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Chapter 6

INSIGHTS INTO THE ACOUSTIC BEHAVIOUR OF POLAR PINNNIPEDS – CURRENT KNOWLEDGE AND EMERGING TECHNIQUES OF STUDY

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ABSTRACT

This chapter will provide a review of the acoustic behaviour of polar pinnipeds. It will also present a detailed update of new and emerging passive acoustic technologies and how these can further the study of behaviour for polar marine mammals.

Both Arctic and Antarctic pinnipeds are known to exhibit a range of adaptations which enable them to survive and reproduce in an ice-dominated environment. However, large gaps still exist in our understanding of the fundamental ecology of these species, as investigations are severely hampered by the animals' inaccessibility. Improving our understanding of ice-breeding species and the effects that changes in habitat might have on their behaviour is vital, as current climatic trends are rapidly altering the polar environments.

For pinnipeds, acoustic communication is known to play an important role in various aspects of their behaviour. Mother-pup reunions and the establishment of underwater territories during the mating season are examples which, for the majority of species, are known to be mediated by vocal signalling. Acoustic measurements therefore provide an essential tool to study ice-breeding pinnipeds as recordings can be used to remotely monitor sounds, track animal movements and determine seasonal changes in movements and distribution. Recent advances in recording technologies, now allow the acquisition of continuous long-term acoustic data sets, even from the remotest of polar regions.

To date, a range of different types of passive acoustic instruments are used, the choice of which depends largely on the purpose of the study. These instruments in addition to computer-based methods that have been developed for automated detection, classification and localization of marine mammal sounds will be discussed. The autonomous PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA) is presented here as one example of such recording systems.

INTRODUCTION

Dispersal of pinnipeds into polar areas is thought to have begun with the evolution of large body size in the ancestral pinnipeds (Costa 1993). In Costa's (1993) model, early pinnipeds exhibited a primitive form of otariid breeding patterns with females requiring numerous short duration foraging trips to sustain lactation. The evolution of large body size enabled females to separate foraging from lactation as females had increased maternal reserves to rely on. This separation of foraging and breeding is thought to finally have enabled these basal phocids to inhabit and reproduce in less-productive areas such as the Atlantic, in relative absence of resource competitors. Upon reaching higher latitudes, the shortened lactation period would have pre-adapted these early phocids to breeding on unstable substrates, such as ice (Costa 1993). The establishment of ice-breeding along with development of a mainly aquatic life style has influenced many aspects of pinniped behaviour in high latitude habitats e.g. the timing of reproduction, duration of lactation period and the development of different mating strategies. Although ice-breeding pinnipeds share many similarities in behavioural patterns, there is also considerable variance in the social and physical conditions of their breeding habitat (e.g. Lydersen & Kovacs 1999). To date however, clear gaps still exist in what is known about the behaviour of polar pinnipeds. This is due to the fact that behavioural studies in polar pinniped species are severely hampered since many of the behavioural patterns are likely to take place in offshore waters or in remote pack-ice areas, logistically limiting the possibilities of study. All of the ice-breeding pinniped species are however, known to produce underwater vocalizations, the monitoring of which has proved to be a valuable tool to study many aspects of pinniped behaviour (e.g. Thomas & DeMaster 1982; Rogers et al. 1996; Van Parijs et al. 1997; Perry & Terhune 1999; Van Parijs et al. 2003; Van Parijs et al. 2004; Terhune & Dell'Apa 2006; Rouget et al. 2007). This review aims to provide an overview of the existing information and current gaps in knowledge on the acoustic behaviour of ice-breeding pinnipeds. Additionally, we summarize recent developments in recording technologies, which now enable acquisition of long-term acoustic data sets in remote areas and evaluate how these techniques may contribute to the improvement of our fundamental understanding of the behaviour of polar pinnipeds.

POLAR HABITATS

The Southern Ocean surrounds the Antarctic continent. The northern boundary of the Southern Ocean is formed by the Antarctic Convergence or the southern polar frontal zone, which forms a sharp temperature boundary between northern temperate waters and southern polar waters. The polar front is an important factor in the distribution of marine mammals, as it defines the southern extent of tropical and temperate species. There are four species of ice-breeding seals in the Antarctic, all of which occupy different niches in the sea ice habitat:

leopard (*Leptonyx hydrurga*), crabeater (*Lobodon carcinophagus*), Ross (*Ommatophoca rossii*) and Weddell seal (*Leptonychotes weddellii*). The Antarctic sea-ice habitat differs substantially from that in the Arctic. The Antarctic sea-ice offers seasonal habitat hetereogeneity, as most of it melts in austral summer (Dayton et al. 1994). The Arctic sea ice is less dynamic and never melts except at the periphery. However, this may change rapidly within the next decades as the Arctic sea-ice shows substantial decreases in both extent and thickness in response to global warming. The Arctic region is less well defined by environmental characteristics, consisting of the Arctic Ocean with in the center a permanent cover of slowly circulating ice floes surrounded by a zone of seasonal pack-ice and a zone of land fast-ice (e.g. Stonehouse 1989). Polynias, predictable areas of open water within ice-covered seas, are of particular importance in Arctic habitats as they represent areas with high nutrient levels and enhanced productivity (Comiso & Gordon 1987; Dayton et al. 1994). Of all the Arctic pinniped species, only three have a continuous circumpolar distribution (ringed (*Phoca hispida*) and bearded seal (*Erignathus barbatus*) and walrus (*Odobenus rosmarus*) e.g. Stirling et al. 1983). However, several other species associate with the ice seasonally and are dependent on it as a breeding substrate. The Arctic pinniped species covered in this review are: ringed, bearded, harp (*Phoca groenlandica*), hooded (*Cystophora cristata*), grey (*Halichoerus grypus*), ribbon (*Phoca fasciata*), Caspian (*Phoca caspica*), Baikal (*Phoca siberica*), Largha (*Phoca largha*), harbour seal (*Phoca vitulina*) and walrus.

Seasonal or year-round association with ice offers pinnipeds a number of advantages, such as abundant food supply that is readily accessible under the ice in relative absence of competitors and terrestrial predators, a solid substrate to moult, rest, give birth and nurse pups. Dependent on the ice type, ice may also provide shelter in ridges and crevices as well as a milder micro-climate as there is generally less wind and wave action within ice packs (Riedman 1990).

