Underwater vocalization of ice breeding grey seals

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Grey seals (*Halichoerus grypus*) breed both on land and on the ice. In January 1991, 36 h of underwater recordings were made from Amet Island, located in ice-covered waters in the southern Gulf of St. Lawrence. All vocalizations were examined for spectral and temporal structure and then classified into 1 of 7 call types. The majority of calls consisted of guttural "rups" and "rupes" (frequency = 100–3000 Hz), and low-frequency growls (100–500 Hz). Other less common vocalizations were low-frequency clicks (3000 Hz), as well as loud knocks, similar to knocking vocalizations recorded in walrus, and which had not been described previously for grey seals. The total number of vocalizations and the number of specific call types showed seasonal variations. The rate of vocalizations increased with the intensity of social activity and with the number of agonistic behaviors during the progression of the breeding season. Comparisons between night and day showed some changes in the vocal repertoire. Low-frequency clicks were recorded more often during darkness (17.1% of calls) than in daylight (1.9%), and when ice cover was more extensive.

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Le Phoque gris (*Halichoerus grypus*) se reproduit sur les côtes et sur les glaces. En janvier 1991, 36 h d'enregistrement ont été faites sous l'eau à partir de l'île Amet située dans la partie sud du Golfe St Laurent. Toutes les vocalisations ont été analysées en fonction de la fréquence, du temps et de l'aspect physique des spectrogrammes, pour être ensuite classifiées en 7 types. La majorité des vocalisations sont des "rups", des "rupés" gutturaux (fréquence = 100–3000 Hz), ainsi que des grognements de basses fréquences (100–500 Hz). Nous décrivons aussi des clics de basses fréquences (3000 Hz), ainsi qu'un type de vocalisation bien particulier semblable au "cognement" chez les morses. Il se produit des changements saisonniers dans le nombre et le types des appels. La quantité de vocalisations a tendance à augmenter en fonction du nombre d'interactions entre les animaux pendant cette periode. Des comparaisons entre le jour et la nuit démontrent qu'il y a des différences dans le répertoire vocal. Durant la nuit, les phoques gris semblent avoir tendance à utiliser les clics plus que toute autre vocalisation, et ce, particulièrement lorsque le couvert de glace est important. Les proportions de clics dans les répertoires vocaux nocturne et diurne sont respectivement de 17.1% et de 1.9%.

Introduction

The grey seal (*Halichoerus grypus*) is a large phocid found throughout northern temperate waters on both sides of the Atlantic Ocean (Davies 1957; Cameron 1967). Although rare early in this century, most populations are recovering and in some cases increasing rapidly (Harwood et al. 1989; Stobo and Zwanenburg 1990; Zwanenburg and Bowen 1990). In the eastern Atlantic, grey seals occur around the British Isles, in the Baltic Sea, along the coast of Norway, and along the south coast of Iceland. In the western Atlantic, they range from northern Newfoundland to the northeastern United States (Stobo and Zwanenburg 1990). The largest concentrations are found in the southern half of the Gulf of St. Lawrence and around Sable Island (Davies 1957; Cameron 1967; Godsell 1991).

There have been very few studies on the underwater vocalizations of grey seals (Schevill and Watkins 1963; Schusterman 1970; Schneider 1974). They identified roars, trrots, and clicks, but only Schneider provided detailed descriptions, dealing primarily with the in-air repertoire. The paucity of information results from grey seals apparently being rather silent, except during the breeding period, when social interactions are more common (Poulter 1968; Schusterman 1970; Schneider 1974; Chwedenczuk 1985). Most pinnipeds produce striking underwater acoustic signals and greatly increase their calling during reproductive activities (Stirling 1973; Møhl et al. 1975; Watkins and Ray 1977; Wartzok et al. 1981; Ralls et al. 1985).

In grey seals, breeding occurs during the fall in northeastern Atlantic populations, and from the end of December until the end of January in eastern Canada, on land or on shifting pack ice. Lactation lasts for 15–17 d (Boness 1984). After mating, the females disperse from the breeding haul-out site. In terrestrial breeding populations, males maintain territories or compete to lie in close proximity to one or several females (Boness et al. 1982; Anderson et al. 1975). A male's reproductive success is correlated positively with the length of time he remains near a group of females (Anderson et al. 1975; Boness and James 1979; Godsell 1991). Copulation normally occurs on land or ice, approximately 13 d after the birth of the pups (Cameron 1970; Bonner 1972; Boness and James 1979). Bulls require a very strong sexual drive to overcome a cow's aggressive responses, and this reinforces the selective advantage of aggression in bulls (Anderson et al. 1975).

