

Recent impacts of anthropogenic climate change on a higher marine predator in western Britain

Samuel Riou^{1,*}, Catherine M. Gray², M. de L. Brooke³, Petra Quillfeldt⁴,
Juan F. Masello⁴, Christopher Perrins⁵, Keith C. Hamer¹

¹Institute of Integrative and Comparative Biology, University of Leeds, Leeds LS2 9JT, UK

²Peak District National Park Authority, Aldern House, Baslow Road, Bakewell DE45 1AE, UK

³Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

⁴Max Planck Institute for Ornithology, Vogelwarte Radolfzell, Schlossallee 2, 78315 Radolfzell, Germany

⁵Edward Grey Institute of Field Ornithology, University of Oxford, Oxford OX1 3PS, UK

ABSTRACT: Impacts of anthropogenic climate change on marine ecosystems are now widely acknowledged. In the NE Atlantic, abundant evidence from the partly enclosed waters of the North Sea indicates that recent climate-induced changes in primary and secondary productivity have been propagated up the food chain, with marked consequences for higher vertebrate predators such as seabirds. In contrast, however, there is much less indication of such impacts on higher predators in the more open Atlantic waters around the west coast of the British Isles. Through an annual comparison of chick growth and adult food provisioning behaviour of Manx shearwaters in SW Wales, we found that birds bred later and chicks attained lower peak and fledging masses in 2007 and 2008 than in any previous recorded year dating back to 1965. These changes were accompanied by a reduction in parental attendance at the colony, which was probably the result of parents switching to a dual foraging strategy in 2007 and 2008. These events were linked to higher sea surface temperature in the preceding winter and to a reduction in prey quality, as indicated by the mean body mass of 2 yr old herring. These are the first such findings for the west coast of Britain and indicate that within the NE Atlantic region, adverse impacts of climate change on higher marine predators are no longer restricted to the vicinity of the North Sea.

KEY WORDS: Breeding success · Foraging behaviour · Global warming · Manx shearwater · Phenology · Sea surface temperature

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

There is now very strong evidence for a progressive effect of human activity on global climates, with increases in atmospheric CO₂ levels strongly suspected to have induced increases in air temperatures, particularly over the past 50 yr (IPCC 2007). Less certain, however, are the long-term impacts of rising temperatures on different species and ecosystems (Hockey & Midgley 2009, Grémillet & Boulinier 2009). In marine environments, warming of surface waters results in a low-density surface layer that greatly reduces vertical mixing, with a consequent reduction in nutrient inputs into the euphotic zone and hence in the primary pro-

ductivity of surface waters during the summer period (Richardson & Schoeman 2004, Behrenfeld et al. 2006). In polar regions, this effect may then be exacerbated by decreases in surface-water salinity due to increased fresh-water input as a result of the melting of coastal and inland ice as well as Arctic permafrost (Jacobs et al. 2002, Greene & Pershing 2007). However, surface warming can also directly favour phytoplankton growth at high latitudes (Behrenfeld & Falkowski 1997), and in all regions, rising air temperatures can generate large atmospheric pressure differentials, resulting in high wind stress on the surface of the oceans. This in turn increases the upwards transfer of nutrients and so enhances primary productivity (Toggweiler &

*Email: samuel.riou@gmx.fr

Russell 2008). The net effect of these antagonistic processes varies regionally but global ocean primary productivity, as assessed by remote sensing, has decreased significantly since 1999 (Fig. 1 in Behrenfeld et al. 2006). This decrease is highly correlated with large-scale climatic indices, strongly suggesting that global warming has had a net negative impact on marine primary productivity (Le Bohec et al. 2008, Grémillet & Boulinier 2009).

There is growing evidence that decreases in primary productivity can be propagated up the food chain (Beaugrand et al. 2002, Behrenfeld et al. 2006), extending in some cases to higher marine predators such as piscivorous seabirds (e.g. Gjerdrum et al. 2003, Frederiksen et al. 2006). Rising temperatures may also have direct physiological effects on both predatory fish (Perry et al. 2005) and seabirds (Oswald et al. 2008), in some cases exacerbating the impacts of changes in primary productivity (Hamer 2010, Oswald et al. in press). Intense fishing pressure on predatory fish can also have cascading effects on marine food webs (Watermeyer et al. 2008, Baum & Worm 2009) and the greatest threat to fish stocks is likely to be the combined effects of climate change and overfishing (Brander 2007). Recent studies have suggested that these combined effects can also have important consequences for seabird breeding success, survival and population stability (Frederiksen et al. 2004b, Ainley & Blight 2009).

In the Northeast Atlantic Ocean, several species of seabird at sites bordering the North Sea have experienced delayed breeding, reduced breeding success and, in some case, declines in population sizes since the 1990s (Frederiksen et al. 2004a, Mavor et al. 2006). These events have been linked to reductions in the abundance and nutritional quality of their main prey (lesser sandeels *Ammodytes marinus*), which were in turn associated with warming of surface waters (Frederiksen et al. 2004b, Wanless et al. 2007). In particular, an inflow of warm nutrient-poor oceanic water, together with stronger stratification of surface waters, has favoured a northward expansion of warm-water copepod species and a decline in cold-water zooplankton (Beaugrand 2004, Grémillet & Boulinier 2009). Together with impacts of industrial sandeel fisheries (Frederiksen et al. 2004b, Poloczanska et al. 2004), these changes in plankton assemblages have resulted in poor and erratic growth and survival of sandeels, with adverse consequences for North Sea seabirds (Frederiksen et al. 2007). However, studies elsewhere in the region have not previously recorded such adverse effects (Swann 2000, Votier et al. 2005), despite the fact that sea surface temperature has also been rising in these areas (ICES 2007). Indeed, studies at more northerly latitudes have recorded or suggested positive relationships between sea surface temperature and vi-

