

Atlantic Puffin *Fratercula arctica* chick growth in relation to food load composition

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Abstract

Despite a long-term (1989–2013) reduction in size of fish brought to Atlantic Puffin *Fratercula arctica* chicks and a parallel increase in numbers of fish in the food loads, there was no evidence of changes in chick growth rates at Hornøya, NE Norway. Recent declines in chick survival and cessation in population growth suggest, however, that environmental conditions have changed to an extent that breeding success is now compromised.

Introduction

Adult seabirds generally feed their chicks an energy-rich, high quality diet, but quantities and quality can vary tremendously in relation to the availability of suitable prey, often resulting in large differences in growth rates of the chicks (Visser 2002). Atlantic Puffins *Fratercula arctica* (hereafter 'Puffins') feed their chicks on a wide diversity of fish that they carry back to the nest in the beak. Although > 50 fish species plus some invertebrates have been recorded worldwide (Harris & Wanless 2011), at any one colony prey often consists of one or two energy-rich species such as sandeels *Ammodytes* sp., Capelin *Mallotus villosus* or clupeids *Clupeidae* sp. (e.g. Barrett 2002; Baillie & Jones 2004; Harris & Wanless 2011). Numbers of fish in loads delivered to chicks in Norway vary from one large fish to tens of small larvae or self-feeding post-larvae (Figure 1; Barrett *et al.* 1987). Because the mass and energy content of fish increases approximately with length³, a diet consisting of large numbers of small fish in a load is considered a poor alternative to a few large fish and is often associated with reduced chick growth, extended fledging periods and ultimately breeding failure (Anker-Nilssen 1987; Martin 1989; Barrett & Rikardsen 1992; Barrett 2002; Harris & Wanless 2011).

Long-term changes in food load characteristics are not uncommon (e.g. Martin 1989; Baillie & Jones 2004; Harris & Wanless 2011; Miles *et al.* 2015), and a 21-year (1980–2000) study of Puffins at Hornøya, NE Norway (70°23'N 31°09'E) documented a gradual change in chick diet and signs of a deterioration in feeding conditions through increases in numbers of small fish in beak loads (Barrett 2002). A supplementary feeding experiment in 2003 failed, however, to reveal any difference in mass growth rate between extra-fed chicks and control chicks (Dahl *et al.* 2005). Assuming 2003 was representative of the time period, this suggested

that the overall amount and quality of food delivered by their parents over the two decades remained sufficient to maintain normal growth presumably through compensatory behaviour by the adults (Barrett 2002; Eilertsen *et al.* 2008). Until the time of the experiment (2003), this was corroborated by a relatively high rate of chick survival (> 80%) and a steady increase in numbers of occupied Puffin burrows in the colony. Since then conditions seem to have deteriorated further with an evident decline in chick survival (see below) and an apparent culmination of the population increase around 2000 (The National Seabird Monitoring Programme, www.seapop.no).

Using a further 13 years of data, this study addresses the effect of a long-term change in diet (species composition, fish size and number) on the growth and survival rates of Puffin chicks on Hornøya, and tests the association between increases in numbers of fish/load and reduced chick growth (Harris & Wanless 2011).

Methods

Chick food: Each year 1989–2013, diet was assessed by observing loads of fish held by adults using 10 x 40 binoculars. Where possible the number of fish in each bill load was counted and the species composition was identified. In addition, the lengths of the fish were estimated as multiples of the straight bill length of the adult bird (c. 30 mm). In most years a few food samples were also collected as found in burrow entrances or by catching fish-carrying adults with a noose pole. Such loads were used as controls for the visual identification and estimates of numbers and sizes of prey items. This method appears to give a good representation of the diet (Eilertsen *et al.* 2008). The mass of individual items was then calculated from observed lengths (in relation to bill length) based on length/mass relationships determined from the control samples. Data for 1991 were excluded from the analyses because food samples in that year were collected on two days only. For the remaining years, data were collected on at least 8 days spread over the first two thirds of the chick-rearing period (Barrett 2002). All means are given \pm 1 SE.

Chick growth and survival: Growth rates (mass gain g d^{-1} or wing growth mm d^{-1}) were estimated by dividing the change in body mass or wing length by the time interval between measurements made every 5–15 d of chicks in 30–40 control nests. Using wing-length as a proxy for age, these estimates were restricted to measurements made in the linear phases of growth from hatching to an age when wing length = 120 mm for mass gain and 130 mm for wing growth (see Figure 1 in Eilertsen *et al.* 2008). More details are given in Barrett (2002).

Chick survival was determined as the number of chicks hatched that survived until the last inspection day of the field season, by which time a mean of $71.7 \pm 4.1\%$ (range 31–100%) of the surviving chicks had reached the age of 20 d. Survival data from 2011 and 2012 (< 30%) were excluded from the analyses due to observed excessive predation by American Mink *Neovison vison* in the region of the control burrows masking any effect of food supply.



