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# Response of Atlantic Puffins to a Decline in Capelin Abundance at the Gannet Islands, Labrador

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**Abstract.**—In eastern Canada during the early 1990s, a shift in the distribution of Capelin (*Mallotus villosus*) resulted in a prolonged absence (at least 8 years) of the preferred prey for the Atlantic Puffin (*Fratercula arctica*) breeding at Gannet Islands, Labrador. It has been documented that there is no suitable alternative prey to Capelin in the northwest Atlantic for seabirds, thus these extreme changes in food supply may have negative effects on reproduction and adult survivorship. In this study, foraging behavior, chick growth and productivity of Atlantic Puffins at the Gannet Islands, Labrador during 1996-1998 were compared to data in a study undertaken in 1981-1983, prior to the decline in Capelin abundance. It was confirmed that the dramatic change in Capelin abundance was reflected in chick diet as Atlantic Puffin chicks received 50-70% (by mass) less Capelin in 1996-1998 than in 1981-1983. Hatch dates did not differ among decades and breeding success, chick wing growth and fledge mass were unaffected. The only breeding parameter significantly affected by the change in food supply was chick growth (mass gain). Taken together, our data indicated that following a decline in Capelin abundance, the Atlantic Puffin did not experience breeding failure and effectively reared young utilizing suitable alternative prey which included post-larval sand lance and other small fish and invertebrates. Received 24 November 2002, accepted 6 December 2003.

**Key words.**— Atlantic Puffin, *Fratercula arctica*, Capelin, *Mallotus villosus*, chick diet, productivity, chick growth, Labrador.

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Capelin (*Mallotus villosus*), a schooling migratory smelt, has been considered the preferred prey of chick-rearing Atlantic Puffins (*Fratercula arctica*) and central to marine food-web energetics models in Newfoundland and Labrador, eastern Canada (Brown and Nettleship 1984; Carscadden 1984; Gaston and Jones 1998). Capelin are generally abundant in northwest Atlantic waters from Hudson Bay to Greenland and are a circumpolar species (Bigelow and Schroeder 2002a). Puffins that breed in Labrador (Birkhead and Nettleship 1983, 1985), Nunavut (Robards *et al.* 2000) and the Barents Sea (Anker-Nilssen 1987; Barrett *et al.* 1987; Anker-Nilssen and Lorensten 1990) are known to forage on Capelin. Nonetheless, many Atlantic Puffin breeding colonies are located beyond the southern boundaries of Capelin distribution. Puffins breeding in Maine and Nova Scotia harvest mainly Herring (*Clupea harengus*), Hake (*Urophycis* spp., *Merluccius* spp.) and sand lance (= sandeel, *Ammodytes* spp.; Lowther *et al.* 2002). From south Norway to Brittany (Lowther *et al.* 2002) breeding puffins forage mainly on Herring, Sprat (*Sprattus sprattus*) and sandeel (*Ammodytes*

*marinus*; Harris and Hislop 1978; Harris 1984; Harris and Bailey 1992). Despite the broad and varied range of prey types that puffins harvest in other geographical locations, Brown and Nettleship (1984) indicated that there was no alternative prey to Capelin for piscivorous seabirds in Newfoundland and Labrador and without Capelin, breeding failure and even high adult mortality is inevitable. In contrast, Russell (1999) showed that at several colonies in insular Newfoundland, puffins successfully reared nestlings on diets with a highly variable contribution of Capelin (Russell 1999). However, prolonged scarcity of main prey has been shown to have negative affects on Atlantic Puffins (Harris and Hislop 1978; Brown and Nettleship 1984; Anker-Nilssen 1987; Barrett *et al.* 1987; Nettleship 1991; Barrett and Rikardsen 1992). In Norway, a continuous 22-year period of low Herring abundance and the absence of suitable alternative prey were responsible for complete breeding failure of Atlantic Puffins (Anker-Nilssen 1987; Barrett *et al.* 1987; Barrett and Rikardsen 1992). In the North Sea, declines in Sprat abundance may have caused reduction in adult survival rates

though breeding success at the colonies remained high (Harris and Bailey 1992). In 1981, at Witless Bay, Newfoundland, reproductive failure of puffins was attributed to a shortage of prey due to a large-scale international Capelin fishery (Nettleship 1991).

