THE VOCAL BEHAVIOUR OF THE GREY SEAL (HALICHOERUS GRYPUS)

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The vocal behaviour of the grey seal
(*Halichoerus grypus*)

by
Susanne McCulloch

Submitted in fulfilment of requirements for
the degree of Doctor of Philosophy
University of St. Andrews

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"When angels fell, some fell on
the land, some on the sea.
The former are the faeries and
the latter were often said to be
the seals."

Anonymous Orcadian

Abstract

This thesis is an observational and experimental study of the vocal behaviour in the grey seal (*Halichoerus grypus*). It provides the first comprehensive description of in-air and underwater vocalisations for the eastern Atlantic population of grey seals and compares it to the western Atlantic population. Two out of 6 in-air call types were very similar to underwater vocalisations and of the 10 eastern Atlantic underwater vocalisations 5 were comparable to the western Atlantic repertoire described earlier. Most calls were found to occur on their own, while some were preferentially associated in time with other call types. In addition, the number of particular types of underwater vocalisation did not display any diurnal variation, but did vary across the breeding season. Experimental studies were also carried out on the role of pup vocalisations in mother-pup vocal recognition at two reproductively isolated colonies: the Isle of May, Scotland and Sable Island, Nova Scotia, Canada. Pup vocalisations were found to be both stereotyped and individually distinctive, features normally associated with a system of individual recognition. Allo-suckling was observed to be widespread on the Isle of May but was absent on Sable Island. Playback experiments revealed that mothers on the Isle of May did not respond more to vocalisations of their own pup than to those of non-filial pups. In contrast, on Sable Island, mothers were able to discriminate between their own and other pup calls. This suggests that different selective pressures may be affecting the two colonies, and possible reasons are discussed.

Declarations

(i) I, Susanne McCulloch, hereby certify that this thesis, which is approximately 41 000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

Date........................ Signature of candidate.......................

(ii) I was admitted as a research student in October 1996 and as a candidate for the degree of PhD in October 1997; the higher study for which this record was carried out in the University of St. Andrews between 1996 and 1999.

Date........................ Signature of candidate.......................

(iii) I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of PhD in the University of St. Andrews and that the candidate is qualified to submit this thesis in application for that degree.

Date........................ Signature of supervisor.......................

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Acknowledgments

I feel as if I've become part of the decor of St. Andrews. People come and go and after 7 years, I seem to still be here. The reason why I stayed after my undergraduate degree is quite simple and goes back to my first year and to my first taste of animal behaviour. These lectures were a pleasure to attend so it's not surprising that I jumped at the opportunity to do a PhD with that same lecturer. Thanks Peter for introducing me to this exciting field and supporting me throughout my university career.

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To my folks,
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Chapter 1

General Introduction

Animal communication has been said to be "the glue that holds animal societies together" so it is not surprising that the number of studies of the subject have increased enormously in recent years (Bradbury & Verhencamp 1998). Whether communication is honest or deceiving, it involves the transmission of information from one individual to another. In all sexual animals, communication has to occur somewhere in the process of reproduction. However, in highly social animals, communication goes beyond transmitting the necessary information for mating. Indeed, animals can also communicate information on their identity, on the location of feeding places and on the presence of predators. Some signals send information about the identity of the sender such as its species, sex, group membership or individual identity. Others send information about its status and emotional state (dominance rank, fear or aggression), about its subsequent actions (such as groom, fight, eat, flee) and finally about its environment (presence of predators, location of food).

However, although the sender may direct its signal to a specific receiver, rarely do signals lend themselves to private channels of communication. Furthermore, sender and receiver may have conflicting interests in the accurate exchange of information: senders may cheat on receivers, and receivers may exploit senders. Wiley (1983) describes four possible combinations of value of information to senders and receivers (Table 1). The transmission of information is therefore not always beneficial to both parties. An example of manipulation by the sender is illustrated by the female bolas spiders (*Mastophora sp.*) that lures male armyworm moths (*Spadoptera frugiperda*) to their death by emitting a pheromone that resembles the sexual attractant of the female moth (Eberhard 1977). A sender can also provide the receiver with inaccurate information through lies, withholding information, and exaggeration or bluff (Bradbury & Verhencamp 1998). Moreover, some signals can become parasitised by unwanted receivers both at the inter- and intraspecific level. An example of such exploitation of the sender by the receiver is the neotropical bat (*Trachops cirrhosus*) that eavesdrops on the mating calls of male frogs (Ryan et al. 1982). At the intraspecific level, deception is documented, by for example, "mimicry of females by males to gain surreptitious matings, and use of alarm calls to gain temporary advantage in competition for food or territories" (Wiley 1994).

		Receiver value of information	
		Positive	Zero (or negative)
Sender value of information	Positive	True communication	Manipulation (deceit)
	Zero (or negative)	Eavesdropping, cueing (exploitation)	Ignoring (spite)

Table 1. Possible combinations of value of information to senders and receivers (From Wiley 1983)

Therefore, in some situations, communication has advantages for both sender and receiver; in others, one can take advantage of the other. This can be further illustrated by the following examples of prey-predator interactions. Nightjars (*Caprimulgus europaeus*) lure foxes away from their chicks with a broken wing display while female fireflies (*Photuris collustrans*) attract the males of other species by mimicking the appropriate light flash signal for that species (Gerhardt 1983). However, for communication to evolve, it is essential that signal transmission should, on average, benefit the sender and for this to be so, it will in most cases also benefit the receiver. The question arises otherwise of why the receiver should respond. For this reason, cases of deception are rather rare.

Sensory modalities and signal design

The process of maximising the difference between the costs and benefits of communication, leads to an effective signal adapted to a particular context (i.e. "optimisation", Bradbury & Verhencamp 1998). Animals may use conspicuous colours, structures, odours and other displays to attract members of the opposite sex. They may also use different calls to describe different predatory threats (e.g. vervet monkeys, Seyfarth & Cheney 1990). Communication can therefore involve many different sensory modalities with distinctive properties of their own. The effectiveness of transmission, locatability, and energetic cost are some of the features that may determine which sensory modality is most appropriate (Table 2).

Table 2. Advantages of different sensory channels of communication. (Adapted from Alcock (1984) and Bradbury & Verhencamp 1998)

	Type of signal			
Feature of channel	Chemical	Auditory	Visual	Tactile
Medium requirement	Current flow	Air/water	Ambient light	None
Range	Long	Long	Medium	Short
Rate of change of signal	Slow	Fast	Fast	Fast
Ability to go past obstacles	Good	Good	Poor	Poor
Locatability	Variable	Medium	High	High
Complexity	Low	High	High	Medium
Signal duration	Long	Short	Variable	Short

Chemical, auditory, visual and tactile signals each have advantages and drawbacks.

Chemical signals

Chemical signals are energetically cheap to produce. They can be released into air and water, and will diffuse slowly in a stationary medium. The signaller can accelerate the diffusion process by exploiting wind or water currents. Certain moth species travel up wind searching for high concentration of pheromones known as "odour plumes" left by potential mates (Shorey 1977). Pheromones can also be deposited on stationary objects thus leading to durable signals that can be used to scent mark territories, and hence operate when the signaller is absent.

Finally, pheromones can be transferred directly to the receiver such as the "queen substance" in honeybees that inhibits workers from rearing rebel queens and laying eggs themselves (Seeley 1985). However, chemical signals are restricted to certain molecular configurations that maximise transmission or signal duration, thus reducing their specificity and the amount of information they can carry. In addition, their speed and direction of travel is highly dependent on the medium of transmission. Nevertheless, chemical signals are widely used in communication to determine the identity of individual animals, and stimulate aggregation, dispersion, sexual behaviour and aggression (e.g. sex pheromone in hermit crab, Shorey 1977).

Visual signals

Some of the most striking signals belong to the visual modality. Indeed, the peacock tail, the feathers of the bird of Paradise, and the facial colours of certain primates are just a few examples of elaborate visual signals. Animals can easily communicate through the visual channel by altering their posture and their colour. These signals are well adapted for private short range communication and can be in some cases quickly switched off to avoid detection. However, drawbacks are that they can be limited in range and direction by dense vegetation or by low light, and their conspicuousness makes them vulnerable to predation (Gerhardt 1983). Finally, senders can be constrained by physical factors such that body size will determine the maximum size of any visual signal it can produce.

Tactile signals

Tactile signals can be produced by all animals. They are easy to locate and often act instantaneously. These are the least studied form of communication signal. However, a few species of insects have been shown to use contact, compression and boundary vibrations. For example, water strider (*Gerris remigis*) males signal their sex by producing higher frequency surface waves than females. Furthermore, female *Drosophila* fruitflies can detect the wing vibrations made by courting males (Harper 1991).

Acoustic signals

Finally, I would like to concentrate on acoustic signals as this will be the focus of most of this thesis. The study of animal communication has made a great leap forward in recent years, in part due to the technical progress of recording and analysing equipment. Furthermore, many social animals use this sensory modality to communicate therefore adding to scientific interest. Indeed, many recent studies have looked at how acoustic signals are involved in species and individual recognition (e.g. parrotlets, Wanker et al. 1998; king penguins, Jouventin et al. 1999) and how calls are used in maintaining group cohesion (e.g. bottlenose dolphins, Janik & Slater 1998).

Sounds propagate rapidly through air and water, with rapid onset and offset. They are not limited by changes in ambient light and can convey complex information over a long range. Senders can alter sounds rapidly by changing their volume and frequency and sounds can be made to be easily detectable. However, sounds (as well as other forms of communication) can be distorted by atmospheric attenuation, scattering and absorption by obstacles, microclimate effects and reflection (Gerhardt 1983). They can also be affected by ambient noise. Many animals have responded to these problems through behavioural and physiological adaptations. For example, senders often produce low frequency sounds as these travel further in all habitats (e.g. elephants, Poole et al. 1988). Others improve their broadcast efficiency by elevating themselves (e.g. crickets (*Anurogryllus*) in Gerhardt 1983) or by signalling at optimum times (e.g. dusk and dawn choruses in birds). Another example is the king penguin that lives in large colonies resulting in a continuous background noise of calls with similar temporal and spectral properties. In response to the high levels of sound degradation in this environment, parents use a characteristic incubating posture that maximises detection of their mates signal (Lengagne et al. 1999). Other signals have evolved in response to predator pressure. Many small European songbirds produce a high pitched "seeep" alarm call in the presence of hawks (Marler 1955). This alarm call is hard to detect and provides information on predator threat. The similarity in this signal given by distantly related species has been suggested to reflect the convergent evolution of a call that is hard for predators to detect (Marler 1955).

Sound transmission in water

I will now concentrate on the problems of sound transmission in water. Without going into the theory and physics of sound transmission, it still remains necessary to outline some of the problems of sound propagation under water. This will explain some of the difficulties encountered later when trying to record animals communicating in this medium. In water, sounds propagate differently at different depths and are affected by variations in temperature, salinity and bottom structure and composition. Sound travels further under water than in air. In shallow waters, bottom and surface reflections are usually dominant components of sound transmission (Malme 1995). With upward refraction, bottom reflections and resulting bottom losses are reduced; the opposite occurs with downward refraction. Other factors that influence sound transmission are molecular absorption, a sloping bottom, and shallow source and receiver effects. The last of these occurs when the source and/or receiver are close to the surface. This can lead the direct sound and its surface reflection to be out of phase, producing an interference pattern (Malme 1995). At frequencies <1 kHz, absorption is not significant at ranges < 40 km. However, for broadband noise, the absorption coefficient and usually the source level are frequency dependent (Malme 1995). The shallow source and receiver effect occurs when range from source to receiver is long enough for the direct and reflected path lengths to be comparable. Finally, the slope of the bottom influences sound transmission by increasing or decreasing the available volume for sound transmission. Therefore, sound propagation in water is affected in various ways by the physical properties of the medium and the structure of the ocean floor.

In addition, sound transmission can be further affected by ambient and man-made noise. Ambient noise is environmental background noise caused by wind, waves, precipitation, biological organisms, sea ice, thermal noise and sometimes seismic activities (Greene 1995). It determines along with the source level of the sound how far a signal can be detected. The wind source of noise often dominates the total ambient noise from a few hundred hertz to ~30 kHz, while surface waves tend to produce infrasonic noise at frequencies of 1-20 Hz. Precipitation is an important component of total noise above the 500 Hz range, whereas biological noise can extend from ~12 Hz to over 100 kHz (Greene 1995). Sea ice noise can be very important at high latitudes, but is also very variable. Finally thermal noise resulting from molecular agitation is important at frequencies above 30 kHz, whereas seismic noise emits energy at frequencies up to 500 Hz. Another source of noise that will affect sound transmission underwater is man-made noise arising from transportation, dredging, construction, mineral exploration, geophysical surveys, sonars, explosions, and ocean science studies (Greene & Moore 1995). In the past decade, oceans have become increasingly noisy, making it potentially more difficult for marine mammals to communicate. A general concern for underwater noise and habitat degradation has arisen leading to a number of studies investigating the effect of man-made noise on the environment. Although most data remain anecdotal, noise from human activities seems to sometimes cause pronounced short-term behavioural reactions and temporary local displacement of certain marine mammals (Richardson 1995b). It therefore seems essential to investigate how marine mammals and other marine organisms adapt to these new sources of noise.

Signal information

We have seen how signals can be shaped by ecological, environmental and prey-predator constraints and that the modality of signal used depends on the sensory systems of the signaller and the medium the signal travels through. What about the information provided by a signal transmission? Again we will focus on auditory signals and more specifically their use in group membership recognition, parent-infant interaction, and territory defence as these are directly relevant to this thesis.

Group membership recognition

In social groups, it is often important for individuals to respond in particular ways to particular individuals. This discrimination can be done at the species, kin, pair and individual level. Individually distinctive calls have been demonstrated in many birds (e.g. swallows, Loesche et al. 1991), fish (e.g. cichlids, Myrberg et al. 1965, Myrberg et al. 1993), and mammals (e.g. lions, McComb et al. 1993; bats, Balcombe 1990; vervet monkeys, Cheney & Seyfarth 1982; elephant seals, Shipley et al. 1986). Some individuals distinguish between group members and non members based on familiarity. For example, the use of playback experiments has demonstrated that individual pikas (*Ochotona princeps*), a small North American mammal, can discriminate between familiar and unfamiliar calls (Conner 1985). The same technique has been used for many avian species with similar results. The white-throated sparrow (*Zonotrichia albicollis*) performs neighbour-stranger discrimination on the basis of the pitch of the song (Brooks & Falls 1975). Moreover, King penguin partners alternate between brooding and foraging at sea. At the changeover, a parent must recognise its mate among several thousand other individuals. This is achieved through vocal recognition and discrimination is thought to be based on frequency modulation in the penguin's syllables (Aubin & Jouventin 1998, Lengagne et al. 1999). Individual recognition is especially important in the relationship between a parent and its young.

Parent-infant interaction

For the parent, it is essential that they care for their own offspring. For the young, recognition of the parent may be vital for their survival, especially in dense breeding colonies and when the young is mobile. Parent-young recognition is well established in many species of birds (for review see Beecher 1982). The extent to which chicks are able to recognise their parents, and the age at which they become able to do so varies between species (Beer 1970). Except for some marine mammals (e.g. harbour seal (*Phoca vitulina*), Renouf 1984, 1985; California sea lion (*Zalophus californianus*), Hanggi 1992), parent-young auditory recognition in mammals is not so well documented. Nevertheless, parent-young vocal recognition has been shown in reindeer (*Rangifer tarandus L.*) by Espmark (1971), in racoons (*Procyon lotor*) by Sieber (1986) and suggested in timber wolves (*Canis lupus*) by Goldman et al. (1995). Furthermore, acoustic learning of infant "isolation calls" and mothers' "directive calls" has been suggested in the lesser spear-nosed bat *Phyllostomus discolor* (Esser & Schmidt 1989). Many of these studies have used playback techniques to demonstrate vocal recognition. This technique consists of playing sounds to animals and observing their response. The advantage to this method is that it is possible to isolate the sound stimulus from other confounding variables, vary it and see how responses differ between different stimuli. However, it is essential to avoid "pseudoreplication" (i.e. the use of a sample size in a statistical test that does not consist of truly independent trials, McGregor 1992), to be explicit about the question being asked and to minimise or at least acknowledge errors that may occur in carrying out the experiment. Test tapes and test sounds, environmental conditions, test animals, playback equipment and experimental procedures are all sources of such execution errors (eg. subject location, fidelity of equipment, observer bias, degradation effects. see Table I p 8 McGregor 1992). In spite of the problems in designing and carrying out playback experiments (McGregor 1992), these techniques have increased our knowledge of vocal recognition enormously.

Territory defence

Acoustic signals can also be used in territory defence. In many cases, the acoustic structure (i.e. frequency) of the signal is correlated with the size of the animal thus providing the receiver with the possibility of assessing physical and behavioural traits of potential rivals. This can be illustrated by the threat calls of the north elephants seals (Shipley et al. 1986) and the "musth rumble" of African elephants (Poole 1999).

In this study, I investigate the vocal behaviour of grey seals to gain more information on the social systems of this species and the role of its acoustic communication. Grey seals are social animals that breed in large colonies. They spend most of their time at sea foraging in between the breeding and moulting seasons. The noise emanating from the summer haul-outs leaves us in no doubt that on land they are a vocal species. In addition, grey seals have been found to be more vocal underwater than previously thought (Asselin & Hammill 1993). Thus, acoustic signalling seems their most appropriate mode of social communication as sound travels efficiently in air and in water. Are underwater vocalisations similar to the vocalisations produced on land? Under what circumstances do seals call? Do they call more at the start of the breeding season than at the peak or the middle? Are pup vocalisations used in mother-pup recognition? This thesis attempts to answer some of these questions by describing the vocal repertoire of the Grey seal, suggesting a possible functional significance for certain calls and then investigating mother-pup vocal recognition. However, before considering these issues, it is necessary to review the ecology of the Grey seal and the structure of its auditory system along with what has been investigated in the other pinnipeds.

Grey seal ecology: Overview

Classification

The order Pinnipedia include three families: the Odobenidae, which has a single species, the walrus; the Otariidae, the eared seals, containing 14 species, and the Phocidae, the true seals with 19 species (Table 3). In this last group, the only member of the *Halichoerus* genus is the Grey seal, *Halichoerus grypus.*

Distribution

Grey seals, *Halichoerus grypus*, are found in three reproductively isolated populations: those of the north west Atlantic, the north east Atlantic and the Baltic Sea. In the west, grey seals breed on ice in the Gulf of St Lawrence and on the islands off Nova Scotia. The breeding season lasts from mid-December to February. The majority of the north east Atlantic population breeds around the coast of the British Isles from September to December. This population also breeds around Iceland, the Faroes, Norway and as far north as the Murman coast of Russia. The Baltic Sea population is the smallest of the three and is restricted to the Gulfs of Bothnia, Riga and Finland. Births occur on land during poor ice years and/or pack ice during February and March (Anderson 1990).

On the basis of a 1994 survey, the Sea Mammal Research Unit (SMRU) estimated the population around the British Isles at c 108 500 individuals (Hiby et al. 1996). The main breeding sites on the east coast of Britain are the Isle of May, the Farne Islands and Donna Nook, south of the Humber Estuary. Large stocks of grey seals are also found in the Inner and Outer Hebrides, in Orkney and in Wales. Outside the breeding season, grey seals wander widely (Hammond et al. 1993), and spend a large amount of time at sea foraging and travelling between haul-out sites. Until the late 1970's, the Isle of May hosted only a handful of births each year and was mainly used as a haul-out site. In contrast, up to 2 000 pups were born each

Table 3. The order Pinnipedia

ORDER: Pinnipedia

SUBORDER: Phocoidea

FAMILY: Phocidae

SUBFAMILIES:

Phocinae (Northern seals):
10 species

- *Erignathus barbatus* (Bearded seal)
- *Cystophora cristata* (Hooded seal)
- *Phoca sibirica* (Baikal seal)
- *Phoca vitulina* (Harbour seal)
- *Phoca groenlandica* (Harp seal)
- *Phoca fasciata* (Ribbon seal)
- *Phoca hispida* (Ringed seal)
- *Phoca largha* (Spotted seal)
- *Phoca caspica* (Caspian seal)
- *Halichoerus grypus* (Grey seal)

Monachinae (Southern seals):
9 species

- *Monachus tropicalis* (Caribbean monk seal)
- *Monachus schauinslandi* (Hawaiian monk seal)
- *Monachus monachus* (Mediterranean monk seal)
- *Hydrurga leptonyx* (Leopard seal)
- *Lobodon carcinophagus* (Crabeater seal)
- *Ommatophoca rossi* (Ross seal)
- *Leptonychotes weddelli* (Weddell seal)
- *Mirounga angustirostris* (Northern elephant seal)
- *Mirounga leonina* (Southern elephant seal)

SUBORDER: Otarioidea

FAMILY: Otariidae

SUBFAMILIES:

Otariinae (Sea lions)
5 species

- *Eumetopias jubatus* (Steller sea lion)
- *Zalophus californianus* (California sea lion)
- *Otaria flavescens* (South American sea lion)
- *Neophoca cinerea* (Australian sea lion)
- *Phocarctos hookeri* (New Zealand sea lion)

Arctocephalinae (Fur seals)
9 species

- *Arctocephalus australis* (South American fur seal)
- *Arctocephalus philippii* (Juan Fernandez fur seal)
- *Arctocephalus townsendi* (Guadalupe fur seal)
- *Arctocephalus galapagoensis* (Galapagos fur seal)
- *Arctocephalus gazella* (Antarctic fur seal)
- *Arctocephalus tropicalis* (Subantarctic fur seal)
- *Arctocephalus forsteri* (New Zealand fur seal)
- *Arctocephalus pusillus* (Cape fur seal)
- *Callorhinus ursinus* (Northern fur seal)

FAMILY: Odobeninae

SUBFAMILY:

Odobeninae (Walrus)
1 species, 2 subspecies

- *Odobenus rosmarus rosmarus* (Atlantic walrus)

- *Odobenus rosmarus divergens* (Pacific walrus) year at the breeding colony of the Farne Islands. However, since 1975, the number of pups born at the Isle of May has increased substantially. An estimated 1 770 pups were born there in 1997 (C. D. Duck, Sea Mammal Research Unit, personal communication). The sudden expansion of the Isle of May colony is thought to have been the result of intrinsic growth and immigration (Harwood & Wyile 1987). In the early 1970's, the increase in the Farne Islands grey seal population was causing major damage to the habitat of the breeding gulls and puffins there. The radical decision was therefore adopted by the National Trust in 1971, to reduce the number of breeding females to 1000 by culling during the breeding season. This objective was rapidly reached, and the number of pups born at the Farne Islands declined dramatically. However, the density of adult seals did not change on the islands vulnerable to soil erosion. In 1977, a new policy was adopted where wardens were instructed to concentrate their effort on the vulnerable islands and kill all seals attempting to breed there. This led to virtually no pups being born on those islands in the years following the change in management policy (Harwood & Wyile 1987). Since then, the breeding population has stabilised to around 1 000 births a year with a redistribution of breeding sites amongst the different Farne Islands (Hiby et al. 1996). Recent monitoring of branded females and the use of radio and ultrasonic transmitters has given evidence of the immigration of grey seal cows from the Farne Islands to the Isle of May (Harwood & Wyile 1987). The Isle of May (Fig. 1) is now a well-established breeding colony and is easily accessible thus making it an ideal location for fieldwork and research.

Dispersal

On the east coast of Britain, grey seals breed colonially in October and November, usually on isolated uninhabited islands. After the breeding season, they disperse widely, travelling to foraging sites and hauling out on rocky shores and sandbanks. Movements at sea have only recently been investigated with the development of satellite telemetry (McConnell et al. 1992). Hammond et al. (1993) found grey seals to show great variability in their distribution and movement patterns. It was suggested that mature adults travel long distances probably to seek out good feeding sites in the run-up to the breeding season. Stores of energy in the form of blubber are needed for them to survive fasting during the breeding period (Hammond et al.

1993). The tracking of 14 adult grey seals in the North Sea using Argos Satellite Relay Data Loggers confirmed varied but persistent movement patterns (McConnell et al. 1999). Some seals undertook long range trips (up to 2100 km away) to haul out sites while others made local, repeated trips (20-60 km away) to specific off-shore areas (McConnell et al. 1999). Based on diving data, and the presence of pisciverous seabirds, Thompson et al. (1991) suggested that grey seals forage in these off-shore areas.

In addition, large aggregations of grey seals can be found during the annual moult. Males are thought to moult from January to early March and females from February to April (P. P. Pomeroy, personal communication). Seals also spend long periods of time submerged in shallow waters near the haul-out sites. Thompson et al. (1991) suggested that grey seals engaged in periods of resting dives may use less energy than when resting on land or at the surface. This would be due to lower overall metabolic rate when breathing periodically. Adult seals have been recorded to alternate between resting periods, short duration dives and travelling between haul-outs.

Little is known about dispersal of pups from their birth site. Short and long distance travels have been observed and are thought to be caused by differences in post-weaning mass, weather at time of dispersal, and individual differences (P. P. Pomeroy, personal communication).