Figure 1. From one extreme to the other. Atlantic Puffins *Fratercula arctica* carrying a) 30–40 Atlantic Herring *Clupea harengus* larvae and b) a single 1-y old Herring. Hornøya, NE Norway, July 2007. © Robert T. Barrett.

Simple and quadratic regression analyses and ANOVA (1-way unstacked) analyses were carried out using Mintab 15 statistical software.

Results

Chick food: Small larval fish were often impossible to identify from a distance and 13% (annual range 0–35%) of the 3,848 loads noted during the study period contained unidentified larvae. They comprised 13.2% by number of the 29,267 food items recorded, but only 2.0% by mass. Between 1989 and 2013 the composition of food loads by mass brought in to Puffin chicks varied considerably with Capelin common in the first years but gradually being replaced by young Atlantic Herring *Clupea harengus* (hereafter 'Herring') and/or gadids Gadidae sp. (30–60 mm) (Figures 2 & 3). The decline in Capelin and increase in gadid fry (both % by mass) were both significant (arcsine transformed data; Capelin: $y = 38.3 - 0.019x$, $r^2 = 0.581$, $df = 23$, $P = 0.000$; gadid: $y = -33.2 + 0.02x$, $r^2 = 0.258$, $df = 24$, $P = 0.011$), whereas there were no significant trends in amounts of sandeel, Herring or 'other' fish. 'Other' fish was often 40–60 mm long Atlantic Wolffish *Anarhichas lupus* (1994, 1995 and 1997) or, as in 1998, 60–65 mm long Daubed Shanny *Leptoclinius maculatus*.

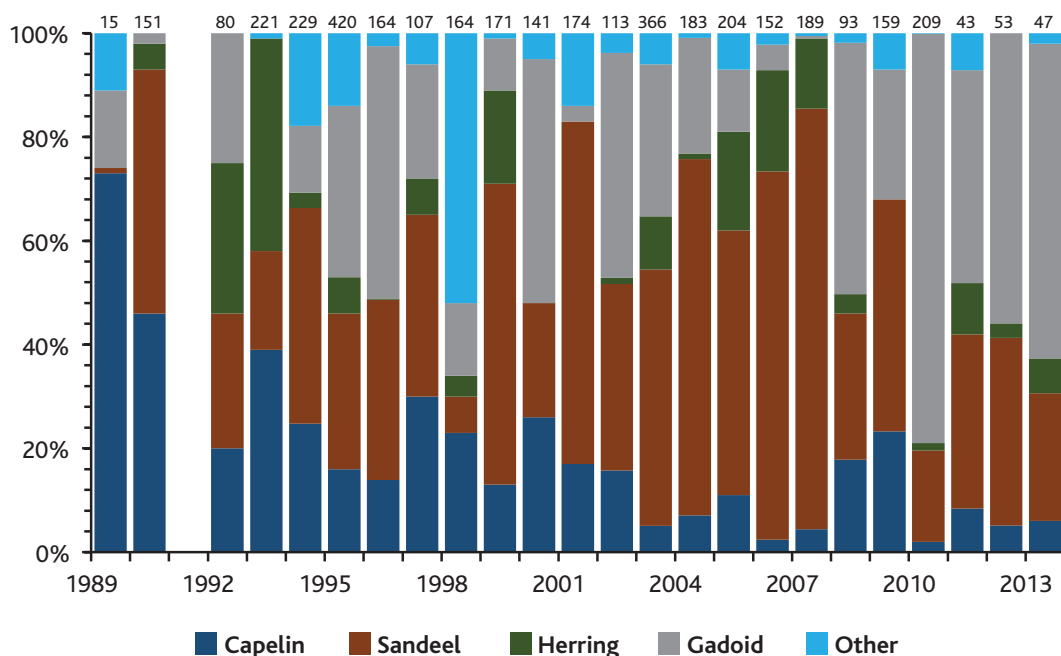


Figure 2. Composition of Atlantic Puffin *Fratercula arctica* chick diet (% by mass) at Hornøya, NE Norway, 1989–2013. Numbers of food loads observed is given above each column.

When considering the numbers and size of prey in food loads, a very different picture emerged with gadid fry and larval and post-larval fish (≤ 60 mm, e.g. Capelin in 1989, 1993 and 2001, sandeel in 2006, Herring in 2007, and unidentified in 2005, 2009 and 2011) comprising much of the diet from 1990 onwards (Figure 3). Between 1989 and 2013 the contribution of gadids and larval fish by number combined nearly doubled ($x = -35.9 + 0.018y$, $r^2 = 0.348$, $df = 23$, $P = 0.002$) while that of Capelin decreased markedly ($x = 9.36 - 0.005y$, $r^2 = 0.468$, $df = 23$, $P = 0.000$). There were no significant time trends in any of the other food categories.