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TABLE 1. Mean quantitative descriptors of each grey seal vocalization type

Call type	Frequency (kHz) Fundamental $\bar{x}$	Fundamental SD	Maximum $\bar{x}$	Maximum SD	Maximum n	Call duration (s) $\bar{x}$	Call duration SD	Call duration n	Series duration Time (s) $\bar{x}$	Time SD	Number of repetitions Range	Repetitions $\bar{x}$	Repetitions SD	Repetitions n	Harmonics
Rup T1	0.2	0.1	2.3	1.5	42	0.04	0.69	42	2.35	4.33	1–84	9.1	14.6	67	Yes
Rup T2	0.2	0.1	2.1	1.7	21	0.11	0.06	21	1.49	1.93	1–61	5.8	4.1	38	Yes
Rupe	0.2	0.1	1.5	1.2	38	0.58	0.52	64	2.74	3.35	1–41	4.9	5.8	244	Yes
Growl T1	0.2	0.5	2.0	1.2	26	1.09	0.52	34	1.24	0.97	1–2	1.1	0.3	32	Yes
Growl T2	0.2	0.1	0.3	0.1	17	1.17	0.60	29	1.20	0.59	1	1.0	0	24	No
Knocking	NA		8.6	5.7	11	0.13	0.09	49	0.39	0.45	1–4	1.5	0.5	94	No
Trrot	NA		3.3	1.9	12	1.06	1.90	71	1.21	1.85	1–6	1.2	0.7	82	No
Click	NA		3.5	3.3	13	1.40	1.21	133	2.09	1.50	1–6	1.5	0.9	296	No
Roar	0.4	0.1	1.8	1.4	15	1.61	1.53	102	1.93	1.98	1–6	1.2	0.8	116	Yes

Owing to logistical difficulties, most research on grey seals has focused on terrestrial breeding populations in the United Kingdom and on Sable Island in eastern Canada, where a large part of their social interactions occur on land, and adults rarely enter the water. In ice-breeding populations, both males and females regularly enter the water through holes in the ice or via leads (open water within the ice cover). Hence, underwater vocalizations may have an important function in male–male or male–female interactions.

The objectives of this study were to describe the underwater vocal repertoire of grey seals during the breeding season, to determine the spectral and temporal characteristics that define each vocalization, and to relate underwater vocalizations to changes in behavior as the brief breeding season unfolded.

Material and methods

Study area

The study was conducted at Amet Island, an islet approximately 120 by 55 m wide and 5 m high, located approximately 5.4 km off the northern Nova Scotia coast, in Northumberland Strait (45°51′ N, 63°10′ W). The island provides an ideal vantage point for observing seals, both on the beach and on the surrounding ice, without disturbing them. The water surrounding the island is shallow (3–4 m), and during winter drifting ice is trapped on reefs surrounding the island. Pups are born on the narrow beach or on the trapped ice. In some years the prevailing westerlies and eastward-moving current may cause large amounts of ice to pile up along the west and northwest sides of the island, trapping animals between the island and rafted ice, and limiting their access to water. Such conditions occurred in 1991. As a result, only seals along the northeastern, eastern, and southeastern sides of the island had access to water.

Ice conditions change considerably throughout the study. On January 6 there was only 0–20% ice cover around the island, in small patches, particularly along the west side. Ice cover increased on January 9 to 21–41%, with ice concentrated along the west coast where cover was 100% and without breathing holes. Ice cover continued to increase along the eastern side of the island, reaching 41–60% on January 12 and 61–80% by January 15. This ice was primarily very thin grey ice and slush, and was unable to support the seals. Seals often surfaced in this ice by pushing their heads through the slush to make breathing holes. By January 17 ice cover on the eastern side reached 100% (grey-white ice). At this time the ice was sufficiently thick to support the seals, and animals began using breathing holes.

Data collection

Underwater vocalizations were recorded between 6 and 27 January 1991 using a Sony cassette recorder (model TCM-5000 EV; frequency response was flat between 0.09 and 9.0 kHz, but the sensitivity extended beyond that range), and a Vemco hydrophone (frequency response was flat between 0.03 and 20.0 kHz) lowered 2–3 m below the surface, about 30 m off the east side of the island. One hydrophone was continually in the water and was connected to the recorder on top of the island with 100 m of cable. A second hydrophone beside a breathing hole was also used.

Fifteen-minute recordings were made every 2 h between 08:00 and 22:00, and again at 04:00. During three 24-h periods (14, 18, and 23 January), we recorded for 15 min every 2 h.

During the study, daily counts of the total number of males, females, and pups, and their approximate location were noted at 08:00, 12:00, and 16:00. In addition, during each daylight recording period the number of males and females on land or ice were counted. Sampling all occurrences of some behaviors, as described by Altmann (1974), was conducted for visible animals during each 15-min recording session. Observations were conducted from a small blind on the island, about 5 m above the ice. All animals were ≤100 m from the blind. Recorded behaviors were agonistic, attempted copulation, or successful copulation (Boness 1984).

Vocalization analysis

All frequency and time–domain analyses were made from spectrograms, using the Signal system (V 2.10; Engineering Design, Belmont, Massachusetts). Frequency resolution was set at 48.8 Hz, and time resolution at 0.02 s.

A vocalization series was defined as a number of vocalizations emitted without a pause of 2 s or more. In the majority of cases 2 successive series were separated by much more than 2 s. Ten of 124 recording bouts were discarded because of background noise resulting from ice or water movement, masked vocalizations, or because of equipment malfunctions. The remaining recordings were analysed: 18 h 8 min of recording between 7:00 and 17:00 (daylight recordings), and 13 h 42 min of recording between 17:00 and 7:00 (nighttime recordings). During the study period sunset occurred around 17:30 and sunrise at around 07:30. A total of 3856 vocalizations were recorded, measured and classified. Vocalizations were classified using a combination of audible and visual differences between sonograms, using the frequency range of the fundamental (where most of the energy is concentrated), call duration, number of calls per series, and the presence or absence of harmonics (multiples of the fundamental frequency). One hundred and ninety-five of these vocalizations, which were more distinct, were analysed in detail to obtain the mean value and the standard deviation of the fundamental and of the highest frequency, as well as the duration. A total of 993 series of vocalizations were measured for duration (mean and standard deviation), total number of calls per series of vocalization, and presence or absence of harmonics (Table 1). The pulse repetition rate of trrots and clicks was measured using 1 of 2 methods. Below repetition rates of 100 pulses per second, each pulse appeared distinctly in a spectrogram, covering a broad band of frequencies (Fig. 1G). In this case, the number of pulses per second was counted directly from the spectrogram. Above rates of 100 pulses per second, the spectrum analyser

