biology letters
Marine biology

Biol. Lett. (2007) **3**, 185–188
doi:10.1098/rsbl.2006.0588
Published online 9 January 2007

Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change mean more starving porpoises?

Colin D. MacLeod[1,*], M. Begoña Santos[1], Robert J. Reid[2], Beth E. Scott[1] and Graham J. Pierce[1]

[1]*School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK*
[2]*Wildlife Unit, Scottish Agricultural College Veterinary Services, Drummondhill, Stratherrick Road, Inverness IV2 4JZ, UK*
**Author for correspondence (c.d.macleod@abdn.ac.uk).*

Sandeels are known to be negatively affected by climate change in a number of ways. This study investigated whether these changes are affecting the harbour porpoise (*Phocoena phocoena*), a species which consumes sandeels. Porpoise diet was examined in spring (March–May), a critical time of year for survival when sandeels are important prey, from 1993 to 2001 to provide baseline information on the proportion of sandeels consumed. When data from spring 2002 and 2003 were compared to these baseline data, the diet was found to be substantially different, with a significant and substantially smaller proportion of sandeels being consumed in March and May. There were also differences in the number of porpoises starving between the two time periods (33% in spring 2002 and 2003 died of starvation, but only 5% in the baseline period). This suggests that a lower proportion of sandeels in the diet of porpoises in spring increases the likelihood of starvation. Therefore, we suggest that the negative effects of climate change on sandeel availability may have serious negative effects on harbour porpoise populations in the North Sea by increasing the likelihood of starvation in spring.

Keywords: harbour porpoise; sandeels; climate change

1. INTRODUCTION

Climate change has the potential to affect marine mammals in a wide variety of ways (Learmonth *et al.* 2006). However, investigating whether potential effects are actually happening is often limited by a lack of sufficient data to undertake the detailed analyses required to identify them. In this study, information from other, better studied, marine predators with similar dietary preferences (seabirds) is used as a framework to place the effects of variation in the diet of a marine mammal species, the harbour porpoise (*Phocoena phocoena*), in the context of a potential impact of climate change. Specifically, this study investigated whether changes in the availability of their main prey in spring, sandeels (*Ammodytes* spp.), that have been linked to changes in climate through detailed long-term studies on seabirds, could also have an effect on porpoises.

At around 1.5 m length and 50 kg weight, the harbour porpoise is the smallest cetacean in Europe. Its small size limits the amount of stored energy it can carry, and it can only survive very short periods (as little as 3 days) without feeding (Kastelein *et al.* 1997). Therefore, a relatively continuous availability of the right prey is important. Any changes in prey availability may affect energy stores, and ultimately survival. While porpoises will consume a wide variety of prey species, a few key species dominate the diet at specific times of the year in Scottish waters (Santos *et al.* 2004). In particular, in spring, sandeels are among the most important prey items for porpoises in the Scottish North Sea (Santos *et al.* 2004).

Spring is a critical time for porpoises in terms of energy requirements. Some of the coldest water temperatures in the Scottish North Sea occur in March, placing the greatest thermodynamic stress on porpoises and requiring the thickest blubber layer to limit heat loss. Since the blubber layer is also the site of energy storage, any reduction in the size of energy stores due to poor feeding will increase thermodynamic stress by reducing the level of insulation provided by the blubber and increasing the risk of lethal cooling. This, in turn, will increase the energy required to maintain a stable internal body temperature (Watts *et al.* 1993) and, therefore, will increase the amount of energy used each day. In addition, young animals are weaned and become independent in spring. As inexperienced foragers they may be less able to cope with changes in prey availability.

