

## Aquatic mating in pinnipeds: a review

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### Abstract

The goals of this review are to summarize existing information available on aquatic mating strategies in pinnipeds. Considerable advances in knowledge concerning the reproductive strategies of aquatic mating pinnipeds have been made over recent years. Studies have showed that aquatic mating pinnipeds exhibit a range of evolutionary adaptations in their reproductive strategies that differ considerably from those of land-breeding species. However, clear gaps still exist, particularly amongst ice-breeding species. This review introduces the topic and then is divided into 1) techniques for studying aquatic mating pinnipeds, of which acoustic, telemetry, and genetic technologies are discussed, 2) evolutionary consequences of lactation and whelping habitat, 3) male reproductive strategies and, 4) conclusions and future research directions. Based on current evidence, aquatic-mating species are thought to maintain aquatic display areas using vocal and dive displays for the purpose of male–male competition and likely for the attraction of females. Between species, mating behaviour ranges from lek mating, female defense polygyny, to the use of alternative mating tactics. Observed variations within species in mating behaviour appear to be linked to the influences of local habitat type and changes in female behaviour. Therefore, it is appropriate to reassess our knowledge concerning aquatic breeders and reflect how this alters the development of theories on the evolution of pinniped reproductive strategies.

Key words: underwater vocalizations, display behaviour, pinniped, mating, reproductive strategies, whelping habitat.

### Introduction

#### *Adaptations to aquatic feeding*

The pinnipeds comprise three families; the Odobenidae, containing the walrus, *Odobenus rosmarus*, the Otariidae, containing the eared and fur seals and the Phocidae, containing the true or haired

seals (Rice, 1998). Pinnipeds evolved from a terrestrial ancestry to a mainly aquatic life style. In 1970, Bartholomew identified terrestrial parturition and aquatic foraging as the prerequisites for the evolution of polygyny in pinnipeds. This spatial and temporal separation of feeding from reproduction is a fundamental component influencing the reproduction of all pinnipeds, regardless of their breeding system.

Adaptations to aquatic feeding have resulted in reproduction patterns that incorporate varying periods of time spent fasting on land or ice and feeding at sea. In most pinnipeds, oestrus is seasonally synchronous. Females therefore are highly synchronized in the timing of parturition (Stirling, 1975, 1983). In addition, the relative rarity of suitable pupping sites on land or ice also results in females being highly aggregated. Consequently, females are clumped in both time and space during parturition and weaning (Boyd, 1991). This clumping results in predictable distributions of females on land or ice and therefore, in an increase in the potential for polygyny (Bartholomew, 1970). In pinniped species where females are highly clumped on land or ice, both in space and time, female or resource defence polygyny is frequently observed.

#### *Why study aquatic mating pinnipeds?*

Pinnipeds often are used as a prime example for demonstrating trends in mammalian reproductive strategies (e.g., Le Boeuf & Reiter, 1988). They offer numerous advantages for studying reproductive success in polygynous, long-lived mammals. Pinnipeds have evolved from a terrestrial ancestry, retaining certain terrestrial traits while adapting to pelagic foraging (Stirling, 1975, 1983). Therefore, the critical factors, shaping mating systems in pinnipeds such as foraging behaviour and distribution, may vary considerably from land mammals. Studies of pinniped reproductive strategies offer an opportunity for examining the evolutionary adaptations of a long-lived mammal to a semi-aquatic environment. Previously, studies of pinniped reproductive strategies have concentrated on those species that remain ashore during the entire breeding season. However, the

Odobenidae and at least 15 of the 18 phocid species mate aquatically, representing 47% of the pinnipeds. Current lack of knowledge concerning aquatic-mating species results in a large gap in the understanding of pinniped reproductive systems. Otariid species mate predominately on land; however, recently studies showed that some species appear to partially or wholly use the aquatic environment for the purpose of mating (e.g., Francis & Boness, 1991; Gemmell *et al.*, 2001). Knowledge of aquatic mating in otariids is still very limited and will not be discussed in detail in this review.

