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On the pupping season of grey seals (*Halichoerus grypus*) off Amrum, Northern Germany

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The grey seal *Halichoerus grypus* (Fabricius, 1791) is distributed along several coasts of the North Atlantic and adjacent seas (Bonner 1981; Anderson 1992). Within this range, the species shows a highly variable timing of reproduction, as compared to other phocids. Grey seals breed from September to March, with distinct seasons in the three commonly recognized sub-stocks of the West Atlantic, East Atlantic, and the Baltic (King 1983; Anderson 1992). Geographic variation is further evident within the East Atlantic stock, particularly around Great Britain (Bonner 1981; Anderson 1992), and along the Norwegian coast (Wiig 1986). Originally, geographic patterns of reproductive timing were simply related to population structure (Davies 1957; Hewer 1974; Summers 1978). However, various other explanations have been suggested (Harrison 1963; Coulson 1981; Boyd 1991).

In the North Sea, the largest aggregation of grey seals is found on the Farne Islands (Fig. 1, King 1983), where pupping occurs mainly from late October to mid December (Coulson and Hickling 1964). A number of smaller breeding colonies has arisen in recent decades on the British east coast and in the Wadden Sea, one of which is situated on the shoal Jungnamensand (54°40′ N, 8°15′ E) off the German island of Amrum (Fig. 1). Although these colonies are commonly assumed to descend from the prolific Farne Islands stock (Harwood and Wyile 1987; 't Hart et al. 1988; Vogel and Koch 1992), there is evidence that in some colonies breeding is considerably later than on the Farnes (Bonner 1981; Vedder et al. 1992; Vogel and Koch 1992). To make this phenomenon more distinct, we analysed reports of grey seal birth dates from the breeding site off Amrum.

Pupping on Jungnamensand was monitored over 10 seasons from autumn 1988 to spring 1998. Sightings of pups were made by volunteers on boat trips, for the most part by the crew of a customs patrol boat routinely passing the site. With some exceptions, surveys took place at least weekly. The proportion of missed pups is thus believed to be small, although an occasional pup may have been lost through flooding of the rookery during storms.

Approximate – sometimes even exact – birth dates were derived from morphological clues (e. g. Davies 1949; Radford et al. 1978). The latter also allowed for easy discrimination of pups of different ages, since numbers per season are usually small. However, as survey intensity was not constant and experience of observers limited, the precision of the assumed birth dates varied, with ranges of uncertainty between 1 and 10 days (mean = 3.7).

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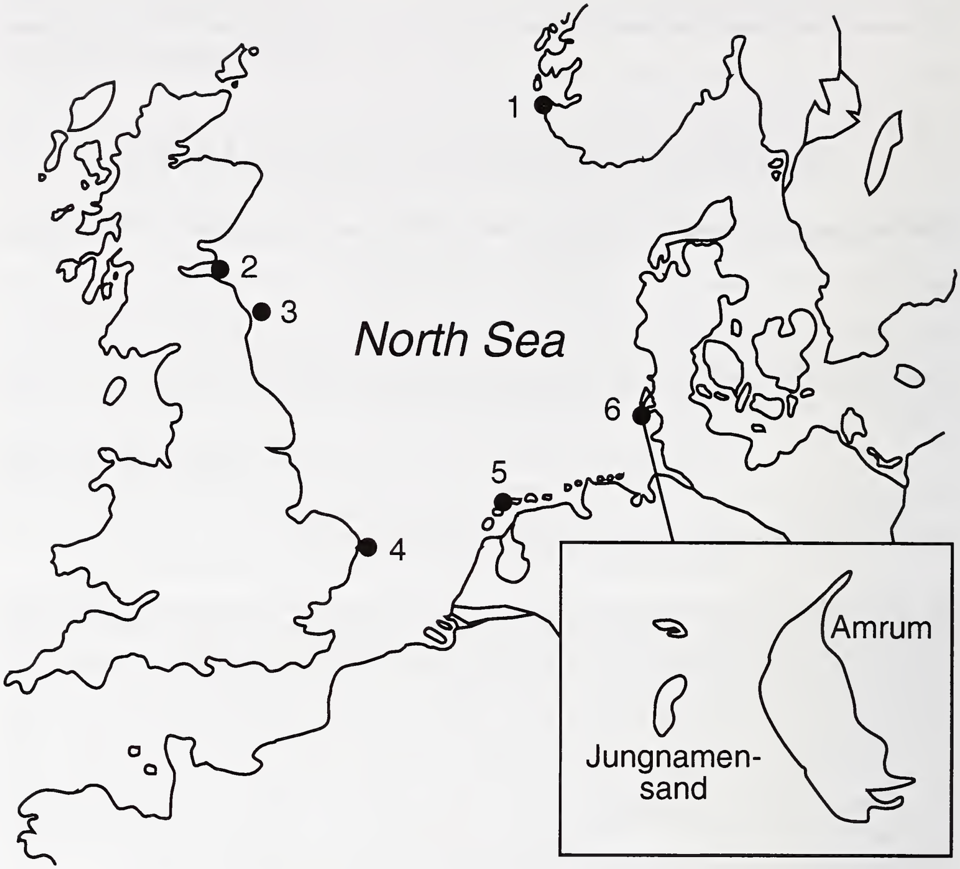

Fig. 1. Location of the study area and other grey seal breeding sites mentioned in the text; 1 = Kjør (S-Norway), 2 = Isle of May, 3 = Farne Islands, 4 = Scroby Sands, 5 = Vlieland (The Netherlands), 6 = Amrum (N-Germany).

