CHICK DIET AND NESTLING CONDITIONS AMONG ATLANTIC PUFFINS AT THREE NORTHWEST ATLANTIC COLONIES

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Chick diet and nestling condition among Atlantic Puffins at three Northwest Atlantic colonies

by

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Abstract

Seabirds forage in a variable environment. Theoretical investigations into seabird foraging ecology and practical efforts to utilize seabirds as sampling agents of marine dynamics have been hampered by an inadequate base of natural history data. Prior to this study, the nestling diets of Atlantic Puffins along the coast of insular Newfoundland in the northwest Atlantic were assumed to be homogeneous. Successful breeding by Atlantic Puffins in the region had been linked to the availability of mature capelin which was thought to be an essential component of puffin nestling diet due to the paucity of suitable alternative prey.

This study reports data on the diets and condition of nestlings collected at Baccalieu, Funk and Small Islands between 1992 and 1995. Bill-loads of fresh prey were collected from adult Atlantic Puffins provisioning nestlings. Bill-load size and the contribution to the diets made by mature capelin were compared between areas and years in conjunction with nestling condition, measured as body mass at a given wing-length. Proximate organic composition analyses were conducted on the lesser known prey items and energy densities estimated.

These data were used to test the assumptions that 1) the diets of puffin nestlings along the coast of insular Newfoundland are homogeneous and 2) that there are no prey of comparable quality to mature capelin available to breeding puffins in the region. The data do not suppport either assumption. Diets of nestling puffins along the northeast coast of insular Newfoundland are not homogeneous. Rather than uniformly dominated by mature capelin, the diets of nestling puffins on Funk and Small Islands were sometimes composed principally of either postlarval 0-group sandlance or larval 1-group capelin. The condition of nestlings fed on post-larval 0-group sandlance was the best observed in this study, exceeding that of nestlings fed diets dominated by mature capelin. 1-group capelin had a wet energy density similar to male capelin while postlarval 0-group sandlance had a wet energy density which exceeded that of mature capelin during a comparable time of year.

I conclude that the diets of Atlantic Puffin nestlings in the northwest Atlantic are more variable than previously considered, and that there are occasions when prey of at least comparable energetic density to that of mature capelin are available to adult puffins provisioning young in this region.

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1.0 Introduction

1.1 General Introduction

Studies comparing the diets of conspecific seabird species at different colonies and at the same colony between years are useful in assessing the environmental variation encountered by a species in time and space (e.g. Harris and Hislop 1978; Schneider and Hunt 1982; Barrett et al. 1987; Anker-Nilssen and Lorentsen, 1990; Baird 1990; Hatch and Sanger 1992; Bertram and Kaiser 1993; Montevecchi 1993; Montevecchi and Myers 1995; Springer et al. 1996). If one assumes that conspecific seabirds at different colonies in the same oceanographic region have the same basic food requirements for survival and rearing offspring it would follow, all other things being equal, that these conspecific seabirds would employ roughly equivalent foraging strategies. If this assumption is valid, differences in conspecific seabird diets between locations and at different times would be due to variation in local menus.

The two general sources of variation in seabird nestling diet are parental foraging behavior and foraging conditions. In addition, these two sources of variation interact. There is evidence of changes in seabird nestling diets in association with changes in the availability of commonly taken prey species which demonstrates the plasticity of seabird foraging behavior (e.g. Hislop and Harris 1985, Barrett et. al. 1987, Martin 1989, Anker-Nilssen 1992, Montevecchi and Myers 1996). Seabirds are not so rigid in their behavior that in the absence of usual prey they refrain from provisioning their young. Rather, they provision them differently, with varying degrees of success (e.g. Anker-Nillssen 1987, Martin 1989).

The dynamic interaction between foraging conditions and seabird foraging behavior complicates the interpretation of seabird nestling diets with regard to the foraging conditions they represent (see Hunt et al. 1991 for an excellent discussion of seabirds as sampling agents). Because of the flexible nature of foraging behavior the potential range of such behavior within a seabird species is unlikely to change on the temporal scale with which we are interested, i.e. on the scale of decades, unless there is a new selection pressure exerted within that time frame such as a profound change in environmental variability. The potential range of foraging behavior under given conditions is roughly illustrated at any given time by the variation in nestling diets among conspecific individuals present within a colony.

The inherently flexible but often predictable nature of puffin foraging behavior illustrated by long-term studies in the northeast Atlantic (Anker-Nilssen 1987, Martin 1989) is consistent with assuming that the driving force behind variation in nestling diet among years at a given colony or among colonies in a given year is not differences in the potential foraging behavior of the parents but rather differences in the foraging environment, the same variable environment in which it would have been advantageous to have evolved a plastic foraging phenotype. Changes in nestling diet variation can therefore reasonably be assumed to reflect a combination of changes in foraging conditions and the interaction between foraging conditions and parental foraging behavior. It is unlikely that they reflect changes in parental foraging behavior alone as this is not expected to change from year to year. Differences in nestling diet among conspecific seabirds nesting at different colonies or at the same colony in different years therefore to some degree measure differences in foraging conditions. However, differences in foraging conditions are not always manifest as differences in nestling diet. For example, in a year of very low sandlance abundance near Shetland, Scotland murre nestling diet was still dominated by sandlance because adults were able to increase their foraging energy expenditure to compensate for the lower abundance of preferred prey (Monaghan et al. 1994, 1996). As a consequence, nestling diet did not reflect large changes in prey abundance.

The ability of adult seabirds provisioning chicks to adjust foraging effort and thus maintain stability in nestling diet composition complicates the use of nestling diet as an indicator of changes in prey availability. When changes in nestling diet composition do occur it is therefore likely, but not necessarily the case, that such changes have been preceded by efforts to maintain historical nestling diet composition by increasing parental foraging effort (e.g. increasing foraging distance). The ability to increase the frequency with which chicks are provisioned is another way in which seabirds provisioning young can compensate for changes in foraging conditions (e.g. Uttley et al. 1994 but see also Burger and Piatt 1990). Increased feeding frequency can compensate for a decrease in the dietary value of individual meals but does not mask changes in the species composition of nestling diet.

Feeding conditions that affect the composition of seabird nestling diet are a composite of the presence, abundance, relative abundance and behavior of various prey types 1) within the bird's foraging range of the colony, 2) within the bird's foraging depth range and 3) during a time period which overlaps with the bird's nestling period.

Puffin colonies situated off the northeast coast of insular Newfoundland (Fig 1.1) are all under the influence of the inshore branch of the Labrador Current which is a mixture of low salinity Hudson Bay water and the arctic waters of the Baffin Island Current which then flow the length of Labrador and the east coast of insular Newfoundland (Drinkwater 1996). Interannual variability in foraging conditions off insular Newfoundland is largely a consequence of interannual variation in the temperature and salinity of the ocean and its effect on somatic growth of prey, phenology of prey reproduction and behavior, distribution and prey availability within the relevant foraging distance and depth for the seabird species under consideration (e.g. Nakashima 1994, Carscadden et. al. 1997).

The main source of intercolony variability in foraging conditions in a given year are differences in local biophysical conditions, some of which are constant such as bottom topography and some of which vary from year to year such as water temperature and salinity.

Large scale pelagic surveys conducted off the northeast coast of insular

Newfoundland and the coast of southern Labrador since 1994 divide the region into four broad scale zoogeographic domains: 1) the shelf waters of the Northeast Newfoundland Shelf and the Southern Labrador Shelf; 2) the Northern Grand Bank; 3) the Southern Grand Bank; and 4) the inshore bays along the northeast coast of Newfoundland (from Anderson and Dalley 1997a). Puffin colonies off the coast of insular Newfoundland differ in their proximity to the different zoogeographic domains identified above. Starting from the south, the Witless Bay seabird colonies (e.g. Gull and Great Islands where most data on Atlantic Puffins in the northwest Atlantic have been gathered) are located inshore of the deep Avalon Channel and directly adjacent to the extensive and shallow Grand Banks (e.g. Nettleship 1991, Rodway and Montevecchi 1996). Baccalieu Island is located inshore in relatively shoal free deep water off the headland separating Trinity and Conception Bays and near the boundary between the Grand Banks to the south and the Northeast Newfoundland Shelf to the north. Small Island, in the Wadham Island archipelego is located inshore in shoal waters, just south of Notre Dame Bay with the deep Northeast Newfoundland Shelf directly offshore. Funk Island is in shoal waters surrounded by deeper water and is directly offshore from Small Island and within the Northeast Newfoundland Shelf area. The above descriptions are based on the broad-scale delineation of the Newfoundland region into subareas adopted by the Pelagic Juvenile Fish Survey conducted by the Canadian Department of Fisheries and Oceans (DFO) in each of the years since 1994 (Anderson and Dalley 1997a).

Capelin in the northwest Atlantic for the most part migrate inshore during the summer months to spawn on or near beaches (Templeman 1948, Carscadden et al. 1989). While inshore, spawning capelin provide an aggregated source of lipid rich food within foraging range of all puffins breeding off the northeast coast of insular Newfoundland. Because they swim in aggregations, spawning schools of capelin, once encountered, provide the opportunity for seabirds to forage exclusively on one species and maturity stage of prey and this has generally been observed to be the case for Atlantic Puffins provisioning young (Brown and Nettleship 1984, Piatt 1987, Creelman and Storey 1991). The arrival of capelin inshore to spawn varies both annually (e.g. roughly 1 month later in the early 1990s than during the 1980s) and geographically, i.e. progressively later as one moves north along the northeast coast of insular Newfoundland (Templeman 1948, Shackell et al. 1994, Nakashima and Winters 1996, Carscadden et al. 1997, Therriault et al. 1996). The puffin nestling period is sufficiently long so that direct overlap with the availability of spawning capelin while not gauranteed for the full duration of the nestling provisioning period is bound to overlap with some portion of it (Harris and Birkhead 1985). Which portion overlaps and for how long is of relevance to puffin nestling diet.

The diets of Atlantic Puffin (*Fratercula arctica)* nestlings have been compared among colonies and years throughout much of the northeast Atlantic (e.g. Corkhill 1973, Harris and Hislop 1978, Ashcroft 1979, Barrett et al. 1987, Martin 1989, Anker-Nilssen and Lorentsen 1990) but not in the northwest Atlantic (i.e. limited to Nettleship 1972, 1991, Creelman 1991, Rodway and Montevecchi 1996). In a review of the importance of mature capelin to Newfoundland seabirds, Brown and Nettleship (1984) concluded that capelin were essential for the successful fledging of Atlantic Puffin chicks and that there were no suitable alternate prey available in southeast Newfoundland waters. Nettleship (1972) assumed further that Atlantic Puffin nestling diets at various colonies along the northeast coast of insular Newfoundland (namely Funk, Small and Great Islands) were essentially the same. Absence of mature capelin in puffin nestling diets at Great Island has been associated with breeding failure (Nettleship 1991). Prolonged periods of breeding failures attributed to scarcity of energy rich prey have been reported in northern Europe (Anker-Nilssen 1992, Baird 1990) and concern has been expressed that the breeding success of seabirds in Newfoundland is directly dependent on the availability inshore of spawning capelin (Brown and Nettleship 1984, Nettleship 1991).

Although puffins specialize in feeding on small pelagic fish, prey harvests are often variable (Corkhill 1973, Harris 1984, Barrett et al. 1987, Martin 1989). However, the menu offered puffin nestlings by provisioning adults at the major Newfoundland colonies appears much less varied than in the northeast Atlantic. In all periods sampled, capelin dominated the diet in the northwest Atlantic (Brown and Nettleship 1984, Bradstreet and Brown 1985, Piatt 1987, Creelman and Storey 1991, Rodway and Montevecchi 1996). The apparent consistency of Atlantic Puffin nestling diets in the northwest Atlantic in contrast to the diversity experienced in the northeast Atlantic may be an artifact of the short time series of data available for the northwest and/or the small geographic area over which the data were collected. All published data for puffin nestling diet off insular Newfoundland has been collected at either Gull or Great Island, both located in close proximity to one another off the southeast coast in Witless Bay (Figure 1.1; Piatt 1987, Creelman and Storey 1991, Nettleship 1991, Rodway and Montevecchi 1996).

Atlantic Puffins breed in several locations along the east coast of the island of insular Newfoundland (Cairns et al. 1989) and off the southern Labrador coast. Major breeding sites are indicated in Figure 1.1. Breeding adults arrive at their respective colonies in early April at Baccalieu and Great Islands (Harris and Birkhead 1985) and depart in August/September. Breeding phenology is variable and progressively later as one moves northward from Great Island. One egg is laid in a ground burrow or less frequently in a rock crevice and incubated for roughly 40-45 days. After a brooding period of 6-7 days, hatched nestlings are able to thermoregulate and the continuous presence of the parents is no longer required. Both parents provision the young with food (Creelman and Storey 1991, Corkhill 1973) which is carried crosswise in the bill and delivered to the chicks in a fresh state. Nestlings are fed by the parents until they fledge. Feeding occurs on the order of 2 to 8 times per day during daylight, usually for 38-41 days, with extremes to more than 70 days (Harris and Birkhead, 1985).

1.2 Study sites

Data on the diet and condition of Atlantic Puffin nestlings were collected from Baccalieu Island (48° 09'N, 52° 48'W) in 1992, 1993 and 1994, Funk Island (49° 45'N, 53 ° 11'W) in 1992, 1993, 1994 and 1995, and Small Island (Wadham Islands Figure 1.1; 49° 35'N,53° 46'W) in 1994 and 1995 (see Figure 1.1 for location of study colonies).

Baccalieu Island measures aproximately 1 x 6 km and is located approximately 4 km off shore from the northern tip of the Avalon Peninsula on the northeast coast of Newfoundland (see Figure 1.2 and 1.3). The puffin population includes about 45,000 pairs and is expanding (Montevecchi 1996). The island is surrounded by cliffs and steep slopes of grass and/or talus. Baccalieu is the largest seabird island in the northwest Atlantic and there is an abundance of suitable nesting habitat for puffins. Colony expansion outside the more densely occupied areas is evident from newly excavated burrows. A small fox population has deterred gulls from nesting directly on Baccalieu Island though they do nest on nearby Puffin Island (Sklepkovych and Montevecchi 1989). Eleven species of seabirds also breed on Baccalieu, including Leach's Storm-Petrels *(Oceanodroma leucorhoa)*, murre spp. *(Uria aalge, U. lomvia)*, Black-legged Kittiwakes *(Rissa tridactyla)* and Razorbills *(Alca torda;* Montevecchi and Tuck 1987*)*. Puffin burrows on Baccalieu Island are usually on steep seaward slopes. Tunnels often extend for distances longer than 1 m, with boulders and scree incorporated into the substratum creating narrow and winding tunnel paths. The slope gradient allows very dense burrowing as tunnels do not limit the surface area available for entrances as is the case in level habitat (i.e. Funk and Small Islands).

Funk Island measures approximately 800 x 400 m and is situated 50 km off the northeast coast of insular Newfoundland (Montevecchi and Tuck 1987; Figure 1.3). The island supports a small Atlantic Puffin population of about 2000 pairs (Montevecchi unpubl. data) restricted to the one central meadow composed of gravel and the decomposed remains of the Great Auks (*Pinguinus impennis*) that once nested and were slaughtered there (Montevecchi and Tuck 1987, Montevecchi and Kirk 1997). The puffin nesting area is surrounded by bare rock on which many thousands of murres nest and gannets. Several pairs of Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*) nest among the puffins. Both gull species steal prey being delivered to puffin chicks, and some Great Black-backed Gulls kill adult puffins (Russell and Montevecchi 1996). The puffin population on Funk Island is limited by the small surface area of the island into which burrows may be dug, the majority of the island being exposed granite, and the level nature of the puffin habitat which limits the potential density of burrows as tunnels are not deep and erosion is a problem. In the shallow soil of the island, nest chambers are frequently less than 1 m from the tunnel entrance.

Small Island measures approximately 520 x 360 m and is one of seven islands in the Wadham Islands archipelago situated at the entrance to Hamilton

Sound on the northeast coast of insular Newfoundland (Figure 1.3). An Atlantic Puffin population of some 20,000 breeding pairs occupy the flat meadowy habitat that covers roughly 20 ha of the island (Rodway and Montevecchi 1996). The island perimeter is the most densely burrowed area, although there is extensive suitable habitat and expansion into the island's center is ongoing. As on Funk Island there are nesting Great Black-backed Gulls. Their presence is a recent development, and the source of relatively heavy predation on adult puffins (Russell and Montevecchi 1996). Puffins on Small Island burrow in level ground composed of gravel and peat in varying mixtures ranging from pure peat to almost pure gravel with some boulders. As on Funk Island, nest chambers are frequently less than 1 m from the burrow entrance.

1.3 Study objectives

The present study will describe and compare the diets of Atlantic Puffin nestlings from three colonies: Baccalieu (1992, 1993 and 1994), Funk (1992 - 1995 inclusive) and Small (1994 - 1995) Islands in the northwest Atlantic off the northeast coast of insular Newfoundland to test the assumptions that

1. the composition of puffin nestling diets off insular Newfoundland is homogeneous and
2. that there are no prey of comparable quality to mature capelin available to breeding puffins in the region.

Diet quality will be measured directly through proximate composition analyses of prey items and indirectly through measurements of nestling body condition.

These data will constitute an important extension in time and space of what is a relatively limited set of natural history data on the nestling diets of Atlantic Puffins in the northwest Atlantic.

Figure 1.1. **Map of the northwest Altantic showing the location of major Atlantic Puffin breeding sites along the east coast of insular Newfoundland and off the southern Labrador coast.**

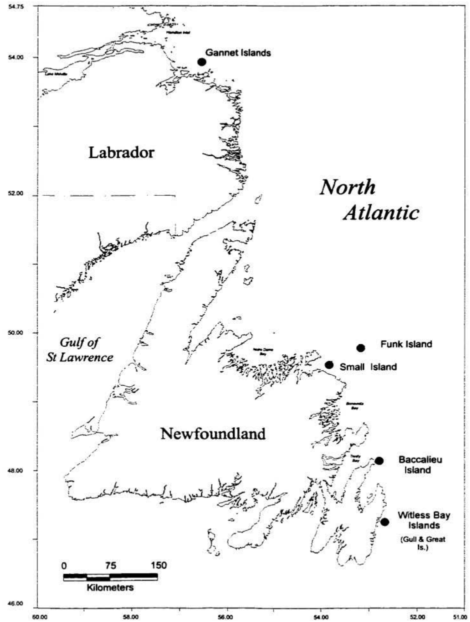

54.75
54.00
52.00
50.00
48.00
46.00
60.00
58.00
56.00
54.00
52.00
51.00
Gannet Islands
Labrador
North
Atlantic
Gulf of
St Lawrence
Funk Island
Small Island
Newfoundland
Baccalieu
Island
Witless Bay
Islands
(Gull & Great
Is.)
0
75
150
Kilometers

Figure 1.2 Topographic map and aerial photograph of Baccalieu Island showing the locatin of the four Atlantic Puffin sub-colonies sampled during 1992 and 1993 including Woody Cove, the only sub-colony sampled in 1994 and corresponding to the top right arrow.

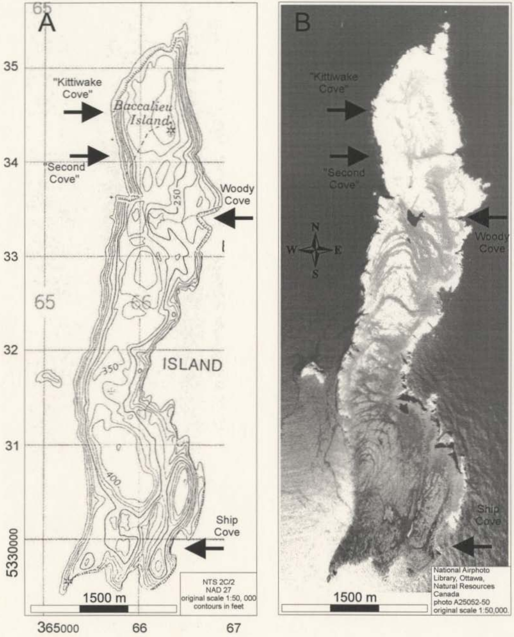
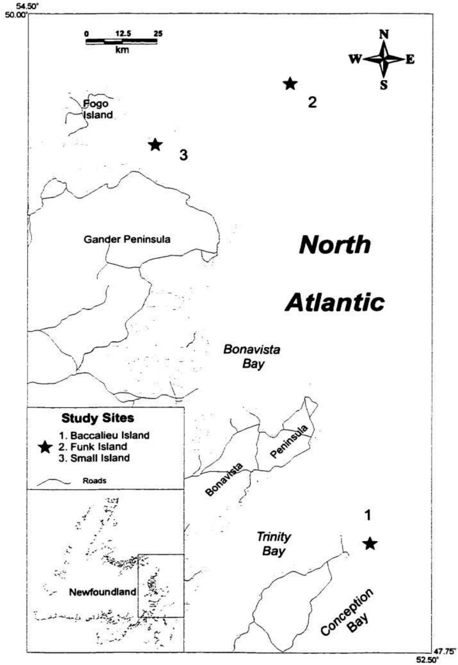

A
65
35
34
33
32
31
5330000
"Kittiwake Cove"
Baccalieu Island
"Second Cove"
Woody Cove
250
65
66
ISLAND
350
400
Ship Cove
1500 m
NTS 2C/2
NAD 27
original scale 1:50, 000
contours in feet
365000
66
67
B
"Kittiwake Cove"
"Second Cove"
N
W
E
S
Woody Cove
Ship Cove
1500 m
National Airphoto Library, Ottawa, Natural Resources Canada
photo A25052-50
original scale 1:50,000.

Figure 1.3 Map of the northeast coast of insular Newfoundland showing the location of seabird breeding islands sampled for this study (Baccalieu, Funk and Small Islands) and their proximity to shore.


54.50°
50.00°
0 12.5 25
km
N
W
E
S
Fogo Island
2
3
Gander Peninsula
North Atlantic
Bonavista Bay
Study Sites
1. Baccalieu Island
★ 2. Funk Island
3. Small Island
Roads
Bonavista Peninsula
Newfoundland
1
Trinity Bay
Conception Bay
47.75°
52.50°

2.0 Composition of Atlantic Puffin nestling diets

2.1 Introduction

There is much theoretical and practical interest in how seabirds sample their environment and to what extent an understanding of this may be used to understand variation in seabird mortality rates (Harris and Bailey 1992), reproductive success (Anker-Nilssen and Lorentsen 1990) and indicate changes in the behaviour, distribution, recruitment, and/or absolute or relative abundance of prey species (Cairns 1987, 1992, Bertram and Kaiser 1993, Montevecchi and Myers 1995). Data on seabird diets also contribute to the estimation of natural mortality experienced by prey species (e.g. Anker-Nilssen 1992, Barrett et al. 1990, Hatch and Sanger 1992, Rodway and Montevecchi 1996). Changes in seabird diets may reflect shifts or conversely the stability of oceanographic regimes and marine food webs (Springer et. al. 1984, Montevecchi and Myers 1996). Studies using dietary information from seabirds depend on an adequate foundation of natural history data. Serious consideration of the general foraging ecology of Atlantic Puffins, for instance, relies on an adequate description of their prey consumption.

For colonially breeding birds which provision dependent land-based chicks, nestling diet may be observed without the need to sacrifice or inordinately disturb animals (Rodway and Montevecchi 1996). The constraint on breeding birds of having to obtain prey from within foraging range of the colony fortuitously limits the potential sources of prey which the researcher must consider and facilitates comparisons of prey harvested with prey known to be present in the area at the time if such additional information is available.

Prey species within the foraging range of adult Atlantic Puffins provisioning nestlings vary in abundance, availability to predators, susceptibility to capture, digestibility and energetic and nutrient content (Bradstreet and Brown 1985). At any given time there is inter- and intra-specific variation in size, maturity, reproductive status, abundance, availability and dietary value of prey (Clarke and Prince 1980, Montevecchi and Piatt 1984, Hislop et al. 1991). Therefore, in addition to taxonomic identification, information on prey size, maturity and reproductive status is needed for a proper consideration of differences between prey items.

Data on the diets of Atlantic Puffin nestlings in the northeast Atlantic have been reported more frequently than in the northwest Atlantic (order of 100 breeding seasons compared with 10), over a broader geographical area (> 10 degrees latitude compared with < 1 degree latitude) and from more varied foraging contexts (forage fish assemblages dominated by fish species other than capelin i.e. sandlance and herring). The diets of puffin nestlings in the northeast Atlantic have varied considerably both within (inter and intra-annually) and between colonies (e.g. Harris and Hislop 1978, Martin 1989). While puffin nestling diets are often dominated by a single prey type (i.e. capelin at the northern tip of Norway and post-larval 0-group herring further south in Norway, Barrett et al. 1987; 0-group and 1-group sandlance in the Shetland Islands, Martin

1989), 23 prey types at the species level alone have been reported from a single colony (Anker-Nilssen 1987). Replacement of the usual dominant prey type by another at a given site (in association with both failed and successful breeding) has been reported (Anker-Nilssen 1992). In contrast, the diet of puffin nestlings in the northwest Atlantic has been reported as dominated uniformly both in space and time by reproductively mature capelin (Brown and Nettleship 1984, Piatt 1987, Creelman and Storey 1991, Rodway and Montevecchi 1996) with the exception of one year when the replacement of capelin by juvenile gadids was associated with breeding failure. In 1981, a year of apparent low capelin availability in Witless Bay, Newfoundland, puffins on Great Island fed their chicks 68 % immature gadids, 16 % sandlance and only 10 % capelin versus 78 - 100 % capelin in the six other years previously sampled (Nettleship 1991). The apparent lack of diversity in the diet of Atlantic Puffin nestlings in the northwest Atlantic as compared with the northeast is likely an artifact of the short time series and small geographical extent of sampling effort in the northwest as compared with the northeast Atlantic. Nonetheless, a comparison of the effect of kleptoparasitism by gulls on puffin breeding success at different colonies assumed that the diets of nestling puffins on Funk, Small and Great Islands did not differ (Nettleship 1972).

The objective of this study was to test the assumption of homogeneity of the diets of nestling Atlantic Puffins along the northeast coast of Newfoundland by documenting the diversity of prey fed to nestlings at Baccalieu, Funk and Small Islands between the years 1992 and 1995.

2.2 Methods

Adult puffins provisioning nestlings were intercepted and the dropped bill-loads collected for direct measurement. Mist-nets and fine meshed gillnets deployed vertically on poles were used to intercept birds in flight and were also used to cover burrow entrances inducing some landing birds to drop bill-loads at burrow entrances.