In the past, the study of aquatic-mating pinnipeds was restrained by the logistic difficulties of acquiring information on these species while they are at sea. However, in recent years our knowledge of the aquatic-mating pinnipeds has grown. Studies show that aquatic-mating pinnipeds exhibit a range of evolutionary adaptations in their reproductive strategies that differ considerably from those of land-breeding species. Based on current evidence, aquatic-mating species are thought to maintain aquatic display areas using vocal and dive displays for the purpose of male–male competition and likely for the attraction of females. Between species, mating behaviour ranges from lek mating, female defence polygyny, to the use of alternative mating tactics. Observed variation, within species in mating behaviour appears to be linked to the influences of local habitat type and changes in female behaviour. Therefore, it is appropriate to reassess our knowledge concerning aquatic breeders and reflect how this alters the development of theories on the evolution of pinniped reproductive strategies.

### Techniques for Studying Aquatic-Mating Pinnipeds

In recent years acoustic, telemetry, and genetic technologies progressively have become more mainstream and affordable. The integration of these techniques along with behavioural observations has enabled substantial advances in knowledge of aquatic-mating pinnipeds (Table 1). This section concentrates mainly on the use of acoustic techniques, while the techniques of behavioural observation, telemetry and molecular genetics will be covered briefly.

#### *Behavioural observations*

Until relatively recently, most knowledge concerning aquatic-mating pinnipeds was restricted to behavioural observations made in 'nearshore areas' i.e., within the direct vicinity of haul-out sites (Thompson, 1988). However, it is important to remember that these data often only represent a small section of the behavioural patterns of aquatic pinnipeds and that a significant proportion of mating behaviour occurs 'offshore' i.e., away from

haul-out sites. To obtain a complete picture of aquatic mating strategies it is important to combine studies within the 'nearshore' with those 'offshore'.

#### *Acoustic methods*

The two main acoustic approaches used for studying aquatic-mating pinnipeds involve remotely monitoring their sounds or tracking individuals acoustically, using transponders, such as pingers, attached to the subject animal. Underwater playback experiments using species' sounds is also a potentially valuable tool, which requires further exploration.

Acoustic tracking using pingers attached to the subject animal has been previously applied to study the movement patterns of a variety of pinnipeds (e.g., Siniff *et al.*, 1977; Wartzok *et al.*, 1992). It requires the attachment of an acoustic transmitter on an individual animal then using either a directional hydrophone or multiple hydrophones configured in an array formation to acquire the sound signals. Recently this technique has been adapted to collect detailed information on three-dimensional behaviour of male Weddell seals, *Leptonychotes weddellii*, during the breeding season (Harcourt *et al.*, 1998, 2000). For this technique to be useful for studying aquatic-mating species, it must be feasible to capture and tag individual animals. Furthermore, this system is reliant on the tagged animals remaining within range of the acoustic receiving system, which limits the technique to a small number of individuals within a restricted area.

Play-back experiments can be of great value in determining the functional significance of vocalizations within a species (e.g., Insley, 2000; Charrier *et al.*, 2001, 2002; Hayes, 2002). In aquatic-mating phocids, few attempts have been made to use these techniques to ascertain the role of vocalizations during the breeding season and this area research requires further development (Watkins & Schevill, 1968; Thomas *et al.*, 1983; Hayes, 2002). The difficulty with using playbacks in aquatic-mating species is likely a function of the limited ability to observe behavioural responses beyond listening for other vocal responses. The use of underwater video in areas where the visibility is adequate may provide a solution to this problem. Determining how to deal with this problem is one of the bigger challenges facing studies on aquatic-mating species.

