Analysis of historical and recent diet and strandings of sperm whales (*Physeter macrocephalus*) in the North Sea

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Abstract: The increasing frequency of sperm whale (*Physeter macrocephalus*) strandings during the winter in the North Sea has resulted in many theories about why this phenomenon occurs. Using a newly updated catalogue of North Sea sperm whale strandings, the possible roles of environmental drivers, which might affect the entry of migrating sperm whales into the North Sea and/or their stranding, were investigated using generalised additive mixed models. Little or no evidence was found of effects of sunspot activity, the North Atlantic Oscillation (NAO) Index or sea surface pressure around Iceland (a component of the NAO) on the occurrence of strandings. Several sea and land surface temperature indices were positively correlated with the occurrence of strandings. There is evidence of changing relationships between strandings and environmental variables during the last three decades and, given the absence of an obvious mechanism by which the temperature-strandings link might operate, it is important to recognise that several different processes may contribute to the strandings, including the recovery of the sperm whale population following the cessation of commercial whaling in the late 20th century. In addition, and since temperature could also be affecting the whales´ prey and changes in prey distribution could explain whale stranding patterns, this paper updates previous studies of diet, confirming the continued dominance of the Boreoatlantic armhook squid *Gonatus fabricii* in stomach contents of sperm whales stranded on North Sea coasts, although remains of small numbers of North Sea species were also found, suggesting some feeding within the North Sea.

Keywords: sperm whale, Boreoatlantic armhook squid, stranding, sea surface temperature, land surface temperature, diet, stomach contents analysis.

Introduction

Sperm whales (*Physeter macrocephalus*) are known to have entered the North Sea and stranded since at least the 13th century. Almost invariably these animals seem to have been males, travelling southwards in the winter from summer feeding grounds in the Arctic (Smeenk 1997, Smeenk & Evans, this volume). The presence – and deaths – of large numbers of sperm whales in a shallow sea area such as the North Sea in the 1990s and the wide year-to-year fluctuation in numbers of whale deaths led to considerable attention and speculation about causes (e.g. the set of papers collected in Jacques & Lambertsen 1997). Possible explanations relate to the distribution, abundance, health and navigational skills of the whales as well as effects of a range of anthropogenic stressors including climate change as well as the possibility that we are documenting rare, random events. It is also important to bear in mind that reasons for sperm whales entering the North Sea may be unrelated to the ultimate cause of death; the explanation for the strandings in the North Sea needs to consider both questions.

The occurrence of feeding migrations in sub-adult and adult male sperm whales is well-documented. The need for the whales to return southwards from Arctic feeding grounds puts them in proximity of the entrance to the North Sea but generally they travel southwards through deep Atlantic waters along the west coast of the UK. Past dietary studies have consistently revealed little evidence of sperm whales feeding within the North Sea; stomach contents of whales stranded on North Sea coasts are usually dominated by the remains of the hard structures (mandibles) of the Boreoatlantic armhook squid *Gonatus fabricii* (e.g. Santos et al. 1999, 2001, 2002, Simon et al. 2003), a species found in Arctic and sub-Arctic waters (Bjørke 2001), and with little evidence of recent feeding.

Gonatus fabricii is the most abundant squid in Arctic and sub-Arctic waters; Bjorke (2001) estimated that it reached a biomass of 1.5 million tonnes in the Norwegian Sea in 1994. As speculated by Santos et al. (1999), it is possible that year to year changes in the distribution and abundance of *Gonatus* influence the likelihood of sperm whales entering the North Sea, for example because the distribution in some years extends closer to the North Sea (e.g. into the Norwegian Deeps). Alternative possibilities are that more sperm whales are present in the Arctic in years of high squid abundance and that a higher proportion of whales migrate southwards in years of low abundance. While few data exist on distribution and abundance of *Gonatus*, there is evidence of substantial year to year variation in its abundance (see Dalpadado et al. 1994).

Sperm whale populations have presumably recovered since the cessation of commercial whaling on this species around 1988 (Whitehead 2002) and increasing whale density may have resulted in more males undertaking feeding migrations to the Arctic. Evans (1997) reported evidence for a higher frequency of younger males among strandings on eastern North Atlantic coasts in recent years and suggested this may have been due increased competition for females on the breeding grounds as populations recovered from the earlier harvesting of the more mature males. Thus we might expect a steady increase in numbers of whales entering the North Sea, although perhaps starting only once a threshold density had been achieved. However, sperm whale population size probably reached an all-time low in the latter half of the 20th century and it is unlikely that abundance has recovered to pre-whaling levels (see hypothetical population trajectories in Whitehead 2002).

Vanselow & Ricklefs (2005) and Vanselow et al. (2009, 2017) have pointed to the possible effect of solar disturbances on sperm whale navigation as a plausible explanation for many strandings, although the statistical support for this is weak. The role of great storms (documented in the North Sea by Lamb (1991)) was investigated by Nielen (2018), who found no apparent relationship. Smeenk (1997) referred to the North Sea as a "sperm whale trap", in which shallow sloping sandy seabeds in coastal waters rendered sperm whale navigation ineffective. The normal migration route of males which have been feeding in the Arctic passes through deep waters to the west of the United Kingdom and it is likely true that a high proportion of sperm whales which enter the North Sea subsequently perish on its coasts. If so, the key question is likely to be why more sperm whales enter the North Sea in some years than in others.

Studies on carcasses of stranded sperm whales on North Sea coasts have revealed high contaminant burdens (Holsbeek et al. 1999) and the presence of significant quantities of plastics in the digestive tracts (Unger et al. 2016). While such findings highlight anthropogenic pressures faced by cetaceans, the pollutants and plastics were not thought to have been responsible for the deaths. Evidently not all sperm whales which strand are healthy animals, and in some cases poor health may contribute to navigational errors, perhaps explaining entry into the North Sea (Hansen et al. 2016). However, in general, even if the North Sea is a sperm whale trap, it seems unlikely that it is also a sperm whale graveyard; it is not a gathering place for ailing and moribund whales. It is worth noting that effects of plastics and PCBs or indeed seismic surveys and naval sonar are modern day threats and could not explain the occurrence of strandings over a half a millennium, nor are they likely to explain the wide year to year variation in numbers of strandings.

