

# Atlantic Puffin (*Fratercula arctica*) chick diet and reproductive performance at colonies with high and low capelin (*Mallotus villosus*) abundance

Shauna M. Baillie and Ian L. Jones

**Abstract:** We compared nestling diet and growth, breeding phenology, breeding success, and adult mass of Atlantic Puffins (*Fratercula arctica*) between two seabird colonies adjacent to ocean habitat with presumed high and low capelin (*Mallotus villosus*) abundance in 1996–1998. We hypothesized that puffins at their colony at Gannet Islands, Labrador, where capelin were scarce, would exhibit lower reproductive performance than at Gull Island, Witless Bay, where capelin were abundant. Historically, capelin comprised approximately 60%–95% of the chick diet biomass at both colonies. In the late 1990s, puffin chicks at the Gannet Islands received 3%–24% capelin (by mass), which was 39%–97% less than was received at Gull Island. Postlarval sand lance (*Ammodytes* sp.) comprised up to 49% (by mass) of the chick diet at the Gannet Islands. Hatching success and fledge success estimates at the Gannet Islands in 1997–1998 were statistically similar to those at Gull Island in 1998. Fledge mass (expressed as percentage of adult mass) was similar between Gannet Islands (69%) and Gull Island (68%). The high interyear variability in chick diet at both colonies and the low variation in breeding performance during our study suggest that Atlantic Puffins in Labrador are resilient to large-scale prey-base changes.

**Résumé :** Nous avons comparé le régime alimentaire et la croissance des petits au nid, la phénologie de la reproduction, le succès de la reproduction, ainsi que la masse des adultes chez le macareux moine (*Fratercula arctica*) dans deux colonies d'oiseaux marins adjacentes à des habitats marins, l'un présumé contenir de fortes densités de capelans (*Mallotus villosus*), l'autre que de faibles densités, en 1996–1998. Notre hypothèse voulait que les macareux de la colonie des îles Gannet au Labrador, où le capelan est rare, aient une performance reproductive plus faible que ceux de l'île Gull dans la baie Witless où le capelan est abondant. Dans le passé, le capelan représentait environ 60 % à 95 % du régime alimentaire des poussins dans les deux colonies. À la fin des années 1990, les poussins des îles Gannet recevaient 3 % à 24 % de capelan (en masse), ce qui représentait 39 % à 97 % moins que ceux de l'île Gull. Les lançons (*Ammodytes* sp.) ayant terminé leur stade larvaire représentaient jusqu'à 49 % de la masse du régime alimentaire des poussins aux îles Gannet. Le succès de l'éclosion et celui de l'envol aux îles Gannet en 1997–1998 étaient statistiquement semblables à ceux de l'île Gull en 1998. La masse à l'envol (en pourcentage de la masse adulte) était semblable aux îles Gannet (69 %) et à l'île Gull (68 %). La grande variabilité du régime alimentaire des poussins d'une année à une autre dans les deux colonies et la faible variation de la performance reproductive durant notre étude laissent croire que les macareux moines du Labrador résistent bien aux changements à grande échelle de leurs sources de proies.

[Traduit par la Rédaction]

## Introduction

Capelin (*Mallotus villosus*), a small migratory pelagic smelt, was considered to be the preferred prey for Atlantic Puffins (*Fratercula arctica*) in the northwest Atlantic from Witless Bay, southeastern Newfoundland, to southern Labrador (Brown and Nettleship 1984; Montevecchi 1993). As a commercially important fish resource, information on bio-

mass, distribution, and age-class structure of capelin has been studied in detail by the Canadian Department of Fisheries and Oceans (e.g., Carscadden 1984; Miller and Lilly 1991; Nakashima 1992; Mann and Drinkwater 1994; Carscadden et al. 1997). However, relatively little is known of noncommercially important pelagic forage fish consumed by alcids such as sand lance (*Ammodytes* sp.). Throughout the 1990s, capelin biomass estimates were higher in Witless Bay than estimates combined for eastern Newfoundland and southern Labrador (Carscadden 1984; Carscadden et al. 1997). Capelin migrate from the offshore banks of Newfoundland and Labrador to inshore coastal waters and beaches each spring to spawn (Nakashima 1992; Nakashima and Winters 1997). The spawning aggregations consist of 3- to 5-year-old fish (gravid females, spent females, and mature males) mixed with immature or 1-group fish as well as young of the year 0-group fish. In Witless Bay, capelin spawn on beaches of the Avalon Peninsula, Newfoundland,

Received 4 December 2002. Accepted 28 July 2003.  
Published on the NRC Research Press Web site at  
<http://cjz.nrc.ca> on 14 October 2003.

**S.M. Baillie.**<sup>1</sup> Canadian Wildlife Service, Environment Canada, 6 Bruce Street, Mount Pearl, NL A1N 4T3, Canada.  
**I.L. Jones.** Biology Department, Memorial University of Newfoundland, St. John's, NL A1B 3X9, Canada.

<sup>1</sup>Corresponding author (e-mail: shaunabaille@canada.com).

in June and July. This spawning aggregation coincides with the chick-rearing period of seabirds at the Witless Bay Ecological Reserve, southeast Newfoundland. In south and central Labrador, capelin typically migrate north along the beaches of south Labrador in late July and August and are available to seabirds provisioning chicks at the Gannet Islands Ecological Reserve. Before the onset of our study, Atlantic Puffins at both the southeastern Newfoundland and south Labrador colonies were known to feed chicks 60%–95% (by mass) capelin (Nettleship 1972, 1991; Birkhead and Nettleship 1985; Rodway and Montevecchi 1996). Then, a dramatic change occurred in the spawning migration pattern of capelin in Labrador. During the late 1980s, capelin exhibited a population shift offshore and south to the Northeast Newfoundland Shelf (Carscadden et al. 2001). Capelin had ceased to spawn in Labrador in 1992 (Rose 1999). Thus, to our knowledge, for at least 5 consecutive years at the Gannet Islands prior to our study, puffins were unable to access spawning aggregations of capelin during the breeding season.

Behavioural responses of seabirds to environmental change have been found to occur at different temporal and spatial scales for parameters such as population size, clutch size, breeding phenology, chick growth, diet, and feeding rates (Schneider and Hunt 1984; Cairns 1987; Montevecchi 1993). In a previous study, we had investigated large-scale temporal behavioural changes of Atlantic Puffin at the Gannet Islands, Labrador, to a major shift in prey base from the early 1980s to the late 1990s (Birkhead and Nettleship 1983, 1985; Baillie 2001; S.M. Baillie and I.L. Jones<sup>2</sup>). In this study, we put these behavioural changes in perspective with other geographic regions of the northwest Atlantic in which capelin is thought to be the base of the marine food web. We compared Atlantic Puffin chick diet and breeding performance between colonies at Gull Island, Witless Bay, southeastern Newfoundland, and the Gannet Islands, Labrador. These two colonies exist in very different ecological systems. Some of the disparate environmental variables include latitude, climate, breeding habitat, population size (Birkhead and Nettleship 1983; Rodway et al. 1998; Chardine 1999; Calvert and Robertson 2002), kleptoparasitism, predation, and human disturbance levels (S.M. Baillie, personal observation). In the absence of a true control, as is the case with most intercolony comparisons, the validity of contrasting various diet and breeding parameters between unique colonies can be increased by considering the relative changes over decades at each respective colony. Various studies on Atlantic Puffins with respect to changes in environmental variables at their colonies have been conducted at Great Island, Witless Bay, southeastern Newfoundland (a colony similar and proximal to Gull Island), throughout the 1980s and 1990s (Nettleship 1972, 1991; Rodway and Montevecchi 1996; Rodway et al. 1998; Regehr and Rodway 1999).