All 15 phocid species that mate aquatically produce underwater vocalizations during the breeding season (e.g., Schusterman *et al.*, 1970; Stirling, 1973; Thomas & Kuechle, 1982; Cleator *et al.*, 1989). In some species, both sexes produce underwater vocalizations (e.g., harp seals, *Phoca groenlandica*; Møhl *et al.*, 1975), while in others only



males vocalize (e.g., harbour seals, *Phoca vitulina*; Nicholson, 2000). These vocalizations can be used to study individual strategies, seasonal, tidal, diurnal, and geographical behaviour, as well as distribution and density patterns of aquatic-mating species (e.g., Thomas *et al.*, 1988; Cleator *et al.*, 1989; Pahl *et al.*, 1996; Serrano & Miller, 2000; Van Parijs *et al.*, 2000a, 2003). The technology for accomplishing this requires that vocal behaviour be monitored throughout a study area; such tracking of individual movement patterns and behaviour currently can be accomplished through the use of acoustic arrays. Acoustic arrays have been primarily used to study cetaceans (e.g., Watkins & Schevill, 1972; McDonald & Fox, 1999; Clark & Ellison, 2000). However, this technique is easily adaptable for studying pinniped behaviour (e.g., Kelly & Wartzok, 1996; Hayes *et al.*, 2000; Van Parijs *et al.*, 1998, 2000b; Janik *et al.*, 2000).

There are several problems with using the sounds produced by the animals themselves to study their behaviour including knowing which sex is making the sound and the response of others who might be recipients. In most aquatic-mating species, either detailed knowledge of the vocal repertoire is lacking or no distinct vocalizations can be attributed to one sex only. This question remains difficult to answer in several species and requires targeted studies to determine whether males and/or females produce distinctive vocalizations and under what contexts free-ranging animals do not vocalize. However, for certain species, there is more information available on this topic than is often given credit.

Harbour seals, *Phoca vitulina*, have been one of the key species where aquatic mating behaviour has been studied in recent years (e.g., Hanggi & Schusterman, 1994; Van Parijs *et al.*, 1999). This was done by using the typical underwater roar vocalization produced by this species as a tool for gathering behavioural information on males. How do we know that only males produce the underwater roar vocalizations? The problem with answering this question is that little of the evidence has made it to the refereed literature. The 'grey literature' does provide convincing evidence. Although females occasionally vocalize under water, several studies have shown that only adult males produce the typical underwater roar vocalization (Mohr, 1975; Wilson, 1978; Ralls & Gish, 1983; Ralls *et al.*, 1985; Nicholson, 2000).

Evidence for sexual differences in vocal behaviour also exists for male bearded seals, *Erignathus barbatus*, where trill vocalizations are ascribed to males during the breeding season (Cleator *et al.*, 1989; Cleator & Stirling, 1990). Similarly, male walrus vocalize under water during the breeding season and use distinctive stereotyped vocalization patterns (e.g., Stirling *et al.*, 1987; Sjare &

Stirling, 1996). Harp seals have a very diverse underwater vocal repertoire used by both males and females (Møhl *et al.*, 1975). However, recent evidence shows that at least three of the 26 known call types are used by males only (Serrano, 2001). A number of other species have distinctive vocalizations used by males during the breeding season, in particular hooded seals, *Cystophora cristata* (Ballard & Kovacs, 1995) and Weddell seals (Thomas & Kuechle, 1982; Oetelaar *et al.*, this issue). In some species, such as the leopard seal, *Hydrurga leptonyx* (Rogers *et al.*, 1996), available evidence suggests that while these seals do vocalize neither males nor females use distinguishable call types. The underwater acoustic repertoire of most other aquatic species is insufficiently known to determine whether sex-specific calls exist (Table 2).

#### Telemetry techniques

Radio and satellite telemetry are widely used to study pinniped movement, distribution, and foraging patterns. This technique is useful for studying aquatic-mating phocids when applied to studying movement patterns prior to and during the breeding season (e.g., Boness *et al.*, 1994; Coltman *et al.*, 1997; Van Parijs *et al.*, 1997; Boness *et al.*, in press). As movement patterns of males at sea during the breeding season are frequently restricted to small-scale movements, fine-scale collection of data is needed (Nowicki *et al.*, 1997; Van Parijs *et al.*, 1997; Boness *et al.*, in press). The errors associated with positions from satellite tags ( $\pm 2.0$  to 20.0 km) are too inaccurate to be of much use for studying fine-scale movement patterns, but positions from VHF telemetry ( $\pm 0.1$  to 1.0 km) can provide this level of detail. In certain cases, it is possible to collect data on individual dive behaviour using time-depth recorders. During the breeding season, diving depths of many species frequently are restricted to short, shallow display dives (Stirling *et al.*, 1987; Nowicki *et al.*, 1997; Van Parijs *et al.*, 1997) therefore if data collected are to be of use, time-depth recorders need to be programmed to target short, shallow dive behaviour (e.g., Coltman *et al.*, 1997). However, before these data can be used, independent calibration of behaviour occurring during diving, especially during shallow diving, is needed. If this analysis is not carried out, inferences derived from dive data can be misleading or false.