The mass of loads brought in varied significantly from year to year ($F_{23,3542} = 9.84$, $P = 0.000$, range $5.2 \pm 0.3 - 12.2 \pm 0.6$ g), but there was no change over the years ($r = 0.259$, $P = 0.222$) with an overall mean of 7.7 ± 0.3 g (Appendix 1). The number of food items/load, however, increased significantly by a factor of two (1989–2013: $y = -452 + 0.230x$, $r^2 = 0.326$, $df = 23$, $P = 0.004$) with a corresponding decrease in mean size of food items (1989–2013: $y = 1108 - 0.529x$, $r^2 = 0.315$, $df = 23$, $P = 0.004$) (Appendix 1, Figure 4).

Chick growth and pre-fledging survival: Mean annual chick growth rates varied considerably (mass: $F_{28,773} = 11.2$, $p = 0.000$; wing: $F_{27,773} = 4.6$, $P = 0.000$) with mean mass increments between $5.7\text{--}13.3$ g d^{-1} and wing-length increments between $3.1\text{--}4.1$ mm d^{-1} (Appendix 2). There was an insignificant tendency towards declines in wing growth during the years of the study ($r^2 = 0.122$, $P = 0.062$) with marked dips in both parameters in 1993 (wing only), 2001, 2007 and 2011 (Figure 5).

Both growth parameters were negatively related to increases in the overall number of fish/load (wing: $y = 4.17 - 0.0748x$, $r^2 = 0.458$, $df = 22$, $P = 0.000$; mass: $y = 14.8 - 0.447x$, $r^2 = 0.401$, $df = 22$, $P = 0.001$; Figure 6) but there was no effect of load mass on chick growth ($r = 0.000$, $P > 0.98$ for both chick mass and wing). Nor was there any significant correlation between the diet composition (by mass) and chick growth (daily mass or wing length increment) among any of the main diet components. Correlated with diet proportions by number, however, there was a negative relationship between both mass and wing increments and larvae numbers (≤ 60 mm) and a positive one with gadid fry (Table 1), but none with any of the other diet components.

Until 2000, 75–95% of the hatched chicks survived the first four weeks post-hatch, but the survival rate dropped to 60–65% ten years later (Figure 7). In 2011 and 2012 only 28% and 33% of the chicks survived, respectively, but these were years when exceptional Mink activity was seen in parts of the colony (pers. obs.).

Table 1. Atlantic Puffin *Fratercula arctica* chick daily growth (mass and wing length) increments as linear functions of % (by number, arcsine transformed) of larvae (≤ 60 mm) and gadid fry, Hornøya, NE Norway, 1989–2013.

Growth parameter	Diet composition % by no.	Regression equation	r^2	P	df
Mass g^{-1}	larvae	$y = 12.60 - 4.26x$	0.443	0.001	22
Wing $mm\ d^{-1}$	larvae	$y = 3.79 - 0.66x$	0.437	0.001	22
Mass g^{-1}	gadid	$y = 9.54 + 3.10x$	0.301	0.007	22
Wing $mm\ d^{-1}$	gadid	$y = 3.29 + 0.52x$	0.350	0.003	22

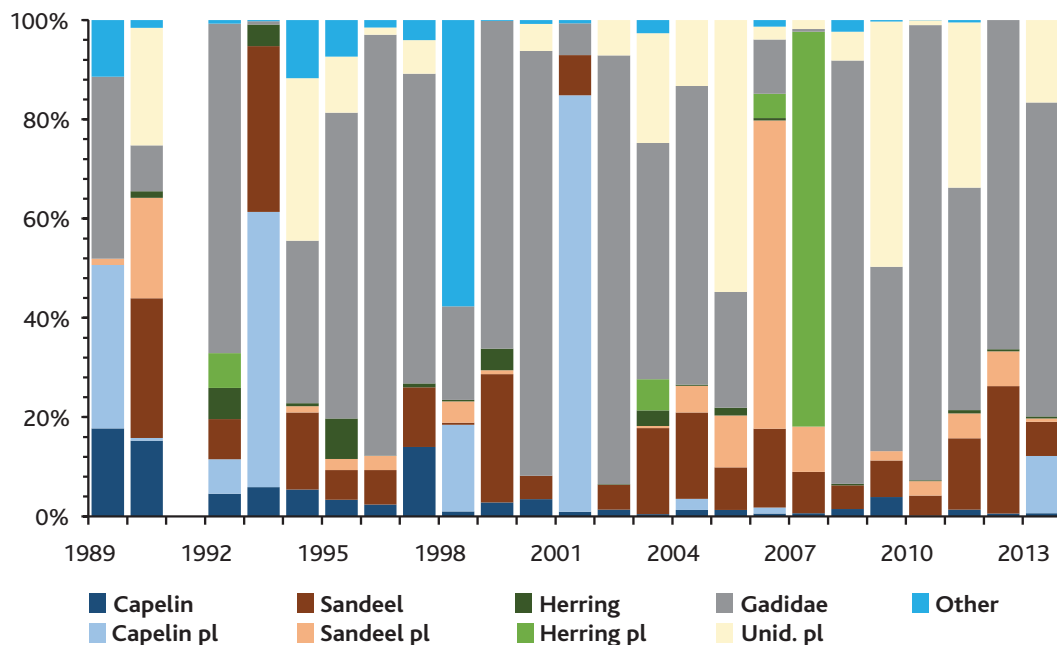


Figure 3. Composition of Atlantic Puffin *Fratercula arctica* chick diet (% by number of prey items) at Hornøya, NE Norway, 1989–2013. pl = larval and postlarval fish (≤ 60 mm). For numbers of food loads see Figure 2.