In addition to being important for porpoises, sandeels are a critical component of the North Sea ecosystem as a whole (Greenstreet 1996). The availability of sandeels plays an important role in the demography of many seabirds. For example, the black-legged kittiwake (*Rissa tridactyla*) requires sufficient availability of sandeels both to get into breeding condition and, later, to feed to the chicks (Frederiksen *et al.* 2004). Kittiwake populations, and those of other seabirds in the North Sea, have been monitored for long periods of time and the effects of changes in sandeel availability upon them have been studied in more detail (e.g. Frederiksen *et al.* 2004; Wanless *et al.* 2004, 2005; Scott *et al.* 2006).

This study examined whether there is any link between sandeel consumption and the likelihood of starvation in porpoises. Information from studies of kittiwakes and other seabirds was then used to place the link between sandeel consumption and mortality of porpoises in a wider ecological context with particular reference to the effects of climate change on sandeels.

2. MATERIAL AND METHODS

Stomach contents were collected from stranded porpoises from the coasts of eastern Scotland, Orkney, Shetland and the Pentland Firth (collectively the Scottish North Sea coasts) as part of a dedicated strandings reporting scheme that also investigated the cause of death and other biological parameters. Full details of the methods used to analyse stomach contents, identify prey remains

Received 10 November 2006
Accepted 14 December 2006

Table 1. A comparison of the diet of porpoises during spring 1993–2001 with spring 2002–2003. (There were insufficient sandeels to undertake a statistical comparison of size of sandeels in the diet in March.)

	number stomachs examined		average number of prey per stomach		percentage of animals with sandeels in stomach		percentage of prey that were sandeels		*p*-values from χ^2-test	comparison of size of sandeels consumed					
										percentage of sandeels					
										>10 cm		<10 cm			
month	1993–2001	2002–2003	1993–2001	2002–2003	1993–2001	2002–2003	1993–2001	2002–2003		1993–2001	2002–2003	1993–2001	2002–2003	*p*-values from χ^2-test	percentage of animals starved 1993–2001	2002–2003
Mar	14	4	243.4	40.3	50	25	60.8	6.6	<0.001	42.6	0.0	53.4	100.0	—	5	33
Apr	17	8	361.8	110.4	65	62	93.1	89.4	<0.001	48.8	42.1	49.2	54.9	<0.001		
May	20	4	218.9	86.2	70	75	96.4	39.7	<0.001	15.3	85.3	84.1	14.7	<0.001		

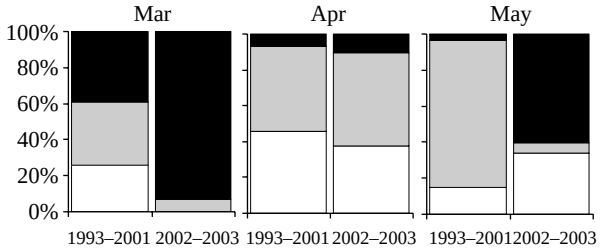

Figure 1. A comparison of the numerical proportions of different types of prey in porpoise diet in porpoises during spring 1993–2001 and 2002–2003. White bars, sandeels larger than 10 cm; grey, sandeels smaller than 10 cm; black bars, other prey species.

and estimate prey size, and results on overall diet composition, can be found in Santos *et al.* (2004). The numerical proportion of sandeels in the diet in spring from 1993 to 2001 was calculated by combining data from all stomach contents for each month and this was used as a baseline for the contribution of sandeels to porpoise diet in spring. Data from spring 2002 and 2003 were then compared to this baseline using the average number of prey remains per stomach, the proportion of individuals that contained sandeels and the numerical proportion of sandeels in the diet. In addition, sandeels were divided into two size classes (smaller than 10 cm representing fish aged 1 year or less and larger than 10 cm representing multi-year fish) and the relative importance of each size class was compared between the two time periods. Finally, the proportions of porpoises where a cause of death was determined as starvation in the baseline period and in spring 2002 and 2003 were compared to differences in diet. Causes of death were determined during veterinary post-mortem examinations at the Scottish Agricultural College (SAC), conducted as part of the UK Cetacean Strandings Project.