Our main objective in this study was to assess the degree to which Atlantic Puffins responded to the dramatic decline in capelin abundance in Labrador by comparing nestling diet and growth, breeding phenology, breeding success, and adult mass between two seabird colonies with high and low cap-

elin abundance (Frank et al. 1996; Carscadden et al. 2001). We also conducted a comparative analysis of the proximate composition of puffin prey items between the two colonies. This information on puffins during their breeding season is the first collected during such a dramatic prey population shift and contributes to long-term monitoring and conservation efforts. We hypothesized that in a region of low capelin abundance, Atlantic Puffin reproductive success and chick growth parameters would be dramatically lower (both absolutely and relative to historical records) than for puffins in a region of high capelin abundance.

## Materials and methods

### Study sites

Fifty-seven percent (or 213 750 breeding pairs) of Atlantic Puffins in the northwest Atlantic breed within the Witless Bay Ecological Reserve on the Avalon Peninsula, Newfoundland (Chardine 1999). The first of our two study colonies, Gull Island (Gull), Witless Bay (47°15.8'N, 52°46.3'W), is the second largest puffin breeding colony within this reserve (Cairns et al. 1989). Gull Island lies less than 5 km from land and 50- to 74-m cliffs surround the island that supports a declining coniferous forest bordered by tussock grass and areas of bare rock and soil. Summer temperatures averaged 20 °C and landfast ice in nearby bays dissipated by late April (Birkhead and Nettleship 1995). The Gannet Islands (Gan) archipelago (53°56'N, 56°32'W), Labrador, is located approximately 770 km north of Witless Bay and is home to approximately 100 000 pairs of auks including 39 300 pairs of puffins (Lock et al. 1994). Our study was conducted at islet GC2, which is a 16-ha relatively steep-sloped island with a maximum elevation of 40 m covered with low-cropped ericaceous and herbaceous vegetation and exposed bedrock (Birkhead and Nettleship 1995). Summer temperature averaged 10 °C with extensive sea ice between December and mid-June (Birkhead and Nettleship 1995).

Median hatch and fledge dates for Atlantic Puffins at Gull Island are late June and mid-August (Cairns et al. 1989). Median hatch and fledge dates at the Gannet Islands are early August (Birkhead and Nettleship 1995) and late September (Birkhead and Nettleship 1985). We conducted fieldwork on Gull Island from early June to late July in 1997 and to late August in 1998 and at the Gannet Islands in early August to mid-September.

### Field methodology and data analyses

We collected bill loads from adult puffins at the Gannet Islands and Gull Island using a 3-m net pole and a large 12 m × 24 m nylon monofilament barrier net with 5-cm mesh. Prey samples were measured immediately then preserved by sun drying on a metal mesh rack. Upon capture, puffins were marked with numbered stainless steel leg bands to ensure that bill loads were collected from each individual only once. In 1997 and 1998, the total length of each fish was recorded to the nearest 0.1 mm. Prey items, including invertebrates, were individually weighed to the nearest 0.1 g using an electronic balance. A list of species keyed to the

<sup>2</sup>S.M. Baillie and I.L. Jones. Response of Atlantic Puffins (*Fratercula arctica*) to a decline in capelin (*Mallotus villosus*) abundance at the Gannet Islands, Labrador. Submitted for publication.

closest possible taxon is contained in Appendix A. Puffin chick diet was collected consistently among colonies during the weeks 3–6, inclusive, after chick hatch date; therefore, interannual comparisons and statistical analyses were limited to this period. All statistical analyses were conducted in Systat 10 (Systat Software Inc., Richmond, Calif.). Whenever  $2 \times 2$   $\chi^2$  contingency tables exist, we used the Yates correction equation (Zar 1984). We categorized chick meals as “full” or “partial” bill loads and used only “full” meals for statistical analyses.

Adult Atlantic Puffins were captured for wing, bill, tarsus, and mass measurements using a 12 m  $\times$  24 m barrier net with 5-cm mesh size set at the base of a densely occupied grassy slope. To avoid resampling, each bird was marked with a stainless steel leg band. We excluded immature puffins (with less than two bill grooves) (Harris 1984) from analysis.

After the onset of chick provisioning at each colony, a sample of 60–120 burrows was checked every 3 days and the contents of each nest recorded as “egg”, “chick”, or “empty”. We determined median hatch date for individual chicks to within 2 days of age by calculating the midpoint between burrow visits when an “egg” and “chick” were recorded (Birkhead and Nettleship 1983). At the Gannet Islands, for burrows in which hatch date was unknown, we used an estimate for Atlantic Puffin incubation period of 37 days (Birkhead and Nettleship 1983). At Gull Island, we estimated median hatch date for 1997 by adding the time interval between first chicks and median hatch (12 days), observed in 1998, to the date of first chicks in 1997. Median laying dates for Gull Island puffins were based on previously reported estimates for the incubation period in Witless Bay of 42 days (Nettleship 1972). We estimated median fledge date as the midpoint between burrow visits when contents were recorded as “chick” and “empty”. Hatching success was determined as the percentage of chicks that hatched from eggs. Fledging success was derived from the percentage of chicks that fledged (or reached over 30 days of age) from nests with chicks.

To measure chick morphology and growth, we used methods similar to those of Birkhead and Nettleship (1985). Body mass was rounded off to the nearest gram with a Pesola spring scale. Flattened wing chord was measured to the nearest millimetre, excluding downy feathers and including the emerging feather shaft (except in 1996 when the emerging feather shaft was not measured). To lessen disturbance, the chick was not measured if an adult was present unless it had not been measured in three visits (except in 1996 when burrows were checked regardless of adult presence). Growth rates and fledge success were collected at Gull Island in 1998 only. We determined chick growth rates by the time period in which the rate of mass and wing gain was linearly dependent on time by inspecting residuals of linear regressions on pooled data of growth parameters through time. We proceeded to eliminate data from the upper and lower ages of the curve until residuals first became linear, which was between chick ages 13 and 25 days. We then performed a linear regression on growth and age for each chick to obtain the mathematical slope of the linear equation and averaged the slopes to obtain growth rates representative of the population. We compared the mass of

**Table 1.** Relative proportions of prey items delivered to young Atlantic Puffins (*Fratercula arctica*) at Gull Island, Witless Bay, and the Gannet Islands, Labrador, during middle chick-rearing period in the late 1990s.

	Gannet Islands			Gull Island	
	1996	1997	1998	1997	1998
<b>Percent mass</b>					
Capelin	3	15	24	92	62
Sandlance	49	49	21	3	29
Larval fish	35	30	51	4	6
Invertebrates	12	5	4	1	4
Total mass (g)	597	1107	981	842	752
<b>Percent frequency</b>					
Capelin	0.5	8	7	34	45
Sandlance	9	16	6	3	14
Larval fish	72	68	82	60	33
Invertebrates	18	9	5	3	8
Total no. of items	473	276	1219	776	1261
<b>Percent occurrence</b>					
Capelin	3	11	10	49	40
Sandlance	32	28	15	4	15
Larval fish	53	37	75	61	16
Invertebrates	32	12	13	13	6
Total no. of bill loads	109	80	99	71	107

known-age chicks at discrete age classes (i.e., 1–3, 10–12, and 37–40 days, peak mass, fledge mass) and chick growth rates between colonies. Chick mass was expressed as a percentage of adult mass to account for geographic differences in morphology (Barrett and Rikardsen 1992) and the resultant percentage data were arcsine-transformed for statistical analyses to meet assumptions of residual normality. Other statistical methodologies are outlined in the Results section where necessary.