Bill-loads and individual prey items (unless desiccated) were weighed to the nearest 0.1 g with 10 g Pesola scales (1995 only) or to the nearest 0.5 g with 100 g scales. In the absence of weigh scales of adequate precision, the mass of individual larval fish from bill-loads containing numerous items of a single prey type and length class was estimated by dividing the bill-load mass by the number of fish in the bill-load. Crustaceans and the heads and tails of partial specimens were counted. Most prey were identified to species level in the field and otherwise retained for further identification on shore (Scott and Scott 1988, J. Green, D. Methven, D. Steele and G.H. Winters, pers.comms.). Total length of the larger whole fish specimens (snout or lower jaw tip to tip of longest tail fin smoothed back) was measured to the nearest mm using a stopped metal ruler. Often only the range of total length was recorded for the numerous larval fish from a given bill-load. Squid mantle length was measured to the nearest mm.

Larval and juvenile fish are distinguished from each other on the basis of settling behaviour and/or metamorphosis to adult pigmentation and body form. Larval fish are transparent, have not metamorphosed to the adult form and are found in the upper water column (Kamler 1992). Juvenile fish may have assumed both adult pigmentation and form and/or exchanged pelagic life for a benthic one. The term larval is used here to refer to fish with transparent bodies while the term juvenile refers to fish which have not reached adult sizes but whose bodies are no longer transparent. The year class distinction common in fishery science whereby young of the year are designated as 0-group and young of the previous spawning year as 1-group is used whenever there is reasonable confidence in prey age. Fish possessing the complete form, size and coloration of adults but showing no obvious sign of sexual maturity are referrred to as immature. The term post-larval is also used to refer to any or all fish beyond the transparent larval body phase without consideration of age.

The larger capelin (*Mallotus villosus)* and sandlance (*Ammodytes* spp*.)* were surgically opened for examination of reproductive status. Fish containing egg masses are referred to as gravid while those with residual eggs (i.e. one to several eggs in an otherwise empty body cavity) are referred to as spent. Reproductively mature male capelin are easily identified by the presence of spawning ridges (Templeman 1948). Reproductive maturity was inferred from the presence of eggs or spawning ridges in the case of capelin, and from the presence of eggs or milt in the case of sandlance.

The estimation of percent occurrence (percent of bill-loads in which a prey type is present), percent frequency (numerical frequency of a prey among all those sampled), percent mass (percent of total sampled prey mass) and percent estimated energy (percent of total sampled estimated energy) of various prey required the assignment of mass to those items without one. Mass of un-weighed specimens was estimated following Rodway and Montevecchi (1996) by calculating the mean mass per cm length class of comparable prey (Table 2.1). The mass of those prey which lacked a length measurement was estimated by calculating the mean mass of comparable prey for that sampling location. Small and/or rare items for which no mass data were available from this study were assigned a minimal mass according to criteria outlined in Table 2.2.

The energy value of prey items was estimated by multiplying the measured or estimated mass (see above) of a prey item by an energy density value (kJ/g) obtained from this study (see Chapter 3 and Tables 3.1 - 3.4) or extrapolation from published values (see Table 2.3 for details). Values from this study were estimated from proximate composition data (dry mass energy density ([dry energy]) = (% protein * 20.0 kJ/g dry mass) + (% lipid * 38.0 kJ/g dry mass) , Ricklefs and Schew 1994 ; wet mass energy density ([wet energy]) = ((100 - % water) * [dry energy]) / 100). Energy density values reported in Table 2.3 from Percy and Fife 1981 are derived from proximate composition data using the mid-range values of proximate composition values reported by Percy and Fife as input to the equations provided above.

The timing of sampling varied between islands and years limiting the inter-annual and inter-colony comparisons which could reasonably be made. Data were aggregated using a seven day week as the unit of aggregation. To facilitate the organisation and presentation of the data nine standard weeks covering the nestling period were defined by calendar date beginning on July 13. Comparisons between years and colonies were made when there were sufficient data for weeks of the same ordinal rank. A minimum sample size of 5 was arbitrarily selected and weeks which did not meet this criteria were eliminated from consideration. As puffin nestling diet is not homogeneous throughout the breeding season (Harris and Hislop 1978, Rodway and Montevecchi 1996) data are presented graphically such that the temporal distribution of sampling and gaps in sampling are evident. To avoid confusion the x and y axes are consistent for those figures likely to be compared. To facilitate consideration of differences among colonies and years in bill-load size, mass and energy content, the 95 % confidence intervals around the median are shown on Figures 2.5 - 2.7.

2.3 Results

2.3.1 Size of prey types

Overall the size of prey items fed to nestlings ranged from 1.5 - 21.1 cm in length and 0.1 - 28.0 g in mass (Table 2.4). The heaviest prey item collected was a male capelin while the longest was an ovid sandlance. 1-group capelin and 0-group sandlance were generally similar to each other in size (range 3.0 - 9.9 and 3.5 - 9.1 cm) with the notable exception of 1995 when 0-group sandlance were post-larval in form (i.e. metamorphosed to adult form, size range 7.2 - 12.9 cm) and much larger than in other years. In 1995 post-larval 0-group sandlance had a median mass of 2.3 g compared with a median mass of 0.5 g when in the larval form.

2.3.2 Contribution made by mature capelin to puffin nestling diets

The sample sizes relevant to nestling diet composition and the contribution made by mature capelin by percent occurrence, frequency, mass and estimated dietary energy content are summarised in Table 2.5. A graphical summary using barplots to illustrate the proportionate contribution made by mature capelin to the nestling diet of puffins at Baccalieu, Funk and Small Islands between 1992 - 1995 and described below is shown in Figures 2.1 - 2.4 inclusive.

Percent occurrence

On Baccalieu Island adult capelin were usually present in the majority of bill-loads (Figure 2.1). In 1993, the only year with full season coverage, the proportion of bill-loads containing adult capelin increased over the first few weeks from an initial low of 45 % to remain consistently high for the latter half of the season at between 89 and 100 %. The same pattern was apparent in 1994 although sampling coverage was not as complete. In contrast, on Funk Island the presence of adult capelin in bill-loads was infrequent in all of the 4 years sampled with a maximum occurrence of 30 % in one week of 1993 compared with a range of 0 - 11 % otherwise. Adult capelin were only slightly more common in bill-loads on Small Island where they were more often present in 1994 (range: 17 - 37 %) than 1995 (range: 4 - 16 %).

Percent frequency

The numerical abundance of adult capelin in sampled nestling diet was greatest on Baccalieu Island where it often exceeded 70 % compared with Funk and Small Islands where percent frequency never exceeded 5 % and was usually closer to zero (Figure 2.2). Numerical abundance on Baccalieu Island was variable with a pattern of lower abundance during the early season compared with the late season for the two years with extended sampling. Adult capelin accounted for a smaller proportion of dietary items in late 1992 than in late 1993 and 1994.

Percent mass

The contribution of adult capelin by mass was greater than by numerical frequency and less variable (Figure 2.3). As with percent frequency, the proportionate contribution of adult capelin by mass was greatest on Baccalieu Island compared with Funk and Small Islands. The same pattern observed with percent frequency of lower levels in early season increasing to higher levels later was evident in 1993 on Baccalieu Island but the differences in magnitude were not as pronounced as with percent frequency. The contribution by mass of mature capelin on Small Island was greater in 1994 than in 1995 and during 1994 was also greater on Small than on Funk Island (58 vs 8 % respectively during a comparable sampling period), but much less than on Baccalieu Island (33 vs 90 % respectively during a comparable sampling period).

Percent estimated dietary energy

The contribution to estimated nestling dietary energy by adult capelin closely resembled the proportionate representation by mass described above, both in magnitude and overall pattern (Figure 2.4).

2.3.3 Contribution made by prey other than mature capelin to nestling diet

A detailed summary of the prey types present in the diets of Atlantic Puffin nestlings by percent occurrence, frequency, mass and energy is shown in Appendices 2.1 - 2.12. In all, a minimum of 10 fish and 5 invertebrate species were present in the puffin nestling diet. While mature capelin dominated the diet by percent occurrence, mass and energy consistently on Baccalieu Island and by percent mass and energy on Small Island in week 5 of 1994, the diet on Funk Island in each of the years 1992 - 1994 was dominated by 1-group capelin by percent frequency, mass, occurrence and energy. In 1995, post-larval (metamorphosed) 0-group sandlance dominated by percent frequency, mass, occurrence and energy on both Small and Funk Islands. A brief description of results organised by prey type follows.

1-group capelin

1-group capelin were present in the nestling diet of all colonies sampled in all years, but not in all weeks (Appendix 2.1). On Baccalieu in 1993 when the entire season was sampled the presence of 1-group capelin was greatest and most important energetically early in the season. Among the three years (1992-1994 inclusive) sampled on Baccalieu, 1-group capelin were most common in bill-loads and important energetically during 1994. Among the three colonies sampled 1-group capelin were most common on Funk Island where they were present in most bill-loads in most years with the notable exception of 1995. They were also important energetically except in 1995. On Small Island they were more common and made a greater contribution to dietary energy content in 1994 than 1995 although never reaching levels of occurrence or energetic contribution observed on Funk Island.

Mature sandlance (*Ammodytes* sp.)

Mature sandlance were only observed on Baccalieu Island where they were infrequently fed to nestlings (Appendix 2.2). When present, however, their energetic contribution was usually in the range of 19 - 44 %. They were observed from both early season (1993) and late season (1992).

0-group sandlance (*Ammodytes* sp.)

Because of the appearance of two distinctly different size classes of 0-group sandlance with different morphology, the two size classes are presented separately and referred to as either larval or post-larval.

Larval 0-group sandlance were not always present, being generally scarce and unimportant energetically on Baccalieu Island (Appendix 2.3). They were common on Funk Island in all years except 1994, although energetic contribution never exceeded 10 % and while 1992 and 1993 were similarly near this maximum, their contribution in 1994 and 1995 was negligible. On Small Island they were often present in bill-loads in 1994 but not in 1995.

Post-larval 0-group sandlance dominated nestling diet in every way, i.e. percent occurrence, frequency, mass and energy, on both Funk and Small Islands in 1995 (Appendix 2.4). On Small Island they were also present in 1994 but less frequent and important energetically. They were notably absent from Baccalieu Island and in every year sampled on Funk Island except 1995.

Stichaeids

All Stichaeids present in the nestling diets were larval and were not identified to species (Appendix 2.5). The two most likely species to which they belong are Arctic Shanny *Stichaeus punctatus* and Radiated Shanny *Ulvaria subbifurcata* (J. Green pers. com.).

Stichaeids were observed at all colonies and in all years although not all weeks sampled. They were somewhat common in the early season on Baccalieu and generally absent there later on except for 1992. Energetic contribution on Baccalieu never exceeded 3 %. Stichaeids were more common in bill-loads on both Funk and Small Islands where energetic contribution ranged from a high of 7 to < 1 %. On Funk Island they were more common and contributed more energetically in 1992 and 1994 than in the other two years. On Small Island they were more common and contributed more energetically in 1994 than 1995.

Cottids

Cottids were present in the nestling diets at each of the three colonies although not in all weeks sampled, particularly on Baccalieu Island where they were absent or scarce in August-September samples and most common in late

July (Appendix 2.6). They were more common on Baccalieu in 1994 than 1993 and rather than the usual < 1 % contribution to dietary energy the contribution in early 1994 reached 11 %. Cottids were always present in periods sampled on Funk Island and usually on Small Island. Energetic contribution at both colonies was usually negligible with the exception of 1992 on Funk Island.

Herring

Herring were generally absent from nestling diets with the notable exception of Small Island in 1994 when 0-group Herring in weeks 5 and 6 respectively contributed 13 and 7 % by frequency, 13 and 12 % by mass, occurred in 32 and 50 % of bill-loads and contributed 10 % of the estimated dietary energy delivered to nestlings (Appendix 2.7).

White Hake

White Hake were recorded at each of the colonies but not in all years (Appendix 2.8). They were generally absent or very scarce and made negligible energetic contributions. White Hake occurred most commonly in bill-loads on Funk Island in 1993. They were recorded from both the early and late season on Baccalieu Island.

Agonidae

Agonidae were either absent or scarce in sampled nestling diet (Appendix 2.9). They occurred most commonly (22 %) in the early season of 1994 on Baccalieu Island. On Funk Island they were most common in 1992 (11 %) and were absent there in 1995. They were not recorded from Small Island and at no time did their energetic contribution anywhere exceed 1 %.

Liparis sp.

Liparis sp. were scarce everywhere with the exception of 1992 on Funk Island when they occurred in 23 % of bill-loads (Appendix 2.10). They were notably absent from Funk Island in 1994 and 1995 and were never observed on Small Island. They appeared more often in the early season than at any other time on Baccalieu. Nowhere did they ever contribute more than 1 % of dietary energy.

Squid

Squid rarely occurred on Baccalieu and Small Islands, although in the late seasons of 1992 and 1993 on Baccalieu their energetic contribution reached 5 - 9 % (Appendix 2.11). On Funk Island they were most common in bill-loads in 1992 (23 %) contributing 18 % of dietary energy at that time. In 1994 their energy contribution was also not negligible at 11 % while in the other years sampled on Funk Island they were less important, particularly in 1995.

Crustaceans

Although crustaceans were observed at each of the colonies in each of the years sampled except for 1995, they were often absent (Appendix 2.12). On Baccalieu crustaceans were most common in the early season. On Funk Island they were less common in 1994 than in the previous 2 years. They were equally as scarce on Small Island in 1994 as on Funk Island and at no time or place did they contribute > 1 % of the dietary energy.

Miscellaneous

The balance of collected nestling diet was made up of rarely occurring prey items which included unidentified juvenile gadids, *Nereis* sp., larval Pleuronectidae and another unidentified larval fish.

2.3.4 Size, mass and energy content of bill-loads delivered to puffin nestlings

The enumeration of bill-load contents and measurement of bill-load mass were not collected from every sample (see methods) and thus the sample size for bill-load size is often greater than the sample size for bill-load mass. A summary of the sample sizes, masses, numbers of prey items and estimated energy content of bill-loads intercepted from adult puffins provisioning nestlings is shown in Tables 2.6 - 2.8. A graphical summary of the same data using boxplots to display the range and distribution of data values and showing the 95 % confidence intervals around the median is shown in Figures 2.5 - 2.7.

2.3.4.1 Number of individual prey items in bill-loads collected from Atlantic Puffin nestlings

The number of prey items in bill-loads collected from Atlantic Puffin nestlings was quite variable (range: 1 - 50; see Table 2.6 and Figure 2.5 for details). Bill-loads were smallest on Baccalieu Island and generally much larger on Funk and Small Islands. On Baccalieu during the 2 seasons with both early and late sampling coverage (1993 and 1994) bill-loads were dramatically larger at the beginning of the nestling period than there after. As well, bill-loads in early 1994 contained more prey items than in early 1993. On Funk Island bill-loads were largest and most variable in 1992 and 1993, less so in 1994 and contained the fewest prey with the least variation in 1995. While the 95 % confidence intervals around median bill-load size on Funk Island during 1992 - 1994 overlapped with each other, those for 1995 did not overlap with the others. On Small Island in 1994 bill-loads contained more prey during week 6 than in 1995 and were more variable in week 5 than in 1995.

During sampling periods when data are available from more than one site, there are some clear differences, for example, during weeks 4 and 5 of 1993 bill-loads on Funk Island were dramatically larger and more variable than those on Baccalieu Island. During week 6 of 1994 bill-loads on Small Island were also larger and more variable than on Baccalieu Island. A week before, when comparison is possible between Small and Funk Islands, bill-loads on Funk Island are larger than on Small Island. A year later, in 1995, during the same time period bill-load size was notably reduced and the Funk and Small Island bill-loads contain similar numbers of prey.

2.3.4.2 Mass (g) of bill-loads collected from Atlantic Puffins provisioning nestlings

The magnitude of variation in bill-load mass was generally greater and more consistent than that of bill-load size (see Table 2.7 and Figure 2.6 for details). Overall bill-load mass had a range of 0.5 - 33.5 g . On Baccalieu Island during 1993 and 1994, there was a reciprocal relationship between bill-load mass and size. Early season bill-loads weighed less than during the balance of the season in 1993. Bill-load mass was less variable in the latter part of 1992 than in the same period during 1993 and 1994.

Funk Island bill-loads were generally somewhat heavier in 1995 but the 95 % confidence limits around the median bill-load mass among the four years sampled on Funk Island all overlapped . The smallest median bill-load mass on Funk Island was 7.6 g in 1994 while the largest median was 11.0 g during 1995. Bill-loads were heavier on Small Island in 1995 than in 1994.

Between colony differences in bill-load mass are much less pronounced than was the case for bill-load size. In 1993 during a comparable time period (weeks 4 and 5) Funk Island bill-loads were generally lighter and less variable than on Baccalieu Island but 95 % confidence limits around the medians still had some overlap. In 1994 during comparable weeks the median bill-load mass was roughly similar between colonies. In 1995 during a comparable week median bill-load mass on Small Island tended to exceed that of Funk Island.

2.3.4.3 Estimated energy content (kJ) of bill-loads collected from Atlantic Puffin nestlings

Estimated energy content of bill-loads collected from Atlantic Puffin nestlings ranged from a low of 0.5 kJ to a high of 189 kJ. Estimated energy content of bill-loads followed much the same pattern as that of bill-load mass (see

Table 2.8 and Figure 2.7 for details). The same intra-seasonal pattern of lower values early in the nestling season compared with later, observed for bill-load mass on Baccalieu Island in 1993, is also apparent for energy content. Bill-loads on Baccalieu Island from comparable weeks between years contained the least energy in 1994, as did those on Funk and Small Islands. Bill-loads on both Funk and Small Islands had highest energy contents in 1995. On Funk Island, 1995 bill-load energy contents were also more variable than in previous years.

Median values of bill-load energy content range from a low of 20.7 kJ on Funk Island in 1994 to a high of 84.7 kJ on Small Island in 1995. Bill-loads on Funk Island in 1993 contained less energy than those on Baccalieu Island during the same time period. Bill-loads on Funk Island in 1994 contained less energy than those on Small Island, while those on Small Island tended to contain less than those on Baccalieu Island, although the difference between Small and Baccalieu Islands (medians: 33.4 vs 39.0 kJ) was not as great as the difference between Small and Funk Islands (medians: 33.7 vs 20.7 kJ).

2.3.4.4 The relationship between bill-load size, mass and energy content

The relationships between bill-load mass and size, bill-load mass and energy content and bill-load size and energy content are illustrated for a comparable sampling period (week 5 of nestling season) for Baccalieu Island 1993, Funk Island 1992 - 1995 and Small Island 1994 - 1995 in Figures 2.8 - 2.10.

There is dramatic variation in the relationship between bill-load mass (g) and bill-load size (number of prey items per bill-load) among colonies and years during a comparable time period (e.g. week 5 of the nestling season in 1993, Figure 2.8). On Baccalieu in 1993 the heaviest bill-loads were also the largest. However, the extremely small variation in bill-load size suggests something else is responsible for increasing bill-load masses, i.e. size of individual fish. On Funk Island, the relationship between bill-load mass and size is different for each of the four years sampled ranging from non-existent in 1994 through loosely positive with a lot of variation in 1992, to a low slope tight positive association in 1995 and a steep slope positive association in 1993 with variation intermediate between the extremes of 1992 and 1995. On Small Island, the relationship between bill-load mass and size also differs distinctly between 1994 and 1995. In 1994, there are two groups of points, one a loose cluster resembling Funk Island in 1992 and the other a flat string of points resembling Baccalieu in 1993. These two patterns represent bill-loads containing multiple and variable prey items in the first instance and bill-loads containing varying numbers of a single dominant prey (adult capelin) in the second. The pattern on Small Island in 1995 is different again and resembles Funk Island in 1995. Both instances depict bill-loads containing variable numbers of a single dominant large prey type (post-larval 0-group sandlance).

The relationship between bill-load mass and estimated energy content is strongly positive and generally tight with minimal variation (Figure 2.9). Funk

Island in 1992 was notably more variable than the other years and colonies examined during the same sampling period.

The number of prey items in a bill-load had a varying effect on energy content (Figure 2.10). On Funk Island the relationship was similarly positive and variable in 1992 and 1993, ambiguous in 1994 and steeply positive in 1995. Small Island in 1995 resembled Funk Island in the same year. Baccalieu Island had a distinct pattern due to the lack of variation in bill-load size and Small Island 1994 contained two patterns including one similar to Baccalieu Island and the other resembling Funk Island in 1992 and 1993.

2.5 Discussion

Sampling of bill-loads from adults provisioning nestlings relied on retrieval of a dropped sample from the ground. Direct examination of retrieved prey items is possible but recovery of 100 % of the bill-load is not assured (Rodway and Montevecchi 1996). The smaller transparent prey items are more likely to be over-looked among the ground cover than larger or fleshier prey. Consequently, numbers of larval fish and crustaceans are underestimated with these methods (Rodway and Montevecchi 1996). These data therefore represent minimal estimates of the percent occurrence and numerical frequency of the smaller prey items and especially the transparent larval forms. Even so, the number of these prey types present in nestling diets was far greater than expected. The estimation of contribution by mass of these prey is not strongly biased by the tendency to underestimate numerical abundance as the mass contribution per unit fish is very small. Therefore, while reported percent frequency and occurrence for small prey should be treated as minimal estimates the percent contribution by mass and energy of these same prey are more robust to the sampling bias identified above.

Consideration of differences among colonies and years was based on comparing weeks of the same ordinal rank, i.e. comparisons were among similar calendar periods. Nestling age of Atlantic Puffin nestlings may affect meal size, i.e. the youngest chicks may be unable to ingest the larger prey consumed when older and may be fed smaller prey by the provisioning adult (Bradstreet and Brown 1985). Comparing diets of nestlings among colonies for the same calendar period is potentially confounded by differences among colonies in breeding phenology. If the question being addressed is limited to consideration of the differences in foraging conditions among colonies at a particular time then this is not a problem unless confounded by the tendency of adults to feed the smallest chicks smaller prey. The timing of puffin breeding on Funk and Small Islands was roughly a week later than on Baccalieu Island during the years of this study (Russell and Montevecchi unpubl. data). The puffin breeding season on Funk and Small Island in the periods sampled by this study was further advanced than that which would present a concern for the interpretation of nestling diet comparison with Baccalieu Island. Therefore, the difference in puffin breeding phenology among the study colonies is insufficient to explain the observed differences in nestling diet and I infer that the abundance in nestling diet on Funk

Island during 1992 - 1994 of small prey items is a reflection of foraging conditions and not confounded by nestling age.

The composition of Atlantic Puffin nestling diets at Baccalieu, Funk and Small Islands (1992 - 1995) were not homogeneous. Mature capelin dominated nestling diets in all years on Baccalieu and Small Island in 1994 but otherwise were replaced as the primary diet constituent by larval 1-group capelin (Funk Island: 1992-1994) or post-larval 0-group sandlance (Funk and Small Islands 1995). Contributions to estimated nestling dietary energy of 10 % or more were occasionally made by a number of prey types other than mature capelin. In addition to the principal exceptions mentioned above, the following made lesser but noteworthy contributions to puffin nestling diet in the northwest Atlantic during 1992 - 1995: 1) adult sandlance on Baccalieu Island, 2) 0-group larval sandlance on Funk and Small Islands, 3) cottidae on Baccalieu and Funk Islands, 4) 0-group Herring on Baccalieu and Small Islands and 5) squid on Funk Island. Invertebrates were uncommon prey items but much more frequent than recorded in the northeast Atlantic. In 27 colony years in Great Britain, Harris and Hislop (1978) observed only 1 load containing squid and one crustacean. In contrast, although infrequent, crustaceans were recorded from all locations and years in this study and squid made up 11 % by mass of the nestling diet on Funk Island in 1992.

The small miscellaneous prey which are most common in the early seasons at Baccalieu Island and in each year sampled on Funk Island are available throughout the nestling season and in the absence of adult capelin could constitute the principal ingredients of nestling diet as indeed they do on Funk Island during the sampled period 1992 - 1994. Some of these prey although abundant contribute very little to dietary energy content e.g. stichaeids. The energy content of bill-loads composed of miscellaneous and numerous prey was less than that containing fewer larger items. The bill-loads delivering the most energy were either from Baccalieu where adult capelin dominated or from 1995 on Small and Funk Islands when large bill-loads of large post-larval 0-group sandlance were the norm. There was a four-fold increase in bill-load energy content between the poorest loads of 1994 on Funk Island and the richest loads of 1995. The poorest year at all three colonies with respect to the energy content of bill-loads was 1994.

Energy content of bill-loads is highly associated with bill-load mass but not necessarily with bill-load size. Depending on prey type the number of items in bill-loads has a lesser or greater influence on bill-load energy content. In the case of bill-loads dominated by a single large prey type, each additional prey item added to a bill-load increases the energy content by a large factor. The size of this incremental factor limits the maximum number of prey per bill-load to much less than if the prey type was a small one. In the case of bill-loads dominated by a variety of small prey, each additional prey item does not increase the energy content of the bill-load by very much. The less energetically rewarding the prey and the more consistent this is for all prey collected, the less pronounced will be the unavoidable association between number of prey in a bill-load and energy content. This limits the potential of single bill-loads based on harvesting small prey to compete with the energetic potential of single bill-loads based on large prey. The slope of the relationship between number of prey per bill-load and bill-load energy content could be considered analogous to a measure of foraging efficiency if one assumes the same energy requirement for each additional prey regardless of identity. If all prey types are equally available for the same investment of foraging energy then bill-loads composed of larger prey items are more efficient than those composed of small prey. Therefore, when a complete range of acceptable prey types are locally available, on the basis of bill-load efficiency one would predict the provisioning of chicks with the larger prey. However, if one has to fly considerably further to obtain the larger prey than the smaller prey then it may become more efficient to provision the young with smaller prey of lower energy content. This may have been the case on Funk Island during 1992 - 1994.

The limitation on efficiency at the scale of the bill-load mentioned above may be compensated for at the scale of daily nestling dietary intake by an increase in provisioning frequency. This study does not report on the frequency with which nestlings were provisioned. While feeding frequency information is necessary for the estimation of total nestling dietary intake it is not required to describe the composition of nestling diet which has been the emphasis here.