Stobo et al. (1990) examined the distributional range of Northwest Atlantic grey seals using bounty and tag recoveries of the 1977-87 cohorts. Two primary breeding areas were identified, the Gulf of St. Lawrence and Sable Island, with direct evidence of transfer of animals between the two groups. Stobo et al. (1990) found the Sable Island seals to have a post-breeding dispersal phase (Jan.-Apr.), followed by a moulting phase (May-June), a summer movement northward (July-Sept.) and finally a return towards the breeding area of Sable Island in late Fall (Oct.-Dec.). In contrast, Gulf of St. Lawrence seals appeared to have a more restricted distribution. However, Stobo. et al. (1990) did suggest that the Gulf of St. Lawrence results could be an artefact of the recovery program and the problems associated by the annual formation and movement of sea ice. Ongoing research using satellite telemetry of the movements at sea of Sable Island adults should in the near future provide us with more information on these distribution and dispersal patterns (C.A. Beck, personal communication). Preliminary examination of satellite telemetry data indicates that adult grey seals use a broad range of areas across the entire Scotian Shelf and the Gulf of St. Lawrence, at scales up to 1000 km during the non-breeding season. There also appears to be a large degree of individual and seasonal variation in the foraging locations used (C. A. Beck, personal communication).

In conclusion, great variation exists amongst individuals in their movements and dispersal patterns. The monitoring of branded animals and the increasing use of radio and ultrasonic transmitters are needed to increase our knowledge of the behaviour of grey seals at sea.

Breeding

Grey seals breed in polygynous colonies. The timing of breeding varies around Britain in a clockwise direction. Pups are born in September-October in the south west, October-November in the west and north of Scotland and finally in late October through to December at the Isle of May, Farne Islands and Donna Nook colonies (Bonner 1981, Anderson 1990). Males are larger than females and compete aggressively with each other for a position among the aggregated females (Amos et al. 1995). A strong site-fidelity is shown by both males and females and older females also show consistency in the time of pupping (Pomeroy et al. 1994, Twiss et al. 1994). Females spend around 18 days ashore during which they give birth to a pup, nurse it and then mate before returning to sea (Bonner 1981). Copulation generally occurs on land shortly before or after weaning. The gestation period is 10-11 months despite the period of active embryonic growth of only 6.5-8 months (Bonner 1981, 1989, Boyd 1983, Anderson 1990). This delay in implantation allows the female to recover from the breeding season before investing in a new pup. The white coated pups weigh about 14 kg and are suckled every 5-6 hours for up to 3 weeks (Bonner 1989). During this period, pups spend most of their time sleeping and keeping out of the way of aggressive females. After lactation, pups enter a postweaning fast and remain ashore for a few more weeks (Bonner 1989).

In a study of grey seal breeding behaviour, Anderson et al. (1975) found that males at colonies are either dominant males that spend 6 to 57 days ashore (mean = 18.79 days for 31 bulls observed) or subordinate ("transient" Boness & James 1979; "roaming" Pomeroy 1996) males that remain ashore for less than four days. Although this division of males is an oversimplification, as suggested by Twiss et al (1998), dominant males can nevertheless be expected to father most pups. However, an analysis of pups born on the island of North Rona, Scotland revealed that dominant males fathered rather few of the large number of full siblings born in successive years (Amos et al. 1993, Amos et al. 1995). Timing of births and site fidelity could in itself account for a certain proportion of pups being full siblings. However, full siblings were also produced by the least site-faithful females. Mate fidelity suggests that grey seals are able to recognise each other and that mating preferentially with previous partners might increase pup survival in certain situations (partner fidelity could reduce pup mortality due to disturbances arising from aggressive interactions between males), an advantage that is yet to be demonstrated (Amos et al. 1995). However, Worthington Wilmer et al. (1999) suggests that the latter preliminary study of paternity might have been biased by sampling methods. Indeed, very few samples were taken from peripheral males and pups belonged to a small sample of study females (including full-sibs) thus reducing further the independence of paternity (Worthington Wilmer et al. 1999). With the analysis of a larger data set, Worthington Wilmer et al (1999) confirmed that a skew in reproductive success does exist with a few males having a higher than average rate of success. However, 54 % and 70 % of pups sampled on North Rona and the Isle of May respectively still could not be allocated a father. The authors then suggested that the deficit of paternities could be explained by an underestimation of the importance of aquatic matings in the grey seal breeding system.

Indeed, an aquatic mating between a mature grey seal bull and a mature grey seal cow has been reported off the Shetland Isles (Watkins 1990) and further observations have been made at the Isle of May colony (personal observations of inshore aquatic matings during 1997 and 1998 breeding seasons). Furthermore, fifteen of the 18 species of phocid seals mate exclusively in the water and, in 12 of these, aquatic mating is associated with the use of ice as breeding habitat (Boness et al. 1993). Given that, uniquely among pinnipeds, grey seals use all three major substrates (land, land-fast ice and free-floating pack-ice) for breeding, the possibility of aquatic mating is not surprising. In addition, Coltman et al. (1999) found that the most successful male harbour seals (*Phoca vitulina*) were of moderate size and suggested that large body size was not such an advantage in the 3-dimension aquatic environment. Therefore, aquatic mating in grey seals could be an alternative mating strategy used by non-dominant males sneaking copulations as females leave the breeding colony (Amos et al. 1993). Alternatively, Worthington Wilmer et al. (1999) suggested that some dominant males maintain some form of territories within tidal inlets. A distinction would need to be made between inshore and offshore matings as the latter would give little opportunity for a male to control access to females and would be more likely to arise through female choice (Worthington Wilmer et al. 1999). Unfortunately, no study has looked at underwater matings directly. In harbour seals however, males have been observed to engage in patrolling, making vocalisations, flipper-slapping displays, inter-male aggression and courtship during shallow dives in the breeding season (Coltman et al. 1997). Van Parijs et al. (1997) suggested a form of lekking where males defend preferred areas near haul-out sites, around female foraging areas or along female transit routes. Therefore, males seem to be influenced by the distribution of food and availability of oestrous females (Coltman et al. 1998) and subsequently adapt their temporal and spatial behaviour patterns according to female distribution and density (Van Parijs et al. 1999).

In conclusion, the study of paternity in the grey seal, using microsatellite analysis, suggests that their mating system is not as clear as previously thought. Further studies with larger data sets are needed to assess the importance of mate fidelity and aquatic matings in this species.

Mortality

Whereas sharks, and to some extent killer whales, are an important cause of death in the north west Atlantic population, man remains the major predator of adult grey seals (Anderson 1990). Most populations of grey seals are now stable or increasing due to the reduction in hunting. Culling is however still used to control population size in Britain, Canada, Norway and Iceland (Bonner 1981).

Mortality of adult grey seals increased in 1988 due to a viral epidemic caused by a virus from the *Morbillivirus* genus (Bonner 1989, Harwood & Reijnders 1988). Little is known about their resistance to parasites and their response to pollutants. Diseases of the respiratory system and alimentary tract, infection of the reproductive tract and trauma from injury are the commonest causes of death in mature grey seals. Baker and Baker (1988) investigated the effects of environment on grey seal pup mortality on the Isle of May. Death was mainly due to starvation, peritonitis, other infectious diseases and injuries following adult aggression. Crowded beaches led to a failure of the mother-pup bond to form and subsequent starvation. Young pups were more likely to suffer from crowded, dirty environments with higher occurrence of infections than older pups. Beach environment and topography therefore influence the cause of death of grey seal pups (Baker & Baker 1988). The survival rate of grey seal pups in their first year is 0.51, and it is 0.95 per annum thereafter (Harwood & Wylie 1987).

Grey seals are therefore at their most vulnerable in their first year of life when they need to survive the postweaning fast and learn to forage successfully.

Grey seal auditory system

Grey seals spend most of the year at sea but come ashore to breed, thus requiring their auditory sensory system to be adapted to both the marine and the terrestrial environment. When leaving the oceans, vertebrates adapted their sensory systems to their new habitat. The middle ear evolved to reduce the impedance mismatch between the atmosphere and the liquid-filled apparatus (Møhl & Ronald 1975). It acts as a transformer that amplifies airborne sounds sufficiently for them to be perceived (Renouf 1991). However, this transformer is unnecessary underwater and is even thought to introduce a hearing impediment (Renouf 1991). In humans, directional discrimination underwater is poor and a loss of sensitivity up to 30 dB is apparent and is assumed to be caused by the inefficiency of the air-adapted middle ear apparatus to conduct sound from water to the cochlea (Møhl & Ronald 1975). These adaptations for terrestrial life have therefore become handicaps for species that require amphibious hearing.

However, behavioural experiments with phocids have shown better sensitivity and sound direction discrimination underwater which could suggest a water adapted auditory system (Riedman 1990). Indeed, Kastak and Schusterman (1999) found the hearing sensitivity of a female northern elephant seal (*Mirounga angustirostris*) to be generally poor, with its greatest sensitivity at 6.3 kHz (43 dB re: 20 μPa). The underwater audiogram was similar to other phocids. The thresholds obtained in water were lower than those in air indicating that elephant seals are adapted for underwater hearing. Nevertheless, in-air hearing via the meatal orifice is better than expected. The closing of this orifice during submergence suggests that the seal must use another method in water than the conventional air conduction mechanism (Ramprashad 1975). This has led to speculation on the nature of the pathway of sound from the two different media to the inner ear. Experiments have shown that sound is transmitted via the meatus in air, and through an area ventral to the orifice in water. This suggests separate inputs for hearing or alternatively an impedance switching mechanism within the inner ear (Møhl & Ronald 1975). Phocids have therefore developed small modifications for hearing underwater and to cope with the increasing pressures they sustain during their deep dives. The outer ear has lost the external pinna and there have been changes in the auricular muscles so that seals can voluntarily shut the external entrance of the meatus. Another distinction between terrestrial mammals and phocids is the presence of cavernous tissue within the middle ear mucosa and the thick wall of the auditory tube. The mass of the ossicles has also been increased and the round window is about three times bigger than the oval window.

This acoustical isolation and the structural changes to the middle ear have provided the phocids with enhanced sound reception and directionality in water. As a result of these modifications, grey seals appear to be better equipped for hearing sounds in water than in air. Unfortunately, little is known about fundamental aspects of hearing in the grey seal. Richardson (1995a) suggested that the hearing abilities of any mammal are a complex function of at least six specific abilities and processes: absolute threshold, individual variation, motivation, frequency and intensity discrimination, localisation, and masking. An understanding of these hearing abilities is important in evaluating the capabilities of mammals to detect various sounds and could give an insight into the communicative functions of different calls. What is known about the hearing abilities of phocids is therefore of relevance to the work in this thesis and is reviewed below, when possible with special emphasis on the grey seal.

The sensitivity to sounds of different frequencies is calculated using behavioural tests carried out on captive and trained animals and illustrated by audiograms. No audiogram exists for the grey seal, but it has been suggested that enough data are available to generalise about phocid hearing abilities, although this generalisation should be treated with care (Richardson 1995a). Therefore, it is believed that for their underwater hearing phocids possess flat audiograms from 1 kHz to ~30-50 kHz, with thresholds between 60 and 85 dB re: 1 μPa, and that their sensitivity is poor above 60 kHz. In-air, the high-frequency cutoff of grey seals is ~20 kHz. Ridgway and Joyce (1975) investigated sensitivity thresholds in grey seals using a auditory evoked potential method (AEP). AEP results suggested that grey seals are most sensitive between 20 and 25 kHz in water and 4 kHz in air. They are also thought to be able to detect frequencies as high as 150 kHz. Comparisons between aerial and underwater hearing levels showed a 15 dB loss of sensitivity in air for harbour seals and a 28 dB loss for harp seals (Riedman 1990). Such measurements have not been made in the grey seal.

Unfortunately very little is known about the frequency and intensity discrimination abilities of pinnipeds (Richardson 1995a). Although hearing abilities have been studied in some phocids, direct measurements for grey seals are still lacking. However, studies with harbour seals provide us with some clues on how vocal communication, whether in air or water, is affected by the detection abilities of the receiver and by the environment the signal travels in. It seems as if neither ringed seals nor harbour seals are able to discriminate frequencies above 60 kHz, and that harbour seals may be more sensitive to descending-frequency than to ascending-frequency swept tones (Turnbull & Terhune 1994). As for intensity discrimination, information only exists for the California sea lion where tones differing in level by as little as 3 dB could be distinguished at 16 kHz (Moore & Schusterman 1976).

Directional hearing and source localisation underwater have only been investigated in the harbour seal. In a two-alternative, forced-choice experiment, a harbour seal had to determine correctly (on 75 percent of presentations) which of two underwater transmitters were producing a 2 kHz tone (Møhl 1968). The threshold found in water appeared to be 3° as opposed to 1° in air for humans and even finer in other animals (Møhl 1968). However, Terhune (1974) found the threshold to be 9°± 4° underwater and 3°± 4° in air. Furthermore, he found harbour seals to have a better ability to localise broadband sounds than narrowband noise and pure tones.

Although audiograms are determined in a quiet environment, the real world is far from quiet whether due to man-made noise or just the ambient background noise. The calculation of critical ratios and masking bands help to estimate the frequencies at which sounds are actually detected and how background noise affects hearing thresholds. Furthermore, the distances at which seals are able to distinguish between signal and noise can be estimated by keeping the source level constant and measuring the distance at which a signal can be detected. It is also important to establish the potential harmful effects of anthropogenic noise on marine mammals. Again, data are absent for grey seals. However, harbour seals indicated a critical ratio ranging from 21 dB to 26 dB when tested in air with sounds of between 2 kHz and 16 kHz. Richardson (1995a) defines the critical ratio as "the amount by which a pure-tone signal must exceed the spectrum level background noise in order to be audible". Underwater, the critical ratio varied from 19 dB to 27 dB when tested between 4 kHz and 32 kHz (Turnbull & Terhune 1990). Renouf (1985) found that a harbour seal mother should not be able to hear a 70 dB aerial pup call when separated by more than 8 meters in relatively low background noise (25 dB). In response, pups follow their mother very closely (Renouf 1984). Reiman and Terhune (1993) further investigated the role of vocal communication in air between a pup and its mother. They observed that on days with optimal experimental conditions (low ambient noise levels, calm and sunny), a pup calling at 90 dB re 20 μPa and 0.5 kHz could be detected by its mother to up to 1 km away and audibly identified up to 140 m away. However, a pup calling at 70 dB re 20 μPa at 0.5 kHz may not be recognised more than 20 m away (Reiman & Terhune 1993). Furthermore, worse experimental conditions will hinder the ability of seals to communicate effectively and reduce the maximum distance of communication to a few meters as found by Renouf (1984).

Geographical variations in vocal repertoire

As previously mentioned, pinnipeds are rather vocal and structural changes to the skull and the inner ear make them well equipped for hearing sounds in water and in air. Studies of their in-air and underwater repertoires have shown some geographical differences in vocalisations. This has been described in detail in five species of pinnipeds: the leopard seal (*Hydrurga leptonyx*), the Weddell seal (*Leptonychotes weddelli*), the northern elephant seal (*Mirounga angustirostris*), the bearded seal (*Erignathus barbatus*) and the harp seal (*Phoca groenlandica*). Microgeographical variation has also been observed in Weddell seals, northern elephant seals and bearded seals. This variation occurs between neighbouring populations that can potentially interbreed. Speculation on the function and cause of geographical variations in repertoire has arisen and is reviewed below.

Leopard seal

Leopard seals are solitary, non-migratory pinnipeds, with a circumpolar distribution throughout the Antarctic packice. Stirling and Siniff (1979) described four underwater vocalisations, recorded near King George Island in the South Shetlands, Antarctica. The calls were classified as low, medium and high frequency double trills and a low hoot followed by a double trill. A later study by Thomas and Golladay (1995) investigated geographic differences in the underwater vocal repertoire of leopard seals between Palmer Peninsula and McMurdo Sound, Antarctica. Nine types of calls were recorded at Palmer Peninsula and five at McMurdo Sound. Calls at Palmer Peninsula showed more components, lower frequency measurements (beginning, ending, maximum, and minimum frequencies), more frequency modulation and both shorter component durations and total call durations than at McMurdo Sound. Thomas and Golladay (1995) concluded that the repertoire differences between the two geographically separate areas suggest two different breeding populations. This may reflect a low probability of encounter between these two populations.

Rogers et al. (1995) described twelve calls, of which nine were new, in a study on captive and free-ranging leopard seals. Of the five calls commonly recorded in Prydz Bay, Antarctica, three were shared with the South Shetland Islands repertoire. The medium double trill was unique to the South Shetland Islands, while the medium single trill and the low descending single trill were only recorded in Prydz Bay. A comparison between these calls and those of Stirling and Siniff (1979) supports Thomas and Golladay's (1995) finding of geographical variation in the repertoire of leopard seals. In all three studies, extensive recordings were made throughout the area suggesting a genuine geographical variation in repertoire rather than an artefact of sampling methods. However, it remains uncertain whether leopard seals have discrete populations and/or whether the variation in underwater calls is due to geographic segregation.

Weddell seal

During the austral spring, Weddell seals congregate at traditional breeding sites around the Antarctic. They show high site fidelity and have a large repertoire of twelve underwater calls subdivided into 34 call types. Thomas and Stirling (1983) investigated the possibility that geographically different vocal repertoires might have evolved due to the high site fidelity and that these differences could be used to identify different populations. Their study showed that the repertoires of underwater vocalisations recorded at McMurdo Sound and at Palmer Peninsula, Antarctica, were different. Although some vocalisations were recorded at both sites, significant structural and usage differences were found. Twenty-one vocalisations were used at Palmer Peninsula against 34 at McMurdo Sound. The former were shorter in duration, tended to be lower in frequency and lacked auxiliary sounds. Mirror-image pairs (i. e. one call ascending in frequency followed by a mirror-image descending form, see Fig. 1 & 2, Thomas & Stirling 1983), vocalisation trios (3 calls given in apparent association) and descending and ascending sweeps were however unique to Palmer Peninsula. Vocalisations that are shared between populations are expected to be more important in social interactions. Thomas and Stirling (1983) concluded that the strong site fidelity at breeding colonies produces enough geographic isolation for different vocal repertoires to develop.

In another study of variations in underwater vocalisations, Thomas et al. (1988) predicted that variations in Weddell seal repertoires would reflect the extent of geographic isolation between breeding populations. A comparison between sounds recorded at East Prydz

Bay near Davis Station, Palmer Peninsula and McMurdo Sound was undertaken. Vocalisations at Davis Station, situated half way between Palmer Peninsula and McMurdo Sound, showed similarities with the other two sites. Sounds from Davis station shared the use of prefixes and suffixes with sounds from McMurdo, and shared the use of both ascending and descending trills and whistles with calls from Palmer Peninsula. However, despite sharing spectral and temporal structures, no calls were identical and all major categories seemed to be variable in acoustic structure at different sites. It was therefore concluded that underwater vocalisations are probably a good indication of the degree of mixing between different populations.

These studies have therefore confirmed the presence of geographic variation in repertoires of Weddell seals around the Antarctic continent and the importance of site fidelity. Morrice et al. (1994) investigated this further by studying microgeographic variation in an attempt to measure the level of site fidelity and the degree of intermixing between populations of the same region. Recordings were made in two fjords of the Vestfold Hills near Davis Station, and separated by only 20 km of ice and land. Despite these short distances, unique vocalisations were recorded at each site, supporting strong site fidelity and low degree of mixing between breeding populations. However, during recordings of Weddell seal calls from seven fjords near Davis, Pahl et al. (1997) found microgeographic differences to be weak and not consistent between sites and years. Furthermore, analysis of tagging data indicated a low site fidelity: 5 out 55 females returned the following year to the same site. Therefore, the presence of dialects needs to be confirmed by assessing the temporal stability of repertoires and the genetic variability between and within populations. Finally, Morrice et al. (1994) also described seven male songs that could have an important role in communication during the breeding season and help to maintain group integrity.

In conclusion, the strong evidence for geographic variation in underwater vocalisations of Weddell seals suggests discrete breeding populations. The degree of overlap between repertoires could indicate the extent of mixing between populations and provide more information on the ecology of the Weddell seal.

Northern elephant seal

Northern elephant seals breed on several islands off the coast of Mexico and California. During the breeding season, from mid-December to March, adult males form dominance hierarchies and compete for access to females. Dominance status is usually maintained by discrete and highly stereotyped threat calls (Bartholomew & Collias 1962, Shipley et al. 1981, Shipley et al. 1986). Consistent differences in these threat vocalisations were found among four island populations (Le Boeuf & Peterson 1969). The mean pulse rate of male vocalisations at San Nicolas Island (2.53 per second) was more than the double the rate of males at Año Nuevo Island (1.02 pulses per second). Mean pulse rates at Isla de Guadalupe and San Miguel Island were intermediate between the two. Variation was also recorded in the mean pulse duration and prolonged terminal pulses (mean duration between penultimate and last pulse). Le Boeuf and Peterson (1969) proposed that these geographical differences might resemble the local dialects seen in birds and humans.

The concept of dialects implies consistency over the years. In order to investigate the reliability of elephant seal dialects, Le Boeuf and Petrinovich (1974, 1975) examined the stability of the Año Nuevo Island threat calls over a 5-year period. Their results showed that the mean pulse rate varied systematically and significantly over the years. It increased every year from 1968 to 1972 at Año Nuevo Island but still remained slower than at all southern colonies. Individual adult males showed a consistency of at least three years. Tagging studies gave evidence that juveniles disperse northward from their birthplace and that mature adults show site fidelity for a rookery. Ninety percent of the seals tagged were 1 month-old newly weaned pups and the majority of resightings occurred when they were between 9 and 16 months of age (Le Boeuf and Petrinovich 1974). Le Boeuf and Petrinovich (1974) then suggested that the yearly increase in pulse rate at Año Nuevo Island was due to immigration from southern populations with faster pulse rates. During the last century, northern elephant seals were reduced to a small population on the remote Isla Guadalupe due to extensive hunting. Le Boeuf and Petrinovich (1974) concluded that the dialects arose as a result of isolation and recolonisation of the former breeding locations and "not to maintain isolation". The dialects are therefore expected to disappear with time if immigration continues. Pulse rate did not vary over the years in a rookery with few immigrants like San Miguel Island.

In conclusion, northern elephant seals dialects arose as a result of isolation and not to maintain or promote isolation (Le Boeuf & Petrinovich 1974, 1975).

Bearded seal

Bearded seals are patchily distributed in low densities throughout the Arctic. They prefer areas of unstable ice and avoid regions of thick shorefast ice (Cleator & Stirling 1990). Little is known about their breeding behaviour and social structures. Cleator et al. (1989) suggested that bearded seals are relatively sedentary and promiscuous. During the breeding season, male bearded seals produce loud frequency modulated trills suspected to be used in territorial and mating behaviour. Cleator et al. (1989) recorded bearded seals' vocalisations at six different locations in the Arctic to investigate geographical variation and the possibility of discrete breeding populations. Their results showed geographic differences in frequency of occurrence of different trill types and in the percentage of single trills versus sequences. There were also site-differences in start frequency, end frequency and duration of trills. The authors suggested that bearded seals may display the same site-fidelity to overwintering areas as shown in Weddell seals. Microgeographic variation in repertoire was also observed and could be explained by the presence of large areas of multiyear ice that may reduce the movements of bearded seals during most of the year (Cleator et al. 1989).

Further study of the geographical variation of bearded seal vocalisations should establish whether these site-differences are due to discrete breeding stocks or isolation following restriction of movement by the ice patterns.

Harp seal

Harp seals are circumpolar in distribution and breed on ice in late February or early March. Møhl et al. (1975) described a rich repertoire of 16 underwater calls. Since then, a few more have been observed and their usage suggested as concerned with breeding behaviour (Terhune et al. 1987, Terhune 1994). Terhune (1994) recorded underwater calls of harp seals from the

Jan Mayen and Gulf of St. Lawrence herds to investigate the possibility of vocal differences. Variation in repertoires would suggest that the two herds are reproductively isolated. The results of this study showed 17 of the calls to be shared often in different proportions between the populations, with the presence of one unique call at each site. However, most of the calls that were shared between the two herds had different pitch, duration and repetition patterns. Variation in the function of the call between herds was proposed as an explanation for these interherd differences. Temporal and within herd stability in call types was also found. Terhune (1994) concluded that these findings and other separate tagging studies suggest that geographical differences in the underwater calls of harp seals exist.

In conclusion, the continuing study of geographical variation in repertoires will provide more information on the social and breeding structure of seal populations. Further research will determine the degree of site-fidelity and the extent of intermixing between populations. Knowledge of the effect of the environment such as the ice patterns is important for our understanding of the ecology of circumpolar populations of seals.

Individual recognition

The previous section has shown how vocalisations could be used to identify discrete populations. It is also well known that certain calls advertise breeding condition as in the bearded seal, and fighting ability as in the elephant seal. In dimorphic species such as the elephant seal and the northern fur seal, marked frequency differences are found between male and female vocalisations, with those of the cows higher (Poulter 1968). Studies of individual recognition have focused on male vocal threats in male-male competition and on reproductive displays. It has been suggested that some threat calls are learnt and can assist individual seals to recognise their own intraspecific social group at a particular location (Shipley et al. 1981, Shipley et al. 1986). However, although the acoustic structure of calls may allow for individual recognition, it nevertheless remains to be advantageous to the animal to transmit its identity. In many species of birds and mammals, individually distinct vocalisations advertise that a territory is occupied by a particular individual (eg. great tits, *Parus major*, see Catchpole & Slater 1995 for review). The ability to discriminate between individual vocalisations allows an individual to balance the costs and benefits of engaging in agonistic interactions. Advertising one's identity therefore becomes adaptive when time and energy is saved by not fighting individuals who may not pose any threat.

