Relationships between underwater vocalizations and mating systems in phocid seals

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Abstract

In this paper, we considered the number and diversity of underwater vocalizations given by aquatic-breeding phocids, and two species that copulate both in the water and on ice, in relation to what is known or hypothesized about their mating systems. Underwater recordings made throughout the year by both bearded (*Erignathus barbatus*) and Weddell (*Leptonychotes weddellii*) seals indicated that most of the vocalizations could be attributed to males and were given almost exclusively during the breeding season. Less extensive studies of other species indicated the same pattern. Thus, for this study, we considered only underwater vocalizations known, or suspected, to be given by adult males during intra-specific agonistic behaviour, defence of territories or access to females, or attraction of females. A one-way ANOVA and linear regression indicated a significant relationship between the numbers of underwater vocalizations given by individual species and their mating systems. A Pearson's correlation analysis discerned the following: the mating system and the number of vocalizations were positively correlated; female gregariousness was positively correlated with the number of underwater vocalizations and geographic variation in vocalizations, but there was no correlation with the duration of lactation. The degree of predation was negatively correlated with the number of vocalizations, geographic variation in vocalizations, and the number of days of lactation. A principal component analysis showed that 66.1% of the variation in this data set was explained by Factor 1, a suite of variables that included mating system, number of underwater vocalizations, intensity of predation, female gregariousness, and geographic variation in vocalizations. The number of days of lactation explained an additional 19.5% of the variability. These results suggest that additional selection pressures, more specific to the ecological circumstances of individual species, also influence the size of the underwater repertoire. The development of a diverse underwater repertoire with geographic variations was consistently associated with the development of population genetic structure and geographic fidelity. Within each category of social system, the species with the greatest number of underwater vocalizations consistently occurred at higher densities during the breeding season than did the species with the lowest vocal diversity. The role of predators on the evolution of social systems is not well known, but could be significant for some species.

Characteristics of the underwater vocalizations of walruses during the breeding season were found to share similar characteristics to phocids occurring at similar densities in similar habitats, suggesting that the most important selection factors influenced both phocids and odobenids similarly. On the basis of the available information from better-studied species, some testable hypotheses are proposed for further investigations of spotted (*Phoca largha*), Ross (*Ommatophoca rossii*), Hawaiian monk (*Monachus schauinslandi*), and ribbon (*Phoca fasciata*) seals.

Key words: vocalization, pinnipeds, phocid, social behaviour, geographic variation, mating systems, predation.

Introduction

The two most fundamental features of pinniped life history that shaped the evolution of their mating systems are marine feeding and terrestrial parturition (Bartholomew, 1970). Ecological factors, in particular availability and access to suitable habitat for pupping, also are critical in determining a social system. Particularly important are the facts that birth of pups takes place out of water, females develop fidelity to suitable pupping sites, females mate shortly after weaning pups, and males are attracted by the presence of oestrous females (Stirling, 1983). Additional papers also have documented the significance of availability of habitat,

gregariousness of females, the influence of marine and terrestrial predators, strategies of maternal care, and energetic requirements (Bartholomew, 1970; Stirling, 1977; Boness & Bowen, 1996; Lydersen & Kovacs, 1999).

The phocid seals (order Carnivora, family Phocidae) also are known as the 'true' or 'earless' seals. There are 19 species (Rice, 1998) that are most abundant in polar and temperate waters, although there are tropical representatives as well. The ease of observing and documenting details of mating systems of terrestrially breeding phocids, such as elephant (*Mirounga* sp.) and grey (*Halichoerus grypus*) seals, and of terrestrially breeding otariids (all fur seals and sea lions), has led to a comprehensive comparative understanding of species-specific differences in social systems, the role of individual vocalizations, and even details, such as individual variability in vocalizations (e.g., LeBoeuf & Laws, 1994; Gentry, 1998). In contrast to the terrestrially breeding phocids, observations of the reproductive behaviour of aquatically breeding phocids, and the details of their social organization, often are limited because of the difficulty inherent in observing them underwater.

When under water, seals like other marine mammals vocalize to communicate in an environment where individuals may not be able to see each other because of distance, darkness, or turbidity. Also, the use of vocalizations to advertise for mates, deter competitors, or provide information to help females identify or select individuals is far more energy-efficient than swimming over wide distances in search of mates or fighting with each possible challenger, although obviously some of the latter is necessary as well. Not surprisingly, at least some degree of underwater vocalization has been documented for virtually every species of marine mammal it has been practical to study and in some cases, the extent and diversity of vocal development is quite remarkable (see review in Tyack & Miller, 2002).

From reviewing the literature, it is clear there is great variability in the vocalizations given by individual species of phocid seals, as well as species-specific geographic variations in repertoires (Table 1). At the same time, because there is so little direct information on the structure of underwater mating systems of most phocid species, it is difficult to interpret how variations in a species-specific underwater vocal repertoire might relate to the evolution of different patterns of social behaviour. Thus, in this paper we consider the number of different underwater vocalizations given by aquatic-breeding phocids in relation to what is known or hypothesized about their mating systems. We also compare subsets of data from species that appear to share important ecological or behavioural

attributes. We did not include the aerial vocalizations of terrestrially breeding elephant or grey seals because the selection factors operating in a two-dimensional environment where females and access to them can be more easily defended are quite different from the three-dimensional underwater habitat where males communicate over much longer distances and access to females is much more difficult to control. Furthermore, comparing the underwater and aerial vocalizations of terrestrially breeding phocids logically would extend to comparisons with the otariids because of the similarities in their mating systems and that is beyond the scope of what we propose to deal with in this paper.

At the simplest level of analysis, we first hypothesized that the number of different underwater vocalizations given might be related to the complexity and structure of the mating system as first suggested by Thomas & Stirling (1983). If this was correct, seals with serial monogamy might have the least complex mating system and thus the simplest repertoire (with fewest different vocalizations), polygamous seals in which males are capable of defending underwater territories and accessing more than one female at a time might have the most structured mating systems (with the greatest number of different vocalizations), and promiscuous species would be intermediate between the other two in the complexity and number of different vocalizations.

Second, we hypothesized that the number of different underwater vocalizations might be greater in dense breeding colonies than where seals are widely distributed because of the increased competition among males for mates and possibly a greater need for females to be able to identify and select potential mates among individual males.

Third, we hypothesized that the development of a diverse underwater repertoire with geographic variations would indicate a mating system in which there was geographic fidelity and thus, recognition of vocalizations and possibly (although not necessarily) recognition of individuals between years.

Fourth, we compared data on the vocalizations and social system of the Atlantic walrus (*Odobenus rosmarus rosmarus*, family Odobenidae) which is a highly vocal and social pinniped that also breeds in ice-covered waters. We did this to test how applicable our conclusions on phocid seals might be when applied to a distant relative living in a habitat similar to several phocids and thus, theoretically subject to the same or similar ecological selection factors.

Comparisons of available data, coupled with our own field experience with a majority of the species, helped us speculate further about mating systems or

Table 1. Number of underwater vocalizations given by aquatically mating male phocids during the breeding season in relation to mating system (serially monogamous, promiscuous, polygamous), geographic variation in vocalizations (yes/no/unknown), gregariousness of females (yes/no), mating location (aquatic, aquatic/ice), population genetic structure (yes/no/unknown), length of lactation (in days), sexual dimorphism (small, moderate, large), and predation during the breeding season (l-low, m-medium, h-high or u-present but level unknown).