## Results

### Prey composition

Pairwise comparisons of the relative proportions of four prey categories by mass, numbers, and occurrence in bill loads showed that no two colony years were statistically homogeneous ( $\chi^2$  statistic values ranged from 18.7 to 1135.9,  $df = 3$ , and all  $P < 0.001$ ) (Table 1). Adult capelin were the predominant prey item, by mass, at Gull Island, while sandlance was more important at the Gannet Islands except in 1998 when larval fish were more prominent. However, prey other than capelin and sandlance, i.e., larval sandlance, cottids, and blenniids, were as or more important in percent frequency and percent occurrence in bill loads at both colonies.

We found that the proportion of mature capelin, by mass, fed to Atlantic Puffin chicks was significantly higher at Gull Island in 1997 and 1998 (92% and 62%, respectively) than at the Gannet Islands during 1996, 1997, and 1998 (3%, 4%, and 24%, respectively;  $\chi^2$  ranged from 65.0 to 1135.4 and all  $P < 0.001$  for all pairwise contingency tables comparing capelin and colony year). Although capelin diet biomass increased significantly each year at the Gannet Islands, there was no significant difference in capelin between 1997 and

1998 by numbers ( $\chi^2_1 = 0.1$ ,  $P = 0.7$ ) or occurrence ( $\chi^2_2 = 0.09$ ,  $P = 0.8$ ). The number of capelin brought to chicks at Gull Island was almost 20 times higher than that at the Gannet Islands. Capelin occurred in up to 49% of chick meals at Gull Island and only in 3%–11% of chick meals at the Gannet Islands (Table 1).

Proportions of postlarval sand lance were significantly higher at the Gannet Islands during 1996 and 1997 (49% by mass) than at Gull Island in 1997 and 1998 (3% and 29%, respectively) ( $P < 0.001$  for all pairwise contingency tables comparing capelin and colony year by mass). The difference between sand lance contribution to chick diet at the Gannet Islands during 1996 and 1997 was not significant by mass ( $\chi^2_2 = 0.04$ ,  $P = 0.8$ ) or by occurrence in bill loads ( $\chi^2_2 = 0.4$ ,  $P = 0.5$ ) (Table 1). All other differences in sand lance, by mass, among colony years were significant with  $\chi^2$  values ranging from 14.9 (Gan 1998 : Gull 1998) to 293.9 (Gan 1996 : Gull 1997) and  $P < 0.001$ .

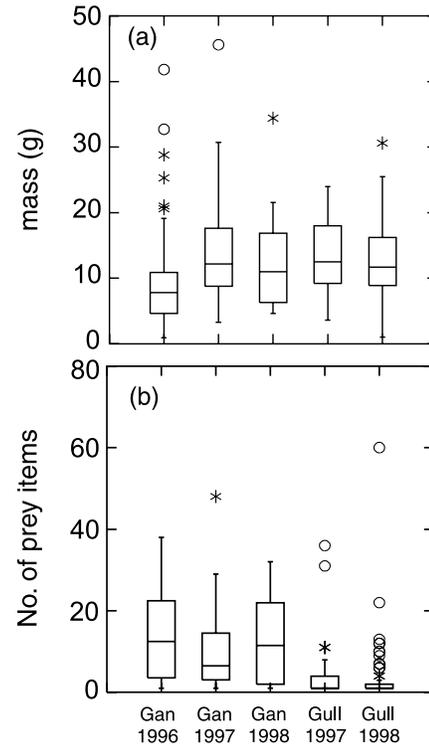
During middle chick rearing, mean bill-load mass for Gull Island in 1997 and 1998 was  $13.4 \pm 5.1$  g ( $N = 38$ ) and  $12.5 \pm 5.4$  g ( $N = 117$ ), respectively. Mean bill-load mass for the Gannet Islands in 1996, 1997, and 1998 was  $9.8 \pm 7.7$  g ( $N = 61$ ),  $14.1 \pm 8.1$  g ( $N = 48$ ), and  $12.1 \pm 6.5$  g ( $N = 36$ ), respectively. We found the difference among colony years to be significant ( $F_{[4,295]} = 3.5$ ,  $P = 0.008$ ) (Fig. 1a). However, post hoc examination showed that bill-load mass was significantly different only among colony years Gan 1996 and Gan 1997 (Tukey pairwise probabilities with Gan 1996 : Gan 1997,  $P = 0.005$ ; Gan 1998, not significant; Gull 1997, not significant; Gull 1998, not significant). Number of items per bill load during the middle chick-rearing period was  $4.4 \pm 7.6$  ( $N = 37$ ) and  $2.6 \pm 6.2$  ( $N = 117$ ) at Gull Island in 1997 and 1998, respectively. Number of items per bill load at the Gannet Islands during the middle chick-rearing period was  $13.9 \pm 11.5$  ( $N = 60$ ),  $9.8 \pm 9.4$  ( $N = 48$ ), and  $12.1 \pm 10.2$  ( $N = 36$ ) in 1996, 1997, and 1998, respectively. As the number of items per bill load did not meet assumptions for normality owing to high sample variance, we did not perform statistical analyses. However, the data show that the number of items per bill load were much lower at Gull Island than at the Gannet Islands (Fig. 1b).

### Size and nutritional value of prey

Capelin were significantly heavier than sand lance in our study ( $F_{[1,389]} = 11.6$ ,  $P = 0.001$ ) and we detected significant differences in fish sizes among colony years ( $F_{[4,389]} = 13.6$ ,  $P < 0.001$ ). However, the interaction between species and colony year also was significant ( $F_{[4,389]} = 13.6$ ,  $P < 0.001$ ) because sand lance were much smaller than capelin at Gull Island in 1997 and much larger in 1998 (Fig. 2a). Similarly, the differences in fish length among colony years were significant (species:  $F_{[1,389]} = 11.6$ ,  $P = 0.001$ ; colony year:  $F_{[4,389]} = 13.6$ ,  $P < 0.001$ ; species  $\times$  colony year:  $F_{[4,389]} = 33.8$ ,  $P < 0.001$ ) (Fig. 2b). Again, the significant interaction indicates inconsistency in fish size at Gull Island, but the data show little difference in length between capelin and sand lance at the Gannet Islands.

The nutritional value of capelin was significantly lower than that of postlarval sand lance at both colonies (Table 2). Postlarval sand lance were 38% higher in lipid content, 20% higher in protein content, and 26% higher in energy density

**Fig. 1.** Median mass (a) and number of items (b) per Atlantic Puffin (*Fratercula arctica*) chick meal during middle chick-rearing at the Gannet Islands (Gan), Labrador, and Gull Island (Gull), Witless Bay, during middle chick rearing. Lower and upper box boarders (25th to 75th quartiles, respectively) contain 50% of values, whiskers extend to the highest and lowest values, and asterisks and circles indicate outliers. Sample sizes: 61 (Gan 1996), 48 (Gan 1997), 36 (Gan 1998), 38 (Gull 1997), and 117 (Gull 1998).



(Baillie 2001). However, we found that energy per fish did not differ significantly, as sand lance at the Gannet Islands were generally smaller (by mass) than capelin. Despite this, there was no significant size difference between species in Gull Island fish specimens subjected to proximate composition, and energy density, protein content, and lipid content remained significantly higher (Table 2). Because of a significant interaction between species and colony, we examined fish size differences at each colony separately. No significant interactions were seen in any other test. We found no significant intercolony variation in nutritional content of capelin and sand lance (lipid:  $F_{[1,19]} = 0.002$ ,  $P = 1.0$ ; protein:  $F_{[1,19]} = 0.2$ ,  $P = 0.7$ ; energy per gram of fish:  $F_{[1,19]} = 0.1$ ,  $P = 0.7$ ; energy per fish:  $F_{[1,19]} = 0.07$ ,  $P = 0.8$ ).