Furthermore, individual recognition does also appear to play an important role during separations of the mother-pup pair in crowded rookeries (e.g. Riedman & Le Boeuf 1982, Roux & Jouventin 1987). Individual differences making recognition possible may arise through genetic differences or complex vocal learning. Evidence for individual vocal recognition is reviewed below to assess its distribution and function in pinnipeds.

Northern elephant seal

During the breeding season, mature male elephant seals engage in frequent confrontations over access to females. Fighting is rare and disputes are most often settled by threat displays. Bartholomew and Collias (1962) suggested that the stereotyped threat call is used to establish dominance status. Individual variation in threat calls might then provide vocal signatures that could be used for individual recognition. Shipley et al. (1981) recorded the threat calls of individual elephant seal bulls during one breeding season to investigate their range and variability. Two distinct male calls were described: the clap threat and the burst threat. The parameters for assessing range and reliability of differences between individual elephant seal bulls were: call type, spacing of pulses within calls, addition of snorts to calls, pulse rate of calls, and number of pulses in calls. A comparison between the threat calls of dominant and subordinate animals led the authors to suspect that vocal signatures could be used to establish dominance status. Further data are necessary to confirm this hypothesis. However, the study of Shipley et al. (1981) did suggest that elephant seals recognise each other on the basis of vocal differences. Rather than using a specific parameter of the threat call, which would assume a clear relationship, yet to be confirmed, between call character and dominance status, it was hypothesised that bulls associate distinctive characteristics of a threat call with an individual. Recognition would then be based on experience. These features, including complex patterning of individual claps or burst calls, have been measured to be relatively stable over time and within individuals, and thus to provide the necessary differences for individual recognition. The threat calls of juveniles were also found to be more variable than the those of mature adults.

In a later study, Shipley et al. (1986) recorded the threat vocalisations of juvenile and adult elephant seals to investigate the development of adult vocal patterns. The ability to advertise dominance status through vocal signatures would clearly be advantageous to dominant males, since a vocal threat would be sufficient to displace a subordinate male. A greater variability in juvenile and subordinate bull calls might be expected as this would disguise their identity (Shipley et al. 1986). Juvenile calls had previously shown to lack a structural pattern and sound strikingly different from adult calls (Bartholomew & Collias 1962). A comparison of call characteristics across different age groups led to the hypothesis of a developmental sequence where juveniles would gradually acquire the characteristics of adult threat calls during adolescence. Shipley et al. (1986) demonstrated that juvenile elephant seals go through a transitional stage during development and later acquire the stability and characteristics of the adult repertoire. They also concluded that elephant seal bulls present the necessary acoustic parameters for individual recognition. Whether elephant seals use these vocal signatures in their social interactions remains uncertain.

By contrast, mother elephant seals produce a high-pitched vocalisation to attract their pup ("pup attraction call", Bartholomew & Collias 1962; "mother primary call", Insley 1992). Females of high dominance status often drive subordinate females away causing them to be momentarily separated from their pups. The movement of males through the colony, the scarcity of good breeding sites and severe weather are factors that all lead to frequent mother-pup separations (Riedman & Le Boeuf 1982). Lost pups can suffer serious injuries from other females so it is essential that the mother-pup pair is quickly reunited. Bartholomew & Collias (1962) observed that elephant seal pups vocalise in conditions likely to be of distress or discomfort. Both pup calls and female calls were found to vary highly between individuals, exhibiting sufficient stereotypy to allow them to be used in individual recognition ("offspring primary call", Insley 1992). Responses to the pup calls are apparent in the behaviour of the females and, as expected, evoke the most vigorous response from their own mother. In contrast, males seem to completely ignore these vocalisations (Bartholomew & Collias 1962).

A female barks directly to her pup whenever it calls, but also to maintain a vocal contact when it is silent. Riedman & LeBoeuf (1982) found that females attempted to reunite with their pup following a separation 66% of the time (n=97), that pups attempted to reunite with their mother 14% of the time (n=21) while both mother and pup actively attempted to reunite 19% of the time (n=28). Therefore, calling between mother and pup is thought to function to inform her of the location and condition of the pup and as a way to keep the pair together in the densely populated rookery. Recognition is mutual even though mothers take the more active role.

Harbour seal

Harbour seals congregate in mixed breeding groups on isolated islands, rocky beaches and intertidal sandbars (Bigg 1981). Although no direct observation has been made, harbour seals are assumed to mate aquatically (Coltman et al. 1998). Van Parijs et al. (1997) suggested that the male mating system may be a lek. Indeed, adult males have been found to engage in stereotypic diving and acoustic displays thought to be used in defending preferred areas and/or as an advertisement to females (Hanggi & Schusterman 1994, Van Parijs et al. 1997). Adult males produce five underwater vocalisations, described as groans, grunts, creaks, roars and bubbly growls (Hanggi & Schusterman 1994). Nicholson & Harvey (personal communication) found that a primary social function of underwater vocalisations is display among males to establish and maintain dominance hierarchies. They then observed that high ranking males have longer roars, roar while other males maintain passive muzzle contact and engage in flipper splashing.

Hanggi and Schusterman (1994) recorded underwater vocalisations of male harbour seals during the breeding season at Point Lobos State Reserve, California, to investigate individual variation in calls. Although only male vocalisations were recorded, the sampling area did however contain seals of all age classes and both sexes. Furthermore, recordings were made around haulouts rather than in areas where displays were thought to occur. It was then hypothesised that male harbour seals use acoustic displays in male-male competition to advertise their dominance status without having to engage in fighting. It was also suggested that the vocalisations are used to attract females. This study gave evidence of individual variation in underwater vocalisations. Roars varied in mean frequency, and minimum and maximum frequency, between individuals but not within individuals. In contrast, duration showed intra- and inter-individual differences and was thus excluded as a reliable parameter for individual recognition. Hanggi and Schusterman (1994) concluded that the variation in males' calls necessary for individual recognition exists but that further studies are needed to determine their function.

Renouf (1984) investigated the call of the harbour seal pup and its role in the mother-pup bond. This study showed that pups have individually distinct calls distinguishable by their fundamental frequency and harmonic pattern. Pup calls, brief sheep-like bleats, are restricted to the lactation period and can be transmitted simultaneously in air and in water when the pup's head is in air. Renouf (1984) suggested that pup calls convey enough information for the mother to monitor precisely her pup's location by comparing the arrival times of the in-air and in-water vocalisations. However, females do not apparently produce a "pup attraction call" as observed in other seal species (Schusterman et al. 1970).

Renouf (1984) found the aerial and underwater versions of the pup call to differ significantly in certain physical characteristics such as the frequency of harmonics and intercall intervals. Pup calls also varied in intensity depending on the motivational state of the pup and their awareness of their mother's location. In a later study, Renouf (1985) demonstrated the discrimination ability of a captive adult female using playbacks from different pups. Perry and Renouf (1988) suggested that it is the information in the pup vocalisations that informs the female of an increasing risk of separation.

Genus Arctocephalus and genus Zalophus

Individual vocal recognition has been investigated in four species of *Arctocephalus*: the Subantarctic fur seal (*Arctocephalus tropicalis*), the New Zealand fur seal (*Arctocephalus forsteri*), the South Australian fur seal (*Arctocephalus pusillus doriferus*) and the Galapagos fur seal (*Arctocephalus galapagoensis*). It has also been investigated in two races of *Zalophus*: the California sea lion (*Zalophus californianus*) and its Galapagos subspecies (*Z. c. wollebaeki*).

Individual vocal recognition was also suggested during a preliminary study of the vocal behaviour of the South American fur seal (*A. australis*).

Subantarctic fur seals breed in high-density colonies within which most males hold territories. Roux and Jouventin (1987) recorded the territorial calls of males on Amsterdam Island to investigate individual recognition between neighbouring males. The duration, two frequencies of highest amplitude and the pattern of the calls showed sufficient inter-individual variability to be used in individual recognition. Roux and Jouventin (1987) performed playback experiments and demonstrated that males are indeed able to discriminate between a neighbour's territorial call and an unknown call. A male produces fewer agonistic reactions to a neighbour than to a call from a male from a different colony. Once territories have been determined males show habituation to their neighbour's call. In the same study, Roux and Jouventin (1987) investigated individual recognition between female and pup Subantarctic fur seals. Their observations suggested that a pup is not able to discriminate visually between females. If its mother stops producing her pup attraction call, the pup will wander around the colony and will often fail to localise her. Females may also not rely on visual cues as the appearance of their pup often changes due to being wet and/or muddy. Thus, visual cues do not seem to play an essential role in the recognition process. Playback experiments confirmed that vocalisations play the most important role in mother-pup recognition and that recognition is mutual even though the mothers play the most active part. To date, no information on underwater vocalisations has been presented.

Stirling and Warneke (1971) compared the structure of male airborne vocalisations of the South Australian fur seal and the New Zealand fur seal. The South Australian fur seal produces two calls associated with male-male interactions: the bark and the guttural threat. As well as these two vocalisations, the New Zealand fur seal emits a low-intensity threat and a full threat call. Stirling and Warneke (1971) measured consistent inter-individual differences in the structure of threat calls. As a result of these observations, they suggested that these calls are used in advertising dominance status and individual identity. Furthermore, Stirling (1971) reported that female South Australian fur seals produce one of two pup-attraction calls to find their pup after a separation. The most common call is a high pitched whine while the other is a low pitched monotonic call. Pups answer with a high pitched call that becomes deeper and stronger with age (Stirling & Warneke 1971).

Trillmich (1981) carried out field observations and playback experiments on the Galapagos fur seal and the Galapagos sea lion. Intense calling from the pup and the mother immediately after birth suggested early vocal recognition. The rapid response of pups to their mothers' attraction calls and the aggressive behaviour of females towards strange pups strongly supports mutual mother-pup vocal recognition.

Gisiner and Schusterman (1991) observed California sea lion mother-pup reunions at a rookery on San Nicolas Island, California. Observations of focal females showed that mothers are able to discriminate between pup calls and move towards them to reunite. Pups were capable of identifying their mother's attraction call and played a greater role in the reunion as they grew older (Schusterman et al. 1992). Reunions without female movement increased as the lactation period went on. Evidence of mother-pup vocal recognition was further confirmed by a playback experiment carried out by Hanggi (1992). A female California sea lion responded consistently to the recorded vocalisations of her pup and ignored the calls of an unrelated pup. The female moved towards the recorder/speaker even though she was in physical contact with her pup, thus implying that vocal cues are important in the mother-pup recognition system in California sea lions.

Trillmich and Majluf (1981) described the vocalisations of the South American fur seal in Peru. They found greater between than within individual variation in the frequency of the female pup attraction call (PAC). Similar variation was found for the calls of immatures and pups suggesting the possibility of individual recognition. However, these findings are based on only an hour of recordings so further studies are needed in this species to confirm these preliminary results.

Therefore, the vocalisations of some pinnipeds are similar in air and in water. For example, the different species of fur seals, the Steller sea lion, the California sea lion and other otariids such as the South American, the Australian and New Zealand sea lions are all capable of barking under water without emitting any bubbles (Poulter 1968). In addition, they can occasionally produce clicks in air similar to the ones recorded underwater (Poulter 1968).

Walrus

Finally, male walruses (*Odobenus rosmarus*) exhibit a particular display pattern in the vicinity of conspecifics of all-ages during the breeding season. The acoustic part of the display is stereotyped and repetitive. It has been defined as a song due to its structural characteristics and territorial and courtship functions (Ray & Watkins 1975). Stirling et al. (1987) recorded the stereotyped vocalisations of male Atlantic walruses (*O. r. rosmarus*) to investigate whether these songs display individuality. Stability over the years was suggested after a male was recorded in two separate years and exhibited identical structure in its call. This study showed a high level of consistency within individual vocalisations and variability between adult male calls suggesting that they could be used in individual recognition during the breeding season.

Female walruses give birth to a single calf in the spring, then nurse and protect it for two years. Since their sense of vision is poor, olfactory and auditory signals are more likely to play an important role in communication. Kastelein et al. (1995) recorded airborne vocalisations of two captive Pacific walrus pups (*O. r. divergens*). The vocalisations differed between the two pups. However, both pups did produce similar alarm or surprise signals when frightened by new objects, suggesting a possible species-specific function to this call. Furthermore, the caretakers were able to recognise both pups by their sounds. The authors then suggested that pup calls may be individually distinctive and/or probably age-related and that these could be used in maternal recognition.

Aims of this thesis

In conclusion, this brief review shows that, despite extensive research in the last 50 years, the functions of in-air and underwater vocalisations are unclear for many species of pinnipeds (Table 4 & 5). This is especially and surprisingly the case for the grey seal. In Chapter 2, I describe the in-air and underwater repertoire of grey seals from an eastern Atlantic population during the breeding season. I then compare the underwater vocalisations with those recorded at a reproductively isolated population from the western Atlantic and finally suggest some possible functions for these calls on the basis of behavioural observations. Chapter 3 describes the seasonal and diurnal variation in underwater vocalisations. It also investigates the possibility of associations between certain call types. In Chapter 4, I record and analyse sonagrams of pup vocalisations to evaluate individual differences at the Isle of May breeding colony, Scotland. I document behavioural observations of fostering behaviour and then use playback experiments to investigate mother-pup vocal recognition. Chapter 5 is another study of mother-pup vocal recognition but this time, based on playback experiments carried out on Sable Island, Nova Scotia, Canada, a population reproductively isolated from the one on the Isle of May. Finally, Chapter 6 looks at some of the questions that remain to be investigated, and gives suggestions on how they can be answered.

Table 4: Phocids: Research review

SPECIES	REPERTOIRE SIZE	CALL TYPES	DIURNAL VARIATION	SEASONAL VARIATION	ANNUAL VARIATION	GEOGRAPHICAL VARIATION	INDIVIDUAL RECOGNITION	MATERNAL RECOGNITION
Hawaiian monk seal *Monachus schauinslandi*	8 +[1, 2]	In-air	?	?	?	?	?	No[3]
Leopard seal *Hydrurga leptonyx*	4-12[4, 8]	Underwater	Yes[5]	Yes[6, 9]	No[8]	Yes[4, 7, 8]	?	?
Crabeater seal *Lobodon carcinophagus*	1[4]	Underwater	Yes[5]	Yes[4]	?	?	?	?
Ross seal *Ommatophoca rossi*	1-2[10]	In-air and underwater	?	?	?	?	?	?
Weddell seal *Leptonychotes weddelli*	12[11, 12, 13, 14, 15, 16]	Underwater	Yes[18]	Yes[18]	?	Yes[13, 16, 17, 19]	?	?
Northern elephant seal *Mirounga angustirostris*	Large[20, 29]	In-air	Yes[27]	?	No[22]	Yes[21, 22, 24]	Yes[25, 27, 28]	Yes[23, 26, 29]
Bearded seal *Erignathus barbatus*	6[30, 31]	Underwater	Yes[31]	Yes[30, 31, 32]	?	Yes[31]	?	?
Hooded seal *Cystophora cristata*	3[34, 35, 36]	In-air and underwater	?	?	?	?	?	Not in-air[36]
Harbour seal *Phoca vitulina*	5[39, 42]	Underwater and in-air	?	Underwater[39]	?	?	Underwater[42]	No[33] Yes[37, 38, 40, 41]
Harp seal *Phoca groenlandica*	15-19[43, 47, 48, 49]	Underwater	No[47]	Yes[45]	No[46]	Yes[49]	?	No[44 ,50, 51]
Ribbon seal *Phoca fasciata*	2[52]	Underwater	?	Yes[52]	?	?	?	?
Ringed seal *Phoca hispida*	4[53, 54]	Underwater and in air	?	Underwater[53]	?	?	?	?
Spotted seal *Phoca largha*	3[2]	In-air	?	?	?	?	?	No[55]
Grey seal *Halichoerus grypus*	7-12[56, 57, 58, 59, 60, 61, 62, 63] This study	In-air and underwater	No[61] This study	Underwater[61] This study	?	?	?	Suggested[57] This study

[1] Eliason et al. 1990, [2] Miller & Job 1992, [3] Job et al. 1995, [4] Stirling & Siniff 1979, [5] Thomas & DeMaster 1982, [6] Cleator & Stirling 1990, [7] Thomas & Golladay 1995, [8] Rogers et al. 1995, [9] Rogers et al. 1996, [10] Watkins & Ray 1985, [11] Watkins & Schevill 1968, [12] Thomas & Kuechle 1982, [13] Thomas & Stirling 1983, [14] Thomas et al. 1983, [15] Terhune et al. 1994, [16] Pahl et al. 1997, [17] Thomas et al. 1988, [18] Green & Burton 1988, [19] Morrice et al. 1994, [20] Bartholomew & Collias 1961, [21] Le Boeuf & Peterson 1969, [22] Le Boeuf & Petrinovich 1974, [23] Petrinovich 1974, [24] Le Boeuf & Petrinovich 1975, [25] Shipley et al. 1981, [26] Riedman & Le Boeuf 1982, [27] Shipley & Strecker 1986, [28] Shipley et al. 1986, [29] Insley 1992, [30] Ray et al. 1969, [31] Cleator et al. 1989, [32] Cleator & Stirling 1990, [33] Burns et al. 1972, [34] Schevill et al. 1963, [35] Terhune & Ronald 1973, [36] Ballard & Kovacs 1995, [37] Renouf 1984, [38] Renouf 1985, [39] Ralls et al. 1985, [40] Perry & Renouf 1988, [41] Reiman & Terhune 1993, [42] Hanggi & Schusterman 1994, [43] Møhl et al. 1975, [44] Terhune et al. 1979, [45] Watkins & Schevill 1979, [46] Terhune & Ronald 1986, [47] Terhune et al. 1987, [48] Miller 1991, [49] Terhune 1994, [50] Kovacs 1995, [51] Miller & Murray 1995, [52] Watkins & Ray 1977, [53] Stirling 1973, [54] Kunnasranta et al. 1996, [55] Burns et al. 1972, [56] Schusterman et al. 1970, [57] Fogden 1971, [58] Schneider 1974, [59] Oliver 1977, [60] Boness & James 1979, [61] Asselin et al. 1993, [62] Caudron et al. 1998, [63] McCulloch et al. chapter 5.

Table 5: Otariids: Research review

SPECIES	REPERTOIRE SIZE	TYPE OF CALLS	DIURNAL VARIATION	SEASONAL VARIATION	ANNUAL VARIATION	GEOGRAPHICAL VARIATION	INDIVIDUAL RECOGNITION	MATERNAL RECOGNITION
California sea lion *Zalophus californianus*	7 [1,4]	In-air	?	?	?	?	?	Yes [1, 2, 3]
Galapagos sea lion *Z. californianus wollebaeki*	2 + [4]	In-air	?	?	?	?	?	Suggested [4]
South American sea lion *Otaria flavescens*	4 [5]	In-air	?	Yes [5]	?	?	?	Suggested [5]
South American fur seal *Arctocephalus australis*	Large [6]	In-air	?	?	?	?	?	Yes [6]
Galapagos fur seal *A. galapagoensis*	2 + [4]	In-air	?	?	?	?	?	Suggested [4]
Subantarctic fur seal *A. tropicalis*	?	In-air	?	?	?	?	Yes [7]	Yes [7]
New Zealand fur seal *A. forsteri*	6 [8, 9]	In-air	?	?	?	?	Suggested [8]	Yes [8]
Antarctic fur seal *A. gazella*	5 [8]	In-air	?	?	?	?	?	Yes [8]
South Australian fur seal *A. pusillus doriferus*	4 [8]	In-air	?	?	?	?	Suggested [8]	Yes [8]
Alaska fur seal *Callorhinus ursinus*	4 [10, 11]	In-air	?	?	?	?	?	Suggested [10]

Walruses:

Atlantic walrus Odobenus rosmarus rosmarus	Complex, large [14]	In-air and underwater	?	Yes [12]	No [13]	?	Yes [13, 14]	?
Pacific walrus Odobenus rosmarus divergens	Age-related [15]	In-air and underwater	?	?	?	?	?	Suggested [15]

[1] Peterson & Bartholomew 1969, [2] Gisiner & Schusterman 1991, [3] Hanggi 1992, [4] Trillmich 1981, [5] Vaz-Ferreira 1975, [6] Phillips 1998, [7] Roux & Jouventin 1987, [8] Stirling & Warneke 1971, [9] Stirling 1971, [10] Bartholomew 1959, [11] Insley 1992, [12] Ray & Watkins 1975, [13] Stirling et al. 1983, [14] Stirling et al. 1987, [15] Kastelein et al. 1995.

Chapter 2

In-air and underwater vocal repertoire of grey seals

Abstract

In-air and underwater vocalisations were recorded during the breeding season on the Isle of May, Scotland, in October and November of 1997 and 1998, and on Sable Island, Nova Scotia, Canada, during January of 1999. Underwater calls were also recorded in Scotland during mid-September 1997 and late March 1998 at the haulout site of Abertay Sands. Six call types were identified for the in-air repertoire and a further ten call types for the underwater repertoire. Underwater call types 1, 2, 4 and 5 accounted for over 70% of all calls recorded. A comparison between in-air and underwater vocalisations suggested that call types B and 5, and A and 1, may be the same call but used in different mediums. Furthermore, call type 1 is thought to be produced by males only and call type 5 by females only. The usage and acoustic structure of type 1 calls also suggested that this call might contain identity and dominance status clues that may be used in individual recognition. Finally, the function of certain call types based on behavioural observations of male-female interactions was suggested. However, further studies in which the caller is identified, thus providing clues on the function of each call, are essential for an understanding of the acoustic communication of grey seals.

Introduction

Recordings of pinniped vocalisations have been collected and described anecdotally since the early 1960's, but it is only since the early 80's that detailed descriptions and the investigation of individual recognition, and of seasonal and geographical variation have been made. The number of studies increased with the development of sophisticated listening and recording equipment and when it became apparent that acoustic communication may have an important role in the reproductive behaviour of pinnipeds. It was also thought that sounds could be used for identifying discrete breeding stocks and for locating some of the more elusive polar species. Otariids clearly use pup attraction calls and female attraction calls to enable a successful reunion of the mother-pup pair after a separation in their crowded colonies (eg. South Australian fur seal, *Arctocephalus pusillus doriferus*, Stirling & Warneke 1971; California sea lion, *Zalophus californianus*, Gisiner & Schusterman 1991). Male northern elephant seals use vocal threats to communicate their dominance status (Bartholomew & Collias 1962). Furthermore, acoustic communication may be essential not only to defend a harem but where finding a sexually receptive mate during the often brief breeding season is difficult. Mature male bearded seals (*Erignathus barbatus*) produce an underwater song consisting of 6 types of narrow-band, frequency-modulated trills, that are probably only used during the spring courtship season (Cleator et al. 1989). Leopard seals (*Hydrurga leptonyx*) engage in a pattern of alternate underwater singing and breathing, during which males are believed to advertise their presence and females their sexual receptivity (Stirling & Siniff 1979; Rogers et al. 1996). Although the function of in-air and especially underwater vocalisations remains largely speculative, spectrograms and estimation of repertoire size now exist for most phocids.

Three types of in-air vocalisations have been described for northern elephant seal males, snort, clap-threat and roar, while females produce a threat and an attraction call (Bartholomew & Collias 1962). To date, no underwater vocalisations have been recorded in this species (Fletcher et al. 1996). The Ross seal, however, produces in-air "chugging" sounds and "siren" calls, as well as underwater calls. The latter are similar to the in-air calls although they have a greater range of frequencies and often more harmonics (Watkins & Ray 1985). Harp seals

(*Phoca groenlandica*) have the largest underwater repertoire, with 19 calls recorded during the breeding season in the Gulf of St. Lawrence (Terhune 1994). Furthermore, Weddell seal (*Leptonychotes weddelli*) sounds can be heard above and below the ice. They have been classified into 13 broad call categories, many with subdivisions, from booming territorial sounds to birdlike chips and whistles (Pahl et al. 1997). However, despite extensive study of the ecology, physiology and breeding patterns of grey seals (*Halichoerus grypus*), acoustic communication has been the focus of relatively few studies, such as those of Asselin and Hammill (1993) and Caudron et al. (1998) for example.

Grey seals are sexually dimorphic pinnipeds which breed in polygynous colonies. They are found in three reproductively isolated populations in the north west Atlantic, the north east Atlantic and the Baltic sea (Bonner 1981). The majority of the north east Atlantic population breeds from September to December on isolated islands or beaches around the coast of the British Isles. Females spend around 18 days ashore during which they give birth to a pup, nurse it and then mate before returning to sea. Copulation has been observed on land shortly before or after weaning (Anderson 1990).

Grey seal vocalisations have been anecdotally described by Fogden (1971), Anderson (1978) and Oliver (1977). Schneider (1974) provided the first description of in-air calls while Schusterman et al. (1970) provided the first sonagram of an underwater call. This latter study involved the recordings from a male and a female of about 6 or 7 months old that had been captured as pups and kept in a concrete pool. It was then over twenty years before a study focused on free swimming grey seal vocalisations. In 1993, Asselin and Hammill discovered ice-breeding grey seals in the Gulf of St. Lawrence to be rather more vocal underwater than earlier thought. More recently, Caudron et al. (1998) analysed the acoustic structure and individual variation of pup calls at a breeding colony in the Barents sea. Nevertheless, studies of the acoustic communication of grey seals remain sparse.