tal rates (breeding success, recruitment, adult survival, etc.) of several species (Aebischer et al. 1990, Hamer et al. 1991, Thomson & Ollason 2001, Durant et al. 2003, D'Alba et al. 2010). Moreover in Shetland, recent low abundance of sandeels coincided with record-high abundance of herring *Clupea harengus* (Frederiksen et al. 2007), in keeping with the notion that food webs in cooler waters may be more strongly influenced by 'top-down' effects of predation than by 'bottom-up' effects of changes in primary and secondary production (Hunt et al. 2002, Frank et al. 2007).

Seabirds differ in their vulnerability to adverse effects of low prey availability (Furness & Tasker 2000). For instance, species foraging relatively close to the colony are typically more vulnerable than longer distance foragers, because they have less flexibility in their foraging locations and time-activity budgets (Diamond 1978, Hamer et al. 2007). Procellariiform seabirds (albatrosses, petrels, shearwaters, etc.) typically forage at great distances from the colony (Brooke 2004), and several species have been recorded to employ a dual-foraging strategy entailing a combination of short foraging trips mainly used to feed the chick, interspersed with longer trips during which the adult rebuilds its reserves (Weimerskirch et al. 1994, Weimerskirch 1998). There is also growing evidence that procellariiforms can adjust their food provisioning strategy according to food availability and foraging costs (Granadeiro et al. 1999, Duriez et al. 2000, Quillfeldt et al. 2007). For these reasons, procellariiforms have been viewed as the least vulnerable to changes in the distribution and abundance of their prey (Furness & Tasker 2000).

Manx shearwaters *Puffinus puffinus* breed in large colonies around the Northeast Atlantic (Brooke 1990). They typically make foraging trips lasting 1 to 3 d with little indication of a dual-foraging strategy (Gray & Hamer 2001, Hamer et al. 2006). On the islands of Skomer and Skokholm, Southwest Wales, they have been studied sporadically since the 1920s and annually since about 1990, yet there have been no accounts of feeding conditions that have led to poor chick growth or breeding failures (Lockley 1930, Harris 1966, Brooke 1990, Hamer & Hill 1997). During chick-rearing, Manx shearwaters from these islands prey mainly on clupeid fish such as herring *Clupea harengus* and sprat *Sprattus sprattus* (Brooke 1990), with foraging effort concentrated in the Irish and Celtic Seas (Guilford et al. 2008). Stocks of herring in the Celtic Sea have declined steadily following a recovery in the 1980s and have reached critically low levels in recent years (ICES 2007). There are no comparable data for stock sizes of sprat in the region or herring in the Irish Sea, but they are also thought to be low (ICES 2007). Here, we use data for years spanning the period from 1965 to 2008 to investigate annual variation in the phe-

nology, breeding success and foraging behaviour of Manx shearwaters in Southwest Wales and to relate these data to annual variation in climatic and prey population indices.

MATERIALS AND METHODS

Fieldwork was carried out at the large colony of Manx shearwaters (>100 000 pairs) on Skomer Island, Southwest Wales (51.73°N, 5.28°W), each year from 1995 to 2008 and on the neighbouring island of Skokholm (ca. 4 km away) from 1965 to 1967 and from 1973 to 1976. Manx shearwaters are burrow nesters, and chicks were reached via short access tunnels in the roof of each burrow, capped with removable earth lids. This system reduced overall disturbance and had no adverse effects on burrow occupancy, food-provisioning rates or breeding success (Brooke 1990, Hamer & Hill 1997). We determined hatching dates of chicks (between 40 and 60 nests each year, with mostly different study burrows being sampled each year) by direct observation or by calibrating wing length (maximum flattened chord measured to the nearest 1 mm) against wing growth in chicks of known age (Brooke 1990). Chicks were then weighed daily to the nearest 5 g using a Salter spring balance (RS Components). Manx shearwater chicks gain weight for about 50 to 55 d post-hatching before losing mass prior to fledging at around 70 d. Mass growth was monitored until fledging in 1965, 1973–1976, 1995, 1998–2000 and 2007–2008; peak and fledging masses are described for these years only. In addition, every night from the end of August in 2007 and 2008, we caught and weighed a sample group of young Manx shearwaters on the surface prior to fledging for comparison with published Skokholm data from 1965 to 1967 (Perrins et al. 1973).

Food provisioning behaviour of adults. Parents are nocturnal at the colony, and overnight nest attendance was monitored by simultaneously radio-tracking both adults at each of 10 nests in 1999 and 2002, 21 nests in 2007 and 19 nests in 2008. In each case, both adults were caught when chicks were 15 to 25 d old, weighed and fitted with a VHF radio-transmitter (Biotrack) weighing 2 g in 1999 and 2002 and 4.5 g in 2007 and 2008 (<1.5% of adult body mass). Transmitters were attached to the central tail feathers using self-amalgamating tape (RS Components). Attendance of each adult at the colony was then monitored using a scanning receiver for an average of 15 and 16 consecutive nights in 1999 and 2002, respectively, and until chicks reached ca. 60 d of age in 2007 and 2008. Trials at the colony indicated that weak and intermittent signals were sometimes received if a bird was on the water in the vicinity of land, but consistent, strong signals were

obtained only from birds returning to their nests (Riou & Hamer 2008). Chicks were weighed twice daily (at dawn and dusk), and mass increments between successive weighings overnight were used as estimates of meal sizes.