### Adult puffin morphology

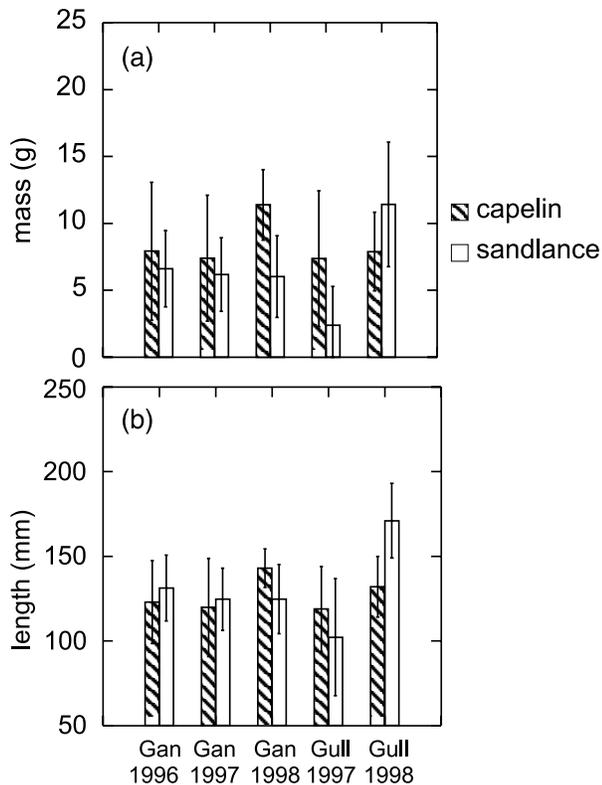
At the Gannet Islands, a two-way ANOVA for adult puffin mass by period and year showed no significant difference between years ( $F_{[2,955]} = 0.6$ ,  $P = 0.8$ ) but a significant mass loss through the chick-rearing period ( $F_{[2,955]} = 3.2$ ,  $P = 0.004$ ). The sampling period at Gull Island in 1997 (20–27 August) was later than in 1998 (4 July – 14 August); thus, we controlled for a date-related effect using an ANCOVA for mass by year with date as a covariate. This showed that mass decreased linearly dependent on date and there was no

**Table 2.** Comparison of the nutritional value of postlarval sandlance and capelin delivered to Atlantic Puffin chicks at the Gannet Islands and Gull Island.

	Capelin	Sandlance	Species effect
Mass (g)			
Gannet	11.0 ± 2.4 (8)	5.3 ± 1.9 (51)	$t_{[57]} = 6.2, P = 0.001$
Gull	7.9 ± 3.7 (11)	8.7 ± 3.9 (19)	$t_{[28]} = -0.5, \text{ not significant}$
Percent lipid content			
Gannet	3.0 ± 1.9 (5)	3.9 ± 1.9 (7)	$F_{[1,19]} = 4.4, P = 0.05$
Gull	2.2 ± 1.8 (4)	4.7 ± 2.0 (7)	
Percent protein content			
Gannet	14.7 ± 1.7 (4)	19.2 ± 1.0 (7)	$F_{[1,19]} = 11.3, P = 0.003$
Gull	15.5 ± 1.1 (4)	19.1 ± 5.4 (7)	
Energy density (kJ·g <sup>-1</sup> )			
Gannet	4.6 ± 0.6 (4)	6.4 ± 1.2 (8)	$F_{[1,19]} = 17.4, P = 0.001$
Gull	4.5 ± 0.8 (5)	6.0 ± 0.8 (7)	
Energy per fish (kJ·fish <sup>-1</sup> )			
Gannet	47.4 ± 18.2 (4)	44.7 ± 29.0 (8)	$F_{[1,19]} = 0.6, \text{ not significant}$
Gull	38.5 ± 20.8 (4)	59.1 ± 31.4 (7)	

Note: Values are means ± SD and sample sizes are in parentheses.

**Fig. 2.** Comparison of mass (a) and length (b) for postlarval capelin (*Mallotus villosus*) and sandlance (*Ammodytes* sp.) delivered to Atlantic Puffin chicks during the middle chick-rearing period among colony years. Values are means ± SD. Capelin sample sizes: 4 (Gan 1996), 22 (Gan 1997), 19 (Gan 1998), 46 (Gull 1997), and 70 (Gull 1998). Sandlance sample sizes: 71 (Gan 1996), 88 (Gan 1997), 46 (Gan 1998), 8 (Gull 1997), and 46 (Gull 1998).



significant difference in puffin mass between 1997 and 1998 ( $r^2 = 0.008, F_{[1,305]} = 3.3, P = 0.07$ ) during the chick-rearing period at Gull Island. We pooled data on adult puffin size

between years at Gull Island in 1997 and 1998 and the Gannet Islands in 1996–1998 during the chick-rearing period and compared the colonies (Table 3). Puffins at Gull Island in 1997 and 1998 weighed 8% less than those at the Gannet Islands in 1996–1998. Other body size measurements including wing length, tarsus, bill length, and culmen length were also significantly smaller in puffins at Gull Island.

#### Timing of breeding and productivity

Annual variation in onset of breeding was much greater between colonies than within colonies (Table 4). Atlantic Puffins at Gull Island in 1998 laid their eggs approximately 35 days earlier by calendar date than puffins at the Gannet Islands in 1996–1998 ( $U = 16.0, z = -9.8, P < 0.001$ ). Similarly, the first chicks to fledge from Gull Island went to sea 32–40 days earlier by calendar date than chicks reared at the Gannet Islands. The difference in hatch success among colony years was significant ( $\chi^2_3 = 12.0, P = 0.007$ ) (Table 5). Inspection of the data showed that hatch success at the Gannet Islands in 1997 (80%) was anomalously high. A subsequent  $\chi^2$  test, excluding Gannet Islands in 1997, showed no significant difference in hatch success between colony years ( $\chi^2_2 = 1.8, P = 0.4$ ). Hatch success and overall performance at the Gannet Islands during 1996 was poorer than in any other colony year. However, fledge estimates were similar in 1996 and 1997 at the Gannet Islands. Although the data show that fledging success was lower at the Gannet Islands in 1996–1998 than at Gull Island in 1998, there was no significant difference in fledging success ( $\chi^2_3 = 3.0, P = 0.4$ ) (Table 5). The overall puffin breeding-success estimate did not differ among colonies, except in 1996 at the Gannet Islands when breeding success was 24%–42% lower than for other colony years.

#### Chick growth

Rates of chick mass gain during the linear phase of chick growth were not significantly different between colony years, except for the Gannet Islands in 1996. In 1996, growth rates were significantly lower compared with those

**Table 3.** Comparison of adult Atlantic Puffin morphology at Gull Island in 1997 and 1998 and the Gannet Islands in 1996–1998.

	Gull Island*	Gannet Islands	<i>t</i> test results
Mass (g)	431.6 ± 34.7 (308)	468.2 ± 35.1 (401)	$t_{[707]} = 13.8, P < 0.001$
Wing length (mm)	169.0 ± 4.6 (304)	174.4 ± 13.5 (308)	$t_{[610]} = 6.5, P < 0.001$
Tarsus length (mm)	33.6 ± 1.7 (303)	34.5 ± 1.4 (310)	$t_{[611]} = 7.6, P < 0.001$
Bill length (mm)	29.0 ± 1.5 (278)	29.9 ± 2.8 (275)	$t_{[551]} = 4.6, P < 0.001$
Bill depth (mm)	37.3 ± 2.4 (270)	39.0 ± 2.2 (274)	$t_{[542]} = 1.3, P = 0.2$
Culmen length (mm)	47.7 ± 2.2 (261)	49.9 ± 2.5 (261)	$t_{[536]} = 11.0, P < 0.001$

**Note:** Values are means ± SD and sample sizes are in parentheses.

\*G. Robertson, Canadian Wildlife Service, unpublished data.