PINNIPED ADAPTATIONS FOR LIFE ON ICE

Apart from a number of physiological adaptations for life in ice-dominated environments, such as sharp and strong claws for locomotion on the ice, the lanugo fur of pups which maintains body heat and thick subcutaneous blubber layers to restrict heat loss in adult seals (e.g. Lydersen & Kovacs 1999), polar pinnipeds also developed behavioural adaptations to life in their habitat. In temperate regions, the onset of parturition in terrestrial breeding pinnipeds is to a large extent determined by ambient temperature. Polar pinnipeds, however, depend on ice for breeding. Consequently, parturition does not occur in late spring and early summer, but rather in the late winter and early spring, when snow accumulation is at a maximum and temperatures are well below freezing (Pierotti & Pierotti 1980). This is the time of year when the ice is most extensive and stable and pup mortality as a result of ice breakup is minimized (Pierotti & Pierotti 1980). As this period of optimal ice conditions is relatively short, pupping is generally synchronous within ice-breeding pinniped populations compared to pinnipeds breeding on land. Grey seals provide a unique illustration in this respect as some grey seal populations breed on ice, whereas others breed on land. The grey seal populations that breed on ice have much more condensed lactation and birthing periods than the populations that breed on land, which is thought to be a response to the higher risk of premature separation of mother and pup on ice (Pierotti & Pierotti 1980; Haller et al. 1996). Nevertheless, within the ice habitats of polar pinnipeds there also exists considerable variation which appears to be of influence on behavioural patterns and the timing of behaviour as well (Trillmich 1996; Lydersen & Kovacs 1999). Variability in e.g. the temporal and structural stability of the platform, risk of predation, availability of food within the breeding habitats and access to the water are factors that have been suggested to have resulted in the evolution of different maternal strategies and consequently in differences in development of mother-pup acoustic communication in ice-breeding phocids (Insley 1992; Trillmich 1996; Lydersen & Kovacs 1999). In the light of current trends in climate change, knowledge on small scale local adaptations of behaviour in ice-breeding pinnipeds is of great importance in order to understand changes in abundance, distribution and behaviour. In the following section we provide an overview of the current state of knowledge on the role of in-air acoustic cues in polar pinniped mother-pup pairs and relate this to maternal strategies and breeding habitat characteristics.

ACOUSTIC BEHAVIOUR OF POLAR PINNIPED MOTHER-PUP PAIRS

In all pinniped species studied to date, pups have been found to vocalize in a similar fashion when interacting with the mother (e.g. Perry & Renouf 1988; McCulloch et al. 1999; Van Opzeeland & Van Parijs 2004; Collins et al. 2006). Individual stereotypy in calls is an important aspect of vocal recognition, as it enables individuals to distinguish between one and another, although individual vocal stereotypy does not necessarily indicate individual recognition (Insley 1992; Insley et al. 2003). Vocal signalling has been shown to play an important role in successful otariid mother-pup reunions upon the female's return from regular foraging trips (Trillmich 1981; Gisiner & Schusterman 1991; Insley 2001; Charrier et al. 2002). In phocids, however, the role of vocal signals in the recognition process, has been found to be more variable and has to date only been investigated in few species (see Table 1; Renouf 1984; Insley 1992; Job et al. 1995; McCulloch et al. 1999; McCulloch & Boness 2000; Van Opzeeland & Van Parijs 2004; Collins et al. 2005; 2006). Within ice-breeding phocids, evidence for individual stereotypy in pup calls has been found in the three colonial breeding species: Weddell seals (Collins et al. 2005; 2006), grey seals (McCulloch et al. 1999; McCulloch & Boness 2000) and harp seals (Van Opzeeland & Van Parijs 2004). However, the patterns in pup call individual stereotypy reported in these species are markedly different and are likely to reflect the complex interactions between e.g. the degree of coloniality, the likelihood and predictability of separations due to maternal foraging or ice break-up and the ontogeny of acoustic behaviour in ice-breeding pinnipeds (McCulloch & Bonness 2000; Insley et al. 2003; Van Opzeeland & Van Parijs 2004). In Weddell seals, females form breeding aggregations in fast ice areas where ice cracks provide access to the water. Compared to other phocid species, the lactation period in Weddell seals is relatively long, lasting 6-7 weeks (Laws 1981; 1984). During the first two weeks post-partum, females attend their pup on the ice continuously. However, during the second half of the nursing period, females spend increasingly more time in the water (Tedman & Bryden 1979; Hindell et al. 2002; Sato et al. 2003). Pups also start entering the water around this time, although the age at which pups first enter the water varies and is thought to depend on differences in local ice conditions and colony density (Tedman & Bryden 1979). Weddell seal pups vocalize and their vocalizations have been found to be moderately individually distinctive (Collins 2006). Unlike many other phocid mothers, Weddell seal females vocalize frequently to their pups (Kaufman et al. 1975; Collins et al. 2005). Female in-air calls have also been investigated in this species and have been found to exhibit individual stereotypy, although vocalizations are not unique (Collins et al. 2005). The critical amount of distinct information in both female and pup calls combined with an individual's visual and olfactory cues is likely to allow mother-pup pairs to recognize each other (Collins et al. 2005; 2006).

In grey seals, vocal behaviour of mother-pup pairs has to date only been studied in land-breeding populations. This has led to the finding of some remarkable differences between land-breeding colonies, which have been related to the ice-breeding ancestry of the species (McCulloch et al. 1999; McCulloch & Boness 2000). Through playback experiments, McCulloch et al. (1999; McCulloch & Boness 2000) were able to show that in the Sable Island colony, grey seal females discriminate between the vocalizations of their own and unfamiliar pups, whereas this ability appeared absent in the Isle of May grey seal colony. It was suggested that the female's ability to recognize the vocalizations of their own pup in the Sable Island colony could be a vestige of the ice-breeding ancestry of that colony, where it might have evolved in response to the higher risks of mother-pup separations (Pierotti & Pierotti 1980; McCulloch & Boness 2000). Acoustic behaviour of grey seal mother-pup pairs has, however, to date not been studied in any of the ice-breeding grey seal populations. As grey seals breed both on fast-ice and pack-ice, comparisons between these populations might provide interesting insights into the impact of breeding substrate stability on mother-pup acoustic behaviour.

Harp seal females form large breeding aggregations on seasonal Arctic pack-ice. During the 12 day lactation period, females forage a few hours per day (Lydersen & Kovacs 1993; Kovacs 1987; 1995), leaving their pup alone on the ice. Pups are relatively sedentary, rarely leaving the ice flow or entering the water. Harp seal pups vocalize in air during the lactation period, their vocalizations being structurally complex and variable (Miller & Murray 1995). Pup vocalizations were found to exhibit a relatively low percentage of individual variation (Van Opzeeland & Van Parijs 2004; Van Opzeeland et al. in prep). In the Greenland Sea population, vocalizations of female pups however, were found to be significantly more individually stereotyped within individuals than males, biasing maternal recognition towards female pups. However, in the Canadian Front harp seal population, no significant difference in pup vocal individuality between the sexes was found (Van Opzeeland et al. in prep). These differences in vocal individuality between the sexes may reflect different selection pressures working on female and male harp seals (Van Opzeeland & Van Parijs 2004). Alternatively, these population differences may be related to small scale local adaptations to i.e. site-specific ice conditions (Van Opzeeland et al. in prep). Clearly, further study is needed to investigate what is driving these differences in harp seal pup vocal behaviour.