Effects of climate variation and change may be suspected, not least due to the known sensitivity of squid (the sperm whale´s main prey) distribution and abundance to changing environmental conditions. However, this suggests only a rather vague general hypothesis. In its favour is a weak but statistically significant positive relationship between occurrence of strandings and sea temperature (Pierce et al. 2007) but the underlying mechanism (if any) remains unclear. Indeed, it is not obvious whether warming would have a positive or negative influence on *Gonatus* abundance. Higher abundance could result in wider distribution of *Gonatus* and draw whales closer to the North Sea while lower abundance could favour more whales undertaking the southward migration rather than remaining in the Arctic.

An obvious question is whether sperm whale strandings in the North Sea are chance events. In some respects, they are obviously not: sub-adult and young adult male sperm whales tend to move around in groups and a stranding of multiple animals cannot be considered as multiple independent events. The likelihood of strandings being reported has probably increased with the density of coastal human populations and in the last century with the emergence of dedicated strandings networks, many of which have become increasingly professional and better funded over the last two or three decades. In addition, publicity likely begets publicity: after a recorded stranding the efficiency with which subsequent strandings are reported may increase. This does not preclude strandings events themselves being essentially random, i.e. whether and how many strandings occur in a given year are independent of what happened in the previous year – something easily tested. Finally, we cannot rule out the possibility that there are multiple causes of the North Sea strandings.

The first two decades of the 21st century have also seen substantial numbers of sperm whale strandings in the North Sea and it is therefore appropriate to revisit evidence about causes. Here we re-examine two specific questions, about the diet of these whales (is there any evidence that they enter the North Sea to feed; has the diet changed over time?) and causes of variation in numbers stranded.

Methods

Diet

We compiled dietary data from our previous publications (which included samples from 1990 to 2004 as well as one from 1937), adding data from stomach contents for four additional individuals stranded in Scotland (UK) during 2002 to 2014 (see table 1). In most cases, only a sample of the stomach contents could be obtained (e.g. samples from Cruden Bay, Aberdeenshire (UK) in 1996 were taken when the carcasses exploded due to buildup of decomposition gases) and the absolute amount of prey remains recovered is not necessarily indicative of stomach fullness. No fresh prey remains were recovered in this

Table 1. Sources of stomach contents samples.

Stranding ID	Date	Season	Location	Area	Event	Age	Sex	Length (cm)	Source
PM1937	23/02/1937	W	Terneuzen NL *	NS	M (2)		Male	1600	2
CN 719	17/11/1990	W	Nymindegab DK	NS	S		Male	1185	1
CN 850	01/12/1991	W	Fanø DK	NS	M (3)		Male	1173	1
M2583/94 3	07/12/1994	W	Orkney UK	NS	M (11)	***	Male	1280	1
M2583/94 6	07/12/1994	W	Orkney UK	NS	M (11)	***	Male	1340	1
M2583/94 9	07/12/1994	W	Orkney UK	NS	M (11)	***	Male	1280	1
M2583/94 11	07/12/1994	W	Orkney UK	NS	M (11)	***	Male	1250	1
M0546/95	23/03/1995	W	Inverness UK	NS	S	23	Male	1370	1
M143/96B	28/01/1996	W	Cruden Bay UK	NS	M (6)		Male	1285	1
M143/96C	28/01/1996	W	Cruden Bay UK	NS	M (6)		Male	1210	1
M143/96D	28/01/1996	W	Cruden Bay UK	NS	M (6)	24	Male	1375	1
M143/96E	28/01/1996	W	Cruden Bay UK	NS	M (6)	19	Male	1365	1
M143/96F	28/01/1996	W	Cruden Bay UK	NS	M (6)		Male	1365	1
1	27/03/1996	W	Rømø DK	NS	M (16)	20	Male	1280	1
5	27/03/1996	W	Rømø DK	NS	M (16)	22	Male	1295	1
8	27/03/1996	W	Rømø DK	NS	M (16)	26	Male	1190	1
12	27/03/1996	W	Rømø DK	NS	M (16)	20	Male	1215	1
1996_009	29/03/1996	W	Tory Island IE	Atl	S		Male	1480	2
PM281197	27/11/1997	W	Wassenaarseslag NL	NS	S		Male	1175	2
Potvis 1	28/11/1997	W	Ameland NL	NS	M (4)		Male	1320	2
Potvis 2	28/11/1997	W	Ameland NL	NS	M (4)		Male	1421	2
Potvis 3	28/11/1997	W	Ameland NL	NS	M (4)		Male	1360	2
M1695/98	06/08/1998	S	Bettyhill UK	Atl**	S		Male	1220	2
M172/02	26/08/2002	S	Lewis UK	Atl	S		Male	1290	4
2004_057	05/05/2004	S	Quilty IE	Atl	S	Calf	Male	580	3
M305/06	10/12/2006	W	Burghead UK	NS	S		Male	1320	4
M133/12	18/05/2012	S	N. Uist UK	Atl	S		Male	1183	4
M11/14	11/01/2014	W	Edinburgh UK	NS	S		Male	1395	4

Seasons: W = winter, S = summer. Location: countries are indicated by two letter codes (DK, IE, DK, UK). Areas: NS = North Sea (east of 4˚W), Atl = Atlantic. Strandings: M = multiple (with number of animals), S = single. Ages of Scottish animals are taken from Mendes et al. (2007). Sources: 1 = Santos et al. (1999), 2 = Santos et al. (2002), 3 = Santos et al. (2006), 4 = this study. Notes: * Smeenk (this volume) records this stranding as occurring at Middelplaat (Westerschelde), just north of Terneuzen, on 24/2/37. ** The location is very close to the boundary at 4˚W. *** Three other animals from this mass stranding, not sampled for stomach contents, had estimated ages of 20-24.

mass stranding or in previous ones or in single animals analysed (at least by us).