Phocid species	Number of underwater vocalizations	Location	Geographic variation in vocalizations	Mating system	Females gregarious
Arctic					
Hooded seal	3	Gulf St. Lawrence	unknown	serial monogamy	yes
	10	Gulf St. Lawrence			
Harp seal	19	Gulf St. Lawrence	yes	promiscuous	yes
	18	Jan Mayen			
	18	captive			
Bearded seal	5	Alaska	yes	promiscuous	no
	6	Ramsay Island			
	4	Hudson Bay			
	3	Baffin Island			
	2	Dundas Island			
	6	Table Island			
Ringed seal	4	Amundsen Gulf	unknown	territorial, polygamous	no
	6	High Arctic			
Ribbon seal	2	Bering Sea	unknown	possibly promiscuous	no
Spotted seal	unknown		unknown	serial monogamy	
Temperate/Tropical					
Grey seal (ice-breeding stock)	7	Gulf St. Lawrence	unknown	polygamous	yes
Harbour seal	5	California	unknown	promiscuous	yes
	2	Scotland			
Hawaiian monk seal	2	NW Hawaiian Islands	unknown	serial monogamy	no
Antarctic					
Weddell seal	34	McMurdo Sound	yes	territorial, polygamous	yes
	21	Palmer Peninsula			
	49	Davis Station			
Leopard seal	4	South Shetland Islands	yes	promiscuous	no
	9	Palmer Peninsula			
	5	McMurdo Sound			
	12	captive			
Ross seal	3	western Ross Sea	yes	polygamous	no
	5	eastern Ross Sea			
	5	western Ross Sea			
	5	Davis Station			
Crabeater seal	1	Palmer Peninsula	no	serial monogamy	no

Table 1. Continued.

Phocid species	Mating location	Population genetic structure	Lactation	Sexual dimorphism	Predation in mating season	References on vocalizations
Arctic						
Hooded seal	aquatic	unknown	4	large	polar bear, l–m; shark, u	Terhune & Ronald, 1973; Ballard & Kovacs, 1995
Harp seal	aquatic	yes	12	small	polar bear, l–m; shark, u	Møhl et al., 1975; Perry & Terhune, 1999; Serrano 2001
Bearded seal	aquatic	yes	24	small	polar bear, l–m	Cleater et al., 1989
Ringed seal	aquatic	no	39	small	polar bear, h; shark, l	Stirling 1973; Stirling et al., 1983
Ribbon seal	aquatic	unknown	21+?	small	polar bear, l	Watkins & Ray 1977
Spotted seal	aquatic	unknown	24		polar bear, l	
Temperate/Tropical						
Grey seal (ice-breeding stock)	mainly aquatic, some on ice	unknown	15	moderate	shark, l–m	Asselin et al., 1993
Harbour seal	aquatic	yes	24	small	shark, l–m	Hanggi & Schusterman, 1994; Van Parijs et al., 2001
Hawaiian monk seal	aquatic	unknown	39	small	shark, h	F. Parrish, pers. comm.
Antarctic						
Weddell seal	aquatic	yes	53	small	killer whale, l	Thomas & Keuchle, 1982; Thomas & Stirling, 1982; Pahl et al., 1997
Leopard seal	aquatic	unknown	unknown	small	killer whale, l	Stirling & Siniff, 1979; Thomas & Goladay, 1995; Rogers et al., 1996
Ross seal	aquatic	unknown	unknown	moderate	killer whale, u; leopard seal, l	Watkins & Ray, 1985; Stirling, unpublished 2003; Stacy unpublished 2003; Rogers unpublished 2003
Crabeater seal	mainly on ice? some aquatic?	no	28	small	leopard seal, h; killer whale, l–m	Stirling & Siniff, 1979; Thomas & DeMaster, 1982

other aspects of the behaviour of species that currently are little known.

Materials and Methods

Vocalizations included and categories of behaviour and ecology considered
For this analysis, we focused predominantly on the underwater vocalizations known or suspected to be given by male phocids during the breeding season to defend territories, defend access to females, attract potential mates, or possibly enable females to identify and select individual males for mating. In the case of harp (*Pagophilus groenlandicus*) and leopard (*Hydrurga leptonyx*) seals, we included data from studies of captive animals. We did not include vocalizations known or suspected to be given between females and pups, aerial vocalizations, or vocalizations recorded from captive seals other than those listed above.

To the degree possible for each species, we also tabulated: (1) the number of different underwater vocalizations, (2) the presence of geographic variation in vocalization structure, (3) the preferred pupping and mating habitat, (4) degree of predation, (5) presence or absence of gregariousness among females (defined as density/km² or numbers of females hauled out within a few body lengths of each other while nursing and weaning pups), (6) duration of lactation in days, (7) degree of sexual dimorphism (small, moderate, large), (8) known or suspected mating system, and (9) presence or absence of population genetic structure, if known (Table 1). From these data, we grouped subsets of vocal information in relation to behavioural or ecological data to seek common threads or to evaluate possible reasons for differences.

Terminology
We use the term *repertoire* to refer to the total number of different underwater vocalizations given by an individual phocid species in a particular geographic area during the pupping and mating season. Limiting the use of the term to geographic area is important because seals in geographically separated populations can give particular vocalizations in one area, but not in another. Thus, the total repertoire of the species is sometimes considerably larger than the repertoire of a single population, which of course is part of what contributes to geographic variation in the repertoire of that species. The underwater repertoire of most phocids is made up of a variety of different, but easily recognizable (to a human), vocalizations. In some cases, two or more different vocalizations may be easily recognizable as variants of a single 'type'. For example, Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica have 15 different

'calls' or vocalizations that are easily separable by the human ear. One of the most common calls is the trill, of which there are 11 different types, ranging in duration from 4.5 to 35.5 s, and are markedly different in profiles on a sound spectrograph both within and between geographically separated populations (Thomas & Stirling, 1983). Since we do not understand possible differences in function of individual calls within or between call types, we use the term *vocalization* for each recognizable underwater call, regardless of how many types. In the literature, different investigators sometimes report different numbers of vocalizations for a particular species. Part of this is due simply to geographic variation, but also can be influenced by factors such as the extent of recording done in a study. Thus, when we compared the total number of different underwater vocalizations given by each species we list the total number of underwater vocalizations reported from each study and if more than one total is reported, we include the range in our summary.

Definitions of mating systems
For this paper, we recognize three different broad categories of mating systems: (1) *serial monogamy*, in which an adult male defends a female and her pup from other males until the pup is weaned, after which the male mates with the female and then seeks another female to defend and mate with, (2) *promiscuity*, in which males are not able to defend either exclusive territories and both individual males and females likely mate with more than one seal, and (3) *polygamy*, where adult males defend three-dimensional aquatic territories and thereby a significant amount (although likely not all) access to reproductive females within that territory by competitors (Stirling, 1983). We use the term polygamy (where males may mate with more than one female), rather than polygyny (where males or females may mate with more than one member of the opposite sex) because in this paper we are focusing on the underwater vocalizations of males.