3. RESULTS

Stomach contents were available for 51 porpoises from spring 1993 to 2001 (the baseline period) and 16 from spring 2002 and 2003 (table 1). The average number of individual prey items per stomach was much less (between 17 and 39% of the monthly averages in the baseline period) in each month in spring 2002–2003 in comparison to 1993–2001 (table 1). In addition, the proportion of porpoises from which any sandeel remains were recovered in March 2002–2003 was 50% of that in the baseline period. However, the proportions of porpoises with sandeels in their stomach in April and May were similar for the two time periods (table 1).

Sandeels made up a significantly smaller proportion of the diet in each month in spring 2002–2003 than expected based on the proportion of sandeels in each month recorded in 1993–2001. This was particularly marked in March and May, but much less so in April (figure 1). In addition, where it could be calculated, there was a significant difference in the proportions of sandeels of different size classes in the diet, with a smaller proportion of large-sized and a greater proportion of smaller-sized sandeels being consumed in April 2002–2003 than expected from the baseline period, while the opposite was true in May (table 1 and figure 1).

These differences in diet between spring 1993–2001 and spring 2002–2003 coincide with a change in the proportion of porpoises dying due to starvation. In the baseline period, only four (one in each year between 1997 and 2000) out of 85 porpoises where the cause of death was determined died from

starvation (5%). This compares with seven (three in 2002 and four in 2003) out of 21 porpoise (33%) deaths in spring 2002–2003. This difference is significant ($\chi^2 = 14.52$, $p = 0.0001$). These starving animals were primarily young, post-weaning individuals and were of similar body sizes to the animals whose stomach contents were analysed.

4. DISCUSSION

This study found that harbour porpoises in the Scottish North Sea consumed a significantly smaller proportion and different sizes of sandeels in spring 2002 and 2003 in comparison with the baseline period (1993–2001). Although based on a relatively small sample size, the differences are sufficiently marked to be noteworthy. The concurrent increase in the proportion of porpoises starving and the lack of sandeels in the diet suggest that there is a link between the two. There are at least three possible reasons why such a link could exist: (i) alternative prey types (such as whiting *Merlangius merlangus* or haddock *Melanogrammus aeglefinus*) have a lower energy content than sandeels, (ii) there are higher energetic costs associated with locating and catching alternative prey, and (iii) sandeels were not replaced by another species and the total number of prey consumed was reduced, increasing the reliance on stored energy in the blubber. This would reduce the insulative properties of the blubber and increase the risk of starvation-induced hypothermia. The substantially lower average number of prey recorded per stomach in spring 2002–2003 in comparison with the baseline period (table 1) provides some support for the third hypothesis.

This raises the question of why a lower proportion of sandeels was consumed in spring 2002–2003. It has been well documented that some population parameters of seabirds that feed on sandeels are linked to sandeel availability. As a result, changes in oceanographic conditions resulting from climate change have been hypothesized to affect seabirds through their negative effects on sandeel availability, body size and energy content. This leads to a reduction in the proportion of sandeels in the diet, with less energy being obtained from each individual sandeel, which reduces breeding success and adult survival (Frederiksen *et al.* 2004; Wanless *et al.* 2004, 2005; Scott *et al.* 2006). With reference to the time periods used in this study, both the spawning stock biomass and sandeel recruitment in the North Sea were substantially lower in 2002 and 2003 than at any point from 1993 to 2001 (Anonymous 2006). Similarly, in 2002 and 2003, in seabirds such as the common guillemot (*Uria aalge*) and the black-legged kittiwake that rely heavily on sandeels, the breeding success was relatively low in the Scottish North Sea in comparison with the period 1993–2001 (Anonymous 2005).

