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Geographical variation in temporal and spatial vocalization patterns of male harbour seals in the mating season

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In the aquatically mating harbour seal, *Phoca vitulina*, oestrous females show marked differences in spatial and temporal distribution between geographical areas. This suggests that the males' display behaviour may also vary between areas. We recorded male vocalizations in two areas, the Moray Firth and Orkney, U.K. In the Moray Firth, females haul out on a few intertidal sandbars and travel along predictable routes to forage at sea. In Orkney, female haul out sites are much less influenced by tidal availability and females are much more dispersed. In the Moray Firth, males vocalized only during a short mating season, from 1 July to 12 August. Vocalizations varied significantly with the tide, the peak at high tide clearly coinciding with the period when most females were in the water. In contrast, vocalizations in Orkney were significantly related to both tidal and diel patterns. We suggest that the timing of male vocalizations reflects differences in female availability between sites. In the inner Moray Firth, vocalizations were heard throughout the females' range, whereas vocalizations in Orkney were heard only in two discrete areas. However, at both sites the density of vocalizing males was highest in narrow channels and/or along predictable female travel routes. Therefore, males clearly adapt their temporal and spatial behaviour patterns to variations in female distribution and density. These results suggest that male mating strategies in aquatically mating pinnipeds are more variable than was previously envisaged.

Since phocids show considerable diversity in breeding habitats and sexual dimorphism (Boness 1991; LeBoeuf 1991), they are excellent subjects for studying the influences of ecological and physiological constraints on mating systems. In land-breeding phocids, such as the northern elephant seal, *Mirounga angustirostris* (Deutsch et al. 1989) and the grey seal, *Halichoerus grypus* (Anderson et al. 1975), females are highly clumped in both space and time, and they remain on land with their pups for several weeks (Costa 1991). During this period males also remain ashore to defend groups of several females (Shipley et al. 1980; Haley et al. 1994). Land-breeding phocids also show a clear temporal and spatial separation between foraging and reproduction. Less is known about the reproductive strategies of phocids that mate in the water. In these species oestrous females are generally more dispersed (Costa 1991; Boness & Bowen 1996) and the temporal and spatial division between foraging and reproductive activity is less distinct. Theoretical (Boness 1991; LeBoeuf 1991), as well as limited empirical, evidence suggests that male reproductive strategies may be very different to those of land-breeding phocids (Boness 1991; Bartsch et al. 1992; Coltman et al. 1997; Van Parijs et al. 1997).

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Harbour seals, *Phoca vitulina*, mate aquatically (Sullivan 1981; Allen 1985) and the distribution of oestrous females varies considerably in space and time. Geographically, they are the most widely distributed of the pinnipeds. They can be found on a variety of habitats including ice, intertidal sand bars and rocky beaches, and occur in breeding groups of one or two up to several hundred females (Bigg 1981). During the breeding season, energetic demands force females to forage during late lactation, and they are widely distributed in space throughout oestrus (Boness 1991; Bowen et al. 1992; Thompson et al. 1994). Not only do different habitats influence the spatial distribution and size of female haul out groups, but the temporal distribution of oestrous females also varies geographically. At one scale, populations can differ markedly in how synchronous pupping and oestrus are (Bigg 1981; Boyd 1991; Temte 1994). At finer scales, populations also differ in the relative