Statistical analyses
For some species, such as Weddell or harp seals, more than one investigator independently reported on the number of underwater vocalizations given by a species, either in the same general area several years apart or from widely separated geographic areas. One consequence is that considerable intraspecific variation has been reported for some species and, from careful examination of different studies, it is clear that much of the variation reported is real and not spurious. For example, the number of vocalizations reported for bearded seals (*Erignathus barbatus*) ranged from 2 to 6 (Cleator *et al.*, 1989) (Table 1). The smallest repertoire of only two vocalizations was recorded at Dundas

Island in the Canadian High Arctic Archipelago at a site where underwater recordings were made for several weeks at a time, often through several-consecutive 24-h periods, and over a period of about 10 years so clearly the small repertoire did not result from under sampling. This diversity in the repertoires of the same species at different locations suggests that much of the variability within a species occurs because of ecological or behavioural influences that we do not understand, but which may vary considerably. Thus, we evaluated and included the results of most studies on as many species as possible (Table 1) in our analyses. Species for which the number of vocalizations were listed as unknown were not included in analyses.

To examine whether the number of underwater vocalizations was related to the mating system used, we conducted a one-way ANOVA and linear regression tests at the alpha equals 0.05 significance levels and graphed this relationship by species. To examine the role that other ecological and behavioural variables played in the number of underwater vocalizations we used Pearson's correlation analysis and principle component analysis (PCA).

Results and Discussion

Seasonality of vocalizing

A basic, often unstated, assumption in interpreting recordings is that underwater vocalizations are given mostly by males and related to intra-specific agonistic behaviour, defence of territories or access to females, or attraction of females. While this seems a reasonable *a priori* assumption, it is hard to test because it is difficult to confirm the age and sex of the submerged vocalizing animal. Furthermore, recordings of most species have only been made during the pupping and mating season and few studies have systematically recorded for underwater vocalizations throughout the year to test whether or not such vocalizing is seasonal or continuous.

Thorough, year-round underwater recording data exist only for two species: Weddell and bearded seals. Green & Burton (1988) recorded under water to monitor vocalizations of Weddell seals, one of the two most vocal phocids, near Davis Station, Antarctica. They demonstrated low rates of vocalizing through the winter, a marked increase in October when pupping occurs, a peak in November when most breeding occurs, and high, but rapidly declining levels through the post-breeding period in December from 213 vocalizations/h in the first week, to 94 vocalizations/h mid-month, to 19 vocalizations/h in the last week. At least some Weddell seals remain under the landfast ice throughout the winter at places where tidal action or glacial movement help maintain cracks where animals are able to maintain their breathing holes

(Wilson, 1907; Stirling, 1969). A limited amount of vocalizing continues throughout the winter, probably to defend access to self-maintained, breathing holes by the limited number of animals that remain and keep them open. Even so, the vocalization rates recorded in July and August (austral winter) were very low (Green & Burton, 1988). Similarly, Stirling (1973) reported that during the dark period in the Arctic winter ringed seals (*Phoca hispida*), like Weddell seals, had low levels of agonistic vocalizing during the time they self-maintain breathing holes in fast-ice, presumably to restrict access by other seals. The vocalization rate of the ringed seals increased considerably during the spring breeding season when the sea is still ice-covered but, like bearded seals, vocalizations were virtually absent during the post-breeding, open-water period in summer when there was no need to self-maintain breathing holes (Stirling, 1973; Calvert & Stirling, 1985).

Van Parijs *et al.* (2001) monitored under water for vocalizing male bearded seals in a fjord in Svalbard which had some open water throughout the winter and found they were silent (despite 24-h darkness), began vocalizing in April, peaked during the pupping and mating season in May, declined through June, and ceased by mid-July. Other authors reported a similar pattern of vocalization rates for the period between March and July for bearded seals although they did not collect comparative data from other seasons (e.g., Chapskii, 1938; Ray *et al.*, 1969; Stirling *et al.*, 1983). The absence of vocalizations during winter by bearded seals contrasts markedly with Weddell seals and could be because bearded seals occur in areas of moving ice where self-maintenance and defence of breathing holes is not necessary.

The occurrence and rates of vocalizing by other species also vary significantly between the known breeding and non-breeding seasons. For example, Van Parijs *et al.* (2000a) reported that underwater vocalizing by male harbour seals (*Phoca vitulina*) was limited to a 40-day period in June and July and they were silent in the weeks before and after that time, although they did not actually do extensive underwater recording through the balance of the year. From these studies, we conclude that most of the underwater vocalizing during the breeding season is done by males and is related to intra-specific agonistic behaviour, defence of territories or access to females, or attraction of females and possibly to facilitate individual recognition or selection of males by females.

Number of vocalizations in relation to mating system

The one-way ANOVA showed there was a significant difference ($F=6.09$, df$=29$, $P=0.006$) in the
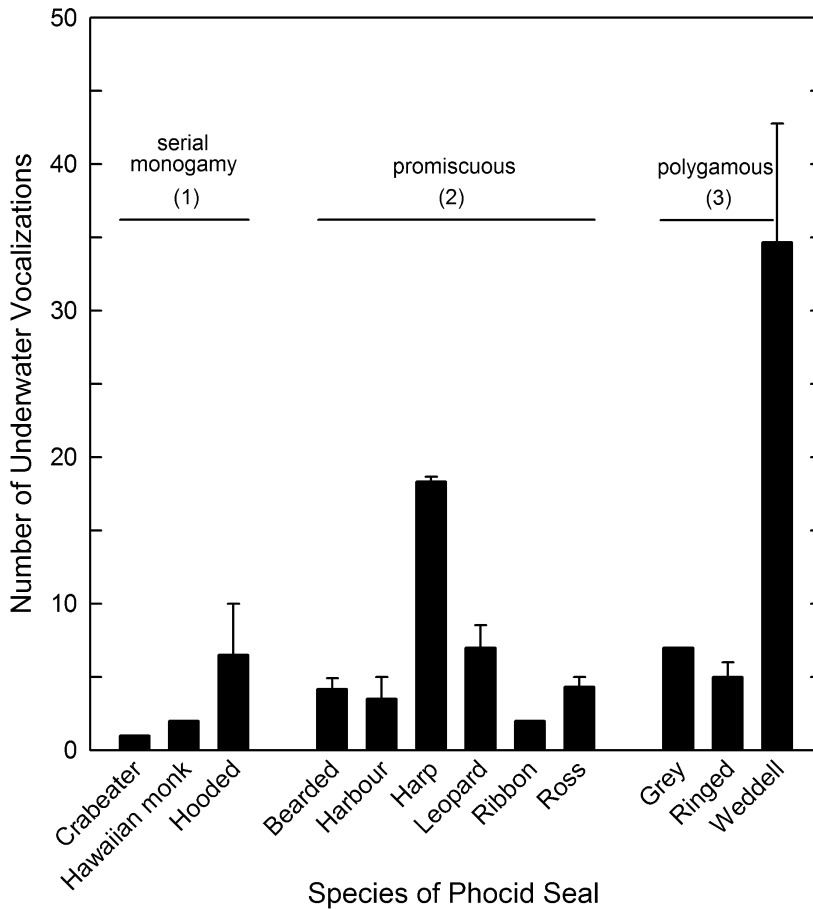
Figure 1. The mean (± SE) number of underwater vocalizations of individual species of phocid seals, in relation to their mating systems, calculated from data in Table 1.

number of underwater vocalizations by mating system (Fig. 1). The Bonferroni adjustment showed the difference was between the number of underwater vocalizations in polygamous species compared to both serially monogamous and promiscuous species). There also was a significant linear relationship (F=9.76, df=29, P=.004) between the number of underwater vocalizations and the mating system.