There was no discernible effect of radio-tracking on chick growth in 1999 or 2002 (Gray & Hamer 2001, Quillfeldt et al. 2004). As a further check in 2007 and 2008, we compared the growth of chicks at nests where both parents had been radio-tracked with a separate sample of 30 nests where parents were never handled. There was no significant effect of radio-tracking on average chick peak mass (\pm SE) (radio-tracked: 505.1 \pm 11.9 g; controls: 515.7 \pm 12.6 g; likelihood ratio test: $\chi^2_1 = 0.1$, $p = 0.7$), nor was there an effect on fledging mass (radio-tracked: 394.5 \pm 11.4 g; controls: 393.3 \pm 7.2 g; $\chi^2_1 = 0.01$, $p = 0.9$).

Environmental variables. Monthly sea surface temperature (SST) data were obtained from the UK Meteorological Office (Hadley Centre; HadISST 1.1 Global sea-ice coverage and SST 1870 to present, available from <http://climexp.knmi.nl>) and used to calculate the average winter (December to April) SST for waters surrounding Skomer. Winter North Atlantic Oscillation (NAO) index values were obtained from the Climatic Research Unit, Norwich, UK. We used data for these months to characterize climate over the period preceding the birds' breeding season each year. Both winter SST and winter NAO have previously been linked to fish and seabird productivity (Borges et al. 2003, Frederiksen et al. 2004b), and in the Baltic Sea, mild winters (as indicated by a positive winter NAO index) have a positive effect on year-class strength of herring in spring (Axenrot & Hansson 2003). In the waters around Skomer, herring spawn on the south coast of Ireland during the winter and move to feeding grounds in the Celtic and Irish Sea during the summer. Here, we used spawning stock biomass (SSB; data from the ICES Herring Working Group; ICES 2009) as an index of prey abundance each year. The modal length of prey regurgitated by birds at the colony (15 cm; Brooke 1990) best corresponds to fish aged 2 yr, and so we used SSB 2 yr previously, which accurately predicts year-class strength of age-2 herring (Axenrot & Hansson 2003). We also examined prey quality, in terms of the mean mass of individuals aged 2 yr (data from ICES 2009).

Statistical analyses. Chick growth and food provisioning were compared across years using general linear modelling in R (www.R-project.org). Hatching date and chick peak mass were first analysed as a function of year using *F*-tests. Growth rates during the phase of linear growth (10 to 30 d post-hatching) were examined by modelling chick mass as a function of year and age, with chick ID included as a random effect to account for repeated measurements (Pinheiro & Bates

2000). Hatching date and peak mass were then analysed as a function of SST, NAO and herring mass and abundance, starting with all the variables in the initial model and including year as a random effect. Finally, parental attendance was modelled as a function of year in a binomial model with parent ID included as a random effect. Attendance was measured as the probability of an individual bird being present at the colony each night during the period with the most intense and least variable food provisioning rhythm when chicks are between 20 and 50 d of age (Hamer & Hill 1997). In all cases, model simplification was carried out by sequential removal of the least significant terms, using likelihood ratio tests (F -tests and, when a random effect was included, χ^2 tests). All significant terms remained in the minimum model used for statistical inference. All models met the assumptions of normality and homoscedasticity.

RESULTS

Timing of breeding and growth of chicks

Hatching occurred significantly later in both 2007 and 2008 than in previous years ($F_{16,734} = 3.3$, $p < 0.0001$; Fig. 1), but there was no annual trend in hatching date ($\chi^2_1 = 1.4$, $p > 0.2$) and no effect of either NAO or winter SST (all $\chi^2_1 < 1.2$, $p > 0.3$). Chick mass during the linear phase of growth differed significantly between years ($\chi^2_3 = 225$, $p < 0.0001$), with an average growth rate of $14.9 \pm 0.1 \text{ g d}^{-1}$ from 1965 to 1976, $12.7 \pm 0.2 \text{ g d}^{-1}$ from 1995 to 2000 and $11.3 \pm 0.3 \text{ g d}^{-1}$ in 2007

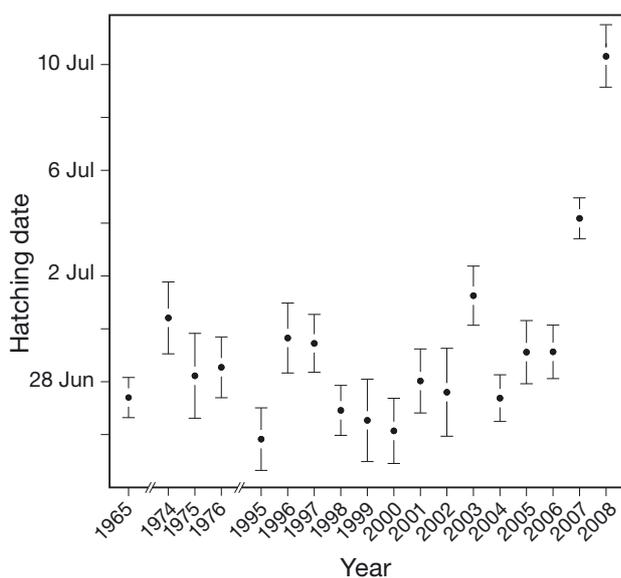


Fig. 1. *Puffinus puffinus*. Hatching date as a function of year (mean \pm SE)

(Fig. 2). In 2008, chicks had an intermediate rate of growth to 30 d post-hatching ($13.2 \pm 0.3 \text{ g d}^{-1}$), but in both 2007 and 2008, chicks showed very poor growth from then until fledging (Fig. 2).