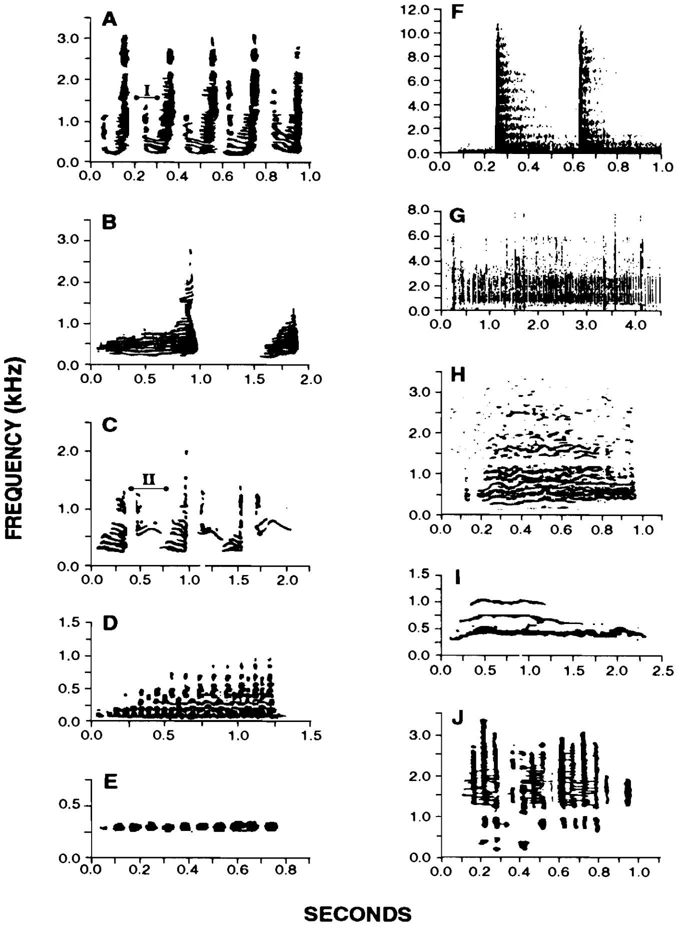

FIG. 1. Examples of underwater call types emitted by grey seals during the breeding period. (A) Series of 5 type-1 rups with an auxiliary structure (I). (B) Series of 2 type-2 rups. (C) Series of 3 rupes with an audible auxiliary structure (II). (D) Growl type 1. (E) Growl type 2. (F) Series of two knocks. (G) One example of a click: 72 pulses per second in this particular train. (H) One example of a click: 125 pulses per second in this particular train. (I) Roar. (J) Trrot: 13 pulses per second.

could no longer distinguish between individual pulses of sound, because individual pulses coalesced together and horizontal bands appeared (Fig. 1H). When this occurred, the pulse repetition rate was determined by measuring the width between two horizontal bands (Watkins 1967).

To document temporal and seasonal changes in vocalizations, we expressed vocalization rates as the total number of vocalizations per hour of recording per seal in the water. The number of calls was counted using the function real time spectrogram function of Signal. Occasionally, series of calls were emitted very rapidly, but these never overlapped. The number of seals in the water was determined as the greater of either the number of seals actually counted in the water during the recording session, or, the difference between the number of resident animals in the study area, based on the daily counts minus the number of animals hauled out during the daylight recording session. No vocalizations were heard when no seals were observed in the water, therefore, we believe that our measure provides a valid index of vocalization rate per seal. During January and February no other species of marine mammals were sighted in Northumberland Strait. Therefore, we believe that our recordings were only from grey seals.

Statistical analysis

Differences between periods in the rate of vocalizations per seal, and changes in the number of vocalizations and clicks per hour with time of day, were compared using a Kruskal–Wallis one-way analysis of variance by rank (Siegel 1956; Scherrer 1986). Differences in the number of agonistic behaviors, the number of vocalizations, and the number of clicks between night and day were compared with a Mann–Whitney U test (Siegel 1956). Differences in the vocal repertoire during the progression of the breeding season were compared with a χ^2 test for goodness of fit (G test), with Williams' correction (Sokal and Rohlf 1981).

Results

Vocal repertoire

Seven types of vocalizations were identified. These were the guttural rup, guttural rupe, growl, knock, click, roar, and trrot (Table 1 and Fig. 1).