A total of 78 pups was recorded, with the number per season varying between 3 and 11 (Tab. 1). The entire range of birth dates was from mid October to late February, i. e. about four months. However, these extreme values occurred only in the season of 1997/98, whereas in 9 of the 10 seasons, pupping did not start prior to mid November, and in 7 seasons ceased by late December or earlier (Tab. 1). In order to avoid bias in parametric analyses through extreme values (which might represent different populations in the statistical and/or biological sense), the joint distribution was truncated at the 2.5- and 97.5-percentiles. In the remaining 74 birth dates, ranging from mid November to mid January (Tab. 1), the average date did not vary significantly between seasons (ANOVA, $df = 9$, $F = 0.815$, $p = 0.604$). Therefore, the peak pupping date was calculated from the pooled data. The latter were not normally distributed (Lilliefors test, $n = 74$, $p = 0.005$), which could be attributed to positive skewness ($S = 0.724$). A log-normal distribution was therefore suggested, the parameters of which were determined by $\log(x - k)$ transformation of the data, and fitting k (the origin) to give a minimum departure from normality. With $k = 27$ October, as found by an iterative least squares procedure, the data conformed remarkably well to a log-normal distribution (Lilliefors test, $n = 74$, $p = 0.516$). The corresponding median birth date was 5 December, whereas the mode, i. e. the peak

Table 1. Numbers of grey seal pups born off Amrun, Northern Germany, from autumn 1988 to spring 1998, by pupping season and decade. Figures within the two dotted lines represent the central 95%-mass of the pooled birth dates, from which the peak pupping date (1 December) was calculated.

Pupping season	Month/(Decade)															Σ
	Oct			Nov			Dec			Jan			Feb			
	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	
88/89					1	1	4	1	2							9
89/90							1	2								3
90/91					2		3	1	1							7
91/92					1	3	1		1							6
92/93					1	3		2	1	1	1	1				10
93/94					2	3	1		1							7
94/95						3		1		1						5
95/96						4	6		1							11
96/97						2	5	4								11
97/98		2				2	2	2							1	9
Σ		2			7	21	23	13	7	2	1	1			1	78

pupping date, was 1 December. The central 68%-mass of the probability distribution of births (corresponding to the area between the mean date +sd and –sd on the log scale) occurred from 24 November to 19 December (25 days).

Close genetic relationships and a similiar timing of reproduction among grey seals in the North Sea might be expected. However, with peak pupping in early December, seals off Amrum give birth 3–4 weeks later than on the Farnes (Coulson and Hickling 1964) and on the Isle of May (Caudron 1998). Pupping in a colony in the Dutch Wadden Sea, near the island of Vlieland, is even later, with a peak in early January (Vedder et al. 1992) or, more recently, in late December (P. Reijnders, pers. comm.). Similarly, grey seals at Scroby Sands off the Norfolk coast give birth in late December or early January (Bonner 1981). Thus, pupping in the southwestern North Sea occurs 7–8 weeks later than on the Farnes, while off Amrum it is intermediate. It is interesting in this regard that there is also a north-south gradient in the time of pupping along the west and north coast of Great Britain, but in the opposite direction, i. e. ranging from September in Cornwall until November in northern Scotland (Coulson 1981; King 1983; Anderson 1992). Only in southern Norway, grey seals appear to have a similar birth season as of Amrum (Wiig 1986).

Factors that regulate – and thus may cause geographic variation in – the annual cycle of the grey seal seem to be poorly understood, although having received much attention by scientists. In fact, neither the relevance of genetic differences between sub-stocks (cf. Davies 1957; Hewer 1974), nor the concept of photoperiodical regulation (Harrison 1963), have yet been generally accepted. Coulson (1981) rather suggested response of seals to ambient sea-temperature as the mechanism of – and source of variation in – reproductive timing. Boyd (1991) instead proposed a proximate relation of the time of breeding to seasonal food abundance, which is equivalent to an indirect influence of temperature.

However, none of these ideas seem to help explaining why grey seals off Amrum and Vlieland give birth significantly later than those on the Farne Islands. Some researchers related this phenomenon to a presumably high proportion of primiparous females in the former two sites (Vedder et al. 1992; Caudron 1998; P. Reijnders, pers. comm.). Considering this to be a characteristic of recently founded colonies, they expect a shift towards earlier pupping with rising proportion of multiparous females (cf. Vedder et al. 1992), which would gradually lead to a similar birth season as on the Farnes. However, no such trend is evident from our data. Further, the idea does not appear to be compatible with the virtually well-defined, unimodal pupping season found in the present study.

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