**Table 4.** Atlantic Puffin breeding phenology for Gull Island during 1997 and 1998 and the Gannet Islands during 1996–1998.

	Gull Island		Gannet Islands		
	1997	1998	1996	1997	1998
Median lay date	29 May	23 May	26 June	27 June	26 June
First chicks	2 July	20 June	3 Aug.	1 Aug.	28 July
Median hatch date	13 July*	2 July	5 Aug.	6 Aug.	5 Aug.
First fledging	—	11 Aug.	15 Sept.	18 Sept.	12 Sept.
Median fledge date	—	—	20 Sept.	21 Sept.	17 Sept.

\*Median date was estimated from first chick dates at Gull Island in 1998.

**Table 5.** Atlantic Puffin productivity estimates at Gull Island and the Gannet Islands during the late 1990s.

	Gull Island, 1998	Gannet Islands		
		1996	1997	1998
Nests with eggs	47	82	38	40
Nests with eggs hatched (initially found as eggs)	27/43*	42	32	24
Hatching success (%)	63	51	84	60
Total nests with chicks (%)	37	112	42	85
Total nests that fledged	21	47	19	43
Fledging success (%)	57	42	45	51
Overall success (% hatched × % fledged)	36	22	38	29

\*Total number of nests reduced, as we were unable to track egg/chick progress.

**Table 6.** Comparison of Atlantic Puffin chick growth parameters at Gull Island and the Gannet Islands in the late 1990s.

	Gull Island, 1998	Gannet Islands			ANOVA results
		1996	1997	1998	
Mass gain (g/d)	9.4 ± 3.2 (16) b	7.1 ± 2.8 (40) a	9.0 ± 1.8 (18) b	9.4 ± 2.2 (35) b	$F_{[3,99]} = 9.1, P < 0.01$
Wing growth (mm/d)	4.1 ± 0.4 (16) a	—	3.9 ± 0.3 (18) a	4.1 ± 0.4 (35) a	$F_{[2,61]} = 1.4, P = 0.3$
Age 1–3 days*	12 ± 1.5 (28) a	11 ± 1.7 (60) a	13 ± 2.6 (12) b	12 ± 0.5 (46) ab	$F_{[3]} = 3.6, P = 0.01$
Age 10–12 days*	27 ± 6.0 (26) a	25 ± 5.3 (56) a	28 ± 2.6 (7) ab	31 ± 3.6 (41) b	$F_{[3]} = 6.8, P < 0.001$
Age 37–40 days*	51 ± 13.4 (21) a	57 ± 8.9 (37) b	76 ± 6.7 (18) c	72 ± 8.4 (23) c	$F_{[3]} = 35.0, P < 0.001$
Peak mass*	63 ± 12.7 (11) a	71 ± 7.4 (29) a	81 ± 5.3 (20) b	77 ± 8.4 (41) b	$F_{[3]} = 15.0, P < 0.001$
Fledge mass*	68 ± 3.6 (3) a	63 ± 1.1 (2) b	71 ± 5.3 (14) a	73 ± 3.2 (5) a	$F_{[3]} = 4.1, P = 0.04$

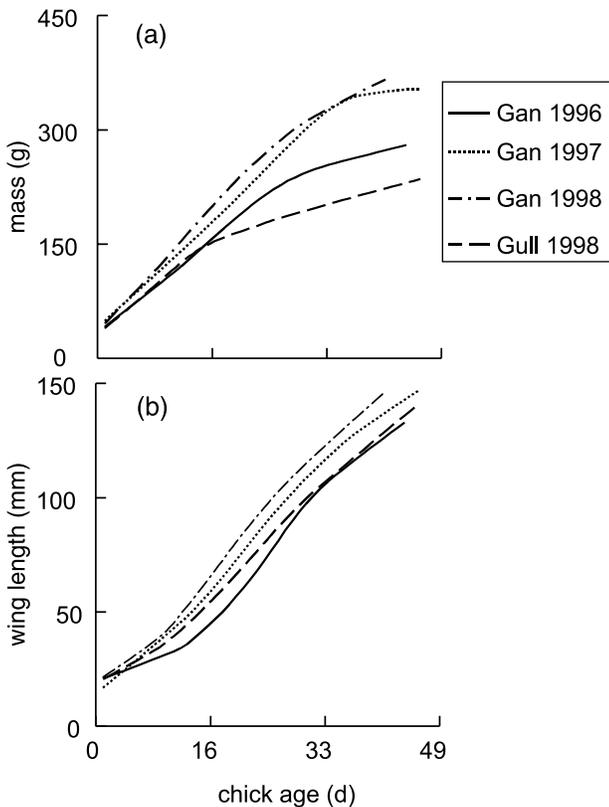
**Note:** Values are means ± SD and samples sizes are in parentheses. Matching letters show where the Fisher's PLSD post hoc examinations did not find a statistically significant difference.

\*Chick mass expressed as a percentage of adult puffin mass during the chick-rearing period: Gull Island, 431.6 ± 34.7 g ( $N = 308$ ); Gannet Islands, 468.2 ± 35.1 g ( $N = 401$ ).

at Gull Island in 1998 and the Gannet Islands in 1997 and 1998 (Table 6, Fig. 3). Wing length at the Gannet Islands in 1996 was measured slightly differently than in other colony years; therefore, 1996 nestling wing measurements were not

included in the statistical analyses. Wing growth rates did not differ significantly between Gull Island and the Gannet Islands chicks. The Gannet Islands chicks during 1997 and 1998 were significantly heavier than Gull Island chicks in

**Fig. 3.** Intercolony comparison of Atlantic Puffin nestling growth curves (unadjusted for adult mass) for mass (a) and wing length (b). Sample sizes: 436 (Gan 1996), 189 (Gan 1997), 331 (Gan 1998), and 190 (Gull 1998).



1998 for most age classes even when expressed as a percentage of adult mass, except that fledge mass between colonies was statistically similar (Table 6). We found no significant differences in parameters between study years 1997 and 1998 at the Gannet Islands, although in 1996, chicks weighed significantly less. Despite this, chicks at the Gannet Islands in 1996 were significantly heavier than those at Gull Island at age 37–40 days and peak mass.