The guttural rup was the most common call, accounting for 47% of the 3856 vocalizations recorded. Rups typically consisted of a relatively constant frequency followed by a sharp upsweep in frequency at the end of the call (Figs. 1*a*, 1*b*). Type 1 rups also had an additional short downsweep (I), without harmonics, at the start of the call. There were no obvious audible differences between type 1 and type 2 rups. In both types of call most of the energy in the fundamental during the period of relatively constant frequency was between 0.1 and 0.4 kHz (N = 63). During the sharp upsweep at the end of the call the frequency typically increased from 0.4 to 4.7 kHz. In type 1 rups, the initial downward sweep had a fundamental frequency of 0.4 ± 0.1 kHz ($\bar{x}$ ± SD). The total duration of type 1 and type 2 rups ranged from 0.04 to 1.01 s. These calls usually occurred in series. The duration of these series ranged from 0.05 to 28.76 s (N = 105 series). Type 1 series were slightly longer in duration than type 2, but these differences were not statistically significant.

The second most common call, the guttural rupe, accounted for 29% of all vocalizations. Guttural rups and rupes often were recorded together (18% of occurrences), although no consistent pattern in the occurrence of these vocalizations together was observed. The fundamental frequency of the guttural rupe ranged from 0.1 to 0.4 kHz (Fig. 1C). Numerous harmonics varying from 0.4 to 3.6 kHz were observed (N = 38 calls). The duration of this call was also quite variable, ranging from 0.13 to 2.84 s. The guttural rupe also had a downsweep (II), at 0.4 ± 0.3 kHz, which occurred at the end of the vocalization. However, contrary to type 1 rups this auxiliary structure had harmonics and was audible. A series of rupes lasted from 0.13 to 21.31 s.

Growls represented 5% of the underwater vocal repertoire (Figs. 1D and 1E). This vocalization was monotonic. Most of the energy was limited to the fundamental frequency, which ranged from 0.1 to 0.3 kHz. Two types of growls were identified. Both sounded exactly the same, but only type 1 had harmonic structures. The highest frequency recorded was 3.4 kHz for type 1, and 0.4 for type 2. Growl types 1 and 2 lasted from 0.13 to 2.36 s. Compared with rups and rupes, growls were less variable in duration (0.13 to 5.75 s) and were recorded in much shorter series.

Knocks represented 4% of all vocalizations recorded (Fig. 1F). This call had the highest frequency range of all vocalizations, and it sounded like a hammer hitting metal. The harmonics may be the cause of the "ringing" quality (lingering tone) of the call. The higher frequency was between 1.9 and 15.8 kHz. The sound duration of one knock ranged between 0.02 and 0.41 s.

Clicks sounded like a "creaking door," and represented 8%

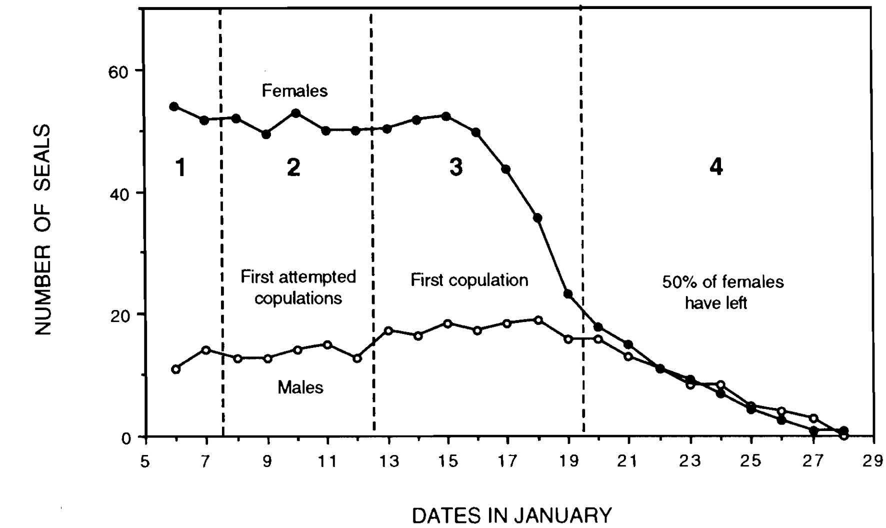

FIG. 2. Total number of male and female grey seals around the island (both on the ice and in the water) during the breeding period.

of all underwater vocalizations. Clicks displayed may cover a frequency spectrum of 0.2 to 10.0 kHz (Figs. 1G and 1H). They were recorded most often (87% of 296 cases) in series. The duration of one click (or click train) ranged from 0.13 to 5.88 s. The difference in the contour component between clicks (Figs. 1G and 1H) was affected by the speed of the sound production (pulses per second). The rate at which clicks were repeated varied between and within series of clicks, and ranged from 60 to 537 pulses per second (mean, 172 ± 118 pulses per second). However, this physical parameter was not sufficient to classify them into different types.

The roar vocalization sounded like a roaring or howling dog. The fundamental frequency of roars had energy in the 0.2 to 0.6 kHz range, with some harmonics (Fig. 1I). Sound duration ranged from 0.08 to 6.48 s, and a series of roars ranged from 0.08 to 10.89 s. Forty-five percent of roars were recorded with guttural rups and rupes. This call type constituted only 4% of the vocal repertoire.

The trrot vocalization (Fig. 1J) sounded like a jackhammer (Schneider 1974). It was the least common type among the calls recorded, representing only 2% of the underwater vocal repertoire. Trrots displayed energy between 0.1 and 7.6 kHz. Ten percent of trrots were recorded with clicks, and the pulse repetition rate ranged from 24 to 46 pulses per second (mean, 34 ± 8 pulses per second). This call lasted from 0.06 to 12.47 s.