Peak masses of chicks decreased significantly with year ($F_{1,411} = 225$, $p < 0.0001$) and were lower in 2007 and 2008 than in all previous years (Fig. 2). Variation in peak mass closely matched SST in the immediately preceding winter in the waters around the colony ($\chi^2_1 = 10.6$, $p = 0.001$; Fig. 3) but was not related to winter NAO (all $\chi^2_1 = 0.5$, $p = 0.5$). In a separate model dealing with the effects of herring mass and abundance, chick peak mass was strongly dependent on mean body mass of 2 yr old herring ($\chi^2_1 = 8.6$, $p = 0.003$; Fig. 4) but was not significantly related to spawning stock biomass ($\chi^2_1 = 2.8$, $p = 0.09$). In a model that included both SST in the preceding winter and herring body mass, both terms showed significant independent effects on chick peak mass ($\chi^2_1 = 4.5$, $p = 0.03$ and $\chi^2_1 = 5.4$, $p = 0.02$, respectively).

Body masses of fledglings were substantially lower in 2007 and 2008 than from 1965 to 1967 (Fig. 5). Chicks that fledged at earlier dates in 2008 were heavier than later fledglings that year and than all fledglings in 2007 (interaction between date and year; $F_{1,380} = 10.7$, $p = 0.001$; Fig. 5).

Parental attendance and food provisioning

The probability of a parent returning to the nest overnight differed significantly between years ($\chi^2_3 = 20.7$, $p = 0.0001$), being substantially lower in 2007 and

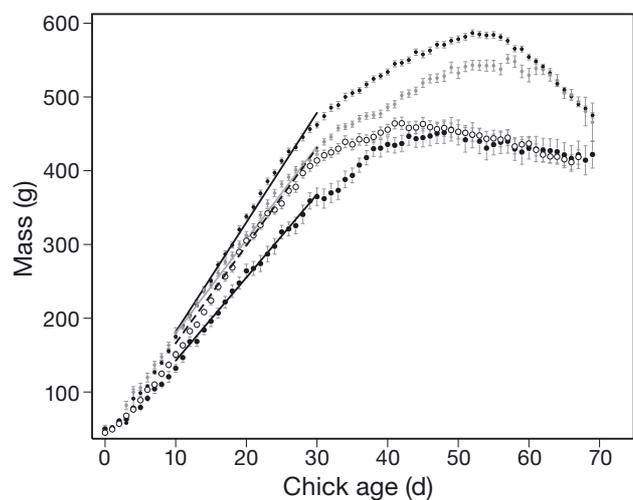


Fig. 2. *Puffinus puffinus*. Chick mass (mean \pm SE) as a function of age across years 1965 to 1976 (small black dots), 1995 to 2000 (grey dots), 2007 (large black dots) and 2008 (large white dots). Lines show model growth rates between 10 and 30 d post-hatching

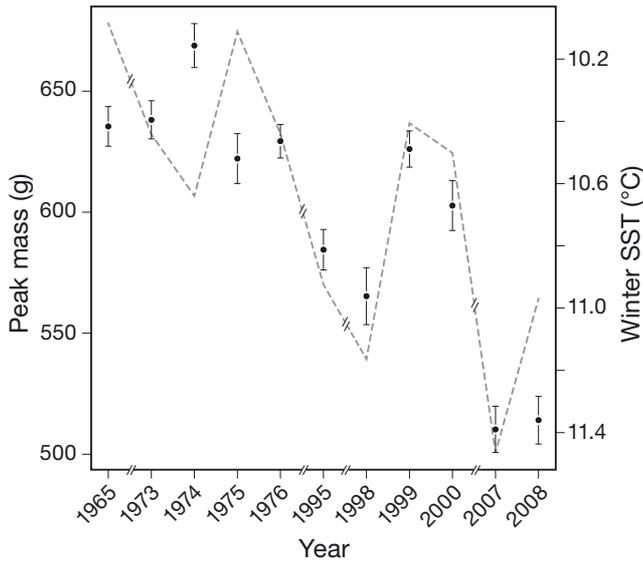


Fig. 3. *Puffinus puffinus*. Peak mass of chicks (dots) as a function of year (mean \pm SE). Winter sea surface temperature (SST) in the area around Skomer Island in the immediately preceding winter is shown as a dashed line. Note inversion of scale for SST

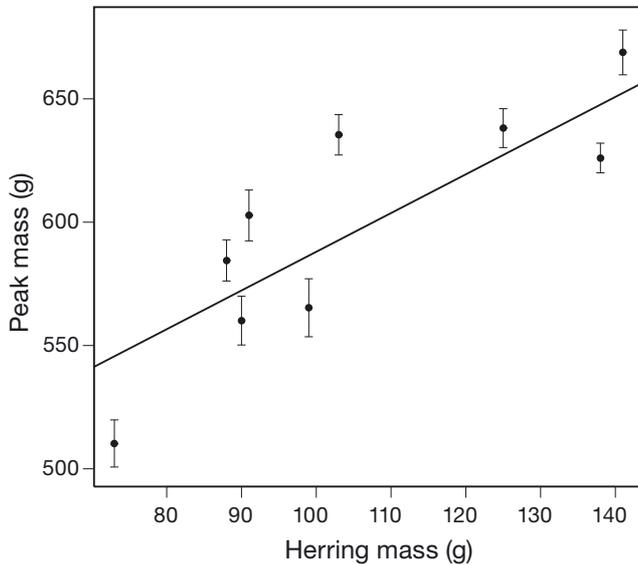


Fig. 4. *Puffinus puffinus*. Chick peak mass each year (mean \pm SE) as a function of the mean body masses of herring aged 2 yr (i.e. spawned 2 yr previously). The line shows the model prediction