However, recent studies of the mating behaviour of grey seals on land have led to a renewed interest into their vocal communication. Indeed, a discrepancy between the observational measures of male mating success and paternity, as determined by DNA fingerprinting (Amos et al. 1993, Amos et al. 1995) has been found. In principle on the breeding beaches, dominant males exclude subordinates and so increase their chances of mating with a female when she comes into oestrus. Dominant males are therefore expected to be highly successful and father most pups (Amos et al. 1993). Surprisingly, they did not father as many pups as expected. Fertilisation outside the colony has been suggested to explain the disparity between the observations and the DNA data (Worthington Wilmer et al. 1999). One possible explanation is that significant matings occur in the sea below the surface around the breeding beaches and that underwater vocalisations may be used as a display to competing males and/or to attract females. Support for this idea was found when underwater copulations were observed during the breeding season of October 1996 off the island of Faray, Orkney Islands, Scotland (McCulloch, Slater, Janik, Fedak & Loyer, unpublished data). In addition, males were seen to produce wave-like body movements while producing water-borne calls, similar to the ones described by Boness (personal communication). Finally, underwater copulations and calls were also observed as part of this study during the breeding seasons of October-November 1997 and 1998 off the Isle of May, Scotland.

The relationship between the underwater vocalisations and social behaviour of grey seals remains speculative. Schneider (1974) described three types of grey seal underwater calls: wails, moans and clicks. Calls were recorded at the New York Aquarium, Brooklyn, N. Y., and off the Basque Island, Nova Scotia, Canada. Schneider suggested they were used in warning, arousal and perhaps aggression. Asselin and Hammill (1993) recorded seven types of vocalisations in the ice breeding grey seals of the Gulf of St. Lawrence, Canada. They observed changes in the vocal repertoire during the progression of the breeding season but were unable to relate specific calls to particular behaviours. The difficulty of identifying the caller and observing the associated behaviour leads to speculation on the function of these underwater vocalisations. These calls might be used in mate attraction and/or function in territorial defence.

In this study, I describe the in-air and underwater repertoires of grey seals at the Isle of May colony during the breeding seasons of 1997-1998, and the in-air vocalisations of adult grey seals on Sable Island, Nova Scotia, during the breeding season of 1999. I also compare the underwater repertoire to the one previously reported for ice-breeding grey seals. The Isle of May grey seals belong to the north-east Atlantic stock and form a reproductively isolated population from the Canadian grey seals, and hence may show differences in their underwater repertoires. It has been suggested that the eastern and western populations have been isolated for around the last 100 000 years (Davies 1957), which could explain morphological and behaviour differences between them. This chapter therefore provides new and comprehensive information from an acoustical survey at a new location. The recent development of sophisticated listening, recording and analysing equipment is such that sonagrams of much better quality are now possible. The aim is therefore to produce clear sonagrams of all types of vocalisations for past and future comparison with other colonies. This data also generates important questions on the function of underwater vocalisations and suggests further testing.

Methods

Study animals, sites and data collection

The major part of this study was conducted on the Isle of May (56°10'N, 2°35'W), a small uninhabited island (2 x 0.5 km) in the Firth of Forth, Scotland. A colony of grey seals breeds on the island during October and November with an annual production of c 1 400 pups (Hiby et al. 1996). Females come ashore, give birth to a single pup and mate before returning to sea. Pups are weaned after 14-18 days. The mean birth date for 1997 was 1 November (C. D. Duck, Sea Mammal Research Unit, personal communication).

In-air vocalisations were recorded during the breeding seasons of 1997 and 1998 on a Marantz CP430 tape recorder (frequency response, 20 Hz to 18 kHz) using a Sennheiser ME80 gun microphone with integral windshield. Recordings were made at East Tarbet, Kirkhaven, Kaimes and Rona (Figure 1). The aim was to produce examples of clear sonagrams of grey seal in-air vocalisations. To achieve this, recordings were made on calm sunny days by simply approaching animals on the periphery of the colony which were seen to be vocalising. The topography of the Isle of May is such that one is able to approach peripheral animals without causing unnecessary disturbance to the colony. A number of vocalisations for each call type were recorded so as to allow a quantitative description. For most call types, vocalisations were recorded from more than one individual to provide information on individual variation.

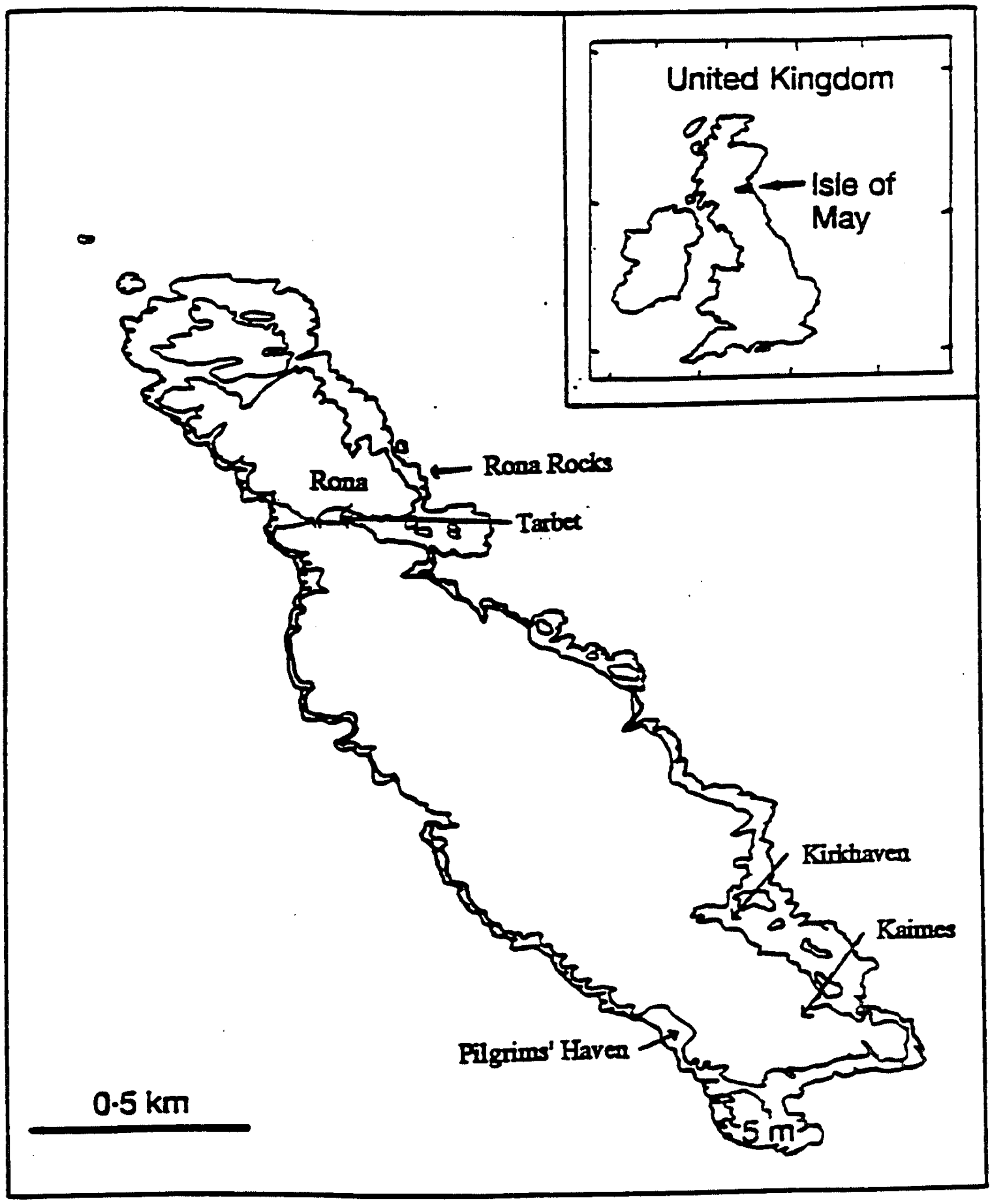


Figure 1. Location of study sites on the Isle of May, Scotland

However, as it was noted that one particular male produced a vocalisation similar to one heard underwater, this vocalisation was also recorded from him for comparison with the underwater call.

Underwater recordings were first carried out at Kirkhaven, the harbour area of the Isle of May. These recordings were made at the very start of the breeding season in 1997 on a Marantz CP430 tape recorder using an AQ18 hydrophone (frequency response, 1 Hz to 10 kHz, n= 492 calls, 3-5 October, 810 minutes of recording). The hydrophone was mounted on trailer tyre (Figure 2) and placed on the end of the lower pier. The timing of these recordings (i.e. early in the season) was such that only four males were seen in the area at any one time and females were only transient through the site.

The main recordings were made at East Tarbet (Figure 3a & 3b), a channel that divides the island along a north-south axis at high tide and allows seals to move between west and east coasts. Underwater vocalisations were recorded between 6 October and 25 November 1997 (n= 12 days) and 11 October and 24 November 1998 (n= 17 days). Thirty six and 51 hours of recordings were made for 1997 and 1998, from which 1 995 and 2 849 series of vocalisations were analysed respectively. This site provides easy access to the island tops and is constantly used by females going to and from the sea. Interactions between females, males and pups were therefore frequent due to the continual movement of seals in this area. The hydrophone was deployed at the start of the breeding season (early October in both seasons) before any pups were born to avoid disturbance to breeding females. It was then removed at the end of November just prior to departure off the island. The hydrophone was fixed underwater to a rubber tube attached to a leaded trailer tyre (Figure 2). Its depth varied with tide levels. The hydrophone cable was laid on the sea floor through the intertidal area and up to the hide situated 20m above the study site. As a result of damage caused by seals and mice during the first season of recordings, the cable was subsequently threaded through a standard garden hosepipe for protection. Weights were then needed to keep it on the sea bed. Due to the tidal nature of this area, recordings were only possible when the hydrophone was submerged at high tide. Therefore, underwater vocalisations were recorded for 90 minutes around the peak high tide. Numbers of males and females in the water were recorded at regular 10 min intervals

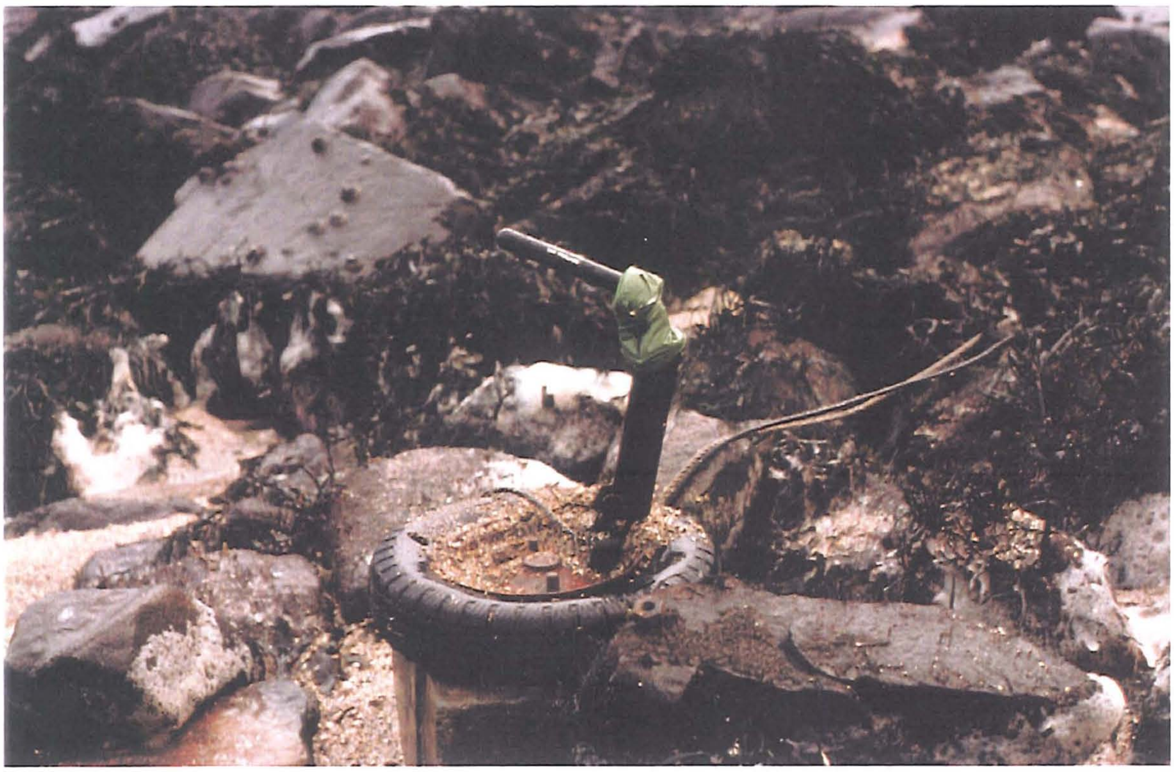


Figure 2. Hydrophone set-up.

Figure 3a. East Tarbet at low tide (note hydrophone in centre of picture fixed by ropes onto large boulder).

Figure 3b. East Tarbet at high tide.

throughout the recording sessions. The mean number of seals per session was then calculated. Notes were taken when vocalisations were followed or preceded by surface behaviour. Unfortunately, this provides limited anecdotal behavioural observations due to half of the sessions being made in darkness and the often heavy surf. No other marine mammal was observed around the island during this period so that the assumption was made that the recordings are from grey seals. Although this assumption is valid for previously documented calls (other papers, behavioural observations and underwater video footage), it is however not valid for newly described calls. These calls will nevertheless be described below but further data is needed to confirm that they are produced by grey seals and not by other marine organisms.

In addition to the Isle of May recordings, underwater vocalisations of grey seals were recorded on 11, 12 and 17 September 1997 and 25 March 1998 at the haul-out site of Abertay sands, Scotland (Figure 4). This totalled 585 minutes of daytime recording. The number of vocalising seals and their distance from the hydrophone were unknown.

In-air recordings were also made in 1999 at the breeding colony at Sable Island (45° 55' N; 60° 00' W), Nova Scotia, Canada (Figure 5). Sable Island is a crescent shaped, vegetated sandbar (42 x 1.5 km), located 296 km south east of Halifax. A colony of grey seals estimated at 100 000 in 1999 breeds on the island from mid-December to early February with an annual production of c 25 000 pups (W. D. Bowen, personal communication). The same equipment was used as on the Isle of May except that the microphone was fitted with an additional two core windshield made of silk and 3/4 inch wire mesh to compensate for constant 25 knot winds. Recordings of pup vocalisations were made in preparation for mother-pup vocal recognition playback experiments (see chapter 5). During this recording session, it was noted that an individual female produced vocalisations that resembled underwater calls previously recorded during the 1997 breeding season on the Isle of May. Consequently, recordings were made from this individual female during a calm sunny day for comparison with the underwater vocalisation. In addition to this female vocalisation, males were heard to produce particular calls specific to the western Atlantic population of grey seals. To add to the survey of grey seal vocalisations, recordings were made on a calm and clear night which provided ideal conditions

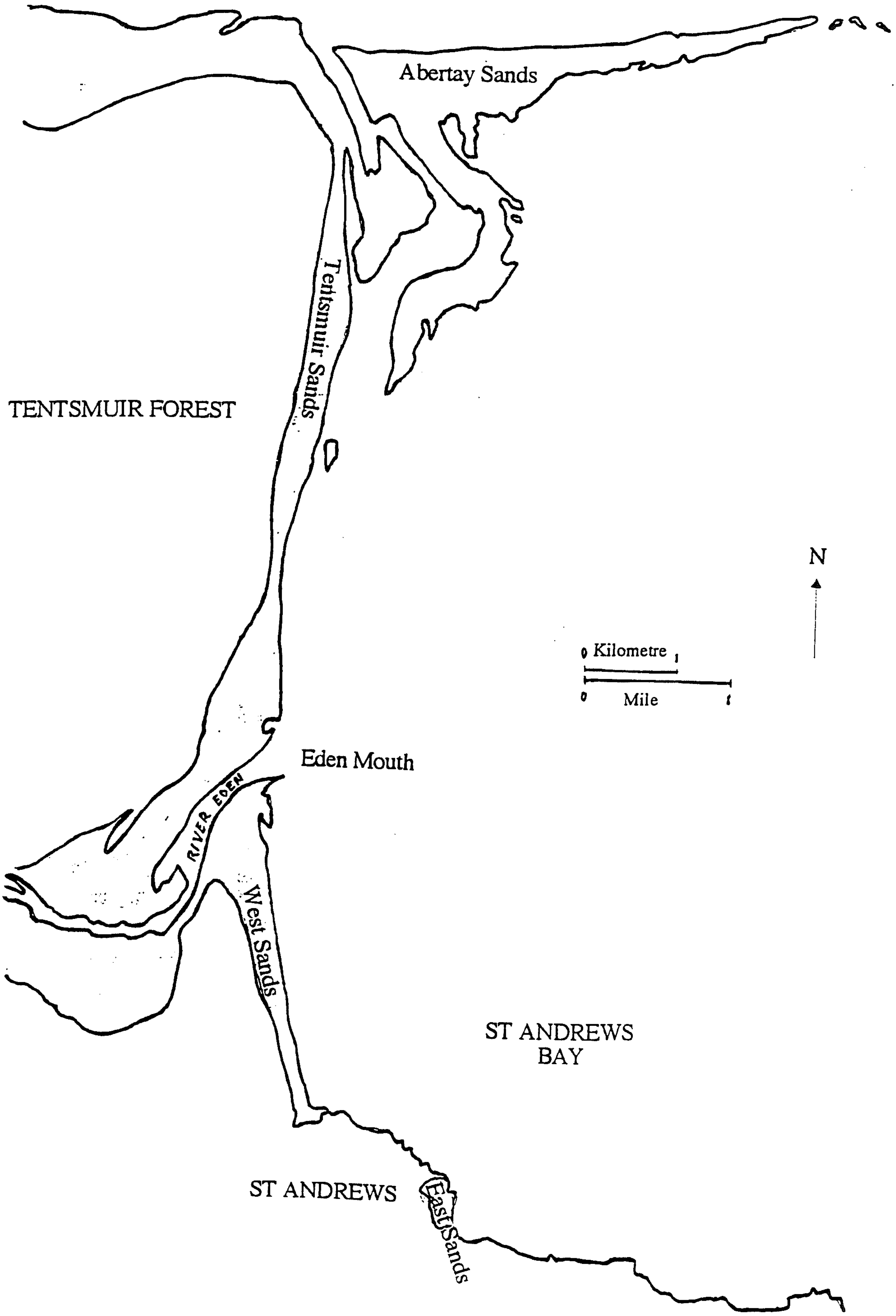
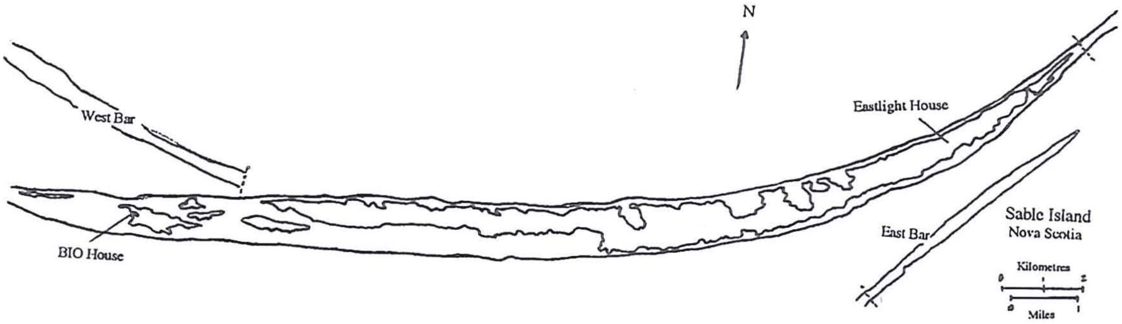


Figure 4. Abertay sands haul-out, Scotland

a) aerial photograph from helicopter



b) map of island

Figure 5. Sable Island, Nova Scotia, Canada:

for good quality sonagrams. Unfortunately, darkness meant that no behavioural observations were possible. The identity of the callers were therefore unknown. However, daylight recordings (personal observations), and previous observations by Boness & James (1979), confirmed that these vocalisations are produced by males only.

Sound analysis

Recordings were analysed with the RTS digital sound analysis system (Engineering Design, Belmont, Massachusetts). Although most vocalisations extended to >3.5 kHz, this was largely through the addition of harmonics rather than distinct structures. Therefore, a low pass filter was used. Where necessary, further analysis was performed with a higher frequency range. All measurements of temporal and frequency parameters were made directly from the spectrograms on the screen (cursor error: ± 9 ms, ± 10 Hz).

In-air repertoire

A total of 214 clear in-air vocalisations were examined from 315 minutes of recordings. Temporal and frequency parameters were measured directly from the spectrograms. The time variables measured, where applicable, were (i) total duration and (ii) cadence (duration between start of one element to the start of next element). The frequency variables measured on the fundamental (H_o) were (where applicable) (iii) beginning frequency (Bfreq), (iv) ending frequency (Efreq), (v) maximum frequency (Maxfreq), (vi) minimum frequency (Minfreq). Other variables measured were (vii) number of elements, and (viii) presence or absence of harmonics.

Underwater repertoire

A total of 1 120 calls were recorded in September 1997 at Abertay Sands (n= 6 days, 495 min) and 41 calls were recorded in March 1998 (n=1 day, 90 min). A total of 4 844 clear underwater vocalisations were recorded during the 1997 (n= 1 995 calls) and 1998 (n=2 849 calls) breeding seasons on the Isle of May. The calls from the 1997 breeding season were examined to prepare an initial subjective classification based on visual and auditory characteristics. Series of calls were chosen in preference to counting individual calls to take into account the fact that some calls occur in long series. Asselin and Hammill (1993) defined a series as a number of vocalisations emitted without a pause of 2 seconds or more. From this twelve provisional call categories were initially identified, three of which contained subgroups. The line spectrograms of 62 vocalisations were printed on separate sheets of paper and five observers were asked to classify them by their shape into as many groups and subgroups as they thought necessary. This information was used to establish a final 10 category classification which was then validated by measuring the inter-observer reliability between three observers.

A subset of clear vocalisations from each category was analysed in detail to measure temporal and frequency variables. Measurements of temporal variables consisted of the same ones as for the in-air vocalisations with in addition, where applicable, the measurement of (ix) element duration(s), and (x) intercall duration (duration between two successive calls of the same type in a series). The frequency variables were also the same as the ones measured for the in-air repertoire, but a further variable described was (xi) overall call shape (ascending, descending, constant frequency, modulated, segmented, etc.).

The frequency of occurrence of each call type was also investigated. This, with diurnal and seasonal variation in calling rates will be discussed in chapter 3. Finally, the number of elements making up each type 1 call was recorded to test for any possible individual recognition based on element repetition rate.

Statistical analysis

The Kappa coefficient (Siegel & Castellan 1988) was calculated to measure the index of inter-observer reliability and the subsequent validity of the classification.

Results

In-air repertoire

Classification and call description

A total of 214 clear vocalisations were analysed to obtain a qualitative description of each call type (Table 1) and six clear categories were identified. These are as follows:

Type A (Figure 6a) is a multiple element call. The mean number of elements per call was 1.67 (± 0.21 SD) and the cadence varied between 106 and 234 ms. This call was produced in-air by one young male from the Isle of May colony but is thought to be generally emitted underwater. The frequency of calling was not directly measured. However, this call was heard both in 1997 and 1998 on a regular basis when researchers walked by or from a nearby hide (personal observations) suggesting that this call is a regular component of his repertoire.

Type B (Figure 6b) consists of two components, a sharp upsweep followed by a brief descending frequency part. The number of elements per series varied between 2 and 10 and the maximum duration of the call was 3.16 s. This call was emitted by one mother from the Sable Island colony and was produced during female-male and female-female interactions. The frequency of this call within the colony is not known. As previously mentioned, this call was recorded while carrying out another experiment on mother-pup vocal recognition; an experiment during which long behavioural observations of mother-pup pairs were made. None of the other 27 females involved in that study were found to produce this call. It is therefore not known whether this call was specific to this female or whether the context in which it was produced did not arise during any of the other observations.

Moans (Type C, Figure 6c & 6d) were the longest calls heard with a mean duration of 3.56 s (±2.3 SD) and a maximum duration of 12.5 s. Most moans were produced at a constant frequency although some showed frequency modulation. These calls often had a higher beginning than ending frequency. Moans were recorded on the Isle of May and on Sable Island.