Table 1. Review of current knowledge on polar pinnipeds concerning whelping habitat, gregariousness, duration of the lactation period, female foraging during lactation and the type of inidividualistic vocalization and recognition tested

Species		*Whelping habitat*	*Gregarious*	*Duration of lactation (days)*	*Females at sea during lactation*	*Individualistic vocalization tested*	*Type of recognition tested*
Harp seal	Arctic	Pack-ice	Yes	12	Yes	Pup calls	None
Grey seal	Arctic	Pack-ice, fast ice and land	No, No, Yes	12-17	Yes	Pup calls	Pup by mother
Harbour seal	Arctic	Pack-ice and land	Yes, Yes	24-42	Yes	Pup calls	Pup by mother
Hooded seal	Arctic	Pack-ice	No	3-4	No	None	None
Bearded seal	Arctic	Pack-ice	No	24	Yes	None	None
Ringed seal	Arctic	Fast-ice	No	39-41	Yes	None	None
Largha seal	Arctic	Pack-ice	No	14-21	No data	None	None
Caspian seal	Arctic	Fast-ice	No	20-25	No data	None	None
Baikal seal	Arctic	Fast-ice	No	60-75	Yes	None	None
Ribbon seal	Arctic	Pack-ice	No	21-28	No data	None	None
Walrus	Arctic	Pack-ice, Fast-ice	Yes	~730	Yes	Pup calls	Pup by mother
Weddell seal	Antarctic	Fast-ice	Yes	33-53	Yes	Mother + Pup calls	None
Crabeater seal	Antarctic	Pack-ice	No	17-28	No	None	None
Leopard seal	Antarctic	Pack-ice	No	~30	No data	None	None
Ross seal	Antarctic	Pack-ice	No	~30	No data	None	None

Table 2. Overview of passive acoustic techniques that are currently used to study marine mammals and their suitability to study polar pinnipeds (partially based on information derived from Van Parijs et al. 2007)

Technique	*Duration deployment*	*(near) real-time data*	*Vessel requirements*	*Data storage capacity*	*Suitable for use on pinnipeds in polar areas*	*Available types*
Ship-towed arrays	Hours to weeks	YES	Dedicated ship time	Essentially unlimited	Dependent on ice conditions	Ecologic Ltd., MAPS, many more
Acoustic tags	Hours to days	NO	Deployment and retrieval	A few gigabytes	YES	Bprobe, DTAG
Moored autonomous hydrophones (bottom, deep-sea mooring, ice based)	up to several years (dependent on sampling regime)	NO	Yearly or bi-yearly deployment and retrieval (but dependent on sampling regime)	Giga- to terabytes	YES (iceberg shifting in deeper waters)	Popup, HARP, ARP, AURAL-M2, EARS
Gliders and underwater vehicles	Weeks to months	YES	Deployment and retrieval	Gigabytes	YES	SeaGlider, WHOI
Radio-linked sonobuoys	Hours to months	YES	Dedicated ship/air time	Essentially unlimted	YES	Military surplus, DIFAR
Cabled systems	Years to decades	YES	One-time deployment; maintenance	Essentially umlimited	NO	SOSUS, ALOHA, NEPTUNE, AUTEC, CTBTO
Autonomous listening stations	Years to decades	YES	One-time deployment; maintenance	Essentially unlimited	YES	PALAOA

Although most harbour seal populations form dispersed breeding colonies on land, few also give birth on ice (Streveler 1979; Calambokidis et al. 1987). Research on these populations is limited and to date no study has addressed mother-pup behaviour in ice-breeding harbour seals. In land-breeding harbour seals, pups often accompany their mothers on foraging trips from birth (Wilson 1974). Pups vocalize both in-air and in water and although airborne and underwater vocalizations were found to differ, pup calls were individually stereotyped (Renouf 1984; Perry & Renouf 1988). However, to what extent these findings can be extrapolated to ice-breeding harbour seals is unknown.

For solitary ice-breeding pinnipeds the selective pressures favouring development of individually stereotyped vocalizations may be less strong as there is little confusion possible over maternal investment. Crabeater and hooded seals are solitary pack-ice breeders and have short lactation periods, during which females remain with their pup on the ice throughout the nursing period (Siniff et al. 1979; Riedman 1990). Consequently, there is little opportunity for mother-pup pairs to become separated. Hooded seal pups emit snorts, grunts or brief low-frequency moans while attended by their mothers. Ballard & Kovacs (1995) concluded that these vocalizations are unlikely to be used by a female to identify her pup as these sounds contain little frequency or amplitude modulation which in many other species have been found to bear the individually distinctive cues (e.g. Phillips & Stirling 2000; Charrier et al. 2002). In crabeater seals, nothing is known on the role of vocal behaviour in mother-pup interactions, although vocalizing has been reported to occur when the pair is separated (Siniff et al. 1979). In bearded and ringed seals, both pup and female are known to forage throughout the lactation period (Hammill et al. 1991; Lydersen & Hammill 1993; Hammill et al. 1994; Kelly & Wartzok 1996; Krafft et al. 2000). Vocal cues might therefore serve a function to coordinate and synchronize mother-pup behaviour during the lactation period. However, to date the role of acoustics in mother-pup interactions in these species has not been investigated.

In the other pack-ice breeding pinnipeds, Ross, leopard, Largha, Caspian, Baikal and ribbon seals, knowledge on the species' general biology is to a large extend still lacking and nothing is known on acoustic behaviour in mother-pup pairs.

Walruses also breed on pack-ice, forming dense aggregations in spring. Calves enter the water immediately after birth and are nursed for at least one year both on the ice and in the water (Riedman 1990; Kastelein 2002). However, most calves associate with their mothers in groups of adult females for longer periods and are weaned after three years (Kastelein 2002). Walrus female-offspring acoustic recognition has been suggested by observation to be well developed in walruses (Kibal'chich & Lisitsina 1979; Miller & Boness 1983; Miller 1985; Kastelein et al. 1995) and was recently also experimentally demonstrated. Walrus calf vocalizations were found to be highly stereotyped and females were found to respond more strongly to playbacks of vocalizations of their own calf than to the calls of an alien calf (Charrier pers. comm.).