During the late 1980s, Capelin off Labrador exhibited a population shift south and offshore beyond the summer foraging range of the Gannet Islands puffin colony (Miller and Lilly 1991; Mann and Drinkwater 1994). This event was believed to be associated with a cold ocean water event that began in the late 1980s (Drinkwater 1996; Frank *et al.* 1996; Anderson *et al.* 2002; Carscadden *et al.* 2002). Spawning aggregations were delayed and then in 1992 Capelin ceased to spawn on the south and central coast of Labrador (Rose 1999; Anderson *et al.* 2002). This study is the first to investigate Atlantic Puffin response to declines of Capelin stocks in Labrador. Composition of Atlantic Puffin chick diet, fish size, timing of breeding, productivity, chick growth and fledge mass at the Gannet Islands, Labrador in 1997 and 1998 were incorporated with data collected in 1996 from this colony by colleagues and compared to findings on puffin prey selection and reproduction in 1981, 1982 and 1983 when Capelin were plentiful (Birkhead and Nettleship 1985). Based on the opportunity provided by the decrease in Capelin abundance along the south Labrador coast between the early 1980s and the late 1990s, we evaluated two alternative hypotheses: a) that Atlantic Puffins at the Gannet Islands would experience breeding failure in the absence of Capelin, or b) that puffins would maintain their moderate to high breeding success by switching to alternative prey.

#### STUDY AREA AND METHODS

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

Methods in this study were based on those employed by T. R. Birkhead and D. N. Nettleship during 1981-1983 in a similar study at the Gannet Islands, Labrador. Where methods differed, they are explained below. Data in electronic form for 1981 and 1982 were not available, thus it is clearly footnoted in the Tables where these data were not included in ANOVAs. Data for 1983, on chick growth and fish size only, were available for re-analysis and used in ANOVAs (see footnotes in Tables). All other 1981-1983 findings were taken directly from the text of Canadian Wildlife Service reports (Birkhead and Nettleship 1983, 1985). In some cases, data from 1981-1983 could not be included in the inter-decadal comparisons as results were not published or methods varied too greatly among studies for comparison.

#### Timing of Breeding and Productivity

During 1996-1998, a sample of 60-120 burrows each year was checked every three days, beginning when adult puffins were first observed delivering meals to chicks. Burrow contents were recorded as "egg", "chick" or "empty". Hatch and fledge dates for individual chicks were determined to within two days of age from the midpoint between burrow visits (Birkhead and Nettleship 1983). Fledge dates may have been underestimated in the late 1990s because investigators left the breeding colony by 22 September, before the last chicks fledged, whereas T. N. Birkhead and D. N. Nettleship remained on the colony two to 17 days longer, except in 1981 when they left on 6 September. For chicks that reached peak mass before we left the colony in the 1990s, the relationship between peak mass and fledge date for known-age chicks was used to estimate fledge date (Birkhead and Nettleship 1985; Baillie 2001). Medians for hatch and fledge date were used to facilitate comparison with other studies as they represent central tendency of skewed distribution better than the mean (Sokal and Rohlf 1995). Hatch success was determined as the percentage of chicks that hatched from eggs. Fledge success was estimated as the percentage of chicks that reached 31 days of age. The mathematical product of proportionate hatch and fledge success was used to calculate overall breeding success. No breeding success data was available for 1981 and only overall breeding success and sample size were available for 1983.

#### Chick Growth

Body mass of 60-120 regularly visited chicks was measured to the nearest 2 g with a 600 g Pesola scale. Flattened wing chord was measured to the nearest mm, excluding downy feathers and including the emerging feather shaft (except in 1996, when emerging feather shaft was not measured). Growth patterns of puffin chicks in all study years did not consistently fit conventional growth equations such as logistic curve or Gompertz equation. As an alternative method, linear growth rate (the rate at which mass and wing length gain was linearly dependent on chick age) was determined by eliminating the upper and lower ages of the linear regression curve until residuals first became linear. In all study years, linear growth occurred between chick age 13 and 25 days. The slope of the linear equation for each chick was used to estimate growth rate. Wing growth rates for 1996 were excluded from analyses as a different wing measurement technique was used.