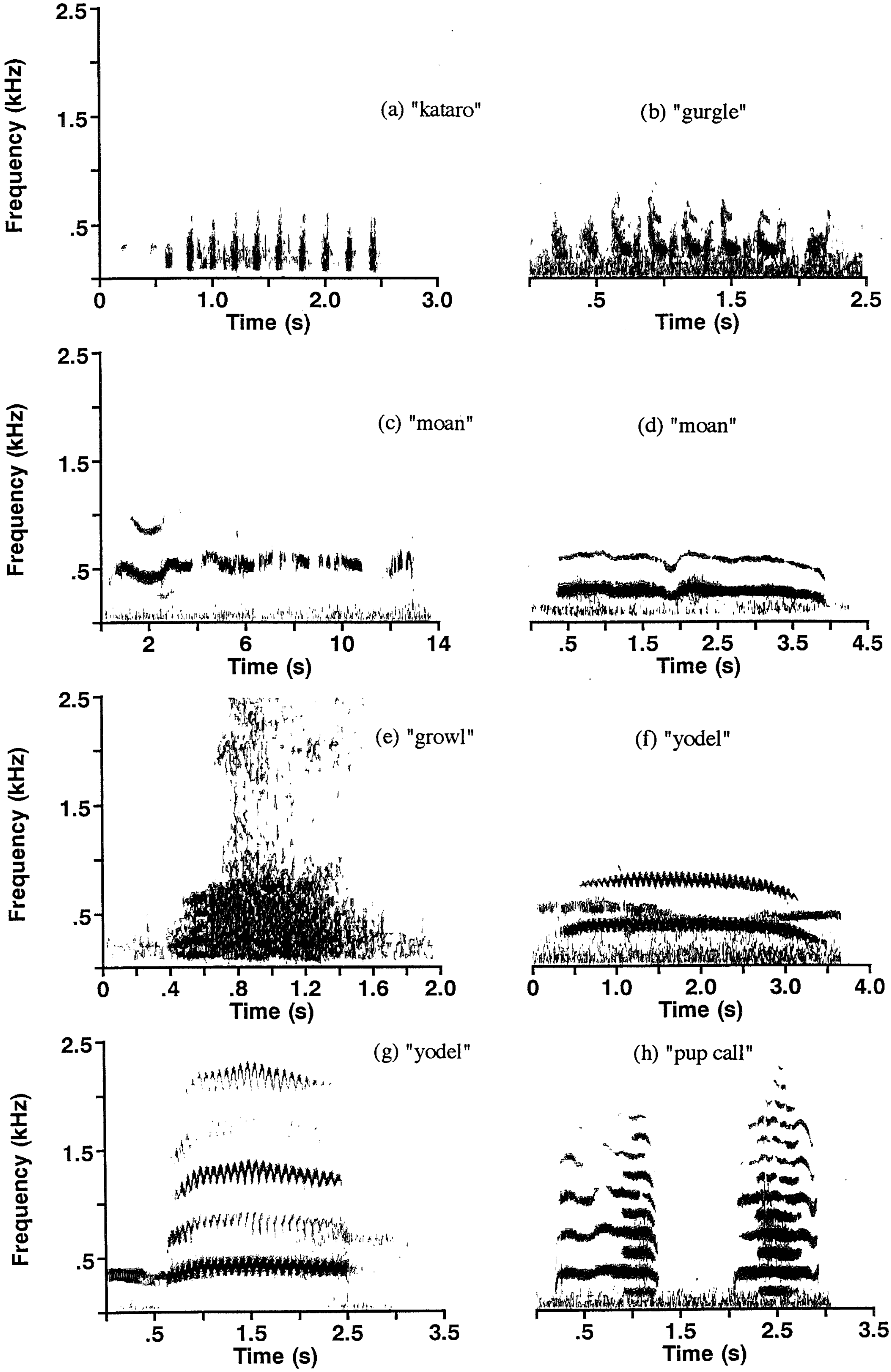


Figure 6. In-air repertoire of grey seals: call type A "kataro" (6a), call type B "gurgle" (6b), call type C "moan" (6c & 6d), call type D "growl" (6e), call type E "yodel" (6f & 6g) and call type F "pup call" (6h)

Table 1. Quantitative description of each in-air call type.

		N	Mean±SD	Range
Call type A ("kataro")	Series duration (s)	11	1.67±0.21	1.14-1.91
	N° of elements/series	11	9±1	6-10
	Cadence 1st-2nd (ms)	11	144±51	106-234
Call type B ("gurgle")	N° of elements/series	35	5±2	2-10
	Series duration (s)	35	1.39±0.58	0.43-3.16
Call type C ("moan")	Call duration (s)	94	3.56±2.30	0.30-12.5
	Bfreq (Hz)	94	356±98	195-713
	Efreq (Hz)	94	310±117	117-830
	Maxfreq (Hz)	94	451±128	244-1006
	Minfreq (Hz)	94	287±86	117-488
	N° of harmonics	94	0.01±1	0-2
Call type D ("growl")	Call duration (s)	27	2.7±1.25	0.71-5.13
	Bfreq (Hz)	19	202±57	117-322
	Efreq (Hz)	19	134±34	28-193
	Maxfreq (Hz)	18	214±49	62-242
	Minfreq (Hz)	18	123±20	98-176
	N° of harmonics	16	3±1	1-6
Call type E ("yodel")	Call duration (s)	47	3.77±1.34	0.63-5.67
	Bfreq (Hz)	47	333±26	244-391
	Efreq (Hz)	47	265±72	166-449
	Maxfreq (Hz)	47	399±24	332-449
	Minfreq (Hz)	47	246±51	166-342
	N° of harmonics	36	1±1	0-4
Call type F ("pup calls")	see chapter 4 for quantitative analysis			

Growls (Type D, Figure 6e) were often found to follow or precede moans. They were often noisy, shorter in duration (range 0.71-5.13s) and had harmonics (range 1-6). Their fundamental frequency was lower than for any other call type. They were recorded at both colonies.

Type E (Figure 6f & 6g) is a male produced call and was recorded on Sable Island during the breeding season. It was also recorded on the Basque Island off the SE coast of Cape Breton by Schneider (1974). Boness and James (1979) described it as "the falsetto part of a yodel". It is essentially a pure tone with a gradual onset and some rapid frequency modulation. Males were seen to vibrate their chest and neck while producing this call. The duration of this call ranged from 0.63 to 5.67 s with a mean beginning frequency of 333 Hz (±26 SD) and a mean ending frequency of 265 Hz (±72 SD). The number of harmonics in this call ranged from 0 to 4. Boness and James (1979) found it easy to discriminate males by their yodel suggesting the possibility of individual recognition based on this vocalisation.

Finally, type F (Figure 6h) consists of the pup vocalisation. These are analysed in detail in chapter 4.

Underwater repertoire

Classification and call description

The human observer classification identified 10 clear call types based on visual characteristics of the sonagrams, with call types 1, 3, 4 and 5 all having subgroups (Figure 7 & 8). The inter-observer agreement for these 10 categories was high (Kappa statistic, $\kappa = 0.81$, $z = 40.92$, $p < 0.0001$).

One thousand and forty clear vocalisations from the 1997 season were further analysed to obtain a qualitative description of each call type (Table 2). These are as follows:

Type 1 (Figure 7a & 7b) is a multiple element call. Each element had a sharp upsweep and occurred in series ranging from 2 to 20 elements with a mean duration of 1.53 s per series (±0.75 SD). A subtype was identified. It had an additional sharp upsweep structure which was not audible (Figure 7b, arrow). The cadence, time between the start of the first element to the start of the next, varied between 36 and 276 ms.

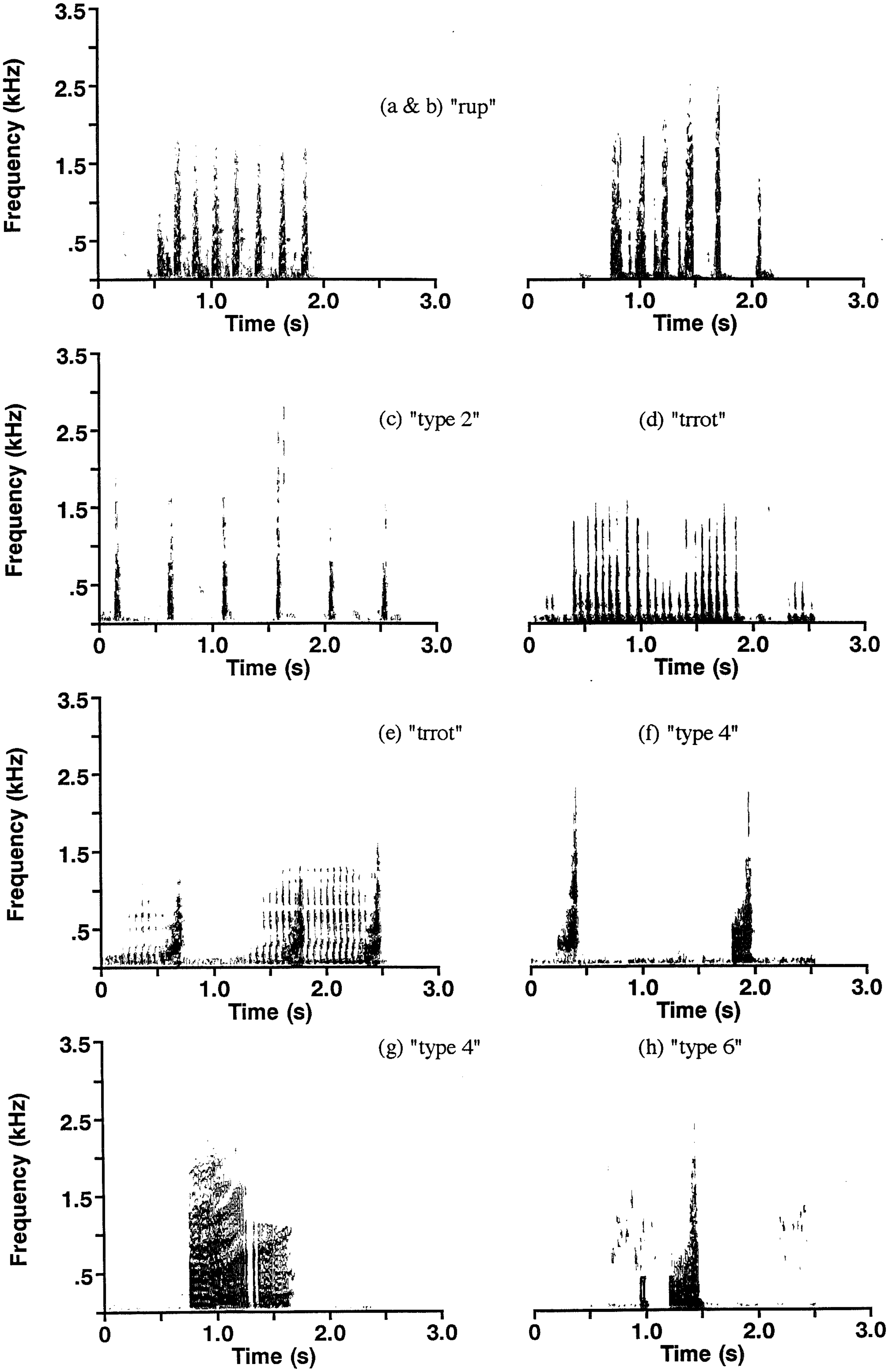


Figure 7. Underwater repertoire of grey seals: call type 1 "rup" (7a & 7b), call type 2 (7c), call type 3 "trrot" (7d & 7e), call type 4 (7f & 7g), call type 6 (7h)

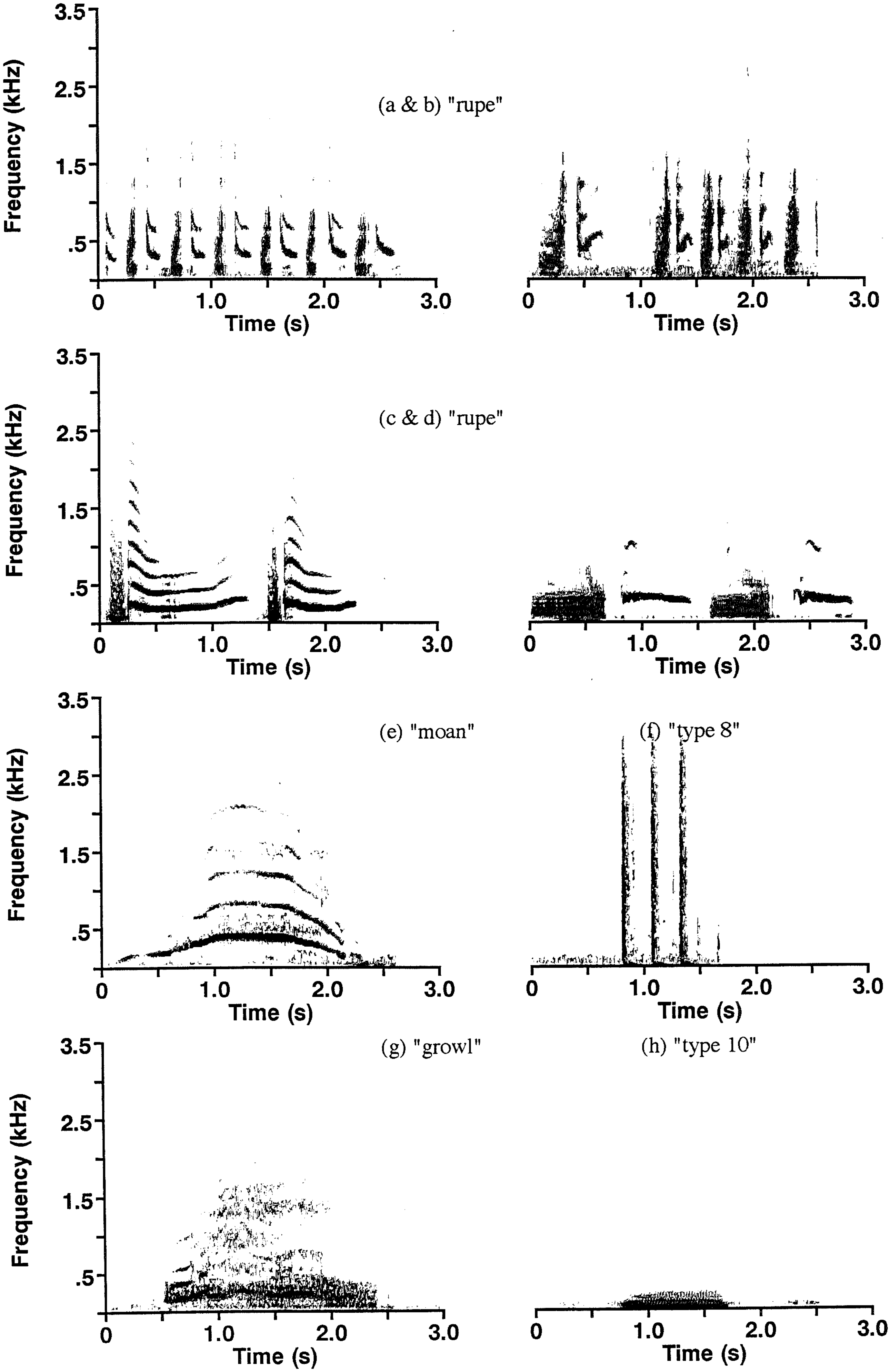


Figure 8. Underwater repertoire of grey seals: call type 5 "rupe" (8a 8b, 8c & 8d), call type 7 "moan" (8e), call type 8 (8f), call type 9 "growl" (8g), call type 10 (8h)

Table 2. Quantitative description of each underwater call type.

		N	Mean±SD	Range
Call type 1 ("guttural rup")	N° of elements/series	135	7.86±3.15	2-20
	Series duration (s)	135	1.53±0.75	0.25-4.49
	Cadence 1st-2nd (ms)	135	95.6±36.5	36-276
Call type 2	N° of elements/series	269	3.14±3.97	1-36
Call type 3 ("trrot")	Series duration (s)	116	1.47±1.08	0.27-6.73
	N° of elements/series	116	23.2±14.8	5-80
	N° of elements/s	116	16.4±2.98	14.6-18.2
Call type 4	Call duration (s)	211	0.26±0.15	0.09-0.97
	Fo (Hz)	79	90.4±30.2	47-219
Call type 5 ("guttural rupe")	N° of elements/series	181	4.14±3.87	1-37
	Series duration (s)	80	2.31±1.33	0.37-6.41
	Inter-call duration (ms)	96	483.6±340.7	139-2026
	Fo (Hz)	35	347.8±124	146.5-713
Call type 6	Call duration (s)	15	0.57±0.16	0.26-0.80
	N° of components	15	2±0	2-2
	Dur 1st element (ms)	15	0.19±0.09	0.06-0.34
	Cadence 1st-2nd (ms)	15	0.40±0.15	0.11-0.62
	Dur 2nd element (ms)	15	0.17±0.08	0.08-0.37
	Fo (Hz)	11	75±23.1	49-127
	Max freq (Hz)	15	1964±573	1077-2853
Call type 7 ("moan")	Call duration (s)	36	1.98±1.42	0.35-6.31
	Bfreq (Hz)	36	267.7±149.5	59-664
	Efreq (Hz)	36	185.7±141.4	20-605
	Fo (Hz)	36	265.8±138.1	59-708
	N° of harmonics	36	2.53±2.29	0-9
Call type 8	N° of elements	144	1.75±1.05	1-5
Call type 9 ("growl")	Call duration (s)	22	1.58±0.89	0.47-4.11
	Bfreq (Hz)	22	153.7±67.0	69-387
	Efreq (Hz)	22	90.9±44.4	28-193
	Fo (Hz)	22	127.7±44.6	62-242
	N° of harmonics	22	3.5±3.11	0-9
Call type 10	Call duration (s)	122	1.21±0.25	0.5-1.76
	Fo (Hz)	122	35.1±22.4	20-131
	Max NRJ (Hz)	122	295.5±121.3	83-870

Type 2 is a single element call with a brief duration and a wide frequency range (Figure 7c). These calls were produced in bouts ranging from 1 to 36 calls with variable inter-call durations.

Type 3 calls (Figure 7d) could be described as slow clicks and were found in series ranging from 5 to 80 components. The mean number of components per second was 16.4 (±2.98 SD). Some calls were followed by type 4 calls (Figure 7e).

Type 4 (Figure 7f) was often noisy with a harmonic structure, frequency modulation and its major energy ranged between 47 and 3500 Hz. The highest frequency recorded was however 7.5 kHz. The mean call duration was 0.26 s (±0.15 SD). and this call type was the most variable in shape of all call types. Formants, " parts of the frequency range spectrum that are reinforced by resonant properties of the vocal tract" (Miller & Murray 1995) were found in a small sample of these calls and are illustrated in Figure 7g.

Call type 6 (Figure 7h) was a two part call, with a mean duration of 0.57s (±0.16 SD) and energy up to c. 2800 Hz. The first component of the call had a very sharp and brief onset while the second component of the call was very similar to type 4 calls.

The duration of call type 5 ranged from 0.37 to 6.41 s with a mean of 4.14 calls per series. This call consisted of two variable components as illustrated in the 4 subgroups in figure 8a, b, c & d (e.g. short descending, short ascending, long constant frequency and medium length constant frequency, the last associated with a long part 1). A harmonic structure was often present in the second element which had a fundamental frequency range of 150 to 700 Hz. This call was often recorded together with type 4 calls (see chapter 3).

Moans (call type 7, Figure 8e) were often heard simultaneously underwater and in-air. Calls ranged between 0.35 and 6.31 s in duration with a mean fundamental frequency of c 250 Hz (±138.1 SD). These calls had harmonics, some frequency modulation and a start frequency often greater than the end frequency.

Type 8 calls were very brief single element calls with a sharp onset and were often found in series of 1 to 5 calls (Figure 8f). Energy ranged up to 10 kHz in this call type. These vocalisations sounded like a loud piercing clap.

Growls (call type 9, Figure 8g) were noisy, with some frequency modulation and a mean duration of 1.58 s (±0.89 SD). Harmonics were also present, but almost all the energy in the call was below 3.5 kHz.

Type 10 calls (Figure 8h) had a mean duration of 1.21s (±0.25) and a fundamental frequency of 35.1 Hz (±22.4 SD). No energy was displayed above 870 Hz in this very low frequency "buzz" sounding vocalisation.

All call types identified during the breeding season on the Isle of may were also recorded at Abertay Sands during September. However, only 6 of the call types were heard in March. The 4 missing call types (6, 8, 9 and 10) correspond to the less common calls accounting for less than 16.5% of call usage. The low frequency of occurrence of these calls types and the short recording session (n=1 day, 90 min) could explain their absence.

Frequency of occurrence of each call type

The frequency of occurrence of each call type as a percentage of the total number of vocalisation series is illustrated in Figure 9. In 1997, call type 4 was the most prominent call, accounting for 20.5% of the 1 995 calls recorded. The second most common call (19.6% of call usage) was type 5. Type 2 calls made up 18.8% of the underwater repertoire while type 1 calls accounted for 17.7%. In 1998, call type 1 was the most common call accounting for 32.2% of the 2 849 calls recorded. In addition, call types 5, 4 and 2 represented 23.2%, 11.1% and 8.3% of call usage, respectively. Combining the two years of data showed type 1 calls to be the most prominent call overall with 26.2% of the 4 844 calls recorded. Temporal differences in call usage is described in chapter 3.

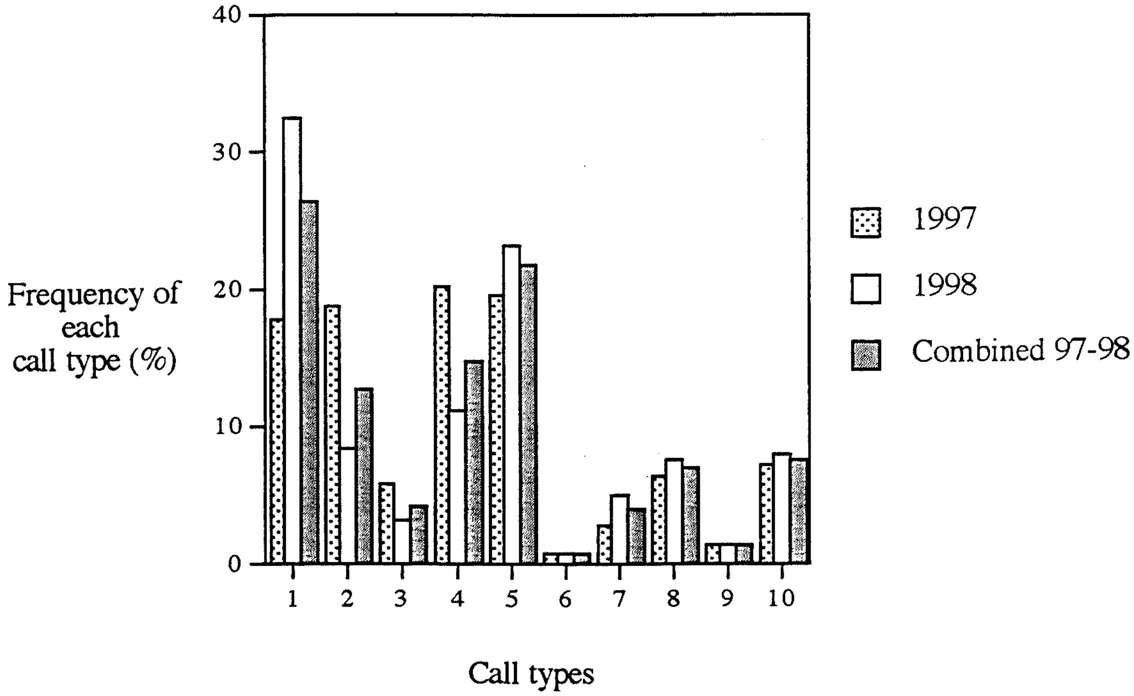


Figure 9. Frequency of occurrence of each call type during the 1997 and 1998 breeding seasons.

A specific case: type call 1

As previously mentioned type 1 is a multiple element call and thought for several reasons to be produced by males only. That males produce this call has been documented through underwater video footage (B. Loyer, personal communication), and surface behavioural observations, and at no point have females been seen to produce it. The variation in the number of elements is illustrated in the four sonagrams of Figure 10. The distribution of type 1 calls based on their number of elements per series is illustrated in Figure 11. During recordings in the Kirkhaven area, up to four males were observed at any one time. Two males were present for the 3 days and were seen to engage in parallel swimming and bottling behaviour. No fighting was observed but one male did constantly move away when approached by the other. Despite taking notes describing any surface behaviour and the relative position of males during vocalisations, it was not possible to ascribe any function to this call. Few male-female interactions were observed as females only passed through the area during this eraly part of the breeding season.

The East Tarbet calls correspond to 135 clear vocalisations used for the quantitative description of this call type and were recorded during the 1997 breeding season (Table 2). Male

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present during any one recording session. However, in both data sets, the caller was not identified. Therefore calls were not necessarily independent of one another such that they could have been produced by the same or by different individuals.