#### Molecular genetics

Understanding the links between phenotype and reproductive success is critical to the study of the evolution of mating systems and life-history patterns (Boness *et al.*, in press). Few detailed genetic studies have been carried out to examine the relationship between phenotype and mating success of

Table 2. Review of current knowledge concerning acoustic and aquatic mating behaviour in phocids and walrus.

Species of seal	Sex-related aquatic vocalizations			Aquatic male strategies
	Aquatic vocalizations	Sex-related aquatic vocalizations	Aquatic male displays	
Harbour, <i>Phoca vitulina</i>	Five call types: Grunts, bubbly growl, groans, creaks and roars	Adult males: Roar vocalization	Males perform stereotypic visual, acoustic and dive displays	Lek mating in water
Spotted, <i>Phoca largha</i>	Six call types: Growl, drum, snort, chirp, bark and creaky door	No data	Males perform stereotypic visual, acoustic and dive displays	No data
Ringed, <i>Phoca hispida</i>	Four call types: high and low pitched barks, yelps and chirps	No data	No data	No data
Baikal, <i>Phoca sibirica</i>	No data	No data	No data	No data
Caspian, <i>Phoca caspica</i>	No data	Adult males: 2, 7, 15, 20	No data	No data
Harp, <i>Phoca groenlandica</i>	Twenty-six call types	Adult males and females: 1, 3, 13, 14, 18, 21–26	No data	No data
Ribbon, <i>Phoca fasciata</i>	Two call types: Sweeps and broadband puffs	No data	No data	No data
Bearded, <i>Erignathus barbatus</i>	Six to eight call types: Groans, sweeps, moans and several trill variants	Adult males: Trills	Males perform stereotypic acoustic and dive displays	Alternative strategies: Males hold aquatic territories or 'roam' over larger display areas Mate guarding on ice with copulation in the water
Hooded, <i>Cystophora cristata</i>	Six call types: Clicks, trills, beating, knocking and paired pulsed signals.	No data	No data	No data
Crabeater, <i>Lobodon carcinophagus</i>	One call type: Groans	No data	No data	No data
Ross, <i>Ommatophoca rossii</i>	One call type: Siren calls	No data	No data	No data
Leopard, <i>Hydrurga leptonyx</i>	Twelve call types: Roars, nose blasts, blasts, growls, snorts, high, medium, low and low descending trills, hoots, hoots with single trill and groans	Adult males and females: Broadcast calls	No data	No data
Weddell, <i>Leptonychotes weddellii</i>	Thirty-four to thirty-nine call types	No data	Males perform stereotypic acoustic and dive displays	Aquatic territories
Mediterranean monk, <i>Monachus monachus</i>	No data	No data	No data	No data
Hawaiian monk, <i>Monachus schauinslandi</i>	No data	No data	No data	No data
Grey, <i>Halichoerus grypus</i>	Ten call types	No data	No data	Female defence on land with some mating occurring at sea Female defence polygyny
Walrus, <i>Odobenus rosmarus</i>	Numerous	Males: Short repetitive pulses	Males perform acoustic and dive displays	

aquatic-mating species, with the exception of the harbour seal (Coltman *et al.*, 1998, 1999; Perry & Amos, 1998) and the hooded seal (McRae & Kovacs, 1994). The reason for the lack of information primarily is because of the logistical difficulty of capturing and recapturing animals. The use of behavioural estimators to determine probable paternity has little likelihood of success because copulations rarely are seen. This is why genetics analyses (i.e., paternity assessments) are so critical to determining success in aquatic-mating species. For example, Walker & Bowen (1993) suggested that harbour seal males hauled out alone on beaches were likely to be reproductively successful males; however, a further study combining genetic analysis with haul-out pattern data showed that these males were, for the most part, unsuccessful (Coltman *et al.*, 1998, 1999). Similar studies on other species combining behavioural data with genetic paternity analyses are needed.