Chick Diet

During August and September 1996-98, chick meals were collected from adult puffins using a 3 m net-pole, a large 12 × 24 m nylon monofilament barrier net with 5 cm mesh and by using a fleg. Prey samples were placed in plastic bags and either measured immediately or frozen. Upon capture, puffins were marked with numbered stainless steel leg bands to ensure that bill-loads were collected from each individual only once. In 1997 and 1998, the total length of each fish was recorded to the nearest 0.5 mm. Prey items, including invertebrates, were individually weighed to the nearest 0.1 g using an electronic balance. In 1996, I. L. Jones (during August), M. Hipfner and T. Roberts (during early September) collected puffin chick diet samples. They measured larger prey items immediately and preserved bill-loads containing smaller items in 70% isopropyl alcohol. In 1998, bill-loads collected in 1996 were re-measured and because specimens stored in alcohol weighed less and were shorter than when fresh, a conversion factor for each species and size class was devised from fish with known fresh mass and lengths.

Methods for bill-load sampling differed among decades. T. R. Birkhead and D. N. Nettleship quantified average bill-load mass and content based on visual records of bill-loads being delivered to chicks (Birkhead and Nettleship 1985). To collect and determine fish sizes, they used a fleg (as in this study) and collected prey items from grass in the vicinity of burrows (Birkhead and Nettleship 1985). All percent data in this study were arcsine transformed for parametric statistical tests to produce normality.

RESULTS

Timing of Breeding and Productivity

Median hatch during 1996-1998 was similar to that in 1981-1983, as reported by Birkhead and Nettleship (1985), with a maximum difference of 5 days (Table 1).

However, fledging dates in the late 1990s were at least 8-12 d later than the 1980s. During 1996-1998 at the Gannet Islands, there was no significant difference in mean hatch date of Atlantic Puffin chicks (7 Aug. ± 5 d (112), 7 Aug. ± 5 d (39) and 6 Aug. ± 4 d (82), respectively;  $F_{2,230} = 0.7$ , n.s.).

Hatch success was significantly different among study years 1982, 1996, 1997 and 1998 ( $\chi^2_3 = 12.7$ ,  $P < 0.005$ ; Table 1). When 1997 is excluded from the test, we found no significant difference in hatch success in 1982, 1996 and 1998 ( $\chi^2_2 = 3.8$ , n.s.). There was no significant difference in fledge success between available 1980s estimates and the 1990s ( $\chi^2_3 = 2.6$ , n.s.). Fledge success estimates in 1997-1998 were similar to 1982-1983 and the data indicate that the overall breeding success estimate in 1983 was similar to that in 1982, 1997 and 1998 (Table 1). The low overall breeding estimate in 1996 was attributed to low hatch success in that year.

Chick Growth

Chick growth (mass gain) during the linear phase (13-25 d) was significantly highest in 1983 among study years 1983, 1996, 1997 and 1998 (Table 2). Findings reported by Birkhead and Nettleship (1985) showed that growth rates in 1981-1982 (calibrated for linear phase growth with a simple conversion factor based on 1983 data) also were higher

**Table 1. Comparison of Atlantic Puffin breeding phenology and productivity estimates at the Gannet Islands, Labrador during the 1980s and 1990s. See footnotes for sources of the following data. Productivity values are means ± SE (represented as percentages).**

	1981†	1982	1983†	1996*	1997*	1998*
Median lay date	23 June	30 June†	30 June	26 June	27 June	26 June
Median hatch date	1 Aug.	9 Aug.†	2 Aug.	5 Aug.	6 Aug.	5 Aug.
Median fledge date	9 Sept.	18 Sept.†	12 Sept.	20 Sept.	21 Sept.	17 Sept.
No. eggs	—	88††	62	82	38	40
No. eggs that hatched	—	58††	—	42	32	24
Hatching success (%)	—	66 ± 5.1	—	51 ± 5.6	84 ± 6.0	60 ± 7.8
No. chicks	—	58††	—	112	42	85
No. fledged chicks	—	31††	22	47	19	43
Fledging success (%)	—	53 ± 6.6	—	42 ± 4.7	45 ± 7.8	51 ± 5.5
Overall success (%)	—	35 ± 5.1	36 ± 6.1	21 ± 3.4	38 ± 7.1	31 ± 5.2

††Taken from Birkhead and Nettleship 1983.  
†Taken from Birkhead and Nettleship 1985; hatching and fledging success not reported.  
\*Taken from Baillie and Jones 2003.