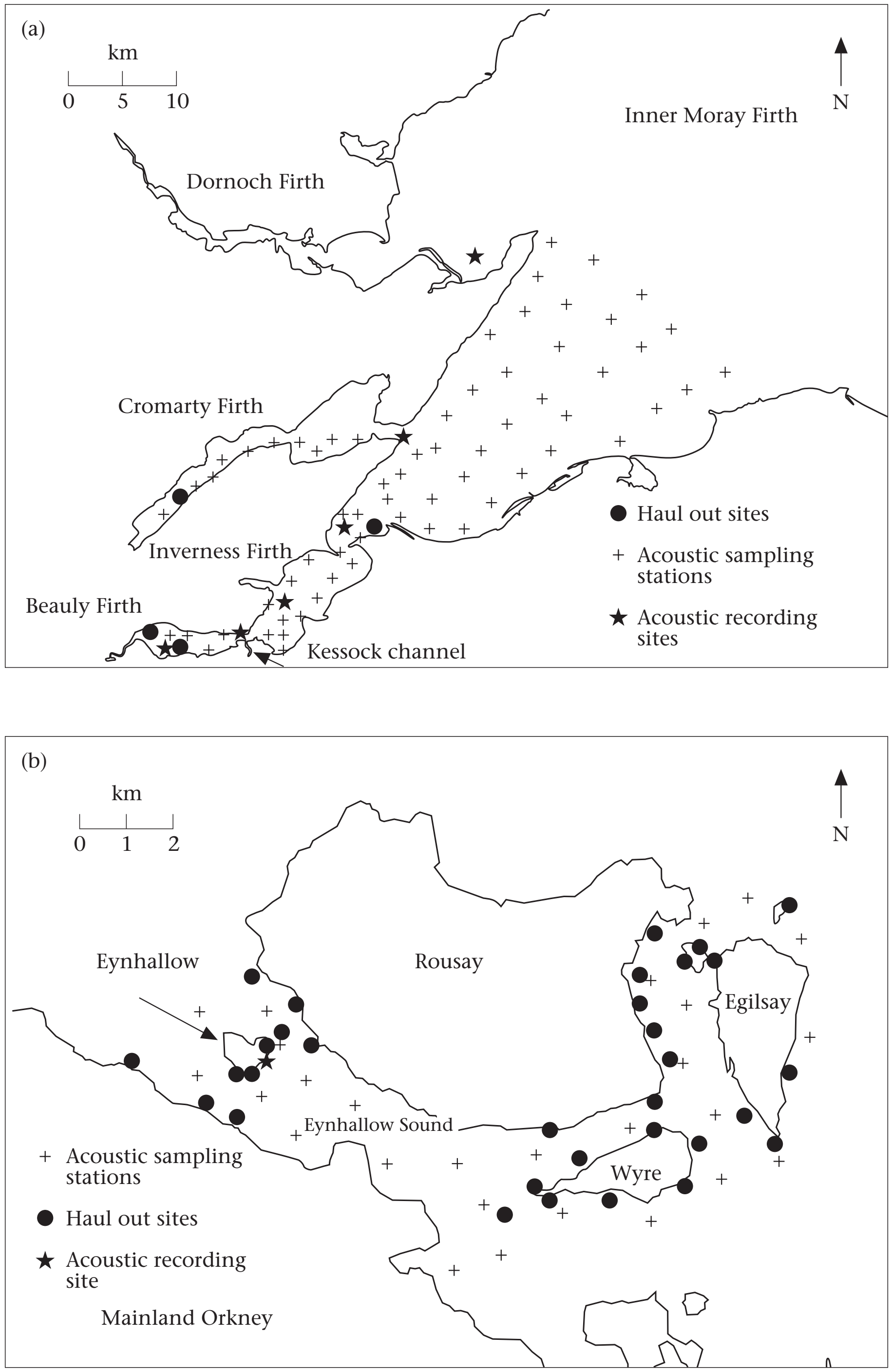


Figure 1. Main sampling stations and other recording sites where male harbour seal vocalizations were recorded in (a) the inner Moray Firth and (b) the Orkneys. Seal haul out sites are also shown.

influence of tidal and diel cycles on female activity patterns (Thompson et al. 1989, 1997). These differences in the spatial and temporal distribution of oestrous females suggest that males may also differ in the spatial and temporal distribution of their display behaviour. A study of nine radiotagged males during the mating season in the Moray Firth, U.K. suggested that males display throughout the females' range, on the females foraging areas, near haul out sites and along transit routes between the two (Van Parijs et al. 1997). However, the spatial or temporal distribution of males is not known in detail in this or other areas.

In this study, we used male vocalizations as a tool for comparing the distribution of displaying males in two topographically different areas in northern Scotland, U.K., an estuarine haul out area in the Moray Firth and the rocky islands of Orkney. Our aims were to compare spatial and temporal patterns of male vocalizations in

