ± 6.5 g, N = 59) to late chick-rearing period (10.4 ± 5.4 g, N = 48) at Gull Island during 1998 ($F_{2,164} = 0.4$, $p = 0.644$). In contrast, there was a marked decline in number of items per bill-load throughout the season from 7.8 ± 11.5 (N = 60) to 3.3 ± 4.5 (N = 59) and 1.7 ± 1.4 (N = 48) items per chick meal ($F_{2,164} = 10.2$, $p < 0.0001$).

3.3.1.3 Inter-annual comparison, Gull Island and Gannet Islands

The majority of prey species fed to young puffins at Gull Island, Witless Bay 1997-98 and the Gannet Islands, Labrador 1996-98 occurred in remarkably different proportions (Figure 3.3). Adult capelin and post-larval sandlance were the most utilized prey, together consisting of no less than 45 % diet biomass. During my study, capelin was markedly more abundant in the diet at Witless Bay whereas sandlance had the dominant role in Labrador. Species diversity of smaller fish in chick diet at Gull Island and the Gannet Islands was remarkably similar though prey composition was slightly more diverse at the more northern colony.

The proportions of capelin were markedly higher at Gull Island than at the Gannet Islands (Table 3.1, Figure 3.3). Puffin diet collected at the Gannet Islands was completely devoid of male and gravid capelin with very little 1-group capelin relative to capelin assemblage in the Gull Island chick diet. At the Gannet Islands, percent mass of capelin was highest in 1997 during middle chick-rearing yet this was less than half the proportion of capelin at Gull Island in any year. Numerical frequency of capelin at Gull Island was twenty-fold that of Gannet Islands. Percent occurrence of capelin was highest at Gull Island in 1998 and lowest at the Gannet Islands in 1996.

Proportions of post-larval sandlance were highest during 1996 and 1997 at the Gannet Islands and lowest at Gull Island in 1997. However, in 1998 at Gull Island, annual percent of sandlance biomass, numerical frequency and occurrence in bill-loads was over double that for the Gannet Islands in 1998.

At the Gannet Islands in 1998, provisioning puffins fed a greater proportion of small fish and invertebrates to nestlings than in any other colony-year. At the Gannet Islands, the most common species of smaller fish, in descending order by percent occurrence in bill-loads, were sculpins, blenniids and larval sandlance, while at Gull Island larval sandlance and 1-group capelin predominated. Invertebrates at Gull Island consisted of crustaceans for the most part, while at the Gannet Islands polychaetes, squid and pterapod molluscs were important.

One-group capelin were rare at the Gannet Islands yet comprised a considerable proportion of the Gull Island chick diet, especially in 1997. Larval sandlance were most abundant in diets of 1997 at Gull Island but appeared to be comparably utilized at the Gannet Islands, especially in 1998. I found no species overlap between colonies within the gadid group, arctic cod appears in the Gannet Islands nestling diet and white hake at Gull Island. Blenniids and cottids occurred at both colonies in all years. Flatfish occurred at both colonies but only in 1998. Polychaetes, pterapods, and daubed shannies also present at the Gannet Island were non-existent at Gull Island.

Mean bill-load mass for Gull Island 1998 was 9.9 ± 6.3 g (N = 167) and 4.4 ± 3.2 g (N = 71), 10.4 ± 8.3 g (N = 105) and 6.8 ± 5.8 g (N = 120) for the Gannet Islands 1996, 1997 and 1998, respectively. Number of items per bill-load was 4.5 ± 7.8 (N = 167) at

Gull Island 1998, and 14.4 ± 10.7 (N = 77), 9.4 ± 7.7 (N = 108), and 12.5 ± 7.5 (N = 120), at the Gannet Islands 1996, 1997 and 1998, respectively. It is important to note that the means for colony-year Gannet Islands 1997 do not include early chick-rearing.

During middle chick-rearing, there was no significant difference in bill-load mass between colony or year at Gull Island during 1997-98 and the Gannet Islands during 1997-98 ($F_{1,203} = 3.6$, $p = 0.06$). However, mean number of items per bill-load was significantly lower at Gull Island, 5.3 ± 6.8 (N = 126) than the Gannet Islands, 11.3 ± 8.7 (N = 84) ($F_{1,206} = 28.1$, $p < 0.0001$).

3.3.1.4 Intra-annual comparison Gull Island and Gannet Islands

Proportions of all major prey types by percent mass, frequency and occurrence changed through the nestling period (Figure 3.4a-c and Appendix B). Temporal tends for most prey types differed between Gull Island 1998 the Gannet Islands 1996-98.

There was a marked decline in proportions of adult capelin at the Gannet Islands from early to middle chick-rearing while at the Gull Island puffin colony adult capelin increased from early to middle chick-rearing (Figure 3.4a-c). Gravid capelin were most prevalent early in nestling period at Gull Island and completely absent from puffin diet at the Gannet Islands. Initial appearance of 1-group capelin at the Gannet Islands was much later in the nestling season than at Gull Island where proportions were highest in the first bi-weekly period of chick-rearing.

Proportions of post-larval sandlance in chick diet were highly variable among colony-years according to stage of the breeding season (Figure 3.4a-c). At Gull Island 1998, sandlance occurred in high proportions throughout the nestling season, a situation very similar to that at the Gannet Islands 1997. Conversely, at the Gannet Islands in 1996 post-larval sandlance did not appear until middle chick-rearing and decreased in late chick-rearing, while in 1998 at the Gannet Islands post-larval sandlance occurred in very low proportions early in the season and increased through the entire season.

At Gull Island 1998, smaller prey including hake, larval capelin and sandlance, cottids and crustaceans were most prevalent early in the nestling period. In contrast at the Gannet Islands smaller prey, as in gadids and cottids, either persisted or increased in diet through the summer months. At Gull Island, crustaceans appeared in diet early in nestling period and were absent in later season, yet at the Gannet Islands they persisted throughout the season and in higher proportions that at Gull Island.

In general, there was a negative relationship between change in load mass and numbers of prey items per load from period to period. This relationship was most prevalent at the Gannet Islands in 1996-98. Interestingly, at Gull Island in 1998, the overall trend of increase in load mass in 1998 corresponded to an increase in load size. The Gannet Islands scatterplots typically were dominated by a clumped distribution replete with multiple larval/juvenile prey loads, especially in August (Figure 3.5). At Gull Island in 1998, there was a clumped distribution of small fish loads and a few one fish loads during the early chick-rearing period then the distribution became even during middle chick-rearing, and in late chick-rearing the distribution was clumped and dominated by one fish loads (Figure 3.5).

3.3.2 Size distribution of prey

3.3.2.1 Inter-annual variation Gull Island 1997-98

Atlantic Puffin chicks at Gull Island, Witless Bay 1997-98 were fed prey items that ranged in mass and length from 0.1 g and 15 mm to a 21.8 g male capelin and a 212 mm post-larval sandlance (Table 3.2). Mean mass of adult capelin at Gull Island was 8.7 ± 4.5 g (N = 157) and 129.0 ± 20.9 mm (N = 148) was the mean 'total fish' length over the two study years. Though individual post-larval sandlance, of the same length as capelin, generally weighed less (Appendix C(ii)), the overall mean for individual mass in 1997-98, 9.2 ± 5.6 g (N = 69), was greater than that for adult capelin, due to a higher proportion of longer sandlance averaging 153.0 ± 39.6 mm (N = 68). Other individual prey items were well under 100 mm in length with the exception of one 103 mm post-larval White Hake.

Mean mass and length of adult capelin including gravid females, males and immature or spent capelin at Gull Island in 1998 was 9.0 ± 3.9 g (N = 106) and 133.2 ± 16.6 mm (N = 95). In 1998, adult male capelin delivered to nestling puffins were heavier and longer than both gravid and immature or spent capelin (Table 3.3). Conversely in

1997, gravid capelin were the heaviest and longest of the adult capelin and in both years immature or spent capelin were the smallest. During middle chick-rearing, mean mass of adult capelin was 8.2 ± 5.6 g (N = 51) and 9.5 ± 4.3 g (N = 41) in 1997 and 1998, respectively. This annual difference in individual capelin mass was not significant (t_{41} = -0.6, p = 1.0) though capelin were significantly shorter (t_{41} = -2.5, p = 0.02) in 1997 than 1998 with total body length of 122.2 ± 25.5 mm (N = 53) and 134.1 ± 19.8 mm (N = 36), respectively.

The morphology and length distribution of sandlance in 1997 was distinctly unlike that of 1998 (Table 3.3). In 1997, puffins provisioned chicks on smaller, unscaled and metamorphosed, post-larval sandlance. The larval sandlance, 15 - 25 mm, and small post-larval sandlance, 60 - 125 mm, prevalent in 1997, were replaced in importance by 125 – 225 mm post-larval sandlance in chick diet of 1998 (Figure 3.6). In 1998, post-larval sandlance ranged from 4.3 - 20.3 g and 127 - 212 mm yet in 1997 only three fish collected, of 71 bill-loads, fell within this range with a mean mass of 5.4 ± 4.0 g (N = 2) and total length 139.3 ± 17.8 mm (N = 3).

3.3.2.2 Intra-annual variation at Gull Island 1998

Mean mass of adult capelin was highest in early July (9.6 ± 3.6 g, N = 27) and lowest in early August (8.0 ± 3.7 g, N = 38) but the difference in mass between bi-weekly periods was not significant ($F_{2,103}$ = 1.7, p = 0.2). The higher mass early in the season is attributed to a greater proportion of gravid capelin. Mean length of adult capelin increased slightly through the season from 131.3 ± 13.1 mm (N = 25) in early chick-rearing to 134.0 ± 15.6 mm (N = 34) in late chick-rearing and, again, this difference was not significant ($F_{2,92} = 0.2$, $p = 0.8$).

Post-larval sandlance generally decreased in size throughout the nestling period. Mean mass of adult sandlance was 12.9 ± 3.7 g (N = 23), 9.2 ± 5.1 g (N = 13) and 10.5 ± 4.1 g (N = 19) in early, middle and late chick-rearing, respectively ($F_{2,52} = 3.8$, $p = 0.03$). Length of post-larval sandlance also declined through the summer and was lowest in late July with means from early to late chick-rearing of 176.3 ± 16.6 mm (N = 23), 158.2 ± 18.5 mm (N = 25.8) and 169.0 ± 18.5 mm (N = 18) ($F_{2,51} = 3.5$, $p = 0.04$). Notable was the steadily increasing trend in length of smaller fish such as 1-group capelin, larval sandlance, cottids and blennies brought to young puffins through the chick-rearing period until they virtually disappeared from the diet in early August.

3.3.2.3 Inter-annual comparison Gull Island and Gannet Islands

The most frequently occurring size class of adult capelin at Gull Island in 1997-98 was 140 – 180 mm and 120 - 160 mm at the Gannet Islands 1996-98 (Figure 3.7). Size of immature or spent capelin increased from 1996 to 1998 at the Gannet Islands and the overall mean mass was 9.9 ± 3.8 g (N = 38). The length, as well as mass, of capelin in

1997 at the Gannet Islands was most similar to that of Gull Island in 1998. Capelin at the Gannet Islands in 1998 were the largest collected during this study.

The most frequently occurring size class of post-larval sandlance at Gull Island was 150 - 200 mm in 1997-98. At the Gannet Islands the most frequently occurring size class of post-larval sandlance was 100 - 150 mm (Figure 3.8). The smallest sandlance in any of the five colony-years were collected at Gull Island 1997 and the largest at Gull Island 1998. The mean mass and length of individual post-larval sandlance at Gull Island in 1998 was approximately 6.0 g heavier and 50 mm longer than sandlance collected at the Gannet Islands in 1996 and 1997. Sandlance collected at the Gannet Islands in 1998 were small and similar to those fed to young puffins at Gull Island in 1997.

Mass and length of immature or spent capelin decrease through the season at the Gannet Islands in 1996 and 1997 yet increased through the 1998 season. At Gull Island, mass remained constant throughout the season though length of fish increased from early to middle chick-rearing (Figure 3.9). Post-larval sandlance length and mass generally increased from middle to late chick-rearing at Gull Island yet a decreasing trend was prevalent at the Gannet Islands (Figure 3.10).

3.3.3 Proximate composition and energy density of chick diet

3.3.3.1 Variation between prey species, Gull Island 1998:

Fat content

In rank order for percent fat of wet body mass, adult sandlance was highest, 4.7 ± 2.0 % (N = 7), then gravid sandlance, 4 %, cottids 3 %, immature or spent capelin, 2.2 ± 1.9 (N = 4), gravid female capelin, 1.5 ± 0.4 % (N = 2), and the lowest fat content was in a sample of male capelin, 0.2 %. Fat content of juvenile fish was 50 % lower than adult fish which had a mean fat content of 3.1 ± 2.2 % (N = 16).