ACOUSTIC BEHAVIOUR AND MATING STRATEGIES IN POLAR PINNIPEDS

The transition from ancestral terrestrial parturition to giving birth on ice is also thought to have had major consequences for the evolution of mating strategies in ice-breeding pinniped species (e.g. Bartholomew 1970; Pierotti & Pierotti 1980; LeBoeuf 1986; Van Parijs 2003). On land, the relative rarity of suitable pupping and haul-out areas causes the formation of very dense female breeding aggregations, enabling males to defend harems or compete with other males for a place within a female breeding group (Bartholomew 1970). However, ice habitats generally offer large areas suitable for parturition and haul-out and consequently many ice-breeding pinnipeds aggregate in loose colonies or breed in a solitary fashion (e.g. Stirling 1975; LeBoeuf 1986; Lydersen & Kovacs 1999). This, along with the fact that females in many ice-breeding pinnipeds forage to sustain lactation, causes female movements to be both spatially and temporally less predictable for males compared to land-breeding females (Van Parijs 2003). As a consequence, ice-breeding pinniped females cannot be economically monopolized by males when they become receptive and male reproductive strategies must aim to attract females for the purpose of mating (Van Parijs 2003). All ice-breeding pinnipeds mate aquatically and underwater vocalizations and stereotypical dive displays are known to form an important part of male-male competition and male advertisement to females in aquatic mating species (see Van Parijs 2003 for a review). The available evidence appears to indicate the existence of different mating systems within aquatic mating species (Kovacs 1990; Rogers et al. 1996; Van Parijs et al. 1997; 2001; 2003; Harcourt et al. 2007; in press). However, due to the difficulties of studying ice-breeding pinnipeds, too few species have been studied to date to compare the relative impact of habitat and female behaviour on male mating tactics. Here we summarize what is currently known on acoustic behaviour related to mating behaviour in ice-breeding pinnipeds.

In colonial breeding species such as Weddell and harp seals, communication generally occurs over relatively short distances as both males and females form seasonal aggregations. Signals are not constrained by propagation needs and consequently many different sound types as well as subtle variations in sounds are used in communication. Accordingly, the vocal repertoires of colonial breeding species are generally broad and consist of a wide variety of sounds that serve local advertisement displays in order to defend territories and to attract mates (Rogers 2003). Male Weddell seals typically defend underwater territories around or near tide cracks used by females, perform short shallow display dives and have a large underwater vocal repertoire, including the male-specific long descending “trill” (Kooyman 1981; Thomas & Kuechle 1982; Bartsch et al. 1992; Oetelaar et al. 2003; Harcourt et al. in press). Vocal activity increases strongly during the breeding season (Green & Burton 1988; Rouget et al. 2007) and trill vocalizations are likely used underwater by males for the purpose of territorial defence, advertisement, dominance and warning signals (Thomas & Kuechle 1982; Thomas & Stirling 1983; Thomas et al. 1983). Although female movements are somewhat predictable as females use tide cracks in the ice to access the water, females have access to all parts of the water column and male monopolization of females may be difficult (Hindell et al. 2002; Sato et al. 2003; Harcourt et al. 2007; in press). It has been suggested that in systems where males cannot monopolize females, male-male competition may play a less important role (e.g. Harcourt et al. 2007). Male territories under the ice may instead primarily serve to maximize exposure of the territory holder to females passing through. Male vocal and dive displays may be used by females to assess quality of a potential mating partner and consequently female choice may have a significant role in mating success. However, male Weddell seal mating tactics have also been found to exhibit plasticity (Harcourt et al. in press) and more detailed investigation of underwater behaviour of male and female Weddell seals is needed to test this hypothesis.

Similar to Weddell seals, harp seals also have a large vocal repertoire consisting of a wide variety of sounds that suit local communication purposes (Møhl et al. 1975; Terhune & Ronald 1986; Terhune 1994; Serrano 2001; Rogers 2003). Harp seal vocal activity increases in both sexes during the breeding season, suggesting that females also may have an important role in mating behaviour (Watkins & Schevill 1979; Serrano & Miller 2000; Serrano 2001). Harp seal females aggregate in colonies and use leads between shifting pack-ice floes to access the water to forage during lactation. Males therefore have access to clusters of females. Merdsøy et al. (1978) reported large male harp seal groups travelling through the breeding herd early in the breeding season. Agonistic interactions between males increased towards the time that pups were weaned and males and females were seen hauled out on the ice (Merdsøy et al. 1978). Males have been observed snorting and bubble blowing at holes used by females (Merdsøy et al. 1978; Kovacs 1995). However, to date it is unknown how vocal behaviour relates to harp seal male and female mating behaviour.

Ringed seals also exhibit a relatively rich vocal repertoire, which is thought to serve the purpose of male local display (Stirling 1973; Kunnasranta et al. 1996; Rogers 2003). Although ringed seals do not breed in colonies, they often form small aggregations on fast-ice. Females are believed to maintain birth lair complexes which are included in an area occupied by a territorial male (Smith & Hammill 1981). Interestingly, Weddell, harp and ringed seals have been found to vocalize year round, with peaks in vocal activity during the breeding season (Green & Burton 1988; Kunnasranta et al. 1996; Serrano 2001; Rouget et al. 2007). Apart from the sole purpose of vocal display during the mating season, vocal behaviour has in these species been suggested to also serve other purposes such as social communicative function during migration or pursuit of prey (Kunnasranta et al. 1996; Serrano & Miller 2000; Rouget et al. 2007). However, only few studies have investigated the vocal behaviour of these species outside the breeding season (Serrano & Miller 2000; Serrano 2001; Rouget et al. 2007)

In contrast to the rich vocal repertoire of Weddell, harp and ringed seals, a number of polar pinnipeds produce single or series of relatively short broadband pulsed sounds, which have been suggested to mainly function in agonistic interactions (Rogers 2003; Hayes et al. 2004). Land-breeding harbour seals perform short dives and produce underwater roar vocalizations in underwater display areas (Hanggi & Schusterman 1994; Van Parijs et al. 1997; Hayes et al. 2004). Male mating strategies were found to be closely linked to habitat type and resulting changes in female behaviour, distribution and density (Van Parijs et al. 1999; 2000). In ice-breeding harbour seals, females have been reported to strongly depend on the limited availability of suitable haul-out ice (Calambokidis et al. 1987; Mathews & Kelly 1996). Similar to land-breeding harbour seals, this may enable males to concentrate and display in areas that are frequented by females. However, the underwater vocal behaviour in ice-breeding harbour seals has not been studied and it is not known if males in these populations also hold underwater territories. Grey seals also breed both on ice and on land and have a similarly simple vocal repertoire consisting of short gutteral sounds, growls and clicks (Schusterman et al. 1970; Asselin et al. 1993). Breeding habitat has in this species been shown to be of great influence on mating behaviour (Anderson & Harwood 1985). Whereas males in land-breeding grey seals defend harems, males in ice-breeding grey seals are unable to monopolize females that are widely dispersed on the ice. Males are usually seen attending one female and her pup on the ice, forming triads (Riedman 1990). Another difference between ice-breeding and land-breeding grey seals is the fact that ice-breeding grey seal males and females regularly enter the water during the breeding season, whereas this is rarely seen in land-breeding populations (Asselin et al. 1993). The underwater vocal repertoire of grey seals has also been found to differ between land- and ice-breeding populations (Asselin et al. 1993). Underwater vocal display may therefore form an important part of ice-breeding grey seal male mating behaviour.