Remains consisted principally of cephalopod beaks and fish otoliths, bones and eye lenses, and skate or ray egg capsules. Otoliths, beaks and bones were identified by MBS and GJP to the lowest possible taxonomic level, consulting reference material and relevant guides (e.g. Clarke 1986, Härkönen 1986). Results are expressed in terms of the minimum number of prey individuals represented (for details of stomach analysis methodology and diet quantification, see Santos et al. 1991, 2002).

For the diet analysis, we divided animals into North Sea (east of 4^0 W) and Atlantic (west of 4^0 W) coasts and considered strandings as belonging to winter (November to early April) or summer (the remainder of the year). Note that here we included animals stranded in the Orkney islands along with the North Sea animals although Smeenk (1997), and Smeenk & Evans (this volume) did not include them in the stranding record for the North Sea, since these islands were considered to be outside the North Sea. However, the Orkney islands are on the continental shelf, some distance from the deep waters to the west of the United Kingdom, including the Faroe-Shetland channel, which normally is used by migrating sperm whales. Therefore, we included them here (and they were included in Santos et al. 1999).

Strandings

The strandings series was compiled from Smeenk & Evans (this volume), thus extending (forwards) and updating that used in Pierce et al. (2007). Note that Smeenk & Evans also extended Smeenk´s (1997) series backwards in time from 1563 to the 1250s but this essentially added only one new occurrence record, of three animals stranded during two stranding events in the Netherlands either in 1254 or 1257, hence we retained the previous first record, from 1563, as the first in the series. We first compiled information on the number of sperm whale strandings on North Sea coasts per calendar year, excluding animals which did not strand or live stranded and escaped. Strandings that were described as "insufficiently documented", e.g. because the species was uncertain, were also excluded. Since strandings normally show a peak between November and March (Smeenk 1997) we also derived an alternative series, with each "year" running from July of the calendar year through to June of the following year. Thus, in the latter case the "1995" strandings refer to July 1995 to June 1996. Since more animals strand in the first six months of the year than in the second (Smeenk 1997), animals for which the month of stranding was unknown were assigned to the first half of the year. Both series of counts were then used to derive occurrence (i.e. presence-absence) series.

The times series of occurrence of strandings were tested for randomness using a non-parametric runs test. Strandings occurrence was then analysed in relation to the following variables (these series extend up to 2016, the last year of the strandings series, unless otherwise stated):

a. Annual (1701-) and winter (1751-) sunspot numbers (as used by Vanselow and co-authors);
b. The NAO index (1825-) and Iceland sea level pressure (i.e. the northern component of the NAO index, 1823-) (data available at https://crudata.uea.ac.uk/cru/data/nao/index.htm, see Jones et al. 1997). The latter index may be more directly relevant to the area in which the whales are found before entering (or not) the North Sea;
c. European (land) surface air temperature (LSAT) reconstructions by Luterbacher et al. (2004, 2006). Here we used winter (December of the previous year to February) and annual series (both 1563-2004);
d. Annual average sea surface temperature (SST) anomaly, available at https://www.eea.europa.eu/ and originating with the UK Meteorological Office´s Hadley Centre. We used global, North Sea and North Atlantic datasets (all 1870-2014).

We initially calculated correlations between the count and occurrence series and each of the environmental series, repeating this for the environmental series lagged by one year. As a way to examine the temporal consistency of the strandings-environment relationships, we plotted correlation "discovery curves", estimating the correlations after each successive year of data was added. This approach was run forwards from the year in which each environmental series started,

Table 2. Summary of stomach contents. The order of appearance of the whales in this table is the same as in table 1.

Date	Season	Country	Area	Fish					Cephalopods																			
									Squid																Octopus			
				Cho	Lop	Mm	Pv	UK	Arc	Chi	Ga	Gf	Hb	His	Hm	Hr	HtA	Lf	Lg	Ms	Td	Tm	Tp	Ts	Ec	Ha	Oct	UK
23/02/1937	W	NL	NS									7																2
17/11/1990	W	DK	NS									279																
01/12/1991	W	DK	NS									1	1															
07/12/1994	W	UK	NS									4260	3									4				1		
07/12/1994	W	UK	NS									1652	2	1								2				1		
07/12/1994	W	UK	NS									17																
07/12/1994	W	UK	NS									344	1									7						
23/03/1995	W	UK	NS	1								1439	2									60				3		
28/01/1996	W	UK	NS									72										1				1		
28/01/1996	W	UK	NS									207										2				2		
28/01/1996	W	UK	NS					1				1432										2		10	1	1		
28/01/1996	W	UK	NS	1								4631	84					1				31		3		5		6
28/01/1996	W	UK	NS	1								402										1						
27/03/1996	W	DK	NS				1																					
27/03/1996	W	DK	NS									98																2
27/03/1996	W	DK	NS									1																
27/03/1996	W	DK	NS					1				1064	2									5						
27/11/1997	W	NL	NS				1					402	5									4					1	6
28/11/1997	W	NL	NS									1546															1	
28/11/1997	W	NL	NS									160										1		1			17	
28/11/1997	W	NL	NS		1			1				151																
10/12/2006	W	UK	NS			14						20																
11/01/2014	W	UK	NS									3170																
01/04/1996	W	IE	Atl						1	1		14	104						3			13				39		
06/08/1998	S	UK	Atl							1		29	2				1				1	9				1		
26/08/2002	S	UK	Atl									290	1									1						2
04/05/2004	S	IE	Atl								7		2		3	65	405			1		73	1					207
18/05/2012	S	UK	Atl							1		134					6					3				1		
Occurrences				3	1	1	2	3	1	3	1	26	12	1	1	1	3	1	1	1	1	17	1	3	1	10	3	6