Water content

A sample of gravid capelin contained the lowest water content, 70 %, while the highest value, 87 %, was tied for a sample of male capelin and white hake (see Table 3.4). All post-larval sandlance had lower water content than immature or spent, male, and gravid capelin with the exception of the aforementioned sample. Water content did not differ statistically between adult and juvenile fish ($t_{21} = 2.0$, $p = 0.06$). This low difference may be a function of translucent, thin-skinned juvenile fish drying faster than more developed. mature fish enroute to colony in bills of provisioning puffins (Montevecchi and Piatt 1987).

Protein content

Percent protein of wet body mass was highest in samples of gravid capelin and gravid sandlance and lowest in smaller hake and a sample of adult male capelin. Adult fish ranked from highest to lowest by mean protein composition are as follows: gravid sandlance 21 %, gravid capelin 20.3 ± 5.8 % (N = 2), adult sandlance 19.1 ± 5.4 % (N = 7), immature or spent capelin 15.5 ± 1.1 % (N = 4) and male capelin 13.5 ± 0.9 % (N = 2). Of the juvenile fish, blenniids then capelin and cottids had the highest protein density. Adult fish had a mean of 17.8 ± 4.5 (N = 16) percent protein while 15.1 ± 2.7 % (N = 7) of juvenile fish was composed of protein.

Energy density

The prey species delivered to puffin nestlings at Gull Island, Witless Bay with the highest energy content were sandlance (mature) and capelin (gravid females). The energy density value from the one sample of gravid sandlance was identical to the mean value for all adult sandlance (A: 5.6 ± 1.1 $\text{kJ}\cdot\text{g}^{-1}$ (N = 7) and B: 6.4 ± 1.2 $\text{kJ}\cdot\text{g}^{-1}$ (N = 7)). Male capelin 140 - 149 mm in length had the lowest energy densities of any sample analyzed. The difference in wet energy density between adult and smaller fish was significant (for A: $t_{21} = -2.2$, $p = 0.04$, and for B: $t_{21} = -2.2$ $p = 0.04$).

3.3.3.2 Inter-colony comparison Gull Island and Gannet Islands

On average, adult capelin from Witless Bay had a lower fat content (2.2 ± 1.8 %, N = 5) than capelin at the Gannet Islands (3.0 ± 1.9 %, N = 4) though energy densities between colonies were similar (Gull Island A: 4.0 ± 0.7 kj·g^{-1}, N = 4 and B: 4.5 ± 0.8 kJ·g^{-1}, N = 4; Gannet Islands A: 4.0 ± 0.6 kJ·g^{-1}, N = 5 and B: 4.6 ± 0.7 kJ·g^{-1}, N = 5) (Tables 3.4 and 2.5). Percent protein of capelin was 10 % higher and ash content was 10 % lower at Gull Island than the Gannet Islands. On the other hand, at Witless Bay, sandlance had a higher fat content (4.7 ± 2.0 %, N = 7) and a slightly higher energy density (A: 5.6 ± 1.0 kJ·g^{-1}, N = 7; B: 6.4 ± 1.2 kJ·g^{-1}, N = 7) than sandlance brought to puffin nestlings at the Gannet Islands, Labrador (lipid: 3.9 ± 1.9 %, N = 8; energy density A: 5.2 ± .8 kJ·g^{-1}, N = 8; and energy density B: 6.0 ± 0.8 kJ·g^{-1}, N = 8). Percent protein and ash content of post-larval sandlance were the same at Gull Island and the Gannet Islands.

There were significant differences in nutritional value between capelina nd post-larval sandlance. Post-larval sandlance was 7 % lower than capelin in water content ($F_{1,20}$ = 15.9, p = 0.001), and 38 % higher in percent lipid ($F_{1,20}$ = 4.4, p = 0.05), 20 % higher in protein ($F_{1,20}$ = 8.4, p = 0.009), and 26 % higher in energy density (A: $F_{1,20}$ = 15.7, p = 0.0008 and B: $F_{1,20}$ = 16.4, p = 0.0006). However, there was no significant inter-colony variation in capelin and sandlance (water content: $F_{1,20}$ = 0.2, p = 0.7; percent lipid: $F_{1,20}$ =

0.002, $p = 1.0$; protein: $F_{1,20} = 0.2$, $p = 0.7$; and energy density values A: $F_{1,20} = 0.1$, $p = 0.7$, and B: $F_{1,20} = 0.1$, $p = 0.7$).

Proximate composition of the several 0-group and 1-group fish were similar between colonies (Tables 3.4 and 2.5). Of the gadids, white hake at Gull Island were lower in fat, protein and energy density than arctic cod of the same size and length at the Gannet Islands.

3.3.4 Adult puffin morphometrics

During the nestling period, mean mass of adult Atlantic Puffins caught at their breeding colony on Gull Island, Witless Bay was 425.6 ± 35.1 g ($N = 95$) in 1997 and 434.3 ± 34.3 g ($N = 213$) in 1998 ($t_{306} = - 2.0$, $p = 0.04$). The sampling period in 1997 (20 - 27 August) was later than in 1998 (04 July - 14 August), thus I controlled for a date related effect using an ANCOVA for mass by year with date as a covariate. This showed that mass decreased linearly dependent on date thus there was no significant difference in puffin mass between 1997 and 1998 ($F_{1,305} = 3.3$, $p = 0.07$; $r^2 = 0.008$) during the chick-rearing period at Gull Island.

I pooled data on adult puffin size between years at Gull Island, Witless Bay 1997-98 and the Gannet Islands, Labrador 1996-98 during the chick-rearing period and compared the colonies (Table 3.5). Puffins at Gull Island 1997-98 weighed 7.9 % less than those at the Gannet Islands 1996-98. Other body size measurements including wing length, tarsus, bill length and culmen were also significantly smaller in puffins at Gull Island with the exception of bill depth.

3.3.5 Timing of Breeding

At Gull Island in 1998, mean hatch date was 06 July ± 10 days (N = 54). Sixty-one percent of puffin nestlings sampled hatched over a nine-day interval from 26 June to 05 July (Table 3.6). Nevertheless, breeding on Gull Island does not appear highly synchronous as chicks hatched over a six week span from 23 June to 03 August, 1998. Fledging dates were obtained for three chicks in 1998 and it is likely that chicks continued to fledge from Gull Island through to mid-September or later assuming a nestling period from 43 to 83 days (Nettleship 1972).

Annual variation in onset of breeding was much greater between colonies than within colonies. Atlantic Puffins at Gull Island 1998 laid their eggs approximately 35 days earlier by calendar date than puffins at the Gannet Islands 1996-98 ($U = 16.0$, $z = -9.8$, $p < 0.0001$; Figure 3.11). Similarly, the first chicks to fledge from Gull Island, Witless Bay went to sea 32 - 40 days earlier by calendar date than chicks reared at the Gannet Islands, Labrador.

3.3.6 Productivity

The overall breeding success estimate for Gull Island in 1998 was 36 % (N = 64), hatching success was 63 % (N = 43) and fledging success, 57 % (N = 37) (Table 3.7). Only three chicks fledged while I was present at the colony, thus my fledging success estimate was based on healthy chicks that reached 30 days of age (Birkhead and Nettleship 1985). The mean overall breeding success estimate for the Gannet Islands, Labrador during 1996-98 (33 %) was similar to that at Gull Island, hatching success (72 %) was higher, and fledging success (49 %) was lower than that at Gull Island. There was little difference in breeding estimates between colonies with the exception of overall breeding estimate, B, where breeding puffins at the Gannet Islands 1996 were much less successful than those at Gull Island 1998.

My multiple fledging and overall breeding estimates contrast differential levels of investigator disturbance (Table 3.7). Chicks not disturbed during incubation had 52 % higher fledging success (fledging estimate B) than those in burrows visited regularly during incubation (fledging estimate A). Similarly, chicks at the Gannet Islands that were disturbed during incubation had a 30 % lower fledging success than those not disturbed during incubation.

3.3.7 Chick growth

3.3.7.1 Inter-annual variation Gull Island 1997-98

Atlantic Puffin chicks with wing length greater than 120 mm at Gull Island, Witless Bay were 20 % heavier in August 1997 than in August 1998 (Table 3.8). As the chicks got older, the difference in mass between years became less pronounced (10 %). Chicks which hatched late were lighter (grew slower) than those which hatched early in chick-rearing. During the linear growth phase, puffin chicks at Gull Island in 1998 gained mass at 9.4 ± 3.2 $g \cdot d^{-1}$ ($N = 16$) and wing length grew 4.1 ± 0.4 $mm \cdot d^{-1}$ ($N = 16$) (Table 3.9). Gull Island puffin chicks reached a peak mass at age 25 - 30 d, then mass dropped sharply followed by an increase to a second, similar or lower, mass peak around 38 d or later. The three chicks that fledged during my presence in the field in 1998 probably fledged at a younger age than subsequent fledglings. The mean mass loss for the two chicks in which mass decreased from peak mass to fledge was 48.0 ± 2.8 g ($N = 2$) or 14 % body mass over a 10 day period.

3.3.7.2 Inter-annual comparison Gull Island and Gannet Islands

Chick mass in 1 cm wing size classes of Gull Island chicks 1997-98 was lower than Gannet Island chicks 1996-98. Annual chick mass was highest at Gull Island in 1997 yet this mass was consistently lower than the lowest recorded annual chick mass of the Gannet Islands in 1996. An annually decreasing trend in chick body condition was apparent at Gull Island during this study, while chicks appeared to be improving in body condition in each year at the Gannets Islands.

Chicks at Gull Island were significantly smaller than chicks at the Gannet Islands (Tables 2.8 and 3.9). Gull Island nestlings at age 1 - 3 d weighed 12 % less than Gannet Island chicks ($F_{3,140} = 6.2$, $p = 0.0005$), 12 % less at 10 - 12 d ($F_{3,98} = 9.8$, $p < 0.0001$), 31 % less at 37 - 40 d ($F_{3,97} = 45.0$, $p < 0.0001$), 24 % less at peak mass ($F_{3,50} = 26.1$, $p < 0.0001$) and 9 % less at fledging mass ($F_{3,10} = 8.2$, $p = 0.005$). Wing length of Gull Island nestlings was significantly shorter than that of nestlings at the Gannet Islands, except for wing length at fledge (1 – 3 d: $F_{3,150} = 2.8$, $p = 0.04$; 10 – 12 d: $F_{2,62} = 16.4$, $p < 0.0001$; 37 – 40 d: $F_{3,97} = 12.1$, $p < 0.0001$; at peak mass: $F_{3,50} = 3.4$, $p = 0.02$; at fledge: $F_{3,10} = 0.1$, $p = 1.0$) (Appendix G).

Rate of mass gain of chicks at Gull Island and the Gannet Islands in 1997 and 1998 were not significantly different yet mass growth was significantly lower in 1996 at the Gannet Islands ($F_{3,99} = 9.1$, $p < 0.0001$) (Appendix G). Rate of wing length increase was not significantly different between Gull Island chicks in 1998 and Gannet Island chicks in 1997-98 ($F_{2,61} = 1.4$, $p = 0.3$). A comparison of chick mass at discrete growth stages expressed as a percent of adult puffin mass (Gull Island: 431.6 ± 34.7 g, N = 308; Gannet Islands: 468.2 ± 35.1 g, N = 401) showed that Gull Island chicks weighed significantly less at peak mass, fledge mass and mass at age 37 - 40 d than the Gannet Islands chicks in 1996-98 (Table 3.10). However, puffin chicks at Gull Island fledged at

68 % of adult body mass which was comparable to the mean for Gannet Islands 1996-98 of 68.5 %.

I found no significant difference in body masses among chicks at Gull Island that were measured frequently and chicks measured only once (Table 3.11). In fact, frequently weighed chicks at Gull Island had slightly greater masses.