2008 than in 1999 and 2002 (Table 1). Adults increased the frequency of long trips (>3 d) and reduced the frequency of 2 to 3 d trips in 2007 and 2008 compared to 1999 and 2002 (χ^2_1 (on a 2×2 contingency table) = 25.0, $p < 0.001$; Fig. 6). The average duration of long trips also increased substantially, from 4.8 ± 0.4 d (maximum = 7 d) in 1999 and 2002 to 5.6 ± 0.1 d (maximum

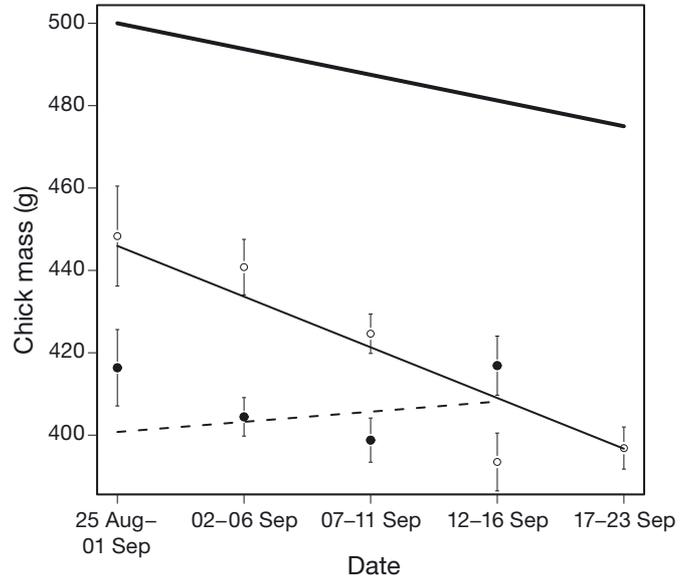


Fig. 5. *Puffinus puffinus*. Body masses of fledglings caught on the surface according to date ranges in 2007 (●, $n = 167$) and 2008 (○, $n = 218$). Lines show fitted model masses for 2007 (dashed) and 2008 (black), and the mass of fledglings in the years 1965 to 1967 (data from Perrins et al. 1973: thick black line)

Table 1. *Puffinus puffinus*. Parental attendance (probability of a parent returning to the nest overnight) and meal sizes delivered by parents at Skomer in different years (means \pm SE)

Year	Adult attendance	Single meals (g)	Double meals (g)
1999	0.60 ± 0.03	43.8 ± 2.6	55.2 ± 5.7
2002	0.63 ± 0.03	46.6 ± 2.0	77.6 ± 5.4
2007	0.49 ± 0.01	44.1 ± 1.1	99.8 ± 1.8
2008	0.51 ± 0.02	42.8 ± 1.3	80.9 ± 2.0

= 10 d) in 2007 and 2008. These changes resulted in a bimodal distribution of trip durations in 2007 and 2008, which was not present in 1999 or 2002 (Fig. 6).

The sizes of individual meals delivered by parents showed little variation among years ($\chi^2_3 = 0.7$, $p = 0.9$; Table 1). However, double meals, resulting from delivery of food by both parents, showed significant variation among years ($\chi^2_3 = 36.8$, $p < 0.0001$), being heavier in 2007 and 2008 than in earlier years. They were close to twice the mass of single meals only in 2007 and 2008.

DISCUSSION

In 2007 and 2008, Manx shearwaters in SW Wales bred later and chicks reached substantially lower peak masses than in any of the years since the 1960s for which

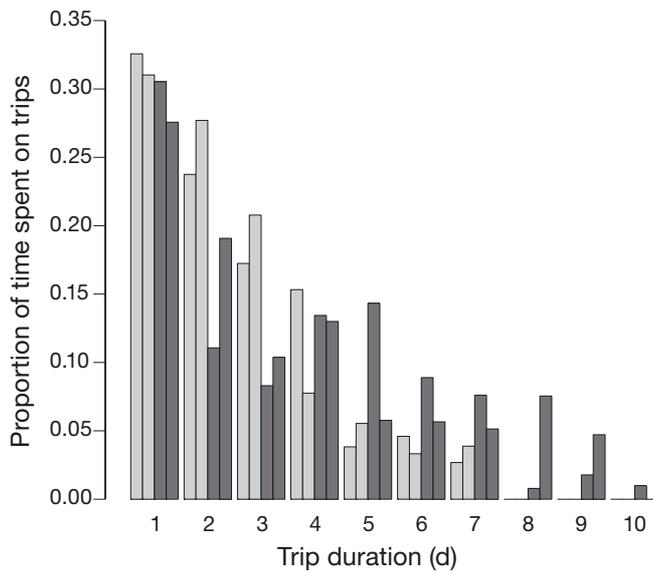


Fig. 6. *Puffinus puffinus*. Proportion of time spent on foraging trips of different durations in 1999 and 2002 (light grey bars) and in 2007 and 2008 (dark grey bars). Data are shown as time spent on trips rather than frequencies of trips to avoid over-emphasizing the shortest trips