## Discussion

### Chick diet

Although chick diet was highly variable among colony years, the greatest differences in diet composition by mass, numbers, and occurrence in bill loads existed between colonies. Atlantic Puffin chicks at the Gannet Islands received 39%–97% less capelin than chicks at Gull Island. Postlarval sandlance dominated the diet at the Gannet Islands in 1996 and 1997 and were replaced by small miscellaneous prey in 1998. Capelin that were brought to chicks at the Gannet Islands in 1997 and 1998 diminished in size from middle chick-rearing onward, possibly indicating that the presence of mature capelin near the colony was short-lived and that capelin had migrated out of the puffin foraging range well before chicks reached peak mass (Baillie 2001; S.M. Baillie and I.L. Jones<sup>2</sup>). The fact that the Witless Bay region off southern Newfoundland has higher concentrations of capelin

than areas like Labrador is also reflected in the Atlantic Puffin chick diets. However, puffins at Gull Island exhibited apparent size selection of capelin, as none of the capelin brought back were 0-group juveniles, although Department of Fisheries and Oceans surveys in Witless Bay suggested that 4- to 200-mm capelin were available during the time of our study (J. Anderson, personal communication). The proportion of prey species biomass in puffin nestling diet at Great Island for 6 of 7 years between 1969 and 1984 ranged from 78% to 94% capelin and from 10% to 15% sandlance and the remainder was immature gadids (*Gadus* sp. and *Boreogadus* sp.) and other small items (Nettleship 1972, 1991). Rodway and Montevecchi (1996) found that Atlantic Puffins at Great Island fed nestlings a diet of 83% (by mass) capelin between 1992 and 1994. Alternative prey consisted, by mass, of mainly sandlance (13%) and miscellaneous items (<5%). At the Gannet Islands in the early 1980s, puffin chick diets comprised mainly capelin (70%–74% by mass) during 2 years of a 3-year study from 1981 to 1983 (Birkhead and Nettleship 1985). However, in 1981 at the Gannet Islands, puffins fed nestlings only 17% capelin (by mass) with no negative breeding repercussions. Despite this, extreme variation in Atlantic Puffin diet and reproductive success in Witless Bay had not been observed in past decades (Nettleship 1972, 1991; Rodway and Montevecchi 1996; Rodway et al. 1998; Regehr and Rodway 1999). Another recent study of Atlantic Puffins (Russell 1999) found that broad displacements of capelin in the diet of Atlantic Puffins were highly visible in chick diet around Funk and Small Islands yet had little influence on breeding performance. It is apparent that puffins do not necessarily depend on one prey species (Russell 1999; Baillie 2001), yet we feel that some colonies may be more sensitive to prey shifts than others depending on availability of alternative prey and other constraints to foraging and breeding ecology.

We found that postlarval sandlance delivered to young puffins were higher in lipid, protein, and energy density values than capelin at both the Gull Island and Gannet Islands colonies. Our results were consistent with those of recent studies on murre (Bryant and Jones 1999; Bryant et al. 1999) and puffin (Russell 1999; S.M. Baillie and I.L. Jones<sup>2</sup>) chick diet in Newfoundland and Labrador which showed that individual capelin may not necessarily provide the highest quality meal to seabird nestlings. Sandlance fed to chicks in our study had more energy (kilojoules) per gram of fish than capelin. However, when sandlance were smaller than capelin, especially at the Gannet Islands, we found no difference in energy (kilojoules) per fish. Thus, sandlance may not be more profitable than capelin if they are significantly smaller, as appears to be the case in Witless Bay but not in Labrador. Variable factors such as fish size and ease of capture likely determine the highest quality meal in terms of energetic return.

### Adult puffin morphology

Results from our study indicate that adult Atlantic Puffins at Gull Island weighed less and had shorter wings and smaller bills than adult puffins at the Gannet Islands. This decline in adult puffin body size from north to south is consistent with northeast Atlantic breeding colonies, even though northwest Atlantic colonies are situated within a

shorter latitudinal distance (Harris 1978; Moen 1991; Gaston and Jones 1998). This is an example of selection for larger body size at high latitudes to offset stress of more severe climate, yet the degree of overlap indicates that they belong to the same subspecies.

Interyear variation in mass of adult puffins during the chick-rearing period was not evident at Gull Island. However, at the Gannet Islands, adult puffins had higher body masses in years when preying on larval fish (Baillie 2001). Adult puffins at the Gannet Islands likely spent more energy to obtain larger, fattier prey such as capelin and sandlance than to obtain small sculpins and blennies in probable high abundance around the colony. Our results are consistent with those of Anker-Nilssen and Lorensten (1990) who found that individual mass declined through the chick-rearing season but that this decline was not statistically significant. It is evident that the food supply was sufficient enough at the Gannet Islands to prevent the adult puffin population from reaching the critical point at which they abandon food delivery to young in favour of self-preservation (Cairns 1992).

### Timing of breeding

The median Atlantic Puffin hatch date at Gull Island was a week later in 1998 than in 1997 yet was similar to hatch dates of puffins at Great Island 30 years earlier in 1968 and 1969 (Nettleship 1972). Puffins at the Gannet Islands had median hatch dates that were roughly 4 days later in the late 1990s than in the early 1980s (Birkhead and Nettleship 1983, 1985; Baillie 2001). The onset of egg laying at Witless Bay was approximately 1 month earlier (by calendar date) than at the Gannet Islands, yet both colonies finished breeding at approximately the same time, in late September. Nettleship (1972) also found that puffins in Witless Bay on Great Island in 1968 and 1969 commenced breeding earlier and had a longer nestling period than those at the Gannet Islands in 1981–1983 (Birkhead and Nettleship 1985). The nestling period was much longer at Gull Island, mostly because breeding was less synchronous. The Gannet Islands puffin breeding phenology is affected by climatic conditions such as changes in sea surface temperatures (Harris et al. 1998), sea ice inhibiting early breeding (e.g., Hipfner and Gaston 1999), snow cover, frozen ground, and drying conditions (Rodway et al. 1998), and early arrival of winter sea storms and cold water at the end of the breeding period in the north. The longer temporal window for breeding in Witless Bay may allow seabirds greater resilience to temporary prey deficiencies (Nettleship 1972; Ydenberg et al. 1995). At the Gannet Islands in 1982, puffins bred a week later than they did in 1981 and 1983, and this was attributed to ice conditions (Birkhead and Nettleship 1983). Similarly, in 1992 and 1993 at Great Island, Rodway et al. (1998) found hatch dates to be a week later and related it to a cold ocean event. These events may in turn delay the timing of spawning in capelin but are not reported to affect puffin productivity (Rodway et al. 1998).

### Productivity

The change in food supply did not negatively affect hatch-success estimates at the Gannet Islands. Fledging success estimates at the Gannet Islands were lower, but not significantly, than those at Gull Island. Despite some annual

variation in hatch success and fledge success, overall breeding-success estimates at the Gannet Islands during 1997 and 1998 ranged from 29% to 38% and were similar to that at Gull Island in 1998 (36%). These estimates at both colonies were similar to estimates recorded in the early 1970s and 1990s in Witless Bay (21%–37% (Nettleship 1972) and 34% (Regehr and Rodway 1999)) and at the Gannet Islands in the early 1980s (36% (Birkhead and Nettleship 1983, 1985)). However, overall breeding success was 24%–42% lower at the Gannet Islands in 1996, when both hatch and fledge success were low. This low breeding-success estimate in 1996 was mainly driven by relatively lower hatching success and not clearly related to the chick-rearing period and fledging success. The presence of an arctic fox (*Alopex lagopus*) on islet GC2 in 1996 early in the breeding season likely caused the reduction in breeding success (Birkhead and Nettleship 1995).

### Chick growth

We found no clear evidence that chick growth was negatively affected by low capelin abundance in Labrador. Chick mass gain and wing growth rates were statistically similar between the Gannet Islands and Gull Island except in colony year 1996 at the Gannet Islands in which chicks grew slower (by mass) and fledged at lower weights. Hislop and Harris (1985) reported that in years when puffins were fed whiting (*Merlangius merlangus*) instead of sandeel (*Ammodytes marinus*) and sprat (*Sprattus sprattus*), chicks fledged at lower weights. Our results show that chick diet, despite the almost complete lack of capelin, was not poor in 1996. We found no difference in the mass of chick meals among colony years, and even if bill loads were smaller, more trips per day could easily compensate for the total mass delivered to the chicks. In 1996, sandlance comprised almost 50% of chick diet by mass and occurred in as many meals as in 1997 when chicks grew better. Although chicks at the Gannet Islands fledged heavier than those at Gull Island, chick fledge mass was similar when expressed as a percentage of adult mass. At the Gannet Islands where chicks are constrained by seasonal climate and sea ice, it is plausible that a chick increases its chances of survival at sea by heavier fledge mass and longer wings (Ydenberg 1989). It is apparent that puffin chicks at the Gannet Islands reached peak mass and fledged at a younger age than chicks at Gull Island, regardless of changes in prey.