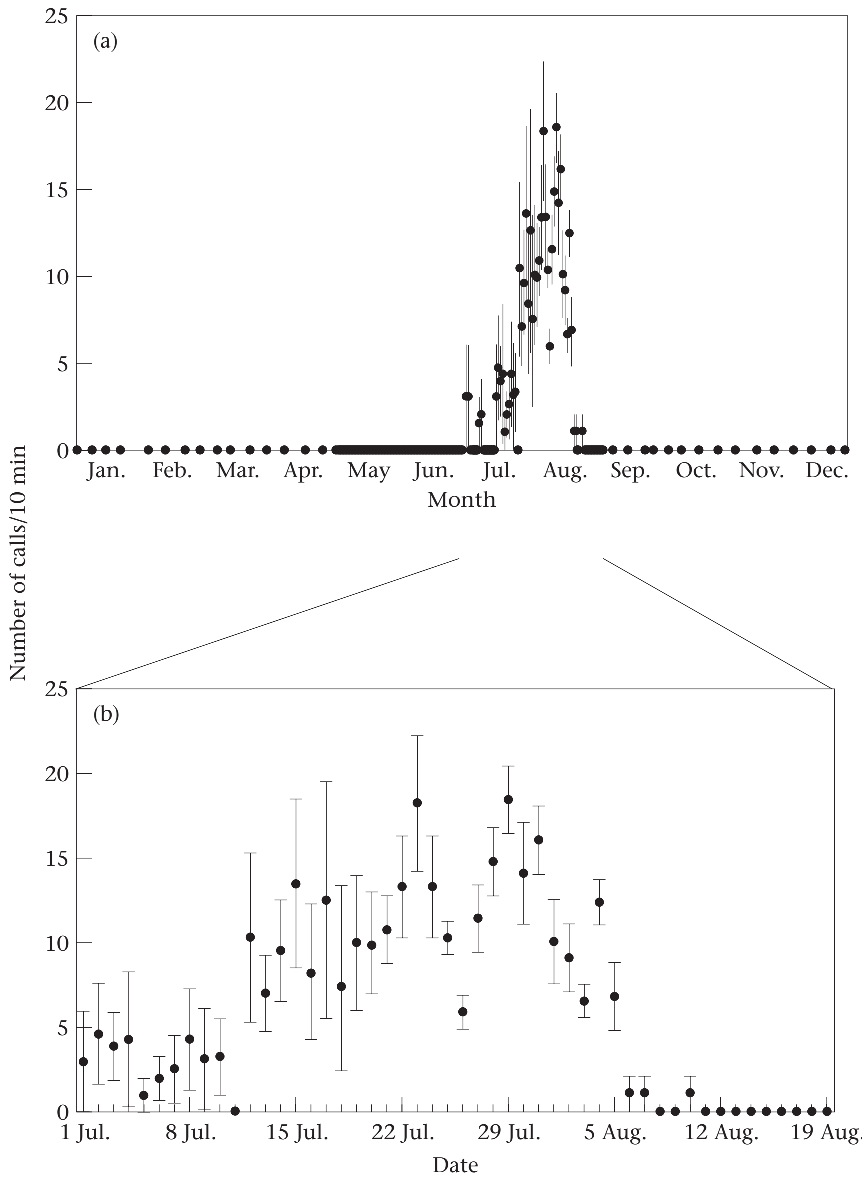


Figure 2. Seasonal variation in the mean number of male vocalizations ±SE per 10-min sample at high tide (*N*=598) in the inner Moray Firth for (a) March 1995 to August 1997 and (b) July to mid-August 1995, 1996 and 1997.

these two areas, and to assess how male display activity varies in relation to geographical differences in female distribution.

METHODS

We studied seals in the Moray Firth (57°41′N, 4°00′W), from July 1995 to October 1997, and throughout the northwest islands of Orkney (59°8′N, 3°8′W), during June and July 1998 (Fig. 1). These two sites impose different environmental constraints on female distribution. The inner Moray Firth contains three sheltered estuaries, the Beauly, Cromarty and Dornoch Firths, with intertidal sandbars that are used for both haul out and pupping by harbour seals (Thompson et al. 1996). Females in this study area give birth to their pups in June or early July and parturition is followed by a 3–4-week lactation period (Thompson 1988; Corpe 1996). Female pupping sites are limited to a few intertidal sandbars and females are highly clumped in time and space (Thompson et al. 1996). During June and July, female harbour seals travel along these narrow estuaries to forage further out in the inner Moray Firth (Thompson et al. 1994; Van Parijs et al. 1997). In contrast, the study area in Orkney consists of several dispersed islands, Eynhallow, Rousay, Egilsay and the northwest mainland, with rocky coastlines (Fig. 1b). In this area, female pupping sites are much less influenced by tidal availability and females are much more dispersed (Thompson 1988; Thompson et al. 1989). Only limited information is available on foraging areas of seals from Orkney, but females appear to travel west out to more open water to forage during late lactation (P. M. Thompson, unpublished data).