#### Evolutionary Consequences of Lactation and Whelping Habitat

While the females of many phocid species fast throughout lactation, in some small phocid species (average weight  $\leq 100$  kg), such as the harbour seal (Bowen *et al.*, 1992; Boness *et al.*, 1994; Thompson *et al.*, 1994) and the ringed seal, *Phoca hispida* (Kelly & Wartzok, 1996), females forage during late lactation (Table 3). It is thought that this is due to either small body size, which renders it energetically impossible for females to sustain late lactation (Boness & Bowen, 1996) or to the relative richness of the local environment, which may influence a female's decision to forage during lactation (Boyd, 1998). In at least three of the larger phocids, the bearded seal, *Erignathus barbatus* (Gjertz *et al.*, 2000; Krafft *et al.*, 2000), the Weddell seal (Testa *et al.*, 1989), and the harp seal (Lydersen & Kovacs, 1993, 1996), females also appear to forage or spend time at sea during late lactation. In the walrus, pups accompany their mothers to the foraging grounds (Fay, 1982), thus reducing the foraging costs to mothers.

The nursing habitats of pinnipeds are also thought to exert a strong influence on the evolution of lactation behaviour (Bowen, 1991; Lydersen & Kovacs, 1999). The length of lactation is highly variable among phocid species (see Table 3). This variation is thought to reflect differences in the stability, predictability, and harshness of the whelping habitat (Bowen, 1991; Siniff, 1991; Lydersen & Kovacs, 1999). Several of the phocids and the walrus are known to give birth and nurse their pups on a floe or fast ice. Five of the large phocids give birth predominately on floe ice, and there is a wide degree of variability in the breeding habitats of seals

that do not breed on land. Ice is a highly unstable environment and is thought to force ice-breeding females to spend more time at sea during lactation, compared to those breeding on fast ice or land. Therefore, whether it is a large or small species, if females are mobile at sea when they become receptive they cannot be economically monopolized by males.

#### Male Reproductive Strategies

Behavioural and morphological indicators suggest that most aquatical-mating species are polygynous (Bartholomew, 1970). Therefore, the strategies by which these males obtain matings with females are fundamental in determining pinniped mating systems. For those species where data are available, a common feature shared by many pinniped species during the breeding season is the production of simple or complex underwater vocalizations and stereotypical dive displays during the breeding season (Table 2). In some species, these vocalizations are thought to be used predominately in male–male competition and could play a role in male advertisement to females (e.g., Stirling *et al.*, 1987; Bartsch *et al.*, 1992; Hanggi & Schusterman, 1994). Empirical evidence, gathered from underwater video or play-back experiments, showed that vocalizations are used in male–male competition (Nicholson, 2000; Hayes, 2002). However, no clear data exist to prove that vocalizations are used for female attraction, mainly due to the difficulties of assessing female responses in reaction to male vocalizations at sea. Nonetheless, the reality of the matter is that somehow males must attract females for the purpose of mating and although vision or smell might function over short distances, there is no other obvious solution to the problem of long-range attraction at sea other than the use of sound.

As noted above, the harbour seal, which has been studied in some detail, provides several insights into the relationship between male strategy and mating systems. Harbour seals exhibit a low level of polygyny consistent with predictions based on their breeding ecology (Coltman *et al.*, 1998, 1999; Hayes, 2002), as females are highly mobile and widely dispersed at sea during oestrus. Within-species variation in male behaviour appears to be closely linked with habitat type and resulting changes in female behaviour (Van Parijs *et al.*, 1999, 2000a). To date, male harbour seal mating strategies have been studied in relation to three main habitat types: 'riverine' (complex of narrow channels leading to an estuary or open ocean, see Perry, 1993), 'estuarine' (a firth or fjord system, see Van Parijs *et al.*, 1997) and 'open ocean' (islands or coastal haul-out sites open to the ocean,



**Table 3.** Review of current knowledge concerning body size, weaning habitat, duration and behaviour during lactation in phocids and walrus. Note that these may vary between different sites.