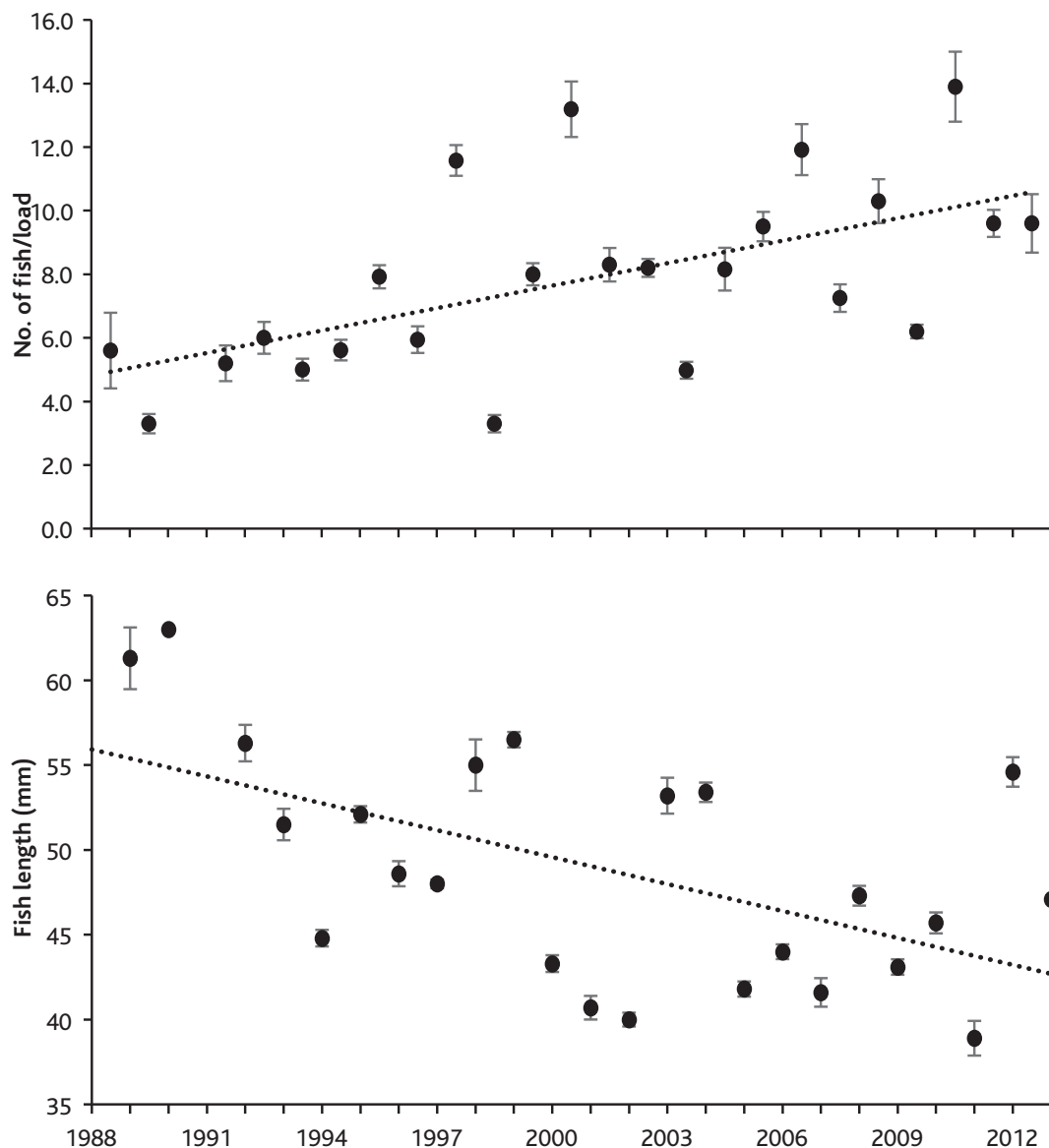


Figure 4. Changes in mean numbers of fish and mean fish length (± 1 SE) in loads brought to Atlantic Puffin *Fratercula arctica* chicks at Hornøya, NE Norway, 1989–2013.