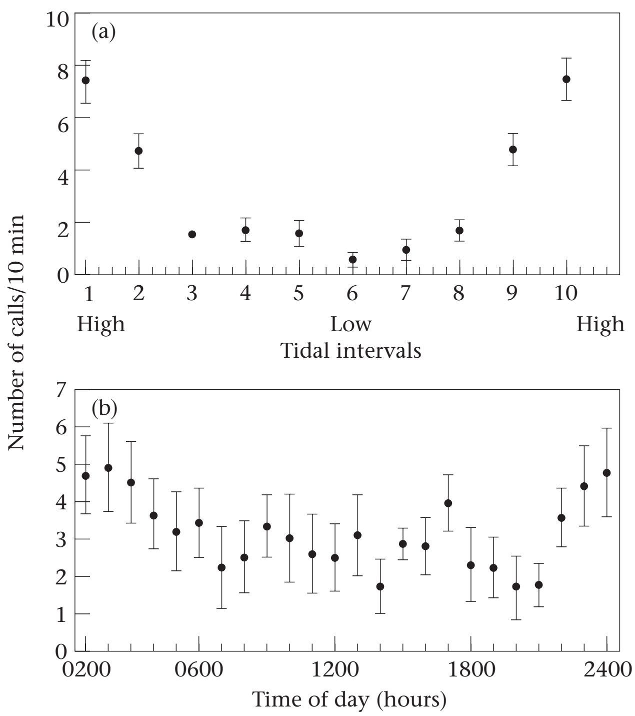


Figure 3. The tidal and diel patterns in the mean number of male vocalizations ±SE counted for all 10-min sampling periods in the Kessock channel in the inner Moray Firth during July and August 1995 and 1996. The tidal cycle was divided into 10 intervals for presentation.

Temporal Patterns

We investigated seasonal patterns in male vocalizations in the inner Moray Firth by making regular acoustic recordings between July 1995 and October 1997. We used a fixed hydrophone in the Kessock channel, at the mouth of the Beauly Firth (Fig. 1a). We recorded for 10 min at each high tide during July and August of each year and, outside the mating season, for 10 min at two randomly chosen high tides each week (one day and one night) from September to March. Between March and July we increased our sampling rate to 10 min on each high tide to determine the onset of the mating season more precisely. In addition, data were collected at five other 'recording sites' spread throughout the inner Moray Firth for shorter periods during 1996 and 1997 (Fig. 1a). In Orkney, recordings were made at high tide every day from 14 June to 23 July 1998 at one site in Eynhallow Sound (Fig. 1b).

We determined tidal and diel patterns in male vocalizations by making acoustic recordings at the same six sites in the inner Moray Firth (Fig. 1a) and one site in Eynhallow Sound in Orkney (Fig. 1b). In the inner Moray Firth, we recorded underwater vocalizations in July and August 1995 and 1996. In Orkney, recordings were made for 24 h every 3 days from 14 June to 23 July 1998. For clear representation of the tidal patterns of vocalizations, we split each tidal cycle into 10 separate intervals.

In the Kessock channel, recordings were made using a HTI-94-SSQ hydrophone mounted to the end of a pier. The signal from the hydrophone was transmitted via a MICRON TX 101.1 pocket radiomicrophone to a land-based receiving station. Signals were recorded on to a Grundig video cassette recorder using a YAESU FRG-9600 receiver and an S5Y YAGI aerial. At each of the five other sites throughout the inner Moray Firth, a sonobuoy (Van Parijs et al. 1998) was anchored at sea and used to record underwater vocalizations. Each sonobuoy consisted of a SSQ 906A navy hydrophone and transmitted a VHF radio signal to a land-based receiving station (resembling that in the Kessock channel) located 500–2000 m from the sonobuoy. In Orkney, recordings were made using a SSQ 906A navy hydrophone, fixed underwater by a leaded car tyre, and a shore-based receiving station comprising a custom-made preamplifier and a Marantz audiocassette recorder.

All recordings were played back and we counted the number of vocalizations heard in 10 min for each tidal interval and time of day. To determine the relationship between the number of vocalizations and the tidal and diel cycles for each geographical area we used a two-way ANOVA.

Spatial Patterns

We determined the spatial distribution of male vocalizations by making acoustic recordings at predetermined 'sampling stations' spaced every 2 km throughout the inner Moray Firth in July 1997 and throughout the study site in Orkney in July 1998 (Fig. 1). Male vocalizations in the Moray Firth can be recorded up to 1.2 km away (Van Parijs 1998). Males display consistently within the same small area throughout the mating season (Van Parijs et al. 1997; Van Parijs 1998). Therefore, by sampling at 2-km intervals, we assumed that there was limited overlap between vocalizations from adjacent sampling stations.

In the Moray Firth, acoustic surveys were designed to record at between five and seven sampling stations on each calm day (Beaufort scale 1–3) for a minimum of 10 min during July 1997. The total recording period was restricted to 3 h either side of high tide, the time during which we heard the greatest number of harbour seal vocalizations at all sites in the inner Moray Firth (see Results). Recordings were made using SSQ 906A hydrophones, custom-made preamplifiers and a Tascam Porta II cassette recorder. In Orkney, acoustic surveys were carried out on an opportunistic basis over 6 days during July 1998 (Beaufort scale 1–3). Recordings were made for a minimum of 10 min at each sample station, using a SSQ 906A navy sonobuoy, a custom-made preamplifier and a Marantz cassette recorder. Owing to the limitations imposed by the harsh weather conditions, we were unable to restrict our recording periods to the period when most vocalizations were observed.