Species of seal	Average adult weight (kg)	Weaning habitat	Duration of lactation (days)	Females at sea during lactation
Harbour, <i>Phoca vitulina</i>	80–140	Fast ice or land	24–42	Yes
Spotted, <i>Phoca largha</i>	82–123	Floe ice	14–21	No data
Ringed, <i>Phoca hispida</i>	50–70	Fast ice	39–41	Yes
Baikal, <i>Phoca sibirica</i>	63–66	Fast ice	60–75	Yes
Caspian, <i>Phoca caspica</i>	≈ 86	Floe ice	20–25	No data
Harp, <i>Phoca groenlandica</i>	≈ 130	Floe ice	12	Yes
Ribbon, <i>Phoca fasciata</i>	≈ 90	Floe ice	21–28	No data
Bearded, <i>Erignathus barbatus</i>	200–250	Floe and fast ice	24	Yes
Hooded, <i>Cystophora cristata</i>	300–400	Floe ice	3–4	No
Crabeater, <i>Lobodon carcinophagus</i>	80–110	Floe ice	17–28	No data
Ross, <i>Ommatophoca rossii</i>	≈ 200	Floe ice	≈ 30	No data
Leopard, <i>Hydrurga leptonyx</i>	350–400	Floe ice	≈ 30	No data
Weddell, <i>Leptonychotes weddellii</i>	400–600	Fast ice	33–53	Yes
Mediterranean monk, <i>Monachus monachus</i>	240–300	Land	42–49	No data
Hawaiian monk, <i>Monachus schauinslandi</i>	≈ 270	Land	39–41	Yes
Grey, <i>Halichoerus grypus</i>	200–350	Land, floe and fast ice	12–17	Yes (at some sites)
Walrus, <i>Odobenus rosmarus</i>	800–1300		≈ 730	Yes

see Coltman *et al.*, 1997; Van Parijs *et al.*, 1999; Nicholson, 2000). In the riverine and estuarine habitats, the topography of the local areas is such that females are forced to move from pupping haul-out sites to and from foraging areas along relatively predictable routes (Perry, 1993; Thompson *et al.*, 1994), while in open-ocean sites female movements are much less predictable (Boness *et al.*, 1994).

Several observations suggest that males adapt their mating strategies in accordance with the degree of uncertainty in female movement patterns between the haul-out sites and feeding habitats. Current evidence suggests that male harbour seals from open-ocean habitats display primarily around haul-out sites (Coltman *et al.*, 1997), while in estuarine habitats males can be found displaying throughout haul-out sites and feeding grounds and in transit routes between the two (Van Parijs *et al.*, 1997, 1999). Whether males restricted themselves to haul-out sites or are wider spread is not yet known for riverine habitats. In the open-ocean habitat, male display areas are clustered around principal haul-out sites (Coltman *et al.*, 1997; Nicholson, 2000), in riverine areas males can be found holding territories throughout the narrow channels (Perry, 1993), while in estuarine areas male territories are clustered in narrow channels and areas where females are more likely to pass during their foraging trips out to sea (Van Parijs *et al.*, 1997, 1999). Further evidence, particularly of male movements away from the haul-out site, is needed to test these observations.

Studies from all habitat types report that male harbour seals perform stereotypic underwater displays consisting of short dives combined with the production of underwater roar vocalizations during the period when females are in oestrus (e.g., Hanggi & Schusterman, 1994; Bjørge *et al.*, 1995; Coltman *et al.*, 1997; Van Parijs *et al.*, 1997; Nicholson, 2000). The occurrence and frequency of display behaviour can vary among geographic areas and habitat types. For example, males in Scotland restrict their displays to the breeding season (Van Parijs *et al.*, 1997; Van Parijs & Kovacs, 2002), while males in California display all year round with a peak in frequency during the breeding season (Nicholson, 2000; Hayes, 2002).