**Table 2. Comparison of mean daily growth rates (grams/day) and growth parameters (g) of Atlantic Puffin chicks at the Gannet Islands, Labrador in the early 1980s and late 1990s. Values are means  $\pm$  SD (N); where N = number of chicks. Matching subscripts show where the Bonferroni post hoc examinations did not find a statistically significant difference.**

	Chick growth rate	Peak mass	Fledge mass
Mass (g)			
1981†	11.4	—	—
1982†	13.0	—	361.9 $\pm$ 37.3 (79)
1983*	12.1 $\pm$ 3.1 (29) <sub>a</sub>	400.3 $\pm$ 28.9 (35) <sub>a</sub>	362.3 $\pm$ 34.4 (34) <sub>a</sub>
1996	7.1 $\pm$ 2.8 (40) <sub>b</sub>	290.4 $\pm$ 34.6 (29) <sub>b</sub>	295.5 $\pm$ 5.0 (2) <sub>b</sub>
1997	9.0 $\pm$ 1.8 (18) <sub>c</sub>	370.3 $\pm$ 24.8 (20) <sub>c</sub>	344.3 $\pm$ 25.0 (14) <sub>a</sub>
1998	9.4 $\pm$ 2.2 (35) <sub>c</sub>	345.5 $\pm$ 39.1 (41) <sub>d</sub>	348.0 $\pm$ 15.2 (5) <sub>a</sub>
ANOVA results	$F_{3,118} = 21.1, P < 0.001$	$F_{3,121} = 60.0, P < 0.001$	$F_{3,51} = 3.8, P < 0.02$
Wing length (mm)			
1983*	4.0 $\pm$ 0.7 (29) <sub>a</sub>	128.4 $\pm$ 9.7 (33) <sub>a</sub>	142.6 $\pm$ 5.0 (30) <sub>a</sub>
1996	—	120.0 $\pm$ 21.8 (29) <sub>b</sub>	142.5 $\pm$ 2.1 (2) <sub>a</sub>
1997	3.9 $\pm$ 0.3 (18) <sub>a</sub>	133.1 $\pm$ 7.1 (20) <sub>a</sub>	141.4 $\pm$ 4.5 (14) <sub>a</sub>
1998	4.1 $\pm$ 0.4 (35) <sub>a</sub>	126.6 $\pm$ 9.1 (41) <sub>a</sub>	141.8 $\pm$ 4.9 (5) <sub>a</sub>
ANOVA results	$F_{2,114} = 0.3, n.s.$	$F_{3,119} = 4.3, P < 0.001$	$F_{3,49} = 0.2, n.s.$

†Taken from Birkhead and Nettleship 1985. Not available for statistical analyses.

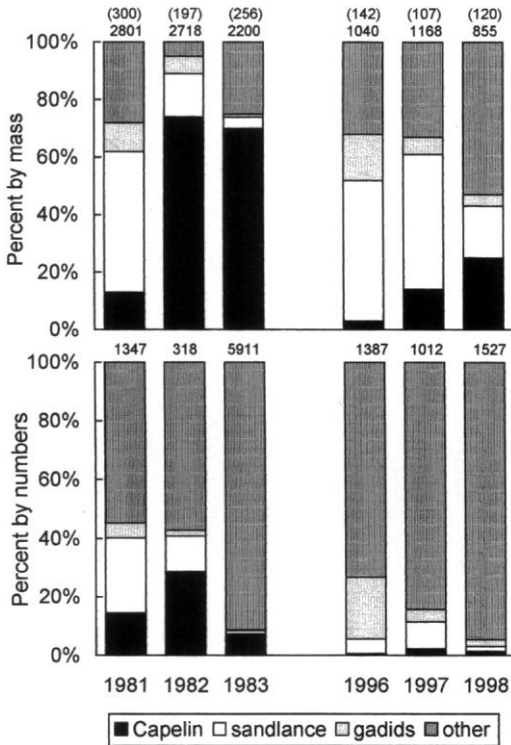
\*Re-analyzed data collected by D. N. Nettleship and T. R. Birkhead.