Discussion

Estimated load masses of 6–10 g (Appendix 1) brought to chicks by adults at Hornøya in 1989–2013 were lower than the 11–12 g measured in what have been characterised as optimal years 1980–1982, and similar to those collected at Røst, NW Norway during years of poor breeding success (Barrett *et al.* 1987; Anker-Nilssen & Aarvak 2006 (Figure 3.5); Eilertsen *et al.* 2008). They were also similar to the typical load (8–9 g) for Puffins at the Isle of May, SE Scotland (Harris & Wanless 2011). In relation to body mass (c. 390 g at the Isle of May when feeding young,

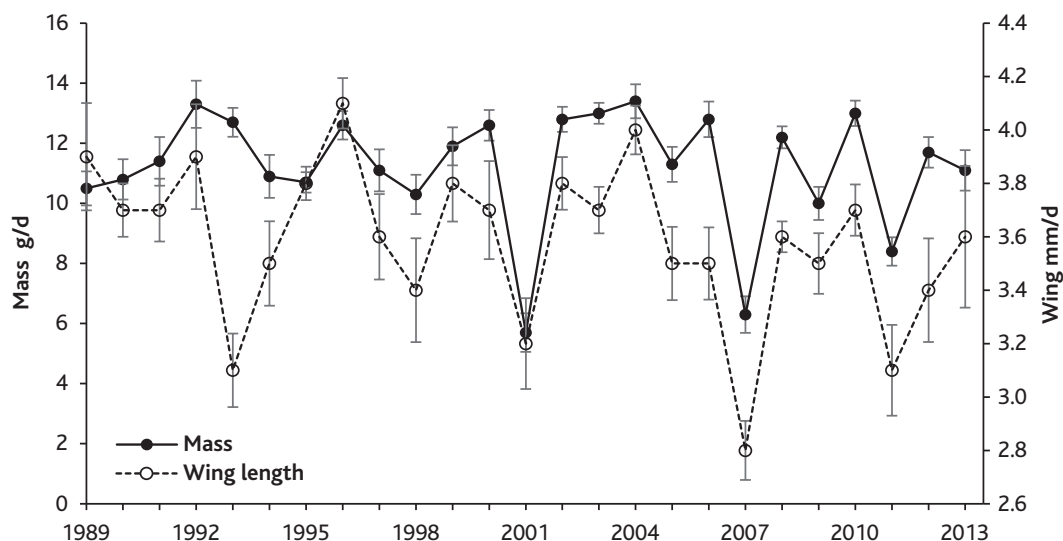


Figure 5. Mean growth rates (body mass g d^{-1} and wing length $\text{mm d}^{-1} \pm 1 \text{ SE}$) of Atlantic Puffin *Fratercula arctica* chicks at Hornøya, NE Norway, 1989–2013.

480 g at Hornøya; Barrett *et al.* 1985; Harris & Wanless 2011), however, load masses were much lower (1.7% of body mass) at Hornøya than at the Isle of May (2.3%). There are admittedly shortcomings in sampling Puffin food through direct observations (Rodway & Montevecchi 1996), but counts of fish and mass measurements of samples collected in the field suggested that the data presented here are adequate (Barrett 2002). Whereas there was no time trend in the load mass over the 25 years (1989–2013) of the study at Hornøya, other long-term studies have shown the converse. For example, at the Isle of May, SE Scotland, the mean load mass, which was initially slightly higher (8–11 g) than at Hornøya, decreased over the last 10 years of the 38-year study period 1973–2010 (Harris & Wanless 2011). Similarly, at Hermaness, Shetland, a decrease of c. 50% was recorded over 15 years (1974–1988; Martin 1989) and at Fair Isle, Shetland a 68% decrease was recorded between 1987 and 2013 (Miles *et al.* 2015). Although not declining, the overall statistic of low meal masses since 1989 at Hornøya corroborates earlier suggestions that after seemingly optimal years in the early 1980s (Barrett *et al.* 1987), Puffins here have been experiencing a reduction in feeding conditions that have possibly been compensated for by changes in feeding behaviour patterns including increases in feeding frequency (Dahl *et al.* 2005; Eilertsen *et al.* 2008). Unfortunately, annual feeding frequency data do not exist at Hornøya.

The suggestion of deteriorating feeding conditions at Hornøya is enhanced by the near doubling of the numbers of fish in a load brought to Puffin chicks over the 25 years. A similar increase (from c. 4 to 12 fish/load) was recorded over the 38-year period at the Isle of May (Harris & Wanless 2011), and at Røst numbers of prey items were generally high with means of 10–11 in years of good breeding success and 15–20 in poor years over a 27-year period (1979–2005; Anker-Nilssen & Aarvak 2006). At Hermaness, fish numbers also increased over a 14-year period, and both at