The most obvious explanation for the paucity of mature capelin in the diets of Funk Island nestlings during the period sampled (limited to first half of August in each year) is that at that time of year the migration of reproductively mature capelin inshore to spawn, has placed them outside of some threshold foraging distance for puffins on Funk Island. Funk Island is roughly 50 km offshore. The migration of capelin inshore to spawn either passes Funk Island earlier in the season than the period sampled in this study in which case adult capelin may have contributed to the nestling diet during the period preceding that sampled by this study, or capelin migrate from distant areas south of Funk Island and then along shore to reach progressively more northerly areas inshore from Funk Island. Depending on capelin migration routes, puffins on Funk Island may or may not be aware of the presence inshore of spawning capelin. There is no evidence from this study from which to infer whether or not puffins at Funk Island prior to our visit had more immediate access to migrating capelin. Murres on Funk Island during the periods sampled were observed returning from inshore with mature capelin for their nestlings (Russell and Montevecchi pers. obs.). In 1994, this behavior of murres in conjunction with data on the puffin nestling diet on Small Island confirm that mature capelin were available inshore from Funk Island.

While 50 km is within the maximal foraging range observed for Atlantic Puffins, puffins from Funk Island were not flying inshore to forage for their assumed preferred prey. This raises questions concerning how Atlantic Puffins sample their foraging space and under what conditions this space is extended or compressed (Anker-Nilssen and Lorentsen 1990).

The ubiquity of post-larval sandlance in both an inshore and an offshore diet in 1995 (i.e. Small and Funk Islands) also raises questions concerning the conditions under which capelin would be preferentially fed to puffin nestlings. Capelin spawning occurred along the northeast coast of insular Newfoundland in each of the years 1992 - 1995 (Anderson and Dalley 1997b) and so it is likely that capelin were available to foraging puffins on Small Island in 1995, and if so, their displacement in the puffin nestling diet by sandlance suggests that at those locations in 1995 post-larval sandlance were either more likely to be encountered than mature capelin, were selected in preference to mature capelin, or both.

Independent information on prey availability

On Great Island, Witless Bay during 1992 - 1994, adult capelin dominated the nestling diet of Atlantic Puffins by proportionate mass at all times except very early in 1994, when larval capelin and sandlance were the principal prey (Rodway and Montevecchi 1996). Larval capelin and sandlance were numerically abundant in the nestling diet on Great Island in each of the years 1992 - 1994. Crustaceans and cottids were most common in 1994. Adult sandlance were present in each year and most common in 1993. As on Baccalieu Island, miscellaneous and smaller prey items were displaced by adult capelin as the nestling season progressed (Rodway and Montevecchi 1996). Foraging conditions at Great Island appear similar to those at Baccalieu Island during the overlapping years and are consistent with the assumption that Atlantic Puffin nestling diet in the northwest Atlantic with the exception of the earliest part of the season is dominated by adult capelin. The nestling diets at Funk and Small Islands in which prey other than adult capelin dominated during the middle of the nestling period indicate that foraging conditions at the main puffin colonies off the northeast coast of insular Newfoundland are not homogeneous. The continued importance of capelin on Great Island during years when their importance elsewhere is questioned parallels the findings of DFO's juvenile fish survey for the 1990s, namely that the northwest Atlantic pelagic environment off the coast of insular Newfoundland is subject to some broadscale differences between the inshore and the two principle shelf regions, i.e. the broad and deep northeast shelf and the massive and shallow Grand Banks (Anderson and Dalley 1997a).

Various indices of adult capelin biomass and spawning phenology are available from several annual surveys conducted by DFO (Winters 1995). In recent years a multiplicative approach has been taken which incorporates multiple indices in the formation of an objective standardised time series (Winters 1995). The standardised estimates of annual capelin biomass since 1980 indicate 1981 as the lowest estimate in the time series, followed by a fairly consistent increasing trend up to 1989 after which estimates declined during 1990 - 1992 before increasing again (Nakashima and Winters 1997). It is noteworthy that 1981, the lowest estimate in the time series, is the only year for which puffin breeding is reported to have failed due to poor nestling diet (Nettleship 1991).

In the context of a time series beginning in 1980, the years 1992 - 1995 during which the nestling diet data reported here were collected, represent a period of generally greater capelin biomass than in the early 1980s. Within 1992 - 1995, the standardised biomass estimate was lowest in 1992 and those during 1993 - 1994 were roughly similar (Nakashima and Winters 1997). In a time series beginning in 1978, the timing of peak capelin spawning was about one month later in the early 1990s than during previous years (Carscadden et al. 1997). Later spawning was linked to cold spring ocean conditions and slowed somatic growth in capelin, smaller fish spawning later (Carscadden et al. 1997). However, capelin did spawn along the northeast coast of insular Newfoundland in each of the years 1992 - 1995 (Anderson and Dalley 1997b).

The spawning periods of 1994 and 1995 were similar (Nakashima and Winters 1996). Deposition of eggs on capelin spawning beaches sampled by DFO was similar in 1992 and 1995 being intermediate between the highest estimate in 1993 and the lowest in 1994 when no eggs were present at Cape Freels in the vicinity of Small Island (Nakashima and Winters 1995, 1996). The absence in some cases and relative shortness in others of the beach spawning period in 1994 is suggestive of a greater degree of offshore spawning in that year (Anon. 1995). A relative decrease and in some areas the absence of beach spawning behavior by capelin may reduce their availability as prey to puffins. Beach spawning is preceded by the aggregation of capelin in shallow near shore waters where they are well within the diving depth range of puffins. Off beach spawning may not include the aggregation of capelin in comparable depths to the same extent as on beach spawning. This may explain the delivery to puffin nestlings in 1994 of the least energy rich bill-loads in the years 1992 - 1995. Since the biomass of capelin in 1994 is not low relative to the time series, this may represent an example of the importance of distinguishing between prey abundance and availability (Montevecchi and Berutti 1992).

A large biomass of prey does not guarantee their availability to foraging puffins. Particularly for prey that aggregate nearshore in summer as capelin do, one would expect their availability to foraging puffins to be relatively independent of population biomass. It may be that the degree to which capelin engage in off beach spawning is of equal if not more importance to puffins than how many there are.

Since 1994, DFO has conducted an annual survey for pelagic juvenile fish off the northeast coast of insular Newfoundland and southern Labrador (Anderson and Dalley 1997a,b). The IGYPT trawl used in this survey samples the same part of the water column in which puffins forage, i.e. 20 - 60 m depth (Piatt and Nettleship 1985, Burger and Simpson 1986, Anderson and Dalley 1997) and therefore provides a reasonable depiction of what Atlantic Puffins would encounter if foraging in the area sampled by the trawl during late August - early September. That is, assuming no important difference between foraging conditions at 20 - 60 m depth and 0 - 20 m depth where puffins may spend a significant portion of their time foraging (Piatt and Nettleship 1985, Burger and

Simpson 1986). From 1991 - 1993, DFO also collected data on juvenile fish abundance but using a different protocol than in subsequent years (Anderson and Dalley 1995). As the surrounding nekton is dominated by 1-group capelin and arctic cod (Anderson and Dalley 1997a) the large contribution of 1-group capelin to the diets of nestlings on Funk Island and elsewhere when mature capelin were not abundant in the diets is not surprising. However, it is worth noting the apparent absence of arctic cod (other than as potential members of the unidentified gadids collected) in the nestling diets in contrast to their abundance in the surrounding waters (Anderson and Dalley 1997a). Given the high occurrence of various prey in nestling diet which are not as common in the nekton as arctic cod, i.e. cottids, stichaeids, *Liparis* sp., it would seem that puffins may be selecting against arctic cod, and/or that the catchability of arctic cod for puffins is less than the other prey. Arctic cod are also scarce in common murre nestling diets 1990 - 1998 (Montevecchi unpubl. data).

The offshore Northeast Shelf area has been noted during the early 1990s for an abundance of juvenile fish and squid, and Funk Island is ideally situated to forage in those waters (Anderson and Dalley 1997a,b). While the energetic content of bill-loads made of juvenile fish and squid is lower than those made of larger fish, the fact that Funk Island is surrounded by waters rich in miscellaneous nekton may mean that the relative ease with which meals can be collected makes up for their individual energetic inferiority. This study does not report on the frequency with which nestling were fed. Bill-load energy content alone is insufficient to infer dietary quality. The freshness and in some instances presence of life in the miscellaneous small prey delivered to nestlings on Funk Island 1992 - 1994 however suggest that they were collected in close proximity to the colony. If such bill-loads were readily available close to the colony, parental feeding frequency could presumably easily be increased to make up for a relatively lower energetic content of individual bill-loads.

The inshore area as defined by DFO's juvenile fish survey was noted for its importance as a spawning area and with regard to herring, Notre Dame Bay (just north of Small Island) is particularly important (Anderson and Dalley 1997a). The importance of 0-group Herring in nestling diet on Small Island in 1994 indicates that puffins there are able to benefit from their proximity to a herring spawning area.

Differences in puffin nestling diets at colonies off the northeast coast of insular Newfoundland reflect differences between the main zoogeographical zones identified by DFO's annual juvenile fish survey. Puffins at Baccalieu Island and in Witless Bay forage inshore and on the Grand Banks and may, at least in the years in common between this study and the juvenile fish survey, be more sensitive to changing availability of spawning capelin than Small and Funk Islands to the north. Small Island has access to inshore spawning herring in addition to capelin and the greater productivity of the Northeast Shelf. Funk Island is surrounded by the richer waters of the northeast shelf and could also presumably access the inshore. In addition, at least on Small and Funk Islands and possibly to the south as well (there were no 1995 data on nestling diet from Baccalieu and Great Islands), there are years in which oceanographic conditions favour the production of metamorphosed 0-group sandlance such that may benefit puffins provisioning young.

In the northeast Atlantic, puffins on Hermaness and in northern Norway suffered breeding failures during several years when the mean load mass delivered to nestlings dropped below 5 g. In both locations the decrease in load mass was associated with an increase in the number of prey items per load and a decrease in the size of dominant prey taken (Anker-Nilssen 1987, Martin 1989). Bill-loads delivered to nestlings on Funk Island in 1992 - 1994, Small Island in 1994, exhibited the same general pattern of decreasing bill-load mass with increasing number of bill-load contents and size of prey items but the median bill-load mass did not drop below 5 g (median bill-load mass ranged from 8.3 - 11.9 g) and there was no evidence of breeding failure (Chapter 4). The only time during this study when median bill-load mass fell below 5 g was in early 1994 on Baccalieu Island when it was 4.5 g. The ability to maintain bill-load mass while foraging for multiple tiny prey from Funk Island may be an indication of the ease with which these prey are captured there compared with Baccalieu Island.

Summary

Differences among the diets of nestling Atlantic Puffins on Baccalieu, Funk and Small Islands reflect inter-annual differences in availability of prey as well as differences in the availability of prey due to differences in colony location.

Differences were evident between locations in the same year (eg. Baccalieu Island and Funk Island in 1993) and also between years in the same location (eg. 1995 compared with 1992 - 1994 on Funk Island). With regard to location, differences may be associated with latitude (Funk and Small Islands to the north versus Baccalieu Island to the south) and/or proximity to shore (Baccalieu and Small Islands as inshore versus Funk Island as offshore) as these relate to proximity to the major zoogeographic zones delineated by recent large scale pelagic juvenile fish surveys (Anderson and Dalley 1997a). The availability inshore of spawning capelin may over-ride such broadscale differences for the colonies near shore except in years when changes in capelin breeding phenology, vertical distribution or degree of offbeach spawning limit their availability to puffins provisioning nestlings. Funk Island may be interesting as an example of how well puffins breeding off the coast of insular Newfoundland may provision nestlings independent of significant dietary contributions from adult capelin. However, Funk Island may also be better situated to harvest the relatively richer nekton population of the Northeast Shelf waters. That is, assuming that the differences in nekton biomass between the Grand Banks and the Northeast Shelf observed for the early 1990s holds for other years.

With regard to interannual variation, the domination by 0-group sandlance of puffin nestling diet at both Funk and Small Island in 1995 illustrates the potential in this region for sandlance to successfully displace adult capelin as an efficient source of dietary energy for puffins provisioning nestlings. The coherence between all three colonies indicating 1994 as a season of reduced foraging efficiency indicates the influence of some broad scale source of variation which over-rides local differences to some degree, e.g. oceanographic thermal phenology (e.g. Drinkwater et al. 1994).

The data presented do not support the previously held assumption of homogeneity of Atlantic Puffin nestling diets along the northeast coast of insular Newfoundland (Nettleship 1972, Brown and Nettleship 1984, Nettleship 1991). While the diets of puffin nestlings on Baccalieu Island were dominated by mature capelin the diets of nestlings on Small and Funk Islands were more variable and composed of a more diverse suite of prey items. This finding is important for the interpretation of other ecological data which are potentially confounded by differences in the diets of puffin nestlings at these colonies (i.e. Nettleship's (1972) comparison of the effects of kleptoparasitic behaviour by gulls toward puffins rested on the assumption that nestling diets among Funk, Small and Great Islands did not differ). In addition, these data suggest differences in the foraging regimes experienced by Atlantic Puffins breeding at the major puffin colonies which parallel differences between major pelagic regimes delineated by recent broadscale pelagic surveys along the northeast coast of insular Newfoundland and southern Labrador (Anderson and Dalley 1997a).

Table 2.1. Mean mass and standard deviation (g) per cm length class of major prey types delivered to Atlantic Puffin nestlings within the study area between 1992 and 1995. Sample sizes in parenthesis. Each x cm class includes measurements from x minus 0.5 to x.4 cm inclusive

Length Class (cm)	Larval capelin	Immature or spent capelin	Gravid capelin	Male capelin	Larval sandlance	Immature or adult sandlance	Hake	Cottid	Herring
1	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	0.1 (1)	-
3	-	-	-	-	-	-	-	0.3 +/- 0.2 (4)	-
4	-	-	-	-	-	-	-	0.8 +/- 0.3 (7)	-
5	0.3 +/- 0.1 (43)	-	-	-	0.2 +/- 0.2 (6)	-	0.9 (1)	-	1.2 +/- 0.5 (8)
6	0.4 +/- 0.1 (42)	-	-	-	0.5 +/- 0.2 (22)	-	1.2 (1)	-	1.1 +/- 0.3 (24)
7	0.6 +/- 0.2 (51)	-	-	-	0.7 +/- 0.1 (26)	0.7 (1)	2.2 +/- 0.4 (6)	-	1.2 (1)
8	0.9 +/- 0.3 (43)	-	-	-	1.0 +/- 0.2 (19)	1.0 +/- 0.1 (9)	2.8 +/- 0.3 (3)	-	-
9	1.5 +/- 0.6 (12)	2.5 +/- 0.5 (5)	-	-	1.3 +/- 0.1 (5)	1.5 +/- 0.2 (31)	4.5 +/- 0.4 (2)	-	-
10	-	3.2 +/- 0.5 (14)	-	-	-	1.9 +/- 0.2 (76)	-	-	-
11	-	4.4 +/- 0.8 (29)	-	-	-	2.6 +/- 0.3 (96)	-	-	-
12	-	6.0 +/- 1.0 (27)	8.1 +/- 1.3 (2)	-	-	3.2 +/- 0.4 (33)	-	-	-
13	-	6.4 +/- 1.1 (72)	8.9 +/- 1.9 (23)	-	-	4.2 +/- 0.9 (4)	-	-	13.0 (1)
14	-	7.5 +/- 1.2 (82)	10.7 +/- 2.3 (18)	-	-	5.5 +/- 1.8 (2)	-	-	17.0 (1)
15	-	9.6 +/- 1.5 (70)	13.6 +/- 2.7 (36)	13.5 (1)	-	6.9 +/- 1.0 (7)	-	-	-
16	-	12.1 +/- 2.3 (35)	15.9 +/- 2.9 (12)	18.9 +/- 3.9 (6)	-	8.7 +/- 1.4 (8)	-	-	-
17	-	13.9 +/- 3.4 (8)	24.5 +/- 0.7 (2)	23.0 +/- 5.3 (3)	-	11.2 +/- 0.6 (7)	-	-	-
18	-	-	-	28 (1)	-	13.1 +/- 1.1(9)	-	-	-
19	-	-	-	-	-	17.3 +/- 1.3 (3)	-	-	-
20	-	-	-	-	-	-	-	-	-
21	-	-	-	-	-	17.8 +/- 2.3 (3)	-	-	-

Table 2.2. Criteria for the assignment of mass (g) to prey items recorded without measurements of either mass or length and for which no other mass data are available from this study. These values used to estimate percent contribution by mass and energy of the various prey.

Prey	Category	Assigned Mass (g)	Criteria
Crustaceans	all	0.15	Modal mean mass of crustaceans reported in Rodway & Montevecchi (1996)
Hake	< 4.5 cm TL	-	As per Rodway & Montevecchi (1996)
Herring	< 4.5 cm TL	0.76	From measured Cottids of the same length (this study)
Gadidae	2.5-3.4 cm TL	0.28	From measured Cottids of the same length (this study)
	3.5-4.4 cm TL	0.76	From measured herring of the same length (this study)
	4.5-5.4 cm TL	1.24	From measured herring of the same length (this study)
Capelin and Sandlance	< 4.5 cm TL	-	As per Rodway & Montevecchi (1996)
Cottidae	4.5-5.4 cm TL	0.9	From hake of the same length (this study)
Nereidae	all	0.8	From 4 cm length class postlarval Cottids (this study)

Table 2.3. Criteria for the assignment of energetic value (kJ/g wet mass) to prey items for the calculation of percent contribution made by different prey to the energy content of nestling diet

Prey	Standard Length (cm)	Assigned [Energy] (kJ/g)	Source
Capelin:			
ovid	all	4.6	Montevecchi & Piatt 1984
male	all	3.8	"
spent	all	3.9	"
immature	all	3.9	"
1+ group	all	3.8	This study; see Table 3.2
Cottidae	all	3.4	This study; see Table 3.3
Crustacea:			
Parathemisto libellula	all	4.38	Percy & Fife 1981
Hyperiid amphipods	all	3.53	"
Gammariid amphipods	all	3.21	"
unidentified amphipods	all	3.89	"
Euphausiacea	all	7.48	"
Gadidae	3.6 - 4.5	3.9	This study; see Table 3.3
	4.6 - 5.5	3.8	"
	5.6 - 6.5	3.5	"
	6.6 - 7.5	3.2	"
	7.6 - 8.5	3.2	"
	8.6 - 9.5	3.2	"
	9.6 - 10.5	3.5	"
	10.6 - 11.5	3.2	"
	11.6 - 12.5	3.2	"
	12.6 - 13.5	3.2	"

Table 2.3. Continued

Prey	Standard Length (cm)	Assigned [Energy] (kJ/g)	Source
Gadidae	> 13.5	3.3	This study; see Table 3.3
Herring	all	3.11*	This study; see Table 3.2
Polychaeta	all	2.81	Percey & Fife 1981
Sandlance			
adult	all	6	This study; see Table 3.2
post-larval 0-group	all	5.37**	"
larval 0-group	all	3.66***	"
Shannies	all	3.57***	"
Squid	all	6.9****	Lawson et al 1998
White Hake	all	3.2	This study; see Table 3.3
Other larval fish	all	3.46	Mean of values for other larval fish

Note: - Values reported from Percy & Fife (1981) are estimated from information on water, protein and fat content using using the conversions factors of 20 kJ/g of protein and 38 kJ/g of lipid.

- Values reported from Percy & Fife (1981) represent the middle of the range of values provided
- Dry energy density = (percent dry mass of protein * 20 kJ/g) + (percent dry mass of lipid * 38 kJ/g)
- Wet energy density = ((100 - % water) * dry energy density)/100

* Water content is assumed to be similar to that of White Hake (mean of three values in this study; see Table 3.3)

** Water content is assumed to be similar to that of immature capelin (this study; see Table 3.1)

*** Water content is assumed to be similar to that of 1-group capelin (this study; see Table 3.1)

**** The value from Lawson et al. 1998 is for *Gonatus* squid. Squid in this study were not identified to species.

Table 2.4. **The median and range of mass and total lengths of the main prey types** collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk **and Small Islands between 1992 and 1995 combined.**

Prey	Group		Mass			Length	
		N	Median (g)	Range	N	Median (cm)	Range
Capelin	1-group	952	0.5	0.1 - 3.2	613	6.5	3.0 - 9.9
	immature or spent	368	7.3	2.0 - 21.0	389	13.8	9.2 - 21.0
	adult male	11	21.0	13.5 - 28.0	12	16.3	15.3 - 18.3
	ovid	94	12.0	4.5 - 25.0	99	14.6	12.2 - 17.5
Sandlance	0-group:						
	larval	150	0.5	0.1 - 1.5	151	6.6	3.5 - 9.1
	post-larval	252	2.3	0.7 - 4.0	617	10.6	7.2 - 12.9
	adult male	5	14.0	6.0 - 14.5	5	17.8	14.7 - 18.0
	ovid	12	11.8	9.5 - 18.0	12	17.5	15.7 - 21.1
Herring	0-group post-larval	33	1.1	0.5 - 2.0	44	5.7	4.5 - 6.6
White Hake	post-larval	14	2.4	0.3 - 4.8	38	4.5	3.0 - 9.1
Stichaeidae	larval	67	0.2	0.1 - 1.0	295	3.4	2.2 - 7.8
Liparis sp.	larval				25	3	2.5 - 4.4
Cottidae	post-larval	38	0.4	0.1 - 1.1	138	3.3	2.1 - 4.9

Table 2.5 Proportional representation of mature capelin in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Mature capelin Proportion (%) Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	79	77	88	81
	8	243 - 249	Aug 29 - Sep 5	10	42	95	70	95
	9	250 - 256	Sep 6 - 8	17	36	69	76	61
1993	2	201 - 207	Jul 19 - 26	56	10	58	45	54
	3	208 - 214	Jul 27 - 31	48	24	60	65	52
	4	215 - 221	Aug 4 - 8	19	76	86	89	80
	5	222 - 228	Aug 10 - 12	35	72	91	94	89
	6	229 - 235	Aug 19 - 23	12	100	100	100	100
	7	236 - 242	Aug 24 - 28	47	79	93	94	90
	8	243 - 249	Aug 30 - Sep 6	42	61	90	93	87
1994	3	208 - 214	Jul 28 - 29	23	10	67	57	70
	6	229 - 235	Aug 22 - 23	11	58	90	73	90
	7	236 - 242	Aug 24 - 25	16	75	95	100	95
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	1	18	11	19
1993	4	215 - 221	Aug 7 - 8	50	2	38	30	41
	5	222 - 228	Aug 10 - 11	77	1	8	5	9
1994	5	222 - 228	Aug 12 - 16	50	1	8	6	8
1995	4	215 - 221	Aug 6 - 8	40	1	4	5	4
	5	222 - 228	Aug 9	22	0	0	0	0
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	5	58	37	64
	6	229 - 235	Aug 18	6	2	33	17	36
1995	5	222 - 228	Aug 13 - 15	49	3	16	16	13
	6	229 - 235	Aug 19 - 20	23	1	5	4	4

Figure 2.1 **Percent occurrence of adult capelin in sampled Atlantic Puffin nestling diets on Baccalieu, Funk and Small Islands during 1992 – 1995. Grey shading = adult capelin, black shading = other.**

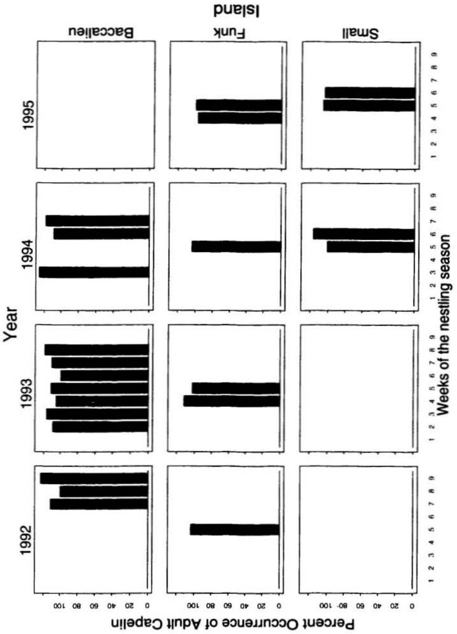

Year
1992
1993
1994
1995
Island
Baccalieu
Funk
Small
Percent Occurrence of Adult Capelin
0
20
40
60
80
100
Weeks of the nestling season
1 2 3 4 5 6 7 8 9

Figure 2.2 **Percent frequency of adult capelin in sampled Atlantic Puffin nestling diets on Baccalieu, Funk and Small Islands during 1992 – 1995. Grey shading = adult capelin, black shading = other.**

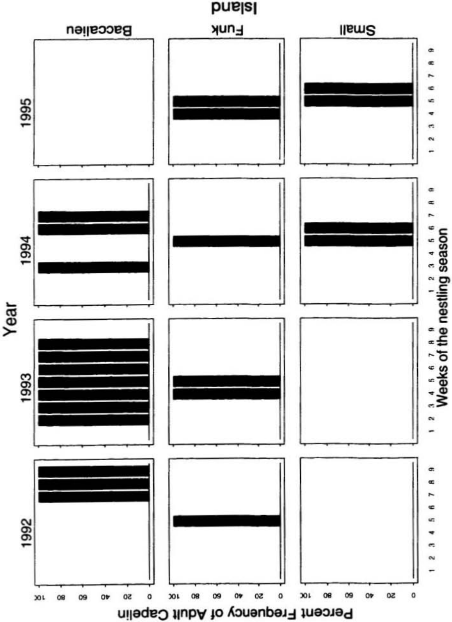

Year
1992
1993
1994
1995
Island
Baccalieu
Funk
Small
Weeks of the nestling season
1 2 3 4 5 6 7 8 9
Percent Frequency of Adult Capelin
0 20 40 60 80 100

Figure 2.3 **Percent mass of adult capelin in sampled Atlantic Puffin nestling diets on Baccalieu, Funk and Small Islands during 1992 – 1995. Grey shading = adult capelin, black shading = other.**

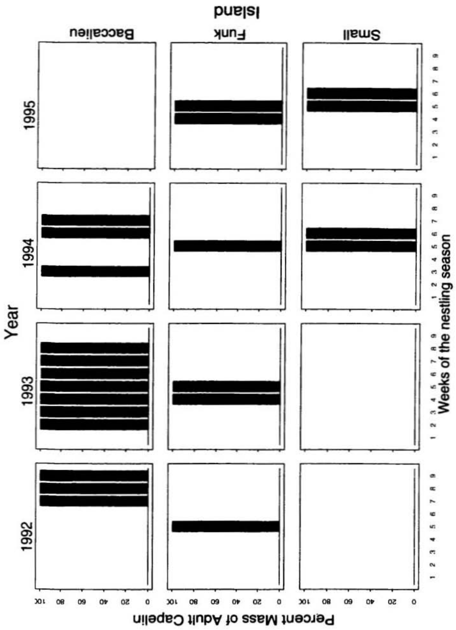
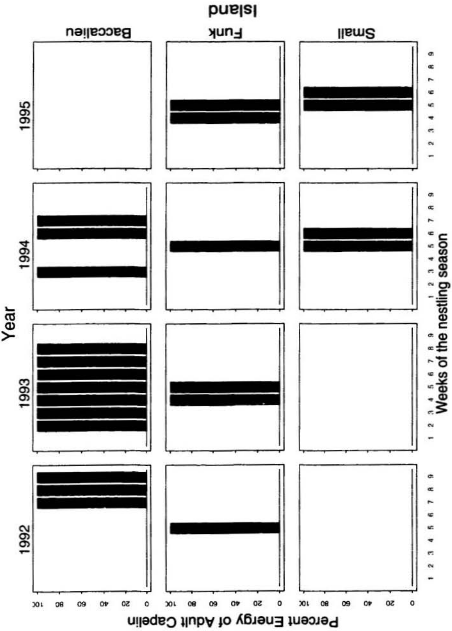

Year
1992
1993
1994
1995
Island
Baccalieu
Funk
Small
Percent Mass of Adult Capelin
0
20
40
60
80
100
Weeks of the nestling season
1
2
3
4
5
6
7
8
9

Figure 2.4 **Percent of estimated dietary energy content represented by adult capelin in sampled Atlantic Puffin nestling diets on Baccalieu, Funk and Small Islands during 1992 – 1995. Grey shading = adult capelin, black** shading = other.