3.4 Discussion

3.4.1 Nestling diet

The predominant prey of adult Atlantic Puffins provisioning young was immature or spent capelin at Gull Island, Witless Bay in 1997 and 1998. Post-larval sandlance dominated the diet at the Gannet Islands in 1996 and 1997 and were replaced by miscellaneous prey in 1998. Similarly, at Gull Island in 1997, higher proportions of larval sandlance and larval capelin were delivered to the colony and replaced by post-larval sandlance in 1998. In Labrador, daubed shannies, sculpins, arctic cod, squid, polychaetes and crustaceans also made up a large proportion of the diet in the absence of capelin and sandlance. These smaller miscellaneous prey items are considered sub-optimal (Harris 1984) though most Northwest Atlantic puffin studies (Rodway and Montevecchi 1996, Russell 1999) have reported higher proportions of squid and crustaceans than are normally fed to chicks in Northeastern Atlantic colonies (Harris and Hislop 1978). Atlantic Puffin diet was extremely variable between and within years at each colony and even more variable among colonies. Russell (1999) also found diet of puffins at several colonies in insular Newfoundland to be heterogeneous. Both our studies do not concur with the idea that puffin diets are relatively homogeneous throughout Newfoundland and Labrador. In fact, even when capelin migrate inshore to spawn near seabird colonies, the diet brought to puffin chicks is not necessarily homogeneous. It was apparent that puffins do not necessarily depend on one prey species, yet certain colonies of disparate geographical and temporal regimes may be more resilient to prey shifts than others for reasons that are not well understood. I suggest that sub-optimal prey should be considered in terms of energetic return and not the nutritional content of individual fish. In some cases, puffins can spend less energy foraging, i.e. avoid traveling long distances and deep diving, and still provide the chicks with adequate energy, lipid and protein by capturing abundant miscellaneous prey like sculpins in shallow waters close to the colony.

Marked population shifts and displacement of supposed preferred prey species in the diet of Atlantic Puffins have been recorded in the Northeast Atlantic and typically were associated with negative repercussions in breeding performance (Hislop and Harris 1985, Anker-Nilssen 1987, Barrett *et al.*1987, Barrett and Rikardsen 1992). Hislop and Harris (1978) reported that in years where puffins were fed whiting instead of sandlance and sprat, chicks fledged at lower weights. A recent study of Atlantic Puffins (Russell 1999) found that in the colder waters of the Northwest Atlantic such broad displacements which are highly visible in chick diet had little influence on breeding performance. Similarly, Bryant (1998) found that Common Murres at the Gannet Islands exhibited no negative breeding response despite the fact that spawning aggregations of capelin off the south Labrador coast (their preferred prey during 1981-83) did not occur between 1992 and 1998. At Great Island, Witless Bay, Nettleship (1972,1991) and Rodway and Montevecchi (1996) reported high proportions of capelin in puffin chick diets and it appears this region and possibly Funk Island, off eastern Newfoundland, are more conducive to higher concentrations of capelin than other localities in which Atlantic Puffin breeding colonies are situated. In 1981, at Great Island, however, a decline in capelin abundance in Witless Bay during spawning season was thought to induce total breeding failure of Atlantic Puffins (Nettleship 1991).

At Gull Island, capelin biomass in chick diet decreased from 70 % in 1997 to 54 % in 1998, this corresponded to an increase in adult sandlance from about 4 to 37 % diet biomass in 1997 and 1998, respectively. Also, a dramatic switch occurred in young sandlance by 94 % and 1-group capelin by 90 % from 1997 to 1998 during the middle chick-rearing period. Larval sandlance were displaced by of white hake, cottids and crustaceans in 1998. Prey base for Atlantic Puffins appears to be highly variable in Witless Bay, especially with regard to sandlance during my study. Additionally, the somewhat lower species diversity in 1997 was likely an artifact of a lower number of sampling sessions, three days in 1997 as opposed to nine days in 1998.

Proportions of adult fish in chick diet in 1996 at the Gannet Islands may have been misrepresented and inflated by the disproportionate sample size late in the season when more adult fish were typically present in the diet. Thus, it is possible that the mass of small, watery fish was underestimated in early and middle chick-rearing due to effects of drying in transit to colony (Montevecchi and Piatt 1987). Numerical frequency of small fish may also be underestimated because many are lost over cliff edges during collection by fleyging (personal observation) or they are disembodied either during flight or upon capture of the adult puffin. Bill-loads in 1996 were typically composed of larval gadids and polychaetes until August when high proportions of adult fish were brought to the colony. These factors considered, I suspect that the actual annual proportion of adult fish in 1996 at the Gannet Islands was probably equal to or less than that in 1998 and that the food supply available to puffins at the Gannet Islands was very poor in 1996.

I found that the nutritional contribution of sandlance fed to young puffins was higher than that of capelin based of calorific contribution, fat and protein at both colonies and that there was no difference in the nutritional value of these fish between colonies. Russell (1999) documented similar findings. Though other studies (Brown and Nettleship 1984, Lawson *et al.* 1998) have suggested that capelin are a higher quality prey than sandlance, these were apparently not based on samples taken from seabirds during the breeding period. Fish vary in composition depending on time of year and even environmental conditions (Carscadden 1984, Montevecchi and Piatt 1987, Lawson *et al.* 1998).

3.4.2 Size distribution of prey

The length of capelin delivered to puffin chicks did not vary significantly between colonies despite the fact that capelin utilized by puffins in Labrador in the late 1990s are much smaller than those brought to nestlings in the 1980s. Adult capelin can grow to a length of 200 mm and are typically captured up to 150 mm by puffins (Harris 1984). None of the capelin brought back to Gull Island were 0-group transparent juveniles, though DFO surveys in Witless Bay suggested that 4 - 200m capelin were available (J. Anderson pers. comm.). Though, sandlance can grow to 320 mm in length, the size of sandlance fed to young puffins was typically below 200 mm in this study. The largest sandlance (212 mm) ever recorded to have been delivered to a puffin chick was documented in my study, though it is not known whether the chick could actually eat it. The sandlance I collected from provisioning puffins appear to change from transparent larval fish at 80 - 90 mm. In 1997, no sandlance greater than 90 mm were harvested by puffins at Gull Island.

It has been suggested that a seasonal size increase in prey could be a function of chick age (Bradstreet and Brown 1985) though this phenomenon is more likely a function of the seasonal growth of the fish themselves. Additionally, in my study, fish size actually diminished from middle chick-rearing onward possibly indicating that schools of mature fish had migrated out of the puffin foraging range. Another possible explanation for the decreasing trend in fish size immediately prior to fledging is that food demands of the growing chicks are curtailed by the necessity a reduction in body mass for flight.

3.4.3 Adult puffin morphometrics

Results from my study indicated that adult Atlantic Puffins at Gull Island, Witless Bay weighed less, had shorter wings, and smaller bills than adult puffins at the Gannet Islands, Labrador. This decline in adult puffin body size from north to south is consistent with Northeast Atlantic breeding colonies even though Northwest Atlantic colonies are situated within a shorter latitudinal distance (Harris 1978; Moen 1991, Gaston and Jones 1998). Montevecchi (1994) also made this argument for Great Auks. Moen (1991) speculated that variation in body size among puffin colonies was attributable to the combined environmental effects of ocean temperature and food quality. This is an example of selection for larger body size at high latitudes to offset stress of more severe climate (I. Jones pers. comm.).

Inter-year variation in mass of adult puffins during the chick-rearing period was not evident at Gull Island between 1997 and 1998. However, at the Gannet Islands adult puffins appeared to have higher body weights when preying on larval fish, enough to allow me to loosely speculate that puffins may have expended more energy to obtain larger, fattier prey such as capelin and sandlance in some years. If so, this would be evidence of a cost of reproduction related to increased investment in 'good' years. My results were consistent with Anker-Nilssen and Lorensten (1990) who found that individual mass declined through chick rearing season but that this decline was not statistically significant. Put forth in existing literature are two possible reasons for mass loss in adult seabirds from incubation to provisioning. First, loss of mass as an immediate consequence of reproductive stress, and second, an adaptive response enable reduction of wing-loading during provisioning (Freed 1981; Norberg 1981). The former scenario can be a function of food supply, and the second, unless driven by specific environmental cues, independent of annual variation in food supply. It is also possible that the extra energy required for provisioning may exceed energy saved by programmed weight loss, resulting in additional mass loss during chick-rearing. Regardless of the mechanism, puffins at Gull Island and the Gannet Islands lost weight coincidentally with an increase in foraging effort. This is consistent with the idea that seabirds will increase energy expenditure to provide for chicks (Cairns 1987).

A confounding factor in the adult puffin mass data was that the breeding or provisioning population may not have been exclusively represented. Though the barrier net was strategically positioned to ensnare breeding puffins, I still had to eliminate sub-adults with less than two bill-grooves from the total sample. Thus it is likely that the sampling method used to capture Atlantic Puffins did not distinguish between successful breeders, unsuccessful breeders and non-breeders.

3.4.4 Timing of Breeding

The median Atlantic Puffin hatch date at Gull Island was a week later in 1998 than in 1997 yet was similar to hatch dates of puffins at Great Island 30 years earlier in 1968-69 (Nettleship 1972). Puffins at the Gannet Islands in Labrador had median hatch dates that were roughly four days later in the late 1990s than in the early 1980s. Onset of egg laying at Witless Bay was approximately one month earlier (by calendar date) than at the Gannet Islands and both colonies finished breeding at approximately the same time, in late September (G. Robertson, J. Chardine pers. comm.). Nettleship (1972) also found that puffins in Witless Bay, on Great Island in 1968-69, commenced breeding earlier and had a longer nestling period than those at the Gannet Islands 1981-83 (Birkhead and Nettleship 1985). Puffins in more northern colonies may be constrained to a shorter breeding season. This is because they are limited by climatic conditions such as sea ice inhibiting early breeding (e.g. Hipfner and Gaston 1999), snow cover, frozen ground, drying conditions (Rodway *et al.* 1998) and early arrival of winter sea storms and cold water at the end of the breeding period in the north. The longer temporal window for breeding in Witless Bay compared to that at the Gannet Islands, Labrador may allow seabirds greater success in recuperation from temporary prey deficiencies (Nettleship

1972). At the Gannet Islands in 1982, puffins bred a week later than they did in 1981 and 1983 and this was attributed to ice conditions (Birkhead and Nettleship 1983). Similarly, in 1992 and 1993 at Great Island, Rodway *et al.*(1998), found hatch dates to be a week later and related it to a cold ocean event. These events may in turn delay the timing of spawning in capelin but are not reported to affect puffin productivity (Rodway *et al.*1998).

A problem associated with accounts of hatch date frequency is that the range of hatch dates is related to effort invested by the researcher. Failure to not continue to sample new burrows after initial sample number is acquired may lead to a hatch frequency within a limited range if subsequent eggs are laid. Also, eggs with prolonged incubation periods must continue to be checked and not regarded as "dead egg". Often cold eggs, thought to be abandoned, would hatch and this was more common at Gull Island than at the Gannet Islands. These may be possible sources of discrepancy where hatch dispersion in the 1960s and 1970s in Witless Bay appeared much shorter than that in 1998.

3.4.5 Productivity

Despite the virtual absence of capelin at the Gannet Islands during 1996-98, hatching success, fledging success and overall breeding success were not much different from estimates at Gull Island in 1998. Contrary to expected, overall breeding success estimates appeared to be higher at the Gannet Islands than at Gull Island and very similar at the Gannet Islands between the 1990s and the 1980s. The one anomaly was that the overall breeding success estimate at the Gannet Islands in 1996 was 40 % lower than any other colony-year at both colonies. Results from this study do indicate that this low breeding performance may have been related to food supply shortage at the Gannet Islands but not exclusively due to the low capelin in chick diet. Alternative prey such as sandlance, apparently were not as accessible as in the past when capelin biomass in chick diet plunged below 20 % (Birkhead and Nettleship 1985). Chick mortality during the nestling period in the case of total breeding failure is more easily assessed and most commonly attributed to food availability (Anker-Nilssen and Rostad 1993) or human interference (Kress 1977). Additionally, it is often difficult to disassociate the compounding effects of a diminished food supply and investigator disturbance when the latter may be equal to or surpass stresses of the natural environment. Hatching success is thought to be the estimate most affected by investigator disturbance (Rodway *et al.* 1996). Despite this, comparability between colonies within one study may be considered valid where the level of investigator disturbance is standardized. However, as is shown in Chapter Two of my study, adult puffins will react to investigator disturbance with varying intensity at different colonies under variable conditions making impact impossible to predict. The lesson here is to create as little disturbance as possible. Breeding success estimates can be improved particularly by limiting frequency of investigator visits to burrows. With previous knowledge of approximate laying, hatching and fledging dates investigators can plan to check nests to two or three times during the breeding season to estimate rate of egg or chick loss, hatching success, fledging success and overall breeding success (Birkhead and Nettleship 1985). Birkhead and Nettleship (1983, 1985) used this method in the early 1980s at the Gannet Islands to calculate an overall breeding success estimate of 78 % when puffins in regularly visited plots had a breeding success of 35 % which was similar to my estimates in the late 1990s.