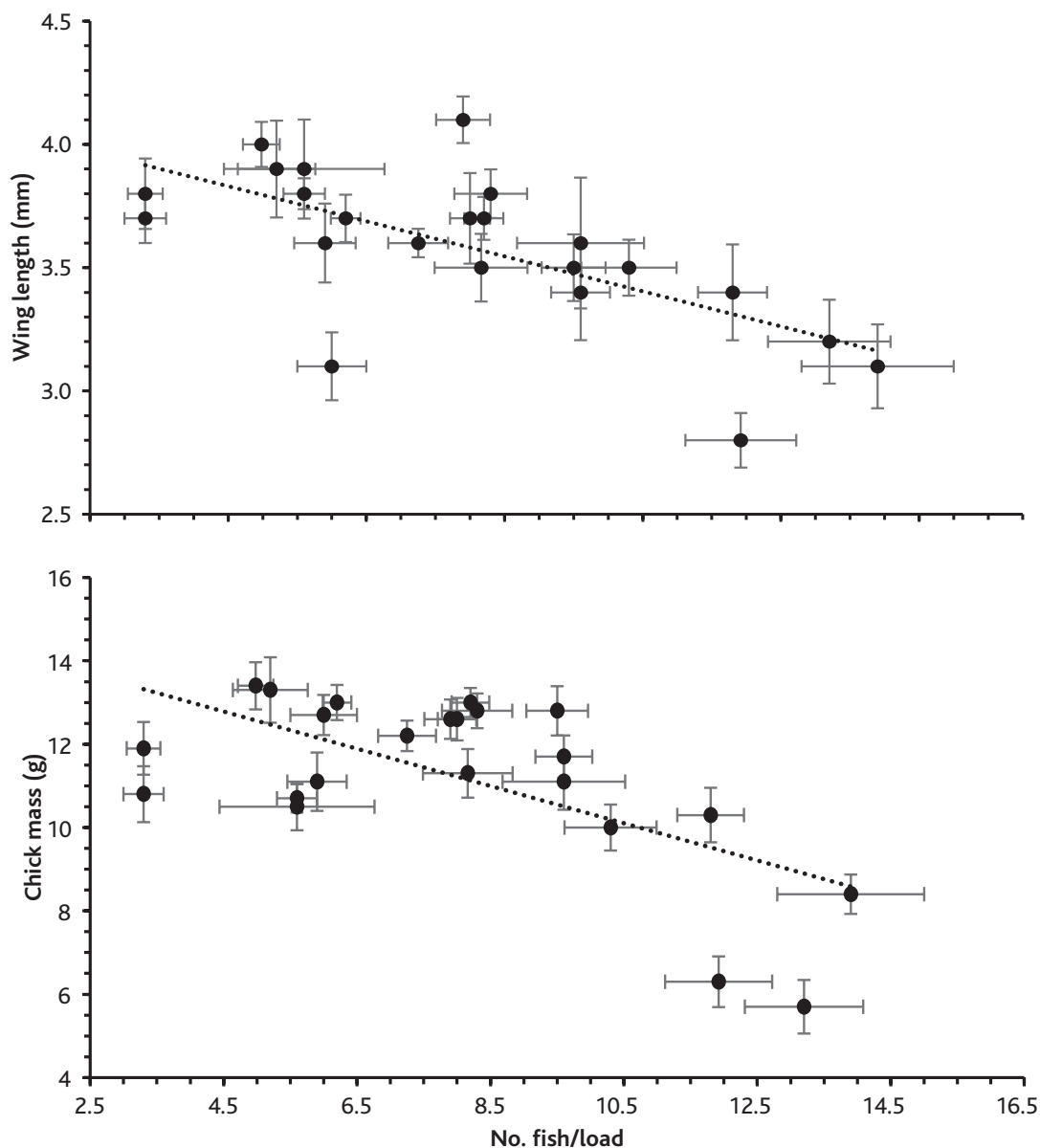


Figure 6. Relationship between chick growth (mean wing length and body mass \pm 1 SE) and number of fish in loads fed to Atlantic Puffin *Fratercula arctica* chicks at Hornøya, NE Norway, 1989–2013.

the Isle of May and Hermaness, increases in numbers of fish in a load were associated with lower load masses and poor feeding conditions, which resulted in reduced chick growth at the former colony (Martin 1989; Harris & Wanless 2011). At Fair Isle, the long-term reduction in load mass was also accompanied by an increase in numbers of fish per load and associated with a reduction in breeding success (Miles *et al.* 2015). Similarly, at Røst large numbers of prey items in a load were associated with low load masses over 26 years (Anker-Nilssen 1987; Anker-Nilssen & Aarvak 2006).