Island
Baccalieu
Funk
Small
Year
1992
1993
1994
1995
Percent Energy of Adult Capelin
0
20
40
60
80
100
Weeks of the nestling season
1
2
3
4
5
6
7
8
9

Table 2.6 **Number of individual prey items in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.**

					Number of Prey Items in bill-loads				
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Min	1st Quantile	Median	3rd Quantile	Max
Baccalieu Island									
1992	7	236 - 242	Aug 23 - 28	17	1	1	1	2	3
	8	243 - 249	Aug 29 - Sep 5	10	1	1	1	3	4
	9	250 - 256	Sep 6 - 8	16	1	1	2	3	13
1993	2	201 - 207	Jul 19 - 26	53	1	1	3	11	25
	3	208 - 214	Jul 27 - 31	47	1	1	1	2	37
	4	215 - 221	Aug 4 - 8	19	1	1	2	2	3
	5	222 - 228	Aug 10 - 12	35	1	1	1	2	12
	6	229 - 235	Aug 19 - 23	12	1	1	1.5	2	2
	7	236 - 242	Aug 24 - 28	46	1	1	1	2	9
	8	243 - 249	Aug 30 - Sep 6	41	1	1	2	2	9
1994	3	208 - 214	Jul 28 - 29	22	1	2	9	13	27
	6	229 - 235	Aug 22 - 23	10	1	2	2.5	4	8
	7	236 - 242	Aug 24 - 25	16	1	1	1	2	5
Funk Island									
1992	5	222 - 228	Aug 8 - 10	55	1	7	14	23	42
1993	4	215 - 221	Aug 7 - 8	49	1	8	18	24	50
	5	222 - 228	Aug 10 - 11	72	1	9.5	16	21.5	48
1994	5	222 - 228	Aug 12 - 16	41	2	10	13	17	31
1995	4	215 - 221	Aug 6 - 8	40	1	3.5	5.5	8	19
	5	222 - 228	Aug 9	22	1	5	7	9	12
Small Island									
1994	5	222 - 228	Aug 11 - 16	100	1	1	7	15	39
	6	229 - 235	Aug 18	6	3	7	16	21	21
1995	5	222 - 228	Aug 13 - 15	49	1	3	7	8	14
	6	229 - 235	Aug 19 - 20	23	1	4	4	6	12

Table 2.7 **Mass (g) of bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.**

Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Mass (g) of bill-loads				
					Min	1st Quantile	Median	3rd Quantile	Max
Baccalieu Island									
1992	7	236 - 242	Aug 23 - 28	16	4.1	6.2	8.6	11.3	30
	8	243 - 249	Aug 29 - Sep 5	5	6	9	11.0	11.1	13.5
	9	250 - 256	Sep 6 - 8	13	5	6.5	11.5	14.0	23
1993	2	201 - 207	Jul 19 - 26	49	0.5	2.3	4.5	13.0	27.3
	3	208 - 214	Jul 27 - 31	44	0.5	7.5	12.7	22.5	33.1
	4	215 - 221	Aug 4 - 8	16	4.5	8.5	13.8	17.5	28.7
	5	222 - 228	Aug 10 - 12	35	4	6.5	9.8	15	26.4
	6	229 - 235	Aug 19 - 23	8	6.5	9.5	14.5	20.2	23.6
	7	236 - 242	Aug 24 - 28	41	6	8.5	10.3	18.0	29.3
	8	243 - 249	Aug 30 - Sep 6	38	5	8	10.9	17.0	30.5
1994	3	208 - 214	Jul 28 - 29	23	2	4.5	6.5	14.0	23.5
	6	229 - 235	Aug 22 - 23	9	4	7	10.0	15.9	18
	7	236 - 242	Aug 24 - 25	13	5.3	7.3	8.4	13.8	19
Funk Island									
1992	5	222 - 228	Aug 8 - 10	50	1	5	10.1	13.8	26
1993	4	215 - 221	Aug 7 - 8	47	3.5	6.5	9.5	12.5	27.3
	5	222 - 228	Aug 10 - 11	72	0.8	5.5	8.5	12	27.5
1994	5	222 - 228	Aug 12 - 16	37	2	5.3	7.6	11.5	24.5
1995	4	215 - 221	Aug 6 - 8	35	3.9	7.5	10.7	16	29.5
	5	222 - 228	Aug 9	21	1.7	3.7	11	18.1	22.5
Small Island									
1994	5	222 - 228	Aug 11 - 16	89	1.3	5.5	9.1	12.5	33.5
	6	229 - 235	Aug 18	6	2.9	5.1	8.8	12.5	29.7
1995	5	222 - 228	Aug 13 - 15	48	3.2	11.8	16.3	19.3	28
	6	229 - 235	Aug 19 - 20	21	2.3	9.7	12.5	13.5	25

Table 2.8 Estimated Energy Content (kJ) of bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

		Julian			Estimated energy content of bill-loads (kJ)				
Year	Week	Dates of Week	Sampling Calendar dates	N	Min	1st Quantile	Median	3rd Quantile	Max
Baccalieu Island									
1992	7	236 - 242	Aug 23 - 28	17	14.4	28.1	35.9	42.7	93.3
	8	243 - 249	Aug 29 - Sep 5	10	2.1	6.3	24.2	42.9	51.3
	9	250 - 256	Sep 6 - 8	17	1.1	23.4	35.1	65.2	110.7
1993	2	201 - 207	Jul 19 - 26	56	2.1	8.9	22.5	53.1	120.8
	3	208 - 214	Jul 27 - 31	48	5.4	30.4	65.2	107.4	189.0
	4	215 - 221	Aug 4 - 8	19	3.4	29.6	61.6	78.8	159.0
	5	222 - 228	Aug 10 - 12	35	15.6	28.3	38.5	68.9	106.9
	6	229 - 235	Aug 19 - 23	12	25.4	37.5	55.7	70.1	92.0
	7	236 - 242	Aug 24 - 28	47	2.6	32.4	39.0	70.2	155.3
	8	243 - 249	Aug 30 - Sep 6	42	19.5	32.1	40.2	71.4	119.0
1994	3	208 - 214	Jul 28 - 29	23	3.5	12.7	26.1	59.3	105.9
	6	229 - 235	Aug 22 - 23	11	3	22.5	39.0	62.0	70.2
	7	236 - 242	Aug 24 - 25	16	20.7	28.9	31.2	56.8	74.1
Funk Island									
1992	5	222 - 228	Aug 8 - 10	55	3.2	13.2	27.5	41.6	153.9
1993	4	215 - 221	Aug 7 - 8	49	1.2	24.4	35.4	55.2	125.6
	5	222 - 228	Aug 10 - 11	77	6	22.2	32.6	47.2	122.9
1994	5	222 - 228	Aug 12 - 16	49	1.1	13	20.7	30.6	80.6
1995	4	215 - 221	Aug 6 - 8	39	11	34.6	55.5	82.9	161.3
	5	222 - 228	Aug 9	22	5.3	12.9	54.6	93.4	129.9
Small Island									
1994	5	222 - 228	Aug 11 - 16	104	0.5	18.6	33.7	55.2	154.1
	6	229 - 235	Aug 18	6	14.8	18.2	33.4	55.0	122.6
1995	5	222 - 228	Aug 13 - 15	49	17.2	63.4	84.7	98.8	145.5
	6	229 - 235	Aug 19 - 20	23	12.4	52.1	65.2	71.7	144.4

Figure 2.5 **Boxplots showing the size (number of prey items per bill-load) of bill-loads delivered by adult Atlantic Puffins to nestlings on Baccalieu, Funk and Small Islands during 1992 - 1995. Boxplot brackets indicate the range of values, black boxes the inter-quartile range, white lines through black boxes the medians and dashes the outliers (defined as points that are further away from the median than 1.5 times the inter-quartile range). The grey shading indicates the 95 % confidence limit around the median. The absence of boxplots rather than representing "null" observations indicates the absence of sampling during that period.**

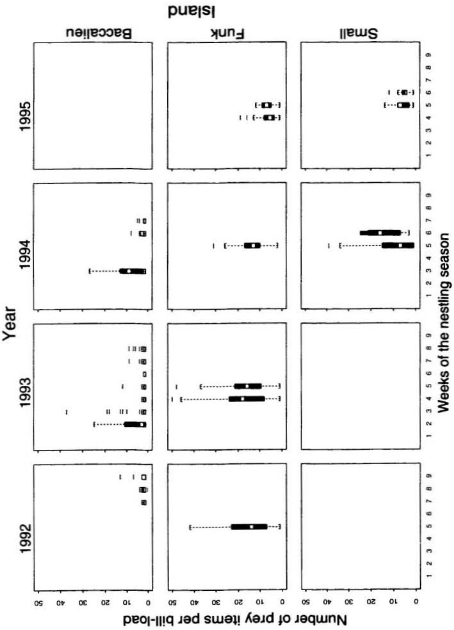

Island
Baccalieu
Funk
Small
Year
1992
1993
1994
1995
Weeks of the nestling season
1 2 3 4 5 6 7 8 9
Number of prey items per bill-load
0 10 20 30 40 50

Figure 2.6 **Boxplots showing the mass (g) of bill-loads delivered by adult Atlantic Puffins to nestlings on Baccalieu, Funk and Small Islands during 1992 - 1995. Boxplot brackets indicate the range of values, black boxes the inter-quartile range, white lines through black boxes the medians and dashes the outliers (defined as points that are further away from the median than 1.5 times the inter-quartile range). The grey shading indicates the 95 % confidence limit around the median. The absence of boxplots rather than representing "null" observations indicates the absence of sampling during that period.**

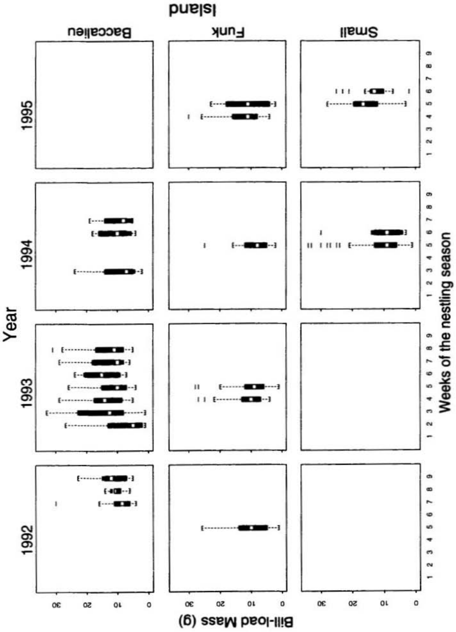

Year
1992
1993
1994
1995
Island
Baccalieu
Funk
Small
Bill-load Mass (g)
0
10
20
30
Weeks of the nestling season
1 2 3 4 5 6 7 8 9

Figure 2.7 Boxplots showing the estimated energy content (kJ) of bill-loads delivered by adult Atlantic Puffins to nestlings on Baccalieu, Funk and Small Islands during 1992 - 1995. Boxplot brackets indicate the range of values, black boxes the inter-quartile range, white lines through black boxes the medians and dashes the outliers (defined as points that are further away from the median than 1.5 times the inter-quartile range). The grey shading indicates the 95 % confidence limit around the median. The absence of boxplots rather than representing "null" observations indicates the absence of sampling during that period.

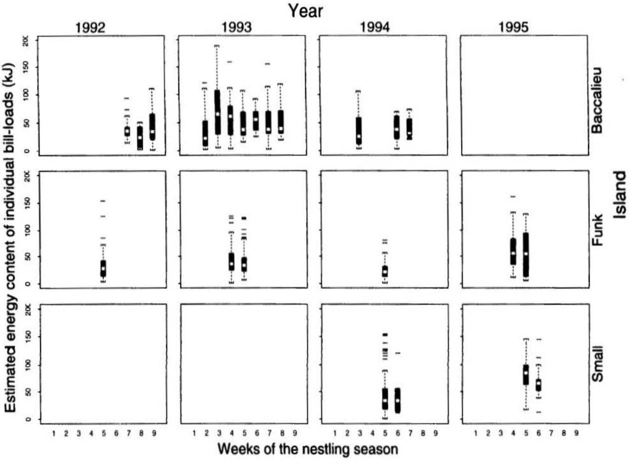
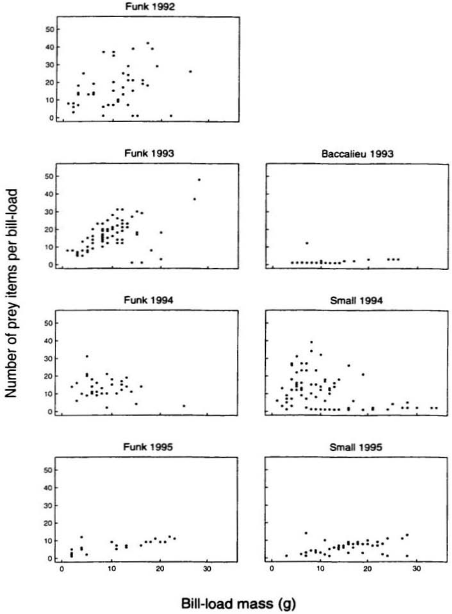

Year
1992
1993
1994
1995
Island
Baccalieu
Funk
Small
Estimated energy content of individual bill-loads (kJ)
0
50
100
150
20
1 2 3 4 5 6 7 8 9
Weeks of the nestling season

Figure 2.8 The relationship between bill-load mass (g) and the number of prey items per bill-load for all locations and years sampled during week 5 of the nestling period on Baccalieu, Funk and Small Islands 1992 - 1995.

Week 5 of puffin nestling season



Funk 1992

Funk 1993

Baccalieu 1993

Funk 1994

Small 1994

Funk 1995

Small 1995

Figure 2.9 The relationship between bill-load mass (g) and estimated bill-load energy content (kJ) for all locations and years sampled during week 5 of the nestling season on Baccalieu, Funk and Small Islands 1992 - 1995.

Week 5 of puffin nestling season

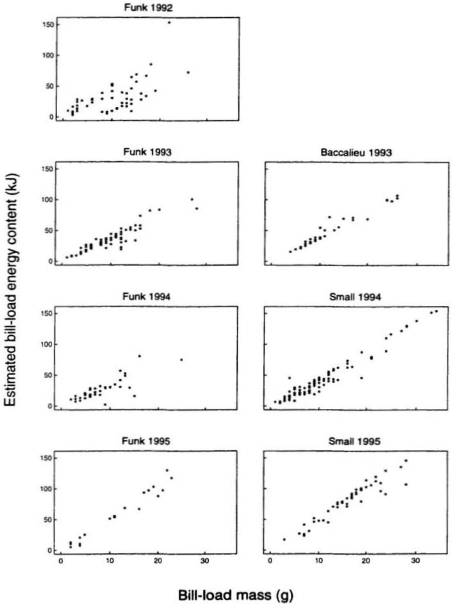
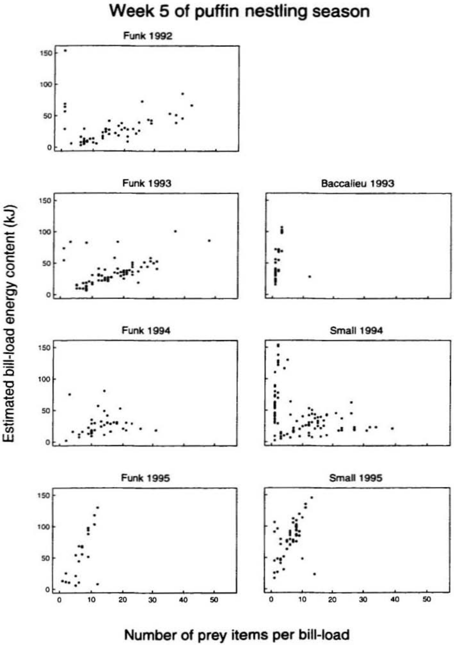


Figure 2.10 **Relationship between bill-load size (number of prey items per bill load) and estimated bill-load energy content (kJ) for all locations and years sampled during week 5 of the nestling season on Baccalieu, Funk and Small Islands 1992 - 1995.**


Week 5 of puffin nestling season
Funk 1992
Funk 1993
Baccalieu 1993
Funk 1994
Small 1994
Funk 1995
Small 1995
Estimated bill-load energy content (kJ)
150
100
50
0
0
10
20
30
40
50
Number of prey items per bill-load

3.0 Proximate composition of prey delivered to Atlantic Puffin nestlings

3.1 Introduction

Prey fed to seabird nestlings differ in nutritional value both within and between species (Clarke and Prince 1980, Montevecchi and Piatt 1984, Hislop et al. 1991). Assumptions concerning prey quality are central to theories on feeding behaviour (Schluter 1980, Perry and Pianka 1997), population level consumption models (e.g. Wiens and Scott 1975, Montevecchi et al. 1984, Diamond et al. 1993, Rodway and Montevecchi 1996), and inferences regarding the suitability of different prey options (e.g. Brown and Nettleship 1984, Nettleship 1991).

Optimal diet theory predicts that predators differentiate between prey items on the basis of their abundance and food value (Schluter 1980, Campbell 1987). Some studies show seabirds feeding the largest and/or most energetically and protein rich prey to nestlings (Harris and Hislop 1978, Piatt 1987, Montevecchi et al. 1987, Baird 1991). Consumption estimates from bioenergetics modelling are sensitive to assumptions concerning prey energy density (Beuchamp et al. 1989, Brekke and Gabrielsen 1994, Martensson et al. 1996). Given the sensitivity of models to, and the large amount of variation in prey energy density, there is need for more published data on the food value of seabird prey. While some published data specific to seabirds in the North Atlantic exist (e.g. Harris and Hislop 1978, Montevecchi and Piatt 1984, Hislop et al. 1991, Brekke and Gabrielsen 1994), there remains a paucity of reported data for the less common prey items of seabirds.

It has been assumed that with regard to size, abundance and nutritional value, no alternative prey to capelin is available to seabirds breeding in eastern Newfoundland (Brown and Nettleship 1984, Nettleship 1991). With regard to nutritional value, information on alternatives to mature capelin for seabirds in the Northwest Atlantic has been insufficient to properly assess this assumption.

This study reports proximate composition data for some of the less common prey species and/or size classes found in the diets of nestling Atlantic Puffins in the Northwest Atlantic. These data will be used to assess the assumption that there are no prey of comparable quality to mature capelin available to puffins provisioning young off the northeast coast of insular Newfoundland.

3.2 Methods

Fish collected from Atlantic Puffins provisioning nestlings were retained on an opportunistic basis for later proximate composition analysis by the Department of Fisheries and Oceans Inspections Branch Laboratory in St. John's, Newfoundland. Fish retained on Baccalieu Island were fresh frozen. On Funk and Small Islands specimens were air and sun dried. In addition to prey intercepted directly from birds, a logistical opportunity presented itself to obtain fish fresh from the water from an inshore juvenile cod survey in Trinity Bay (see Methven et al. 1997 for survey methods). This survey used a beach seine to sample juvenile fish nearshore. These fish were immediately frozen. Percent composition of fat, protein, ash and water were obtained in duplicate. Duplicate values were averaged and the result used as the value for that analysis. Direct measurement during proximate analysis of fresh specimen water content was possible for frozen samples only. The amount of dry matter required for proximate composition procedures often required the inclusion of multiple individuals in any given analysis and, therefore, the number of individuals (n) comprising a single proximate analysis sample varied (i.e. 1 to 47). For some prey types more than one independent sample was analysed and the mean ± standard deviation (SD) and independent sample size (N) is reported for those cases. Total length of fresh specimens collected from birds was measured in the field for most samples. In the absence of sampled prey lengths, measurements from prey of the same type, sampling location and time period are reported instead (indicated by an asterix in Tables 3.1 and 3.2). Fork length rather than total length is reported for fish caught by beach seine.

Proximate composition

Prior to compositional analysis, the thawed or sun dried sample mass was measured to the nearest 0.001 g, then homogenised and dried in a vacuum oven at 100 C until reaching constant mass. The dried matter from frozen samples was weighed and percent moisture calculated by subtraction from thawed sample mass. Fat content of prey was measured by bathing 3 - 5 g of fine ground dry material with 50 ml of diethyl ether before placing on an extraction heater. Solvent removal was followed by drying at 100 C for 30 min. Percent composition of fat was calculated by dividing mass of extracted fat by mass of the original dry matter. Nitrogen composition was estimated by the Kjeldahl Method on a 2 g sample of homogenised prey. Protein composition was calculated as: % Protein = % Nitrogen x 6.25. Ash content was derived from 5 g samples of original homogenate dried for 24 hr at 100 C. Material was further heated in a stepwise fashion to 550 C and maintained at that temperature for 8 hr or until a white ash resulted. All organic matter was oxidised by incineration and remaining material obtained as ash. The ash product was weighed to the nearest 0.001 g after cooling in a dessicator (Fisheries and Oceans 1986).

All data reported on water composition are measurements of the difference between thawed wet mass and dried mass of frozen samples. For those specimens obtained from birds these are minimal estimates of prey water content (as delivered to nestlings), not necessarily representative of prey fresh from the sea (Montevecchi and Piatt 1987). Lipid, protein, and ash content are reported as percent composition of dry mass. Comparative values from the literature have been converted to the same units using the formula: (100 x wet value) / (100-water content) = dry value. Energy densities of prey were estimated using two sets of conversion factors referred to as A and B (A: 20 kJ/g protein and 38 kJ/g lipid (Ricklefs & Schew 1994, Ricklefs 1974 and 1983 in Montevecchi et al. 1984), and B: 23.7 kJ/g for protein and 39.6 kJ/g for lipid (Crisp 1971 in Hislop et al. 1991)). Comparisons made with published values for the North Atlantic are for prey of comparable length collected during roughly the same calendar period.

3.3 Results

Results of proximate analysis and energy density estimation for prey collected from birds are summarised in Tables 3.1 and 3.2, respectively, and the results from beach seined fish in Table 3.3.

Of those prey from seabirds for which water content was measured the lowest value was an adult sand lance (67 %) and the highest a sample of 1+ group capelin at 80 %. Adult fish had the lowest water contents, separated from the higher values of 0 and 1-group fish by at least 5 %. Of those fish collected directly from the sea, water content ranged from a low of 77 % in juvenile shannies (Stichaeidae) to a high of 83 % in juvenile white hake. Nine 1 cm length classes of juvenile cod (4.0 - 18.0 cm total range) had water contents 81 - 82 %. Three 1 cm length classes of juvenile white hake (5.0 to 8.0 cm total range) had water contents of between 82 - 83 %.

Fat content ranged from a low of 5 % in 0-group herring to a high of 37 % in an adult sand lance. The higher values (17 - 37 %) were from fish of adult morphology and the lower values (5 - 17 %) from 0 and 1-group fish which had not completely metamorphosed (e.g. 1995 0-group sand lance had values similar to adult fish but 0-group sand lance in that year were larger than other years and had attained adult morphology). Fat content in juvenile cod declined with increasing length.

Protein content ranged from a low of 51 % in an adult sand lance to a high of 78 % in a sample of 1-group capelin. Immature capelin and adult sand lance had the lowest values (e.g. 56 % and 59 ± 5 %, N=8 respectively). The juvenile and larval fish had higher protein contents of 65 to 78 % (in order of roughly increasing protein content: Cottids: 64 - 67 %, 0-group sand lance from 1995: 66 %, cod: 68 - 75 %, white hake: 70 - 74 %, shannies: 72 %, 0-group sand lance from 1993 and 1994: 74 and 74 %, respectively and herring: 77 %). Protein content in juvenile cod increased with length within the size range sampled (i.e. 4-18 cm total range), while the opposite was apparent for sand lance (i.e. protein content of pre-metamorphosed sand lance was 74 % while that of the larger metamorphosed 0-group sand lance was 66 %).

Ash content ranged from a low of 7 % in an adult sand lance to a high of 21 % in juvenile cod. The lowest values were all associated with metamorphosed fish (e.g. immature capelin: 8 %, adult sand lance: 7 - 10 %, and 0-group sand lance from 1995: 9 - 10 %) while the higher ash contents were all associated with smaller fish (in order of roughly increasing ash content: capelin 1-group: 10 - 11 %, 0-group sand lance 1994 and 1993: 11 %, shannies: 12 - 13 %, white hake: 14 - 20 %, herring: 15 %, Cottidae: 15 % and cod: 15 - 21 %).

The energy density of dry matter using conversion factors A and B (see Methods) ranged from a low of 16.6 and 19.4 kJ/g, respectively, in a sample of juvenile cod to a high of 24.2 and 26.7 kJ/g in an adult sand lance. Wet energy densities (only calculated for samples with water composition data and using factors A and B, respectively) ranged from 3.1 and 3.6 kJ/g in a sample of juvenile white hake to 7.9 and 8.7 kJ/g in an adult sand lance. The highest energy densities based both on dry (e.g. A: 20.1 - 24.2 kJ/g) and wet mass (e.g. A: 4.8 - 7.9) were obtained from fish of adult morphology and largest size (i.e. adult sand lance, immature capelin and 0-group sand lance from 1995). The lowest energy densities were from larval and juvenile fish (e.g. dry A: 16.6 - 20.1 kJ/g and wet A: 3.2 - 3.9 kJ/g).