3.4.6 Chick Growth

Atlantic Puffin nestlings at the Gannet Islands, Labrador 1996-98 were expected to exhibit slower growth and higher mortality than nestlings at Gull Island, Witless Bay 1997-98 because the contribution of capelin to nestling diet had reached a record low for the Gannet Islands. On the contrary, growth rate and nestling condition was similar or better at the Gannet Islands even in 1996, the poorest food year at the Labrador colony. Such inter-annual differences in puffin chick growth may be strongly associated with variation in availability of preferred prey, as is the case for other seabirds (Hamer *et al.* 1991). The pattern of mass gain of Gull Island chicks was distinctly different from those at the Gannet Islands yet wing growth was almost identical. Chicks at Gull Island reach a peak mass earlier than their northern conspecifics and growth slowed whereas chicks at the Gannet Islands generally continued to increase in mass until a few days prior to fledge. Reduced growth rates and prolonged fledging periods are associated with periods of food stress (Anker-Nilssen 1987), however there was no evidence that puffin chicks in Witless Bay were food stressed. In fact, Gull Island chicks received more adult capelin and post-larval sandlance than nestlings in Labrador. On a population level, prediction one of Ydenberg's growth-mortality trade-off theory may proffer an eloquent explanation for the different growth patterns between colonies. Following the logic of Ydenberg's (1989) model, Gull Island chicks may be increasing their chances of survival by staying in burrow longer and they can afford to grow slower and fledge at lower weights because of relatively favourable climatic conditions than chicks in Labrador. Fledging mass was similar between colonies when chick mass was expressed as a percent of adult body mass to correct for geographical body size variation (Barrett and Rikardsen 1992). However, the chicks that I sampled at Gull Island were the first to fledge and I suspect that subsequent chicks, in which I did not have the opportunity to observe leave the colony, fledged at lower masses. It is apparent that puffin chicks at the Gannet Islands must reach peak mass and fledge at a younger age than chicks at Gull Island, because chances of survival at sea may be increased by heavier fledge mass and longer wings (Ydenberg 1989).

It is possible that levels of kleptoparasitism (Grant 1971, Nettleship 1972, Harris and Hislop 1978) or increased inter-specific competition affected foraging efficiency in 1998 but I did not collect data on these factors. Unlike visitation during incubation, there appeared to be little effect of frequent weighing of puffin nestlings at both colonies except at the Gannet Islands in 1998 when frequently weighed chicks were significantly smaller. A confounding phenomenon, which may have reduced the efficacy of my comparison on chick growth as well as productivity, may have resulted from a 'hungry horde effect' (Gaston 1985). A 'hungry horde effect' occurs when breeding performance and fledge mass decrease with increasing colony size because food supply around the colony is subject to greater foraging pressure (Furness and Birkhead 1984, Gaston 1985, Hunt *et al.* 1986). The puffin and collective interspecific breeding populations at Gull Island puffin far exceed population sizes at the Gannet Islands. Therefore, under homogeneous prey conditions, Gull Island puffins should exhibit lower chick growth rates and productivity estimates than at the Gannet Islands.

3.4.8 Conclusions

At the Gannet Islands in the late 1990s, Atlantic Puffins delivered approximately 60 % less capelin to their young than in the previous decade. Despite this, nestlings appeared to be in as good or better condition at the Gannet Islands, except in 1996, than nestlings at Gull Island, Witless Bay. However, overall breeding success at the Gannet Islands was lower due to consistently lower fledging success estimate than at Gull Island.

Seabirds are thought to be useful bioindicators of small fish, planktonic crustaceans, and squid abundance and distribution (Hislop and Harris 1985, Barrett and

Furness 1990, Baird 1991, Montevecchi 1993, Montevecchi and Myers 1996). The high species diversity within Atlantic Puffin diets in my study suggests that puffins are general feeders and are 'haphazard samplers' of the fish populations that they are capable of capturing. Murres at the Gannet Islands in a concurrent study by Bryant (1998) also provided valuable insights into non-commercial fish populations by sampling deeper regions of the water column than the puffins. In study year 1996, anomalous low breeding parameters were evident for puffins. I suspect that this was not completely due to a depauperate capelin source. Post-larval sandlance also were not used to the extent they had been in previous years when capelin plunged below 20 % of puffin chick diet biomass. Furthermore, Common and Thick-billed Murres used benthic daubed shannies instead of pelagic post-larval sandlance as an alternative to capelin though all three fish species were comparable in nutritional value at that time. This use of daubed shannies had not been previously recorded at the Gannet Islands. Were there dramatic changes in the sandlance population in the late 1990s as well?

The extent to which puffins buffered the effects of food stress at the Gannet Islands was considerable. Though negative effects were evident, they successfully reared young where, under prey-depleted conditions, puffins at other colonies have been known to fail. Chicks at both of my study colonies were generally healthy with low obvious parasite loading which lead me to believe that the lower mass of Gull Island chicks reflected genetic and geographic variation in growth and provisioning strategies likely constrained by climate and inter- and intra-specific competition for resources. So what makes the Gannet Islands unique? A colder ocean climate constrains chick-rearing to a shorter season that at Gull Island, thus chicks must grow faster in order to increase the chances of post-fledge survival. There was little to no kleptoparasitism and less avian competition at the Gannet Islands than at Gull Island. The Gannet Islands, situated 35 km offshore, was proximal to alternative prey source of equal nutritional value to capelin. On all counts excluding colder climate, it may be less energetically demanding for puffins to rear young at the Gannet Islands, Labrador than at Gull Island, Witless Bay despite the more consistent abundance of capelin in Witless Bay.

My results and speculations augment the value of long term monitoring at each unique colony however it should not be taken for granted that Atlantic Puffins, or other seabirds, at distinct colonies will respond to investigator disturbance in the same manner and degree. Despite the fact that inter-colony statistical comparison may not be valid for all parameters such as productivity or chick growth, this does not undermine the importance of investigating and contrasting the variable sensitivity of distinct seabird colonies to environmental change.

Table 3.1 Relative proportions (by mass) of prey items delivered to young Atlantic Puffins at Gull Island, Witless Bay during 1997-98 and the Gannet Islands, Labrador during 1996-98. Sample numbers for annual totals are displayed in Figure 3.3.

		Witless Bay		Gannet Islands		
	Species group	1997*	1998	1996	1997**	1998
percent occurrence	capelin	28.2	57.3	4.0	15.0	12.5
	sandlance (larval)	43.7	12.3	28.2	30.8	35.8
	sandlance (post-larval)	4.2	27.5	32.3	35.5	11.7
	gadids	7.0	7.6	52.4	19.6	12.5
	cottids	7.0	12.3	35.5	55.1	54.2
	blenniids	8.4	11.1	37.1	30.8	55.8
	other	12.0	16.0	49.2	31.8	22.5
percent frequency	capelin	25.2	22.3	0.6	2.2	1.3
	sandlance (larval)	61.1	27.7	14.7	22.7	24.4
	sandlance (post-larval)	0.6	7.3	5.0	9.2	1.7
	gadids	1.3	1.3	21.2	4.2	2.3
	cottids	1.7	5.1	12.8	33.4	24.6
	blenniids	6.6	22.1	24.7	18.3	40.8
	other	3.6	14.2	20.9	10.1	5.0
percent mass	capelin	70.7	57.8	3.4	13.9	25.3
	sandlance (larval)	16.2	1.4	8.0	6.8	13.6
	sandlance (post-larval)	2.7	34.3	45.3	47.5	18.3
	gadids	0.8	1.3	12.4	6.0	3.6
	cottids	0.7	0.9	6.3	12.6	15.7
	blenniids	1.8	1.7	10.0	5.5	18.2
	other	0.7	2.6	14.6	7.7	5.2

* Diet collected only during the second bi-week of the nestling period.

** Diet collected during the second, third and fourth bi-weekly period.

Table 3.2 Median and range of mass and total length of fish collected from chick provisioning Atlantic Puffins on Gull Island, Witless Bay during 1997 and 1998.

Prey	Group		Mass			Length	
		N	Median (g)	Range	N	Median (mm)	Range
capelin	1-group	118	1.4	0.4 - 3.6	104	77	50 - 100
	immature or spent	131	7.8	1.5 - 20.5	122	131	72 - 171
	adult male	11	17.8	9.0 - 21.8	11	151	143 - 159
	gravid female	15	9.9	5.2 - 21.1	15	132	118 - 154
sandlance							
	0-group larval	472	0.1	0.1 - 0.8	375	44	15 - 75
	post-larval	69	7.3	0.7 - 20.3	68	161	66 - 212
white hake	0-group post-larval	15	1.7	0.2 - 6.7	15	63	45 - 103
blenniids	larval + post-larval	204	0.2	0.1 - 3.4	145	36	21 - 90
cottids	post-larval	44	0.3	0.1 - 3.1	46	31	23 - 52
alligatorfish	post-larval	10	0.2	0.1 - 0.4	12	36	25 - 39
flatfish	post-larval	3	0.1	0.1 - 0.1	3	22	20 - 25
lumpfish	post-larval	3	0.4	0.1 - 0.4	3	29	29 - 34
crustaceans		87	0.1	0.1 - 4.2	71	~ 27	~ 14 - 65

Table 3.3 Annual mean mass and length of larger prey taxa collected from Atlantic Puffins provisioning chicks at Gull Island, Witless Bay during 1997 and 1998.

		Mass (g)			Length (mm)		
Prey type	Year	X	SD	(N)	X	SD	(N)
capelin							
immature or spent	1997	7.4	5.0	(46)	119.3	25.0	(48)
	1998	8.0	3.0	(85)	131.4	17.5	(74)
gravid	1997	21.1	0.0	(1)	154.0	0.0	(1)
	1998	10.3	3.1	(14)	133.5	7.5	(14)
male	1997	15.7	4.3	(4)	149.8	4.7	(4)
	1998	18.5	1.9	(7)	152.4	4.9	(7)
sandlance							
post-larval	1997	1.6	2.0	(14)	89.6	28.2	(14)
	1998	11.2	4.4	(55)	169.5	20.6	(54)

Table 3.4 Results of proximate composition analysis on prey items collected from Atlantic Puffins provisioning chicks at Gull Island 1998. N, is the number of fish per sample.

Species	Length mm (N)	Water (%)	Fat (%)	Ash (%)	PN (%)	ED (A) $kJ \cdot g^{-1}$ (wet mass)	ED (B) $kJ \cdot g^{-1}$ (wet mass)
capelin							
1-group	75-85 (21)	80.0	1.4	1.8	16.8	3.9	4.5
immature or spent	100-109 (2)	79.4	2.7	1.8	16.1	4.3	4.9
	119-129 (5)	80.0	1.2	2.1	16.7	3.8	4.4
	140-149 (3)	78.7	4.6	1.9	14.8	4.7	5.3
	150-159 (1)	83.3	0.4	2.0	14.3	3.0	3.5
gravid female	130-139 (3)	80.6	1.3	1.9	16.2	3.7	4.3
	140-149 (1)	69.8	1.8	4.0	24.4	5.5	6.5
adult male	140-149 (1)	86.7	0.4	0.0	12.8	2.7	3.2
	150-159 (1)	84.1	0.2	1.6	14.1	2.9	3.4
sandlance							
larval	30-50 (81)	81.7	1.3	2.2	14.8	3.5	4.0
post-larval	120-140 (9)	73.0±9.2	3.1±0.7	2.6 (1.1)	21.3±8.6	5.5±1.6	6.3 ±1.9
	140-155 (3)	76.0	5.6	2.7	15.7	5.3	5.9
	155-170 (3)	72.5	7.7	2.2	17.6	6.4	7.2
	181-190 (2)	72.6	6.6	2.1	18.7	6.2	7.0
	190-200 (2)	76.6	3.5	2.0	17.9	4.9	5.6
gravid female	120-140 (1)	73.1	3.7	2.2	20.9	5.6	6.4
hake	55 (1)	86.7	2.8	2.7	10.0	3.1	3.5
	65-75 (2)	79.3	0.7	1.2	17.6	3.8	4.4
cottids	25-35 (13)	79.4	2.9	0.6	15.1	4.1	4.7
blenniids	20-35 (31)	80.9	0.3	2.4	17.6	3.6	4.3
alligatorfish	30-39 (6)	84.5	0.9	0.9	13.6	3.1	3.6

Table 3.5 A comparison of Atlantic Puffin adult morphometrics during the chick rearing period at Gull Island, Witless Bay during 1997-98 and the Gannet Islands, Labrador during 1996-98.

	Gull Island			Gannet Islands			df	t	p
	X	SD	N	X	SD	N			
mass (g)	431.6	34.7	308	468.2	35.1	401	707	13.8	<0.0001
wing (mm)	169.0	4.6	304	174.4	13.5	308	610	6.5	<0.0001
tarsus (mm)	33.6	1.7	303	34.5	1.4	310	611	7.6	<0.0001
bill length (mm)	29.0	1.5	278	29.9	2.8	275	551	4.6	<0.0001
bill depth (mm)	37.3	2.4	270	39.0	2.2	274	542	1.3	0.2074
culmen (mm)	47.7	2.2	261	49.9	2.5	261	536	11	<0.0001

Table 3.6 Summary of breeding chronology for Gull Island, Witless Bay during 1997-98 and the Gannet Islands during 1996-98. Dates demarked with question marks are not median dates and were estimated from first chick dates at Gull Island in 1998.