Key to species: UK = unidentified fish or unidentified cephalopod. Fish: Cho = chondrithys, Lop = *Lophius* sp., Mm = *Merlangius merlangus*, PV = *Pollachius virens*. Cephalopods: Arc = *Architeuthis* sp., Chi = *Chiroteuthis* sp., Ga = *Galiteuthis armata*, Gf = *Gonatus fabricii*, Hb = *Histioteuthis bonnellii*, His = *Histioteuthis* sp., Hm = *H. meleagroteuthis*, Hr = *H. reversa*, HtA = *Histioteuthis* type A (beak shape consistent with several *Histioteuthis* species including *H. bonnellii* and *H. meleagroteuthis*), Lf = *Loligo forbesii*, Lg = *Lepidoteuthis grimaldi*, Ms= *Mastigoteuthis schmidti*, Td = *Taningia danae*, Tm = *Teuthowenia megalops*, Tp = *Taonius pavo*, Ts = *Todarodes sagittatus*, Ec = *Eledone cirrhosa*, Ha = *Haliphron atlanticus*, Oct = Octopodidae.

and also backwards from the year in which it ended. In both cases, we illustrate the results after excluding the first 10-years of each curve (since results are extremely variable when the series are very short).

Given the non-randomness of the strandings series, we tested them for autocorrelation and partial autocorrelation (PAC). The latter showed autocorrelation values exceeding 0.2 for lags from 1 to 3 or 4 years. Note that with 0-1 data, the confidence intervals generated for AC and PAC are not valid but the plots can still be used as a guide.

Zuur et al. (2012) applied a range of GAM-family modelling approaches to the original strandings and environmental series from Pierce et al. (2007) and all gave rather similar answers. Here, we used binomial GAMMs with an ARMA component to remove autocorrelation in the response variable. In practice, the performance of models accounting for autocorrelation at lag 1 year (corAR1) and for lags of 1 and 2 years (i.e. corARMA(p=2, q=0)) was similar. In both cases autocorrelation was reduced but a few autocorrelation spikes sometimes remained in the residuals, although in the latter the significance of the effect of the explanatory variable was reduced. Hence, we finally used corAR1 and note that some caution is needed in interpreting the results. For all explanatory variables, complexity of smoothers was limited by setting a limit on the number of "knots" (using k=4).

Separate models were fitted for each explanatory variable, for lag 0 and lag 1 year. Note that lag zero does not mean that pairs of points in the strandings and environmental series refer to exactly the same time periods. Thus 1995 winter temperature refers to December 1994 to February 1995 and 1995 July-June strandings refers to July 1995 to June 1996.

Correlations, runs tests, partial autocorrelation and ARMA analyses were carried out using Minitab (Minitab Inc) and Microsoft Excel while GAMMs were fitted using Brodgar (Highland Statistics Ltd) software, which is based on R.

Results

Diet

Diet data were available from 28 individuals stranded in the UK, Ireland, Denmark and the Netherlands between 1937 and 2014, including four animals stranded in Scotland between 2002 and 2014 for which diet results have not previously been published (table 1). All were males, 23 from North Sea coasts (if we include the four animals from Orkney) and five from Atlantic coasts (west Scotland and Ireland).

The main prey species found in stomachs of sperm whales stranded on North Sea coasts in winter (see table 2) was the squid *Gonatus fabricii*, which was present in 22 out of 23 animals, with remains of between 1 and 4600 individual squid recovered. Also frequently occurring, although less numerically important, were the squids *Teuthowenia megalops* (F=12, 1-31 beaks) and *Histioteuthis bonnellii* (F=8, 1-84), and the octopus *Haliphron atlanticus* (F=7, 1-5).

Some evidence of feeding in the North Sea was apparent in the stomach contents, with the appearance of remains of resident fish and cephalopods in stomachs of eight individual whales, including saithe (*Pollachius virens*), whiting (*Merlangius merlangus*), monkfish (*Lophius* sp.), the curled octopus (*Eledone cirrhosa*), and the veined squid (*Loligo forbesii*). Beaks of the latter species were identified only to genus level and assignment of species is based on known squid distribution. Mostly, these remains were of single individual prey specimens, although 28 whiting otoliths were recovered from one whale stomach. Single egg capsules of a shark or ray (Chondrichthyes) were found in three stomachs.

Four of the five individual whales from Atlantic coasts had stranded in summer. The main prey species of three whales from west Scotland were the same as recorded in animals from the North Sea coasts. In the two Irish whales, *Histioteuthis* spp. were the most numerous prey rather than *Gonatus*.

Several cephalopod species were found only in Atlantic samples, namely *Architeuthis* sp., *Chiroteuthis* sp., *Galiteuthis armata*, *Lepidoteuthis grimaldi*, *Mastigoteuthis schmidti*, *Taonius pavo*, *Taningia danae* and two of the