For crabeater seals, only one short broadband call type has been documented and vocal activity is thought to be restricted to the breeding season (Stirling & Siniff 1979; Rogers 2003). Crabeater seals form triads and occur in low densities in pack-ice areas. Males attend one female and her pup on the ice and defend the female against intrusions by other adult crabeater seal males until the female becomes receptive (Siniff et al. 1979). The relatively simple acoustic display of crabeater seal males is thought to function primarily in short-range male-male competition in guarding the female, as loud complex vocalizations would have the potential to attract other distant males to the pre-oestrus female (Rogers 2003).

Male hooded seals have a small in-air and underwater acoustic repertoire, involving five call types, most of which were found to be used in close-range communication in agonistic or sexual contexts during the reproductive period (Ballard & Kovacs 1995). Similar to crabeater seals, hooded seals form triads on the ice. However, hooded seal females are generall less widely dispersed compared to crabeater seals (e.g. Sergeant 1974; Siniff et al. 1979; Boness et al. 1988). Males may therefore move more easily between females resulting in some degree of polygyny (Boness et al.1988; Kovacs 1990). In addition, observations of some males attending a female continuously on the ice, whereas others were more mobile and attended several females for shorter periods of time, are suggestive of the use of alternative mating strategies by hooded seal males (Kovacs 1990). Visual displays involving the hood and septum form an important part of male hooded seal behaviour as male displays to a large part take place on the ice (Kovacs 1990; Ballard & Kovacs 1995).

In walruses, males of Atlantic and Pacific populations have been found to use different mating tactics. In the Atlantic walrus, large mature males were observed to attend and monopolize groups of potentially reproductive females for extended periods (Sjare & Stirling 1996). Male distribution in this population was mainly determined by ice-cracks and polynias that provided easy access to open water (Sjare & Stirling 1996). Pacific walruses breed on drifting pack-ice with a rapidly changing distribution of open water and much higher breeding population densities (Fay et al. 1984). The highly unstable environment combined with higher densities of potentially reproductive females is thought to make it more advantageous for Pacific walrus males to display in small areas for brief periods than to continuously attend and defend one herd (Sjare & Stirling 1996). Male walruses vocalize extensively in the vicinity of females and calves, emitting short repetitious pulses which have been suggested to exhibit individual stereotypy (Stirling et al. 1987).

In solitary pack-ice or fast-ice breeders, individuals need to broadcast their sounds over long distances to advertise their position to potential mates and rival males (Van Parijs 2003; Rogers 2003). These species generally have a medium size repertoire and vocalizations tend to be stereotyped signals to increase the likelihood that they are received by the intended recipient (Rogers 2003). Only limited recordings have been made of ribbon seal vocalizations. Watkins and Ray (1977) recorded ribbon seal high amplitude downward sweeps and puffing sounds towards the end of the breeding season. The sounds are thought to be produced by males, as only males were found to have well-developed air sacs, which may aid in the production of loud underwater sounds (Stirling & Thomas 2003). However, to date nothing is known on the role of vocal behaviour in ribbon seal mating behaviour. No study has investigated the behaviour of Caspian and Baikal seals and no vocalizations have been recorded.

Leopard seal male and females are widely dispersed at the start of the mating season as females give birth, nurse and wean their pups alone on the pack-ice. Communication must occur over long distances and both females and males have been found to produce loud broadcast calls during the breeding season (Rogers et al. 1996; Rogers & Bryden 1997). Lone males are known to vocalize for many hours each day, which may serve as an indicator of male fitness as these displays require the male to be in good body condition (Rogers 2003; 2007). Females are thought to produce broadcast calls to advertise their sexual receptivity to distant males (Rogers et al. 1996). The use of long-distance broadcast calls has also been suggested to occur in bearded and Ross seals (Rogers et al. 1996). Little is known on Ross seal mating behaviour as the species occurs in low densities in heavy pack-ice areas. Vocalizations have only been recorded in December through January, which suggests that these vocalizations are related to the mating season (Watkins & Ray 1985; Stacey et al. 2006; Seibert 2007). Ross seal vocalizations have been described as ‘siren calls’ (Watkins & Ray 1985) and are loud and semi-continuous, which makes them suitable to communicate over long distances (Rogers 2003).

Male bearded seals use loud trilling vocalizations which have been found to carry over large distances to advertise their breeding condition to females (Cleator et al. 1989; Van Parijs et al. 2003). Females are dispersed, but their movements are largely restricted to areas with suitable haul-out ice (Burns 1981). During the breeding season, male bearded seals have been found to vocalize in higher densities in areas where oestrus females are found regularly (Van Parijs et al. 2001; 2003). In Svalbard, bearded seals males have been found to use alternative mating tactics, where some males ‘roam’, displaying over large areas, whereas others are territorial and display over smaller areas (Van Parijs et al. 2003). Territorial males had longer trills than roaming males, which may be used by females as an indicator of male quality (Van Parijs et al. 2003). In addition, male mating success was shown to be dependent on variation in breeding habitat as increased ice cover was found to restrict the number of roaming males, whereas territorial males were present during all ice conditions (Van Parijs et al. 2004). In the light of current climatic trends, changes in ice-associated habitat may therefore alter the long-term mating success of individual male bearded seals. Although predictions on the potential effects of climate change on polar pinnipeds mainly concern regional or seasonal shifts in prey availability and changes in timing and patterns of migration (Tynan & DeMaster 1997; Friedlaender et al. 2007), small scale behavioural changes should not be ignored as important indicators of change. Acoustic techniques are a useful tool to study pinniped behaviour and may therefore also provide important insights in the potential effects of climate change on polar pinnipeds.