data were available. This was associated with a reduction in parental attendance, linked to warming SST in the preceding winter and to a concurrent decline in prey quality. Our finding of delayed breeding in 2007 and 2008 is consistent with a similar, previously reported shift in phenology in several other seabird species breeding at colonies bordering the North Sea (Frederiksen et al. 2004a, Mavor et al. 2006, Wanless et al. 2008) and contrasts with the trend towards earlier breeding in terrestrial species (Crick 2004). The low fledging masses of chicks in 2007 and 2008 (mean = 410 g each year; Fig. 2) likely resulted in very low post-fledging survival (Perrins et al. 1973). However, fledging mass was very variable and about 20% of fledglings each year weighed more than 450 g (Fig. 5), giving them a much higher probability of survival (Perrins et al. 1973) and suggesting that some parents were able to feed their chick adequately. This pattern was consistent with studies elsewhere indicating that a small proportion of individuals often make a disproportionately large contribution to population maintenance and growth (Brooke 1986, Kruger & Lindstrom 2001, Van de Pol et al. 2006).

The observed decrease in adult attendance was the result of a change in foraging behaviour whereby parents increased both the duration and frequency of long trips, with a decrease in the frequency of 2 and 3 d trips. Parents thus switched from using mainly short foraging trips in 1999 and 2002 to a dual-foraging strategy in 2007 and 2008. This change in foraging behaviour is similar to that seen in Cory's shearwater *Calonectris diomedea*, which also switched to dual-foraging

under conditions of low prey availability (Granadeiro et al. 1998, Magalhaes et al. 2008). The sizes of single meals were not affected in this study, but the average yield to chicks from single meals was much lower in 2007 and 2008 than in 1999 and 2002 (21.7 g d^{-1} and 27.8 g d^{-1} , respectively; calculated from data in Table 1) as a result of longer intervals between feeds. Double meals were substantially smaller in 1999 and 2002 than in 2007 and 2008 and were close to twice the sizes of single meals only in the latter period, probably because in the earlier years, when they were fed more frequently, chicks were unable to accept all the food provided by the second parent to return overnight.

The fact that parents performed fewer 2 to 3 d trips in 2007 and 2008 suggests that prey may have been present in sufficient quantity only at longer distances from the colony (Pichegru et al. 2007). This is consistent with a suspected northerly shift in the foraging areas of these birds in recent years (Guilford et al. 2008). Manx shearwaters prey mainly on 1 and 2 yr old clupeids (Brooke 1990), and so the negative effect of both increases in winter SST and decreases in the body masses of 2 yr old herring suggests that warming of surface waters may have had a negative impact on the growth and nutritional quality of prey, as also suggested for sandeels *Ammodytes marinus* in the North Sea since the early 1980s (Wanless et al. 2004, 2005). In waters around western Britain, there is recent evidence that some fish species have also been affected through bottom-up processes (Todd et al. 2008). In our study, peak masses of chicks were negatively related to SST in the immediately preceding winter, suggesting that these effects have now been propagated to a higher trophic level, in a similar manner to that previously recorded in the North Sea (Frederiksen et al. 2004b) and in other oceanographic regions (Guinet et al. 1998, Gjerdrum et al. 2003).

In contrast to Manx shearwaters, guillemots *Uria aalge* and razorbills *Alca torda* (Alcidae) have apparently bred normally in recent years on Skomer (D. Boyle pers. comm.). This difference in responses may reflect differences in foraging depths, with guillemots and razorbills both being capable of diving much deeper than Manx shearwaters (Thaxter et al. 2010), or in the timing of breeding, since chicks of both these species have fledged from the breeding cliffs when Manx shearwaters are still feeding young chicks. However, in contrast to events during the breeding season, there is recent evidence that the over-winter survival of guillemots from Skomer is negatively related to the NAO index, and thus lower in warmer, wetter and windier winters, which have increased in frequency in recent years (Votier et al. 2005). Together, these 2 studies suggest that within the NE Atlantic region, adverse impacts of anthropogenic climate change on higher marine predators are no longer restricted to the vicinity of the North Sea.

Acknowledgements. We thank the Countryside Council for Wales, the Wildlife Trust of South and West Wales, and the Skomer and Skokholm Management Committee for permission to work on Skomer and Skokholm Islands. We also thank D. Boyle, J. Brown, J. and D. Milborrow, and C. Taylor for advice and help with logistics. Thanks to S. Abdalla, A. Harrison and B. Kesso for help in the field.