All recordings were played back and the number of vocalizations in a 10-min sample were counted and represented graphically as densities of vocalizations. The number of vocalizations reflects the number of males within a given area (Van Parijs et al. 1997; Van Parijs 1998). We compared the spatial distribution of male vocalizations within and between sites.

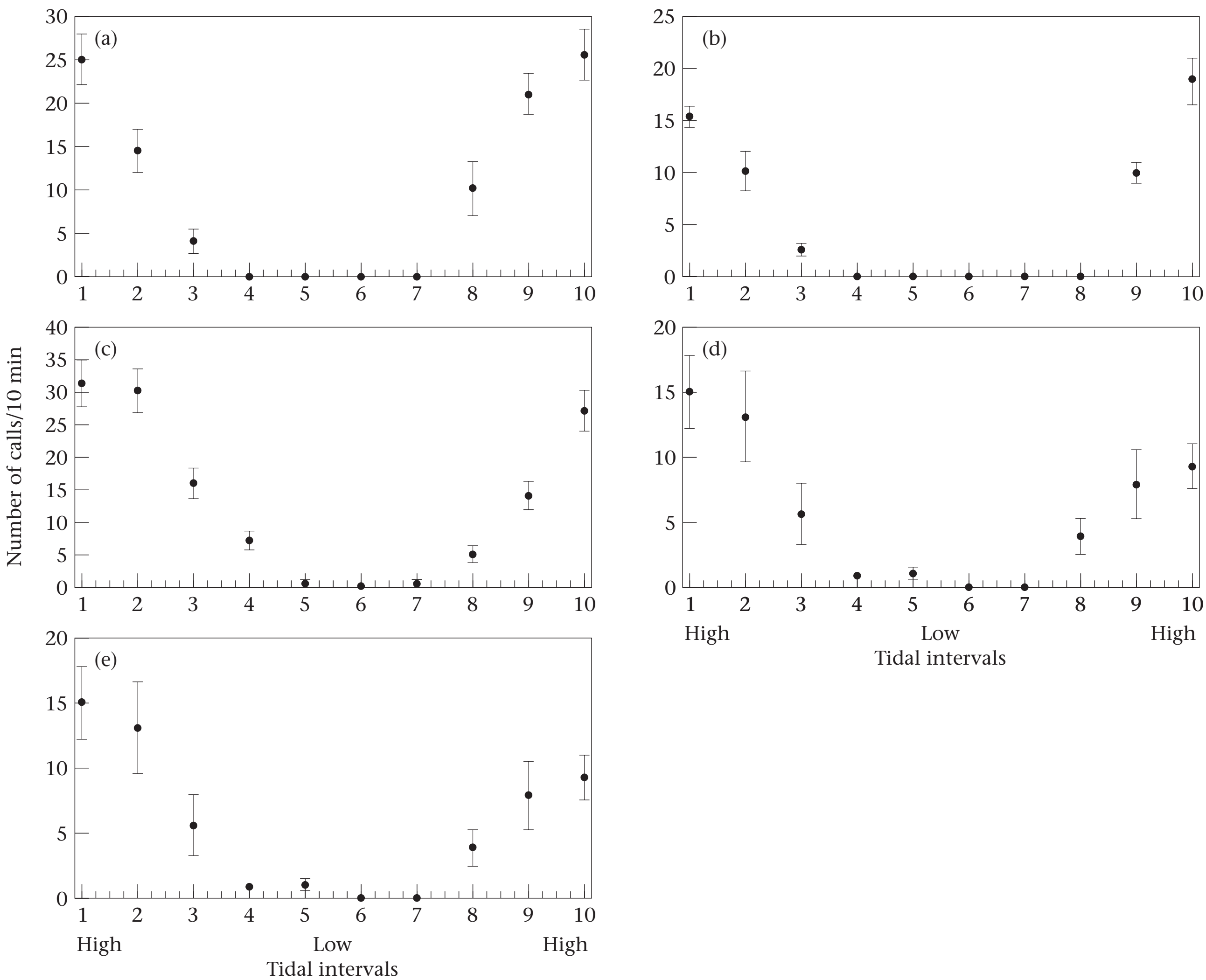


Figure 4. The tidal patterns in the mean number of male vocalizations ±SE counted in all 10-min periods for each tidal interval over several tidal cycles at five sites (a–e) throughout the inner Moray Firth.