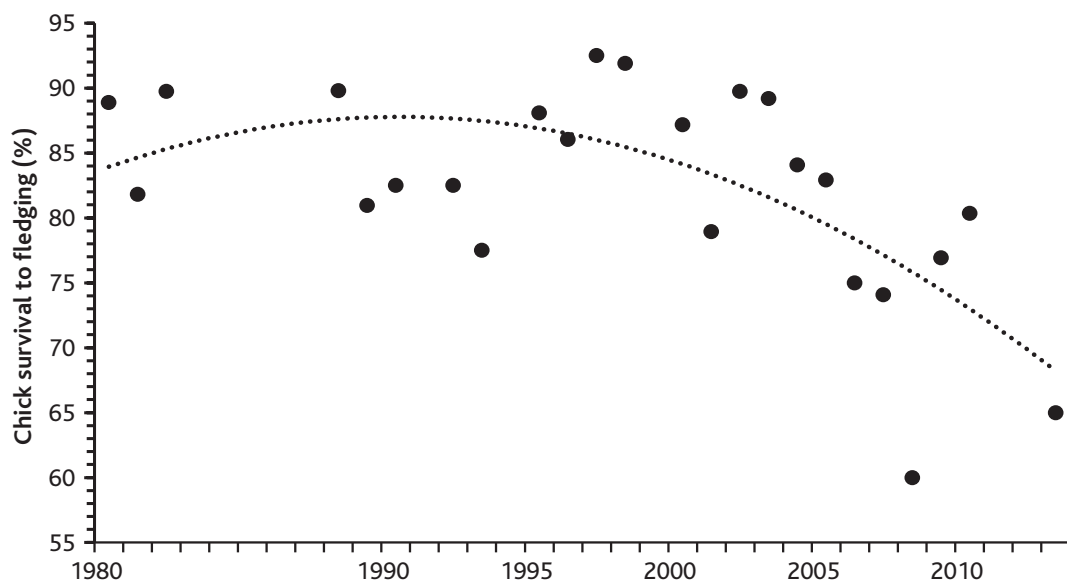


Figure 7. Mean survival rates of Atlantic Puffin *Fratercula arctica* chicks after hatching to age 25–30 d at Hornøya, NE Norway, 1980–2013 (excluding 2011 and 2012 when exceptionally low rates [28% and 33% respectively] were attributed to excessive predation by American Mink *Neovison vison*). (y (%), arcsine-transformed) = $-2440 + 2.45x - 0.0006x^2$, $r^2 = 0.420$, $P = 0.003$)

That there was no corresponding decline in load mass at Hornøya may be due to a more diverse food base being available near the colony compared to the Isle of May and Røst, where Puffins were limited in choice and very dependent on local access to sandeels (and some Sprat *Sprattus sprattus*) and the drift of first-year Herring past the colony, respectively (Durant *et al.* 2003; Harris & Wanless 2011).

This wide food base and steady load mass may have facilitated the high growth rates of chicks throughout the study period. Whereas Isle of May chick growth rate declined from c. 9 g d^{-1} to c. 7 g d^{-1} over 35 years (Harris & Wanless 2011), Puffin chick growth at Hornøya remained in the range of maximum growth rates ($11\text{--}12 \text{ g d}^{-1}$) recorded at the Isle of May and other British colonies (summarised in Gaston 1985) throughout the study period. In relation to adult body mass, Hornøya chicks also had a high daily growth rate equivalent to 2.3% to 2.5% of adult mass whereas Isle of May daily chick growth increments dropped from c. 2.3% to 1.8% of adult mass. In only three years were there markedly reduced rates on Hornøya ($< 10 \text{ g d}^{-1}$ in 2001, 2007 and 2011) and removing these from the analyses results in the negative relationships between chick growth and numbers of items/load (Figure 6) becoming statistically insignificant. The high mass gain but low wing growth in 1993 (Figure 5) when load masses were the lowest measured in this study (5.2 g; Table 1) is an anomaly as long-lived seabirds' chicks generally preferentially allocate resources to structural growth, e.g. wing growth before mass gain (fat deposition) in times of food shortage thus increasing chances of juvenile survival (Øyan & Anker-Nilssen 1996; Morrison *et al.* 2009; Lyons & Roby 2011). Why wing-growth but not mass gain was depressed in 1993 is a mystery.

The fact that Puffin chick growth rates at Hornøya did no more than tend to decline over the 34-year period despite an increase in numbers of items and decrease in size of items brought to chicks demonstrates again how the Puffins were able to compensate for a deterioration in prey quality through behavioural changes such as adjustments of provisioning rates (Johnsen *et al.* 1994; Dahl *et al.* 2005). The dips in growth rates in 2001, 2007 and 2011 (Figure 5) were in years with the highest mean numbers of fish per load (12–14) recorded during the study, mainly as a result of large proportions by number of Capelin and Herring larvae in 2001 and 2007, respectively (Figure 3) and of small fish (unidentified larvae and gadids < 40 mm) in 2011, which in all cases suggested the adults then had problems finding larger, more suitable fish. Until about 2005, adult compensatory chick feeding behaviour (e.g. increased feeding frequency) was enough to ensure more-or-less steady pre-fledging survival rates of chicks of 80% or more (Dahl *et al.* 2005), but a subsequent increase in chick mortality suggests the passing of a critical threshold beyond which some of the adults gave priority to their own survival rather than that of their chick (e.g. Johnsen *et al.* 1994; Wernham & Bryant 1998).