Seasonal variations

When we arrived on January 6, there were 54 females and 11 males around the island. Daily ratios of bulls to cows varied (Fig. 2), but the average ratio was 0.73 ± 0.66 over the 23 d of the study.

To examine seasonal changes in vocalization rates, we divided the breeding season into 4 periods. Period 1 lasted for only 2 d, January 6 and 7. This period was characterized by females with young pups. Males were observed around the island, resulting in an adult sex ratio of 0.24 (N = 2 d), but no male–male, or male–female aggressive interactions were observed. Period 2 was defined as January 8 to 12. Male–male interactions and attempted copulations were observed for the first time on January 8. The sex ratio for this period was 0.26 ± 0.02 (N = 5 d). No successful copulations were observed, pups were fatter, and many were halfway through their lactation period (S. Baker, Laval University, personal communication). Period 3 lasted from January 13 to 19. The first successful copulation was seen on January 13, and increases in male–male, as well as male–female aggressive interactions and copulations, were observed. The number of males remained relatively constant, while the number of females declined throughout this period as the pups were weaned. The mean male to female ratio was 0.43 ± 0.13 (N = 7 d). Period 4 was defined as January 20 to 28. After January 19 more than 50% of the females had copulated and subsequently weaned their pups, and 15% of the males had also left. The adult sex ratio was 1.20 ± 0.82 (N = 9 d). Fewer male–male or male–female aggressive interactions were observed.

The vocalization rate increased with the progression of the breeding season and the number of agonistic behaviors (Fig. 3). The maximal rate occurred in period 3 (52.3 ± 74.4 vocalizations per hour per seal) in spite of the fact that the mean number of animals in the water was lower (2.2 ± 0.1 seals/recording), compared with 6 seals/recording in periods 1 and 2 (Fig. 3). Copulations were most frequent in the third period, and male–male, as well as male–female, aggressive interactions were common (2.65 ± 1.22 agonistic behaviors per hour per seal on the ice). During the fourth period, both vocalization rates (5.8 ± 7.3 vocalizations per hour per seal) and the number of agonistic behaviors (0.36 ± 0.63 agonistic behaviors per hour per seal) declined substantially (Fig. 3), which coincided with a major decline in the total number of animals around the island (Fig. 2). There were no significant differences in the number of vocalizations per hour per seal, between the 4 periods (Kruskal–Wallis, df = 3, p = 0.111), because of the high variability among recording bouts. However, period 3 had a significantly higher rate of agonistic interactions per hour per seal (Mann–Whitney, p = 0.038).

Changes were observed in the vocal repertoire during the progression of the breeding season. Throughout the study guttural rups were the most frequently recorded vocalizations. During the first 2 periods the relative frequency of guttural rups remained constant. This was followed by a significant decline during period 3 (χ^2 for G test, df = 3, p = 0.001).

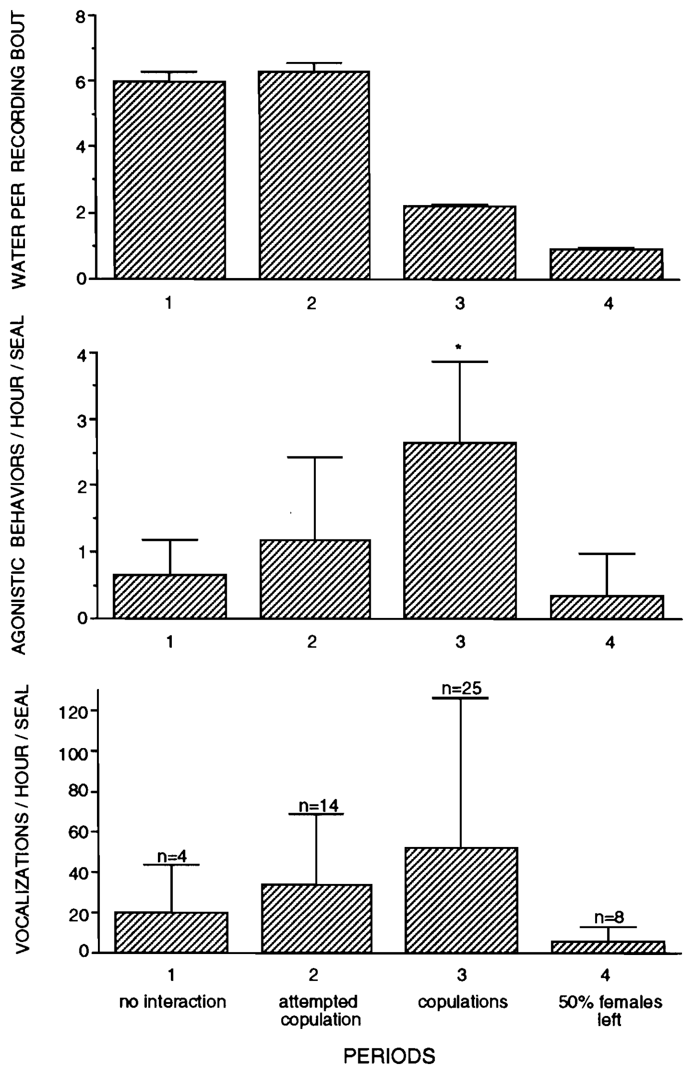

FIG. 3. Temporal variation in the mean number of seals in the water, the mean number of agonistic behaviors observed on the ice, and the mean number of vocalizations per daylight recording bout (n is sample size, bars show SD, and the asterisk indicates significant differences (Mann–Whitney multiple-comparisons test; p = 0.038).