Pearson's correlation analysis (Table 2) showed significant relationships among several variables (critical r=0.457, df=12). The mating system was correlated with all variables and negatively correlated with female gregariousness, the presence of geographic variation in vocalizations, and whether the species showed population genetic structure. The number of underwater vocalizations was correlated with all variables, except geographic variation in vocalizations and whether the species has genetically discreet populations. Predation was correlated with all variables and negatively correlated with the

number of underwater vocalizations and with the length of lactation.

Factor 1 of the principle component analysis (Table 3) showed the variables that explained 66% of the variance in these data. Variables in Factor 2 explained an additional 21.7% of the variance and Factor 3 explained a further 10.9%. In the subsequent discussion, we compare and discuss the variability in numbers of underwater vocalizations given by species of seals that are thought to use the same or similar mating systems to seek possible explanations of the correlations demonstrated above and, in the case of unexpected differences, raise hypotheses that might explain them.

Vocalizations by polygamous species
For polygamy to develop, males must be able to eliminate or at least significantly reduce access by potential competitors to two or more females through defense of an area where reproductive

Table 2. Results from Pearson's correlation analysis of variables related to phocid vocal behaviour. Values in the cells indicate significant values.

Variables	Number of underwater vocalizations	Geographic variation in repertoire	Mating system	Female gregariousness	Population genetic structure	Length of lactation	Predation pressure
Number of underwater vocalizations	1						
Geographic vocal variation	0.778	1					
Mating system	− 0.829	− 0.737	1				
Female gregariousness			− 0.626	1			
Population genetic structure			− 0.737		1		
Length of lactation	0.585		0.644			1	
Predation pressure	− 778	0.737	− 1.000	0.626	0.737	− 0.644	1

Table 3. Factor loadings from principal component analysis of phocid underwater vocalizations in relation to behavioural and ecological variables. Factor loadings are sorted by importance.

Variable	Factor 1	Factor 2	Factor 3
Predation	0.98		
Mating system	− 0.98		
Number of underwater vocalizations	− 0.83		
Genetically discreet populations	0.76	0.63	
Geographic variation in vocalizations	0.76	0.63	
Female gregariousness	0.72		− 0.62
Length of lactation	− 0.54	0.68	− 0.48
Percent variance explained by factor	66%	22%	11%

females are available for mating. In the case of land-breeding pinnipeds, such as the elephant seal or otariid seals, that defend terrestrial territories where females aggregate, males defend territories where they control or at least limit reproductive access by competitors. In those species, airborne vocalizing by males is vital and well-developed (e.g., LeBoeuf & Peterson, 1969; Phillips & Stirling, 2001).

As far as we know, males of only two phocid species, ringed and Weddell seals, are able to physically defend underwater territories because they mate underwater in fast-ice habitats of the Arctic and Antarctic, respectively where they maintain a limited number of their own breathing holes and are able to control access to them. In the absence of terrestrial predators, parturient Weddell seal females are clumped on the surface of the fast-ice around a single or a small number of breathing holes along cracks in the ice during the mating season (Stirling, 1977), separated by an average of about three body lengths during the pupping season (Stirling 1967). In contrast, ringed seal females are distributed individually and at lower densities while maintaining 3–5 breathing holes in home ranges or territories that overlap those of the males (Hammill & Smith, 1990; Kelly & Wartzok, 1996) at densities of about 1.5–2.5 seals/km^2. There are several significant differences in the behaviour and ecology of these species that we suggest could influence the development of vocalizations by adult males. First, judging from studies done on the dispersed distribution of ringed seal birth and haul-out lairs of adult females and haul-out lairs of adult males (Smith & Stirling, 1975; Smith & Hammill, 1981), the number of females whose underwater home ranges overlap that of a male, likely ranges between about two and five. The number of ringed seal females inseminated by an individual male is unknown. The sex ratio of adult female Weddell seals to adult males hauled-out on the ice in breeding colonies is usually around 6–7:1, but can be as high as 10:1 (Stirling, 1969), giving the impression that their sex ratio in breeding habitat is higher than that of ringed seals. However, from genetic determination of paternity, Gelatt (2001) confirmed that one breeding colony in McMurdo Sound had an average of only 2.5–3.3 Weddell seal pups sired per male to a maximum of eight, suggesting that despite appearances the actual reproductive success of male ringed and Weddell seals in a three-dimensional environment may be lower than that of several terrestrial-breeding pinnipeds. Thus, differences in the adult sex ratio alone between ringed and Weddell seals do not appear to be significant enough to influence differences in number of vocalizations.

Second, Weddell seals have a high degree of natal fidelity to individual breeding colonies (Stirling, 1969; Gelatt, 2001), exhibit significant geographic variation in their underwater repertoires (Thomas & Stirling, 1983; Thomas *et al.*, 1988) and have significant differences in population genetic structure (Davis *et al.*, 2000). After weaning, Weddell seal pups and some older seals leave the area of the breeding colonies and move into pack ice and non-breeding habitat along the northern edges of the fast ice (Testa, 1994; Stewart *et al.*, 2000). Most return to their natal area when they are old enough to breed (Cameron, 2001). Thus, recognition and repetition of vocalizations within the repertoire specific to different populations are probably critical for males to establish underwater territories successfully in traditional breeding colonies and for females to identify males from their home population and possibly individuals within it.

Besides having a large repertoire, many of the vocalizations of male Weddell seals are characterized by a high amplitude (i.e., source level of a trill is 193 dB re 1 μPa recorded at a distance of 1 m from the vocalizing seal) and are detectable 80 km

away (Thomas & Kuechle, 1982). When given under water, several vocalizations emitted can easily be heard by a human standing on the surface of the ice (nearly 3 m thick). In comparison, individual vocalizations of bearded seals in the Arctic can be detected by a hydrophone at measured distances of 30 km (Cleator et al., 1989), but can only occasionally be heard by the unaided human ear on the ice surface under quiet conditions.

In complete contrast, the underwater vocalizations given by ringed seals cannot be heard on the ice by a human and are usually faint, even when recorded with the aid of a hydrophone and pre-amplifier (Stirling, 1973; Stirling et al., 1983). The exceptionally low signal strength of ringed seal vocalizations probably evolved, at least in part, to avoid detection by polar bears (Ursus maritimus) because, when ringed seals are committed to breathing at their self-maintained breathing holes, they are highly vulnerable to predation. In a preliminary laboratory study with small sample sizes, Cushing et al. (1988) found two wild polar bears temporarily being held in captivity reacted significantly more to recordings of underwater vocalizations of ringed seals than to recordings of vocalizations given by bearded and harp seals, killer whales (Orcinus orca), and other polar bears. Whether aquatic predation of ringed seals by Greenland sharks (Somniosus microcephalus) also could be a factor selecting for low signal strength in the underwater vocalizations of ringed seals is unknown. However, the presence of a ringed seal in the stomach of one shark (Ridoux et al., 1998), relatively high levels of a contaminant metabolite (oxychlordane) in some sharks, and high organochlorine levels suggested that seals could be a more common food item of some Greenland sharks than previously suspected (Fisk et al. 2002). Thus, it seems likely that because of a significant threat from predation, ringed seal vocalizations have low signal strength and are unlikely to be detected by hydrophones or other seals at distances greater than a few km (Stirling et al., 1983). However, given that potential mates are nearby and have overlapping underwater territories that probably impede the free movement of non-resident seals, there would appear to be little need for vocalizations that could be heard at longer distances or a more developed repertoire.