Time will show whether Hornøya will join the ever-growing list of colonies, large and small, in the NE Atlantic (e.g. Shetland, Faeroes, Iceland, Norway (Runde & Røst)) where breeding success has declined or often failed completely since the turn of the millennium (Harris & Wanless 2011; www.seapop.no). Food shortages, sometimes also weather-related (rain) chick mortality, are often listed as the main cause of poor growth (Harris & Wanless 2011) and survival, but whether they are a result of climate- and/or fisheries-related drivers and whether they have a common, widespread cause is widely discussed (e.g. Irons *et al.* 2008; Gladics *et al.* 2015). These discussions also raise the need for increased focus on ecosystem-based research and management of the marine environment (e.g. Essington & Punt 2011 (and papers therein); Skern-Mauritzen *et al.* 2015)

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Appendix 1. Annual means of load mass, number of fish/load and fish length brought to Atlantic Puffin *Fratercula arctica* chicks at Hornøya, NE Norway, 1989–2013. SE = standard error, N = number of loads. No data for 1991 due to low sample size.

Year	Load mass g			No. fish/load			Mean fish length mm		
	Mean	SE	N	Mean	SE	N	Mean	SE	N
1989	8.8	1.6	13	5.6	1.2	14	61.3	2.2	209
1990	7.6	0.5	139	3.3	0.3	144	63.0	1.8	469
1992	11.0	0.7	56	5.2	0.6	56	56.3	1.5	369
1993	5.2	0.3	212	6.0	0.5	218	51.5	1.1	616
1994	6.4	0.3	179	5.0	0.3	179	44.8	0.9	1166
1995	6.6	0.2	231	5.6	0.3	231	52.1	0.5	2477
1996	7.3	0.4	164	7.9	0.4	164	48.6	0.5	1392
1997	6.2	0.4	104	5.9	0.4	107	48.0	0.7	723
1998	8.3	0.3	149	11.6	0.5	149	55.0	0.3	1959
1999	6.1	0.3	164	3.3	0.3	164	56.5	1.5	485
2000	5.5	0.3	172	8.0	0.3	172	43.3	0.5	1283
2001	7.8	0.5	172	13.2	0.9	172	40.7	0.5	2252
2002	6.7	0.4	113	8.3	0.5	113	40.0	0.7	935
2003	8.0	0.3	366	8.2	0.3	366	53.2	0.4	3090
2004	7.7	0.5	183	5.0	0.3	183	53.4	1.1	910
2005	6.7	0.4	204	8.2	0.7	204	41.8	0.6	1668
2006	9.4	0.5	152	9.5	0.5	152	44.0	0.4	1466
2007	6.8	0.5	189	11.9	0.8	189	41.6	0.4	2253
2008	6.9	0.5	93	7.3	0.4	93	47.3	0.8	675
2009	8.4	0.5	159	10.3	0.7	159	43.1	0.6	1640
2010	6.5	0.2	209	6.2	0.2	209	45.7	0.5	1300
2011	8.0	1.0	43	13.9	1.1	43	38.9	0.6	598
2012	12.2	0.6	53	9.6	0.4	53	54.6	1.0	511
2013	9.6	0.7	47	9.6	0.9	47	47.1	0.9	451



Figure 8. Adult Atlantic Puffins *Fratercula arctica* on Hornøya, July 2008. Note the bird in front carrying a load of small gadoids. © Robert Barrett.

Appendix 2. Mean annual growth increments of Atlantic Puffin *Fratercula arctica* chicks at Hornøya, NE Norway, 1989–2013. Measurements were made in the linear phase of growth and ceased when wing length = 120 mm for mass gain and 130 mm for wing growth. SE = standard error, N = sample size.

Year	Body mass g d ⁻¹			Wing length mm d ⁻¹		
	Mean	SE	N	Mean	SE	N
1989	10.5	0.6	30	3.9	0.2	30
1990	10.8	0.7	20	3.7	0.1	25
1991	11.4	0.8	22	3.7	0.1	26
1992	13.3	0.8	21	3.9	0.2	21
1993	12.7	0.5	19	3.1	0.1	19
1994	10.9	0.7	5	3.5	0.2	10
1995	10.7	0.3	17	3.8	0.1	23
1996	12.6	0.5	28	4.1	0.1	28
1997	11.1	0.7	25	3.6	0.2	25
1998	10.3	0.7	32	3.4	0.2	32
1999	11.9	0.6	24	3.8	0.1	24
2000	12.6	0.5	24	3.7	0.2	24
2001	5.7	0.6	28	3.2	0.2	28
2002	12.8	0.4	36	3.8	0.1	37
2003	13.0	0.3	33	3.7	0.1	33
2004	13.4	0.6	30	4.0	0.1	30
2005	11.3	0.6	34	3.5	0.1	34
2006	12.8	0.6	35	3.5	0.1	35
2007	6.3	0.6	39	2.8	0.1	40
2008	12.2	0.4	27	3.6	0.1	27
2009	10.0	0.6	38	3.5	0.1	38
2010	13.0	0.4	38	3.7	0.1	39
2011	8.4	0.5	28	3.0	0.2	30
2012	11.7	0.5	17	3.3	0.2	18
2013	11.1	0.7	24	3.6	0.3	24