than those during 1996-1998. Conversely, rate of wing length growth in the 1990s was not statistically different from the 1980s (1996 was excluded from analyses due to a different wing measurement technique in this study year). Peak mass was highly and significantly variable among study years and mean mass estimates were highest in 1983 and lowest in 1996. Again, wing length at peak mass was similar among 1983, 1997 and 1998, yet significantly lowest in 1996. Though fledge masses were higher in 1982 and 1983, these differences were not significant as statistical analyses among study years 1983 and 1996-1998 show that only in 1996 was fledge mass significantly lower (Table 2). Chicks that fledged in 1996 weighed 67.2 g (23%) less than chicks in 1983. Fledging mass, as a percentage of adult body mass (puffin adult body mass 1981-1983:  $467 \pm 15.2$  g (231) and 1996-1998:  $468 \pm 35.1$  g (401)), was 78% in both 1982 and 1983 (Birkhead and Nettleship 1985), 74% during both 1997 and 1998, and 63% in 1996. Age at which chicks fledged in 1982 and 1983,  $41.2 \pm 2.7$  d (26) and  $44.9 \pm 2.1$  d (30), respectively, was similar to those in 1996,

1997 and 1998, 45 d (2),  $43.9 \pm 2.3$  d (10) and  $41.7 \pm 1.5$  d (3). Age at which chicks fledged was not significantly dependent on linear rate of chick mass gain ( $t_3 = 0.8, n.s.$ ).

### Prey Composition and Daily Food Intake

Adult puffins annually delivered lower proportions of Capelin (by mass) to chicks during 1996, 1997 and 1998 (3%, 14% and 25% respectively) than in 1981, 1982 and 1983 (13%, 74% and 70%, respectively; Fig. 1). During 1996-1998, Capelin numbers did not exceed 2% of total number of fish yet ranged from 7% to 29% during 1981-1983. Over the six study years, sandlance dominated the chick diet when Capelin did not, except during 1998 when small (20-30 mm) Blenniidae and Cottidae (53% by mass, 95% by numbers) dominated chick diet. In 1981, 1996 and 1997, post-larval sandlance comprised 47% to 49% (by mass) of chick diet. Sandlance comprised 12% to 26% by numbers of chick diet in 1981-1983 and only 2% to 9% by numbers in 1996-1998. A bewildering array of small forage fishes (20 to 89 mm in length) and several benthic and pelagic



**Figure 1.** Composition of Atlantic Puffin chick diet (% by mass and % by numbers) at the Gannet Islands in the early 1980s and late 1990s. Total mass (g) of prey items (number of bill-loads in parentheses) and total number of prey items are displayed above each bar for percent mass and frequency, respectively.

invertebrates including squid, polychaetes, pterapods and crustaceans were utilized by puffins during 1981-1983 (55% to 91% by numbers) and 1996-1998 (73% to 95% by numbers). It was apparent that Arctic Cod (*Boreogadus saida*) was the least important prey category in this study and contributed from 2% to 16% by mass and 0% to 20% by numbers to chick diet in any given year (Fig. 1). Mature Capelin (>100 mm in length) delivered to puffin chicks were significantly larger in 1983 than in 1996, 1997 and 1998 (Table 3). Though statistical tests could not be performed on 1981-1982 results, the data show that individual Capelin were larger in mass in 1983 than in 1981 and 1982. Mass and length of sandlance collected from puffins in 1983, 1996, 1997 and 1998 did not vary significantly (Table 3).

Despite the high variability in chick diet composition, the data showed little variation

during 1980s and 1990s in bill-load size, feeding rates and daily food intake values (Table 4). As the raw data for the 1980s were not available, ANOVA testing was limited to the late 1990s. Among the late 1990s, bill-load mass varied significantly ( $F_{2,142} = 4.4$ ,  $P < 0.02$ ) and *post hoc* examinations showed that load mass in 1996 was significantly lower than in 1997 but not 1998 (see Table 4). There was no statistical difference in items per bill-load among the 1990s ( $F_{2,141} = 2.1$ , n.s.). Estimated daily food intake values ranged from 45 to 57 (g/day) in any given year.

### Relationship Between Chick Diet and Breeding Parameters

Breeding success in 1982-1983 and 1996-1998, was not significantly dependent on percent Capelin in the chick diet ( $t_3 = 1.1$ , n.s.). Similarly fledge mass (expressed as percentage of adult mass) did not vary significantly among years 1981-1983 and 1996-1998 ( $t_4 = 2.3$ , n.s.; Fig. 2). Chick growth (g/day) varied significantly and positively with percent of Capelin in chick diet ( $y = 8.5 + 5.2x$ ;  $r^2 = 0.07$ ,  $t_4 = 2.9$ ,  $P < 0.05$ ). There was no statistically significant relationship between the mean mass of Atlantic Puffin chick meals and the proportion of Capelin (by mass) in the diet during 1981-1983 and 1996-1998 ( $t_4 = 0.6$ , n.s.). Consequently, when regressed against mean bill-load mass, mean chick growth (by mass) was not significantly dependent on meal size ( $t_4 = 2.1$ , n.s.).