POLAR PINNIPEDS AND ANTHROPOGENIC NOISE

Rapidly increasing anthropogenic noise levels in the ocean and the impact of this noise on marine mammals have become a growing concern over the last years. With respect to polar habitats, ice breaker vessels and shipping traffic form the predominant anthropogenic noise sources to which ice-breeding pinnipeds are exposed. Recent computer projections of the National Snow and Ice Data Center have indicated that the receding Arctic sea-ice will leave more and more areas partially or largely ice-free year-round within the near future. Consequently, this opens opportunities to re-route commercial vessel traffic to and from Asia to take advantage of the open Northwest Passage. The increased shipping activity and the year-round presence of vessels in these areas will lead to substantially increased noise levels. These changes are likely to have consequences for polar pinnipeds that aggregate to mate and give birth to pups in traditional areas within these regions. Evidence of the potential impact of vessel sounds on pinniped behaviour and acoustic communication is generally meager (Richardson et al. 1995). In harp seals, calling rates were found to decrease after vessels came within 2km of the whelping area (Terhune et al. 1979). It was uncertain if calling rates decreased because animals stopped vocalizing or because they left the area. Further study is clearly needed and should include the acoustic monitoring of the areas of anticipated increases in vessel activity and the acoustic behaviour of ice-breeding pinnipeds within these regions.

In the next section we provide an overview of new and emerging passive acoustic technologies that can be used to further the study of polar pinnipeds.

ACOUSTIC DATA COLLECTION

Acoustic techniques only recently entered the range of easily accessible research tools, as significant advances in audio and computer technology now allow the acquisition and handling of large acoustic data sets. As a consequence, acoustic techniques have become increasingly important as a tool for remote sensing behaviour of various marine mammal species (e.g. Stafford et al. 1998; McDonald & Fox 1999; Janik 2000; Johnson & Tyack 2003; Mellinger et al. 2007). Compared to visual observation, acoustic recordings are quasi-omnidirectional and independent of light and weather conditions, providing the option of detecting and studying animals at night and under conditions where visual observation are not possible (see Erbe 2000 for a comparative discussion of acoustic and visual censuses). In particular for species in offshore or remote polar areas, newly developed acoustic techniques allow investigation of these animals in their natural habitat for extended time periods. However, not all techniques are equally well suited for collecting data in polar areas, as ice cover and harsh weather conditions can frequently limit deployment. In addition, instrumentation features such as the possibility of recording over longer time spans, the need for a vessel or on-site operators and access to real time data, determine which type of acoustic instrumentation is most suitable for specific research purposes. A comprehensive review of acoustic observation methods can be found in Mellinger et al. (2007). Here we provide a brief overview of the types of passive acoustic techniques that are currently used to study marine mammals. However, given the scope of this review, devices and techniques will be discussed in the light of their suitability for studying pinnipeds in polar environments.

ACOUSTIC INSTRUMENTATION

Ship-towed *hydrophone arrays* allowing coverage of relatively large areas, are in most cases relatively cost-efficient and can be combined with visual surveys (e.g. Spikes & Clark 1996; Norris et al. 1999). Towed systems can be deployed in offshore or remote areas, but often require dedicated ship time and personnel. The time-spans during which towed arrays are deployed are therefore generally relatively short (i.e. hours to weeks). Successful use in polar environments is largely dependent on ice conditions as heavy ice cover may limit access by ships and may damage recording gear. The use of towed arrays in ice-covered areas has nevertheless been shown to be feasible (e.g. Kindermann et al. 2006). Of greater concern are the high noise levels generated by icebreaker vessels which are likely to mask the majority of animal vocalizations, particularly in the mid (< 10kHz) to low (< 1kHz) frequency ranges. However, if the array consists of 10 or more tightly spaced hydrophones, beamforming techniques can be used to significantly improve signal-to-noise-ratios (e.g. Mellinger et al. 2007).

Acoustic tags (e.g. DTAG, Bioacoustic Probe) are miniature acoustic recorders that can be attached to marine animals to collect data on the acoustic stimuli emitted and experienced by the tagged subject (e.g. Johnson & Tyack 2003). Additionally, these devices are also capable of sampling various environmental variables as well as physiological and behavioural data (Fletcher et al. 1996; Madsen et al. 2002). The use of acoustic tags can provide particularly useful information about an individual's behaviour in relation to its vocalizations and sounds from its environment. This technique is also used as a tool to determine correction factors for marine mammal surveys such as the amount of time animals are vocalizing (e.g. Erbe, 2000). However, when animals are in close groups it can be difficult to separate whether the vocalization is produced by the tagged individual or one nearby. Furthermore, acoustic tags can only sample data over periods of hours to days. In contrast to satellite telemetry tags which transmit data back to a receiving station, acoustic tags need to be retrieved before data can be analysed, which might be a difficulty if tags come off in areas that are not easily accessed (i.e. ice covered regions). In addition, as is the case with all tagging studies, the influence of both the tagging event and the presence of the tag on the individual need to be ascertained before major conclusions are drawn from such data.

Autonomous recording devices consist of a hydrophone and a battery-powered data recording system. These instruments are either free-drifting (surface recording units, e.g. Hayes et al. 2000; Collison & Dosso 2003), moored on the sea floor or attached to deep-sea moorings (e.g. Calupca et al. 2000; Newcomb et al. 2002, Wiggins 2003). Alternatively, these devices can be ice-based with hydrophones deployed through holes in the ice (Klinck 2008). Ice-based autonomous recording devices also offer the possibility for in-air recording of vocalizing animals that are hauled out on the ice (e.g. Collins et al. 2005; 2006). These devices are battery-powered and record and store acoustic data internally. Dependent on data storage capacity of the device, recording bandwidth and sampling regime, recordings can be obtained over extended periods of time, in some cases up to several years (e.g. Wiggins 2003;

Sirovic et al. 2003; Moore et al. 2006). In addition, by deploying several synchronized devices in an array, large areas can be acoustically monitored and movements of animals within these areas can be tracked. However, only archival data collection is possible and consequently, data analysis can only occur after a certain period of time when devices have been recovered. Autonomous recording devices have the advantage that they can be deployed in a wide variety of areas, including polar environments (e.g. Wiggens 2003; Moore et al. 2006). Nevertheless, in ice-covered areas, deployment may be restricted to areas with greater water depths (i.e. >250m in Antarctic regions) as in shallow waters, drifting icebergs often cause damage to moored instruments.