LITERATURE CITED

- Aebischer NJ, Coulson JC, Colebrook JM (1990) Parallel long-term trends across four marine trophic levels and weather. *Nature* 347:753–755
- Ainley DG, Blight LK (2009) Ecological repercussions of historical fish extraction from the southern ocean. *Fish Fish* 10:13–38
- Axenrot T, Hansson S (2003) Predicting herring recruitment from young-of-the-year densities, spawning stock biomass, and climate. *Limnol Oceanogr* 48:1716–1720
- Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. *J Anim Ecol* 78: 699–714
- Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog Oceanogr* 60:245–262
- Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–1694
- Behrenfeld MJ, Falkowski PG (1997) Photosynthetic rates derives from satellite-based chlorophyll concentration. *Limnol Oceanogr* 42:1–20
- Behrenfeld MJ, O'Malley RT, Siegel DA, McClain CR and others (2006) Climate-driven trends in contemporary ocean productivity. *Nature* 444:752–755
- Borges MF, Santos AMP, Crato N, Mendes H, Mota B (2003) Sardine regime shifts off Portugal: a time series analysis of catches and wind conditions. *Sci Mar* 67:235–244
- Brander KM (2007) Global fish production and climate change. *Proc Natl Acad Sci USA* 104:19709–19714
- Brooke MdeL (1986) Seasonal, parental, and genetic influences on the chick's age and weight at fledging. *Condor* 88:324–327
- Brooke MdeL (1990) The Manx shearwater. T. & A.D. Poyser, London
- Brooke MdeL (2004) Albatrosses and petrels across the world. Oxford University Press, Oxford
- Crick HQP (2004) The impact of climate change on birds. *Ibis* 146:48–56
- D'Alba L, Monaghan P, Nager RG (2010) Advances in laying date and increasing population size suggest positive responses to climate change in Common Eiders *Somateria mollissima* in Iceland. *Ibis* 152:19–28
- Diamond AW (1978) Feeding strategies and population size in tropical seabirds. *Am Nat* 112:215–223
- Durant JM, Anker-Nylssen T, Stenseth NC (2003) Trophic interactions under climate fluctuations: the Atlantic puffin as an example. *Proc Biol Sci* 270:1461–1466
- Duriez O, Weimerskirch H, Fritz H (2000) Regulation of chick provisioning in the thin-billed prion: an interannual comparison and manipulation of parents. *Can J Zool* 78:1275–1283
- Frank KT, Petrie B, Shackell NL (2007) The ups and downs of trophic control in continental shelf ecosystems. *Trends Ecol Evol* 22:236–242
- Frederiksen M, Harris MP, Daunt F, Rothery P, Wanless S (2004a) Scale-dependant climate signals drive breeding phenology of three seabird species. *Glob Change Biol* 10: 1214–1221
- Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson LJ (2004b) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *J Appl Ecol* 41:1129–1139
- Frederiksen M, Edwards M, Richards AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *J Anim Ecol* 75:1259–1268
- Frederiksen M, Furness RW, Wanless S (2007) Regional variation in the role of bottom-up and top-down processes in controlling sandeel abundance in the North Sea. *Mar Ecol Prog Ser* 337:279–286
- Furness RW, Tasker ML (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Mar Ecol Prog Ser* 202: 253–264
- Gjerdrum C, Vallée AMJ, St. Clair CC, Bertram DF, Ryder JL, Blackburn GS (2003) Tufted puffin reproduction reveals ocean climate variability. *Proc Natl Acad Sci USA* 100: 9377–9382
- Granadeiro JP, Nunes M, Silva M, Furness RW (1998) Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chick-rearing period. *Anim Behav* 56: 1169–1176
- Granadeiro JP, Burns MD, Furness RW (1999) Food provisioning to nestling shearwaters: why parental behaviour should be monitored? *Anim Behav* 57:663–671
- Gray CM, Hamer KC (2001) Food-provisioning behaviour of male and female Manx shearwaters, *Puffinus puffinus*. *Anim Behav* 62:117–121
- Greene CH, Pershing AJ (2007) Climate drives sea change. *Science* 315:1084–1085
- Grémillet D, Boulinier T (2009) Spatial ecology and conservation of seabirds facing global climate change: a review. *Mar Ecol Prog Ser* 391:121–137
- Guilford TC, Meade J, Freeman R, Biro T and others (2008) GPS tracking of the foraging movements of Manx Shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis* 150:462–473
- Guinet C, Chastel O, Koudil M, Durbec JP, Jouventin P (1998) Effects of warm sea-surface temperature anomalies on the blue petrel at the Kerguelen Islands. *Proc Biol Sci* 265: 1001–1006
- Hamer KC (2010) The search for winners and losers in a sea of climate change. *Ibis* 152:3–5
- Hamer KC, Hill JK (1997) Nestling obesity and variability of food delivery in Manx shearwaters, *Puffinus puffinus*. *Funct Ecol* 11:489–497
- Hamer KC, Furness RW, Caldow RWG (1991) The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. *J Zool (Lond)* 223:175–188
- Hamer KC, Quillfeldt P, Masello JF, Fletcher KL (2006) Sex differences in provisioning rules: responses of Manx shearwaters to supplementary chick feeding. *Behav Ecol* 17:132–137
- Hamer KC, Humphreys EM, Garthe S, Hennenke J and others (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Mar Ecol Prog Ser* 338: 295–305
- Harris MP (1966) Breeding biology of the Manx Shearwater *Puffinus puffinus*. *Ibis* 108:17–33
- Hockey PAR, Midgley GF (2009) Avian range changes and climate change: a cautionary tale from the Cape Peninsula. *Ostrich* 80:29–34
- Hunt GL Jr, Stabeno P, Walters G, Sinclair E, Brodeur RD,