Tagging and satellite telemetry studies indicated that large-scale movements, particularly by young-of-the-year and subadult ringed seals of both sexes, are quite common and suggest the likelihood of considerable mixing of individuals among populations (e.g., Kapel et al., 1998; Smith, 1987; Teilmann et al., 1999; Harwood & Smith, pers. comm.). This conclusion is supported by preliminary studies that indicated a lack of population genetic structure between ringed seals from different locations (Davis et al., 1999; Davis, pers. comm.). Similarly, to date there is no evidence of geographic differences in vocal repertoires among ringed seals. Taken together, these results suggest little need for loud vocalizations that could aid young animals in re-locating to their natal population.

Lastly, Weddell seals experience very little predation of any kind in their breeding colonies, while terrestrial predation of ringed seals by polar bears has been so intense (Stirling & Øritsland, 1995) that it has significantly shaped the evolution of ringed seal behaviour and ecology (Stirling, 1977; Kingsley & Stirling, 1991). The location of individual breeding colonies of Weddell seals in the fast-ice is determined by the distribution of tide cracks, glaciers, and other factors that aid the seals with self-maintenance of their breathing holes during winter (e.g., Stirling, 1969). Such sites are often several tens of kilometres (or more) apart so that in the absence of predators, it is advantageous (or necessary) for males to advertise their presence over long distances and possibly aid females to select among males. Taken together, the information above suggests that the presence or absence of strong predation pressures during the pupping and breeding season has been more important than the polygamous mating systems of ringed and Weddell seals to the development of diversity in the number of vocalizations in their respective repertoires, the presence or absence of long-term fidelity to natal colonies for breeding, or a genetically identifiable population structure.

Vocalizations by promiscuous species
In the strict sense of the word, probably all phocid species are polygynous or promiscuous because males or females could mate with more than one individual of the opposite sex, given the opportunity. However, for this discussion, we consider only those polygynous phocid species as promiscuous in which individual males cannot control access to the surface for breathing and instead vocalize underwater, presumably to deter competing males and to attract females for mating.

Male harbour, bearded, leopard, and harp seals vocalize and mate in the water (Ballard & Kovacs, 1995; Hanggi & Schusterman 1994; Van Parijs et al., 2000a; Cleator et al., 1989; Stirling & Siniff, 1979). Male grey seals, in ice-covered areas at least, vocalize in the water below where the females haul-out to pup and nurse, and later mate mainly on the ice, but sometimes in water as well (Asselin et al., 1993; M. O. Hammill, pers. comm.). All of the above species appear to have geographic fidelity to particular areas and, with the exception of grey seals, whose underwater vocalizations from different geographic areas have not been compared, they

also exhibit geographic variation in their repertoires (Cleator *et al.,* 1989; Terhune, 1994; Thomas & Golladay, 1995; Perry & Terhune, 1999; Van Parijs *et al.*, 2000b). Geographically separated subpopulations of all five species are also genetically distinguishable (Allen *et al.,* 1995; Boskovic *et al.*, 1996; Stanley *et al.*, 1996; Davis *et al.*, 1999, 2000, and pers. comm.; Perry *et al.*, 2000).

Terrestrial or marine predation, or both, have been present over evolutionary time for all five species. In the case of harp and grey seals, terrestrial predation (probably by polar bears) has been strong enough to stimulate the evolution of white lanugo on pups at birth to reduce their visibility and vulnerability to predation. Bearded seals are born on the ice at the edges of leads with dark lanugo, but have several white patches on the flippers and body suggesting they may be in the process of evolving white coats (Stirling, 1983). Unlike ringed seals, which have never been recorded hauling out on land, except when killer whales are present in the open water season, bearded seals occasionally are seen hauled out on sand bars, usually in river estuaries. Like the dark lanugo of their pups, the occasional use of terrestrial habitat by bearded seals to haul out on may indicate some of their evolutionary history in the absence of terrestrial predators. Hooded seals moult their white lanugo *in utero,* which facilitates the remarkable accelerated weaning in only 4 days (Bowen *et al.,* 1987). Although some grey seals in eastern Canada breed on ice in the Gulf of St. Lawrence (Asselin *et al.,* 1993), from where polar bears once occurred, but are now extirpated, most now breed on land (e.g., Boness & James, 1979) away from potential predation by polar bears, but the pups are still born with white lanugo. In contrast, harp seals pup in such large aggregations that even fairly heavy predation by those bears that locate the pupping patch is unlikely to have a significant effect in a population sense over the short period (12 days of nursing to wean pups) when the seals are most vulnerable. Although in a few populations, harbour seals pup on ice, most do so on offshore islands, sand bars, or other areas that are not generally vulnerable to terrestrial predators. They have precocious pups that enter the water within a few hours of birth and have young with dark lanugo. Harbour, grey, and harp seals also can be vulnerable to predation by sharks (e.g., Lucas & Stobo, 2000; Lucas & Daoust, 2002). The vocalizations of all these phocids are loud and easily detected when listened to with a hydrophone, suggesting that the pressure of predation has had little effect on reducing the signal strength or diversity of aquatic vocalizations. Even so, only occasional vocalizations of leopard, harp, hooded, and bearded seals have enough signal strength to be heard by the unaided human ear above the surface of the water (Van Parijs, pers. comm.; K.M. Kovacs, pers. comm., J. Terhune, pers. comm.; personal observations). Both bearded seals and leopard seals 'sing', or give repetitive underwater vocal displays, in pack-ice of the open-ocean, as well as in coastal areas. Underwater calls of bearded seals have been demonstrated to travel 25 km (Cleator *et al.*, 1989). So, like Weddell seals, it is likely they need enough amplitude to be able to advertise to more distant conspecifics that also could be distributed at low densities.

The presence of geographic variations in repertoires and population genetic structure also could mean that vocalizations that propagate over relatively long distances aid young animals identifying and returning to natal populations. Four of the five promiscuous species are reported to have five to nine underwater vocalizations (Table 1). The fifth, harp seals, apparently have 19 or more identifiable underwater vocalizations (Table 1). The most obvious behavioural difference from the other promiscuous species is that harp seals aggregate in huge, fairly dense groups in heavy pack ice with densities that can exceed 1000 km^2, although densities of half that value are more common (Sergeant, 1991). While the majority of the pups are born within a few days in early March, whelping can occur over a period of 2–3 weeks or more (Meyers & Bowen, 1989). Pups are weaned in 12 days and mating has been observed shortly afterwards. Given the brevity of the whelping period, it is reasonable to presume that the majority of the underwater mating by large numbers of animals in relatively small areas occurs in a similarly brief period of time and results in a period of intense intrasexual competition among males. During the breeding season in spring, bearded seals are distributed along lead systems and in pack ice at densities of 3–5 km^2 (Kingsley *et al.*, 1985).