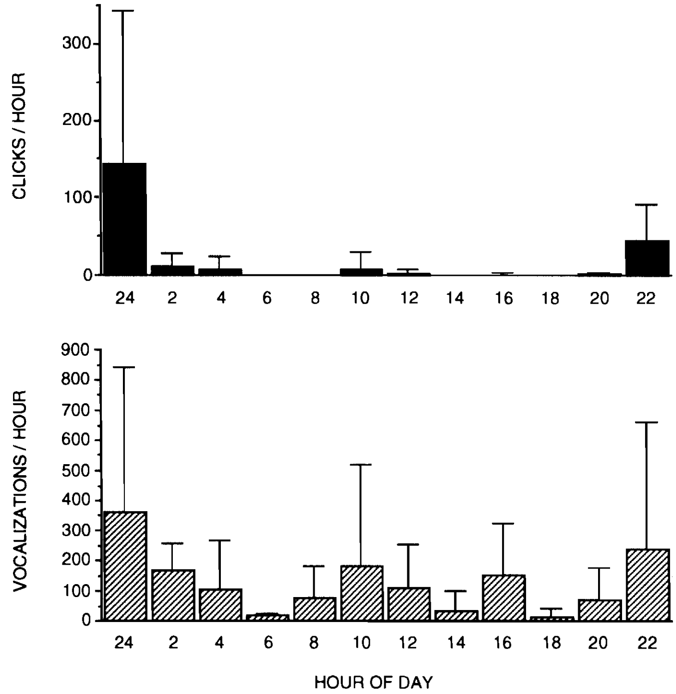

FIG. 4. Changes in the mean number of clicks and vocalizations per hour with time of day. Bars show standard deviation.

During period 4 a significant increase occurred (χ^2 for G test, df = 3, p = 0.001), with rups accounting for 80% of vocalizations.

The rupe was the second most common call. During the first 3 periods the frequency of rupes showed little change, but a significant decline occurred in period 4 (χ^2 for G test, df = 3, p = 0.001).

The remaining 5 vocalizations (knocks, growls, clicks, roars, and trrots) accounted for less than 25% of all vocalizations recorded.

Knocks were the third most common vocalization heard in period 1. A significant decline in the relative frequency of knocks was observed between periods 1 and 2 (χ^2 for G test, df = 3, p = 0.01). Knocks then increased again during period 3, but during period 4, none were recorded. Growls showed a significant increase between periods 1 and 2 (χ^2 for G test, df = 3, p = 0.009), declined significantly during period three (χ^2 for G test, df = 3, p = 0.0001), and then increased again during period 4. During 3 of 4 periods, clicks made up less than 5% of the total number of vocalizations. However, during period 3, a significant increase (from 2 to 20 clicks per hour) was observed (χ^2 for G test, df = 3, p = 0.0004). This increase coincided with changes in total ice cover. During period 3 solid ice formed along the east side of the island for the first time, and seals began to use breathing holes. Roars and trrots also formed only minor components of the vocal repertoire. No significant changes in the frequency of occurrence of these vocalizations were observed throughout the breeding season.

Diurnal cycles

Total vocalization rates showed considerable daily variation, but this was not related to time of day (Fig. 4). The highest rates of vocalizations and clicks were observed at 22:00 and 24:00 (239.6 and 364.4 vocalizations per hour, and 45.4 and 142.0 clicks per hour, respectively) (Fig. 4). The differences between nighttime and daytime vocalization rates were not significant (107.9 ± 129.9 and 114.2 ± 167.3 vocalizations per hour, Mann–Whitney; p = 0.6), (Fig. 5). Clicks tended to be recorded more frequently during the night (17.1 ± 62.5 clicks per hour), than during the day (1.9 ± 4.7 clicks per hour) (Fig. 5), but this difference was not significant (Mann–Whitney; p = 0.4).

Discussion

Vocal repertoire

Fundamental frequency, harmonic structures, and auxiliary sounds have been used in previous studies to classify vocalizations in several species of whale and pinniped. Fundamental frequency range has been used to classify vocalizations of belugas (*Delphinapterus leucas*) (Fish and Mowbray 1962; Sjare and Smith 1986*b*), narwhals (*Monodon monoceros*) (Ford and Fisher 1978), pilot whales (*Globicephala melaena*) (Weilgart and Whitehead 1990), humpback whales (*Megaptera novaeangliae*) (Payne and McVay 1971), harp seals