A lower availability of sandeels in spring in recent years, owing to the effects of climate-driven changes (Frederiksen *et al.* 2004), is consistent with the findings of this study. Therefore, climate-change driven changes in the availability of sandeels identified through longer-term studies on seabirds provides a framework into which the changes suggested by the shorter time-series of data from porpoises can be placed to help explain the observed differences. If, as predicted by climate models (Clark *et al.* 2003), the trends to warmer water temperatures and increased variation in the timing of the spring phytoplankton bloom continue, the availability of sandeels in spring is likely to be further reduced. This will increase the likelihood of starvation in porpoises and have implications for their conservation.

Analysis of stomachs collected up to 1997 was funded by the Commission of the European Communities under Contracts ERB 4001 GT 93/3630 and ERB FMBI CT96 1373. Sample collection and analysis during 1998–2000 was funded under CEC DG XIV Study Project 98/089. Sample collection and analysis during 2001–2003 was funded under CEC project EVK3-CT-2000-00027. The authors would like to thank H. Ross and I.A.P. Patterson (SAC Veterinary Science Division, Inverness, Scotland) for the provision of cause of death data. The SAC necropsy examinations were funded by Defra, previously DETR and DOE. Finally, the authors would like to thank S. Wanless for comments on the earlier drafts of this manuscript.

Anonymous 2005 *UK Seabirds in 2005: results from the UK seabird monitoring programme*. Available from www.jncc.gov.uk/PDF/pub05_ukseabirdsin2005.pdf.

Anonymous 2006 *ICES Advice 2006*, Volume 6. Available from http://www.ices.dk/advice/icesadvice.asp.

Clark, R. A., Fox, C. J., Viner, D. & Livermore, M. 2003 North Sea cod and climate change—modelling the effects of temperature on population dynamics. *Glob. Change Biol.* **9**, 1669–1680. (doi:10.1046/j.1365-2486.2003.00685.x)

Frederiksen, M., Wanless, S., Harris, M. P., Rothery, P. & Wilson, L. J. 2004 The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *J. Appl. Ecol.* **41**, 1129–1139. (doi:10.1111/j.0021-8901.2004.00966.x)

Greenstreet, S. P. R. 1996 Estimation of the daily consumption of food by fish in the North Sea in each quarter of the year. Report No 55. Scottish Fisheries Research, Aberdeen.

Kastelein, R. A., van der Sijs, S. J., Staal, C. & Nieuwstraten, S. H. 1997 Blubber thickness in harbour porpoises (*Phocoena phocoena*). In *The biology of the harbour porpoise read* (eds A. J. Read, P. R. Wiepkema & P. E. Nachtigall), pp. 179–199. Woerden, The Netherlands: De Spil Publishers.

Learmonth, J. A., MacLeod, C. D., Santos, M. B., Pierce, G. J., Crick, H. Q. P. & Robinson, R. A. 2006 Potential effects of climate change on marine mammals. *Oceanogr. Mar. Biol.* **44**, 431–464.

Santos, M. B., Pierce, G. J., Learmonth, J. A., Reid, R. J., Ross, H. M., Patterson, I. A. P., Reid, D. G. & Beare, D. 2004 Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992–2003. *Mar. Mamm. Sci.* **20**, 1–27. (doi:10.1111/j.1748-7692.2004.tb01138.x)

Scott, B. E., Sharples, J., Wanless, S. & Ross, O. 2006 The use of biologically meaningful oceanographic indices to separate the effects of climate and fisheries on seabird breeding success. In *Top predators in marine ecosystems:*

their role in monitoring and management, vol. 12 (eds I. L. Boyd, S. Wanless & C. J. Camphuysen), pp. 46–62. Zoological society of London conservation biology series. Cambridge, UK: Cambridge University Press.

Wanless, S., Wright, P. J., Harris, M. P. & Elston, D. A. 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, M. P., Redman, P. & Speakman, J. R. 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.

Watts, P., Hansen, S. & Lavigne, D. M. 1993 Models of heat loss by marine mammals: thermoregulation below the zone of irrelevance. *J. Theor. Biol.* **163**, 505–525. (doi:10.1006/jtbi.1993.1135)