- Napp JM, Bond NA (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Res II* 49:5821–5853
- ICES (International Council for the Exploration of the Sea) (2007) Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems. ICES Advice Book 5. ICES, Copenhagen
- ICES (2009) Report of the Herring Assessment Working Group for the area south of 62°N (HAWG). ICES Headquarters, Copenhagen
- IPCC (Intergovernmental Panel on Climate Change) (2007) Climate change 2007. Synthesis report. Contribution of Working Groups I, II & III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva
- Jacobs SS, Giulivi CF, Mele PA (2002) Freshening of the Ross Sea during the late 20th Century. *Science* 297:386–389
- Kruger O, Lindstrom J (2001) Lifetime reproductive success in common buzzard, *Buteo buteo*: from individual variation to population demography. *Oikos* 93:260–273
- Le Bohec C, Durant JM, Gauthier-Clerc M, Stenseth NC and others (2008) King penguin population threatened by Southern Ocean warming. *Proc Natl Acad Sci USA* 105:2493–2497
- Lockley RM (1930) On the breeding habits of the Manx Shearwater, with special reference to its incubation- and fledging-periods. *Br Birds* 23:202–218
- Magalhaes MC, Santos RS, Hamer KC (2008) Dual-foraging of Cory's shearwaters in the Azores: feeding locations, behaviour at sea and implications for food provisioning of chicks. *Mar Ecol Prog Ser* 359:283–293
- Mavor RA, Parsons M, Heubeck M, Schmitt S (2006) Seabird numbers and breeding success in Britain and Ireland, 2005. UK Nature Conservation No. 30. Joint Nature Conservation Committee, Peterborough
- Oswald SA, Bearhop S, Furness RW, Huntley B, Hamer KC (2008) Heat stress in a high-latitude seabird: effects of temperature and food supply on bathing and nest attendance of great skuas. *J Avian Biol* 39:163–169
- Oswald SA, Huntley B, Collingham YC, Russell DJF, Anderson BJ, Arnold JM, Furness RW, Hamer KC (in press) Physiological effects of climate on distributions of endothermic species. *J Biogeogr*
- Perrins CM, Harris MP, Britton CK (1973) Survival of Manx shearwaters *Puffinus puffinus*. *Ibis* 115:535–548
- Perry AL, Low PL, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915
- Pichegru L, Ryan PG, van der Lingen CD, Coetzee J, Ropert-Coudert Y, Grémillet D (2007) Foraging behaviour and energetics of Cape gannets *Morus capensis* feeding on live prey and fishery discards in the Benguela upwelling system. *Mar Ecol Prog Ser* 350:127–136
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-Plus. Springer, New York, NY
- Poloczanska ES, Cook RM, Ruxton GD, Wright PJ (2004) Fishing vs. natural recruitment variation in sandeels as a cause of seabird breeding failure at Shetland: a modelling approach. *ICES J Mar Sci* 61:788–797
- Quillfeldt P, Masello JF, Hamer KC (2004) Sex differences in provisioning rules and honest signalling of need in Manx shearwaters, *Puffinus puffinus*. *Anim Behav* 68:613–620
- Quillfeldt P, Strange IJ, Masello JF (2007) Sea surface temperatures, variable food supply and behavioural buffering capacity in thin-billed prions *Pachyptila belcheri*: breeding success, provisioning and chick begging. *J Avian Biol* 38:298–308
- Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305:1609–1612
- Riou S, Hamer KC (2008) Predation risk and reproductive effort: impacts of moonlight on food provisioning and chick growth in Manx shearwaters. *Anim Behav* 76:1743–1748
- Swann B (2000) Integrated seabird monitoring studies on the island of Canna, Scotland 1969–99. *Atlantic Seabirds* 2:151–164
- Thaxter CB, Wanless S, Daunt F, Harris MP, Benvenuti S, Watanuki Y, Grémillet D, Hamer KC (2010) Influence of wing loading on the trade-off between pursuit-diving and flight in common guillemots and razorbills. *J Exp Biol* 213:1018–1025
- Thompson PM, Ollason JC (2001) Lagged effects of ocean climate change on fulmar population dynamics. *Nature* 413:417–420
- Todd CD, Hughes SL, Marshall CT, MacLean JC, Lonergan ME, Biuw EM (2008) Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Glob Change Biol* 14:958–970
- Toggweiler JR, Russell J (2008) Ocean circulation in a warming climate. *Nature* 451:286–288
- Van de Pol M, Bruinzeel LW, Heg D, Van der Jeugd HP, Velhurst S (2006) A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (*Haematopus ostragalus*). *J Anim Ecol* 75:616–626
- Votier SC, Hatchwell BJ, Beckerman A, McCleery RH, Hunter FM, Pellatt J, Trinder M, Birkhead TR (2005) Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecol Lett* 8:1157–1164
- Wanless S, Wright PJ, Harris MP, Elston DA (2004) Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. *Mar Ecol Prog Ser* 279:237–246
- Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar Ecol Prog Ser* 294:1–8
- Wanless S, Frederiksen M, Daunt F, Scott BE, Harris MP (2007) Black-legged kittiwakes as indicators of environmental change in the North Sea: evidence from long-term studies. *Prog Oceanogr* 72:30–38
- Wanless S, Harris MP, Lewis S, Frederiksen M, Murray S (2008) Later breeding in northern gannets in the eastern Atlantic. *Mar Ecol Prog Ser* 370:263–269
- Watermeyer KE, Shannon LJ, Roux JP, Griffiths CL (2008) Changes in the trophic structure of the northern Benguela before and after the offset of industrial fishing. *Afr J Mar Sci* 30:383–403
- Weimerskirch H (1998) How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. *J Anim Ecol* 67:99–109
- Weimerskirch H, Chastel O, Ackermann L, Chaurand T, Cuenot-Chaillet F, Hindermeyer X, Judas J (1994) Alternate long and short foraging trips in pelagic seabird parents. *Anim Behav* 47:472–476