An emerging passive acoustic technique involves the use of *autonomous underwater vehicles and gliders*, which originally were developed for oceanographic research (e.g. Eriksen et al. 2001; Sherman et al. 2001). More recently these devices have been used for various research purposes and have been successfully deployed in ice-covered areas (e.g. Brierley et al. 2002; Owens 2006). Gliders move vertically and horizontally and can be remotely controlled at regular time intervals through an intrinsic two-way communication system, which also allows stored data to be transmitted back to the lab for immediate analysis. However, the type of bi-directional satellite transmitters that are currently used in gliders allow transmission of limited amounts of data only (see also the discussion on satellite transmission below). Furthermore, gliders require significant resources to build and maintain. In cases where they are deployed for acoustic recording purposes, devices need to be recovered after weeks or months to retrieve data. With respect to polar areas, gliders could nevertheless provide a tool for remotely controlled acoustic sampling of (periodically) inaccessible areas. Bioacoustic research using these devices is nevertheless still limited (Baumgartner et al. 2006; Fucile et al. 2006).

Free-drifting *radio-linked sonobuoys* enable short term real time acoustic monitoring as they transmit acoustic recordings as a radio signal and are often deployed from vessels or aircraft. In order to transmit recordings in good quality, radio signals require a receiver to be in relative proximity of the recording device, which makes these systems suitable for use during ship-based surveys where visual and acoustic observations are combined (e.g. Clark et al. 1994; Rankin et al. 2005). Some drifting radio-linked sonobuoy types also allow localization by giving a compass bearing to the sound source (DIFAR buoys, e.g. Greene et al. 2004). The duration of the period over which these devices transmit acoustic recordings and the cost of devices strongly depends on the type that is used. With respect to polar areas, successful use of these devices will largely depend on ice coverage as shifting ice may cause damage or block transmission of the radio signal. In heavy ice-covered areas, radio-linked sonobuoys can be fixed on the ice surface while the hydrophone is deployed through a borehole or crack in the ice (e.g. Clark et al. 1996).

Cabled passive acoustic recording stations can be operated continuously in offshore areas without limitations on data storage capacity and power supply. In addition, cabled recording stations allow near-real time monitoring which enables the linking of acoustic recordings to visual observations. However, the majority of cabled arrays in offshore areas require significant resources and are predominately operated by government institutions. An example of such a station is the US Navy sound surveillance system (SOSUS array), which consists of a network of hydrophones covering the deep offshore waters throughout the Atlantic and Pacific oceans. Due to the military purposes of these systems, access to the acoustic data is often restricted, only off-line available and the recording bandwidth of these systems is often limited to lower frequencies. These systems have nevertheless been used successfully to study baleen whales and other species calling at low frequencies (e.g. Clark 1995; Clark & Charif 1998; Moore et al. 1998; Stafford et al 1998; 1999).

In recent years, however, a growing number of non-military cabled acoustic observatories are operated in coastal areas (e.g. ALOHA, Petitt et al. 2002; NEPTUNE, Barnes et al. 2007; AUTEC). These systems record continuously over broad frequency bandwidths, allow real time monitoring and localization of marine mammals and have no restrictions to data storage, data access and power supply. These characteristics would make cabled systems ideal if they could be used for data acquisition in remote polar environments. However, monitoring of polar regions with a network of hydrophones connected by cables to shore-based stations requires extreme cable length which would imply extensive deployment and maintenance costs. In addition, ice movements and cable melt-in can cause damage to long cables in polar environments. The use of cables can nevertheless be overcome by satellite or iridium phone mediated transfer of acoustic data directly from recordings units to receiver stations where data are analysed. As mentioned previously, the type of transmitter systems that are suitable to be integrated in recording units limit satellite data transmission rates, rendering them too low to allow continuous broadband acoustic data to be transmitted. This can be surmounted by only transmitting acoustic snippets or events (e.g. click detectors, TPODs; e.g. Tregenza 1999), which requires pre-processing of the signal within the buoy to detect and select events that are transmitted.

Transmission of continuous broadband acoustic data instead of snippets is possible if data transmission is mediated by a station with enlarged satellite receivers. Acoustic data from the recording unit can be transmitted to the satellite-linked station using a radio signal or a wireless local area network (WLAN) link, provided that the area is relatively flat and the satellite-linked station and the recording unit are not too far apart. The satellite-linked station can then be used to transmit acoustic data to receiver stations over large distances (an example of such a system will be discussed in the next section). Real time data transmission of autonomous recording units has the additional advantage that data does not necessarily have to be stored locally and that analyses can be performed near-real time (e.g. Simard et al. 2006).

In addition to data transfer, cables also serve to secure the continuous power supply of cabled systems. A system with satellite- and radio-linked data transmission is devoid of this option and therefore either dependent on batteries that need regular exchange or requires autonomous power supply. With respect to polar areas, autonomous power supply secures continuous powering of the station also when the area is periodically inaccessible.

PALAOA

The PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA) is an example of a stationary autonomous listening station that records sound continuously year-round and provides online access to the real time data (see http://www.awi.de/acoustics). The PALAOA observatory is located at 70°31'S 8°13'W, on the Ekström Ice Shelf, Eastern Weddell Sea, at 1 km distance from the ice shelf edge (Figure 1). The main sensor was designed as a 520m baseline tetrahedral hydrophone array deployed through boreholes underneath the 100m thick floating Antarctic ice shelf (Boebel et al. 2006; Klinck 2008b)[1]. It is energetically self-sustained by utilizing solar and wind energy. A CTD probe is mounted to collect oceanographic readings while sea ice conditions of the adjacent ocean are monitored with a webcam. A 13km WLAN link connects the station to the German Antarctic Neumayer Base, which is manned year-round and has a leased satellite internet connection. Development efforts focused on the one hand on the real time transmission of a highly compressed live stream (24kbit/ogg-vorbis-coded) via a satellite link to the Alfred Wegener Institute for Polar and Marine Research (AWI) in Bremerhaven, Germany for immediate processing. On the other hand, acoustic data of very high quality (up to 4 channels, 192 kHz/24Bit uncompressed) is buffered on request at PALAOA and Neumayer Base respectively and can be downloaded for detailed analysis. PALAOA has been operational since December 2005 and has collected a total of 10000 hours audio so far (by January 2008). Recordings contain vocalizations of four Antarctic pinniped species (crabeater, Weddell, Ross and leopard seals) and a variety of cetacean vocalizations. In addition, the recordings contain sounds of abiotic origin, such as iceberg calvings and collisions. Current analyses aim to explore temporal and spatial distribution patterns of vocalizing individuals of the different species. Additionally, the PALAOA recordings are used to gauge the local ocean noise budget and monitor the impact of human activities on marine mammal behaviour. PALAOA provides an example of a state-of-the art system which allows data to be obtained for long term monitoring of acoustic underwater sounds in the Antarctic which has never been attempted previously.