Colony	Year	Median Laying	First Chicks	Median Hatching	First Fledge
Gull Island	1997	29 May	02 Jul	10-15 Jul ?	_
	1998	23 May	20 Jun	02 Jul	11 Aug
	1996	26 Jun	03 Aug	05 Aug	15 Sep
Gannet Islands	1997	27 Jun	01 Aug	06 Aug	18 Sep
	1998	26 Jun	28 Jul	05 Aug	12 Sep

Table 3.7 Calculations for Atlantic Puffin hatching success, fledging success (A,B and C) and breeding success (A and B) at Gull Island, Witless Bay in 1998 and the Gannet Islands during 1996, 1997 and 1998.

Productivity parameters	Gull Island	Gannet Islands		
	1998	1996	1997	1998
No. eggs$_{A}$	47	82	38	40
No. chicks (initially found as eggs)$_{B}$	27/43*	42	32	24
Hatching success (%)$_{B/A}$	(62.8)	(51.2)	(84.2)	(60.0)
No. fledged$_{C}$	10/21	14	14	14
Fledging success A (%)$_{C/B}$	(47.6)	(33.3)	(43.8)	(58.3)
No. chicks (initially found as chick)$_{D}$	20	70	10	42
No. fledged$_{E}$	11/15*	33	5	20
Fledging success B (%)$_{E/D}$	(73.3)	(47.0)	(50.0)	(47.6)
Total nests in study$_{A+D}$	64	152	48	117
Total nests with chicks N(%)$_{B+D}$	37	112 (73.7)	42 (87.5)	85 (72.6)
Total no. chicks that fledged$_{C+E}$	21	47	19	43
Fledging success C (%)$_{F=(C+E)/(B+D)}$	(56.8)	(42.0)	(45.0)	(51.0)
Breeding success A: (%$_{B/A}$ x %$_{C/B}$)	30 %	17 %	37 %	34 %
B: (%$_{B/A}$ x %$_{F}$)	36 %	22 %	38 %	29 %

*Note that the denominator is lower than total number of eggs or chicks originally found. I was rendered unable to track egg/chick progress as adult puffins made these burrows longer. They could not be classed as abandoned or failed as the burrows continued to show signs of activity. This problem did not occur at the Gannet Islands.

Table 3.8 Mean mass and standard deviation of Atlantic Puffin nestlings which were measured only once at Gull Island, Witless Bay during 1991 and 1998.

		Intra-annual comparison					Inter-annual comparison				
Wing length (mm)		August 1997	September 1997	df	t	p	August 1997	August 1998	df	t	p
	X	211.7	190.8				211.7	186.8			
110-119	SD	47.1	34.6	19	1.2	0.3	47.1	37.4	12	1.0	0.3
	N	9	12				9	5			
	X	243.7	198.0				243.7	195.0			
120-129	SD	30.3	19.8	38	5.7	<0.0001	30.3	14.9	22	3.7	0.001
	N	18	22				18	6			
	X	258.8	207.5				258.8	233.0			
130-139	SD	29.7	25.3	74	8.1	<0.0001	29.7	31.0	44	2.0	0.06
	N	40	36				40	6			
	X	289.4	227.2				289.4	258.8			
140-149	SD	29.8	29.8	73	8.9	<0.0001	29.8	18.5	51	2.8	0.007
	N	45	30				45	8			
	X	298.3	190.0				298.3	–			
150-159	SD	24.7	75.7	4	2.4	0.08	24.7	–			
	N	3	3				3	–			

Table 3.9 Comparison of Atlantic Puffin chick growth parameters for Gull Island, Witless Bay during 1998 and the Gannet Islands, Labrador during 1996, 1997 and 1998.

Growth Parameter	Units	Gull Island			Gannet Islands								
		1998			1996			1997			1998		
		x	SD	N	x	SD	N	x	SD	N	x	SD	N
Linear Phase	mass increase (g.d-1)	9.4	3.2	(16)	7.1	2.8	(40)	9.0	1.8	(18)	9.4	2.2	(35)
Growth Rate	wing increase (mm.d-1)	4.1	0.4	(16)				3.9	0.3	(18)	4.1	0.4	(35)
Age 1 - 3 d	mass (g)	48.2	6.4	(28)	51.1	8.0	(60)	59.6	12.0	(12)	54.2	9.3	(46)
	wing (mm)	22.6	1.6	(28)	23.0	4.1	(60)	22.7	1.1	(12)	24.4	2.6	(46)
Age 10 - 12 d	mass (g)	114.3	26.0	(26)	116.7	24.8	(46)	126.9	16.9	(7)	139.9	20.0	(41)
	wing (mm)	36.0	7.1	(26)	32.1	4.2	(46)	38.7	7.7	(7)	40.2	5.1	(41)
Age 37 - 40 d	mass (g)	220.7	58.0	(21)	268.7	41.6	(37)	355.8	31.3	(18)	337.7	39.2	(23)
	wing (mm)	117.7	15.9	(21)	121.2	11.8	(37)	131.8	4.9	(18)	134.2	7.6	(23)
Peak Mass	mass (g)	271.0	54.7	(11)	290.4	34.6	(29)	370.3	24.8	(20)	345.5	39.1	(41)
	wing (mm)	120.0	21.8	(11)	120.0	21.8	(29)	133.1	7.1	(20)	126.6	9.1	(41)
	age (d)	38.2	5.6	(10)	38.9	12.7	(29)	38.8	3.0	(17)	33.8	3.5	(33)
Fledge	mass (g)	293.3	15.5	(3)	295.5	5.0	(2)	344.3	25.0	(14)	348.0	15.2	(5)
	wing (mm)	142.5	2.1	(3)	142.5	2.1	(2)	141.4	4.5	(14)	141.8	4.9	(5)
	age (d)	48.0	2.6	(3)	45.0	0.0	(2)	43.9	2.3	(10)	41.7	1.5	

Table 3.10 Inter-colony comparison of Atlantic Puffin nestling mass at discrete stages along their growth curves between Gull Island 1998 and the Gannet Islands 1996-98. Nestling mass is expressed as a percent of adult puffin mass during the chick-rearing period at respective colonies.

Discrete stage of growth	Gull Island	Gannet Islands			ANOVA results		
	1998	1996	1997	1998	df	F	p
Age 1-3 days	12	11	13	12	3	3.6	0.01
Age 10-12 days	27	25	28	31	3	6.8	0.0003
Age 37-40 days	51	57	76	72	3	35.0	<0.0001
Peak mass	63	71	81	77	3	15.0	<0.0001
Fledge mass	68	63	71	73	3	4.1	0.04

Table 3.11 Mean mass comparison of frequently weighed Atlantic Puffin chicks and those only weighed once at Gull Island during 1998.

Wing length class (mm)	Weighed once			Frequently weighed			T-test results			
	X	SD	N	X	SD	N	Mean Diff.	df	t	p
110-119	186.8	32.4	5	191.6	16.1	8	4.8	11	0.3	0.8
120-129	195.0	14.9	6	210.3	17.8	3	15.3	7	1.4	0.2
130-139	233.0	31.0	6	229.4	16.7	7	-3.6	11	-0.3	0.8
140-149	258.8	18.6	8	265.8	23.4	4	7.0	10	0.6	0.6
110-159	222.9	38.7	25	219.7	32.0	22	-3.2	45	-0.3	0.2

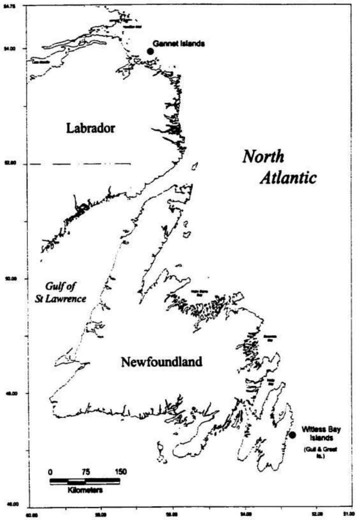

Figure 3.1 Map showing geographical position of study sites at Gull Island in the Witless Bay Ecological Reserve, south eastern Newfoundland and at the Gannet Islands Ecological Reserve, Labrador, Canada.

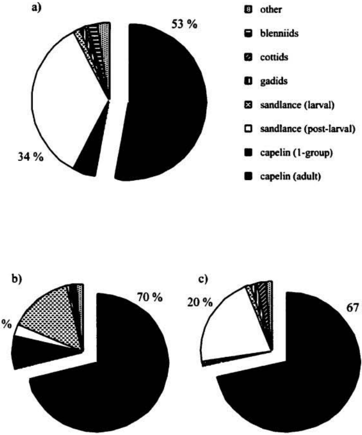

Figure 3.2 Relative contribution of prey taxa to diet biomass of Atlantic Puffin nestlings at Gull Island. The top graph (a) represents annual diet biomass in 1998 and the bottom graphs contrast 1997 (b) and 1998 (c) during the middle chick-rearing period.

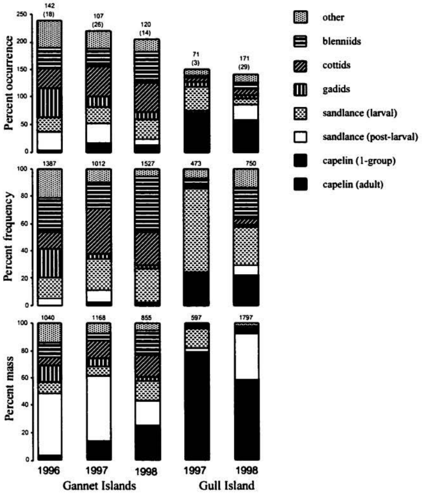

Figure 3.3 Inter-colony comparison of annual proportions of prey delivered to Atlantic Puffin chicks at Gull Island 1997-98 and the Gannet Islands 1996-98. Number of bill-loads (number of sampling days in parentheses), number of prey items and total mass (g) of prey are displayed above each bar of the percent occurrence, percent frequency and percent mass graphs, respectively.

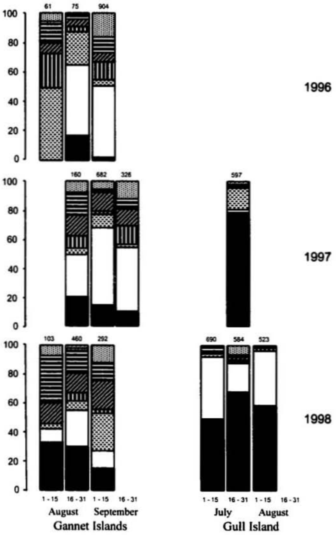

Figure 3.4a Seasonal change in percent mass of prey delivered to Atlantic Puffin nestlings at Gull Island 1997-98 and the Gannet Islands 1996-98. Legend and explanation of numbers are in Figure 3.3.

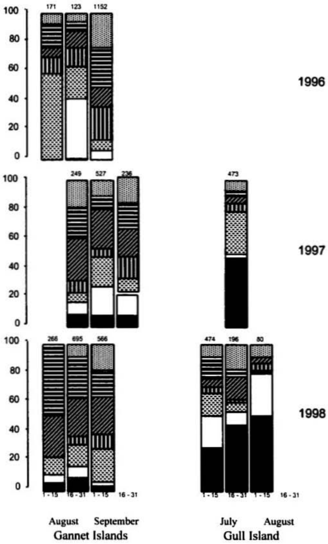

Figure 3.4b Seasonal change in percent frequency of prey delivered to Atlantic Puffin nestlings at Gull Island 1997-98 and the Gannet Islands 1996-98. Legend and explanation of numbers are in Figure 3.3.

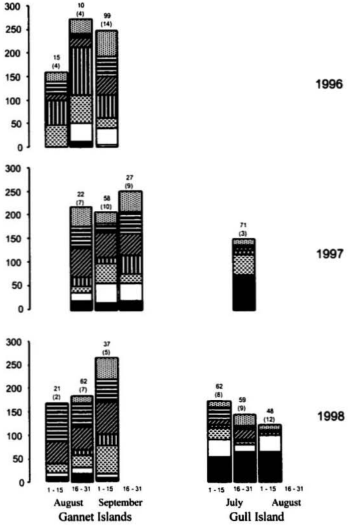

Figure 3.4c Seasonal change in percent occurrence of prey taxa in bill-loads delivered to Atlantic Puffin nestlings at Gull Island 1997-98 and the Gannet Islands 1996-98. Legend and explanation of numbers are in Figure 3.3.