The structure of male vocalizations also varies among different harbour seal populations. Comparative analyses of the roar vocalization of male harbour seals from ten sites throughout their distribution showed that vocal variation occurs at the oceanic, regional, population, and sub-population level (Van Parijs *et al.*, in press). Genetic barriers based on the physical distance between harbour seal populations presented a likely explanation for some of the observed vocal

variation. However, site-specific vocal variations were present between genetically mixed sub-populations in California. A tree-based classification analysis grouped Scottish populations together with eastern Pacific sites, rather than among Atlantic sites, as would be expected if variation was based purely on genetics. Lastly, within the classification tree no individual vocal parameter was consistently responsible for consecutive splits between geographic sites. Combined, these factors suggest that site-specific variation in habitat type influences the development of vocal structure in harbour seals.

Too few studies are available in other aquatic-mating species to compare the relative effects of habitat and female behaviour on male mating tactics. The current knowledge on these species is summarized below. Of the larger phocids, the Weddell seal is the only species to breed solely in a fast-ice area. In this habitat, females use 'predictable' breathing holes during their long lactation period and males appear to use visual and acoustic displays to maintain three-dimensional underwater territories around or near female breathing holes (e.g., Cline *et al.*, 1971; Bartsch *et al.*, 1992; Harcourt *et al.*, 1998, 2000).

Several of the large phocids breed on either ice floes or on the edge of the fast ice (Siniff, 1991; Lydersen & Kovacs, 1999). Their size enables females to range over greater distances and to use resources that may be spatially and temporally unpredictable (*cf.* Stewart & Delong, 1995). Furthermore, the continually changing ice conditions render female movements, even when hauled out, unpredictable in time and space. Do male reproductive strategies reflect the 'unpredictable' distribution of females breeding in a highly variable habitat?

In bearded seals, females haul out with their pups on loose ice floes and the edge of fast ice during the breeding season (Hammill *et al.*, 1994; Gjertz *et al.*, 2000; Krafft *et al.*, 2000; Lydersen & Kovacs, 1999), thereby exhibiting highly variable behaviour. Bearded seal females forage at sea during lactation, however, female movements are mostly limited to areas containing suitable haul-out ice. During the breeding season, male distribution at sea reflects the areas where females are found regularly, suggesting that males are preferentially targeting areas frequented by oestrus females (Van Parijs *et al.*, 2001). As is the case in several other species, bearded seal males produce underwater vocalizations (Ray *et al.*, 1969) and perform dive displays (Van Parijs *et al.*, 2003) during the breeding season. In Svalbard, bearded seal males use alternative mating tactics, exhibiting at least two different types of display tactics, the 'roaming' tactic, where males display over large areas and the 'territorial' tactic where males display over small areas (Van Parijs *et al.*, 2003).



Little is known about the reproductive strategies of other floe-ice species. In the crabeater seal, *Lobodon carcinophagus*, and hooded seal, males appear to attend females and pups on land or on ice floes until the female becomes receptive, suggestive of a form of mate guarding (Kovacs, 1990). Copulation, however usually occurs in the water. In hooded seals, males fight on ice and in the water to obtain access to females and vocalize in both media (Boness *et al.*, 1988; Kovacs, 1990, Ballard & Kovacs, 1995). As mentioned previously, since copulation occurs in the water, it is unclear whether the observed 'mate guarding' on ice enables males to increase their copulation rate in the water.

Harp seals breed on floe ice (Lavigne & Kovacs, 1988). This substrate is extremely transient in both time and space, which favours birthing synchrony and a relatively short lactation period (Kovacs *et al.*, 1991; Kovacs, 1995). Female harp seals are highly mobile during lactation and frequently leave their pups to return to the sea (Kovacs, 1987; Lydersen & Kovacs, 1993). Male harp seals spend the early part of the breeding season in large male groups travelling throughout the whelping patch; there are no signs of competition or aggression between individual males (Merdsoy *et al.*, 1978; Kovacs, 1995). Towards the end of lactation, male groups become smaller or disperse, and individual males can be seen on the ice among clusters of females. Agonistic encounters become increasingly frequent, and males often have fresh wounds during the second half of the breeding season. Additionally, males commence snorting and bubble blowing at holes used by females (Merdsoy *et al.*, 1978; Kovacs, 1995), and they emit a variety of underwater vocalizations (Serrano, 2001).