3.4 Discussion

3.4.1 Water content

In practical terms, measuring the water content of prey collected from birds is the Achilles' heel of assessing prey quality. Dehydration of prey prior to collection from birds is common, variable and unquantifiable. As Atlantic Puffins dangle food for nestlings cross-wise in the bill a variable portion of prey surface area is exposed to the air depending on the number of prey items being carried, the size of prey, and the portion inside the puffin's gape. Exposure to the drying effects of the atmosphere also depends on weather conditions and foraging distance from the breeding colony, which varies from less than 1 to 10s of km with extremes of 100 km recorded (Bradstreet and Brown 1985, Piatt 1987, Anker-Nilssen and Lorentsen 1990). Assessment of water content from such prey is biased and inflates wet mass energy density estimates (Montevecchi and Piatt 1987). Water content measurements of prey collected from incoming puffins are useful in estimating wet energy content of that particular prey only and are misleading when used to estimate wet energy density for extrapolation to other data.

On an individual basis smaller prey and prey caught farthest from the colony should suffer more dehydration than larger prey which have less surface area relative to body volume. However, on a bill-load basis smaller prey are more often accompanied by many individuals (see Chapter 2), minimising surface area exposed to the air, while the largest prey are often carried singly, maximising air exposed surface area. Furthermore, during this study smaller prey were often still alive on arrival at the colony indicating nearby capture and minimal transport time while large prey were rarely delivered live, indicating capture and thus air transport from further afield. These factors combined suggest that for the data reported here large prey may have suffered more dehydration than small prey.

Studies on intra-specific variation in water content with prey length reveal that fish generally have greater percent water composition early in their life history than later (Hislop et al.1991). The few estimates of water composition reported here concur with this pattern although for the reasons stated above the values for those collected from birds represent water content on colony arrival (expected to vary in response to several unquantified factors), rather than the beach seined values which represent the water content of fresh live prey .

Water content information is necessary for the estimation of wet mass energy density and total amount of energy delivered to nestlings. Of the six prey types in this study for which water content delivered to nestlings was measured, 0 and 1-group fish had the highest values and mature fish the lowest. The observed pattern of decreasing water content with increasing age of fish is widespread and associated with increasing fat content (Winters 1970, Sidwell et. al. 1974, Hislop et al. 1991). In terms of energy it is the total energy content of prey received by the nestling that is the parameter of biological significance. Therefore, dry energy density alone is of limited use in understanding meaningful differences in prey dietary quality. Prey water content, although difficult to assess in a standardised way, remains of interest for this reason, and because it is the only source of nestling water. In the absence of accurate water composition the estimation of the wet energy density of fresh fish is not possible. Fish of equivalent dry energy densities but differing water contents provide quite different numbers of total energy units to a nestling on a fresh mass basis (see also discussion of energy density below).

3.4.2 Lipid content

Lipid content of fish is generally negatively correlated with water content (Hislop et al. 1991). Low lipid values in this study were also coupled with high water contents and vice versa. High levels of dietary lipid content are associated with greater assimilation efficiency and absorption of other nutrients (Brekke and Gabrielsen 1994). When the main difference between prey is in lipid content, higher lipid items may offer more than simply an increase in dietary energy density (i.e. increased assimilation of other nutrients may also result). If as suggested, the relationship between lipid and assimilation efficiency is linear (Brekke and Gabrielsen 1994), the considerably lower lipid content of pre-metamorphosed size classes of fish compared with adult forms (e.g. 5 - 17 %

versus 18 - 37 % lipid on a dry mass basis, respectively) would be accompanied by lower assimilation efficiency. As assimilation efficiency also declines with increased consumption (McClintock 1986), the need to eat greater quantities of food low in energy due to low fat content and the low fat content itself may interact to further reduce assimilation of nutrients consumed. Small fish with low fat content would be less desirable on these grounds when compared with larger fish with higher fat content.

3.4.3 Protein content

The protein content of prey may be equally, if not more important, than overall energy content to nestling growth demands (Baird 1991, Robbins 1993, Bowen et al. 1995), although it has been assumed that fish is an adequate source of dietary protein for growing chicks (Harris and Hislop 1978). Protein, while inferior to lipid as a source of energy, can also serve as an energy source, while at the same time providing amino acids which are essential for tissue growth (Ricklefs 1979). Montevecchi and Piatt (1984) found the amino acid compositions of capelin, squid and herring slightly below the minimum required for poultry to maintain nitrogen equilibrium. Squid was low in Valine, capelin and herring low in Arginine and all three species low in Isoleucine. The relevance of poultry amino acid requirements to Atlantic Puffin nestlings is not known but the ubiquity of healthy puffin fledglings raised on diets of adult capelin in Newfoundland (Bradstreet and Brown 1985) and 0-group herring in Norway (Anker-Nilssen 1992), suggests that the discrepancy identified does not translate into inhibited growth or survival to fledging for puffin nestlings. At lower trophic levels increased consumption of poor quality foods can compensate for low energy density but not for low dietary protein (Bowen et al. 1995). It is not clear whether differences in protein content among fish eaten by puffin nestlings require compensation or if in the absence of compensatory feeding there are consequences for nestling growth. Among those prey examined in this study those known to be associated with successful puffin chick rearing (i.e. mature sand lance and immature capelin) had the lowest dry protein compositions suggesting that gross protein is not a limiting factor among these prey choices. However, the possibility that certain amino acids may be lacking in some species or size classes remains (Ricklefs 1974).

3.4.4 Ash content

Assimilation efficiency is variable within consumer species and influenced by food quality. Ash content serves as an indication of food quality (i.e. the higher the ash content the lower the assimilation efficiency; Valiela 1995). Ash content was lowest in fish of adult form (i.e. mature sand lance, immature capelin and 0-group sand lance from 1995) with Gadids, Cottids and shannies having the highest values. The observed pattern fits the suggestion that ash content indicates food quality as the prey of lowest ash content are known as high quality seabird nestling food while puffin nestling diets high in Gadids have been associated with reduced nestling growth and breeding success (Brown and Nettleship 1984, Hislop et al. 1991, Nettleship 1991). Smaller fish have a greater proportion of indigestible body parts to total mass than larger fish. A food load of tiny 0-group fish will contain more fins, bones and scales per volume than a single large fish. This perhaps explains the pattern of increased ash content in the smaller forms and may be a factor decreasing the overall quality of these forms as nestling food by way of decreased assimilation efficiency.

3.4.5 Energy densities

Energy content varies significantly between marine prey species and the differences are most obvious when comparing wet mass values (Steimle and Terranova 1985). In the absence of bomb calorimetry, energy density is estimated indirectly from proximate composition data. Variation in energy density values between studies is confounded by the choice of conversion factors for estimating prey energy density from protein and lipid content (Table 3.4). As discussed earlier, wet mass energy densities, while more appealing biologically, are also a confounding source of variation in reported values due to problems associated with the assessment of water composition for prey items collected from birds. While dry energy density is a more reliable measure for comparative purposes, real differences in prey quality are dampened and sometimes reversed by removal of the influence of water content. Lipid and water content are inversely proportional (Winters 1970, Sidwell et. al. 1974, Hislop et al. 1991), and most of the variance in energy content is due to variation in lipid content (Sidwell et al. 1974). Therefore, the direction of differences between prey types in dry energy densities might be expected to mirror differences between the same prey in wet energy densities. This is not always the case. Differences in water content often reverse ordinal relationships between prey energy densities when moving from consideration of dry to wet energy density (e.g. in this study beach seine caught white hake had greater dry energy densities than beach seine caught Cottids (using conversion factors A: 17.6 - 17.7 kJ/g versus 17.5 kJ/g, respectively) although the Cottids had greater wet energy density (3.5 versus 3.1 - 3.3 kJ/g)). A 10 g food load of juvenile white hake would yield a nestling 30.9 - 32.5 kJ whereas an equivalent meal of the juvenile Cottids would yield 34.5 kJ, a clear difference not apparent from or consistent with a consideration of dry energy density alone. Atlantic Puffin nestlings which fledged on Great Island in 1993 consumed an average of 12506 kJ (Rodway and Montevecchi 1996); assuming a 40-day nestling period an average of 312 kJ was consumed per day. To deliver the white hake equivalent of 312 kJ would require 95 - 101 g/day versus 89 g for juvenile Cottids. Assuming a median bill-load mass of 10 g for simplicity (i.e. Baccalieu Aug 22 - 23 1994, see Table 2.7), a puffin feeding a nestling with white hake would make 22 - 46 more provisioning trips over the nestling period than a puffin preying on Cottids. This illustrates the importance of wet energy density to the birds. A consideration of dry energy density would have suggested birds were better off foraging on white hake. While this may well be the case for other reasons, dry prey energy density is not one of them.

The fine scale ordinal pattern of measured wet and dry energy densities for prey were not always equivalent, and neither were the ordinal patterns of dry or wet energy densities estimated using two different sets of conversion factors from the seabird literature (see Methods). Variation in methods used to measure and/or estimate the proximate composition, energy density and energy content of marine prey make comparisons between studies inconvenient if not impossible. Comparisons with relevant published values are hindered by variation in the measures and units reported. Protein, lipid and ash content are variously reported as percent wet mass (e.g. Montevecchi and Piatt 1984, Hislop et al. 1991, Lawson et al. 1998) or as percent dry mass (e.g. Harris and Hislop 1978). As proximate composition and energy densities change with prey length and time of year, few published values are directly comparable due to differences in, or absence of, prey length and time of year data.

Marine ecologists would benefit by the adoption of a standard protocol for assessing and reporting the food quality of prey species. This study supports Montevecchi and Piatt's (1987) suggestion that dry energy densities be reported for comparisons of prey quality between sampling locations and periods. In addition, it is desirable to 1) report ash and lipid content for their influence on Assimilation Efficiency (Valiela 1995), 2) standardise the conversion factors in use for estimating energy density from protein and lipid content and/or ideally, 3) retain sufficient samples to measure both energy density and proximate composition directly (i.e. measure energy using bomb calorimetry and percent protein, lipid and ash using proximate composition analyses) and 4) when possible report prey length, maturity status and date of collection with any associated energy and proximate composition data. The precision and reliability of wet mass energy density estimates are dependent on the precision and reliability of fresh water content measurements of prey (Montevecchi and Piatt 1987).

If freezing of samples is not an option, as it rarely is on seabird islands, prey must be preserved by drying. Field scales used to measure fresh specimen mass before drying are rarely as precise or accurate as scales used in the laboratory where final dry mass measurements are made during proximate composition analysis. Ideally, specimens should be frozen and their thawed and dried masses measured on the same scales. Alternatively, the advent of affordable lightweight electronic field scales will enable researchers to weigh the individual masses of tiny prey items more precisely in the field.

Energy densities in this study were greatest among fish of adult morphology and largest size, especially among sandlance. These prey, when abundant in nestling diets, are all associated with good puffin chick growth and breeding success (e.g. Martin 1989, Nettleship 1991, Anker-Nilssen 1992). While it is not always explicitly stated, the assumption that there are no suitable alternatives to mature capelin available to Atlantic Puffins breeding off the east coast of Newfoundland refers in particular to alternatives to adult capelin which have migrated inshore to spawn. The energy density of adult capelin is lower in summer than winter (Lawson et al. 1998). This may reflect the decrease in lipid content observed by Winters (1970) to occur in mature capelin during the pre-spawning months of spring. Due to seasonal variation in capelin energy density it is important to only compare values obtained from similar seasons. Proximate composition and energy density data on adult capelin during summer (June) exist for this region (Montevecchi and Piatt 1984; Table 3.5) but does not include data on 1-group and immature capelin which are provided here.

Another recent study reporting on the energy density of important prey species in the northwest Atlantic provides information on summer time capelin although reproductive status and month of collection is not given (Lawson et al. 1998; Table 3.5). 1-group capelin reported here had the same wet energy density as adult male capelin reported elsewhere (Montevecchi and Piatt 1984) and the value obtained by this study for immature capelin exceeded other values reported for capelin in this region during a comparable time period (Tables 3.2 and 3.5 respectively). It must be noted that most adult capelin fed to puffin nestlings in the northwest Atlantic have been ovid and spent females or immature. Male capelin are rarely fed to puffin nestlings (Nettleship 1991, Rodway and Montevecchi 1996, this study) or common Murre nestlings (Montevecchi unpubl data).

The high energy density obtained for immature capelin is surprising, as previous data indicated that immature capelin had much lower lipid content than mature capelin (Winters 1970). At the time of spawning, feeding intensity is low in mature capelin and does not decrease for immature fish (Winters 1970). This provides one possible explanation for the unexpectedly high energy density value obtained in the present study for immature capelin. As this study did not remove stomach contents of prey species before proximate composition analysis, the presence of a stomach full of prey could raise energy values. However, given that the surprising value for immature capelin was obtained from a single fish, the result should be treated with caution.

Adult sandlance and the post-larval 0-group sandlance from 1995 collected in this study had energy densities that exceeded those reported for mature capelin (including gravid fish) during a comparable time period in this region (Montevecchi and Piatt 1984, Lawson et al. 1998, Table 3.5). There appear to be prey alternatives to adult capelin available to foraging puffins in the northwest Atlantic with equal if not greater energy value than adult capelin. However, the following qualification is in order. Interannual differences in intra-species energy densities have been found in the northwest Atlantic for other species (Lawson et al. 1998). This study did not collect data on adult capelin and therefore relies on comparison with values for adult capelin from other years. The possibility that capelin from the same years as prey reported in this study had higher energy density value than those previously reported in the literature, can not be ruled out.

Assuming equivalent availability and catchability among the prey species known to occur in puffin nestling diet, and assuming that comparisons made with capelin in this study are not confounded by unknown interannual variation in capelin energy density, then on the basis of energy density alone one would predict that even in the presence of adult capelin, puffins provisioning nestlings would feed them sandlance.

Table 3.1 Proximate composition (% dry mass) of prey items fed to Atlantic Puffin nestlings

Species/ group	Age status	Mean length (cm) N	(SD)	Year	Month	Colony	N	Mean % (SD) water	protein	fat	ash
Capelin	1-group	6	8.3 (1.3)	1993	July	Baccalieu	1	80.2	72.5	11.8	10.4
		174*	6.1 (0.9)	1993	Aug	Funk	7		76.3 (0.6)	8.6 (0.9)	10.6 (0.6)
		75*	6.7 (0.8)	1994	Aug	Small	1		74.8	8.3	11.1
	immature	3	11.5 (0.6)	1993	July	Baccalieu	1	75.9	55.7	30.2	7.9
Cottidae	juvenile	5*	3.6 (0.2)	1993	Aug	Funk	3		65.2 (0.4)	13.7 (1.3)	14.7 (2.4)
		7*	3.7 (0.5)	1994	Aug	Small	2		67.4 (0.1)	11.6 (0.8)	15.4 (0.7)
White hake	0-group	18*	6.5 (1.8)	1994	Aug	Small	1		73.5	9.0	14.1
Herring	0-group	65*	5.7 (0.5)	1994	Aug	Small	1		77.0	5.3	14.5
Sand lance	adult	11	16.6 (2.1)	1993	July	Baccalieu	8	72.7 (3.0)	59.1 (5.3)	26.9 (6.5)	8.9 (1.2)
	0-group	38*	6.4 (0.6)	1993	Aug	Funk	1		74.3	8.7	11.3
		60*	6.9 (1.4)	1994	Aug	Small	3		74.0 (2.4)	9.7 (2.4)	11.2 (0.2)
		65	10.2 (0.9)	1995	Aug	Funk	7		66.3 (1.9)	23.7 (2.3)	9.1 (0.4)
Shannies	0-group**	13*	3.3 (0.2)	1993	Aug	Funk	1		73.5	10.0	12.0
		63*	3.6 (0.1)	1994	Aug	Small	2		71.5 (1.6)	8.7 (0.2)	13.0 (0.0)

N.B. * lengths of prey items fed to Atlantic Puffin nestlings for the same period and location as the proximate composition samples

** Shannies (Stichaeidae) were not identified to species and depending on which of the two most likely species they belong to (Arctic Shanny *Stichaeus punctatus* or Radiated Shanny *Ulvaria subbifurcata*)

Table 3.2 Dry and wet mass energy density estimates for prey items fed to Atlantic Puffin nestlings using two commonly presented sets of energy equivalents - A (20 kJ/g protein; 38 kJ/g lipid), and B (23.7 kJ/g protein; 39.6 kJ/g lipid)

Species/ group	Age status	Mean N	Length (cm) (SD)	Year	Month	Colony sampled	N	Mean [energy] kJ/g (SD)			
								Dry mass		Wet mass	
								A	B	A	B
Capelin	1-group	6	8.3 (1.3)	1993	July	Baccalieu	1	19.0	21.9	3.8	4.3
		174*	6.1 (0.9)	1993	Aug	Funk	7	18.5 (0.4)	21.5 (0.5)		
		75*	6.7 (0.8)	1994	Aug	Small	1	18.1	21.0		
	immature	3	11.5 (0.6)	1993	July	Baccalieu	1	22.6	25.2	5.5	6.1
Cottidae	juvenile	5*	3.6 (0.2)	1993	Aug	Funk	3	18.3 (0.4)	20.9 (0.5)		
		7*	3.7 (0.5)	1994	Aug	Small	2	17.9 (0.3)	20.6 (0.3)		
White hake	0-group	18*	6.5 (1.8)	1994	Aug	Small	1	18.1	21.0		
Herring	0-group	65*	5.7 (0.5)	1994	Aug	Small	1	17.4	20.3		
Sand lance	adult	11	16.6 (2.1)	1993	July	Baccalieu	8	22.0 (1.4)	24.7 (1.3)	6.0 (1.0)	6.7 (1.0)
	0-group	38*	6.4 (0.6)	1993	Aug	Funk	1	18.1	21.0		
		60*	6.9 (1.4)	1994	Aug	Small	3	18.5 (0.5)	21.4 (0.4)		
		65	10.2 (0.9)	1995	Aug	Funk	7	22.3 (0.6)	25.1 (0.6)		
Shannies	0-group**	13*	3.3 (0.2)	1993	Aug	Funk	1	18.5	21.4		
		63*	3.4 (0.1)	1994	Aug	Small	2	17.6 (0.4)	20.4 (0.4)		

N.B. * = lengths of prey fed to Atlantic Puffin nestlings for the same period and location as the proximate composition sample

** Shannies (Stichaeidae) were not identified to species and depending on which of the two most likely species they belong to (Arctic Shanny *Stichaeus punctatus* or Radiated Shanny *Ulvaria subbifurcata*), their age could be

Table 3.3 Proximate compositions (% dry mass) and dry and wet mass energy densities for beach seined fish, Trinity Bay (1994), using two commonly presented sets of energy equivalents - A (20 kJ/g protein; 38 kJ/g lipid), and B (23.7 kJ/g protein; 39.6 kJ/g lipid). All N = 1 and represent a sample of greater than n=1 individuals.

Species/ group	Age status	Length (cm)	%				Energy Density (kJ/g)			
			Water	Protein	Fat	Ash	Dry (A)	Wet (A)	Dry (B)	Wet (B)
cod	0-group	4.5	80.6	67.7	17.2	15.1	20.1	3.9	22.9	4.4
cod	0-group	5.5	80.6	68.3	15.5	15.1	19.6	3.8	22.3	4.3
cod	0-group	6.5	81.2	69.1	12.5	14.8	18.6	3.5	21.3	4.0
cod	0-group	8.5	81.6	70.1	9.1	17.8	17.5	3.2	20.2	3.7
cod	0-group	9.5	81.4	71.5	8.4	18.1	17.5	3.2	20.2	3.8
cod	0-group	10.5	81.1	74.9	9.5	16.3	18.6	3.5	21.5	4.1
cod	0-group	12.5	81.0	72.4	5.6	21.1	16.6	3.2	19.4	3.7
cod	0-group	13.5	81.1	73.3	5.9	20.2	16.9	3.2	19.7	3.7
cod	0-group	17.5	80.9	72.7	7.3	18.1	17.3	3.3	20.1	3.8
cottidae	1-group		80.3	64.0	12.3		17.5	3.4	20.0	4.0
hake	0-group	6	81.7	69.8	9.9	19.3	17.7	3.2	20.5	3.7
hake	0-group	7	82.2	71.6	8.7	20.2	17.6	3.1	20.4	3.6
hake	0-group	8	82.5	71.6	8.7	19.3	17.6	3.1	20.4	3.6

N.B. Length is mid-point of length class i.e. 4.5 represents fish 4-5 cm fork length

(A) = energy density (dry) = (%protein dry x 20 kJ/g) + (%lipid dry x 38 kJ/g)

(B) = energy density (dry) = (%protein dry x 23.7 kJ/g) + (%lipid dry x 39.6 kJ/g)

cod are *Gadus morhua*, hake are White Hake *Urophysis tenuis*, cottidae are cottid spp.

Table 3.4 A sampling of lipid and protein conversion factors in use for estimation of energy density from proximate composition data

Energy conversion factors (kJ/g) lipid	protein	Source
35.4	22.6	Brekke & Gabrielsen (1994)
37.7	16.8	Sidwell et al. (1974)
37.7	16.8	Schakel et al. (1997)
38	20	Montevecchi & Piatt (1984)
38	29	Lawson et al. (1998)
39.5	18	Taylor et al. (1997)
39.6	23.7	Hislop et al. (1991)
39.8	16.8-18.9	Valiela (1995)

Table 3.5 Recent energy density values for adult capelin in summer reported from the northwest Atlantic

Status	N	Length (cm) Mean (SD)	Year	Month	Area sampled	%water Mean (SD)	kJ/g wet Mean (SD)	Source
Male	15	18.3 (0.62)	1982	June	SE Nfld.	80.2 (1.4)	3.8 (0.5)	Montevecchi and Piatt 1984
Gravid	10	15.8 (1.86)	1982	June	SE Nfld.	76.5 (1.0)	4.6 (0.3)	Montevecchi and Piatt 1984
Spent	10	15.8 (1.27)	1982	June	SE Nfld.	80.0 (2.6)	3.9 (0.8)	Montevecchi and Piatt 1984
-	33	-	-	summer	near shore	-	4.7 (0.8)	Lawson et al. 1998
-	-	-	-	summer	near shore	-	3.4 (0.3)	Nakasima and Kennedy unpubl. data reported in Lawson et al. 1998

N.B. Dry energy density conversion factors used were 38 kJ/g for lipid and 20 kJ/g for protein.

Chapter 4: Atlantic Puffin nestling condition

4.1 Introduction

Seabird nestling condition reflects the quality of nestling diet (Ricklefs & White 1975, Harris 1984, Cruz & Cruz 1990, Anker-Nilssen 1992, Rodway 1997). Cairns (1987) predicted that nestling growth should exhibit a threshold pattern in response to variation in feeding conditions, remaining positive during good conditions but deteriorating under conditions of intermediate food availability. Many studies support this prediction (e.g. Anker-Nilssen 1992).

Investigations of intra- and inter-colony and interannual variation in prefledging growth related to diet quality have been pursued by many researchers (e.g. Harris 1980, Rodway 1997) and have confirmed the correlation between nestling diet and growth (Cruz & Cruz 1990, Uttley et al. 1994, Gebczynski et al. 1996, Phillips et al. 1996, Cook & Hamer 1997).

Atlantic Puffin nestlings fledge at roughly 69 - 75 % of adult mass following a nestling period of about 38 - 44 days, although extreme periods of up to 82 days have been observed (Nettleship 1972, Harris 1984, Rodway 1994). Maximum mass acheived during the nestling period precedes fledging by about a week, after which 8 - 10 % of this peak is lost (Harris 1984) although individual nestlings gain and lose mass in an erratic fashion. While trends in body mass changes by nestlings are generally a reflection of diet, the peculiar daily zig-zag pattern of mass change is not understood (Hudson 1983).

The dependent variable most commonly employed to measure effects of feeding conditions on nestling health is body mass, which is more sensitive than either wing-length, tarsus or culmen to dietary variation (Ricklefs & White 1975, Hudson 1979, Kirkham & Montevecchi 1982, Harris 1984, Cook & Hamer 1997). The independent variable of choice is age. Techniques vary for the measurement of body mass as an indicator of change in nestling diet quality. Measures frequently used for comparisons include mass at fledging (Nettleship 1972), regressions of the linear phase of mass increase (e.g. Wilson 1993), and instantaneous rate of growth at the inflection point where growth rate decelerates shortly before fledging (e.g. Wehle 1983). Several studies have found that the linear phase of mass increase and peak nestling mass are more sensitive to variation in diet than mass at fledging (e.g. Hudson 1979, Bost & Jouventin 1991). Significant differences in the linear growth phases often disappear during the prefledging mass recession resulting in chicks fledging at similar masses. It is possible that this relationship is part of a threshold effect whereby fledging masses are only compromised when feeding conditions worsen beyond that which may affect maximal prefledging mass. Examples of dire feeding conditions for breeding birds have certainly found significant reductions in fledging masses (Anker-Nilssen 1992). Ydenberg et al. (1995) found that faster growing nestlings fledge heavier and younger than those growing at a slower rate. The ability to slow growth of body parts during times of depressed feeding conditions is a plausible adaptation to variable feeding conditions which allows nestlings with prolonged pre-fledging periods such as puffins to survive intra-seasonal variability in food supply (Øyan & Anker-Nilssen 1996). In the case of Atlantic Puffins in the northwest Atlantic this would be of significant benefit in years when the arrival inshore of spawning capelin is delayed, assuming no alternative comparable food source.

Establishing age of Atlantic Puffin chicks requires either the regular inspection of marked burrows during the late incubation period for direct confirmation of hatching or the inference of hatching from observations designed to record the first delivery of food to the burrow. Both methods require colony visits during hatching. This is problematic for two reasons: (1) hatching is not synchronous and may extend over a period of weeks (Harris & Birkhead 1985), therefore a random sample of burrows requires investigator presence in the colony for an equivalent period which may not be logistically feasible, (2) Atlantic Puffin breeding success is vulnerable to investigator disturbance especially during incubation, hatching, and brooding making investigator presence in the colony at these times undesirable (Rodway et al. 1996).

Measurements of culmen, tarsus and wing-length have been used as age proxies in the absence of known nestling age (e.g. Montevecchi & Porter 1980, Wehle 1983). To predict age from a morphometric such as wing-length the relationship between the two must be established from a sample of known age chicks from the same colony and time period as that of the chicks whose ages will be estimated (Harris 1984, Rodway 1997). In the absence of this calibration the morphometric age proxy (e.g. wing length) is a poor estimator and represents relative age only.