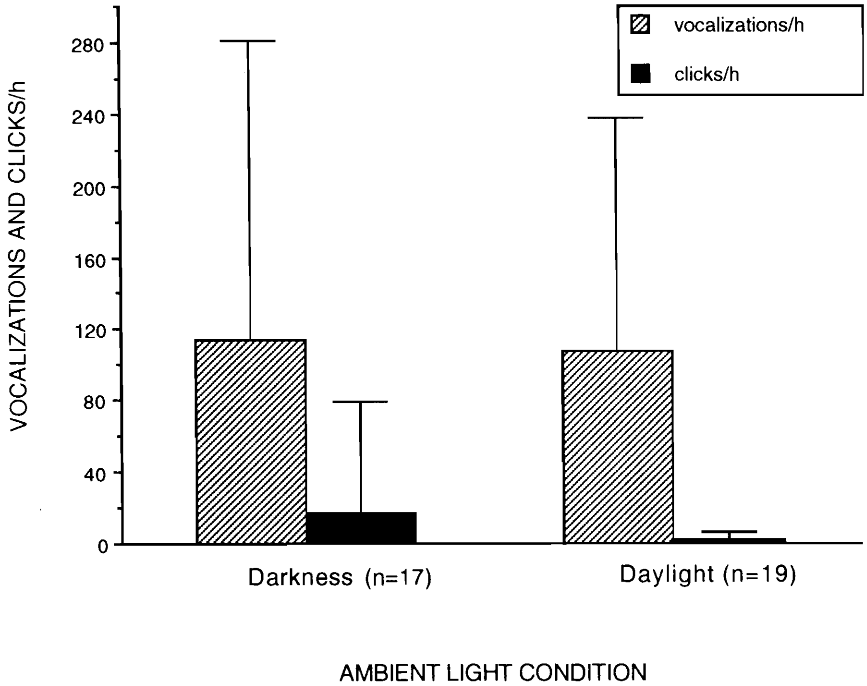

FIG. 5. Difference in the number of vocalizations and clicks between night and day. Daily means with their standard deviations (*n* is the number of nights or days).

(*Phoca groenlandica*) (Møhl et al. 1975), leopard seals (*Hydrurga leptonyx*) (Stirling and Siniff 1979), Weddell seals (*Leptonychotes weddelli*) (Thomas and Kuechle 1982), and bearded seals (*Erignathus barbatus*) (Cleator et al. 1989). Auxiliary sounds have been used to classify vocalizations of Ross seals (*Ommatophoca rossi*) (Watkins and Ray 1977), harp seals (Møhl et al. 1975), Weddell seals (Thomas and Kuechle 1982), and belugas (Fish and Mowbray 1962). The presence or absence of harmonics has been used by Thomas and Stirling (1983) and by Møhl et al. (1975) for classifying Weddell and harp seal vocalizations. However, the number of harmonics is affected by the intensity of the vocalization and the distance from the hydrophone; consequently, we used only the presence or absence (not the number) of harmonics to classify call types in this study.

We recognized 7 audibly different vocalizations. Rups and growls were subdivided further, on the basis of the presence of auxiliary sounds, or the absence of harmonics. All of the vocalizations showed some variability in the physical parameters measured (Table 1). This variability may reflect intersexual or interindividual differences in vocal capabilities or responses to social situations (Busnel and Poulter 1968). Spectral characteristics for some types of vocalizations may vary among individuals (Stirling et al. 1987; Cleator et al. 1989).

The same vocalization can also vary in relationship to the social rank of the animal. Vocalizations were the most highly rank-related aggressive behaviors in southern elephant seals (*Mirounga leonina*) (McCann 1981), and hierarchy could be reliably identified on the basis of consistent acoustic parameters in northern elephant seals (*Mirounga angustirostris*) (Shipley et al. 1986). In the vervet monkey (*Cercopithecus aethiops*), what appears to a human listener to be only 1 vocalization, is in fact several different vocalizations, each evoking a different response depending on whether it is played back to a dominant or to a submissive group member (Cheney and Seyfarth 1990). Unfortunately, during underwater recordings we were unable to identify the caller or the receiver of the signal. Consequently, we are unable to relate specific behaviors to particular call types.

Clicks, trrots, and roars have been described before in the grey seal (Schevill and Watkins 1963; Schusterman 1970; Schneider 1974) with a few sonograms, but the vocalizations have not been described quantitatively. Schevill and Watkins (1963) reported that clicks were recorded singly, or in series, at a rate of 60 pulses per second, with dominant frequencies between 6 and 12 kHz. Schusterman (1970) reported that grey seals emitted clicks at 70 and 80 pulses per second, with a frequency range of 0.5–12 kHz. Schneider (1974) recorded some clicks with an energy of up to 15 kHz. The findings presented here are consistent with these results for frequency ranges, although in our study we obtained a higher pulse repetition rate (172 pulses per second) for many clicks.

Schneider (1974) recorded the clicks of grey seals, both in association with other vocalizations and during feeding. Oliver (1977), working with captive grey seals trained to navigate through an obstacle course, found an inverse relationship between light intensity and vocalization rates, the majority of signals being clicks with a frequency range of 0–30 kHz We did not observe any difference in overall rates of vocalization between daylight and night recordings, which is consistent with Anderson and Hawkins (1978) who found no difference between day and night activity levels for 11 of 12 behavioral categories in grey seals. However, we did observe a significant increase in the number of clicks between periods 2 and 3, which coincided with the formation of thick ice when seals were forced to use breathing holes. This suggests that grey seals used clicks to help find their way under the ice.

The possibility of echolocation in phocids has been discussed for several species (Schevill and Watkins 1963; Poulter 1963, 1966, 1968, 1969; Schusterman 1970; Terhune and

Ronald 1973; Hewer 1974; Møhl et al. 1975; Oliver 1977; Thomas and Kuechle 1982; Hyvärinen 1989; Terhune 1989). The structure of the clicks of grey seals and other pinnipeds, as for Weddell seals (Thomas and Kuechle 1982) or harp seals (Møhl et al. 1975) resembles "restricted-frequency click" series emitted by odontocetes for echolocation. However, the frequency range of 0.2 – 10 kHz and maximum repetition rate of 172 pulses per second emitted by grey seals are much lower than the frequencies of 20 – 120 kHz, with a repetition rate of 3100 pulses per second, emitted by beluga whales (Sjare and Smith 1986*b*).