RESULTS

Temporal Variation

In the inner Moray Firth, vocalizations were heard only during the summer with the first on 1 July (Fig. 2a). The number of vocalizations varied throughout the mating season, from 1 to 18 in each 10-min high tide sample, with a notable peak between 15 July and 5 August (Fig. 2b). In Orkney, vocalizations were first heard on 24 June, a week before they were heard in the inner Moray Firth.

In the inner Moray Firth, variations in the number of vocalizations were closely related to the tidal cycle at all six sites (Figs 3a, 4). Peak vocalizations were recorded within 1–2 h of high tide, while vocalizations were virtually absent within 1 h of low tide. Analyses of the larger data set from Kessock showed that in the inner Moray Firth the number of vocalizations was significantly related to the tidal cycle; however, there was no relationship between the number of vocalizations and time of day (Fig. 3, Table 1). In Orkney, the number of vocalizations varied significantly with both the tidal cycle and the time of day (Fig. 5, Table 1).

Spatial Variation

There was considerable spatial variation in the density of vocalizing males throughout the inner Moray Firth (Fig. 6a). The highest densities of vocalizations were found in the Beauly Firth (total number of vocalizations counted in all 10-min samples for this area=124), around the mouth of the Inverness Firth (225 vocalizations) and in the northern part of the inner Moray Firth (186 vocalizations). Few vocalizations were recorded in the Cromarty Firth (62) and none over the southern region of the inner Moray Firth. Overall, male vocalization density was highest around the narrow channel between the Inverness Firth and the inner Moray Firth.

In Orkney, vocalizations were heard in only two distinct areas in the study site: Eynhallow sound (217 vocalizations) and around the southern tip of Egilsay (54

Table 1. A two-way ANOVA comparing the relationship between the number of male vocalizations, tidal stage and time of day for harbour seal populations in the inner Moray Firth and Orkney

	Sum of squares		*df*		*F* ratio		*P*	
Interval	Moray Firth	Orkney	Moray Firth	Orkney	Moray Firth	Orkney	Moray Firth	Orkney
Tidal stage	13 591.6	1002.1	9	9	45.9	3.1	<0.0001	<0.001
Time of day	1017.7	4335.3	23	23	1.3	2.6	0.16	<0.0001
Tide×Time	7099.2	7152.6	206	191	1.1	1.0	0.33	0.44

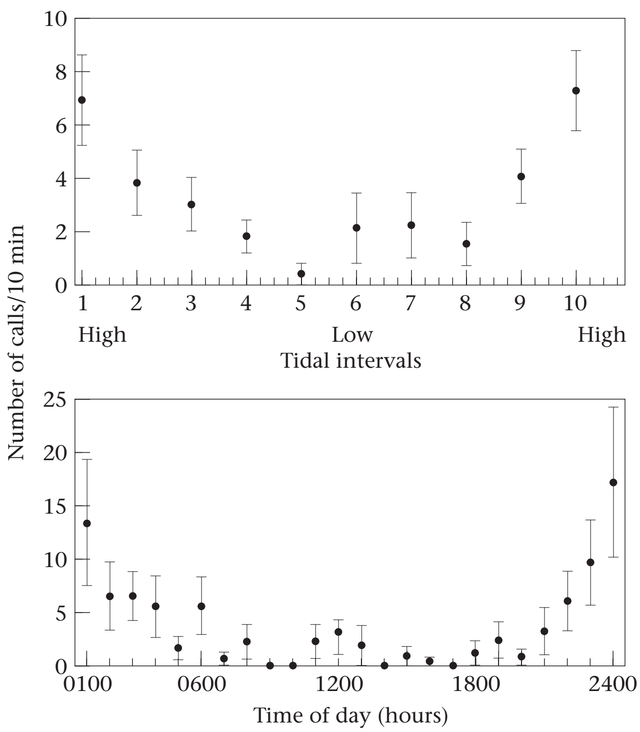


Figure 5. The tidal and diel patterns in the mean number of male vocalizations ±SE counted for all 10-min sampling periods in Eynhallow Sound, Orkney during July and August 1998.

vocalizations; Fig. 6b). No vocalizations were heard at any of the other sampling stations. Our sampling regime differed between areas (see Methods); however, as the temporal patterns of vocalizations were influenced by both tide and time of day in Orkney (Fig. 5), it is unlikely that our unrestricted sampling regime will have influenced male distribution.