The growth trajectories of tarsus, culmen and wing-length are not generally the same (Kirkham & Montevecchi 1982). Any single growth parameter correlates best with age when it is growing fastest (i.e. the linear phase of a sigmoidal growth curve, Harris 1984, Van Heezik 1990). For this reason culmen may be a more reliable predictor than wing-length during the earliest phase of growth, but is then replaced by wing-length as the preferred age metric (Ricklefs & White 1975, Gilliland & Ankney 1992, Rodway 1997), although a recent study which fed captive puffins varying diets found that head measurements differed less between groups fed differing amounts of food than did wing length (∅yan & Anker-Nilssen 1996).

Many studies have assumed wing-length to be relatively insensitive to diet (Ricklefs & White 1975; Rhinoceros Auklet *Cerorhinca monocerata*: Wilson 1993, Harfenist 1995; Common Murre *Uria aalge*: Uttley et al 1994, Hatchwell 1995; Parasitic Jaeger *Stercorarius parasiticus*: Phillips et al. 1996). Some studies support this assumption (Storm-Petrel *Hydrobates pelagicus*: Bolton 1995; Atlantic Puffin: Hudson 1979, 1983, Anker-Nillssen 1987, Cook & Hamer 1997; Yellow-eyed Penquin *Megadytes antipodes*: Van Heezik 1990; Parasitic Jaeger: Phillips et al. 1996). However, wing-length may vary under depressed dietary conditions (Atlantic Puffin: ∅yan & Anker-Nilssen 1996, Rodway 1997; Dark-Rumped Petrel: Cruz & Cruz 1990; Parasitic Jaegers: Phillips et al. 1996; Common Terns: Safina et al. 1988) and as a result of investigator disturbance (see Rodway et. al. 1996 for a recent summary). While variability in wing-length at a given age negates its use for the estimation of individual nestling age, wing-length of Atlantic Puffin nestlings does estimate the average age of a sample of chicks between 5 - 50 days old (Rodway 1997).

This study compares the condition of Atlantic Puffin nestlings, as indicated by body mass at a given wing-length, at three Northwest Atlantic seabird colonies in several years (Baccalieu Island: 1992 - 1994, Funk Island: 1992 - 1995, and Small Island: 1994 - 1995). These data were collected concurrently with nestling dietary data (reported in Chapters 2 and 3) to illustrate the consequences, if any, of differences in diet to nestling condition. The null hypothesis tested was that of no differences in nestling body condition between colonies and years.

4.2 Methods

On Baccalieu Island in 1992 and 1993, nestlings were sampled from four subcolonies (see Figure 1.4). All study sites were within areas of dense burrowing by puffins on steep maritime slopes. Two sites were on the west side of the island and two on the east side. In 1994, all nestlings were sampled from Woody Cove, the most populous subcolony. Each year (1992 - 1995) on Funk Island nestlings were sampled from throughout the grassy area occupied by puffins (Montevecchi & Tuck 1987). On Small Island nestlings were sampled in 1994 and 1995 from the densest part of the colony, a long flat meadow on the eastern shore.

Longitudinal measurements of nestling body mass and wing-length were collected on Baccalieu Island in 1992 and 1993. Cross-sectional independent nestling body measurements were collected from Baccalieu in 1994, and all other sites (see Figure 4.1 for sample sizes and dates by location). Due to the difficulty of retrieving chicks from labyrinthine and rocky burrows, with minimal site disturbance, the sampling method was opportunistic. The population sampled is defined as those nestlings which could be reached within 1 m of the burrow entrance. Since many burrows are too long, irregular or rocky to allow sufficient arm penetration, chicks successfully encountered either occupied shorter burrows or were apprehended on the tunnel side of the nest chamber. It is assumed that the sample obtained is representative of the broader colony.

The body mass of individual nestlings was measured to the nearest 1.0 g in a preweighed nylon bag using the smallest appropriate of 100, 300, or 500 g Pesola scales. Wing-length was measured to the nearest 1.0 mm using a stopped metal ruler. The maximum flattened wing chord, excluding down, was measured from the wrist point to the tip of the longest primary feather, or feather sheath if primaries had not emerged.

Data Analysis

Scatter plots of wing-length and body mass data were initially analysed visually to determine the general data distribution (Appendix 4.1). Prior to statistical analysis, data points with a wing-length less than 50 mm and greater than 110 mm were removed from the data set (Appendix 4.2). This subsetting of the data was done for three reasons: 1) measurement error is greater during the first phase of growth when down plumules precede the eruption of the primary feathers, the consequences of which are known to be significant (e.g. an error of 1 mm can displace a wing length curve by 4 days, Ricklefs & White 1975), 2) wing growth follows a sigmoidal trajectory growing more slowly both during the early phase of growth and near fledging (Gaston 1985). The fastest rate of growth is during the middle linear phase and it is therefore during this time that wing-length most accurately reflects age under normal circumstances (Van Heezik 1990), 3) a linear dataset was desirable to meet the assumption of linearity associated with the selected method of statistical analysis. Repeated measurements from individual nestlings were excluded from the dataset prior to analysis by randomly selecting a single measurement for each nestling (Figure 4.2).

Intra-colony (Baccalieu Island only), inter-colony and inter-annual differences in nestling mass at comparable wing-lengths were investigated with analysis of covariance (ANCOVA, SAS 1988). Measurements of nestling mass and wing-length were log transformed to normalize the variance. A regression of independent measurements of mass on wing-length was conducted using a general linear model (SAS, 1988), and analysis of covariance was applied to the linear portion of the mass/wing-length function. Residuals were plotted and inspected for violation of the assumptions of normality (Appendix 4.3), homoscedasticity (Appendix 4.4) and association with the model (Appendix 4.5). Least squares regression methods are vulnerable to distortion from the presence of outliers (S-plus 1993). To investigate the potential influence of outliers on the results of the above analysis the two largest positive and the two largest negative outliers were removed and the analysis of covariance repeated. Tolerance for Type 1 error was set at α=0.05 and the Bonferroni method was used to maintain this level of experimentwise error among multiple comparisons (Sokal & Rohlf 1995).

4.3 Results

A summary of sample dates, number of observations and summary statistics for nestling body mass and wing-lengh by date are found in Appendix 4.6 (for all nestlings measured including those measured repeatedly) and Appendix 4.7 (for the data used as input to the analysis of covariance). Results of the analysis of covariance are found in Tables 4.1 - 4.6. The raw data used for comparisons are plotted by colony and year in Figures 4.3 - 4.9.

4.3.1. Intra-colony variation in nestling body mass

On Baccalieu Island there was no interaction between the years sampled and the relationship of mass to wing-length for 1992 and 1993 (ANCOVA: homogeneity of slopes, $F_{1,114}$ = 0.34, P = 0.5588; homogeneity of intercepts, $F_{1,115}$ = 0.02,P = 0.8833, Table 4.1) so the following test examined the effect of subcolony alone. There was no difference between the mass of nestlings at a given wing-length from the different subcolonies sampled in 1992 and 1993 (ANCOVA: homogeneity of slopes, $F_{7,102}$ = 0.72, P = 0.6577; homogeneity of intercepts, $F_{7,109}$ = 0.32, P = 0.9429, Table 4.2). Therefore, in 1994 only Woody

Cove, the most populous subcolony was sampled.

4.3.2 Inter-annual and inter-colony variation in nestling body mass

The assumption of homogeneity of regression slopes required by analysis of covariance was met for the preplanned regression comparisons reported below (ANCOVA: $F_{8,423} = 1.59$, $P = 0.1267$, Table 4.3). The repeat analysis with outliers removed gave similar results (ANCOVA: $F_{8,419} = 1.7$, $P = 0.0956$, Table 4.5). The Bonferroni adjusted significance level used for individual comparisons was $\alpha = 0.05/k = 0.0031$ (k=16 comparisons).

Inter-annual variation

For Baccalieu Island, examination of the raw data plotted in Figure 4.3 reveals that at larger wing-lengths the data are more spread out, and an ordinal relationship is apparent between years with nestlings in 1992 heavier than 1993 which in turn are heavier than in 1994. This pattern is not evident at smaller wing-lengths. Statistically nestling mass at wing-length was not significantly different in the years 1992, 1993 and 1994 (ANCOVA: $P > 0.18$ for all comparisons, Table 4.4, Figure 4.3). The repeat analysis with outliers removed yielded similar results (ANCOVA: $P > 0.11$ for all comparisons, Table 4.5).

On Funk Island, examination of the raw data plotted in Figure 4.4 reveals that nestlings were heaviest and similar at a given wing-length in 1992 and 1995 lighter in 1994 and lighter again in 1993. Statistically, nestling mass at wing-length did not differ significantly for the years 1992 and 1995 (ANCOVA: $P = 0.0815$, Table 4.4; with outliers removed $P = 0.1072$, Table 4.6, Figure 4.4), and

1992 and 1994 (ANCOVA: P = 0.0767, Table 4.4; with outliers removed P = 0.0318, Table 4.6). Nestlings in 1993 weighed less at wing-length than nestlings in 1992, 1994 and 1995 (ANCOVA: P = 0.0001, P = 0.0014 and P = 0.0001 respectively, Table 4.4; with outliers removed P = 0.0001, P = 0.0030 and P = 0.0001 respectively, Table 4.6). In 1994 nestlings weighed less than those of 1995 (ANCOVA: P = 0.0001 with and without outliers removed P = 0.0001, Tables 4.4 and 4.6).

On Small Island, examination of the raw data plotted in Figure 4.5 shows nestlings in 1995 heavier than those in 1994 at a similar wing-length. Statistically, nestlings of 1994 did not weigh less at a given wing-length than did those of 1995 (ANCOVA: P = 0.0050, Table 4.4) however with outliers removed the difference was significant (ANCOVA: P = 0.0015, Table 4.4, Figure 4.5) .

Results of the initial analysis contain a contradiction in the comparisons for Funk Island among years: 1992 and 1995 did not differ, and 1992 and 1994 also did not differ, whereas 1995 and 1994 did. The pattern of statistical differences detected is not internally consistent.

Inter-colony variation

In 1992, examination of the raw data plotted in Figure 4.6 reveals no clear difference between Baccalieu and Funk Islands. Neither was there a statistically significant difference between the mass of nestlings at a given wing-length from the two Islands (ANCOVA: P = 0.5538, Table 4.4; and with outliers removed P = 0.5215, Table 4.6, Figure 4.6).

In 1993, examination of the raw data plotted in Figure 4.7 indicates that nestlings on Baccalieu Island were heavier than those on Funk Island at a similar wing-length, a difference which was statistically significant (ANCOVA: P = 0.0001, Table 4.4; with outliers removed P = 0.0001, Table 4.6, Figure 4.7).

In 1994, examination of the raw data plotted in Figure 4.8 reveals no striking difference between Baccalieu and Funk Island nestlings but does show Small Island nestlings as lighter at a given wing-length than elsewhere. There was no significant difference between the mass of nestlings at a given wing-length from Baccalieu and Funk Islands (ANCOVA: P = 0.7052, Table 4.4; with outliers removed P = 0.5453,Table 4.6, Figure 4.8). However, nestlings from Small Island weighed less than those from Baccalieu but not less than Funk Islands at comparable wing-lengths (ANCOVA: P = 0.0012 and P = 0.0057 respectively, Table 4.4). The difference between Small and Funk Islands became significant with outliers removed (ANCOVA: P = 0.0016, Table 4.6).

In 1995, examination of the raw data plotted in Figure 4.9 clearly shows Funk Island nestlings as heavier than those on Small Island at a given wing-length, a difference which was statistically significant (ANCOVA: P = 0.0001, Table 4.4; and with outliers removed P = 0.0001, Table 4.6, Figure 4.9).

4.4 Discussion

The analysis of non-experimental ecological data is necessarily based on many assumptions. The validity of this analysis rests on the following assumptions: 1) nestlings sampled were representative of the general populations on these islands, 2) the three colonies sampled (Baccalieu, Funk and Small Islands), belong to the same population, 3) any disturbance effects created by investigator presence did not differ between years or colonies, 4) the relationship between wing-length and age did not vary between years at a given colony, and 5) the relationship between wing-length and age did not vary between colonies in a given year.

It is assumed that any departures from randomness inherent in the sampling method are not correlated with the parameters under investigation. The assumption that all three colonies belong to the same population requires a more complete understanding of the natural history and genetic structure of the three colonies than exists. Analysis of covariance assumes that subjects have been randomly assigned to treatments (Huitema 1980). This is not so in the present case, where one of the "treatments" is colony location (i.e. island). Each island has a host of variables associated with it which are beyond the scope of this study, any of which may influence the dependent variable.

The principal concern for the validity of this analysis lies in the reliability of wing-length as a proxy for age. Most studies finding wing-length relatively insensitive to nutrition have been supplementary feeding studies (e.g. Cook &

Hamer 1997), while most of those to the contrary have included near starving conditions (e.g. Cruz & Cruz 1990, Anker-Nilssen 1992, Øyan & Anker-Nilssen 1996). When nestling diet is adequate wing growth does not appear to vary with diet. Øyan & Anker-Nilssen (1996) fed several groups of Atlantic Puffin nestlings capelin diets. The daily ration was varied among groups to correspond to increasingly compromised feeding regimes. Dramatic effects on wing growth were only apparent after the rations representing a "good" year were effectively halved to represent a "bad" year (Øyan & Anker-Nilssen 1996). The response of wing growth to both the degree and duration of nutrient variation may exhibit a threshold effect, remaining relatively insensitive to short-term changes in diet but eventually slowing should conditions either worsen or persist. Rodway (1997) found that wing-length in Atlantic Puffin nestlings was a biased predictor of age for inividuals growing faster or slower than the mean but did an acceptable job of estimating the mean age of a sample of nestlings.

Wing-length is used here not to predict individual ages but as a relative age index for comparing samples of nestlings of unknown age among years and colonies. The objective is simply to detect gross ordinal differences between nestling condition in different years and/or between different colonies. The lack of a calibration sample of known age chicks from each colony precludes the estimation of both individual ages and mean sample ages. Therefore, it is not possible to test the assumption that wing-length serves as an unbiased relative indicator of age for these data.

If wing-length was compromised unevenly among the years or colonies compared here, the effect would be to mistakenly compare older chicks (those compromised) with younger ones. Under depressed dietary conditions, loss of body mass is expected to precede any compromise in wing growth (Scenario A: Gaston 1985, Øyan & Anker-Nilssen 1996). Should conditions worsen or persist wing growth will also slow (Scenario B: Øyan & Anker-Nilssen 1996, Rodway 1997). Under the worst case conditions, suppressed growth requirements fail to balance dietary needs with a reduced supply of nutrients and nestlings die (Scenario C: Anker-Nilssen 1992). There was no evidence to suggest that any of the data reported here were collected under Scenario C conditions (i.e. dead nestlings were very rarely observed and occupied burrows with accessable nest chambers were rarely empty). On the contrary, nestlings with very few exceptions appeared healthy. Under Scenario B, assuming homogeneous regression slopes, the analysis provided here would underestimate differences in masses among chicks of the same age (i.e. the underestimation of relative age by compromised wing-lengths would shift compromised regression lines to the left, thus diminishing any differences in comparisons with uncompromised wing growth). However, a decline in the rate of mass gain would likely precede compromised wing growth, resulting in a different, less steeply sloped regression line for nestlings with compromised growth when compared with nestlings with uncompromised growth (Øyan & Anker-Nilssen 1996). Such a comparison would yield heterogeneous regression slopes. The absence of heterogeneity of slopes in the analysis of covariance suggests that Scenario A was the likely regime. Assuming Scenario A (which this study does), wing growth would be relatively unaffected by variation in dietary conditions while body mass would not. This analysis should therefore reflect the direction of detected differences in nestling body condition accurately.

The initial analysis was relatively robust against the influence of outliers. However, removal of the four largest outliers yielded a set of results with one significant comparison in addition to those already obtained with the fuller dataset. The difference in nestling condition between Funk and Small Islands in 1994 became statistically significant when the outliers were removed. There is no biological justification for the removal of these outliers. However, consideration of Figure 4.8 and the known vulnerability of least squares regression to the influence of outliers leads me to infer that the pattern of statistical results obtained on removal of the outliers reflects reality with less bias than does the fuller analysis (S-Plus 1993).

Puffin nestlings on Baccalieu Island appear to have experienced relatively consistent and favorable conditions for growth during 1992-1994 with some suggestion that 1994 was less favorable. In contrast, puffin nestlings on Funk Island and on Small Island experienced less consistent conditions. Nestling condition was similar on Funk Island in 1992 and 1995 with nestlings heavier than in 1994 when in turn they were heavier than in 1993. Small Island also experienced better conditions for growth in 1995 than in 1994. Variation in nestling condition appears limited to variatiion in body mass as opposed to variation in the growth of wing-length in addition to that of body mass, as would be expected under inadequate feeding regimes (Øyan & Anker-Nilssen 1996).

Assuming nestling condition reflects feeding conditions I infer that feeding conditions during the period 1992 - 1995 were most favorable on Baccalieu in 1992 and 1993, Funk Island in 1992 and 1995 and Small Island in 1995. The least favorable feeding conditions as reflected by nestling condition occurred in 1993 on Funk Island and everywhere , particularly Small Island, in 1994. The best feeding conditions were those on Funk Island in 1995. While differences in nestling condition between colonies and years were detected, all diets appeared sufficient such that wing growth was not significantly compromised. This suggests that all diets were adequate to meet the pre-fledging demands of nestlings and provides no evidence that even the poorest feeding conditions encountered in this study compromised basic growth demands. In summary, there is no evidence from comparison of relative nestling condition between colonies and years that any of the feeding conditions experienced by puffins during the colony-years reported on here were "bad" for nestling growth.

Figure 4.1 **Number of measurements of Atlantic Puffin nestling body mass (g) and wing-length (cm) collected at Baccalieu, Funk and Small Islands during 1992 - 1995 by date including some repeated measurements from individuals through time.**

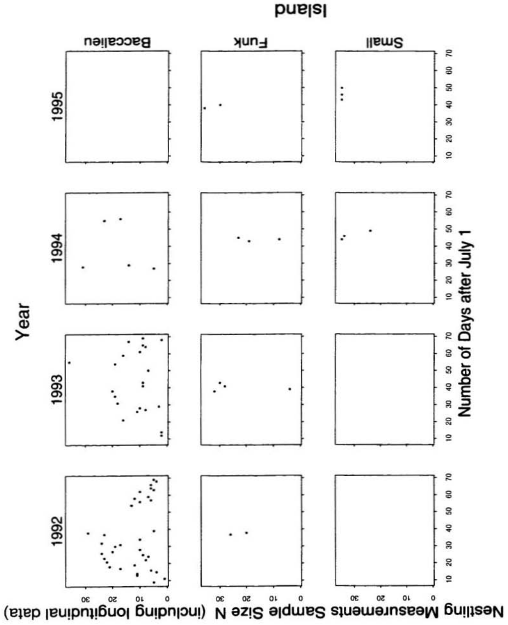

Year
1992
1993
1994
1995
Island
Baccalieu
Funk
Small
Number of Days after July 1
10
20
30
40
50
60
70
Nesting Measurements Sample Size N (including longitudinal data)
0
10
20
30

Figure 4.2 **Number of independent measurements of nestling body mass (g) and wing-length (cm) collected at Baccalieu, Funk and Small Islands during 1992 - 1995 by date and used as the input data for an analysis of covariance.**

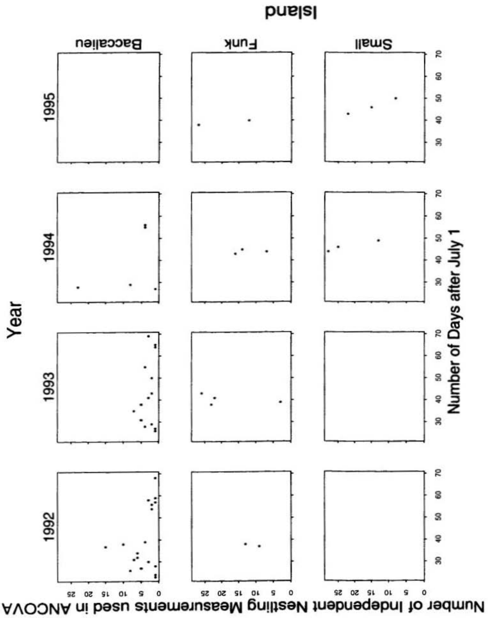

Island
Year
1992
1993
1994
1995
Baccalieu
Funk
Small
Number of Days after July 1
30
40
50
60
70
Number of Independent Nesting Measurements used in ANCOVA
0
5
10
15
20
25

Table 4.1. Results of an analysis of covariance comparing the relationship between Atlantic Puffin nestling mass and wing-length sampled on Baccalieu Island in 1992 and 1993.
Year = year sampled (1992, 1993)
Log Wing = log wing length

a) Test of homogeneity of slopes

Source	df	Type III SS	MS	*F*	Pr > *F*
Year	1	0.0056	0.0056	0.35	0.5544
Log Wing	1	4.3508	4.3508	270.94	0.0001
Log Wing * Year	1	0.0055	0.0055	0.34	0.5588
Error	114	1.8307	0.0161		
Total	117	6.4405			

b) Test of homogeneity of intercepts

Source	df	Type III SS	MS	*F*	Pr > *F*
Year	1	0.0003	0.0003	0.02	0.8833
Log Wing	1	4.5860	4.5860	287.22	0.0001
Error	115	1.8362	0.0160		
Total	117	6.4405			

Table 4.2. Results of an analysis of covariance comparing the relationship between Atlantic Puffin nestling mass and wing-length on the four sub-colonies sampled on Baccalieu Island.

Yr Subcol = Year-subcolony combination i.e. 1992 subcolony 2

Log Wing = log wing length

a) Test of homogeneity of slopes

Source	df	Type III SS	MS	*F*	Pr > *F*
Yr Subcol	7	0.0886	0.0127	0.75	0.6281
Log Wing	1	0.1475	0.1475	8.77	0.0038
Log Wing * Yr Subcol	7	0.0844	0.0121	0.72	0.6577
Error	102	1.715	0.0168		
Total	117	6.4405			

b) Test of homogeneity of intercepts

Source	df	Type III SS	MS	*F*	Pr > *F*
Yr Subcol	7	0.0371	0.0053	0.32	0.9429
Log Wing	1	3.9669	3.9669	240.3	0.0001
Error	109	1.7994	0.0165		
Total	117	6.4405			

Table 4.3. Results of an analysis of covariance comparing the relationship between Atlantic Puffin nestling mass and wing-length on Baccalieu, Funk and Small Islands in 1992 - 1995.
Col Year = Colony Year i.e. Small Island 1995
Log Wing = log of wing length

a) Test of homogeneity of slopes

Source	df	Type III SS	MS	*F*	Pr > *F*
Col Year	8	0.1482	0.0185	1.43	0.1806
Log Wing	1	10.4274	10.4274	806.4	0.0001
Log Wing * Col Year	8	0.1641	0.0205	1.59	0.1267
Error	423	5.4698	0.0129		
Total	440	23.0075			

b) Test of homogeneity of intercepts

Source	df	Type III SS	MS	*F*	Pr > *F*
Col Year	8	1.453	0.1816	13.89	0.0001
Log Wing	1	13.6234	13.6234	1042.22	0.0001
Error	431	5.6338	0.0131		
Total	440	23.0075			

Table 4.4. Results of pre-planned comparisons from within an analysis of covariance (reported in Table 4.2) comparing the relationship between Atlantic Puffin nestling mass and wing-length on Baccalieu (B), Funk (F) and Small (S) Islands in 1992 - 1995.

Pr > [T]   Ho : LSMEANS (i) = LSMEANS (j)

	B92	B93	B94	F92	F93	F94	F95	S94
B93	0.9018							
B94	0.1811	0.2000						
F92	0.5538							
F93		0.0001*		0.0001*				
F94			0.7052	0.0767	0.0014*			
F95				0.0815	0.0001*	0.0001*		
S94			0.0012*			0.0057		
S95							0.0001*	0.0050

* still significant at experimentwise alpha = 0.05 after Bonferroni adjustment for the number of comparisons

Table 4.5. Results of the re-running of an analysis of covariance (reported in Table 4.2) comparing the relationship between Atlantic Puffin nestling mass and wing-length on Baccalieu, Funk and Small Islands in 1992 - 1995, minus the two largest positive and two largest negative outliers.
Col Year = Colony year i.e. Baccalieu 1992
Log Wing = log wing length

a) Test of homogeneity of slopes

Source	df	Type III SS	MS	*F*	Pr > *F*
Col Year	8	0.1409	0.0176	1.55	0.1365
Log Wing	1	10.9164	10.9164	963.24	0.0001
Log Wing * Col Year	8	0.1544	0.0193	1.7	0.0956
Error	419	4.7485	0.0113		
Total	436	23.2132			

b) Test of homogeneity of intercepts

Source	df	Type III SS	MS	*F*	Pr > *F*
Col Year	8	1.4892	0.1861	16.21	0.0001
Log Wing	1	14.6426	14.6426	1275.23	0.0001
Error	427	4.9029	0.0115		
Total	436	23.2132			

Table 4.6. Results of pre-planned comparisons from the re-running of an analysis of covariance (reported in Table 4.4) comparing the relationship between Atlantic Puffin nestling mass and wing-length on Baccalieu (B), Funk (F) and Small (S) Islands in 1992 - 1995 minus the two largest positive and the two largest negative outliers.

Pr > [T] Ho : LSMEANS (i) = LSMEANS (j)

	B92	B93	B94	F92	F93	F94	F95	S94
B93	0.7832							
B94	0.1246	0.1107						
F92	0.5215							
F93		0.0001*		0.0001*				
F94			0.5453	0.0318	0.003*			
F95				0.1072	0.0001*	0.0001*		
S94			0.0001*			0.0016*		
S95							0.0001*	0.0015*

* still significant at experimentwise alpha = 0.05 after Bonferroni adjustment for the number of comparisons

Figure 4.3 **Relationship between Atlantic Puffin nestling mass (g) and wing-length (cm) during the years 1992-1994 on Baccalieu Island.**

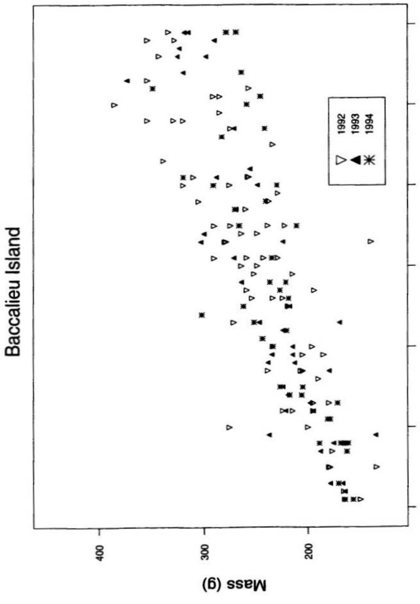

Baccalieu Island
Mass (g)
400
300
200
Wing Length (mm)
50
60
70
80
90
100
110
1992
1993
1994

Figure 4.4 Relationship between Atlantic Puffin nestling mass (g) and wing-length (cm) during the years 1992-1995 on Funk Island.