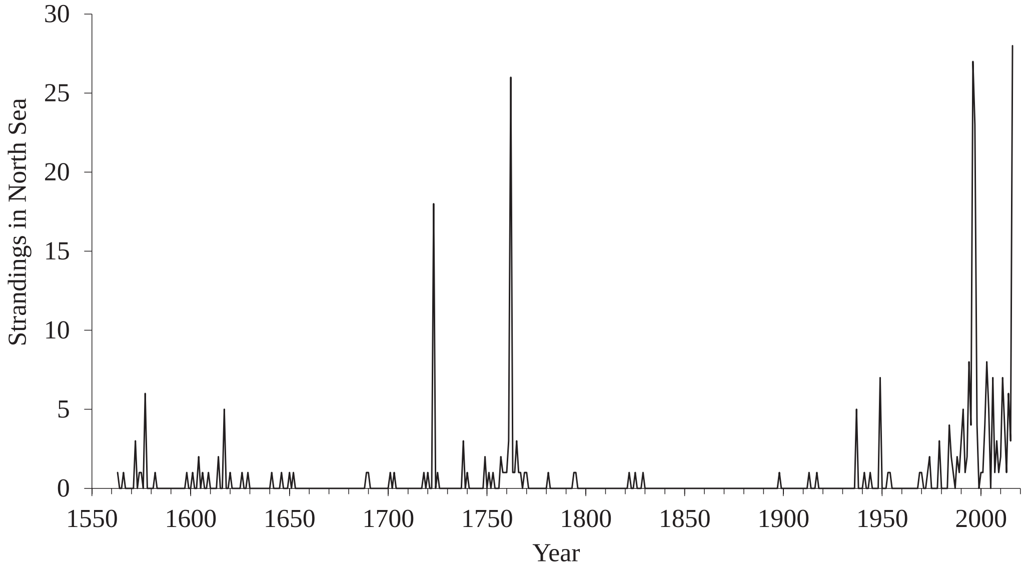

Figure 1. Number of strandings of sperm whales on North Sea coasts per calendar year (data from Smeenk 1997; Smeenk & Evans, this volume).

Histioteuthis species (*H. meleagroteuthis* and *H. reversa*). These samples contained no fish remains.

Strandings

Strandings were recorded in 97 of the 454 calendar years in the series. Twenty-five or more animals were recorded in three years (1762, 1996 and 2016). The series assembled by Smeenk & Evans (this volume) ends in February 2016, by which time it was already the year with most recorded stranded sperm whales (28). The annual number of strandings is illustrated in figure 1. Of 312 stranded whales recorded, more than half (162) have stranded in the last 30 years of the series, a period which includes over a quarter (27) of all the years (since 1563) in which strandings were recorded.

A runs test shows the series of occurrences of strandings per year was clearly more clumped than expected by chance alone ($P<0.0005$) for both calendar years and years running from July to June. Over 454 years, around 154 runs would be expected by chance alone whereas the two series contained just 107 and 105 runs, respectively.

Simple correlations between counts, occurrence, and environmental variables are summarised in table 3. No significant relationships were found between strandings number or occurrence and sunspot numbers. The annual NAO with lag 1 had a weak negative effect on the occurrence of strandings in July-June. Icelandic pressure had a weak negative effect on occurrence of strandings. All strandings variables were positively correlated with all temperature variables; correlations with strandings occurrence were generally higher than those with strandings number and there was little difference between correlations for lags 0 and 1 year. The highest correlations were seen with global SST but this is a relatively short series (145 years). It should be noted that these simple correlations do not account for autocorrelation in the times series, and the significance of correlations may thus be overestimated.

The "discovery curves" of the effect of increasing time series length on the strand-

Table 3. Correlations of standings and environmental variables (SST = sea surface temperature, LSAT = land surface air temperature, NAO = North Atlantic Oscillation, recon = reconstruction).

	n	Count (Cal Year)	Occ (Cal Year)	Count (Jul-Jun)	Occ (Jul-Jun)t
n		454	454	453	453
Lag 0					
Annual sunspots	317	-0.034	0.039	0.000	0.056
Winter sunspots	267	-0.031	0.013	0.001	0.036
Annual NAO	192	-0.072	-0.040	0.008	-0.069
Iceland pressure	194	-0.066	-0.149 *	-0.141 .	-0.178 *
Annual LSAT recon	442	0.186 ***	0.216 ***	0.231 ***	0.227 ***
Winter LSAT recon	442	0.098 *	0.133**	0.152 **	0.164 **
Global SST	145	0.465 ***	0.643 ***	0.473 ***	0.632 ***
N Sea SST	145	0.289 ***	0.431 ***	0.374 ***	0.498 ***
N Atlantic SST	145	0.298 ***	0.362 ***	0.286 ***	0.385 ***
Lag 1					
Annual sunspots	316	-0.002	0.039	0.0006	0.032
Winter sunspots	266	0.006	0.025	0.013	0.003
Annual NAO	191	-0.069	-0.129	-0.098	-0.148 *
Iceland pressure	193	-0.053	-0.072	-0.103	-0.035
Annual LSAT recon	442	0.205 ***	0.174 ***	0.177 ***	0.213 ***
Winter LSAT recon	442	0.148 **	0.138 **	0.097 *	0.167 ***
Global SST	145	0.450 ***	0.651 ***	0.450 ***	0.653 ***
N Sea SST	145	0.268 **	0.465 ***	0.298 ***	0.472 ***
N Atlantic SST	145	0.257 **	0.369 ***	0.246 **	0.397 ***

ings occurrence-environment correlations revealed relatively stable patterns when using the temperature reconstructions and sunspot series (the longest time series available). In the forwards curves (running from 1563 to 2016), these correlations are seen to change in the last 20-30 years of the series. The remaining (shorter) series achieved less stability and again shoe marked changes in the final 20-30 years of the series (figure 2).

GAMM results (table 4) showed no significant relationships between occurrence of strandings and sunspot numbers, NAO or Icelandic air pressure. Some positive relationships were observed with temperature series, the strongest being with the global sea surface temperature series (see also figure 3). However, as noted above, these were the shortest time series (145 years) and, as such, the high correlations with the reconstructed European land surface air temperature series (442 years) is therefore more noteworthy.

Discussion

Diet

Gonatus fabricii is an important resource for many upper level predators in the northeast Atlantic and Arctic (Bjørke 2001) and it has been consistently identified as the main component of prey remains in stomach contents of sperm whales stranded on North Sea coasts (Lick et al. 1995, Clarke 1997, Santos et al. 1999, 2002, Simon et al. 2003).