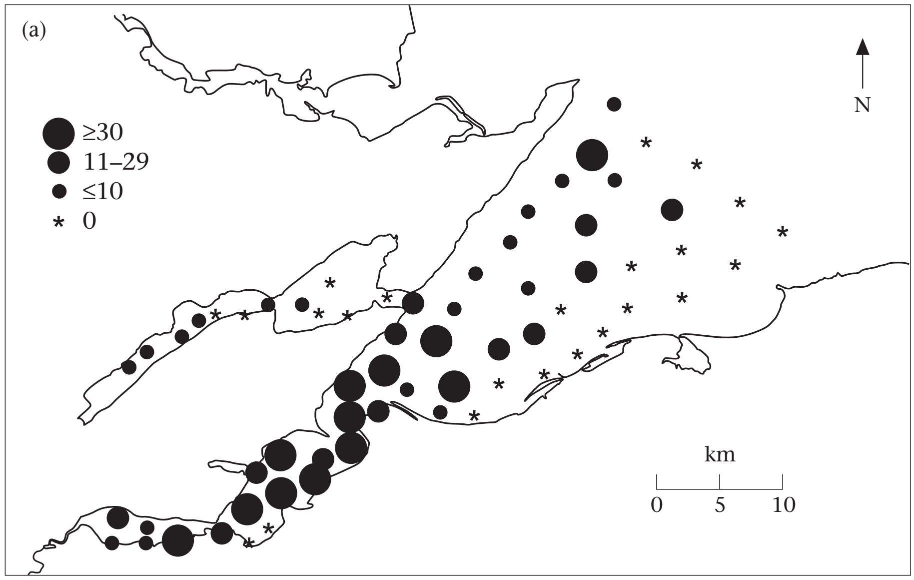
DISCUSSION

Temporal Patterns

In the Moray Firth, harbour seal vocalizations were heard for only a short 40-day period starting in early July to mid-August (Fig. 2), coincident with the onset of weaning in this population (Thompson et al. 1994; Corpe 1996). These were all stereotyped low-frequency calls, occurring at a regular interval of ca. 1 min as described previously (Van Parijs et al. 1997). Although the possibility that females also vocalize cannot be ruled out, considerable research on this species, both in the wild and in captivity, has not previously identified any female vocalizations. Our data therefore support previous studies, which suggest that vocalizations are associated with mating (Hanggi & Schusterman 1994; Bjørge et al. 1995; Coltman et al. 1997; Van Parijs et al. 1997). We suggest that male vocalizations may be used as an indicator of the length of the mating season in northeast Scotland.

In Orkney, male harbour seals began to vocalize 7 days before those in the Moray Firth. There is known to be variation in the timing and duration of the pupping season at different latitudes (Bigg 1981; Boyd 1991; Temte et al. 1991; Temte 1994), and therefore in the timing and synchrony of female oestrus. Formal comparisons of the timing and duration of pupping in these two study areas are not available, but peak numbers of pups are seen slightly later in the Moray Firth (P. M. Thompson, unpublished data) than in Orkney (Thompson & Harwood 1990). Where variations in the duration of the mating season do occur, this may in turn influence male reproductive strategies. For example, where harbour seals have a much longer pupping season in the northeast Pacific (Bigg 1969, 1981), it may not be possible for individual males to restrict their foraging activity and vocalize throughout the mating season. In areas such as the Moray Firth, where the pupping season is shorter, individual males may be able to continue vocalizing throughout the mating season. These acoustic techniques could be used in areas with contrasting pupping phenology to test this hypothesis.

Throughout the Moray Firth, the number of male vocalizations showed a clear temporal pattern in relation to the tidal cycle (Table 1), with an increase in vocalizations around high tide (Figs 3a, 4). In estuarine areas such as this, harbour seal haul out patterns are more strongly influenced by tidal cycles than diel cycles (Thompson et al. 1997), and observed variations in male vocalizations probably reflect the decrease in the number of females present in the water over low tide. In contrast, male vocalizations in Orkney were significantly related to both the tidal cycle and the time of day (Fig. 5, Table 1). Diel cycles in harbour seal haul out patterns are much stronger in these rocky shore areas where site availability is less influenced by the tidal cycle (Stewart 1984; Thompson et al. 1989; Yochem et al. 1987). In these areas, male vocalization patterns are more likely to