Vocalizations by species with serial monogamy
The two species in which serial monogamy has been documented are crabeater seals (*Lobodon carcinophagus*) in the Antarctic (Siniff *et al.*, 1979) and hooded seals (*Cystophora cristata*) in the Arctic (Boness *et al.*, 1988; Kovacs, 1990). Females of both species select solid floes of rafted ice, in fairly dense pack, presumably because these are less likely to break up unexpectedly and therefore, offer a higher probability of safely weaning their pups before the ice disintegrates. In both species, adult males swim among the floes in the ice pack 'spy-hopping' to look at the surface in search of females that have given birth to pups and are nursing them. After locating a mother-pup pair, the male hauls-out and remains on the ice floe, defending her from challengers (or being displaced by one) until the pup is

weaned. A secondary benefit for female crabeater seals, of being attended continuously by an aggressive adult male, is probably deterrence of leopard seals seeking to prey on the crabeater pup prior to its weaning (Siniff & Bengtson, 1977). Although the groupings of an adult male with an adult female and her pup gives the appearance of a 'family' and this term has sometimes been used in the literature (e.g., Corner, 1972), there is no genetic relationship between the male and the pup (e.g., McRae & Kovacs, 1994). Male crabeater or hooded seals that come onto the floes to challenge a male accompanying a female and her pup can have intense intra-sexual fights on the ice. Once hooded seal pups are weaned, the male–female pair leaves the surface of the ice and mate in the water. In contrast, male crabeater seals actively try to prevent females from leaving the floe after the pup is weaned and it appears that copulation occurs on the surface of the ice (Siniff *et al.,* 1979), although to date there has not yet been enough direct observation in the field to confirm the extent of this behaviour.

Like harp seals, hooded seal females pup in large patches of several thousand animals but at lower densities, up to 100 pups/km², although numbers in the range of 20 to 60 km² are more common (Bowen *et al.*, 1987). These values are about one-tenth of the densities reported for harp seals. Like harp seals, most pups are born in a few days, but are weaned in only 4 days (Bowen *et al.*, 1987) and the mating season lasts only 2–3 weeks (Kovacs *et al.*, 1996). Despite some of the similarities between their aggregations and short weaning times of harp and hooded seals, only 10 underwater vocalizations have been recorded from the latter and their social system appears quite different (Table 1).

It is not known if different populations of hooded seals have developed geographic variation in their underwater repertoires, or if their widely separated, but densely clumped, breeding groups are genetically distinct, as neither of these aspects have been studied. However, because they have a diversity of underwater vocalizations (Table 1), and Hammill (1993) documented natal fidelity in hooded seals in the Gulf of St. Lawrence, we predict it is likely that both geographic differences in repertoires and some degree of population genetic structure will be demonstrated in due course.

In the Antarctic pack-ice during spring, crabeater seals are distributed at a density of only 0.7–0.8 seals/km², although on one occasion six male–female–pup triads were found within 2 km of each other (Siniff *et al.,* 1979). Pups take approximately 4 weeks to wean and male–female pairs were seen together on the ice over about a 5-week period, suggesting that is roughly the duration of the mating season (Siniff *et al.,* 1979). Although little has

been published from satellite tracking studies, it appears that crabeater seals move extensively (e.g., Nordøy *et al.*, 1995) and J. L. Bengtson (pers. comm., cited in Davis *et al.,* 2000) recorded individuals travelling at least one-third of the distance around the Antarctic continent in as little as 11 months. Thus, not surprisingly, crabeaters do not appear to show population genetic structure (Davis *et al.*, 2000) or geographic variation in vocalizations (personal observations).

Crabeater and hooded seals apparently produce one and 10 underwater vocalizations, respectively (Table 1). In fact, the greater number and diversity of vocalizations given by hooded seals appears similar to the promiscuous species discussed above and suggests that more of the male–male competition and possible attraction of females takes place in the water compared to on the surface of the ice, as appears to be the case with crabeater seals.

The largest differences in the behaviour and biology of hooded seals, when compared to crabeater seals, are much higher pupping density, much shorter durations of weaning and breeding periods, and the high level of aquatic predation pressure from leopard seals and killer whales on crabeater seals (Siniff & Bengtson, 1977; Siniff *et al.*, 1979) compared to lower, but probably regular, predation on hooded seals by polar bears (Stirling & Holst, 2000) prior to the large-scale disruptions of their respective populations by human activities. Similar to our hypothesis that the intense pressure of terrestrial predation has influenced the development of vocal behaviour in arctic ringed seals, we suggest the reduction in number of vocalizations by Antarctic crabeater seals to one unvaried low-frequency vocalization could be associated with a need to communicate over a distance of a few kilometres, while at the same time being less easily localized by marine predators. Since there is no population genetic structure, there would be no need for a more expanded repertoire to facilitate recognition of different geographic populations.

Male hooded seals are roughly twice the size of females and the scale of this difference in sexual dimorphism, compared to crabeater seals (in which females are larger than males; Laws, 1958) and other ice-breeding phocids is difficult to account for in terms of male strategies for aquatic mating. Clutton-Brock *et al.* (1982) suggested that in ungulates, the degree of development of sexual dimorphism is related to whether or not males use their bodies to push their opponents during intrasexual fighting. However, intrasexual fighting between most male phocids takes place under water where there is nothing to grip or push against so there is much less benefit to being larger. In fact, the most intense fighting involves agility in the water and

biting in the areas of the axilla, penile opening, and hind flippers (e.g., Smith, 1965) so sexual dimorphism is small and in the case of most Antarctic phocids, females are larger than males (Stirling, 1983). In contrast, male pinnipeds that fight on land, where they can grip and push against a substrate, such as elephant and grey seals or otariids, have evolved marked sexual dimorphism. Because the breeding season is so short, even when compared to harp seals, it is possible that the increased intensity of competition among males for mating opportunities coupled with intense intrasexual fighting on ice floes for access to parturient females could be a contributing factor to the development of sexual dimorphism.