Comparison with results from northeast Atlantic coasts outside the North Sea is limited by lack of information. Three samples from west Scotland were quite similar to those

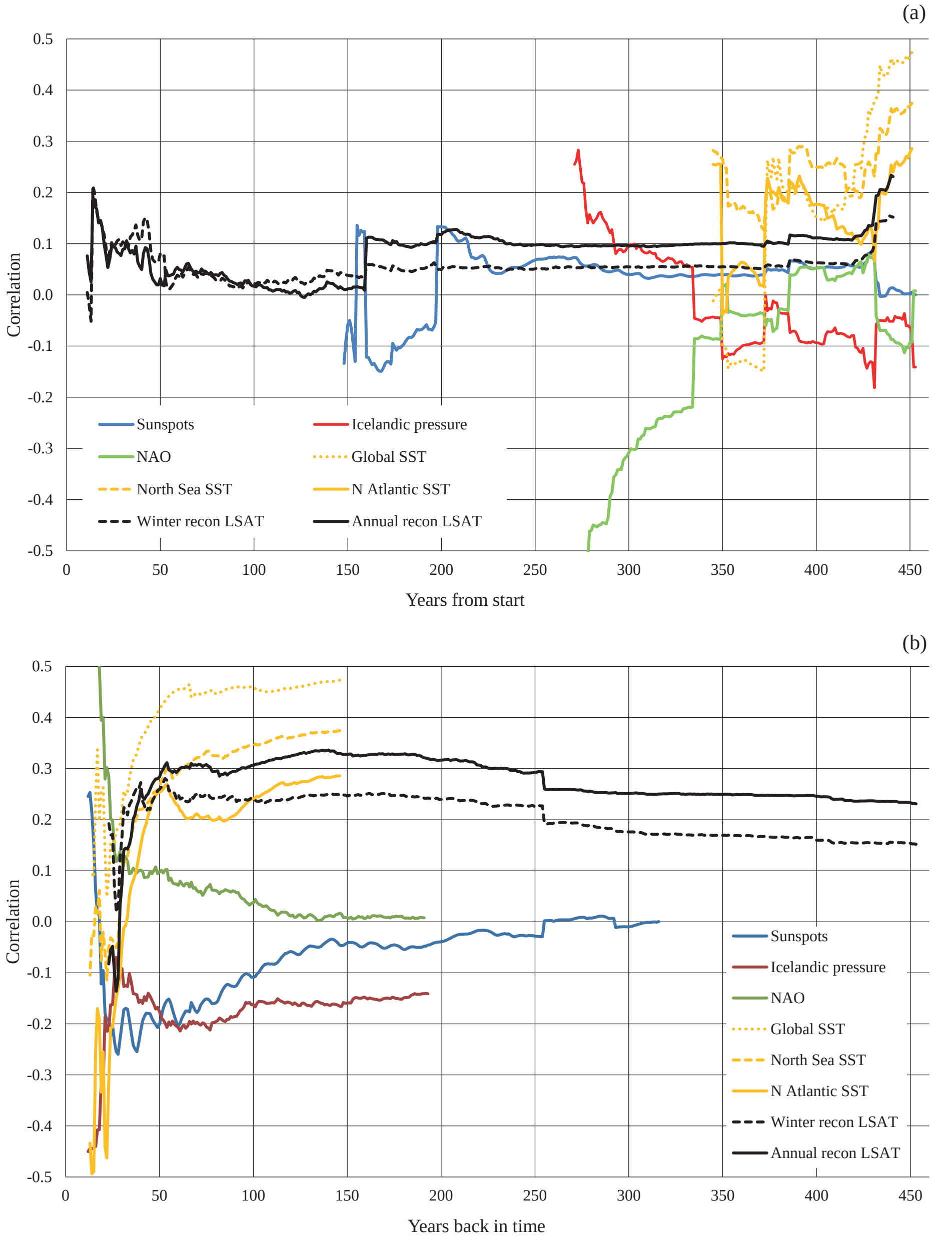

Figure 2. Correlation "discovery curves", running (a) forwards and (b) backwards through time, for occurrence of strandings (July to June) versus selected environmental variables. For each year the correlation refers to the period from when recording of the two variables first coincided through to the year in question. The forwards curves run from the first year of the environmental series towards the present day while the backwards curves start where the series end (i.e. close to the present day) and run backwards through time. The first 10 years of each correlation series are not illustrated (because year to year variation in correlation values is much higher when the series are still very short).

Table 4. GAMM results. For each model the effect of the explanatory variable is described by the degrees of freedom (1 indicates a linear fit, higher values define curves of increasing complexity), probability value (indicating significance) and the direction of the relationship (if significant). Models were fitted using either contemporaneous values of environmental series for each year (lag 0) or values from the previous year (lag 1). All models assume that there is temporal autocorrelation between annual occurrence of strandings and occurrence of strandings in the previous year. (NAO = North Atlantic Oscillation, LSAT = Land Surface Air Temperature, SST = Sea Surface Temperature).

	n	Occ (Cal Year)	Occ (Jul-Jun)
n		454	453
Lag 0			
Annual sunspots	317	1, *P*=0.356	1, *P*=0.409
Winter sunspots	267	1, *P*=0.785	1, *P*=0.570
Annual NAO	192	1, *P*=0.713	1, *P*=0.666
Iceland pressure	194	1, *P*=0.396	1, *P*=0.0540
Annual LSAT recon	442	1.536, *P*=0.0018, +	1.595, *P*=0.0017, +
Winter LSAT recon	442	1, *P*=0.0653	1, *P*=0.0282, +
Global SST	145	1, *P*<0.0001, +	1, *P*<0.0001, +
N Sea SST	145	1.972, *P*=0.0470, +	1, *P*=0.0001, +
N Atlantic SST	145	1.479, *P*=0.0868	1, *P*=0.0146, +
Lag 1			
Annual sunspots	316	1, *P*=0.865	1, *P*=0.686
Winter sunspots	266	1, *P*=0.542	1, *P*=0.954
Annual NAO	191	1, *P*=0.376	1, *P*=0.224
Iceland pressure	193	1, *P*=0.742	1, *P*=0.213
Annual LSAT recon	442	2.116, *P*=0.0032, +	1.005, *P*=0.0025, +
Winter LSAT recon	442	1.629, *P*=0.0695	1, *P*=0.0142, +
Global SST	145	1, *P*<0.0001, +	1, *P*<0.0001, +
N Sea SST	145	1, *P*=0.0041, +	1, *P*=0.0011, +
N Atlantic SST	145	1, *P*=0.0103, +	1, *P*=0.0022, +