### DISCUSSION

A dramatic decrease of 50% to 70% (by mass) in the contribution of Capelin to Atlantic Puffin chick diet at a southern Labrador colony from 1981-83 to 1996-98 was confirmed in this study. Thus, puffin chick diet reflected the broad-scale Capelin distribution shift in Labrador (Miller and Lilly 1991; Mann and Drinkwater 1994; Anderson *et al.* 2002; Carscadden *et al.* 2002), which supported suggestions that seabirds may be good indicators of changes in marine prey (Cairns 1987; Montevecchi 1993; Montevecchi and Myers 1996; Barrett 2002). However,

**Table 3. Inter-annual variation in size of Capelin and sandlance fed to Atlantic Puffin chicks at the Gannet Islands, Labrador in the early 1980s and late 1990s. Values are means  $\pm$  SD (N); where N = number of fish. Matching subscripts show where the Bonferroni post hoc examinations did not find a statistically significant difference.**

		Fish mass (g)	Total fish length (mm)
Capelin	1981†	10.4 $\pm$ 7.5 (86)	—
	1982†	9.9 $\pm$ 2.0 (117)	128.0 $\pm$ 2.1 (117)
	1983*	15.4 $\pm$ 5.3 (209) <sub>a</sub>	154.0 $\pm$ 16.1 (215) <sub>a</sub>
	1996	9.8 $\pm$ 2.4 (3) <sub>b</sub>	132.3 $\pm$ 10.2 (3) <sub>b,c</sub>
	1997	9.8 $\pm$ 3.5 (15) <sub>b</sub>	135.4 $\pm$ 19.0 (15) <sub>b</sub>
	1998	11.6 $\pm$ 2.3 (17) <sub>b</sub>	143.1 $\pm$ 11.0 (17) <sub>c</sub>
ANOVA results		$F_{3,250} = 21.3, P < 0.001$	$F_{3,254} = 30.6, P < 0.001$
Sandlance	1981†	7.4 $\pm$ 1.9 (5)	—
	1982†	4.6 $\pm$ 3.6 (63)	111 $\pm$ 35.0 (63)
	1983*	5.9 $\pm$ 2.4 (30) <sub>a</sub>	129.1 $\pm$ 16.5 (30) <sub>a</sub>
	1996	6.8 $\pm$ 2.7 (68) <sub>a</sub>	132.4 $\pm$ 18.5 (68) <sub>a</sub>
	1997	6.5 $\pm$ 2.6 (81) <sub>a</sub>	126.9 $\pm$ 17.1 (85) <sub>a</sub>
	1998	6.4 $\pm$ 2.8 (24) <sub>a</sub>	127.6 $\pm$ 18.1 (24) <sub>a</sub>
ANOVA results		$F_{3,215} = 1.1, n.s.$	$F_{3,216} = 1.8, n.s.$

†Taken from Birkhead and Nettleship 1985. Not available for statistical analyses.

\*Re-analyzed data collected by D. N. Nettleship and T. R. Birkhead.

as shown below, Atlantic Puffin breeding parameters do not necessarily indicate extreme changes in food supply. In this study, puffins exhibited an ability to prey switch. During two of six study years (1982 and 1983) Capelin dominated puffin chick diet. Sandlance was dominant in three of six years (1981, 1996 and 1997) and in one year (1998), small, miscellaneous fish (20-30 mm in length) and invertebrates dominated puffin chick diets.

Despite the high variability in Atlantic Puffin chick diet at the Gannet Islands during 1981-1983 and 1996-1998, breeding success was not significantly lower in the late 1990s. Even in 1998, when small miscellaneous fish mainly formed chick diet, breed-

ing success did not respond to the change in chick diet. Puffins successfully reared young to fledging in the late 1990s, thus our findings did not support the hypothesis that a prolonged absence of Capelin in Labrador caused breeding failure. In the late 1990s, adult mass (Baillie and Jones 2003), timing of hatch, chick wing growth and chick fledge mass were not affected by the change in food supply and daily food intake of puffin nestlings appeared to be similar to or better than during the 1980s. Timing of fledge dates were delayed by 8-12 days in the 1990s, however, the age at which chicks fledged did not vary statistically among decades. Fledge dates may have been underestimated in the late 1990s because investigators left the