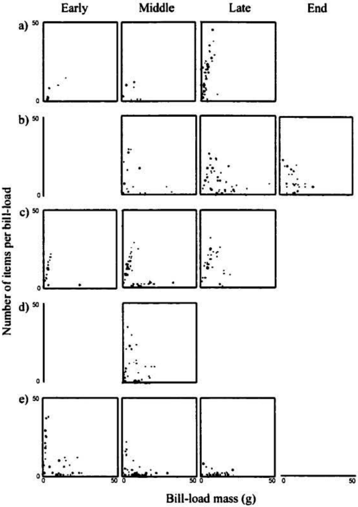

Figure 3.5 Variation through chick-rearing season in the relationship between nestling meal mass and size at the Gannet Islands, Labrador in 1996 (a), 1997 (b), 1998 (c) and Gull Island, Witless Bay in 1997 (d) and 1998 (e).

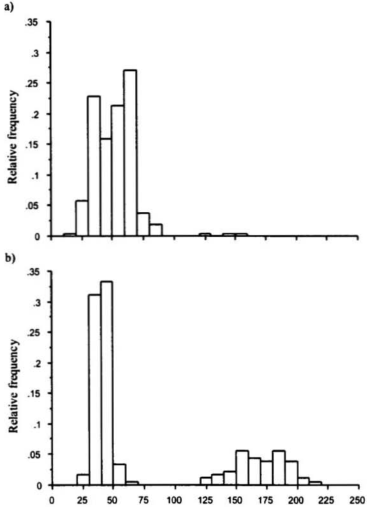

Figure 3.6 Length histograms of sandlance collected from Atlantic Puffins provisioning chicks at Gull Island in 1997 (a) and 1998 (b).

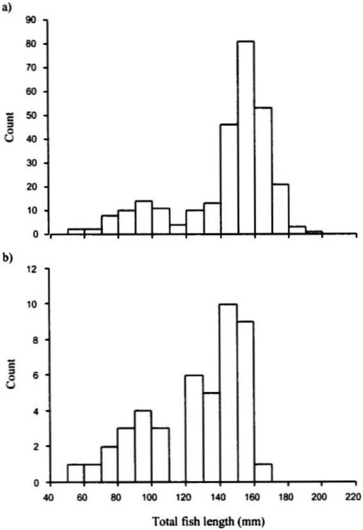

Figure 3.7 Length histograms of capelin delivered to Atlantic Puffin nestlings at Gull Island, Witless Bay in 1997-98 (a) and the Gannet Islands, Labrador in 1996-98 (b).

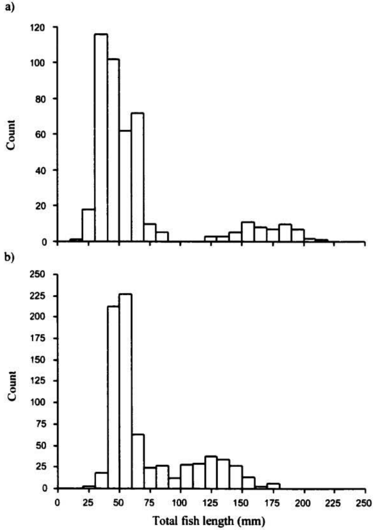

Figure 3.8 Length distribution of sandlance delivered to Atlantic Puffin nestlings at Gull Island, Witless Bay in 1997-98 (a) and the Gannet Islands, Labrador in 1996-98 (b).

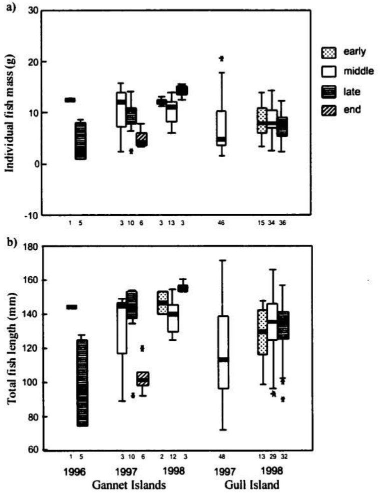

Figure 3.9 Median mass (a) and length (b) of immature or spent capelin delivered to Atlantic Puffin nestlings in early, middle, late and end chick-rearing at Gull Island 1997-98 and the Gannet Islands 1996-98. Lower and upper box boarders (25th to 75th quartiles, respectively) contain 50% of values, whiskers extend to highest and lowest values, and asterisks demark outliers. Sample numbers are displayed below each bar.

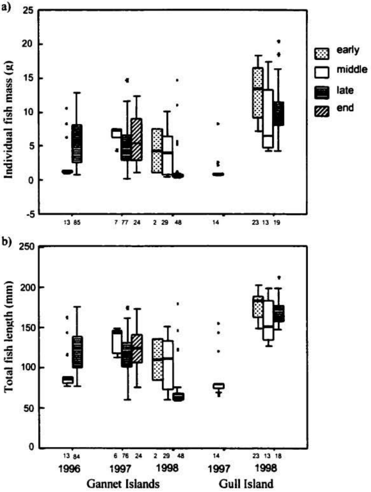

Figure 3.10 Median mass (a) and length (b) of post-larval sandlance delivered to Atlantic Puffin nestlings in early, middle, late and end chick-rearing at Gull Island 1997-98 and the Gannet Islands 1996-98. Lower and upper box boarders (25th to 75th quartiles, respectively) contain 50% of values, whiskers extend to highest and lowest values, and asterisks demark outliers. Sample numbers are displayed below each bar.

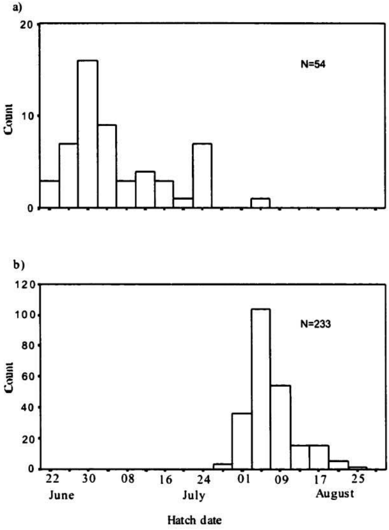

Figure 3.11 Atlantic Puffin hatch date histograms for Gull Island, Witless Bay 1998 (a) and the Gannet Islands, Labrador 1996-98 (b).

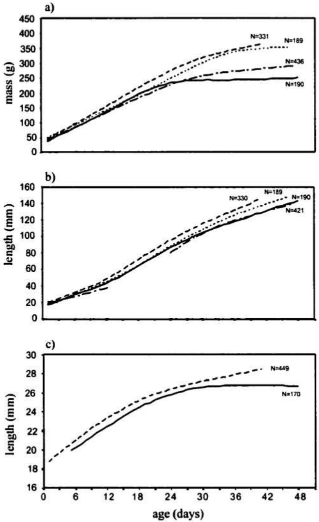

Figure 3.12 Inter-colony comparison of Atlantic Puffin nestling mass increase (a), wing length increase (b) and short tarsus length increase (c). Lowess best fit lines represent chick growth curves: solid lines for Gull Island 1998, dashed lines for Gannet Islands 1998, dotted lines for Gannet Islands 1997, and mixed-dashed lines for Gannet Islands 1996.

CHAPTER FOUR

SUMMARY

The most important finding of my study was that Atlantic Puffins at the Gannet Islands, Labrador were able to successfully fledge young during a supposed period of prolonged food stress. In the absence of spawning aggregations of capelin near the colony, a bewildering array of prey items from post-larval sandlance to tiny sculpins and mollusks were obviously a suitable alternative to capelin during my study. Not only did puffins forage in a variable environment, there appears to be substantial geographical and temporal variability in how they responded to changes. Though the relative abundance of capelin in puffin chick diet was high at Gull Island and very low at the Gannet Islands, breeding success estimates and chick growth rates did not differ substantially. If it is assumed that breeding performance is homogeneous under 'good' food supply conditions, then puffins at the Gannet Islands exhibited a very low degree of negative breeding response to capelin scarcity. I propose two suggestions to explain this, first, that a paucity of capelin is not necessarily equivalent to 'poor' food supply and, second, that geographic differences in puffin demography, population size and other environmental factors confounded my inter-colony comparison. Both suggestions are likely valid and neither prey availability nor breeding response are homogeneous among Northwest Atlantic puffin colonies. I was fortunate in being able to increase the scope and efficacy of my study by contrasting inter-year variability on a broader temporal scale at the same colony. T.R. Birkhead and D.N. Nettleship conducted their study at the Gannet Islands before the shift in capelin distribution in the early 1980s, at a time when the puffin chick diet was similar to that in Witless Bay (Nettleship 1972, 1991). To put things in perspective, indeed there was a reduction in some breeding parameters at the Gannet Islands from the late 1980s to the early 1990s. Nestling growth and survivorship were poorer in 1996 than in any other year for reasons unclear except for a correlation with a drop in capelin diet biomass to three percent (3 %). These changes in diet did by no means result in the catastrophic breeding failure one would project from existing ecological literature on puffins in the northwest and northeast Atlantic (Anker-Nilssen 1987, Brown and Nettleship 1984, Harris and Hislop 1978, Barrett *et al.* 1987, Barrett and Furness 1990, Nettleship 1991). I suspect that the lack of breeding failure can be attributed to the use of post-larval sandlance, which comprised almost half of the chick diet biomass in 1996. It should be pointed out that in other years when capelin diet biomass was below 20 %, puffins utilized much more post-larval sandlance than they did in 1996 and that 1996 small miscellaneous prey mainly comprised larval gadids and not the relatively higher quality sculpins. These may have been contributing factors to lower reproductive and chick mass in 1996 at the Gannet Islands.

Another important finding of my study was that results from proximate composition analyses on the relative nutritional value of capelin and sandlance delivered to young puffins was not consistent with that reported and generally believed among the scientific community. Post-larval sandlance delivered to young puffins were actually higher in lipid, protein and energy density values than capelin. My results, however, were consistent with recent studies on murre (Bryant and Jones 1999, Bryant *et al.*1999) and puffin (Russell 1999) chick diet in Newfoundland and Labrador, which showed that individual capelin may not necessarily provide the highest quality meal to seabird nestlings. The nutritional quality of post-larval sandlance and adult daubed shannies delivered to seabirds was equal to or greater than that of capelin based on the nutritive value of individual fish in proximate composition alone. However, to an adult seabird provisioning its young in addition to replenishing its own energy reserves it is likely the catch-per-unit effort determined by schooling density and depth and time spent traveling to and from the colony that is more important.

Though not a lot is known about non-commercially important forage fish such as sandlance and daubed shannies, it is not likely that these three fish species have similar schooling characteristics. Capelin migrate in dense spawning aggregations in shallow coastal or shoaling waters making them readily accessible to surface feeders like Black-legged Kittiwakes and depth feeding seabirds like Razorbills and murre and puffin species. On the other hand, daubed shannies are a benthic, relatively solitary fish that do not form dense schools and accessibility is restricted to deep divers such as Common and Thick-billed Murres. Byrant (1998) documented a murre chick diet switch from predominantly capelin to daubed shanny in 1997-1998 at the Gannet Islands. Concurrently breeding Atlantic Puffins and Razorbills did not utilize adult daubed shannies, however anecdotally we saw two instances where one adult daubed shanny was delivered to puffin chicks. Sandlance do utilize shallow to mid-waters as do capelin but their aggregations are not as dense and the time when sandlance are gravid in Labrador does not coincide with the puffin breeding period. However, since the nutritional quality of even non-gravid sandlance was similar to or better than capelin, they appear to be an adequate food source and are used consistently utilized by all diving seabirds breeding at the Gannet Islands in varying proportions. Razorbills appear to feed mainly sandlance to their nestlings, puffins deliver 3 - 65 % sandlance by mass and murres deliver consistently less than 10 % sandlance to chicks. Interestingly, the proportion of sandlance fed to razorbill and murre nestlings does not vary with proportion of capelin in diet. However, puffins do alternate the use of capelin and sandlance with chick diet always supplemented by numerous small prey species.

A better understanding of prey preference may be gained by looking at detailed foraging activity of the provisioning parent. The amount of time and effort puffins expend on finding food for their young likely determines which prey species they 'prefer'. The temporal availability of prey species, gravid fish aggregations and the relative ease with which they can be captured and delivered to the chick plays an important role in prey selection. It does not appear possible to conclusively define what 'preferred prey' is for Atlantic Puffins based on such highly variable resource use and resultant breeding response alone. Puffins appear to buffer the effects of changes in prey abundance either by prey switching or increasing foraging effort or both. It is important to keep in mind when considering the information on seabird diet that I and my colleagues have presented that each colony exists in a unique system where factors other than food supply determine reproductive and foraging performance (Phillips *et al.* 1997, Monaghan 1996).