Chicks at Gull Island were significantly smaller than chicks at the Gannet Islands, which was a reflection of geographical differences in body size (Baillie 2001). There were also differences in the growth pattern of chicks among colonies, as the weight of chicks from Gull Island seemed to “peak” at around 25 days, while Gannet Islands chicks gained mass up to 45 days and then rapidly lost weight 2–3 days prior to fledge. Reduced growth rates and prolonged fledging periods often reflect periods of food stress (Anker-Nilssen 1987). There was no evidence in the diet that puffin chicks in Witless Bay were food stressed, and fledge mass at Gull Island in the late 1990s was similar to that reported for Great Island in 1992 (Rodway and Montevicchi 1996). We had expected to see the effects of food stress at the Gannet Islands, and chicks did grow slightly slower in 1996–1998 than in the early 1980s at the same colony (Baillie 2001;

S.M. Baillie and I.L. Jones<sup>2</sup>). However, this change in prey base was not dire enough for the Gannet Islands to exhibit a negative chick growth response relative to a colony that did not undergo a major shift in prey base.

### Conclusions

We have established that Atlantic Puffin chick diet varied greatly among colonies and that there were significantly more capelin fed to chicks at Gull Island than to those at the Gannet Islands. Adult mass and timing of breeding were not affected by these differences and changes in diet. Little intercolony differences in productivity were observed. There was a reduction in chick growth rates and fledgling mass at the Gannet Islands from the late 1980s to the early 1990s (S.M. Baillie and I.L. Jones<sup>2</sup>). However, chick growth rates (by mass) at the Gannet Islands were statistically similar to those at Gull Island in the late 1990s, except that 1996 chicks at the Gannet Islands gained mass significantly slower. Chick wing growth and fledge mass did not vary among colonies. The changes in prey base did by no means result in the breeding failure predicted based on existing ecological literature on puffins in the northwest and northeast Atlantic (Harris and Hislop 1978; Brown and Nettleship 1984; Anker-Nilssen 1987; Barrett et al. 1987; Barrett and Furness 1990; Nettleship 1991; Anker-Nilssen and Rostad 1993). We encourage continued low-impact monitoring of puffin colonies in the northwest Atlantic with attention paid to long-term trends at the Gannet Islands colony and increased data collection on noncommercial forage fish such as sandlance.

### Acknowledgments

We thank Mark Button and Laura Penny (field assistants of S.M.B.), as well as Rachel Bryant, Dreidrich Grecian, Monica Kidd, Tarmo Poldmaa, Tony Roberts, Brian Veitch, and especially Mark Hipfner for assistance with the fieldwork. Thanks to Randy Cahill in Cartwright, Labrador, and the O'Briens and Gatheralls Whale Watch Tour operators in Bay Bulls for vessel transportation to the islands. Glen Ryan and Doug Ballam (Parks and Natural Areas, Department of Tourism, Culture and Recreation, Government of Newfoundland and Labrador) permitted us to conduct research at the Gannet Islands and Witless Bay ecological reserves. We thank Greg Robertson for providing adult puffin measurements from Gull Island. Funding was provided by Atlantic Cooperative Wildlife Ecology Research Network Canadian Wildlife Service (CSW) / Natural Sciences and Engineering Research Council of Canada (NSERC) Industrial Chair, NSERC individual research, and Dean of Science of Memorial University of Newfoundland grants to I.L.J. and by Northern Scientific Training Program support to S.M.B.

### References

- Anker-Nilssen, T. 1987. The breeding performance of Puffins *Fratercula arctica* on Rost, northern Norway in 1979–1985. *Fauna Norv. Ser. C. Cinclus*, **10**: 21–38.
- Anker-Nilssen, T., and Lorensten, S.-H. 1990. Distribution of Puffins *Fratercula arctica* feeding off Rost, northern Norway, during the breeding season, in relation to chick growth, prey and oceanographical parameters. *Polar Res.* **8**: 67–76.
- Anker-Nilssen, T., and Rostad, O.W. 1993. Census and monitoring of Puffins *Fratercula arctica* on Rost, N Norway, 1979–88. *Ornis Scand.* **24**: 1–9.
- Baillie, S.M. 2001. Atlantic puffin response to changes in capelin abundance in Newfoundland and Labrador: an inter-colony and inter-decade comparison. M.Sc. thesis, Memorial University of Newfoundland, St. John's, Nfld.
- Barrett, R.T., and Furness, R.W. 1990. The prey and diving depths of seabirds in Hornoy, North Norway after a decrease in the Barents Sea capelin stocks. *Ornis Scand.* **21**: 179–186.
- Barrett, R.T., and Rikardsen, F. 1992. Chick growth, fledging periods and adult mass loss of Atlantic Puffins, *Fratercula arctica*, during years of prolonged food stress. *Colon. Waterbirds*, **15**: 24–32.
- Barrett, R.T., Anker-Nilssen, T., Rikardsen, F., Valde, K., Røy, N., and Vader, W. 1987. The food, growth and fledging of Norwegian Puffin chicks, *Fratercula arctica*, in 1980–1983. *Ornis Scand.* **18**: 73–83.
- Birkhead, T.R., and Nettleship, D.N. 1983. Studies of Alcids breeding at the Gannet Clusters, Labrador, 1982. Canadian Wildlife Service, Bedford Institute of Oceanography, Dartmouth, N.S.
- Birkhead, T.R., and Nettleship, D.N. 1985. Ecological relationships between Alcids at the Gannet Clusters, Labrador. Canadian Wildlife Service Publication, Ottawa, Ont.
- Birkhead, T.R., and Nettleship, D.N. 1995. Arctic fox influence on a seabird community in Labrador: a natural experiment. *Wilson Bull.* No. 107. pp. 397–576.
- Brown, R.G.B., and Nettleship, D.N. 1984. Capelin and seabirds in the Northwest Atlantic. In *Marine birds: their feeding ecology and commercial fisheries relationships*. Edited by D.N. Nettleship, G.A. Sanger, and P.F. Springer. Canadian Wildlife Service Publication, Ottawa, Ont. pp. 184–195.
- Bryant, R.L., and Jones, I.L. 1999. Food resource use and diet overlap of Common and Thick-billed Murres at the Gannet Islands. *Waterbirds*, **22**: 392–400.
- Bryant, R.L., Jones, I.L., and Hipfner, J.M. 1999. Responses to changes in prey availability by Common and Thick-billed Murres at the Gannet Islands, Labrador. *Can. J. Zool.* **77**: 1278–1287.
- Cairns, D.K. 1987. Seabirds as indicators of marine food supplies. *Biol. Oceanogr.* **5**: 261–271.
- Cairns, D.K. 1992. Population regulation of seabird colonies. In *Current ornithology*. Vol. 9. Edited by D.M. Power. Plenum Press, New York. pp. 37–61.
- Cairns, D.K., Montevecchi, W.A., and Threlfall, W. 1989. Researcher's guide to Newfoundland seabird colonies. Occas. Pap. No. 14, Memorial University of Newfoundland, St. John's, Nfld.
- Calvert, A.M., and Robertson, G.J. 2002. Using multiple abundance estimators to infer population trends in Atlantic puffins. *Can. J. Zool.* **80**: 1014–1021.
- Carscadden, J.E. 1984. Capelin in the Northwest Atlantic. In *Marine Birds: their feeding ecology and commercial fisheries relationships*. Edited by D.N. Nettleship, G.A. Sanger, and P.F. Springer. Canadian Wildlife Service Publication, Ottawa, Ont. pp. 170–183.
- Carscadden, J.E., Nakashima, B.S., and Frank, K.T. 1997. Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* **54**: 781–787.
- Carscadden, J.E., Frank, K.T., and Leggett, W.C. 2001. Ecosystem