from the North Sea while two from Ireland showed greater differences, containing few or no *Gonatus* and including several cephalopod species not recorded from North Sea strandings. The stomach of a juvenile (length 700 cm) sperm whale stranded in Galicia NW Spain on 4 March 1993 contained a few beaks of *Histioteuthis* sp., *Mastigoteuthis* sp., *Chiroteuthis* sp., *Teuthowenia megalops* and *Octopus vulgaris* (Gonzalez et al. 2004) – all but the last of these also occurred in stomach contents of individuals stranded on the west (Atlantic) coast of Ireland (outside the distribution range of *Octopus vulgaris*) (Santos et al. 2002, 2006).

One notable difference between North Sea and Atlantic samples in the present study, albeit again based on a small sample size, was the presence of fish and coastal cephalopod species only in the North Sea samples, suggesting that feeding on such species is unusual, perhaps occurring *in extremis* in animals "trapped" in the shallow North Sea. However, although studies on sperm whale diet based on stranded animals almost invariably indicate them to have fed mainly on cephalopods, it is worth remembering that studies undertaken during the whaling era found evidence of extensive predation on fish (e.g. Martin & Clarke 1986).

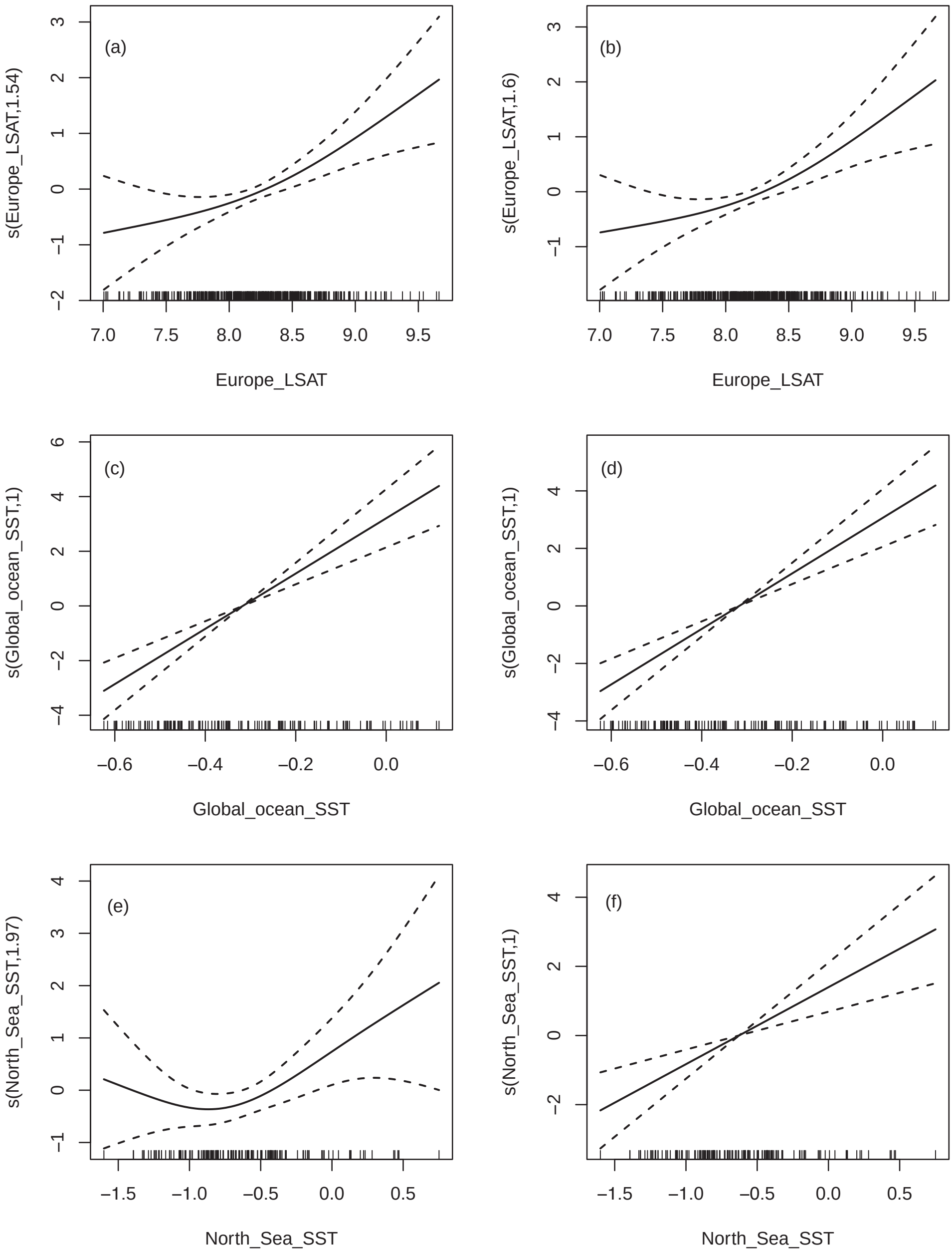

Figure 3. Plots of GAMM smoothers illustrating modelled effects of temperature variables on the occurrence of sperm whale strandings in the North Sea, per calendar year (a,c,e) and per year from July to June (b,d,f): reconstructed annual European land surface air temperature (LSAT) to 2004 (a, b), global sea surface temperature (SST) 1870-2014) (c, d) and North Sea SST 1870-2014 (e,f). In all case the upward slope of the relationhip indicates a positive effect of temperature on the occurrence of strandings. Results are shown for time-lag zero. The "rug plot" of lines along the x-axis indicates the variation of data density as a function of the value of the x-axis variable. Sample sizes associated with each plot are given in table 3.