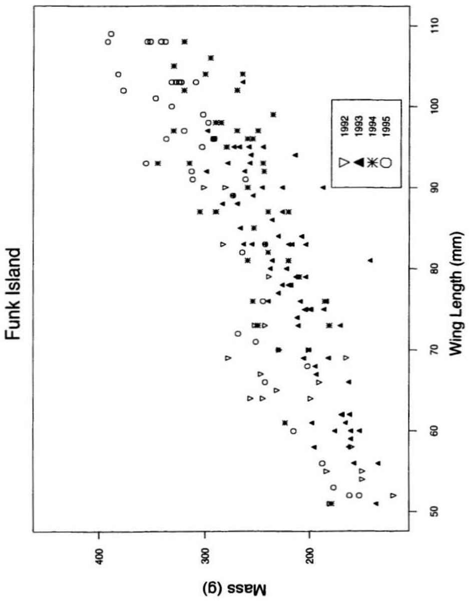

Funk Island
Mass (g)
200
300
400
Wing Length (mm)
50
60
70
80
90
100
110
▽ 1992
▲ 1993
✳ 1994
○ 1995

Figure 4.5 **Relationship between Atlantic Puffin nestling mass (g) and wing-length (cm) during the years 1994-1995 on Small Island.**

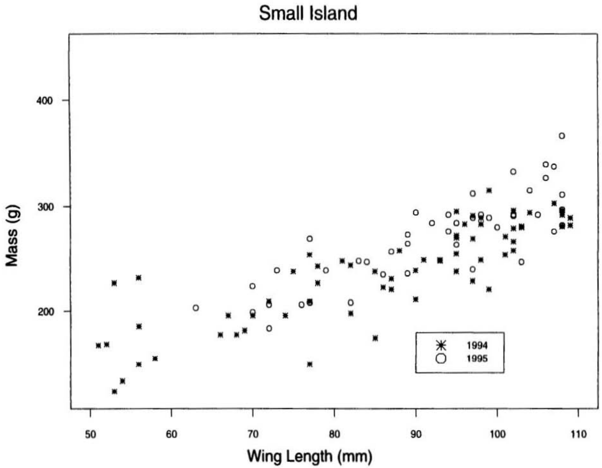

Small Island
Mass (g)
400
300
200
50
60
70
80
90
100
110
Wing Length (mm)
1994
1995

Figure 4.6 **Relationship between Atlantic Puffin nestling mass (g) and wing-length (cm) on Baccalieu and Funk Islands in 1992.**

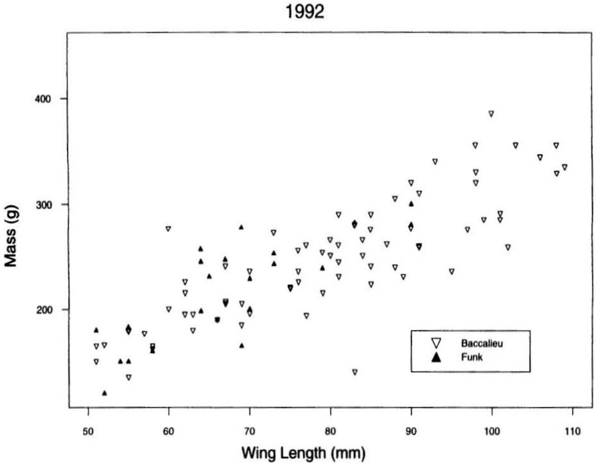

1992
Mass (g)
400
300
200
Wing Length (mm)
50
60
70
80
90
100
110
▽ Baccalieu
▲ Funk

Figure 4.7 Relationship between Atlantic Puffin nestling mass (g) and wing-length (cm) on Baccalieu and Funk Islands in 1993.

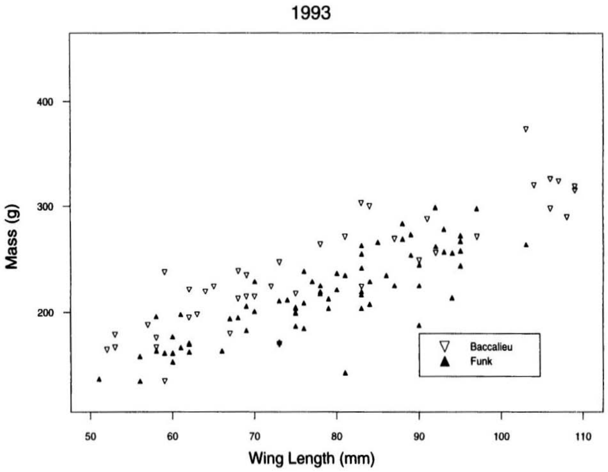

1993
Mass (g)
400
300
200
Wing Length (mm)
50
60
70
80
90
100
110
▽ Baccalieu
▲ Funk

Figure 4.8 Relationship between Atlantic Puffin nestling mass (g) and wing-length (cm) on Baccalieu, Funk and Small Islands in 1994.

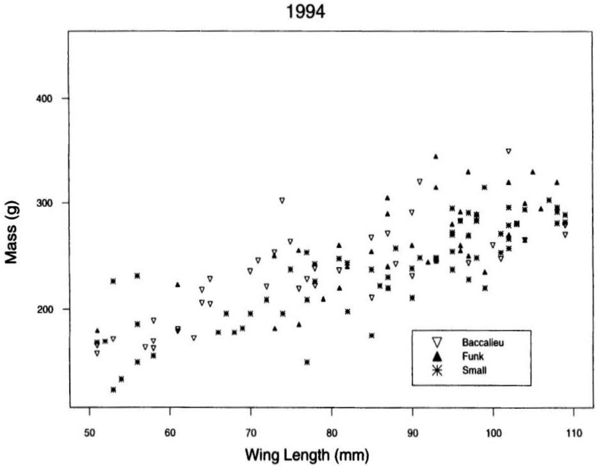
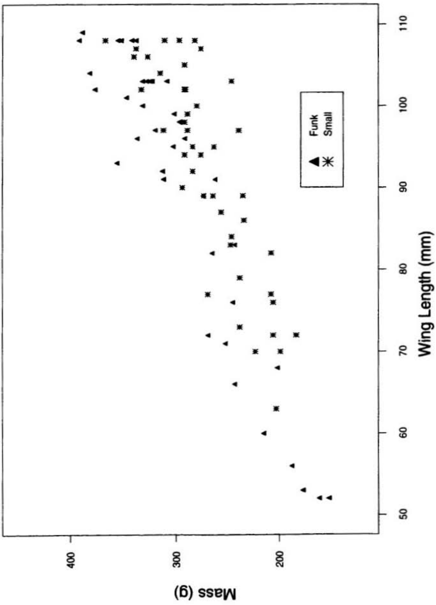

1994
Mass (g)
400
300
200
Wing Length (mm)
50
60
70
80
90
100
110
▽ Baccalieu
▲ Funk
✳ Small

Figure 4.9 **Relationship between Atlantic Puffin nestling mass (g) and wing-length (cm) on Funk and Small Islands in 1995.**

1995


Funk
Small
Mass (g)
200
300
400
Wing Length (mm)
50
60
70
80
90
100
110

Chapter 5. Summary

The data presented do not support previously held assumptions 1) of homogeneity of Atlantic Puffin nestling diets along the northeast coast of insular Newfoundland and 2) that there are no prey of comparable quality to mature capelin available to breeding puffins in the region.

While the diets of puffin nestlings on Baccalieu Island were dominated by mature capelin the diets of nestlings on Small and Funk Islands were more variable and composed of a more diverse suite of prey items (Chapter 2). Notable among these diverse suite of prey items were post-larval 0-group sandlance which dominated nestling diets on Funk and Small Islands in 1995. Bill-loads containing these fish had the highest energy content of any observed during this study. 1-group capelin also made important contributions to nestling diet on Funk Island. There appear to be prey alternatives to adult capelin available to foraging puffins in the northwest Atlantic with equal if not greater energy value than adult capelin (Chapter 3). Prey energy density, bill-load energy content and nestling condition were all greatest in 1995 when post-larval 0-group sandlance dominated sampled nestling diets. While there were differences in nestling condition between colonies and years, it appears that differences in nestling diet were not sufficient to impair wing growth (Chapter 4). I infer that while there were qualitative differences in nestling diet between colonies and years, these differences did not compromise nestling growth to an extent likely to threaten fledging success and therefore reflect the adequacy of nestling diet.

In the spectrum of seabird responses to variation in prey availability, Atlantic Puffins are relatively robust. Surface feeders such as kittiwakes which often share breeding locations with puffins are vulnerable to more subtle changes in the availability of prey than puffins (i.e. small changes in the vertical distribution of prey in the water column may remove food from the foraging range of a kittiwake while not from a puffin able to dive to 60 m (Piatt & Nettleship 1985, Burger & Simpson 1986). Atlantic Puffins provision nestlings for approximately twice as long as the other Alcids with whom they share breeding colonies (Harris & Birkhead 1985). This extended period during which adult puffins must provision their young increases the likelihood that some portion of the nestling period in every year will overlap with the inshore migration of spawning capelin. However, in years when capelin availability near shore is temporally compressed the extended duration of the puffin nestling period means that the inevitable "match" will only represent a small portion of the overall period during which parents are provisioning young. Therefore, given the variable nature of the environment (i.e. spawning phenology one month later than the norm in the early 1990s, Carscadden et al. 1997), it would seem non-adaptive for puffins to be entirely dependent on the availability inshore of spawning capelin.

Breeding failures of Atlantic Puffins in northern Norway have been attributed to a lack of the post-larval 0-group herring which normally dominated nestling diet there. A threshold effect was postulated whereby puffin fledging success plunged suddenly at low herring abundance (Anker-Nilssen 1992). The great variation in puffin fledging success at the threshold level of herring abundance reveals the important role of alternate prey which are also highly variable and which in some instances alleviated the otherwise catastrophic effect of low herring abundance. It is reasonable to expect the same variation in vulnerability to shifts in the availability of mature capelin in the northwest Atlantic. Some years and/or locations may be more difficult than others.

The large increase recorded in this study in the energetic value of 0-group sandlance with metamorphosis from larval to post-larval body form and size has important implications for adults provisioning young. Years and/or locations providing oceanographic conditions conducive to earlier or more rapid development and/or earlier fish spawning phenology and thus older, larger, more developed 0-group fish may in turn provide foraging alternatives comparable to mature capelin. For example, the energy density of the post-larval 0-group sandlance fed to puffin nestlings on Funk and Small Islands in 1995 exceeded that of mature capelin (see Chapter 3) and these prey were delivered in bill-loads with the greatest energy content observed during this study (see Chapter 2). The nestling condition of chicks fed on post-larval 0-group sandlance was the best observed in this study, exceeding that of nestlings fed diets dominated by mature capelin (see Chapter 4).

The large contribution made by 1-group capelin to the nestling diet on Funk Island between 1992 - 1994 and on occasion on Baccalieu (early season) is an interesting aspect of the overall contribution made by capelin as a forage fish.

Capelin live relatively short lives (3 - 5 years) and mortality often follows first spawning (Templeman 1948). Maturation and the timing of the annual inshore spawning migration which brings mature capelin within foraging range of inshore Atlantic Puffin colonies varies considerably with ocean temperature (Carscadden et al. 1997). Capelin were late arriving inshore between 1992 - 1995 in association with cold water temperatures (Nakashima & Winters 1996, Carscadden et al. 1997). During such times and in the absence of sandlance the smaller prey generally present in the nekton community are likely of critical importance. The nekton in the waters off the northeast coast of insular Newfoundland appears to have been dominated by 1-group capelin during the years overlapping with this study (Anderson & Dalley 1997a,b). These larval fish are energetically inferior to mature capelin. However, if locally abundant as they appear to be in the waters around Funk Island, 1-group capelin appear to have potential as an alternative, at least in the short term, to mature capelin.

There are several ways that inshore spawning capelin can become less available to foraging Puffins. On the temporal scale, mature capelin availability to foraging puffins would be diminished by 1) late arrival of capelin inshore, 2) early post-spawning dispersal from the inshore and 3) a compressed spawning period and inshore residency time due to increased synchrony of spawning among capelin. The above would effect the broad scale horizontal spatial distribution of mature capelin within the puffin breeding season. In addition, capelin can become unavailable due to changes in vertical distribution (e.g. replacement of beach spawning with off beach spawning). Assuming an adequate capelin spawning stock biomass and successful spawning in the previous year, the availability of 1-group capelin near shore may well be a reliable alternative to mature capelin during periods when their availability inshore is low. However, the abundance of 1-group capelin depends on successful spawning and recruitment from the previous year. If the capelin spawning stock biomass were severely compromised or recruitment from the previous year was a failure for some other reason, the option to provision chicks with 1-group capelin in the relative absence of adult capelin would not exist. However, at least during the early 1990's, 1-group capelin appear to have dominated the nekton and were widely distributed inshore and on the northeast shelf although not as abundant on the Grand Banks, offshore from Great Island (Anderson & Dalley 1997a,b).

A study comparing Atlantic Puffin breeding success on Great Island, Witless Bay with that on Funk and Small Islands concluded that the greater breeding success of Funk and Small Islands was due to the absence of heavy gull kleptoparasitism on incoming adult puffins observed on Great Island (Nettleship 1972). Food conditions were assumed to be similar for all three colonies. While it is possible that food conditions were then, and are at other times similar for these three colonies, this study shows that in the absence of corroborative contemporaneous data, the assumption is untenable. Falsely assuming homogeneous diets while investigating variables confounded by diet could result in spurious results.

The data I have presented do not support the previously held assumption of homogeneity of Atlantic Puffin nestling diets along the northeast coast of insular Newfoundland. While the diets of puffin nestlings on Baccalieu Island were dominated by mature capelin the diets of nestlings on Small and Funk Islands were more variable and composed of a more diverse suite of prey items. This finding is important for the interpretation of other ecological data which are potentially confounded by differences in the diets of puffin nestlings at these colonies. In addition, these data suggest differences in the foraging regimes experienced by Atlantic Puffins breeding at the major puffin colonies which suggest parallels with three major pelagic regimes delineated by recent broad-scale pelagic surveys along the northeast coast of insular Newfoundland and southern Labrador (Anderson and Dalley 1997a).

A four-fold difference in magnitude between bill-load energy content on Funk Island in 1994 when the principal contents were 1-group capelin and Small Island in 1995 when the principal contents were post-larval 0-group sandlance suggests that when adult capelin are relatively absent from puffin nestling diet the quality of alternative diets off the coast of insular Newfoundland may be sensitive to 1) the presence of a spawning biomass of sandlance, 2) oceanographic conditions conducive to the early spawning and/or rapid development of 0-group sandlance, 3) successful recruitment of capelin from the previous year to provide an abundance of 1-group capelin in the current year and/or 4) proximity to waters with sufficient biomass of miscellaneous nekton to sustain the local population of central place foragers during the nestling season. It would seem that puffins on Funk Island in the early 1990s have benefited at various times from all of the above. In the event of inadequate availability of capelin to meet nestling needs, colonies inshore (Small Island) and to the south (Baccalieu Island and the Witless Bay Islands) may be more sensitive to the availability of sandlance.

Appendix 2.1 Proportional representation of 1-group capelin in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995

				1-group capelin Proportion (%)				
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	4	1	6	1
	8	243 - 249	Aug 29 - Sep 5	10	0	0	0	0
	9	250 - 256	Sep 6 - 8	17	0	0	0	0
1993	2	201 - 207	Jul 19 - 26	56	25	12	32	11
	3	208 - 214	Jul 27 - 31	48	11	1	8	1
	4	215 - 221	Aug 4 - 8	19	10	1	11	1
	5	222 - 228	Aug 10 - 12	35	23	2	9	2
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	2	1	4	1
	8	243 - 249	Aug 30 - Sep 6	42	0	0	0	0
1994	3	208 - 214	Jul 28 - 29	23	16	13	22	13
	6	229 - 235	Aug 22 - 23	11	42	10	36	10
	7	236 - 242	Aug 24 - 25	16	21	5	19	4
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	37	36	80	33
1993	4	215 - 221	Aug 7 - 8	50	68	46	72	44
	5	222 - 228	Aug 10 - 11	77	78	75	97	72
1994	5	222 - 228	Aug 12 - 16	50	64	71	90	68
1995	4	215 - 221	Aug 6 - 8	40	2	1	13	1
	5	222 - 228	Aug 9	22	1	1	5	1
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	12	7	20	6
	6	229 - 235	Aug 18	6	17	12	17	12
1995	5	222 - 228	Aug 13 - 15	49	1	1	4	1
	6	229 - 235	Aug 19 - 20	23	0	0	0	0

Appendix 2.2 Proportional representation of adult sandlance in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Adult Sandlance Proportion (%) Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	0	0	0	0
	8	243 - 249	Aug 29 - Sep 5	10	0	0	0	0
	9	250 - 256	Sep 6 - 8	17	6	18	18	25
1993	2	201 - 207	Jul 19 - 26	56	2	21	11	28
	3	208 - 214	Jul 27 - 31	48	14	35	38	44
	4	215 - 221	Aug 4 - 8	19	10	13	11	19
	5	222 - 228	Aug 10 - 12	35	5	6	9	9
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	0	0	0	0
	8	243 - 249	Aug 30 - Sep 6	42	2	3	5	5
1994	3	208 - 214	Jul 28 - 29	23	0	0	0	0
	6	229 - 235	Aug 22 - 23	11	0	0	0	0
	7	236 - 242	Aug 24 - 25	16	0	0	0	0
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	0	0	0	0
1993	4	215 - 221	Aug 7 - 8	50	0	0	0	0
	5	222 - 228	Aug 10 - 11	77	0	0	0	0
1994	5	222 - 228	Aug 12 - 16	50	0	0	0	0
1995	4	215 - 221	Aug 6 - 8	40	0	0	0	0
	5	222 - 228	Aug 9	22	0	0	0	0
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	0	0	0	0
	6	229 - 235	Aug 18	6	0	0	0	0
1995	5	222 - 228	Aug 13 - 15	49	0	0	0	0
	6	229 - 235	Aug 19 - 20	23	0	0	0	0

Appendix 2.3 Proportional representation of larval 0-group sandlance in bill-loads collected from Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

					0-group sandlance (larval) Proportion (%)			
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	0	0	0	0
	8	243 - 249	Aug 29 - Sep 5	10	16	1	10	1
	9	250 - 256	Sep 6 - 8	17	0	0	0	0
1993	2	201 - 207	Jul 19 - 26	56	2	1	5	1
	3	208 - 214	Jul 27 - 31	48	8	1	2	1
	4	215 - 221	Aug 4 - 8	19	0	0	0	0
	5	222 - 228	Aug 10 - 12	35	0	0	0	0
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	0	0	0	0
	8	243 - 249	Aug 30 - Sep 6	42	1	1	2	1
1994	3	208 - 214	Jul 28 - 29	23	1	1	4	1
	6	229 - 235	Aug 22 - 23	11	0	0	0	0
	7	236 - 242	Aug 24 - 25	16	4	1	6	1
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	12	12	46	10
1993	4	215 - 221	Aug 7 - 8	50	9	7	48	7
	5	222 - 228	Aug 10 - 11	77	11	10	60	9
1994	5	222 - 228	Aug 12 - 16	50	1	1	4	1
1995	4	215 - 221	Aug 6 - 8	40	4	2	20	1
	5	222 - 228	Aug 9	22	7	3	36	2
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	14	9	37	8
	6	229 - 235	Aug 18	6	21	21	83	19
1995	5	222 - 228	Aug 13 - 15	49	1	1	2	1
	6	229 - 235	Aug 19 - 20	23	1	1	4	1

Appendix 2.4 Proportional representation of postlarval 0-group sandlance in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

					0-group sandlance (postlarval) Proportion (%)			
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	0	0	0	0
	8	243 - 249	Aug 29 - Sep 5	10	0	0	0	0
	9	250 - 256	Sep 6 - 8	17	0	0	0	0
1993	2	201 - 207	Jul 19 - 26	56	0	0	0	0
	3	208 - 214	Jul 27 - 31	48	0	0	0	0
	4	215 - 221	Aug 4 - 8	19	0	0	0	0
	5	222 - 228	Aug 10 - 12	35	0	0	0	0
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	0	0	0	0
	8	243 - 249	Aug 30 - Sep 6	42	0	0	0	0
1994	3	208 - 214	Jul 28 - 29	23	0	0	0	0
	6	229 - 235	Aug 22 - 23	11	0	0	0	0
	7	236 - 242	Aug 24 - 25	16	0	0	0	0
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	0	0	0	0
1993	4	215 - 221	Aug 7 - 8	50	0	0	0	0
	5	222 - 228	Aug 10 - 11	77	0	0	0	0
1994	5	222 - 228	Aug 12 - 16	50	0	0	0	0
1995	4	215 - 221	Aug 6 - 8	40	85	90	90	91
	5	222 - 228	Aug 9	22	76	95	91	97
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	1	1	1	1
	6	229 - 235	Aug 18	6	5	9	50	13
1995	5	222 - 228	Aug 13 - 15	49	85	83	90	87
	6	229 - 235	Aug 19 - 20	23	96	95	100	96

Appendix 2.5 Proportional representation of Stichaeids in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

					Stichaeids Proportion (%)			
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	0	0	0	0
	8	243 - 249	Aug 29 - Sep 5	10	26	1	20	1
	9	250 - 256	Sep 6 - 8	17	30	1	24	1
1993	2	201 - 207	Jul 19 - 26	56	33	4	29	3
	3	208 - 214	Jul 27 - 31	48	29	1	13	1
	4	215 - 221	Aug 4 - 8	19	0	0	0	0
	5	222 - 228	Aug 10 - 12	35	0	0	0	0
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	1	1	2	1
	8	243 - 249	Aug 30 - Sep 6	42	10	1	7	1
1994	3	208 - 214	Jul 28 - 29	23	25	4	52	3
	6	229 - 235	Aug 22 - 23	11	0	0	0	0
	7	236 - 242	Aug 24 - 25	16	0	0	0	0
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	16	5	57	4
1993	4	215 - 221	Aug 7 - 8	50	6	1	26	1
	5	222 - 228	Aug 10 - 11	77	6	2	39	1
1994	5	222 - 228	Aug 12 - 16	50	25	7	50	7
1995	4	215 - 221	Aug 6 - 8	40	7	1	20	1
	5	222 - 228	Aug 9	22	14	1	27	1
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	49	7	41	6
	6	229 - 235	Aug 18	6	42	8	67	7
1995	5	222 - 228	Aug 13 - 15	49	10	1	25	1
	6	229 - 235	Aug 19 - 20	23	2	1	9	1

Appendix 2.6 Proportional representation of Cottidae in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

					Cottidae Proportion (%)			
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	0	0	0	0
	8	243 - 249	Aug 29 - Sep 5	10	0	0	0	0
	9	250 - 256	Sep 6 - 8	17	0	0	0	0
1993	2	201 - 207	Jul 19 - 26	56	5	2	16	1
	3	208 - 214	Jul 27 - 31	48	1	1	2	1
	4	215 - 221	Aug 4 - 8	19	0	0	0	0
	5	222 - 228	Aug 10 - 12	35	0	0	0	0
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	4	1	4	1
	8	243 - 249	Aug 30 - Sep 6	42	1	1	2	1
1994	3	208 - 214	Jul 28 - 29	23	29	13	65	11
	6	229 - 235	Aug 22 - 23	11	0	0	0	0
	7	236 - 242	Aug 24 - 25	16	0	0	0	0
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	20	14	66	11
1993	4	215 - 221	Aug 7 - 8	50	8	5	40	4
	5	222 - 228	Aug 10 - 11	77	1	1	12	1
1994	5	222 - 228	Aug 12 - 16	50	4	3	28	2
1995	4	215 - 221	Aug 6 - 8	40	1	1	3	1
	5	222 - 228	Aug 9	22	1	1	9	1
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	2	1	10	1
	6	229 - 235	Aug 18	6	6	5	50	4
1995	5	222 - 228	Aug 13 - 15	49	1	1	4	1
	6	229 - 235	Aug 19 - 20	23	0	0	0	0

Appendix 2.7 Proportional representation of 0-group Herring in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

					O-group Herring Proportion (%)			
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	8	17	6	14
	8	243 - 249	Aug 29 - Sep 5	10	0	0	0	0
	9	250 - 256	Sep 6 - 8	17	0	0	0	0
1993	2	201 - 207	Jul 19 - 26	56	0	0	0	0
	3	208 - 214	Jul 27 - 31	48	0	0	0	0
	4	215 - 221	Aug 4 - 8	19	0	0	0	0
	5	222 - 228	Aug 10 - 12	35	0	0	0	0
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	0	0	0	0
	8	243 - 249	Aug 30 - Sep 6	42	0	0	0	0
1994	3	208 - 214	Jul 28 - 29	23	0	0	0	0
	6	229 - 235	Aug 22 - 23	11	0	0	0	0
	7	236 - 242	Aug 24 - 25	16	0	0	0	0
Funk Island					0	0	0	0
1992	5	222 - 228	Aug 8 - 10	56	0	0	0	0
1993	4	215 - 221	Aug 7 - 8	50	0	0	0	0
	5	222 - 228	Aug 10 - 11	77	0	0	0	0
1994	5	222 - 228	Aug 12 - 16	50	1	1	10	1
1995	4	215 - 221	Aug 6 - 8	40	0	0	0	0
	5	222 - 228	Aug 9	22	0	0	0	0
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	13	13	32	10
	6	229 - 235	Aug 18	6	7	12	50	10
1995	5	222 - 228	Aug 13 - 15	49	0	0	0	0
	6	229 - 235	Aug 19 - 20	23	0	0	0	0

Appendix 2.8 Proportional representation of juvenile White Hake in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