- changes and the effects on capelin (*Mallotus villosus*), a major forage species. *Can. J. Fish. Aquat. Sci.* **58**: 73–85.
- Chardine, J.W. 1999. Population status and trends of the Atlantic Puffin in North America. *Can. Wildl. Serv. Bird Trends No.* 7.
- Frank, K.T., Carscadden, J.E., and Simon, J.E. 1996. Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. *Can. J. Fish. Aquat. Sci.* **53**: 1473–1486.
- Gaston, A.J., and Jones, I.L. 1998. *The Auks: Alcidae*. Oxford University Press, New York.
- Harris, M.P. 1978. Measurements and weights of British Puffins. *Bird Study*, **26**: 179–186.
- Harris, M.P. 1984. *The Puffin*. Poyser, Calton, U.K.
- Harris, M.P., and Hislop, J.R.G. 1978. The food of young Puffins *Fratercula arctica*. *J. Zool.* (1965–1984), **185**: 213–236.
- Harris, M.P., Murray, S., and Wanless, S. 1998. Long-term changes in breeding performance on Puffins *Fratercula arctica* on St. Kilda. *Bird Study*, **45**: 371–374.
- Hipfner, J.M., and Gaston, A.J. 1999. Timing of nest departure in the Thick-billed Murre and Razorbill: tests of Ydenberg's model. *Ecology*, **80**: 587–596.
- Hislop, J.R.G., and Harris, M.P. 1985. Recent changes in the food of young Puffins *Fratercula arctica* on the Isle of May in relation to fish stocks. *Ibis*, **127**: 234–239.
- Lock, A.R., Brown, R.G.B., and Gerriets, S.H. 1994. *Gazetteer of marine birds in Atlantic Canada: Atlas of seabird vulnerability to oil pollution*. Canadian Wildlife Service, Environmental Conservation Branch, Environment Canada, Atlantic Region, Dartmouth, N.S.
- Mann, K.H., and Drinkwater, K.F. 1994. Environmental influences on fish and shellfish production in the Northwest Atlantic. *Environ. Rev.* **2**: 16–32.
- Miller, D.S., and Lilly, G.R. 1991. Observations and studies on SA2 and Div. 3K capelin in 1990. *CAFSAC Res. Doc.* 91/11.
- Moen, S.M. 1991. Morphological and genetic variation among breeding colonies of the Atlantic Puffin (*Fratercula arctica*). *Auk*, **108**: 755–763.
- Montevecchi, W.A. 1993. Birds as indicators of change in marine prey stocks. *In Birds as monitors of environmental change*. Edited by R.W. Furness and J.J.D. Greenwood. Chapman and Hall, London, U.K. pp. 217–266.
- Montevecchi, W.A., and Piatt, J.F. 1987. Dehydration of seabird prey during transport to the colony: effects on wet weight energy densities. *Can. J. Zool.* **65**: 2822–2824.
- Nakashima, B.S. 1992. Patterns in coastal migration and stock structure of capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* **49**: 2423–2429.
- Nakashima, B.S., and Winters, G.H. 1997. Multiplicative trends of biomass cohort abundance, and recruitment of capelin, *Mallotus villosus*. *Dep. Fish. Oceans Atlantic Fish. Res. Doc.* 97/29: 168–188.
- Nettleship, D.N. 1972. Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. *Ecol. Monogr.* **42**: 239–268.
- Nettleship, D.N. 1991. The diet of Atlantic Puffin chicks in Newfoundland before and after the initiation of an international capelin fishery, 1967–1984. *In ACTA XX Congressus Internationalis Ornithologici Symposium 41*. New Zealand Ornithological Trust Board, Wellington. pp. 2263–2271.
- Regehr, H.M., and Rodway, M.S. 1999. Seabird breeding performance during two years of delayed capelin arrival in the northwest Atlantic: a multi-species comparison. *Waterbirds*, **22**: 60–67.
- Rodway, M.S., and Montevecchi, W.A. 1996. Sampling methods for assessing the diets of Atlantic puffin chicks. *Mar. Ecol. Prog. Ser.* **144**: 41–55.
- Rodway, M.S., Montevecchi, W.A., and Chardine, J.W. 1996. Effects of investigator disturbance on breeding success of Atlantic Puffins, *Fratercula arctica*. *Biol. Conserv.* **76**: 311–319.
- Rodway, M.S., Chardine, J.W., and Montevecchi, W.A. 1998. Intracolony variation in breeding performance of Atlantic Puffins. *Colon. Waterbirds*, **21**: 171–184.
- Rose, G. 1999. *Great Auk Lecture Series*. Memorial University of Newfoundland, St. John's, Nfld.
- Russell, J. 1999. Chick diet and nestling condition among Atlantic Puffins at three Northwest Atlantic colonies. M.Sc. thesis, Memorial University of Newfoundland, St. John's, Nfld.
- Schneider, D., and Hunt, G.L., Jr. 1984. Comparison of seabird diets foraging distribution around the Pribilof Islands, Alaska. D.N. *In Marine birds: their feeding ecology and commercial fisheries relationships*. Edited by D.N. Nettleship, G.A. Sanger, and P.F. Springer. Canadian Wildlife Service Publication, Ottawa, Ont. pp. 86–95.
- Ydenberg, R.C. 1989. Growth–mortality trade-offs and the evolution of juvenile life histories in the Alcidae. *Ecology*, **70**: 1494–1506.
- Ydenberg, R.C., Clark, C.W., and Harfenist, A. 1995. Intraspecific fledging mass variation in the Alcidae, with special reference to the seasonal fledging mass decline. *Am. Nat.* **145**: 412–433.
- Zar, J.H. 1984. *Biostatistical analysis*. 2nd ed. Prentice Hall Inc., Englewood Cliffs, N.J.

## Appendix A

**Table A1.** List of prey taxa encountered in the diet of Atlantic Puffin (*Fratercula arctica*) chicks.

Common name	Latin name
Capelin	<i>Mallotus villosus</i>
Sandlance	<i>Ammodytes</i> sp. and (or) <i>Ammodytes americanus</i>
Arctic cod	<i>Boreogadus saida</i>
Blenny	Blenniidae
Sculpin (3–4 spp.)	Cottidae
Alligatorfish (2 spp.)	<i>Aspidophoroides monoptyerygius</i> and (or) <i>Leptagonus decagonus</i>
Hake (2 spp.)	<i>Urophycis tenuis</i> , <i>Urophycis chuss</i>
Daubed shanny	<i>Lumpenus maculatus</i>
Flatfish	Pleuronectiformes
Lumpfish	<i>Cyclopterus lumpus</i>
Snailfish	<i>Liparus</i> sp.
Squid (2 spp.)	<i>Illex illecebrosus</i> , <i>Loligo</i> sp.
Pteropod	<i>Cavelinia</i> sp.
Polychaete	<i>Harmothoe imbricata</i>
Amphipod (2–3 spp.)	Gammaridae
Mysopod	Mysidae
Krill	Euphasidae