SOFTWARE TECHNOLOGIES

As the data storage capacity of acoustic recording instruments has increased substantially over the last years, recordings can be made over longer time spans. In many cases these long term acoustic datasets require the use of automated detection and classification techniques, as manual detection and analysis becomes too time-consuming. A wide variety of software technologies are available to perform automated detection and classification (e.g. open source: Mellinger 2001; Figueroa 2006) and a number of different detection methods have been developed (e.g. see Mellinger et al. 2007 for a summary of methods). However, not all techniques are equally well fitted for different species, research goals and recording types. Species-specific vocal characteristics are one factor to consider when deciding for a specific software tool for analyses. Techniques involving matched filters or spectrogram correlation are most suitable to investigate species with stereotyped vocalizations, whereas more variable vocal patterns (e.g. dolphin whistles) are best detected using energy summation in specified frequency bands (e.g. Oswald et al. 2004). Also, the rarity of a species' vocalizations may determine the optimal configuration of the detector to achieve a trade-off between missed calls (false negatives) and incorrect detections (false positives). In species that are not very vocal or occur infrequently, the importance of detecting as many target vocalizations as possible may overcome the effort of an additional check of the detector's output (either manually or by using subsequent automated classifiers). Similarly, the purpose of the detection will also determine which is the optimal detector type and sensitivity (see Mellinger et al. 2007 for a discussion). A final factor to consider is the type of recordings. As has been

[1] Since mid 2006 the failure of two hydrophones has reduced the array to a two-channel system

mentioned earlier, multi-channel recordings can significantly improve signal-to-noise-ratios through beamforming and allow source localisation

Within marine mammal acoustic research, automated detection has to date almost exclusively been used to scan large data volumes for cetacean vocalizations (e.g. Stafford 1995; Mellinger & Clark 2000; Gillespie 2004; Lopatka et al. 2005; 2006). This likely reflects the fact that long term acoustic observations are much more embedded within cetacean research as compared to studies of pinniped behaviour. However, many of the basic research questions that still need to be addressed for a number of polar pinniped species require acoustic observation over longer time spans and consequently the use of automated detection techniques. Klinck et al. (2008; in press) recently applied various automated detection techniques to long term recordings of pinniped vocalizations and found, for example, that Hidden Markov Models, which are also used for human speech recognition (e.g. Juang & Rabiner 1991) perform well for leopard seal vocalizations. Nevertheless, as mentioned earlier, species-specific vocal behaviour and research goals will ultimately determine the suitability of an automated detection technique.

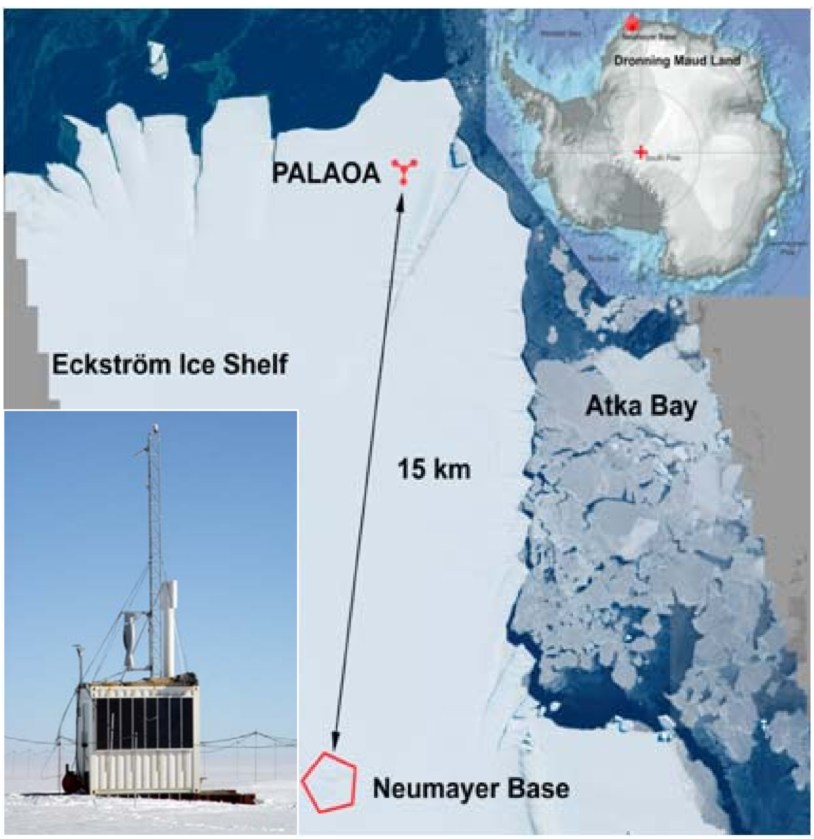

Figure 1. IKONOS-2 satellite image from March 2004, with locations of the Neumayer Base and PALAOA. Top inset: Antarctica with the location of PALAOA indicated by a red dot. Bottom inset: PALAOA Station.

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

Little is known about the acoustics of most ice-breeding pinnipeds. Clearly, the inaccessible nature of their habitat plays an important role in explaining this short coming and has greatly influenced the extent to which these species have been studied. To date mother-pup vocal recognition has not been experimentally tested in any of the ice-breeding species, except for the walrus. Attempting to address these short comings would significantly increase our understanding of ice breeding species requirements in terms of offspring recognition. Investigations of vocal individuality of mother and pup calls show markedly different patterns for each species, which likely reflects the complexity of interactions that shape their vocal behaviour.

With respect to mating strategies, there is a distinction between the species that have been investigated in some detail, such as the bearded, Weddell seal and the walrus and those about which we known very little. Future investigations of well known species' mating systems require more small scale research focussing on individual differences and plasticity in male mating tactics. Additionally, the role of females and female choice also needs to be taken into account. For little known species an attempt at understanding the broader scale role of underwater vocalisations should be the initial focus. Recent changes in acoustic instrumentation technologies and their availability in terms of reduced costs should greatly facilitate the study of little known polar species. Although reseachers have primarily used novel acoustic instrumentation and software technologies for studying cetaceans, the majority of these devices and techniques provide vast opportunities for the study of polar pinnipeds.

It is critical to improve our understanding of both recognition processes and reproductive strategies of polar pinnipeds given current trends in climate driven changes which are altering their ice-dominated environments at hereto unprecedented rates. Ice-associated seals, which rely on suitable ice substrate for e.g. resting, pupping and moulting, are particularly vulnerable to climatic change. Similarly, changing conditions in the ocean basin such as increasing background noise, in terms of anthropogenic sounds, are becoming of heightened concern for polar environments. Among other techniques, acoustic techniques should be recognized as an extremely versatile and useful technology for future studies of pinniped ecology.

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