					Juvenile White Hake Proportion (%)			
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	0	0	0	0
	8	243 - 249	Aug 29 - Sep 5	10	0	0	0	0
	9	250 - 256	Sep 6 - 8	17	0	0	0	0
1993	2	201 - 207	Jul 19 - 26	56	1	1	5	1
	3	208 - 214	Jul 27 - 31	48	0	0	0	0
	4	215 - 221	Aug 4 - 8	19	0	0	0	0
	5	222 - 228	Aug 10 - 12	35	0	0	0	0
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	8	1	4	1
	8	243 - 249	Aug 30 - Sep 6	42	12	1	7	1
1994	3	208 - 214	Jul 28 - 29	23	1	1	9	1
	6	229 - 235	Aug 22 - 23	11	0	0	0	0
	7	236 - 242	Aug 24 - 25	16	0	0	0	0
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	0	0	0	0
1993	4	215 - 221	Aug 7 - 8	50	3	1	22	1
	5	222 - 228	Aug 10 - 11	77	1	1	14	1
1994	5	222 - 228	Aug 12 - 16	50	1	1	8	1
1995	4	215 - 221	Aug 6 - 8	40	0	0	0	0
	5	222 - 228	Aug 9	22	0	0	0	0
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	2	4	9	3
	6	229 - 235	Aug 18	6	0	0	0	0
1995	5	222 - 228	Aug 13 - 15	49	0	0	0	0
	6	229 - 235	Aug 19 - 20	23	0	0	0	0

Appendix 2.9 Proportional representation of Agonidae in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

					Agonidae Proportion (%)			
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	0	0	0	0
	8	243 - 249	Aug 29 - Sep 5	10	0	0	0	0
	9	250 - 256	Sep 6 - 8	17	0	0	0	0
1993	2	201 - 207	Jul 19 - 26	56	1	1	4	1
	3	208 - 214	Jul 27 - 31	48	1	1	2	1
	4	215 - 221	Aug 4 - 8	19	3	1	5	1
	5	222 - 228	Aug 10 - 12	35	0	0	0	0
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	0	0	0	0
	8	243 - 249	Aug 30 - Sep 6	42	0	0	0	0
1994	3	208 - 214	Jul 28 - 29	23	8	1	22	1
	6	229 - 235	Aug 22 - 23	11	0	0	0	0
	7	236 - 242	Aug 24 - 25	16	0	0	0	0
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	3	1	11	1
1993	4	215 - 221	Aug 7 - 8	50	1	1	4	1
	5	222 - 228	Aug 10 - 11	77	1	1	4	1
1994	5	222 - 228	Aug 12 - 16	50	1	1	4	1
1995	4	215 - 221	Aug 6 - 8	40	0	0	0	0
	5	222 - 228	Aug 9	22	0	0	0	0
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	0	0	0	0
	6	229 - 235	Aug 18	6	0	0	0	0
1995	5	222 - 228	Aug 13 - 15	49	0	0	0	0
	6	229 - 235	Aug 19 - 20	23	0	0	0	0

Appendix 2.10 Proportional representation of *Liparis* sp. in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

					Liparis sp. Proportion (%)			
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	0	0	0	0
	8	243 - 249	Aug 29 - Sep 5	10	0	0	0	0
	9	250 - 256	Sep 6 - 8	17	0	0	0	0
1993	2	201 - 207	Jul 19 - 26	56	7	1	9	1
	3	208 - 214	Jul 27 - 31	48	1	1	2	1
	4	215 - 221	Aug 4 - 8	19	0	0	0	0
	5	222 - 228	Aug 10 - 12	35	0	0	0	0
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	2	1	2	1
	8	243 - 249	Aug 30 - Sep 6	42	0	0	0	0
1994	3	208 - 214	Jul 28 - 29	23	1	1	9	1
	6	229 - 235	Aug 22 - 23	11	0	0	0	0
	7	236 - 242	Aug 24 - 25	16	0	0	0	0
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	2	1	23	1
1993	4	215 - 221	Aug 7 - 8	50	1	1	8	1
	5	222 - 228	Aug 10 - 11	77	1	1	3	1
1994	5	222 - 228	Aug 12 - 16	50	0	0	0	0
1995	4	215 - 221	Aug 6 - 8	40	0	0	0	0
	5	222 - 228	Aug 9	22	0	0	0	0
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	0	0	0	0
	6	229 - 235	Aug 18	6	0	0	0	0
1995	5	222 - 228	Aug 13 - 15	49	0	0	0	0
	6	229 - 235	Aug 19 - 20	23	0	0	0	0

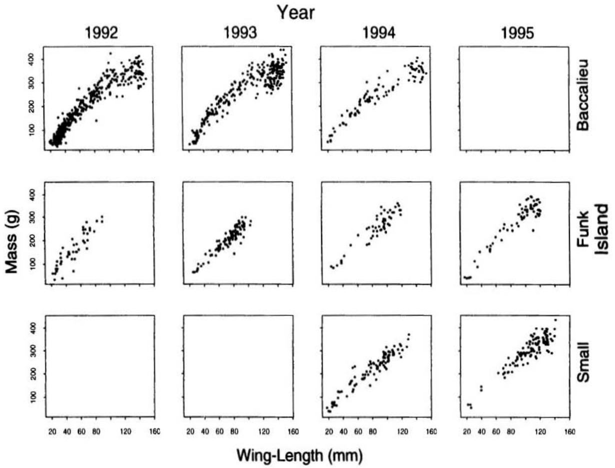
Appendix 2.11 Proportional representation of Squid in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

					Squid			
					Proportion (%)			
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	0	0	0	0
	8	243 - 249	Aug 29 - Sep 5	10	0	0	0	0
	9	250 - 256	Sep 6 - 8	17	2	5	6	8
1993	2	201 - 207	Jul 19 - 26	56	0	0	0	0
	3	208 - 214	Jul 27 - 31	48	1	1	2	1
	4	215 - 221	Aug 4 - 8	19	0	0	0	0
	5	222 - 228	Aug 10 - 12	35	0	0	0	0
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	2	5	4	9
	8	243 - 249	Aug 30 - Sep 6	42	1	3	2	5
1994	3	208 - 214	Jul 28 - 29	23	0	0	0	0
	6	229 - 235	Aug 22 - 23	11	0	0	0	0
	7	236 - 242	Aug 24 - 25	16	0	0	0	0
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	3	11	23	18
1993	4	215 - 221	Aug 7 - 8	50	1	1	6	1
	5	222 - 228	Aug 10 - 11	77	1	3	10	6
1994	5	222 - 228	Aug 12 - 16	50	1	6	12	11
1995	4	215 - 221	Aug 6 - 8	40	1	2	5	3
	5	222 - 228	Aug 9	22	0	0	0	0
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	1	1	2	1
	6	229 - 235	Aug 18	6	0	0	0	0
1995	5	222 - 228	Aug 13 - 15	49	0	0	0	0
	6	229 - 235	Aug 19 - 20	23	0	0	0	0

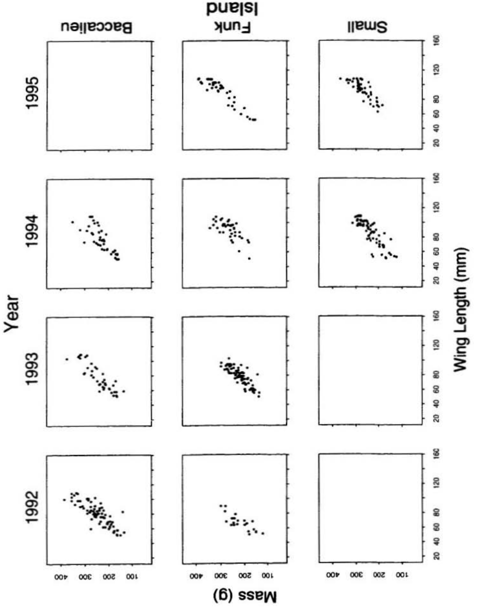
Appendix 2.12 Proportional representation of crustaceans in bill-loads collected from Atlantic Puffins provisioning nestlings on Baccalieu, Funk and Small Islands between 1992 and 1995.

					Crustacea Proportion (%)			
Year	Week	Julian Dates of Week	Sampling Calendar dates	N	Frequency	Mass	Occurrence	Energy
Baccalieu Island								
1992	7	236 - 242	Aug 23 - 28	17	0	0	0	0
	8	243 - 249	Aug 29 - Sep 5	10	0	0	0	0
	9	250 - 256	Sep 6 - 8	17	4	1	6	1
1993	2	201 - 207	Jul 19 - 26	56	6	1	16	1
	3	208 - 214	Jul 27 - 31	48	4	1	14	1
	4	215 - 221	Aug 4 - 8	19	0	0	0	0
	5	222 - 228	Aug 10 - 12	35	0	0	0	0
	6	229 - 235	Aug 19 - 23	12	0	0	0	0
	7	236 - 242	Aug 24 - 28	47	0	0	0	0
	8	243 - 249	Aug 30 - Sep 6	42	3	1	5	1
1994	3	208 - 214	Jul 28 - 29	23	7	1	35	1
	6	229 - 235	Aug 22 - 23	11	0	0	0	0
	7	236 - 242	Aug 24 - 25	16	0	0	0	0
Funk Island								
1992	5	222 - 228	Aug 8 - 10	56	1	1	13	1
1993	4	215 - 221	Aug 7 - 8	50	1	1	12	1
	5	222 - 228	Aug 10 - 11	77	2	1	14	1
1994	5	222 - 228	Aug 12 - 16	50	1	1	6	1
1995	4	215 - 221	Aug 6 - 8	40	0	0	0	0
	5	222 - 228	Aug 9	22	0	0	0	0
Small Island								
1994	5	222 - 228	Aug 11 - 16	109	2	1	3	1
	6	229 - 235	Aug 18	6	0	0	0	0
1995	5	222 - 228	Aug 13 - 15	49	0	0	0	0
	6	229 - 235	Aug 19 - 20	23	0	0	0	0

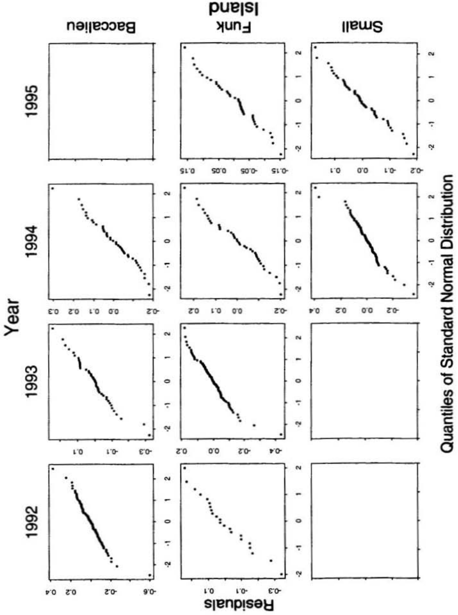
Appendix 4.1 **Atlantic Puffin nestling body mass (g) and wing-length (cm)** measurements from Baccalieu, Funk and Small Islands during 1992 - 1995.


Year
1992
1993
1994
1995
Baccalieu
Funk Island
Small
Mass (g)
100
200
300
400
Wing-Length (mm)
20
40
60
80
120
160

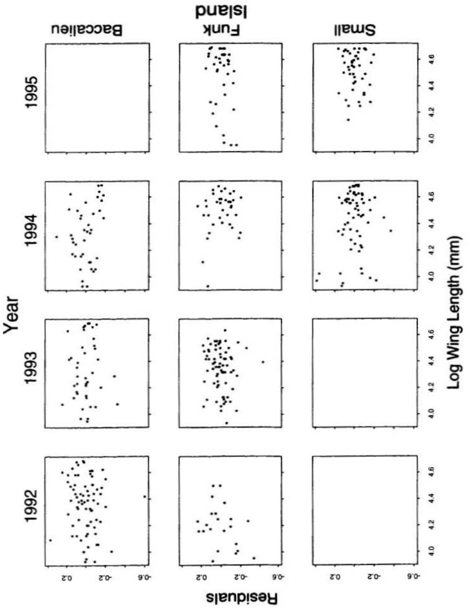
Appendix 4.2 **Truncated data sets of Atlantic Puffin nestling body mass (g) and wing-length (cm) measurements from Baccalieu, Funk and Small Islands during 1992 - 1995 used as input for analysis of covariance.**


Year
1992
1993
1994
1995
Baccalieu
Funk Island
Small
Wing Length (mm)
20 40 60 80 120 160
Mass (g)
100 200 300 400

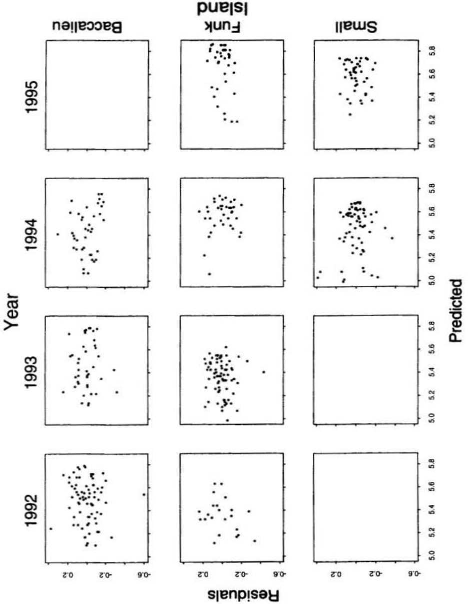
Appendix 4.3 **Residuals from an analysis of covariance on Atlantic Puffin nestling body mass (g) and wing-length (cm) plotted against the quantiles of a standard normal distribution.**


Year
1992
1993
1994
1995
Island
Baccalieu
Funk
Small
Residuals
Quantiles of Standard Normal Distribution

Appendix 4.4 **Residuals from an analysis of covariance on Atlantic Puffin nestling body mass (g) and wing-length (cm) plotted against the independent variable from the same variable (log of nestling wing-length).**


Year
1992
1993
1994
1995
Baccalieu
Funk Island
Small
Residuals
0.2
-0.2
-0.6
Log Wing Length (mm)
4.0
4.2
4.4
4.6

Appendix 4.5 **Residuals from an analysis of covariance on Atlantic Puffin nestling body mass (g) and wing-length (cm) plotted against the predicted values from the same analysis**


Year
1992
1993
1994
1995
Baccalieu
Funk Island
Small
Residuals
0.2
-0.2
-0.6
Predicted
5.0
5.2
5.4
5.6
5.8

Appendix 4.6 Summary of measurements of puffin nestling wing-length (cm) and body mass (g) including longitudinal data

			Nestling wing length (cm)					Nestling body mass (g)				
Year	Month	Day	N	**Mean**	SD	Min	Max	N	**Mean**	SD	Min	Max
Baccalieu Island												
1992	July	9	5	**29.8**	2.4	26	32	6	**53**	5.1	49	60
		11	1	**33**	-	33	33	1	**55**	-	55	55
		13	11	**32.1**	3.8	25	39	12	**54**	10.5	41	73
		14	11	**31.1**	3.7	26	39	12	**71.3**	32	44	152
		15	4	**33.8**	2.2	32	37	4	**60.3**	10.2	48	73
		16	6	**28**	7.1	20	41	6	**54.5**	10.1	46	69
		17	17	**29.9**	4.8	19	37	17	**65.7**	16	39	96
		18	21	**33.2**	8.7	25	59	21	**80.2**	36.4	44	163
		19	12	**31.4**	5.7	23	40	12	**70.3**	19.4	39	95
		21	22	**37.2**	8.5	25	65	23	**98.8**	37.6	45	190
		22	8	**37.3**	9.6	25	50	8	**100.8**	40.3	46	165
		23	23	**40**	15.9	25	78	23	**108.6**	55	49	244
		24	7	**47.6**	9.2	35	61	7	**137.3**	37.1	80	180
		25	9	**33.6**	13.7	21	58	9	**82.4**	55.8	44	185
		26	24	**52.3**	16.1	29	91	24	**162.9**	61.4	60	265
		27	20	**53**	20.9	25	91	20	**168.5**	81	49	299
		28	10	**43.8**	19.3	25	80	10	**123.8**	71.2	32	250
		30	19	**52.8**	23.4	23	85	19	**154.7**	81.8	45	275
		31	17	**68.1**	19.2	31	98	17	**218.5**	68.1	81	320
	August	1	24	**62.7**	22.8	29	102	24	**193.9**	87	45	355
		3	10	**66.5**	23.2	33	98	10	**203**	85.2	110	350
		6	23	**78.7**	26.6	29	109	23	**246.2**	95	70	385
		7	29	**84.9**	27.5	30	123	29	**253**	87.2	65	425
		8	5	**95.2**	14.4	81	118	5	**289**	57.4	235	385
		23	13	**125.7**	20.1	77	145	13	**324.7**	53.2	194	406
		25	10	**120.3**	17	87	141	10	**330.2**	43.2	261	381
		26	6	**127.2**	14.6	102	146	6	**344.8**	49.3	258	396
		27	12	**121.8**	22.3	75	143	12	**331.2**	49.9	219	381
		28	7	**122.4**	35.3	50	148	7	**317.7**	70	183	413
		31	10	**137.4**	8	123	147	10	**364**	20	341	393
	September	1	5	**112.6**	37.8	48	147	5	**263.4**	82	131	339
		2	6	**131.5**	10.2	112	141	6	**329.8**	11.7	321	351
		4	6	**136.2**	14.6	111	151	6	**290.5**	28.6	241	321
		6	4	**125**	23.6	90	141	4	**327.3**	60.1	276	391
		7	5	**133.4**	10.8	116	144	5	**328.2**	49.3	282	406

Appendix 4.6 (continued) Summary of measurements of puffin nestling wing-length (cm) and body mass (g) including longitudinal data

			Nestling wing length (cm)					Nestling body mass (g)				
Year	Month	Day	N	**Mean**	SD	Min	Max	N	**Mean**	SD	Min	Max
Baccalieu Island (continued)												
1993	July	12	2	**28**	1.4	27	29	2	**44**	0	44	44
		14	2	**28.5**	3.5	26	31	4	**51.8**	3.1	49	56
		21	16	**34.6**	4.2	28	43	10	**79.3**	14	50	95
		26	11	**45**	10.5	26	59	11	**130.3**	42.7	51	176
		27	8	**42.3**	13.3	27	69	8	**133.8**	49.4	67	215
		28	10	**47.6**	11.5	30	68	10	**145.1**	47.5	51	213
		29	3	**48.7**	11.2	36	57	3	**156**	47.8	101	188
		31	18	**57.6**	18.2	21	84	17	**194.5**	68.2	40	290
	August	4	19	**79.6**	20	29	108	19	**257.7**	61.6	76	348
		7	20	**84.5**	25.6	25	117	20	**272.5**	75.7	98	384
		10	9	**98.8**	19.2	70	123	9	**299.7**	56.2	215	387
		12	9	**103.1**	17.8	75	128	9	**303.9**	44.8	205	355
		19	7	**120.9**	10.2	109	134	7	**359.7**	37.9	315	416
		23	19	**135.7**	11.5	114	149	19	**361.9**	36.8	253	422
		24	36	**129.7**	20	58	153	36	**346.3**	51.8	167	418
		28	16	**134.5**	6.7	125	146	16	**310.8**	31.4	270	368
		30	10	**139**	8	125	150	10	**351.8**	57.7	290	440
	September	2	8	**127.6**	28.1	59	143	8	**314.3**	79.7	136	385
		3	9	**121.1**	37.5	45	145	9	**305.8**	76.2	179	370
		5	14	**130.1**	25.9	66	149	14	**284.6**	50	155	332
		6	2	**143**	1.4	142	144	2	**296.5**	12	288	305
		7	9	**118.3**	34.9	63	150	9	**283.3**	69.6	170	345
1994	July	27	5	**49.4**	25.6	24	78	5	**146.6**	74.1	53	222
		28	31	**65.4**	23.1	20	102	31	**200**	70.8	50	350
		29	14	**62**	22.8	25	97	14	**196.1**	73	77	320
	August	24	23	**129.6**	23.5	58	151	23	**324.4**	54	162	384
		25	17	**128.8**	23.4	74	155	17	**333.4**	48.5	242	407
Funk Island												
1992	August	6	26	**47.3**	18.5	22	90	26	**134.7**	61.9	41	301
		7	20	**55.2**	19.1	24	83	20	**195.4**	70.9	35	283

Appendix 4.6 (continued) Summary of measurements of puffin nestling wing-length (cm) and body mass (g) including longitudinal data

			Nestling wing length (cm)					Nestling body mass (g)				
Year	Month	Day	N	**Mean**	SD	Min	Max	N	**Mean**	SD	Min	Max
Funk Island (continued)												
1993	August	7	32	**61.8**	17.7	27	90	31	**169.6**	49.3	66	246
		8	4	**74**	33.9	25	103	4	**186.8**	84.9	66	265
		10	28	**77.7**	15.1	32	95	27	**228.3**	36.8	156	284
		12	30	**76.4**	17.7	30	104	30	**209.8**	56.7	70	299
1994	August	12	19	**81.5**	24.4	27	106	19	**249.7**	73.9	85	345
		13	8	**85.6**	16.4	61	115	8	**253.9**	59.6	182	360
		14	23	**91.5**	26.7	24	119	23	**259.3**	75.9	90	350
1995	August	7	36	**92.4**	22.3	38	121	36	**294.3**	65.6	152	392
		9	30	**87.2**	35.9	17	121	30	**266.4**	115.6	41	382
Small Island												
1994	August	13	35	**73.9**	28.5	18	108	35	**205.3**	78.6	40	295
		15	34	**77.7**	28.1	22	130	34	**216.3**	76.6	39	369
		18	24	**90.9**	30.7	25	129	24	**241.3**	81.9	72	349
1995	August	12	35	**89**	28.7	22	126	35	**268.5**	88.3	54	397
		15	35	**107**	18.1	70	131	35	**305.1**	55	199	395
		19	35	**121.1**	15.6	89	141	35	**325.6**	49	235	437

Appendix 4.7 Summary of measurements of puffin nestling wing-length (cm) and body mass (g) used in the analysis of covariance reported in Chapter 4

			Nestling wing length (cm)					Nestling body mass (g)			
Year	Month	Day	N	**Mean**	SD	Min	Max	**Mean**	SD	Min	Max
Baccalieu Island											
1992	July	23	1	**70**	-	70	70	**196**	-	196	196
		24	1	**55**	-	55	55	**180**	-	180	180
		26	8	**64**	14.7	51	91	**204.5**	41.9	150	265
		27	5	**72.4**	15.1	55	91	**253**	42.1	179	279
		28	1	**80**	-	80	80	**250**	-	250	250
		30	3	**83**	3.5	79	85	**226**	12.8	215	240
		31	7	**76.4**	8.4	62	88	**251.9**	38.7	195	305
	August	1	6	**76.7**	14.4	62	98	**265**	59.9	205	355
		3	6	**74.8**	15.2	55	91	**220.8**	63	135	310
		6	15	**84.1**	19	51	109	**268.1**	80.1	140	385
		7	10	**80**	11.2	63	101	**234.5**	37.9	180	285
		8	4	**89.5**	7.7	81	97	**265**	23.5	235	290
		23	2	**89**	17	77	101	**242.5**	68.6	194	291
		25	2	**96.5**	13.4	87	106	**302.5**	58.7	261	344
		26	1	**102**	-	102	102	**258**	-	258	258
		27	3	**90**	16.7	75	108	**278.3**	69.6	219	355
		28	1	**108**	-	108	108	**329**	-	329	329
	September	6	1	**90**	-	90	90	**276**	-	276	276
1993	July	26	1	**58**	-	58	58	**176**	-	176	176
		27	1	**69**	-	69	69	**215**	-	215	215
		28	4	**58.8**	7.6	52	68	**185**	23.2	165	213
		29	2	**55**	2.8	53	57	**183.5**	6.4	179	188
		31	5	**68.2**	7.6	62	81	**235**	21.6	220	272
	August	4	7	**84**	12.3	72	108	**268.7**	29.8	225	303
		7	5	**85.8**	21.3	59	107	**286.8**	59.9	239	374
		10	3	**89**	18.1	70	106	**267**	45.3	215	298
		12	2	**95.5**	12	87	104	**295**	35.4	270	320
		19	2	**109**	0	109	109	**317**	2.8	315	319
		24	4	**84**	21.7	58	106	**245.8**	68.6	167	326
	September	2	1	**59**	-	59	59	**136**	-	136	136
		3	1	**67**	-	67	67	**180**	-	180	180
		7	3	**73**	10	63	83	**197.7**	27.5	170	225

Appendix 4.7 (continued) Summary of measurements of puffin nestling wing-length (cm) and body mass (g) used in the analysis of covariance reported in Chapter 4

Year	Month	Day	Nestling wing length (cm)					Nestling body mass (g)			
			N	**Mean**	SD	Min	Max	**Mean**	SD	Min	Max
Baccalieu Island											
1994	July	27	1	**78**	-	78	78	**222**	-	222	222
		28	23	**73.7**	15.5	51	102	**224.4**	47.6	157	350
		29	8	**74**	15.1	51	97	**234**	50.1	165	320
	August	24	4	**87.3**	22.8	58	109	**228.8**	46.7	162	270
		25	4	**93.8**	15.9	74	109	**272**	25.2	242	302
unk Island											
1992	August	6	9	**67.1**	14.5	52	90	**191.6**	61.2	121	301
		7	13	**67.5**	8.7	51	83	**236.1**	31.8	181	283
1993	August	7	23	**70.8**	10.7	56	90	**193.7**	27.1	154	246
		8	3	**90.3**	11	84	103	**227**	32.9	208	265
		10	22	**81.5**	11	61	95	**233**	35.1	163	284
		12	26	**79**	12.6	51	97	**217.8**	46.4	136	299
1994	August	12	16	**90.1**	14.4	51	106	**275.6**	44	180	345
		13	7	**81.4**	12.1	61	96	**238.7**	44.7	182	292
		14	14	**94**	8.9	79	108	**263.6**	34.1	210	320
1995	August	7	27	**89.9**	17.9	52	109	**295.5**	60.6	163	392
		9	12	**89.3**	18.7	52	108	**294.3**	69.8	154	382
mall Island											
1994	August	13	28	**85.6**	17.5	51	108	**238**	45.5	133	295
		15	25	**86.2**	17.2	52	109	**237.4**	44.1	155	315
		18	13	**86.3**	16.9	53	108	**235.2**	55.6	123	296
1995	August	12	22	**92.3**	14.1	63	108	**279**	45.3	184	367
		15	15	**89.7**	13.5	70	108	**258.5**	46	199	340
		19	8	**96.7**	6.8	89	107	**265**	21.6	235	291

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