**Table 4. Comparison of Atlantic Puffin chick meal size and feeding rates at the Gannet Islands between 29 August and 15 September in all years. Values are means  $\pm$  SD, where SD was available. Matching subscripts for bill-load size show where the ANOVA Bonferroni post-hoc examinations did not find a statistically significant difference.**

Bill-load size				Feeding rates and daily food intake			
	No. loads	Mass (g)	Items/load	No. chicks	No. days	Feeds/day	g/day
1982†	100	14.8	—	19	2	3.1 $\pm$ 0.2	46
1983†	181	12.4	—	28	3	4.3 $\pm$ 0.9	56
1996	61	9.6 $\pm$ 7.7 <sub>a</sub>	13.8 $\pm$ 11.5 <sub>a</sub>	—	—	—	—
1997	48	14.1 $\pm$ 8.1 <sub>b</sub>	9.8 $\pm$ 9.4 <sub>a</sub>	33	3	3.2 $\pm$ 0.4	45
1998	36	12.1 $\pm$ 6.5 <sub>a,b</sub>	12.1 $\pm$ 10.2 <sub>a</sub>	20	2	4.7 $\pm$ 0.8	57

†Taken from Birkhead and Nettleship 1985. Not available for statistical analyses.

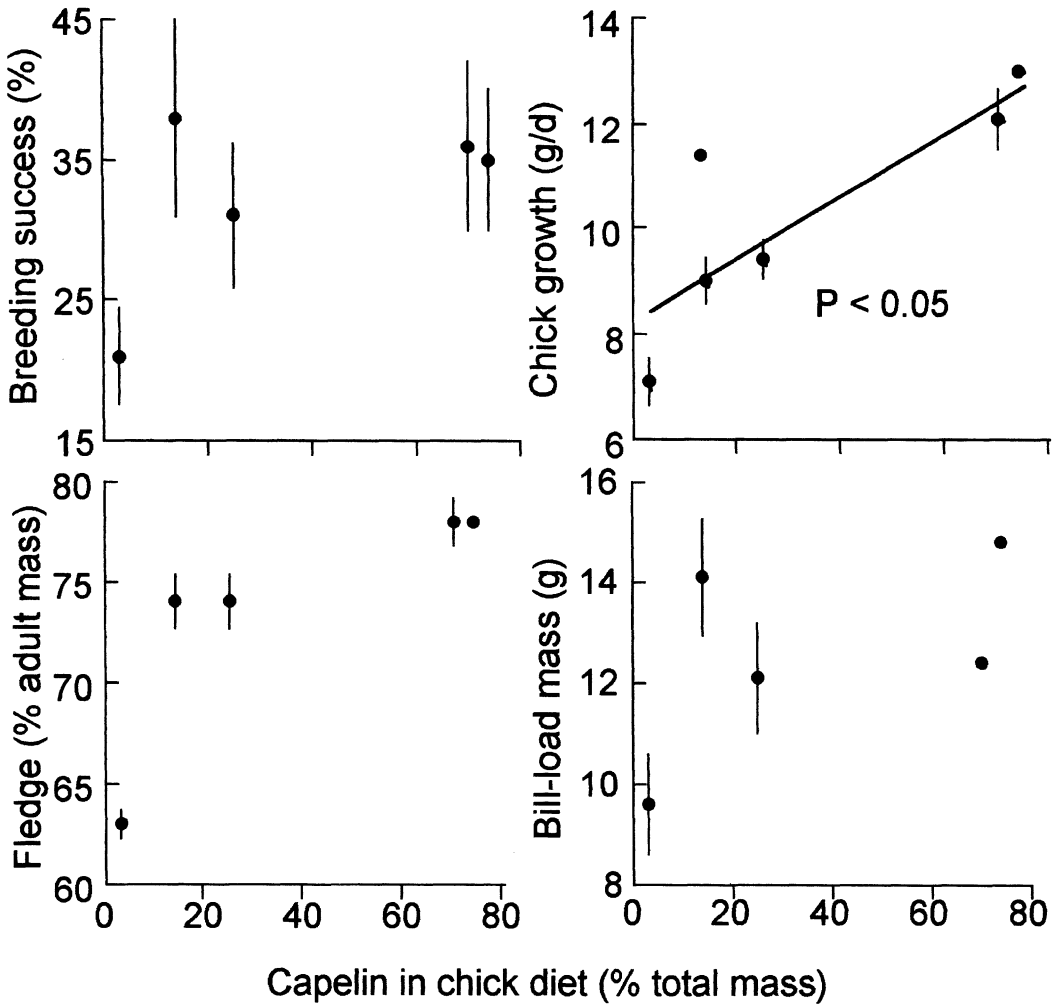


Figure 2. Relationship between means ( $\pm$ SE) of feeding and breeding parameters of Atlantic Puffins at the Gannet Islands and the amount of Capelin in chick diet during 1981-1983 and 1996-1998. In some cases SE was not available for 1980s data (see Tables 2-4).

breeding colony earlier than in the 1980s and before all chicks fledged.

Atlantic Puffin breeding parameters may not be good indicators of marine prey shifts as parent puffins appear able to buffer the effects of food stress on chicks by harvesting more frequently with little visible cost to the adult puffins (Barrett and Furness 1990; Cairns 1992; Russell 1999; Barrett and Krasnov 2002). It appears that chick growth (by mass) was clearly the most sensitive breeding parameter in this study to changes in food supply. This parameter exhibited a significant response as chicks gained mass at slower rates in the late 1990s than in the early 1980s. Tak-

en together, findings in this study supported the alternate hypothesis that puffins would maintain their moderate to high breeding success by switching to alternative prey.

The more easily a prey species can be obtained (and not necessarily the energetic value of the individual fish) is likely to determine which prey species Atlantic Puffins prefer (Barrett 2002). When Capelin schools are not in the vicinity of breeding seabird colonies during chick-rearing, a suitable alternative prey species must be fed to nestlings to prevent starvation and breeding failure. Plausible alternative prey species in the northwest Atlantic are two sandlance species