Female hooded and crabeater seals are aggressive in defensive of their pups prior to weaning and males are extremely aggressive in defense of the females because they wish to retain mating rights once the pup is independent. Hence, males are extremely aggressive to any animal that approaches them on the ice, such as a human or a seal of a different species, when they are attending females with pups. Over evolutionary time, both seal species also had to deal with predators attacking their pups on the surface of the ice (Siniff & Bengtson, 1977; Siniff *et al.*, 1979; Stirling & Holst 2000). Siniff & Bengtson (1977) and Siniff *et al.* (1979) demonstrated that most predation by leopard seals on crabeater seals is on newly weaned pups and yearlings. Since the pup is not the offspring of the guarding male, his concern when approached by a human or a natural predator is solely that the female might abandon the pup and go into the water where control of her movements and access by competitors is considerably more difficult. Male crabeater seals are sufficiently similar in size to leopard seals, and much more aggressive on the surface of the ice when defending females, so that they are probably able to deter this predator. However, adult male polar bears, which are twice the size of female polar bears or male hooded seals, would be considerably more of a threat to an unguarded female seal or her pup than a leopard seal would be to a female crabeater seal. In a dense hooded seal pupping patch with defenceless weaned pups or lone females with unweaned pups, it is likely that the intensely aggressive behaviour of males would deter all but the largest and most determined of male polar bears from persevering with trying to catch a nursing pup that was still being defended by a male. Stirling & Derocher (1990) demonstrated a relationship between the size of different species of bears and the maximum size of their prey. In this analysis, they found that most adult bearded seals, which are large but not aggressive, are killed predominantly by male polar bears that are twice the size of female

bears. We suggest the possibility that the large size of adult male hooded seals in comparison to females and their aggressive nature similar to male crabeater seals, coupled with an extremely short and intrasexually competitive breeding season in relatively unstable habitat may have contributed to the development of their marked sexual dimorphism.

Number of vocalizations in relation to the density of breeding females

When comparing species within each mating system in the above discussion, those that occur at the highest densities in breeding habitat consistently had a larger repertoire, sometimes several-fold, than those at the lowest densities. Furthermore, harp and Weddell seals, the species that form the densest aggregations in breeding areas, are both especially known for the diversity, high rate of occurrence, and amplitude of their calls (Thomas & Kuechle, 1982; Serrano & Terhune, 2001). Harp seal calls have been recorded under water 30 km from their source (Watkins & Schevill, 1979). Watkins & Schevill (1979) also proposed that in addition to giving loud calls that may exceed 60 dB in breeding areas, harp seals increase the number of elements per call in response to higher calling rates by conspecifics as an anti-masking strategy while at the same time increasing the probability of their own calls to be heard in a noisy environment.

The possible importance of both masking and avoiding being masked also may influence the vocal behaviour of some other species, except possibly for ringed and crabeater seals which experience the highest levels of predation and so may have calls with less signal strength and little structural complexity. For example, bearded seals have densities in the medium range for promiscuous seals and have powerful calls, some of which have been measured to transmit under water for 30 km (Cleator *et al.*, 1989). At the height of the breeding season in the Canadian High Arctic, the underwater rate of vocalizing exceeds 10 calls/min. Many trills have a duration of from 15 s to over 1 min and are sufficiently loud that those given close to a hydrophone often obscure more distant ones (Cleator *et al.*, 1989). Terhune (1999) analysed the narrowband frequency-modulated underwater calls of bearded seals and suggested they used pitch separations in excess of one-third octave to avoid having their calls obscured by competitors. It is possible that in areas where breeding Ross or leopard seals occur, some of the louder and repeated calls of some animals may also travel many kilometers under water and interfere with calls of potential competitors, but this has not been studied.

The present paucity of good quantitative data on the densities of adult females in their breeding

habitat for the majority of phocids, or even the total number of vocalizations given by several species, makes it difficult to examine whether there might be a relationship between these two factors. However, on the basis of the above discussion, we raise the hypothesis that the development and transmission of the underwater repertoire of phocid seals is significantly influenced by their density in breeding colonies and the need to both mask the calls of competitors and avoid being masked themselves.

Underwater vocalizations of the Atlantic walrus in relation to its mating system as a comparative test of hypotheses about underwater calls of phocids
The Atlantic walrus mates during late winter in polynyas within island archipelagos or areas of drifting pack-ice. Females aggregate along the ice edge in dense groups of 30–100 or more, often lying in body contact. The most dominant males can be seen vocalizing underwater near groups of females, presumably to attract them into the water to mate, while less dominant males vocalize from further away (Sjare & Stirling, 1996). Open water between floes or around polynyas allows males relatively free movement in areas where females are nearby. Nine walruses were branded adjacent to the polynyas in the area of Penny Strait and Queen's Channel in the Canadian Arctic Archipelago, of which six were seen the following year and two 2 years after that, indicating they had geographic fidelity to the area (Sjare, 1993). If, hypothetically, all we knew about Atlantic walruses was contained in the previous five sentences, then using the data and discussion above about how various selection factors influenced the underwater vocalizations of phocids we might predict that: because walrus females aggregated at high densities, males would have a reasonably large number of different underwater vocalizations, that several males might vocalize simultaneously and compete to attract females, and that individual variations in their vocalizations might be sufficient for females to be able identify and possibly select specific males. Further, if individuals were shown to have geographic fidelity, the repertoires in different areas might differ, and population genetic structure might be present.

Based on our conclusions above of how various selective factors appear to have influenced the relationship between underwater vocalizations of phocids in relation to their mating systems, most of the predictions we hypothetically made about walruses would be more or less correct. Although the basic units of the underwater repertoire of the Atlantic walrus are limited to two main variations on a single-pulsed sound, onomatopoetically described as a sharp relatively low-pitched 'knock' and a higher-pitched 'tap', these calls are given in many combinations and sometimes with harmonics that sound remarkably like a church bell or a stringed instrument being 'strummed' (Stirling *et al*., 1983; 1987). Most dramatic though is that when vocalizing under water, males give repeated stereotyped vocalization cycles made up of variable combinations of several hundred pulses continuously for 1–5 days (Stirling *et al*., 1983; 1987; Sjare & Stirling, 1996; Sjare *et al*., 2003). It is impossible to describe how many individual vocalizations such variability would comprise, but clearly the number is large which is consistent with our conclusion that the repertoire is greater for species in which the adult females are gregarious than in those that are not. Some group patterns and individual variations appear to be consistent between years (Stirling *et al*., 1987; Sjare *et al*., 2003). The vocalizations are loud, can easily be heard by a human standing on the surface of the ice, and some individual vocalizations have been recorded under water at a distance of 48 km (Stirling *et al.*, 1983). Although polar bears are present in walrus habitat and sometimes kill individual animals, usually young animals (Calvert & Stirling, 1990), the bears are not a sufficient threat to have negatively influenced the loudness of the walruses' calls. During the breeding season, many animals vocalize constantly and at the same time so that it can be impossible for a human to monitor the vocalization cycles of more distant individuals because they are obscured by the loudness of closer animals.

Finally, consistent with the observation of geographic fidelity, Born *et al.* (2001) demonstrated population genetic structure. To date, no one has attempted to determine whether or not the vocalizations or repertoires of knocks and taps of Atlantic walruses in other geographic areas, exhibit regional variations although we predict such differences will be demonstrated in due course. Based on a limited sample of underwater vocalizations of Pacific walruses (*O. r. divergens*), substantial differences from the sub-specifically different Atlantic walrus were reported (Stirling *et al*., 1987).

Unknown species and open questions

Caspian and Baikal seals
In this paper, we chose not to deal with land-locked phocid species, such as the Baikal (*Phoca sibirica*) or Caspian (*Phoca caspica*) seals, primarily because there is so little comparative information. There is no geographic variation in genetics or vocalizations since the whole populations are restricted to single inland bodies of water. Although Baikal seal females are gregarious during the breeding season and haul out on the frozen lake ice to give birth to pups, little is known about their underwater vocalizations or other aspects of their social behaviour

(Thomas, 1982). In general; however, we predict their pattern of vocalizing and breeding behaviour to be most similar to the closely related ringed seal.