Figure 11 shows how the number of elements per call is not randomly distributed. Calls of 3, 8, 9 and 10 element are far more frequent than what would be expected by chance. The mean number of elements per series was 7.86 (±3.15 SD) for the East Tarbet data and 8.39 (±0.05 SD) for the Kirkhaven data. Three and four element calls were frequent. During a specific 45 minutes recording session (Kirkhaven, 3 October), ten 3 element, six 8 element and one 7 and 9 element call were heard. At the same time, only two males were observed in the area suggesting that individual seals may produce calls with a specific and

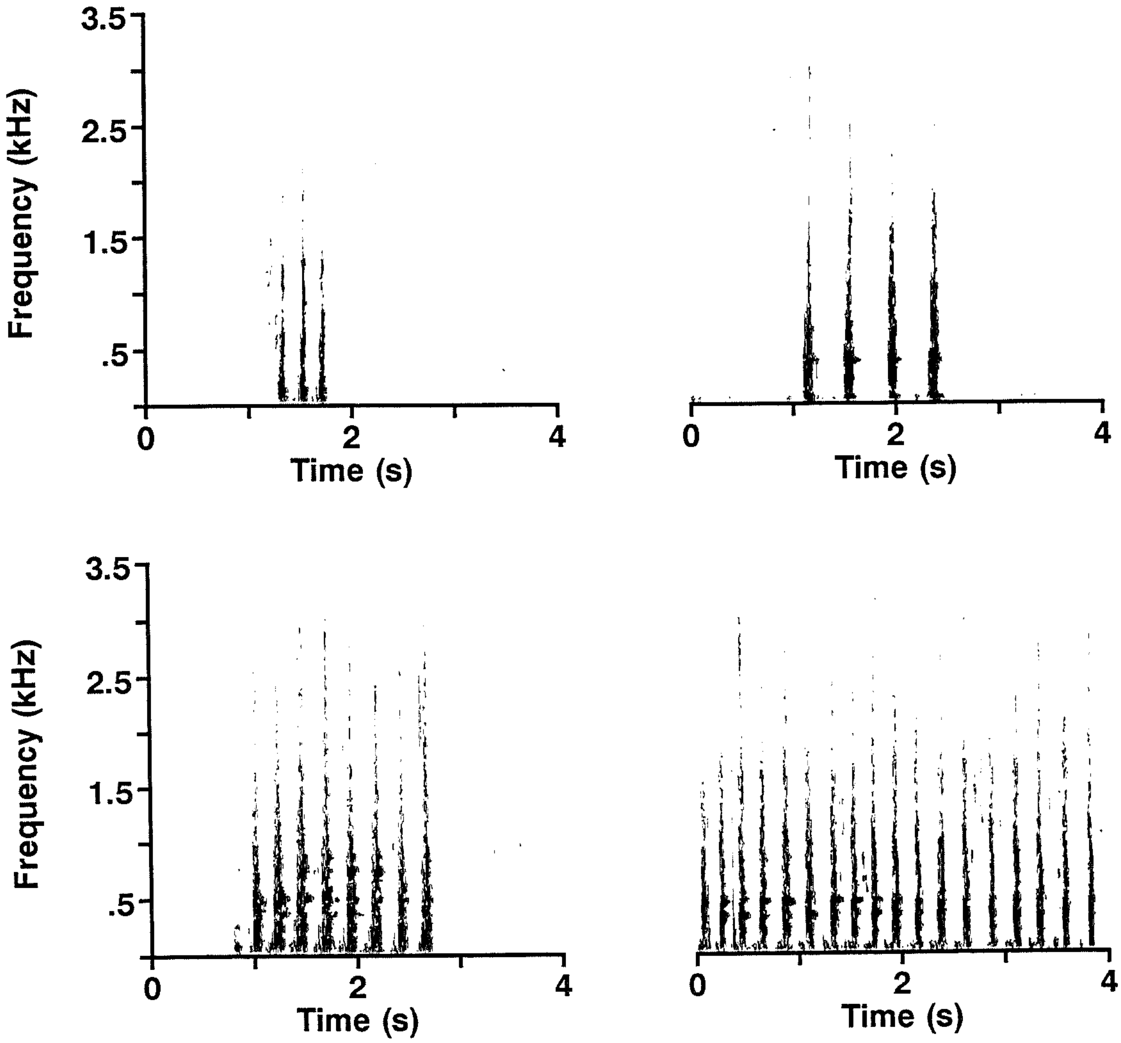

Figure 10. Sonagrams of 4 different call type 1

numbers varied across the breeding season (see chapter 3) but there was never less than 2 males constant number of elements. Interestingly, the in-air type A call produced on land by the young male showed similar consistency in the number of elements. Out of the 11 type A calls recorded, 8 of them had 9 elements, and the remaining 3 calls had 6, 8 and 10 elements respectively. This young male produced the call when females engaged in agonistic interactions and also when researchers walked by.

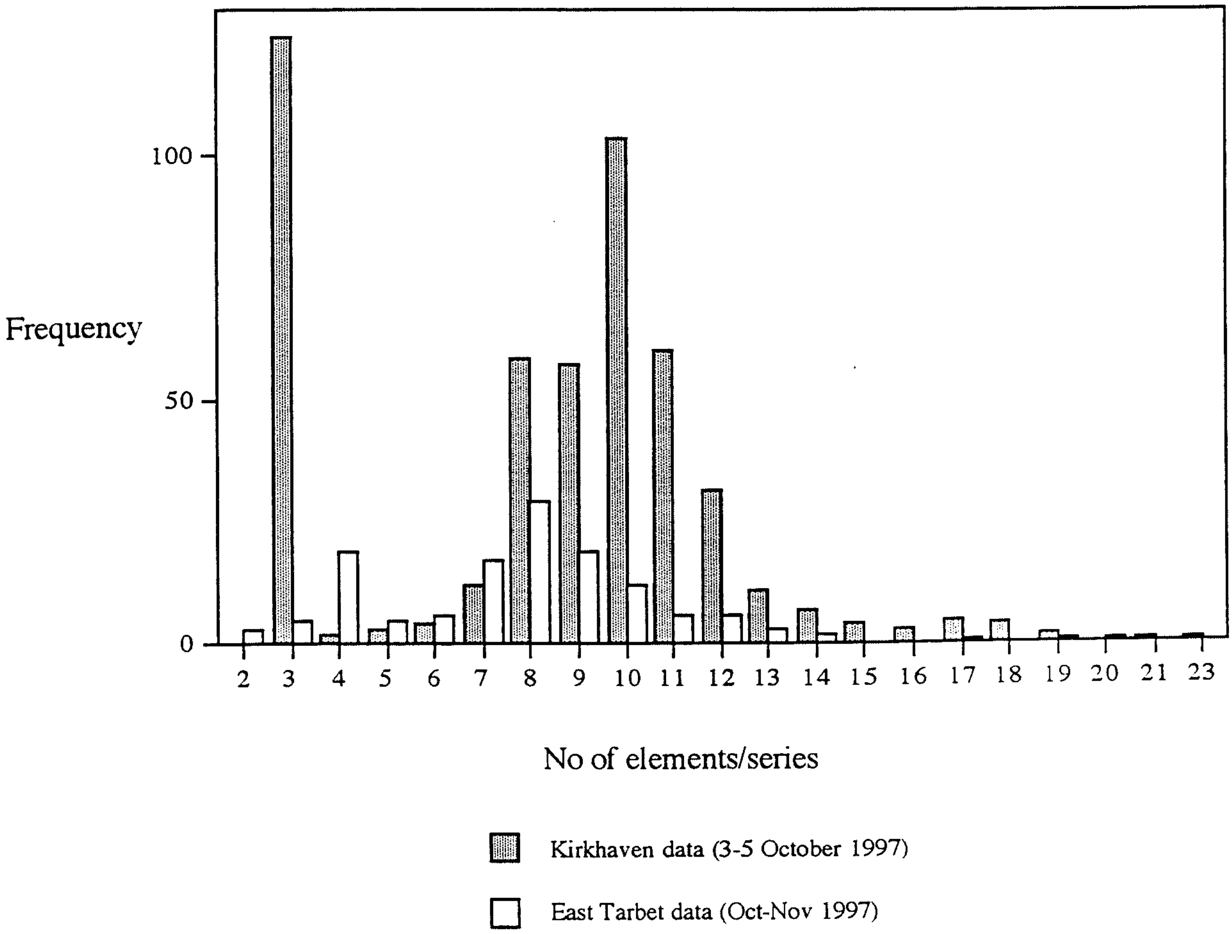

Figure 11. Histogram illustrating the distribution of number of elements per series in recordings of call type 1.

Discussion

Six call types were identified for the in-air repertoire and ten call types were identified for the underwater repertoire using a human observer classification based on visual characteristics. A comparison between in-air and underwater call types suggest that some calls may be the same. Furthermore, call types 1, 2, 4 and 5 accounted for over 70% of all calls recorded (see chapter 3).

Of the call types found here, a few can be compared to call types previously reported. Type 1 corresponds to the "guttural rup" of Asselin and Hammill (1993, see A Figure 12). They suggested that this call might be produced by females only, during female-female or female- male interactions and limited to the breeding season. However, in this study, call type 1 was the only call to be clearly identified as being produced by males. This is because the production of this call was associated with male grey seals close to the surface making wave-like body movements while producing these water-borne calls. Furthermore, call type A is very similar in structure to call type 1 (Figure 13) and was produced by a young male while on land, often when researchers walked by. Moreover, type 1 calls were recorded near the Abertay sands haul-out site at the mouth of the river Tay, Scotland, during summer 1997 and hence are not restricted to the breeding season (see chapter 3). Finally, underwater footage from a wildlife documentary ("Nose no good") also features male grey seals producing type 1 calls (McCulloch & Loyer, unpublished data). The footage was taken during the breeding season off the island of Faray, Orkney, Scotland and showed some male-female interactions and one clear underwater copulation. Viewing of the original and unedited footage gave clear evidence (3 sequences) that males make wave-like body movements while producing type 1 calls. No vocalisations were heard during the aquatic mating. Unfortunately, the limited footage (97 min) and the small field of view provided little information on the identity of the caller. Indeed, out of 53 type 1 calls recorded, only 3 callers were identified. All other calls were heard when no seal was in the field of view. Whether type 1 calls are solely produced my males remains speculation until the emitter of the call can be clearly identified. However, to date no females have been seen to produce this call in the eastern Atlantic population of grey seals.

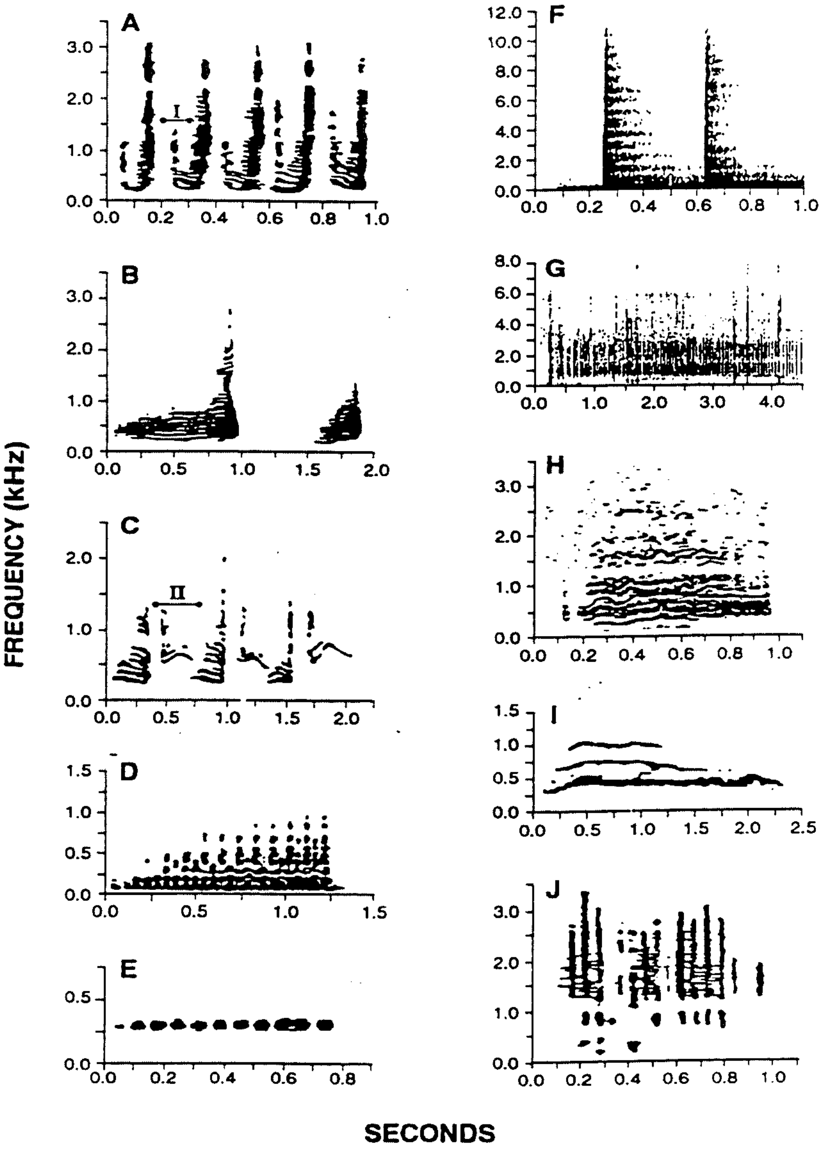

FIG. 1. Examples of underwater call types emitted by grey seals during the breeding period. (A) Series of 5 type-1 rups with an auxiliary structure (I). (B) Series of 2 type-2 rups. (C) Series of 3 rupes with an audible auxiliary structure (II). (D) Growl type 1. (E) Growl type 2. (F) Series of two knocks.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

Figure 12. Figure 1 reproduced from Asselin and Hammill (1993).

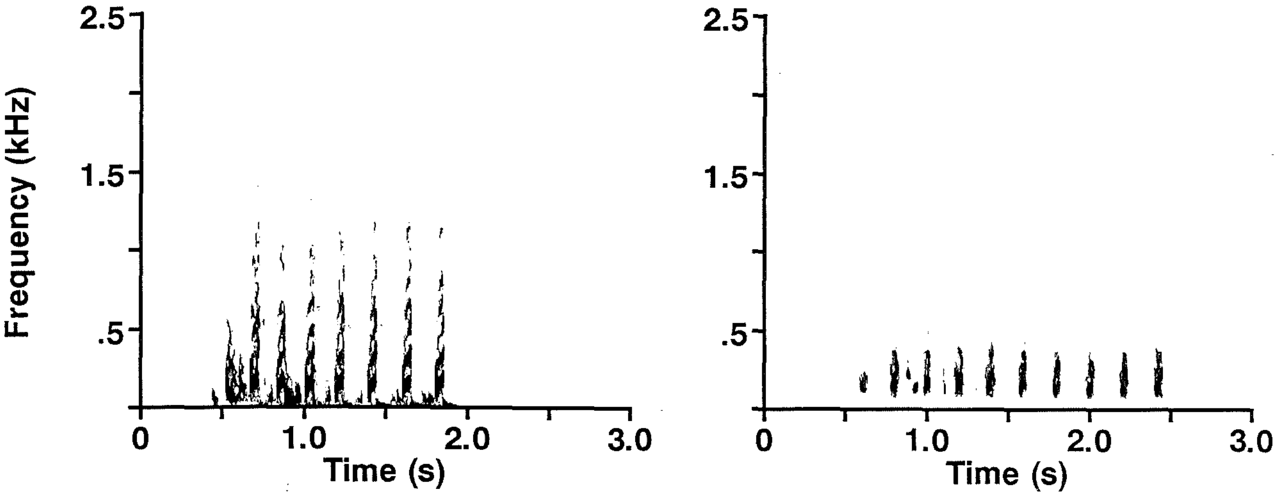

Figure 13. Comparison between call type 1 and call type A "Kataro" .

Call type 5 could be compared to the ice-breeding grey seal "guttural rupe" (Asselin & Hammill 1993, C in Figure 12) by comparing the descriptive features of the calls on sonagrams. This type was suggested to be produced by females only, during agonistic interactions. Although, as previously mentioned, the identity of the caller was unknown during the underwater recordings, in-air recordings on Sable Island suggest this call is indeed produced by females (call type B). Females were seen to produce a gurgling noise on land very similar in sound and structure to the underwater call type 5 (Figure 14). A female produced this call when a male in close proximity interacted with a neighbouring female. Furthermore, a female and a male were often seen interacting at the surface shortly after calls type 5 were heard. It is therefore likely that these calls could be used during female-male social interactions.

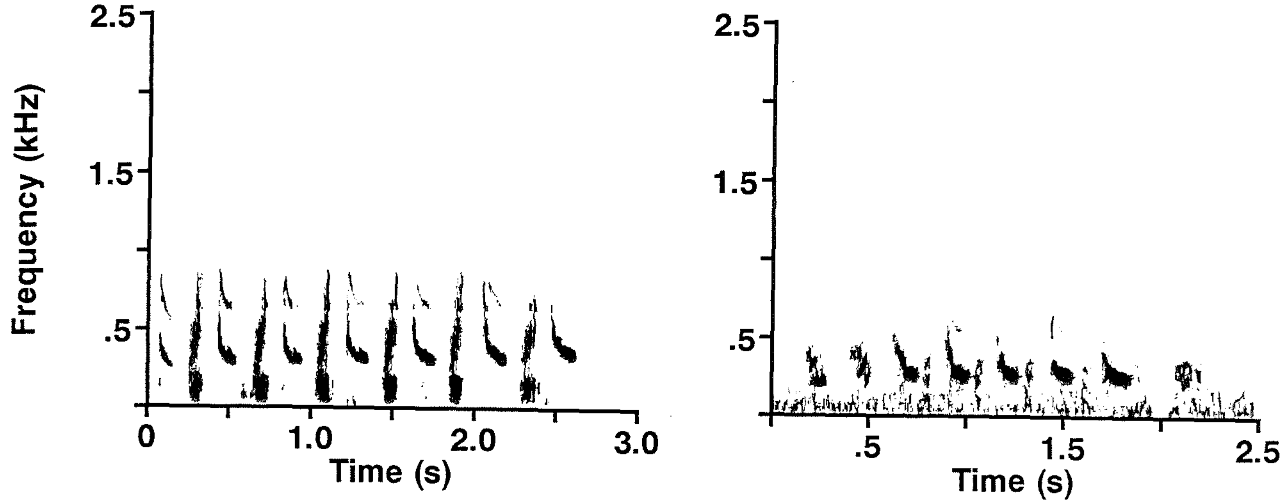

Figure 14. Comparison between call type 5 and call type B "gurgle".

Other calls that have previously been described are call types 3, 7 and 9. Call type 3 was identified as a series of slow clicks similar to the "jackhammer" reported by Schneider (1974) and the "trrot" reported by Asselin and Hammill (1993) in ice-breeding grey seals. Although fast clicks were thought to be used in navigation under the ice, Schneider (1974) observed slow clicks to be produced by males during sexual interactions and situations where dominance might be displayed.

Call type 7 has been described as a hoot (Hewer & Backhouse 1960), a moan (Schusterman et al. 1970), a wail (Schneider 1974) and finally a roar (Asselin & Hammill 1993). Comparisons between calls were made by comparing descriptive features on sonagrams. In this case, the call was produced by males and females, sometimes in-air and underwater simultaneously, during male-female or female-female interactions. Seals were often seen swimming in a circle when producing this call.

Call type 9 has only been previously described by Asselin and Hammill (1993). Only 22 growls were recorded during the present study making up less than 1% of all calls recorded. These calls are probably produced mainly by males during male-male agonistic interactions.

Males were seen to swim with their mouth slightly open while producing these calls, and they were often heard in water and in-air simultaneously. Unfortunately, behavioural observations were limited and rather anecdotal so that inferences about the function of this call can only be speculative. In-air growls were found to be produced by males and females and were often associated in time with moans.

The yodel call (type E call) I recorded on Sable Island has only been recorded at this location and Basque Island. It has never been reported at any European colony. Boness and James (1979) suggested that this call is restricted to the breeding season and occurs in a wide variety of contexts. Neighbouring males and females often ignored a yodelling bull. This call is hard to localise but can be heard several kilometres away. It may therefore be used in advertising dominance status over a relatively long distance. Males from different gullies were also seen to engage in yodelling "duels" (Twiss & Boness, personal communication). Further analysis of this call type is needed to see if these calls are individually distinctive. The data set presented here does not have the required sample size to test for individuality. Furthermore, recordings were made at night so identity of caller is also unknown. Playback experiments may be used to investigate the behavioural response of males to different male calls. It would be interesting to see how so called dominant males respond to young male calls and calls from other dominant males.

The identity of the caller and the function of all other call types are as yet unknown and remain speculative. Call types 2, 4, 6, 8 and 10 have not been described previously as part of the grey seal underwater repertoire. Despite call type 2 being the most common type, representing 21.2% of call usage and, similarly, type 4 accounting for 16.1% of all vocalisations recorded, the function of the calls, and age and sex of the caller remain speculative. The latter call was often recorded in association with type 5 calls (see chapter 3) and hence could have a similar function.

A specific case: type call 1

The distribution and structure of call type 1 leads to a number of hypotheses. The null hypothesis would be for call type 1 to have a random number of elements. While much less likely, it is also conceivable that each individual has a constant number of elements in its call. This feature of the call might then be used in individual recognition, perhaps in combination with variation in features such as frequency, intensity and inter-element duration. Another but not mutually exclusive hypothesis would for this call to reflect the emotional state and status of the sender. Finally, this call may be used to advertise dominance status. Grey seals males produce a wave-like body movement and vibration of their chest when making call type 1. If higher frequency is negatively correlated with body size as in cichlid fishes (Myrberg et al. 1965), and size is positively correlated with dominance, large dominant males would be expected to produce low frequency calls. Males would therefore be able to advertise their dominance status and their identity through calling and females able to choose their mate on the basis of their call. This would be increasingly useful underwater where the visibility is poor. Although none of these hypotheses were directly tested, circumstantial evidence is nevertheless worth noting.

Figure 11 showed that the number of elements per call is not randomly distributed. Furthermore, two males in the water and the young male on land seemed to show some consistency in the number of elements heard in their type A call. So if type A calls are the equivalent of type 1 calls underwater, as suggested by the acoustical structure of the two calls (compare Figure 6a and Figure 6a), type call 1 may therefore be assumed to be produced by males. However, whether this call can be used in individual vocal recognition remains unclear. Certainly variation does exist but whether inter-individual variation is greater than intra-individual is uncertain due to the inability to identify the caller in the present study. Furthermore, the variation in the number of elements per se may not be large enough for individual recognition (range 3-23). However, individual recognition could be based on a combination of variables such as number of elements, frequency, intensity and inter-element duration. For example, bottlenose dolphins (*Tursiops truncatus*) produce "signature" whistles with distinctive frequency modulated contours (Caldwell and Caldwell 1965) whereas the emperor penguin (*Aptenodytes forsteri*) uses the temporal patterning of syllables to identify its mate (Robisson et al. 1993).

However, the number of elements per call may not represent individual distinctiveness or dominance status but could solely reflect the emotional state of the caller. Indeed, Schusterman (1977) showed how territorial California sea lions vary the number and rhythm of barks depending on the social context. Furthermore, Weddell seals have been seen to lengthen certain classes of calls in response to conspecific vocalisations (Terhune et al. 1994). Although these hypotheses are rather speculative, the structure of call type 1 is intriguing and deserves further analysis. However, in order to test for the function of this call, it remains essential to be able to identify the caller. Observation of captive animals is necessary to see if males do produce calls type 1 with a specific and constant number of elements. The use of a hydrophone array could also provide this necessary information to localise calls. During the second year of recordings, two hydrophones were deployed for this very reason, unfortunately equipment failure meant that data collection from only one hydrophone was possible.

This chapter has provided a survey and description of in-air and underwater grey seal vocalisations with examples of clear sonagrams. Unfortunately, limited and mainly anecdotal observations mean that the sex of the caller and the function of each call remain largely a matter of speculation.

Chapter 3

Temporal variation in underwater vocalisations

Abstract

The underwater repertoire of grey seals has only been investigated in the western Atlantic ice-breeding population. This is therefore the first study of the underwater vocalisations of a British Isles population. This yielded 5 220 minutes (n= 29 days) of recordings at the Isle of May during the breeding seasons of 1997 and 1998. Temporal variation in the number and type of underwater vocalisations recorded was investigated to see if certain call types occurred more at a particular time during the breeding season. The results showed that the total number of calls recorded did not vary between years, but did vary between call types and across the breeding season. Furthermore, most calls were found to occur on their own, while some were preferentially associated in time with other call types. Finally, the spatial distribution of males during the breeding season suggested that males may engage in defending underwater territories, the boundaries of which shift as seal numbers and activity levels vary during the course of the breeding season.

Introduction

Phocids are patchily distributed and spend considerable amounts of time under water, thus making studies of their behaviour rather difficult. However, some phocids have been found to be highly vocal underwater and this has led to the possibility of using underwater vocalisations as a way to investigate the social role of acoustic communication in phocids and its part in their reproductive behaviour. Many studies have shown an increase in vocalisations during the mating period. Vocalisations recorded during breeding seasons include the prolonged downward "sweeps" and broadband "puffing" sounds of the ribbon seal, *Phoca (Histriophoca) fasciata,* (Watkins & Ray 1977), the pulses and siren calls of the Ross seal, *Ommatophoca rossi,* (Watkins & Ray 1985), or the wide variety of underwater sounds of the harp seal, *Phoca groenlandica,* (Terhune & Ronald 1986) and the stereotyped cycles of underwater vocalising of the Atlantic walrus, *Odobenus rosmarus rosmarus,* (Stirling et al. 1983, Stirling et al. 1987). Ringed seals, *Phoca hispida,* produce four vocalisations: bark, yelp, growl and chirp, heard at all times of year and day, suggesting that none of them is solely used during reproductive behaviour. However, the frequencies of barks and yelps were reversed between spring and winter recordings. Barks, considered to be threat calls given by males, were more frequent in spring perhaps because of higher levels of aggressiveness in the breeding season (Stirling 1973). During this time, males interact with each other around breathing holes (Stirling et al. 1983). Although these species have complex underwater vocalisations, their role in mating behaviour remains unclear.