The Atlantic walrus is one of the few large aquatic-mating pinnipeds that has been studied in detail. Males aggregate each winter in mating areas called 'polyneas'. Their distribution appears to be determined by sea-ice features and access to the open sea (Sjare & Stirling, 1996). They perform vocal and dive displays at these sites for several days during the breeding season (Stirling *et al.*, 1987; Sjare & Stirling, 1996; Nowicki *et al.*, 1997). Male walrus in the Pacific use a lek-type mating system (Fay, 1982; Fay *et al.*, 1984), while males mating in the Atlantic have been described as using female defense polygyny, since large mature, single males appear to monopolize access to herds containing potentially reproductive females for extended periods of time (Sjare & Stirling, 1996). Given the level of plasticity observed in male harbour seal mating tactics, the observed variation in mating tactics between walrus populations is not surprising and warrants further investigation.

Very little evidence currently is available regarding the aquatic mating behaviour of most other

phocids (see Table 2). In leopard seals, both males and females produce underwater broadcast calls thought to serve in mate attraction (Rogers *et al.*, 1995, 1996, 2002). Captive observations of the spotted seal, *Phoca largha*, show that a male performed underwater vocal and dive displays during the period of oestrus of the captive female (Beier & Warzok, 1979).

The grey seal, *Halichoerus grypus*, mates both on land and in the water (Cameron, 1969; Anderson *et al.*, 1975; Boness & James, 1979; Godsell, 1991; Boness *et al.*, 1993). Recent genetic evidence confirmed that a significant proportion of copulations occur in the water either around the haul-out site or further out to sea (Worthington-Wilmer *et al.*, 1999). Grey seals are vocal both in air and under water (Schusterman *et al.*, 1970; Asselin *et al.*, 1993; McCulloch, 2000) and there is sufficient evidence to believe that aquatic mating forms an important component of male reproductive strategies. A similar study aimed to assess paternity was carried out in the Antarctic fur seal, *Arctocephalus gazella*, with results suggesting that aquatic mating may play a much larger role in male reproductive strategies than was previously thought (Gemmell *et al.*, 2001). Francis & Boness (1991) reported that about half the observed matings of Juan Fernandez fur seal, *Arctocephalus philippii*, males occurred in entirely aquatic territories. The presence/absence of aquatic mating as a component in 'terrestrial' mating species and its relative importance to mating success requires further investigation.

### Conclusions and Future Research Directions

Considerable advances in knowledge concerning the reproductive strategies of aquatic-mating pinnipeds have been made over recent years. However, clear gaps still exist. In particular, there are a number of species about which we know very little (predominately the ice-breeding species), and it is important to begin to look at these species. Studies on the harbour seal have begun to show that multiple factors such as habitat type, female behaviour, and genetic population structure all influence male mating tactics to varying degrees. They have also shown that male behaviour is strongly site-specific and can vary considerably between geographic locations. For those species which have been studied in some detail, such as the bearded seal, Weddell seal, and walrus, there is considerably variability in the mating tactics displayed by each species, and evidence points towards a degree of plasticity in the mating tactics within and between populations. In these species, it is important to begin to ask the next level of questions, that is to look at mating strategies at a finer scale and determining

the relative influence of habitat type and female behaviour on differing populations within a species. Lastly, it is clear that studies of terrestrial-mating pinnipeds are unrepresentative of aquatic-mating species. Although similar factors such as habitat type and female behaviour appear to influence male mating strategies, the logistics and difficulties associated with studying these factors while at sea differ substantially from terrestrial mating species. It is also important to realize that aquatic mating is an important role in the mating system of several terrestrial mating species. Studies examining the relative role and importance of aquatic mating for those species that mate primarily on land are crucial to enable further knowledge concerning pinniped reproductive strategies.

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