Spotted seal

The spotted seal (*Phoca fasciata*) is most closely related to the harbour seal, but their mating system appears to be serial monogamy, like crabeater and hooded seals (Burns, 2002; Burns *et al*. 1972). The pups also have white lanugo, probably to reduce predation by polar bears, and a fairly long, 24-day weaning period. There are breeding populations in both the Bering and Okhotsk Seas, where they occur at very low densities of about 0.3–1 km^2 (Fedoseev *et al*., 1988; Mizuno *et al*., 2002). There is nothing known about their underwater vocalizations, fidelity to breeding areas, or population genetic structure. In particular, quantitative research on spotted seals would be relevant to addressing hypotheses about the differences in the size of their repertoire in relation to the social system and densities in breeding habitat relative to crabeater and hooded seals.

Ribbon seal

The ribbon seal (*Phoca fasciata*) is the closest relative of the harp seal (Árnason, 1995). Male, female, and pup groupings assemble on floes in dense pack-ice, much like crabeater seals in the Antarctic, in at least four different areas in the eastern Bering Sea and Sea of Okhotsk. Like harp seals, ribbon seals remain pelagic during the open water season (Burns, 1981; Fedoseev, 2002). Ribbon seal pups have white lanugo at birth, but take 4 weeks or so to wean, unlike the 12 days taken by harp seals (Table 1). Females and pups are widely dispersed at low densities in the pack (about 0.2–0.6 km^2, Fedoseev *et al*., 1988; Mizuno *et al*., 2002), apparently rather like spotted and crabeater seals, and do not aggregate in dense pupping patches. From a limited sample of underwater recordings made near St. Lawrence Island in the Bering Sea in mid-May, Watkins & Ray (1977) reported two underwater vocalizations from ribbon seals, one of which was a distinctive descending trill of up to 2-s duration, at a maximum rate of 3–5 per 10 s. Because of the limited nature of the sampling it is not known if their repertoire is more extensive. However, males have well-developed air sacs, in comparison to females, which are likely a modification to aid in the production of underwater calls and suggests the possibility of a larger underwater repertoire than has been recorded to date, despite their low density in their breeding habitat. Based on an examination of reproductive tracts, Burns (1981) reported that mating probably occurs in April and early May so the recordings made by Watkins &

Ray (1977) toward the end of the breeding season likely included at least part of the normal underwater repertoire of males in that part of the Bering Sea. There is no information on the presence or absence of geographic variation in underwater vocalizations or population genetic structure, but given the presence of similar characteristics in the five promiscuous ice-breeding phocids discussed above we suggest this is likely.

Ross seal

Ross seal (*Ommatophoca rossii*) females appear to produce pups at low densities in dense pack-ice during November and December (Thomas, 2002), which is about 1 month later than Weddell or crabeater seals at similar latitudes. It appears from the lack of scars on Ross seals, which are so prevalent on crabeater seals, that few Ross seals are attacked by leopard seals (or that they never escape which seems less likely). After weaning their pups and probably mating, individual adults appear to remain hauled-out on large flat floes, well away from the ice edges, for extended periods while they moult (personal observations), after which they go to sea for long individual feeding trips of several weeks interspersed with returning to the northern border of the pack to rest. Loud and semi-continuous underwater vocalizing has been recorded from late December through January (Watkins & Ray, 1985; personal observations), which suggests that represents at least part of the period of mating. Recently, R. Stacey (pers. comm.) identified five underwater vocalizations (Table 1) and found geographic variations in some of the vocalizations of Ross seals. As with the ribbon seal, the development of a vocal repertoire similar to other pack-ice phocids suggests the likelihood of geographic variation in both vocalizations and population genetic structure. However, preliminary analysis of a limited number of Ross seal specimens from three widely separated pack-ice areas in Antarctica revealed no evidence of population genetic structure (Davis, pers. comm.).

Hawaiian monk seal

There are few published data on the social system of the Hawaiian monk seal (*Monachus schauinslandi*). Johanos *et al.* (1994) reported that while pups may be born through most the year, there is a peak in late March and early April, and weaning averages about 39 days. Judging from the presence of fresh injuries inflicted on females by reproductively active males attempting to mount, there is also a fairly long period through which mating can occur, with a peak from late April through June (Johanos *et al.,* 1994). Most adult females are attended by males when they return to shore following the weaning of

their pups (Johanos *et al.,* 1994). From unpublished observations, an attending male defends access to the adult female while the pair is ashore, excluding other males or being displaced in the process. Sometimes a male–female pair appears to remain together at sea for many days (they leave together and are hauled up together upon their return), but it has not yet been confirmed which male is actually successful at mating (T. Johanos, pers. comm.). Because the breeding season is so long, a dominant male monk seal would likely be capable of breeding with more than one female and possibly several. Thus, Hawaiian monk seals could exhibit serial monogamy, similar to that observed with both crabeater and hooded seals, although over a longer time frame. An additional benefit to the female of being successfully guarded by a dominant attending male is that she would be protected from potentially life-threatening wounds that can be inflicted by groups of males that sometimes 'mob' a female while all trying to mate with her (Johanos *et al.*, 1994; Hiruki *et al.,* 1993*a,b*).

There are no published data on underwater vocalizations of Hawaiian monk seals. However, some data on underwater vocalizing by these seals has been documented coincidentally on underwater video footage recorded for studying food habits, along with opportunistic observations made by divers (F. Parrish, pers. comm.). In these observations a single animal hung in the water column or sometimes lay on the bottom, and gave frequent prolonged bouts of underwater vocalizations which sometimes lasted for several hours. Behaviourally, this seems remarkably similar to the vocal pattern reported from Weddell, leopard, and bearded seals (Thomas & Kuechle, 1982; Stirling & Siniff, 1979; Cleater *et al.*, 1989), which all (except for bearded seals) are also in the same subfamily (Monachinae). No other seals were seen in any of the vocalizing sessions and only a single vocalization, reminiscent of a foghorn (or possibly a crabeater seal, Stirling & Siniff, 1979), was given during these bouts although barks also were heard when animals encountered other seals or divers. Although these data have not been analyzed in detail, it appeared the repertoire of vocalizations was limited. One animal that was observed vocalizing hung stationary in mid-water (20 m above the bottom) and inflated its neck, creating an obvious bulge which was sustained throughout the 5–10 s vocalization it emitted. The bulge deflated on completion of one vocalization and re-inflated for the next, but no air was emitted.

From the anecdotal information available on the mating system and underwater vocalizations of Hawaiian monk seals, it seems likely that under normal circumstances they are serially monogamous, like crabeater and hooded seals. Although the data are limited and as yet unanalyzed, it appears that, Hawaiian monk seals have a very limited repertoire, similar to crabeater seals. It is unknown whether sharks, which are known to prey upon monk seals (e.g., Alcorn & Kam, 1986; Bertilsson-Friedman, 2002), especially young animals, partially explains the small number of underwater vocalizations or their signal strength. There are no data on the presence or absence of any geographic variation in underwater vocalizations between island colonies of Hawaiian monk seals, but a preliminary microsatellite analysis of population structure indicated some genetic separation between individuals in the two most widely separated breeding populations (Kretzmann, 2001).

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