(*Ammodytes americanus* and *A. dubius*), which occur from Chesapeake Bay, Maryland, to northern Labrador (Bigelow and Schroeder 2002b). However, identification of fresh specimens is problematic and little is known about differences in biology between these two species. Sandlance is a non-commercial fish species in North America, generally known to form large near-shore spawning aggregations in shallow water (Bigelow and Schroeder 2002b) and post-larval fish are a high quality diet item for seabirds (Russell 1999; Baillie and Jones 2003). Robards *et al.* (2000) reported that puffin chicks at Coburg Island, Nunavut were fed mainly sandlance. At many colonies in the North Sea (Harris and Hislop 1978; Harris and Bailey 1992), around the United Kingdom (Ashcroft 1979; Harris *et al.* 1998), the Faeroes (Stempniewicz and Iliszko 2002), south Norway (Barrett *et al.* 1987) and Barents Sea (Barrett and Furness 1990; Barrett and Krasnov 1996) seabirds heavily rely on the other important species of sandlance, the Lesser Sandeel (*Ammodytes marinus*). In Newfoundland and Labrador, sandlance were abundant throughout the range of Capelin during the 1990s (Anderson *et al.* 2002). Despite a decrease in the size of Capelin fed to puffin chicks from the 1980s to the 1990s, there was no change in post-larval sandlance morphometrics. Evidence in this study, and the fact that puffins are usually very successful when feeding regularly and extensively on sandlance in other regions, shows that sandlance are a suitable alternative prey to Capelin in Newfoundland and Labrador.

It was suspected that the low breeding performance in 1996 was not solely related to poor Capelin or food conditions (Cairns 1987). A higher level of investigator disturbance at burrows in 1996 (Rodway *et al.* 1996; Baillie 2001), late ice and the presence of the Arctic Fox (*Alopex lagopus*) may have caused decreased burrow attendance of parents and survival rates of chicks (Cairns 1985; Nettleship and Birkhead 1995; Craik 1997; Robertson and Elliot 2002). Additionally, Robertson and Elliot (2002) found that numbers of Gannet Islands breeding Atlantic Puffins declined by 23% between 1983 and 2000. A

clear explanation for this decline is lacking, but possible reasons include changes in food availability at breeding and wintering areas, and predation by the Arctic Fox, which were active at this colony during the early 1990s (Birkhead and Nettleship 1995). Harris and Bailey (1992) showed that after a change in Sprat distribution, Atlantic Puffin adult survivorship declined, though breeding success remained high. Further study on adult puffin survivorship at the Gannet Islands, Labrador is warranted and a long-term demographic study has been initiated.

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