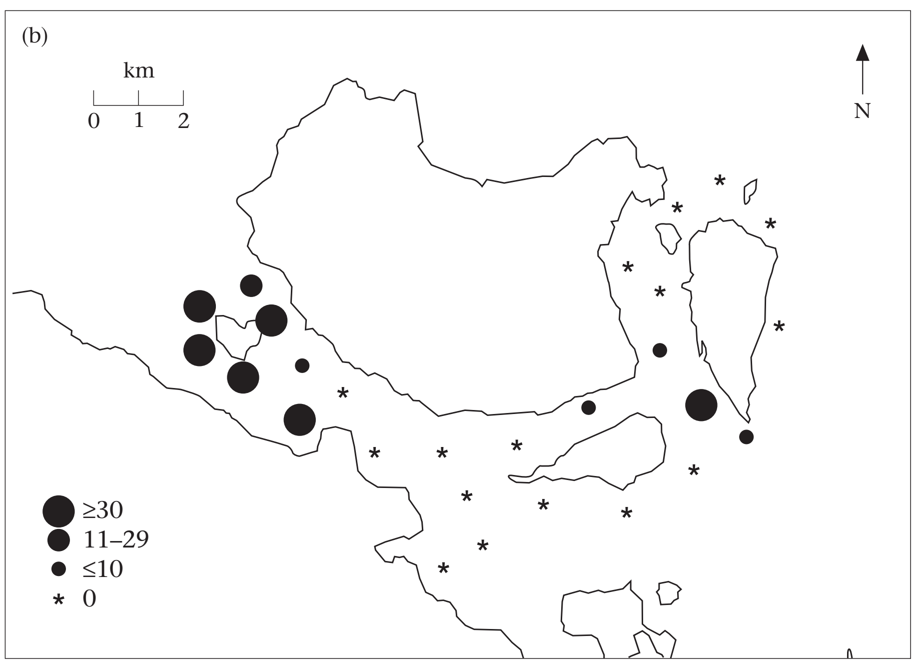


Figure 6. The number of male vocalizations counted during 10-min acoustic recording periods at all sampling stations for (a) the inner Moray Firth during July 1997 and (b) northwest Orkney during July 1998 (note the difference in scale between the two areas).

reflect the combined influences of tide and time of day on female movements. Temporal patterns of male behaviour during the mating season also vary on Sable Island, Canada, where males show a strong diel relationship in their display diving patterns (Coltman et al. 1997). These fine-scale variations in the temporal patterns of male display behaviour therefore probably reflect differences in the ecological constraints on female haul out patterns.

Spatial Patterns

In the Moray Firth, densities of vocalizing males (Fig. 6) showed that males were found throughout the range known to be used by females at this time of year (Thompson et al. 1994). Previous studies also found that nine radiotagged seals made stereotyped dives in all parts of the females' range (Van Parijs et al. 1997), but acoustic recordings could be made only from those seals displaying around haul out sites and transit routes. The results from the present study confirm that males that were located over the females' foraging areas were also making stereotyped vocal displays. Our study also shows that the highest densities of males were found in the narrow channels along female transit routes between their haul out sites and feeding grounds. Lower densities of males were found further out on female feeding grounds, and males were absent from the southeastern part of the study area where previous studies showed that radiotagged females were never located (Thompson et al. 1994; Van Parijs et al. 1997).

In Orkney, male harbour seals were found vocalizing in two discrete areas, around Eynhallow and in the narrow channels between Egilsay, Wyre and Rousay (Fig. 6b). No males were heard vocalizing at any of the other sampling stations, including those around some small haul out sites known to be used by females and pups. These results suggest that displaying males in the Moray Firth may be more widely dispersed, although logistic constraints prevented us carrying out surveys in the more offshore foraging areas in Orkney (Fig. 1). However, there are similarities between those areas in the Moray Firth and Orkney where the highest densities of males were found. Eynhallow represents the largest pupping site in the study area (Thompson et al. 1989), but Eynhallow Sound is also a major transit route between more scattered haul out sites and the open waters to the west and north of the study area where these animals appear to forage (Thompson et al. 1989). Similarly, the highest densities of calling males in the Moray Firth were found along narrow constrictions in the transit routes between haul out sites and foraging areas.

On Sable Island males also use a variety of reproductive strategies, one of which appears to include following females out to their foraging areas (Coltman et al. 1998, in press). Clearly, the relative advantage of these different strategies may differ in relation to an individual's body size and fasting ability (Coltman et al. 1997). The unique aspects of harbour seal behaviour on Sable Island mean that the relative success of the different male strategies observed in that population can be assessed using genetic techniques (Coltman et al., in press). Opportunities to obtain DNA from sufficiently large samples of adults and pups are extremely limited in other areas, where harbour seals inhabit more complex habitats and might be expected to show a broader range of behaviours. Together, these results suggest that male mating strategies in aquatically mating pinnipeds may be more variable than those envisaged by early workers who had focused their studies on terrestrial breeding species (e.g. Bartholemew 1970). Our data illustrate that the focus of work on aquatically mating phocids must move away from the terrestrial pupping sites, and that acoustic techniques should provide a valuable tool for future comparisons of male responses to the much broader differences in female distribution and density that exist in these species.

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