In Weddell (*Leptonychotes weddelli*) and harbour seals (*Phoca vitulina*) a more direct link has been established between underwater vocalisations and territorial defence and/or mate attraction. Siniff et al. (1977, Bartsh et al. 1992) found that male Weddell seals can be divided into three categories (transient, basking and territorial) and that territorial males defend underwater territories along the tide crack of the ice in the pupping colony. In a later study, Green and Burton (1988) recorded their underwater vocalisations and found that the number of seal calls peaked in November and the first week of December, a period thought to correspond to the breeding season. They then suggested that territorial males produce underwater trills and visual displays to advertise their location and compete for females around breathing holes. In a captive study, Rogers et al. (1996) observed broadcast calls being produced by receptive female leopard seals and by a mature male during December and January, again at the presumed time of mating of wild leopard seals. Leopard seals are solitary Antarctic phocids so acoustic communication could be essential in finding a sexually receptive mate. In harbour seals, a similar relationship has been found between underwater visual and vocal displays and reproductive behaviour. Males engage in stereotypic diving and acoustic displays (Hanggi & Schusterman 1992, Coltman et al. 1997, Van Parijs et al. 1997). Nicholson (personal communication) observed male behaviour underwater and found that a primary function of their underwater vocalisations is to establish and maintain dominance hierarchies. It was also observed that high ranking males engage in more flipper flapping and muzzle contact. In a study of distribution and activity of male harbour seals, Van Parijs et al (1997) found that males use dispersed but small display territories in areas near haul-out sites, around female foraging areas and along female transit routes. Furthermore, Coltman et al. (1998) observed that males are influenced by the availability of food and oestrous females. As a result, males seem to adapt their temporal and spatial behaviours according to female distribution and density (Van Parijs et al 1999).

The vocalisations of grey seals (*Halichoerus grypus*) were first described in 1963 by Schevill and Watkins and subsequently by Schusterman et al. (1970) and Schneider (1974). However, it was not until 1993 that the first detailed study of their underwater vocalisations was carried out. Asselin and Hammill (1993) recorded seven types of vocalisations in the ice-breeding grey seals of the Gulf of St. Lawrence, Canada. These seals belong to the western Atlantic population which are reproductively isolated from those in the eastern Atlantic. They breed from the end of December until the start of February on shifting pack ice. Asselin and Hammill (1993) found seasonal variation in both the total number of underwater vocalisations and the number of specific call types. They observed an increase in vocalisation rate as the breeding season progressed and the number of agonistic interactions rose, and they also observed a difference in vocal repertoire between daylight and night-time recordings.

In this study, first, I investigated temporal variation in the underwater vocalisations of grey seals during the breeding season at the Isle of May, Scotland. Secondly, I looked at possible associations between call types during the breeding season. Finally, behavioural observations of surface interactions were recorded. Despite limited data due to adverse weather conditions, the distribution of males was observed suggesting that they may hold underwater territories.

Methods

Study sites and data collection

Underwater recordings were made between 10 October and 25 November 1997 and between 11 October and 24 November 1998 at East Tarbet, Isle of May, Scotland during the breeding season (see Fig. 1 Chapter 2). East Tarbet is a tidal channel that divides the island along a north-south axis. This channel connects the flat grassy top of the north island with the open sea. Males are found throughout the breeding season in the channel. Some males with distinctive scars and pelage marks were relocated from day to day to see if particular males set up residency in the area. Females numbers vary as many only use the channel as an access route to the island tops. Nevertheless, a few females give birth on the edge of the channel and subsequently remain in the area. This site was chosen because of its topography and ease of observation from the shore. Behavioural observations of grey seals in the vicinity of the hydrophone were made during underwater recordings from a small hide located above the study site. Male-male and male-female surface interactions and number of individuals present were recorded to see if underwater vocalisations could be linked to particular behaviours. The number of animals was established by counting the number of seal heads visible. This head count was repeated at regular intervals during the recording session and a mean calculated. The study site was divided into small areas (eg. inner, main, bridge and outer channels, main alcove, west alcove, above hydrophone, see Figure 1). The location of males was then determined relative to these areas at regular intervals during the recording sessions. In addition, weather and sea conditions were noted throughout the recordings. A Marantz CP430 tape recorder and an AQ18 hydrophone were used for this study. As the hydrophone was only submerged at high tide recordings were limited to that period; 90 minutes of recordings were made around both high tides on 12 days in 1997 and on 17 days in 1998. This accounted for 1 260 minutes of recordings during darkness and 900 minutes of daylight recordings for 1997, and 1 440 and 1 620 minutes respectively for 1998.

The total number of series of vocalisations recorded was calculated for each recording session (see chapter 2). Asselin and Hammill's (1993) definition of a series of vocalisations was used in which a series is taken as a number of vocalisations emitted without a pause of 2 seconds or more. To examine temporal variation in calling, the breeding season was divided into 3 periods: start, peak and end. In 1997, the first period (10, 15, 17, 19 October) coincided with a relatively low number of males (mean= 1.25± 0.5 SD) and females (mean= 13.32± 5.09 SD), with most females investigating probable breeding sites and very few hauled-out. The mean birth date for 1997 was 1 November (C. Duck, SMRU, personal communication). Thereafter, equipment failure due to a violent storm prevented recordings during the first few days of November, and the second period was not until 6, 7, 8, 9, 10 November. At this stage there was an increase in female (mean= 22.7± 5.16 SD) and male numbers (mean= 3.17± 1.26 SD), and a high frequency of births. By the third period (23, 24, 25 November), most females had given birth and weaned their pup (mean= 6.43± 1.40 SD). Attempted copulations were frequent at this time (males: mean= 2.0± 1.0 SD). The three recording periods in 1998 were 11, 13, 15, 17, 19 October and 2, 3, 4, 5, 6, 7 November and 19, 20, 21, 22, 23, 24 November. The calculation of the mean birth date requires extensive analysis of aerial photographs, and information for 1998 is not yet available from the Sea Mammal Research Unit. However the mean birth date is expected to be similar to 1997. Fewer females were seen in East Tarbet in 1998 at the start (mean= 3.76 ± 2.08 SD) and peak (mean= 7.77± 3.33 SD) of the breeding season than in 1997, whereas male numbers remained the same (start: mean= 1.09± 0.23 SD, peak: mean= 2.75± 0.61 SD).

Recordings were analysed with the Signal-RTS digital sound analysis system (Engineering Design, Belmont, Massachusetts). Signals were filtered using a lowpass filter (<10 kHz). Minitab 8.2 was used for the temporal variations computations.

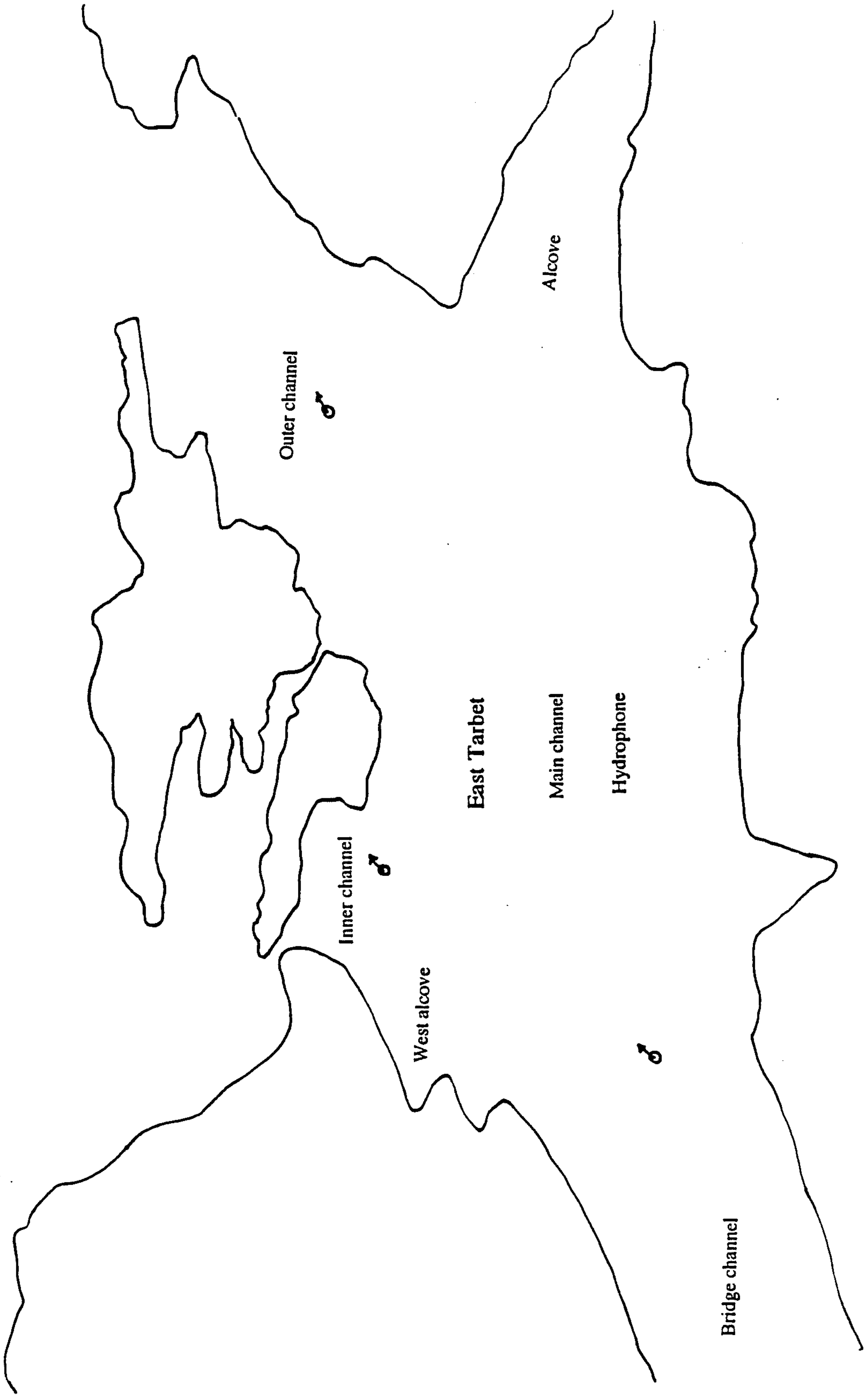

Figure 1. Sketch of the study area showing the location of three males on 13 October 1997.

Temporal variation

Underwater recordings from the Isle of May were analysed and classified into the 10 call types identified previously (see Chapter 2). The aim of the analysis was to investigate the effect of year, season, time of day (am (midnight until noon) vs pm (noon until midnight)), and number of males and females in the water on the total number of calls recorded. Only the daylight data (am data after sunrise and pm data before sunset) were used as no grey seal counts were possible during darkness. This analysis was carried out using a General Linear Model with year, season, call type, time of day, number of males and number of females as main factors, and the latter two factors as covariates. The interactions between call type and year, call type and season, call type and time of day, call type and number of males and finally call type and number of females were also calculated to see if certain call types occurred more at particular times. The null hypothesis was that all call types would be equally represented in all sessions. Therefore, temporal variation was then illustrated for the individual call types by producing a histogram of the transformed adjusted means (± 2SE) for the 3 periods for each call type. These figures show how the total number of calls of a particular call type vary with time or season.

A (ln+1) transformation was used to normalise the data for the General Linear Model.

Associations between call types

A total of 4 844 underwater vocalisations from 1997 and 1998 were examined and classified into 10 call types (see chapter 2). The interest here, was to see if certain call types were associated more than expected with each other. Since no underwater observations were possible, this analysis is restricted to looking at how call types are associated in time, irrespective of the identity of the caller. Calls were coded as events disregarding their duration and repetition rate. If a call was followed by the same call type, this was coded as a single occurrence to avoid autotransitions (Graves & Ruano 1994). Bakeman and Gottman (1997) also refer to the decision to ignore repetitions as having "structural zeros on the diagonal" in transition frequency matrices. A failure to exclude autotransitions would lead to inflated frequencies unless the divisions between bouts of the same behaviour were clear. Bouts of calling were regarded as separate events when there was 2 seconds or more between calls and referred to as sequences of coded events. Data from both years were pooled for the analysis.

Sequential analysis was carried out using the Sequential Data Interchange Standard (SDIS) and the Generalised Sequential Querier (GSEQ) programs (SDIS-GSEQ Version 1 (DOS) with User Interface (SGUI), Bakeman & Quera 1995a, b; GSW Version 3.5, Bakeman & Quera 1996). This program codes the sequences of calls: e.g. call type 1 followed by call type 2 followed by call type 1 followed by call type 3 is coded into a 1213 sequence. It then calculates the frequency of the transitions from each call type to all others (i. e. how many times call type 1 followed by call type 2, preceded by call type 3, etc.). In summary, this program defines particular two-event sequences, counts them and then reports observed and expected frequencies, transitional probabilities and adjusted residuals (i.e. z scores) for those sequences (Bakeman & Gottman 1997). Its purpose is to detect sequences that occur more commonly than expected. The transitional probability is the probability of the second event occurring, given that it follows the first event in a two-event sequence. The z score assesses the extent to which this transitional probability deviates from the base rate for the second event, that is, the simple probability of the second event overall (Bakeman & Gottman 1997). Z scores are computed using an iterative proportional fitting (IPF) procedure, also called the Deming-Stephan algorithm, which takes into account structural zeros resulting from the fact that codes cannot repeat. Bakeman (1999, personal communication) states that a common rule to identify two-event chains whose observed and expected frequencies differ significantly, is to flag any adjusted residual greater than 1.96. This is based on the assumption that adjusted residuals are normally distributed, and so the 1.96 implies an alpha = 0.05 criterion. However, another rule is to flag any adjusted residual greater than 2.58 and so a granted assumption of alpha = 0.01. Since, this study comprises many tests (90 in all) that are not independent, a more stringent alpha level will help control Type 1 error. Therefore, transitions were considered to be significant (Bakeman 1999, personal communication): (1) based on their frequency, and (2) based on adjusted residuals greater than the 2.58 absolute criterion (alpha = 0.01).

In this sequential analysis, the interest is in detecting dependence in the observations. From this, two concerns arise: whether there is an adequate number of events and the assumption of independence. One suggested requirement for using this method of analysis is that the total sample be at least 4 to 5 times the number of cells that are not structurally zero (Bakeman & Quera 1995c). Therefore, with 10 codes (10 K), the total number of transitions expected is: number of cells = K(K-1) * 4 or 5, thus a minimum number of 360 transitions. In this study, the total number of transitions (1 732) is well above the required value. A violation of independence occurs when sequential analysis uses overlapping samples (i. e. two-event sequence begins with the code that ended the previous sequence). However, Bakeman and Dorval (1989) performed a simulation study and concluded that "the apparent violation of sampling independence associated with overlapped sampling was not consequential".

Results

Temporal variation

The results of the General Linear Model are shown in Table 1. These showed that the total number of underwater vocalisations recorded did not vary significantly between years (F=0.46, df=1, p=0.500), nor between periods of the breeding season (F=2.40, df=2, p=0.093) and did not vary with the number of females in the water (F=3.09, df=1, p=0.080). The number of underwater vocalisations varied significantly between am and pm sessions (F=6.20, df=1, p=0.014), with call type (F=3.21, df=9, p=0.001) and with the number of males in the study area (F=10.76, df=1, p=0.001).

However, the results of the various interactions are more important. The breeding season was divided into three periods (start, peak and end) to investigate temporal variation in calling rate and the possible function of certain calls. For example, some calls might be used during courtship and therefore be expected to be more abundant when the females come into oestrus at the end of the breeding season. Table 1 shows that no interactions were significant except for that between call type and season (F=1.78, df=18, p=0.029). The variation in the number of underwater vocalisations recorded during the breeding season could be due to an increase in calling rate and/or an increase in the number of calling individuals. For this reason, the number of males and females visible was taken into account and used as covariates in the analysis. Thus, certain call types did occur more frequently during some periods of the breeding season than others. Figures 2-11 illustrate how each call varies with season. From these, we can see that the total number of underwater calls increases as the breeding season progresses for call type 1 (Fig.2) and call type 8 (Fig.9). It decreases for call types 2, 3, 4, 5, 6 and 7 (Figures 3, 4, 5, 6, 7 and 8 respectively). Finally, call type 9 (Fig. 10) occurs more frequently at the start and end of the breeding season, and call type 10 occurs more at the peak of the breeding season (Fig.11).

Table 1. GLM. Effect of year, season, time of day, call type, number of males and females on the total number of calls recorded.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	1	0.26	0.23	0.23	0.46	0.500
Season	2	8.97	2.38	1.19	2.40	0.093
Am vs Pm	1	5.23	3.07	3.07	6.20	0.001
Call type	9	172.52	14.30	1.59	3.21	0.014
No of males	1	7.04	5.33	5.33	10.76	0.001
No of females	1	1.53	1.53	1.53	3.09	0.080
Call type*Year	9	12.84	7.57	0.84	1.70	0.091
Call type*Season	18	33.34	15.91	0.88	1.78	0.029
Call type*Am vs Pm	9	4.53	4.75	0.53	1.07	0.390
Call type*No of males	9	1.33	1.87	0.21	0.42	0.924
Call type*No of females	9	6.27	6.27	0.70	1.41	0.187
Error	210	104.0	104.0	0.49		
Total	279	357.9				

Behavioural observations

Reliable identification from day to day was only possible for a limited number of very distinctive individuals. Therefore, the description below is biased towards these distinctive males and the number of males described represents a conservative estimate of the total number of males. The East Tarbet channel connects the open sea with Tarbet, a pool area at the foot of a slope leading to the grassy tops of the north island. At the start of the breeding season, males

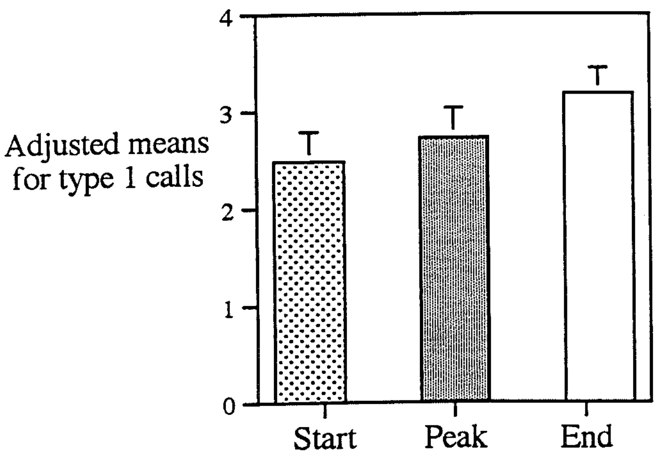

Fig. 2

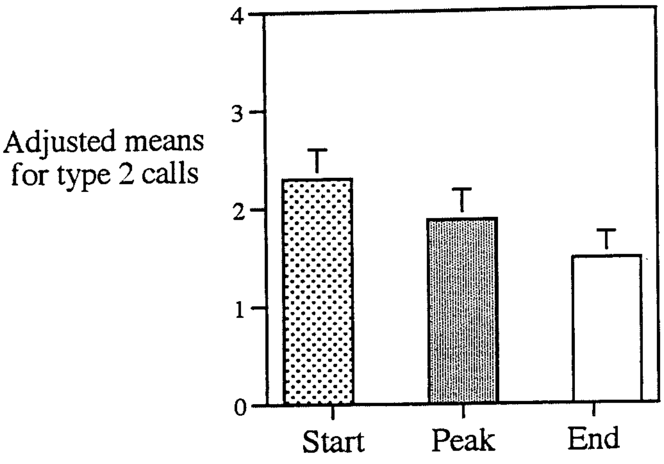

Fig. 3

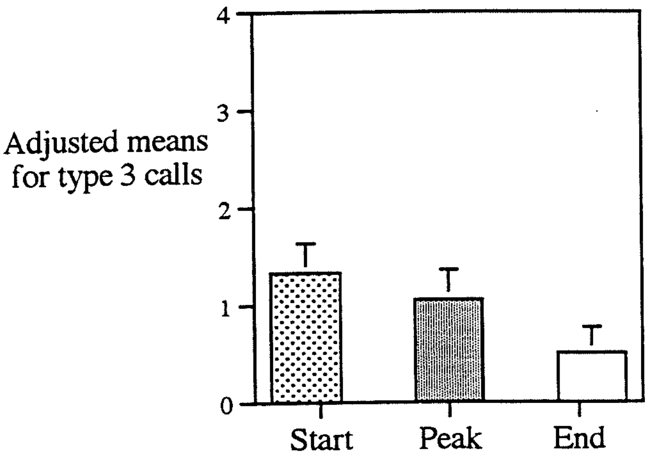

Fig. 4

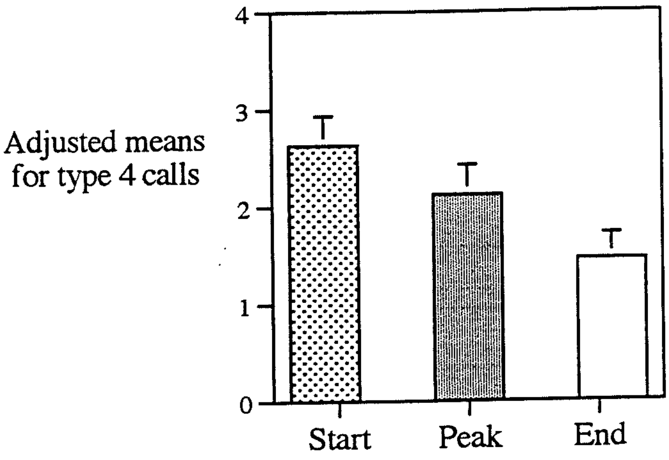

Fig. 5

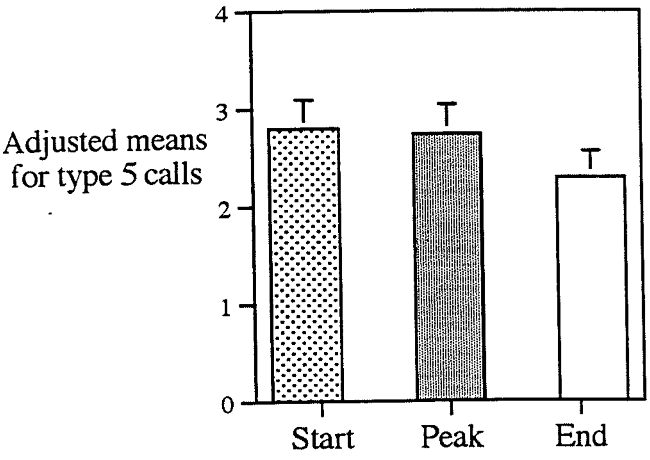

Fig. 6

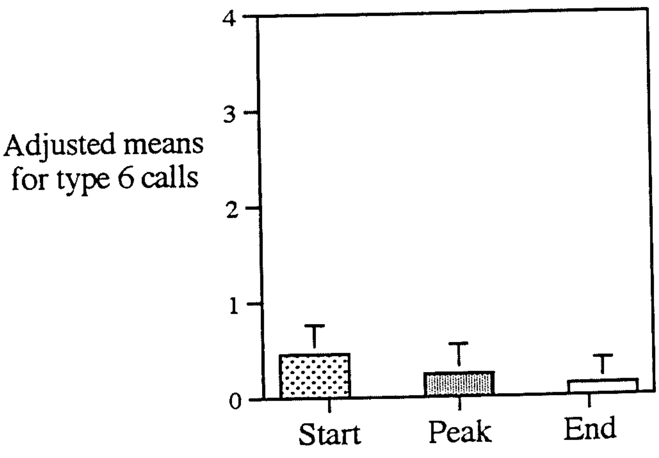

Fig. 7

Figures 2-7. Temporal variation across the breeding season for 6 different call types (Error bars= + 2SE).