Schneider (1974) described a jackhammer sound, which corresponds to our trrots, as a kind of click that would be emitted very slowly. This vocalization was used by males in situations where dominance might be displayed, such as contact during haul out or during sexual interactions (Schneider 1974).

Schusterman (1970) also described a humming or moaning sound that was produced both in air and underwater, and sometimes in both simultaneously. This vocalization corresponds to our roar (Fig. 1I). Described by Schneider (1974) as a wail, the roar showed no variation in structure when emitted in air or underwater. Schneider (1974) reported that this vocalization was emitted by both sexes, often when 2 animals were swimming in coordination, during interactions that involved an animal moving, being crowded, or competing for space or food. In Schneider's (1974) study this was the most common vocalization emitted in captivity, and it is probably the "hoot" threat described by other investigators (Hewer 1957, 1960; Hickling 1962; Hewer and Backhouse 1960; Lockley 1966). In our study, roars accounted for less than 5% of the vocalizations, suggesting that the much higher rate observed by Schneider (1974) may have been partly a result of captivity. The variety of names given to what seems to be one call, as exemplified here (humm, moan, roar, wail, hoot), emphasizes the importance of providing sonograms and quantitative descriptors (e.g., Fig. 1 and Table 1) in addition to names in the description of calls.

The growl vocalization has not been described previously as part of the grey seal vocal repertoire. However, Schneider (1974) described a "male roar" emitted in air at a higher frequency of 200 – 470 Hz, which resembles our underwater growls. Schneider associated this vocalization with dominance and mating. It was sometimes recorded when only males were counted in the water, suggesting that it may be typical of males. Growls resembling our type 2 growls have been described in the Weddell seal, but their function is not known (Thomas and Kuechle 1982).

In this study, the rup and rupe were the most frequently recorded vocalizations. They were often recorded when only females were observed around the hydrophone, or when splashing and swirling were seen at the surface, suggesting a fight or chase. The fact that these vocalizations have not been described before suggests that rups and rupes may be limited to the breeding season, and may be produced mostly by females during female – female or male – female conflicts. Alternatively, most previous studies have been conducted in oceanaria, where animals may vocalize less because of the unnatural conditions, or because dominance relations may be well established, resulting in fewer social interactions involving underwater vocalizations. Schneider (1974) accumulated 1 h of recordings from the Basque Islands, off the east coast of Nova Scotia, during August 1971 and January 1972. The absence of rup and rupe vocalizations in that study may be due to the small sample size, or to seasonal effects on underwater vocalizations. Also, during the 1970s, the grey seal population was much smaller, because of a bounty program and a government-sponsored cull during the breeding season (Zwanenburg and Bowen 1990). Consequently, there may have been fewer interactions and less vocal activity in the water.

The knock vocalization is a very explosive call, which has been described in the walrus vocal repertoire (Ray and Watkins 1975; Stirling et al. 1987; Sjare and Stirling 1991). This vocalization is emitted when the walrus is diving, at the end of the underwater period, and during breathing sequences (Stirling et al. 1987). In the walrus, knocks are emitted in long series (up to 310 calls per series) (Stirling et al. 1987), whereas in grey seals it occurs in 1 – 4 calls per series. Calls that resemble the grey seal knocks have also been described for Weddell seals (Thomas and Kuechle 1982) and harp seals (Møhl et al. 1975). However, these calls are not as explosive (i.e., slower call onset) as the knocking vocalization of grey seals.

Changes in vocalization rates across time often reflect differences in general activity (Shipley and Strecker 1986; Sjare and Smith 1986*a*). We hypothesized that the increasing number of vocalizations should be correlated with the number of interactions. From observations of seals on the ice, social interactions reached a maximum in the third period, coincided with a rapid increase in the total number of vocalizations per hour per seal, which peaked in period 3 and then declined rapidly in period 4 as many animals dispersed from the island. However, we did not observe significant differences between periods in the total number of vocalizations, probably because of the lack of synchrony between females in the lactation stage and variability in vocalization rates. Vocalization rates did show a tendency to increase during periods 2 and 3 before falling off in period 4. These higher rates of vocalizations per seal, recorded during the third period, did not result from a greater number of seals in the water (Fig. 3), but instead were due to a higher rate of vocalization and social activity of each seal present at that time.

It is evident that the underwater vocal repertoire of the grey seal is more complex than previously thought. Our results may reflect changes in behavior due to differences in breeding habitat substrate (Stirling 1983). Ice-breeding grey seals indeed face very different conditions from those breeding on land, such as those on Sable Island. The rate of vocalizations increased with the intensity of social activity. We also found that grey seals used clicks when ice cover was more extensive, suggesting a navigational role for this vocalization. We were unable to relate other specific vocalizations to particular behaviors, since we could not identify the vocalizing animal or the exact social encounter occurring at the time of a given recording. Standardization of the description of the underwater vocal repertoire of grey seals could serve as the foundation for future studies on vocalization functions and on individual and geographic variations.

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