Appendix A. Post hoc examination on one-way ANOVA for Atlantic Puffin bill-load mass (a) and number of items per load (b) at the Gannet Islands in 1996, 1997 and 1998. See Section 2.3.1.1 of this thesis.

a)

Fisher's PLSD for mass
Effect: year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1996, 1997	-3.053	1.936	0.002	S
1996, 1998	1.226	1.872	0.2	
1997, 1998	4.279	1.857	<0.0001	S

b)

Fisher's PLSD for number
Effect: year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1996, 1997	1.056	2.402	0.4	
1996, 1998	-1.982	2.337	0.1	
1997, 1998	-3.038	2.325	0.01	S

Appendix B. Change in Atlantic Puffin diet composition through early, middle and late chick-rearing periods at Gull Island, Witless Bay 1997 (a) and 1998 (b), and the Gannet Islands, Labrador 1996 (d), 1997 (e) and 1998 (f). Number of bill-loads, number of prey items and total grams for percent occurrence, frequency and mass, respectively are in parentheses.

a)

Gull Island 1997	Percent occurrence			Percent frequency			Percent mass		
	Early	Middle (71)	Late	Early	Middle (473)	Late	Early	Middle (597)	Late
capelin									
1-group		21			14			8	
immature or spent		42						57	
male		5						10	
gravid female		2						3	
total mature capelin		49			34			70	
sandlance									
larval		44			28			16	
post-larval		4			3			2	
gadids									
larval cod		–			–			–	
post-larval cod		–			–			–	
1-group:									
white hake		8			6			0	
brown hake		–			–			–	
other 1-group fish									
blenny		7			4			2	
daubed shanny		–			–			–	
cottidae		7			5			1	
alligatorfish		4			2			0	
lumpfish/snailfish		3			1			0	
flatfish		–			–			–	
other		–			–			–	
invertebrates									
crustaceans		11			3			1	
squid		–			–			–	
polychaetes		–			–			–	
pterapods		–			–			–	

Appendix B. (continued)

b) Gull Island 1998	Percent occurrence			Percent frequency			Percent mass		
	Early (62)	Middle (59)	Late (48)	Early (474)	Middle (196)	Late (80)	Early (690)	Middle (584)	Late (523)
capelin									
1-group	16	5	–	7	4	–	12	1	–
immature or spent	19	52	58				18	50	50
male	2	7	4				3	12	7
gravid female	19	5	–			–	16	5	–
total mature capelin	40	64	62	22	42	52	37	67	57
sandlance									
larval	26	9	0	15	6	2	3	1	0
post-larval	36	14	35	21	9	28	43	20	38
gadids									
larval cod	–	–	–	–	–	–	–	–	–
post-larval cod	–	–	–	–	–	–	–	–	–
1-group:									
white hake	5	3	6	3	2	5	1	1	2
brown hake	2	–	–	2	–	–	0	–	–
other 1-group fish									
blenny	26	7	–	16	5	–	3	2	–
daubed shanny	–	–	–	–	–	–	–	–	–
cottidae	11	22	4	6	15	4	0	2	1
alligatorfish	2	7	2	0	3	1	0	0	0
lumpfish/snailfish	–	5	–	–	2	–	–	0	–
flatfish	–	3	–	–	1	–	–	0	–
other	–	–	4	–	–	5	–	–	1
invertebrates									
crustaceans	14	17	–	8	10	–	1	2	–
squid	–	2	2	–	0	3	–	4	1
polychaetes	–	–	–	–	–	–	–	–	–
pterapods	–	–	–	–	–	–	–	–	–

Appendix B. (continued)

c)

Gannet Islands 1996	Percent occurrence			Percent frequency			Percent mass		
	Early (15)	Middle (10)	Late (99)	Early (171)	Middle (63)	Late (1156)	Early (37)	Middle (66)	Late (915)
capelin									
1-group	–	–	2	–	–	0.2	–	–	0.5
immature or spent	–	10	3	–	2	0.4	–	17	2.5
male	–	–	–	–	–	–	–	–	–
gravid female	–	–	–	–	–	–	–	–	–
total mature capelin	–	10	3	–	2	0.4	–	17	2.5
sandlance									
larval	47	60	16	60	22	8	51	22	3
post-larval	–	50	40	–	40	7	–	49	49
gadids									
larval cod	27	99	40	9	15	21	5	3	8
post-larval cod	27	–	8	2	–	1	18	–	6
1-group:									
white hake	–	–	–	–	–	–	–	–	–
brown hake	–	–	–	–	–	–	–	–	–
other 1-group fish									
blenny	27	–	20	16	–	10	16	–	2
daubed shanny	–	10	30	–	6	17	–	2	6
cottidae	13	20	40	6	8	13	6	5	7
alligatorfish	–	–	7	–	–	1	–	–	0
lumpfish/snailfish	–	–	4	–	–	1	–	–	0
flatfish	–	–	–	–	–	–	–	–	–
other	20	–	5	7	–	1	4	–	3
invertebrates									
crustaceans		20	22		6	8		1	3
squid			4			1			3
polychaetes		10	22		2	9		1	6
pterapods			1			1			1

Appendix B. (continued)

d) Gannet Islands 1997	Percent occurrence			Percent frequency			Percent mass		
	Middle (22)	Late (58)	End (27)	Middle (249)	Late (527)	End (236)	Middle (160)	Late (682)	End (326)
capelin									
1-group	5	–	8	2	0	4	1		1
immature or spent	14	16	11	7	8	5	20	14	0
male	–	–	–	–	–	–	–	–	–
gravid female	–	–	–	–	–	–	–	–	–
total mature capelin	14	16	11	7	8	5	20	14	0
sandlance									
larval	14	41	22	6	21	9	4	8	2
post-larval	18	44	37	8	20	15	30	54	44
gadids									
larval cod	14	12	26	6	5	10	1	1	3
post-larval cod	9	1	15	3	1	4	7	1	10
1-group:									
white hake	–	–	–	–	–	–	–	–	–
brown hake	–	–	–	–	–	–	–	–	–
other 1-group fish									
blenny	27	7	17	11	4	2	6	1	1
daubed shanny	27	12	33	11	6	16	9	2	6
cottidae	63	52	–	30	24	9	14	13	13
alligatorfish	9	5	8	3	2	2	0	0	1
lumpfish/snailfish	4	2	8	2	1	2	1	0	2
flatfish	–	–	–	–	–	–	–	–	–
other	4	–	8	2	–	1	0	–	2
invertebrates									
crustaceans	9	7	4	3	2	8	1	0	2
squid	9	9	–	3	4	–	5	5	–
polychaetes	18	3	11	4	1	3	1	0	3
pterapods	–	1	–	–	1	–	–	0	–

Appendix B. (continued)

e)

Gannet Islands 1998	Percent occurrence			Percent frequency			Percent mass		
	Early (21)	Middle (62)	Late (37)	Early (266)	Middle (695)	Late (566)	Early (103)	Middle (460)	Late (292)
capelin									
1-group	–	2	–	–	1	–	–	0	–
immature or spent	10	15	8	7	9	5	35	30	15
male	–	–	–	–	–	–	–	–	–
gravid female	–	–	–	–	–	–	–	–	–
total mature capelin	10	15	8	7	9	5	35	30	15
sandlance									
larval	19	24	60	12	15	22	4	6	26
post-larval	10	22	10	6	8	3	8	26	12
gadids									
larval cod	–	8	24	–	3	10	–	2	2
post-larval cod	–	2	–	–	1	–	–	5	–
1-group:									
white hake	–	–	–	–	–	–	–	–	–
brown hake	–	–	–	–	–	–	–	–	–
other 1-group fish									
blenny	71	47	40	39	28	16	30	16	10
daubed shanny	10	5	11	8	1	2	3	1	3
cottidae	48	48	70	28	26	25	13	12	19
alligatorfish	–	3	11	–	1	7	–	0	1
lumpfish/snailfish	–	5	14	–	2	5	–	0	5
flatfish	–	–	3	–	–	1	–	–	0
other	–	–	–	–	–	–	–	–	–
invertebrates									
crustaceans	–	3	16	–	1	3	–	0	1
squid	–	2	6	–	2	1	–	1	6
polychaetes	–	5	–	–	2	–	–	1	–
pterapods	–	–	–	–	–	–	–	–	–

Appendix C(i). Mean mass and standard deviation per centimetre length class of major prey items collected from Atlantic Puffins provisioning chicks between 1996 and 1998 at the Gannet Islands, Labrador. Each x cm class includes measurements from x.5 tox+1.4 cm inclusive.

Length class (cm)	Immature or spent capelin			Sandlance			Gadids			Cottids			Blenniids		
	x	SD	N	x	SD	N	x	SD	N	x	SD	N	x	SD	N
1	–	–	–	–	–	–	–	–	–	–	–	–	0.1	0.0	2
2	–	–	–	–	–	–	0.1	0.0	2	0.2	0.1	6	0.1	0.0	32
3	–	–	–	0.2	0.1	5	0.2	0.1	63	0.3	0.1	303	0.1	0.2	162
4	–	–	–	0.1	0.0	57	0.3	0.1	117	0.5	0.2	267	0.3	0.1	419
5	0.3	0.0	1	0.2	0.1	236	0.6	0.1	27	0.7	0.2	19	0.2	0.1	125
6	–	–	–	0.4	0.1	95	1.3	0.7	2	–	–	–	0.4	1.1	80
7	0.8	0.2	4	0.7	0.1	29	2.1	0.8	2	–	–	–	0.6	0.1	4
8	1.3	0.5	3	1.1	0.3	28	3.3	0.0	1	–	–	–	–	–	–
9	2.8	0.5	3	1.6	0.4	18	–	–	–	–	–	–	–	–	–
10	3.7	1.0	4	2.9	0.6	21	4.5	3.2	3	–	–	–	–	–	–
11	6.1	0.0	1	3.9	0.7	21	7.6	1.3	4	–	–	–	–	–	–
12	7.8	0.0	1	4.9	1.1	33	10.0	0.8	8	–	–	–	–	–	–
13	8.1	1.0	7	6.3	1.1	33	–	–	–	–	–	–	–	–	–
14	11.2	1.5	10	7.9	1.0	33	–	–	–	–	–	–	–	–	–
15	13.1	1.8	11	9.7	1.1	16	–	–	–	–	–	–	–	–	–
16	12.7	2.2	3	9.9	1.4	7	–	–	–	–	–	–	–	–	–
17	–	–	–	12.5	0.1	4	–	–	–	–	–	–	–	–	–
18	–	–	–	13.5	1.0	3	–	–	–	–	–	–	–	–	–
19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Appendix C(ii). Mean mass and standard deviation per centimetre length class of major prey items collected from Atlantic Puffins provisioning chicks at Gull Island, Witless Bay 1997-98. Each x cm class includes measurements from x.5 to x+1.4 cm inclusive.

Class (cm)	Immature or spent capelin			Gravid capelin			Male capelin			0-group capelin			Post-larval Sandlance			Larval Sandlance			Hake		
	x	SD	N	x	SD	N	x	SD	N	x	SD	N	x	SD	N	?	SD	N	?	SD	N
1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	0.0	18	–	–	–
3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	0.0	108	–	–	–
4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	0.1	101	0.6	0.4	3
5	4.7	–	1	–	–	–	–	–	–	0.5	0.3	8	–	–	–	0.3	0.1	61	0.9	0.2	2
6	4.7	–	1	–	–	–	–	–	–	1.1	0.2	12	0.9	0.2	2	0.4	0.2	70	1.6	1.2	7
7	3.1	0.6	17	–	–	–	–	–	–	1.3	0.3	42	1.1	0.6	5	0.5	0.2	5	2.1	0.4	2
8	4.1	0.8	12	–	–	–	–	–	–	1.7	0.6	36	0.7	0.0	5	–	–	–	3.4	–	1
9	5.0	1.3	10	–	–	–	–	–	–	2.1	1.3	3	–	–	–	–	–	–	–	–	–
10	6.3	2.0	17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6.7	–	1
11	8.8	1.8	24	5.2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
12	10.2	1.7	21	7.6	0.3	3	–	–	–	–	–	–	3.9	1.1	3	–	–	–	–	–	–
13	13.3	2.8	13	10.7	2.3	7	–	–	–	–	–	–	5.3	0.6	3	–	–	–	–	–	–
14	17.0	3.1	3	13.8	2.1	3	14.7	5.0	3	–	–	–	5.7	1.6	4	–	–	–	–	–	–
15	15.2	–	1	21.1	–	1	18.3	0.3	8	–	–	–	7.9	0.8	11	–	–	–	–	–	–
16	–	–	–	–	–	–	–	–	–	–	–	–	9.9	1.6	8	–	–	–	–	–	–
17	–	–	–	–	–	–	–	–	–	–	–	–	11.9	1.4	7	–	–	–	–	–	–
18	–	–	–	–	–	–	–	–	–	–	–	–	14.9	2.5	10	–	–	–	–	–	–
19	–	–	–	–	–	–	–	–	–	–	–	–	16.3	0.9	2	–	–	–	–	–	–
20	–	–	–	–	–	–	–	–	–	–	–	–	16.6	0.9	1	–	–	–	–	–	–
21	–	–	–	–	–	–	–	–	–	–	–	–	20.3	0.0	1	–	–	–	–	–	–