Strandings

Since we published on this topic in 2007, the strandings series has obviously been extended by another decade. However, the only "environmental" data series available for the entire 450-year period are those for sunspots. As previously, statistical modelling carried out in this paper revealed no relationship between strandings and numbers of sunspots.

Positive relationships were again found with temperature series, relatively weak with reconstructed (land surface air) temperature in Europe over the majority of the study period but stronger for (sea surface) temperature in the last 150 years. One problem with this finding is that, at least in the most recent part of the series, we are looking at unidirectional change in the incidence of strandings, i.e. a phenomenon that appears to be increasingly frequent. Thus, other phenomena that are also continuously increasing will appear to be related, making it harder to avoid coincidental relationships. The marked increase in the incidence of strandings over the last 20-30 years suggests a superficial parallel to the famous "hockey stick" fit to long-term temperature records (Mann et al. 1998). What is evident from the correlation discovery curves is that what has happened with strandings over the last few decades, differs from what has gone before. Our new analysis again suggests that there is a relationship with the sea and land surface temperature signals but the underlying mechanism, if this relationship is indeed non-coincidental, is unclear.

It is tempting to ascribe the increased frequency of strandings in the last 30 years to the recovery of the North Atlantic sperm whale population. However, a longer-term perspective casts doubt on this interpretation. Whitehead´s (2002) reconstruction of global sperm whale numbers suggests that whaling mortality led to only a gradual decline from 1700 to around 1950, when the unprecedented catches achieved by the modern whale hunting (peaking in 1964; Rice 1989) caused a sharp decline in abundance. In the North Atlantic, catches reached a peak between 1952 and 1981, and Hiby & Harwood (1981) suggest that numbers declined continuously from 1905 to 1979, especially from 1940 onwards. The cessation of whaling should have allowed some recovery. The global population trajectory proposed by Whitehead (2002) indicates that the population in 2000 would still have been well below the 1950 abundance level and it seems likely that this would also be true in the North Atlantic. Thus, the only part of this story apparent in the strandings record is the increase in strandings in the last three decades as abundance rose from a historical low point.

In conclusion, it is perhaps most likely that multiple phenomena are at work and the functioning of the North Sea sperm whale trap does not have a single simple explanation.

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Samenvatting

Analyses in heden en verleden van het voedsel en de strandingen van potvissen (*Physeter macrocephalus*) in de Noordzee

Het toenemende aantal strandingen van potvissen gedurende de winter in de Noordzee heeft geleid tot veel speculatie over de oorzaken van dit fenomeen. Onder gebruikmaking van een onlangs bijgewerkte lijst van strandingen van de potvis in de Noordzee werd met behulp van zogenoemde *generalised additive mixed models* (statistische technieken waarmee o.a. de ontwikkeling van een populatie kan worden voorspeld) onderzocht wat de mogelijke rol is van diverse milieuomstandigheden die effect zouden kunnen hebben op het binnenzwemmen van de Noordzee door potvissen en/of op hun strandingen rond de Noordzee. Het optreden van zonnevlekken, de *North Atlantic Oscillation* (NAO – een weerfenomeen waarbij gelet wordt op de luchtdrukverschillen op zeeniveau tussen IJsland en de Azoren) index of alleen de luchtdruk op zeeniveau rond IJsland bleken nauwelijks tot geen invloed te hebben. Diverse indexen voor de temperatuur op zee en land vertonen een positieve correlatie met het

optreden van strandingen.

Echter, er zijn daarnaast aanwijzingen voor het optreden van veranderingen gedurende de afgelopen dertig jaar in de correlatie tussen strandingen en milieuvariabelen en, gezien het ontbreken van een duidelijk mechanisme waarmee de relatie tussen de temperatuur en de strandingen kan worden verklaard, is het van belang om in te zien dat verschillende processen kunnen bijdragen aan de veranderingen in de strandingen. Bovendien moet rekening worden gehouden met het herstel van de potvissenstand na het stoppen van de commerciële walvisvangst aan het eind van de 20ste eeuw. Temperatuurveranderingen kunnen namelijk ook invloed hebben gehad op de prooidiersoorten van potvissen en hierdoor veroorzaakte veranderingen in het voorkomen van deze soorten kunnen óók een verklaring opleveren voor veranderingen in het patroon van de potvisstrandingen. Daarom wordt in dit artikel eerder voedselonderzoek herhaald onder gebruikmaking de oorspronkelijke gegevens, aangevuld met nieuw verzamelde gegevens. Hieruit komt naar voren dat de diepzee-inktvis *Gonatus fabricii* (een soort die voorkomt in de noordelijke delen van de Atlantische Oceaan, zoals ook de Engelse naam - *Boreoatlantic armhook squid* - aangeeft) in de maaginhouden van rond de Noordzee gestrande potvissen blijft overheersen. Hierbij wordt opgemerkt dat er ook restanten van in de Noordzee levende soorten inktvissen, zij het in kleine hoeveelheden, werden aangetroffen, op basis waarvan mag worden aangenomen dat er ook sprake is van enig foerageren in de Noordzee zelf. De conclusie wordt getrokken dat er geen sprake is van één verklaring voor het verschijnsel dat de Noordzee als een fuik voor potvissen functioneert maar dat we hierbij zeer waarschijnlijk te maken hebben met een combinatie van oorzaken.

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