Appendix D. Post hoc examination on one-way ANOVA for capelin mass (a) and total length (b) collected from Atlantic Puffins provisioning nestlings at the Gannet Islands in 1996, 1997, 1998 and 1983. See section 2.3.2.1 of this thesis.

a)

Fisher's PLSD for mass
Effect: year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	8.116	6.673	0.02	S
1983, 1997	7.087	2.564	<0.0001	S
1983, 1998	2.839	2.887	0.05	
1996, 1997	-1.029	7.067	0.8	
1996, 1998	-5.276	7.191	0.1	
1997, 1998	-4.247	3.708	0.02	S

b)

Fisher's PLSD for length
Effect: year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	33.026	26.542	0.01	S
1983, 1997	29.163	10.198	<0.000	S
1983, 1998	5.968	11.484	0.3	
1996, 1997	-3.864	28.109	0.8	
1996, 1998	-27.059	28.600	0.06	
1997, 1998	-23.195	14.748	0.002	S

Appendix E. Post hoc examination on two-way ANOVA for mass by year (a) and period (b) of adult Atlantic Puffins breeding at the Gannet Islands in 1996, 1997 and 1998. See section 2.3.4.1 of this thesis.

a)

Fisher's PLSD for mass
Effect: year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1996, 1997	7.066	4.865	0.005	S
1996, 1998	-7.208	12.791	0.3	
1997, 1998	-14.275	12.982	0.03	S

b)

Fisher's PLSD for mass
Effect: period
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	3.915	11.726	0.5	
1, 3	22.564	11.836	0.0002	S
2, 3	18.649	4.808	<0.0001	S

Appendix F. Post hoc examination on a series of one-way ANOVAs for Atlantic Puffin chick growth parameters at the Gannet Islands in 1996, 1997, 1998 and 1983. See section 2.3.7.2 of this thesis.

Fisher's PLSD for rate of mass gain
Effect: year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	4.976	1.241	<0.0001	S
1983, 1997	3.131	1.526	<0.0001	S
1983, 1998	2.777	1.277	<0.0001	S
1996, 1997	-1.845	1.444	0.01	S
1996, 1998	-2.199	1.177	0.0003	S
1997, 1998	-.354	1.475	0.6	

Fisher's PLSD for rate of wing length gain
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value
1983, 1996	.106	.391	0.6
1983, 1997	.142	.470	0.6
1983, 1998	-.018	.393	1.0
1996, 1997	.036	.452	0.9
1996, 1998	-.124	.372	0.5
1997, 1998	-.160	.454	0.5

Fisher's PLSD for chick mass age 1-3 d
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	-2.500	3.256	.1313	
1983, 1997	-11.033	5.250	<.0001	S
1983, 1998	-5.667	3.448	.0014	S
1996, 1997	-8.533	5.044	.0010	S
1996, 1998	-3.167	3.126	.0471	S
1997, 1998	5.366	5.170	.0420	S

Appendix F (continued)

Fisher's PLSD for chick mass 10-12 d
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	-6.570	9.873	0.2	
1983, 1997	-16.710	18.118	0.07	
1983, 1998	-29.707	10.126	<0.0001	S
1996, 1997	-10.140	17.710	0.3	
1996, 1998	-23.136	9.376	<0.0001	S
1997, 1998	-12.997	17.852	0.2	

Fisher's PLSD for chick mass 37-40 d
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	111.948	17.595	<0.0001	S
1983, 1997	24.844	21.413	0.02	S
1983, 1998	42.938	19.886	<0.0001	S
1996, 1997	-87.104	20.766	<0.0001	S
1996, 1998	-69.009	19.187	<0.0001	S
1997, 1998	18.094	22.740	0.1	

Fisher's PLSD for peakmass
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	109.843	16.580	<.0001	S
1983, 1997	30.007	18.508	.0017	S
1983, 1998	54.769	15.196	<.0001	S
1996, 1997	-79.836	19.192	<.0001	S
1996, 1998	-55.074	16.021	<.0001	S
1997, 1998	24.762	18.009	.0074	S

Appendix F (continued)

Fisher's PLSD for fledge mass
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	66.765	44.892	0.004	S
1983, 1997	17.979	19.592	0.07	
1983, 1998	14.265	29.551	0.3	
1996, 1997	-48.786	46.639	0.04	S
1996, 1998	-52.500	51.620	0.05	S
1997, 1998	-3.714	32.144	0.8	

Fisher's PLSD for chick wing length age 1-3 d
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	-.145	1.225	0.8	
1983, 1997	.133	1.975	0.9	
1983, 1998	-1.591	1.297	0.02	S
1996, 1997	.278	1.898	0.8	
1996, 1998	-1.446	1.176	0.02	S
1997, 1998	-1.725	1.945	0.08	

Fisher's PLSD for chick wing length 10-12 d
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	.164	2.110	.8782	
1983, 1997	-6.420	3.872	.0013	S
1983, 1998	-7.913	2.164	<.0001	S
1996, 1997	-6.584	3.785	.0008	S
1996, 1998	-8.077	2.004	<.0001	S
1997, 1998	-1.493	3.815	.4401	

Appendix F (continued)

Fisher's PLSD for chick wing length 37-40 d
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	9.364	4.270	<0.0001	S
1983, 1997	-1.197	5.197	0.6	
1983, 1998	-3.637	4.826	0.1	
1996, 1997	-10.562	5.039	<0.0001	S
1996, 1998	-13.001	4.656	<0.0001	S
1997, 1998	-2.440	5.519	0.4	

Fisher's PLSD for wing length at peak mass
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	8.428	6.628	0.01	S
1983, 1997	-4.656	7.380	0.2	
1983, 1998	1.784	6.090	0.6	
1996, 1997	-13.084	7.569	0.0009	S
1996, 1998	-6.644	6.319	0.04	S
1997, 1998	6.440	7.103	0.08	

Appendix F (continued)

Fisher's PLSD for fledge wing length
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value
1983, 1996	.062	7.072	1.0
1983, 1997	1.205	3.109	0.4
1983, 1998	.762	4.666	0.7
1996, 1997	1.143	7.335	0.8
1996, 1998	.700	8.118	0.9
1997, 1998	-.443	5.055	0.9

Fisher's PLSD for age at peak mass
Effect: YEAR
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1983, 1996	-1.060	3.679	.5690	
1983, 1997	-.894	4.297	.6809	
1983, 1998	4.083	3.562	.0250	S
1996, 1997	.166	4.350	.9397	
1996, 1998	5.143	3.624	.0058	S
1997, 1998	4.977	4.251	.0222	S

Appendix G. Post hoc examination on one-way ANOVAs for Atlantic Puffin growth parameters. Colony-years 1, 2 and 3 represent Gannet Islands study years 1996, 1997 and 1998. Colony-year 5 is Gull Island 1998. See section 3.3.7.2 of this thesis.

Fisher's PLSD for mass gain per day
Effect: colony-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-1.291	1.111	0.02	S
1, 3	-2.249	.947	<0.0001	S
1, 5	-2.225	1.158	0.0002	S
2, 3	-.959	1.163	0.1	
2, 5	-.935	1.340	0.2	
3, 5	.024	1.208	1.0	

Fisher's PLSD for wing length gain per day
Effect: colony-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value
1, 2	-3.894	•	•
1, 3	-4.087	•	•
1, 5	-4.062	•	•
2, 3	-.192	.238	0.1
2, 5	-.168	.275	0.2
3, 5	.024	.247	0.8

Fisher's PLSD for mass at age 1-3 d
Effect: colony-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-8.960	5.572	0.002	S
1, 3	-3.268	3.337	0.05	
1, 5	2.735	3.894	0.2	
2, 3	5.692	5.694	0.05	
2, 5	11.695	6.037	0.000	S
3, 5	6.003	4.067	0.004	S

Appendix G (continued)

Fisher's PLSD for mass at age 10-12 d
Effect: colony-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-11.270	19.169	0.2	
1, 3	-23.846	10.429	<0.0001	S
1, 5	3.460	11.146	0.5	
2, 3	-12.576	19.331	0.2	
2, 5	14.731	19.727	0.1	
3, 5	27.307	11.422	<0.0001	S

Fisher's PLSD for mass at age 37-40 d
Effect: colony-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-86.040	24.771	<0.0001	S
1, 3	-68.985	21.635	<0.0001	S
1, 5	47.069	23.098	0.0001	S
2, 3	17.054	26.369	0.2	
2, 5	133.109	27.582	<0.0001	S
3, 5	116.055	24.804	<0.0001	S

Fisher's PLSD for peak mass
Effect: colony-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-65.386	34.165	0.0003	S
1, 3	-46.892	32.237	0.005	S
1, 5	40.400	35.369	0.03	S
2, 3	18.494	22.053	0.1	
2, 5	105.786	26.422	<0.0001	S
3, 5	87.292	23.877	<0.0001	S

Appendix G (continued)

Fisher's PLSD for fledge mass
Effect: colony-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-37.000	27.261	0.01	S
1, 3	-44.833	30.478	0.008	S
1, 5	2.167	30.478	0.9	
2, 3	-7.833	23.608	0.5	
2, 5	39.167	23.608	0.004	S
3, 5	47.000	27.261	0.003	S

Fisher's PLSD for wing length age 1-3 d
Effect: colony-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	.277	1.954	0.8	
1, 3	-1.447	1.214	0.02	S
1, 5	.390	1.416	0.6	
2, 3	-1.725	2.001	0.1	
2, 5	.113	2.129	1.0	
3, 5	1.838	1.479	0.02	S

Fisher's PLSD for wing length age 10-12 d
Effect: colony-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-6.584	4.383	0.004	S
1, 3	-8.077	2.321	<0.0001	S
1, 5	-3.889	2.651	0.004	S
2, 3	-1.493	4.419	0.5	
2, 5	2.695	4.601	0.2	
3, 5	4.188	2.709	0.003	S

Appendix G (continued)

Fisher's PLSD for wing length at peakmass
Effect: colony-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-13.084	8.267	0.002	S
1, 3	-6.644	6.901	0.06	
1, 5	-3.489	10.072	0.5	
2, 3	6.440	7.757	0.1	
2, 5	9.595	10.677	0.08	
3, 5	3.155	9.658	0.5	

Fisher's PLSD for wing length at fledge
Effect: colony-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value
1, 2	1.143	6.938	0.7
1, 3	.700	7.679	0.9
1, 5	1.167	8.378	0.8
2, 3	-.443	4.782	0.8
2, 5	.024	5.839	1.0
3, 5	.467	6.703	0.9

Fisher's PLSD for %adult mass 1-3 d
Effect: col-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-1.657	1.070	0.003	S
1, 3	-.623	.641	0.06	
1, 5	-.281	.748	0.5	
2, 3	1.034	1.094	0.06	
2, 5	1.376	1.159	0.02	S
3, 5	.342	.781	0.4	

Appendix G (continued)

Fisher's PLSD for %adult mass 10-12 d
Effect: col-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-1.623	2.759	0.2	
1, 3	-3.318	1.501	<0.0001	S
1, 5	-.835	1.604	0.3	
2, 3	-1.695	2.782	0.2	
2, 5	.788	2.839	0.6	
3, 5	2.483	1.644	0.004	S

Fisher's PLSD for %adult mass 37-40 d
Effect: col-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-11.343	3.265	<0.0001	S
1, 3	-8.970	2.851	<0.0001	S
1, 5	3.491	3.044	0.03	S
2, 3	2.373	3.475	0.2	
2, 5	14.834	3.635	<0.0001	S
3, 5	12.462	3.269	<0.0001	S

Appendix G (continued)

Fisher's PLSD for %adult mass peak
Effect: col-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-9.275	4.897	0.0004	S
1, 3	-6.522	4.621	0.007	S
1, 5	2.051	5.070	0.4	
2, 3	2.753	3.161	0.09	
2, 5	11.326	3.787	<0.0001	S
3, 5	8.573	3.423	<0.0001	S

Fisher's PLSD for %adult mass fledge
Effect: col-year
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1, 2	-4.863	3.704	0.02	S
1, 3	-5.892	4.142	0.01	S
1, 5	-2.945	4.142	0.1	
2, 3	-1.028	3.208	0.5	
2, 5	1.918	3.208	0.2	
3, 5	2.947	3.704	0.1	

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