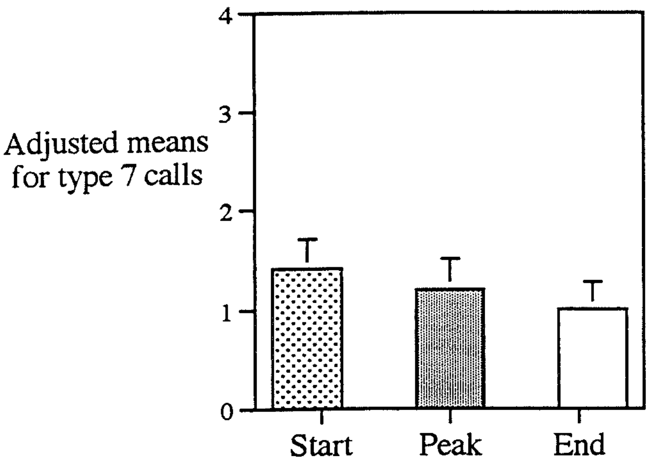

Fig.8

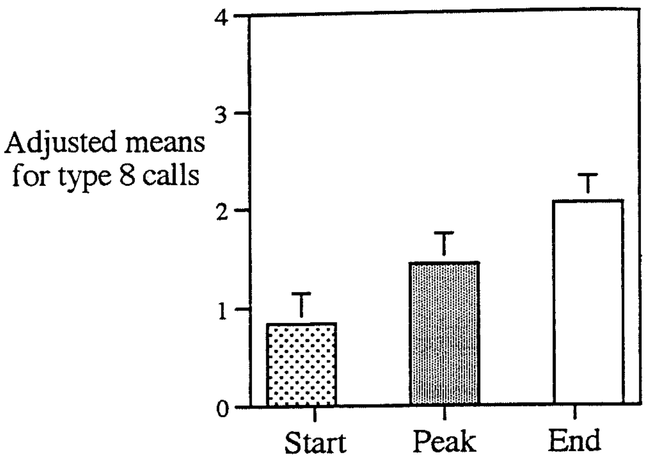

Fig.9

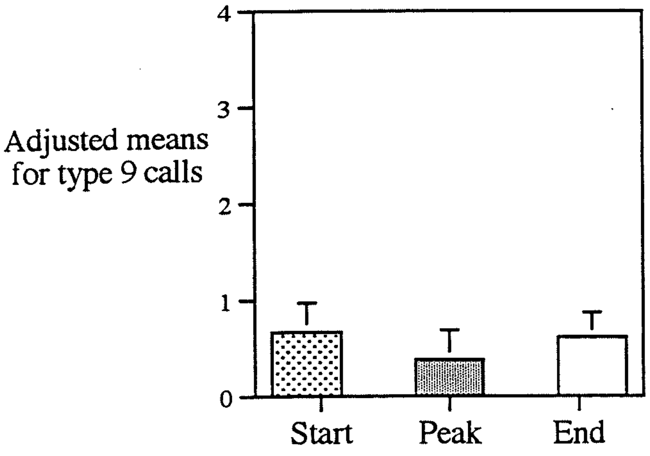

Fig.10

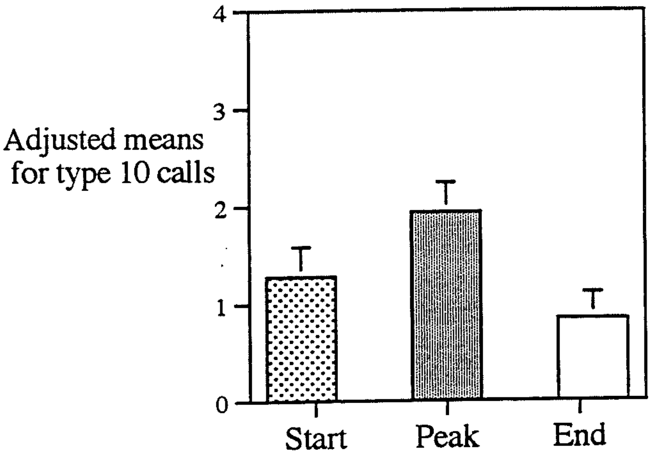

Fig.11

Figures 8-11. Temporal variation across the breeding season for 4 different call types (Error bars= + 2SE).

and pregnant females remain in the channel and only make brief trips up to the pool area. With the unfolding of the breeding season, over a hundred pups are born in the proximity of the pool. Mothers then spend considerable amounts of time in the water between suckling bouts. The increasing numbers of females (in 1997: start: mean= 13.32± 5.09 SD, peak: mean= 22.7± 5.16 SD) make the pool a very valuable area for males to occupy. Behavioural observations of male-male interactions suggest that males establish themselves in the channel before slowly making their way up the channel to challenge the male(s) in the pool.

In 1997, 10 different males were identified on more than one day (mean= 5 days ± 3.13 SD, range 2-11 days, see Figure 12) and their behaviour recorded. Two males M1 and M2 were both seen frequently (11 and 10 days respectively) at the start of the breeding season while M3 was seen less frequently (4 days). However, male M3 was not as distinctive as males M1 and M2 and was seen further away (outer channel) than the other two (main and inner channels respectively) so it is not clear whether these differences are genuine or due to problems in re-identifying individuals. Males M4, M5, M6, M7 and M8 were all seen in the study area during the peak of the breeding season and M9 and M10 during the end of the breeding season. No single male was seen in the channel for the whole duration of the breeding season. However, male M2, which was seen in the channel at the start of the breeding season, disappeared (21 October) following a fight with another male to then later become resident in the pool at the end of the breeding season (24 November). Furthermore, male M7 was seen in the alcove during the peak of the breeding season (9, 10, 11, 14, 18 November) and then reappeared at the end (27 November). At the end of the breeding season, copulations were most frequent for the males resident in the pool or resident in the channel area closest to the pool. Sexually receptive females were obliged to proceed through these areas to reach the open sea.

October 1997

6	7	8	9	10	11	12	13	14	15	16	[...]	20	21	22	23	24
M1		M1	M1	M1	M1	M1	M1	M1				M1	M1			M1
M2		M2			M2	M2	M2	M2	M2	M2			M2			
					M3		M3						M3			M4

November 1997

7	8	9	10	11	12	13	14	15	16	17	18	[...]	24	25	26	27
													M2			
M4			M4	M4			M4									
		M5	M5	M5			M5									
		M6	M6	M6			M6									
		M7	M7	M7			M7				M7					M7
		M8	M8	M8												
													M9			M9
														M10		M10

Figure 12. Diagram illustrating when individual seals were seen in the study site area in 1997.

Male-male interactions were surprisingly not frequent. Male M1 was seen chasing a male out of the study area on October 8 and a young male up Tarbet slope on October 12. Male M2 chased another male out of the study area on October 14.

In 1998, eight males were seen for more than two days (mean= 5.25 days ± 2.81 SD, range 2-11 days, see Figure 13). Male m1 was seen during the start and the peak of the breeding season (6 and 5 days respectively), while males m2, m3 and m4 were seen only during the peak period (6, 5 and 2 days). Males m5, m6, m7 and m8 were only seen at the end of the breeding season (6, 6, 3 and 3 days). Therefore, although observations were not carried out between periods, male m1 could have potentially remained in the Tarbet and East Tarbet areas for 28 days (10 October-7 November).

No male was observed during both of 1997 and 1998 breeding seasons. However, a number of land-based branded males were reliably identified in both years and found in similar areas. This suggests that some of the less distinctive males in the channel could have been the same between years. Furthermore, it can be assumed that less distinctive males may have left and come back later on in the breeding season as male M2 did in 1997.

October 1998

10	11	12	13	14	15	16	17	18	19
m1	m1		m1		m1		m1		m1

November 1998

2	3	4	5	6	7	[...]	19	20	21	22	23	24
m1		m1	m1	m1	m1							
m2	m2	m2	m2	m2	m2							
	m3	m3	m3	m3	m3							
				m4	m4							
							m5	m5	m5	m5	m5	m5
							m6	m6	m6	m6	m6	m6
										m7	m7	m7
										m8	m8	m8

Figure 13. Diagram illustrating when individual seals were seen in the study site area in 1998.

Associations between call types

A total of 2 197 calls occurred as single events (Table 2). Single events are defined as calls that are neither preceded nor followed by a different call type within 2 seconds. 40.6% of isolated calls are type 1. Type 4 was the second most frequent single event call type with 16.1%.

Table 2. Number of single events recorded for the different 10 call types.

Call types	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Totals**
Single events	892	214	62	209	353	7	57	164	18	221	2197
Frequency (%)	40.6	9.7	2.8	9.5	16.1	0.3	2.6	7.6	0.8	10.0	

However, calls were more commonly found to occur in sequences of different call types. As a result, a total of 790 sequences of calls were recorded with 1 732 transitions. The sequential analysis program coded the sequences and tabulated the observed frequencies for two-event sequences. This is illustrated in the matrix of transitions of Table 3.

From the row and column totals of table 3, it is interesting to note that sequences were more likely to begin than end with 2, 4, or 10; that sequences were more likely to end than begin with 5 and 7; and that sequences were as likely to begin as end with 1, 3, 6, 8 and 9.

Table 3. Matrix of transitions. Observed frequencies for two-event sequences.

		FOLLOWS										
	Call types	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Totals**
	1		36	23	44	69	2	16	19	3	22	**234**
P	**2**	36		24	71	98	1	4	7	2	20	**263**
R	**3**	16	38		20	16	1	0	5	0	2	**98**
E	**4**	40	93	21		118	6	8	8	2	16	**312**
C	**5**	88	95	13	180		5	30	39	12	25	**487**
E	**6**	0	8	0	7	3		0	0	0	1	**19**
D	**7**	15	10	2	9	35	0		7	11	6	**95**
E	**8**	21	8	13	11	35	0	9		2	6	**105**
S	**9**	4	2	0	4	12	0	3	6		2	**33**
	10	16	12	2	13	26	1	2	14	0		**86**
	Totals	**236**	**302**	**98**	**359**	**412**	**16**	**72**	**105**	**32**	**100**	**1732**

Moreover, the most frequent 2-event sequences were 5-4 (180 times) and 4-5 (118 times), thus alternating chains of 5-4-5-4-5-4-etc. must have been common. To determine the significant transitions, expected frequencies and adjusted residuals for two-event sequences were calculated (Tables 4 & 5).

Table 4. Expected frequencies for two-event sequences.

		FOLLOWS									
	Call types	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
	1		45.0	13.1	55.9	77.1	2.0	9.6	14.0	4.1	13.2
P	**2**	40.3		15.4	65.8	90.8	2.4	11.3	16.5	4.9	15.6
R	**3**	13.1	17.3		21.5	29.6	0.8	3.7	5.4	1.6	5.1
E	**4**	50.3	66.1	19.2		113.2	3.0	14.1	20.6	6.1	19.4
C	**5**	87.2	114.6	33.2	142.4		5.2	24.4	35.8	10.5	33.7
E	**6**	2.4	3.2	0.9	4.0	5.5		0.7	1.0	0.3	0.9
D	**7**	12.6	16.5	4.8	20.5	28.3	0.8		5.2	1.5	4.9
E	**8**	14.1	18.6	5.4	23.1	31.8	0.8	4.0		1.7	5.5
S	**9**	4.3	5.6	1.6	7.0	9.6	0.3	1.2	1.8		1.7
	10	11.5	15.2	4.4	18.8	26.0	0.7	3.2	4.7	1.4	

Thus, although 4-5 sequences were frequent, their observed frequency is close to that expected, whereas for 5-4 sequences, which are also frequent, their observed frequency is greater than expected. It is then possible to identify frequent transitions based on their frequency and identify different-from-chance transitions based on the 2.58 absolute criterion. From this, 18 transitions are found to deviate significantly from their expected values (Table 5, significant transitions in bold). Of these, 11 transitions have greater than expected observed frequencies and 7 have lower than expected observed frequencies. The significant transitions can then be graphically illustrated with transition state diagrams. Figure 14 therefore includes all transitions that have greater than expected observed values and Figure 15 includes all transitions that have lower than expected observed values. In other words 1-3, 1-10, 3-2, 4-2, 5-4, 6-2, 7-9, 8-3, 8-7, 9-8 and 10-8 two-event sequences occur more often than expected and 2-8, 8-2, 3-5, 5-3, 4-8, 8-4 and 4-7 sequences occur less frequently than expected. It is interesting to note that both 2-8 and 8-2, 3-5 and 5-3, and 4-8 and 8-4 are less common than expected. However, as mentioned before, the identity of the caller was not known. Hence, calls from a particular two-event sequence could be either produced by the same individual, or be produced by two distinct individuals. Sequences could therefore correspond to songs, and call types to syllables like in bird song (for definitions of terms see Catchpole & Slater 1996) or correspond to two animals interacting. The fact that certain calls are rarely found together could possibly reflect opposite motivational states and/or opposite functions in those two call types. Unfortunately, the function of each call type remains speculation until further work is carried out. Nevertheless, this analysis shows that some particular call types are associated in time suggesting a possible functional significance to these sequences.

Table 5. Adjusted residuals for two-event sequences. (Significant transitions in bold)

		FOLLOWS									
	Call types	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
	1		-1.58	**3.05**	-1.92	-1.13	-0.03	2.28	1.47	-0.60	**2.67**
P	**2**	-0.80		2.46	0.78	0.94	-0.99	-2.40	**-2.63**	-1.42	1.25
R	**3**	0.87	**5.65**		-0.37	**-2.95**	0.25	-2.02	-0.18	-1.31	-1.45
E	**4**	-1.73	**4.02**	0.47		0.56	1.92	-1.82	**-3.17**	-1.84	-0.89
C	**5**	0.11	-2.37	**-4.26**	**4.18**		-0.11	1.37	0.66	0.55	-1.82
E	**6**	-1.69	**2.96**	-1.00	1.70	-1.23		-0.85	-1.04	-0.55	0.06
D	**7**	0.76	-1.82	-1.35	**-2.94**	1.48	-0.90		0.86	**8.01**	0.55
E	**8**	2.02	**-2.79**	**3.48**	**-2.91**	0.66	-0.95	**2.68**		0.24	0.24
S	**9**	-0.15	-1.70	-1.33	-1.28	0.88	-0.51	1.70	**3.34**		0.28
	10	1.45	-0.92	-1.21	-1.55	0.00	0.38	-0.72	**4.51**	-1.22	

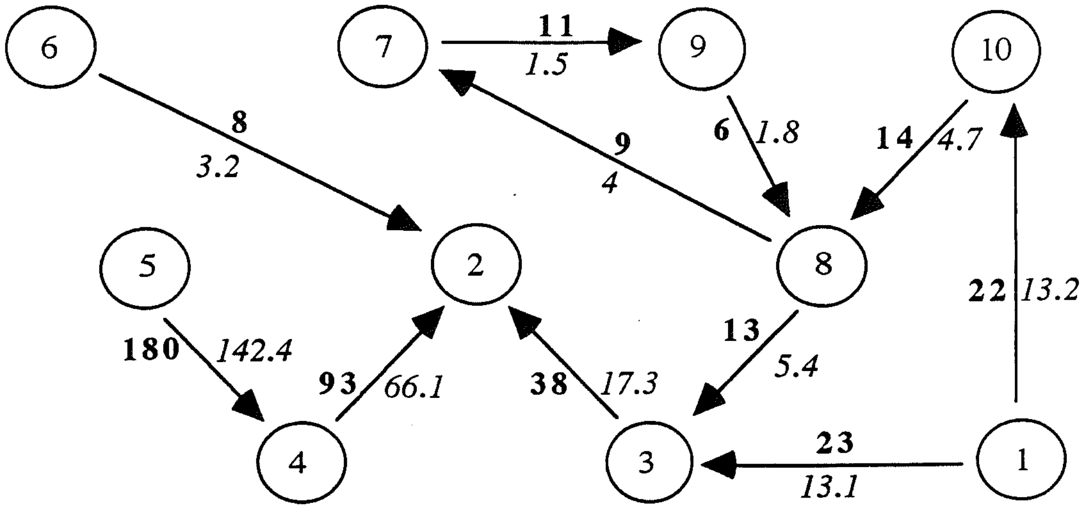

Figure 14. Flow diagram illustrating the two-event sequences with significantly higher than expected observed frequencies. Observed frequencies in bold and expected frequencies in italic

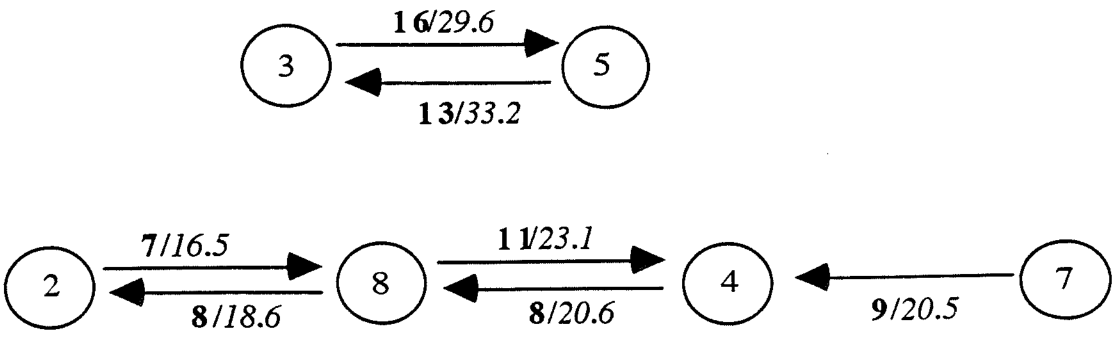

Figure 15. Flow diagram illustrating the two-event sequences with significantly lower than expected observed frequencies. Observed frequencies in bold and expected frequencies in italic

Discussion

An analysis of the temporal variation in the underwater vocalisations of grey seals was carried out to see if certain calls occur more often during a particular period of the breeding season. The idea was that, if a particular call type is only used in mate attraction, for example, it would be more frequent at the end of the breeding season when the females come into oestrus after weaning their pup. However, very little is known about the function of the underwater repertoire, so the temporal trends can only remain descriptive and their function speculative. The total number of underwater vocalisations was found to vary with call type and time of season. For example, call types 1 and 8 showed an increasing trend while call types 2, 3, 4, 5, 6 and 7 all showed a decrease as the breeding season went on. Since the number of males and females were taken into account, these differences are due to changes in calling rates and not caused by an increase in seal numbers. Unfortunately, rough seas and heavy surf did not allow rigorous daily behavioural observations of surface interactions. Only a few male-male encounters were reported. No direct link between call type and a particular surface behaviour was therefore possible. Furthermore, no behavioural observations were possible under the water, so establishing the function of each call type remains entirely speculative. However, the presence of significant associations between particular call types suggests that, either certain calls are only produced by certain individuals or that they vary in function and so in context. Three two-event transitions were found to be significant such that each call type is followed and preceded less often than expected by the other call type (3-5 & 5-3, 2-8 & 8-2, 4-8 & 8-4). These pair of call types could therefore have very different functions. Furthermore, certain calls followed each more than expected by chance. A striking point is that these relationships are not symmetrical suggesting genuine sequences rather than associations. To understand the acoustic communication of grey seals more fully, it will be essential to establish the identity of the caller. The use of captive seals may help although captivity might change their social behaviour. A better alternative might be to use an underwater camera such as the newly developed underwater video camera system Crittercam in conjunction with a underwater tape recorder unit. This camera can be attached to the head or back of the animal and so provide valuable information on the social context and possible function of individual calls.

The observation of the spatial distribution of males within the study area provided some interesting patterns suggestive of possible underwater territories. Grey seals have been assumed to be land breeders. Females come ashore, form predictable breeding aggregations (Pomeroy et al. 1994), and give birth to a single pup. Males compete aggressively to maintain positions within these female aggregations and behavioural observations suggested that a small number of dominant males fathered most of the offspring (Anderson et al. 1975, Boness & James 1979). However, recent discrepancies between behavioural observations and paternity data, as determined by genetic analysis, have suggested that underwater matings may be more frequent than first imagined (Amos et al. 1995, Worthington Wilmer et al. 1999, 2000). The application of molecular genetics to the analysis of paternity in grey seals has revealed a far more complicated mating system than previously assumed. Indeed, Worthington Wilmer et al (2000) showed that behavioural dominance is only found in a handful of males located near the centre of the colony and that the vast majority of the pups are fathered by any of a large number of males who all share equal success. Although intense sampling was carried out, Worthington Wilmer et al. (2000) found that only 200-300 males of the 900+ males having genetic input to each colony's cohort of pups were actually sampled, suggesting that many pups are conceived outside the main colony in either time or space. In support of this, an aquatic mating between a mature grey seal bull and a cow was observed away from the normal breeding beaches by Watkins (1990). Therefore, underwater matings may play a more important role in the grey seal mating system than previously thought. It is necessary at this point to distinguish between the possibility of aquatic matings in the open sea and ones that can be characterised as inshore matings (Worthington Wilmer et al. 1999). These latter would occur within tidal inlets and provide males with an opportunity to defend a relative enclosed space and access to females. It is this relatively enclosed space that males were seen to defend in this study. Although observations of male-male encounters were not frequent in this study, grey seal males did show a spatial distribution suggestive of underwater territories. Indeed, despite the boundaries being not clear and the length of tenure highly variable, particular males remained in the same area and did chase intruders away (eg. Males M1 and M2). Furthermore, grey seals have been found to be more vocal underwater than previously thought. It would therefore not be surprising that grey seals use underwater vocalisations in mate attraction and/or competition between males. As previously mentioned, harbour seal males engage in stereotypic diving and acoustic displays and use dispersed but small territories in areas near haul-out sites, around female foraging areas and along female transit routes (Hanggi & Schusterman 1992, Coltman 1997, Van Parijs 1997). Furthermore, leopard and Weddell seals also use underwater vocalisations to compete for females around breathing holes.

Therefore, although direct evidence in grey seals is weak, behavioural observations of the spatial distribution of males is suggestive of underwater territories and worthy of further research. This could be achieved through a mixture of radiotagging of the males and intense behavioural observations. Improved tracking and resighting of the seals would provide answers to the questions of whether less distinctive seals do actually return to the same area later on in the season, how long males stay in the same area, which males chase others and so on. Then, the relationship between social behaviour and underwater vocalisations could be investigated using underwater cameras and captive seals. So despite extensive work on the physiology and behaviour of grey seals, a lot remains to be done to achieve a better understanding of their acoustic communication.

Chapter 4

Individually distinctive pup vocalisations fail to prevent allo-suckling in grey seals*

Abstract

In crowded aggregations that occur in breeding colonies, female pinnipeds commonly become separated from their pups and may use spatial, olfactory, or auditory cues to locate them. A system of mutual recognition based on vocalisations is known for otariids. Female phocids are known to use location and olfaction to help identify pups, but evidence for vocal recognition is weak. During the 1997 breeding season on the Isle of May, Scotland, vocalisations were recorded from grey seal, *Halichoerus grypus*, pups; playback experiments were carried out; and nursing of non-filial pups was observed. Pup vocalisations were found to be both stereotyped and individually distinctive, features normally associated with a system of individual recognition. However, playback experiments revealed that mothers did not respond more to vocalisations of their own pup than to those of non-filial pups. Furthermore, seventeen cases of allo-suckling were observed during 68 hours of observation on the colony. High densities of animals and frequent separations present challenges to identification of pups by their mothers.

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Introduction

Recognition between females and their offspring is important in many species of mammals, especially where offspring are mobile or separated from their mothers for long periods, as often occurs in pinnipeds. Parental care, fostering behaviour, and mechanisms of mother-pup recognition in pinnipeds have been extensively studied in both the eared (Otariidae) and true (Phocidae) seals.

Breeding systems of otariids and phocids differ, suggesting different selective pressures on individual recognition. Otariids are uniformly polygynous, and normally breed in high-density terrestrial colonies. Females come ashore annually to give birth and copulate with territorial males. Nursing lasts from two months to three or more years in different species (Insley 1992). Mothers remain with their newborn pups for approximately the first week after birth, then alternate between attendance of pups and feeding trips at sea (Anderson 1990). When mothers are absent at sea, pups frequently wander and aggregate in groups with other pups. Mothers often threaten or attack non-filial pups when searching for their own. The frequent separations between mothers and pups, and the danger of injury to pups from non-filial females, have selected for a system of recognition based partly on vocalisations (e.g. Roux and Jouventin 1987; Gisiner and Schusterman 1991; Miller 1991; Hanggi 1992; Insley 1992).

Breeding systems of phocids are more diverse, and the nursing period is briefer, lasting from only a few days to 8 weeks (Anderson 1990). Typically, mothers stay with their pups nearly continuously from birth until weaning, then copulate. However, separations occur in crowded breeding aggregations because of aggressive encounters between adults and their consequential movements, or because of ice movements when females are in the water, which suggest that a system of recognition like that in otariids may occur. This topic has been investigated little in phocids. Renouf (1984, 1985) and Petrinovich (1974) demonstrated mother-pup recognition, in the harbour seal, *Phoca vitulina*, and the elephant seal, *Mirounga angustirostris*, respectively. Conversely, females do not recognise their offspring by vocal cues in the Hawaiian monk seal, *Monachus schauinslandi.* (Boness 1990; Job et al. 1995) or largha seal, *Phoca largha* (Burns et al. 1972).

In spite of extensive research on the grey seal, *Halichoerus grypus*, evidence for mother-pup recognition in this species is sparse (Fogden 1971). High breeding densities, and temporary separations following aggressive encounters between adults, can lead to long term separations between mothers and pups, that can cause confusion among mothers over pup identity. Starvation, as a consequence of long term separations, was found to account for 50% of pup mortality on the Isle of May (Baker and Baker 1988). Fostering and allo-suckling occurs but is highly variable between colonies. Boness (1990) defined fostering behaviour as "care given to a young in replacement of that given by its mother" and described a complex pattern of fostering in the Hawaiian monk seal where mothers started by nursing their own pup, and then went on to nurse one or more non-filial pups in addition to or replacement of their own. Mothers nursed on average 2.3 non-filial pups during the 40-day lactation period some very briefly while others for a longer period of time (mean: 7.7 ± 8.0 days, Boness 1990). The term allo-suckling was preferred to fostering behaviour and defined here as care given to a pup in replacement of or in addition to that given by its mother. In this definition, the mother does not necessarily provide exclusive care for another's offspring and care can be simultaneous or sequential to nursing her own pup. Haller et al. (1996) observed no allo-suckling in a breeding aggregation on landfast ice at Amet Island, Nova Scotia and Boness (1990) reported the incidence of lactating females that fostered to range from 5% on Sable Island, Nova Scotia, to 75% on Ramsey Island, Wales. Kovacs (1987) reported fostering or adoption as "not common" on the Isle of May, Scotland.

In this study, we recorded and analysed sonagrams of pup vocalisations to evaluate individual differences at 3 areas on the Isle of May colony. We then used playback experiments to investigate mother-pup recognition. If pup vocalisations are stereotyped and individually distinctive, we would expect the frequency of allo-suckling to be low in the absence of other factors.

Methods

Study animals, sites and behavioural data collection

The Isle of May is a small uninhabited island (2 x 0.5 km) in the Firth of Forth, Scotland, where grey seals breed in October and November; 1770 pups were born in 1997 (Sea Mammal Research Unit, C. D. Duck, NERC). Typically, a mother comes ashore, gives birth to a single pup, nurses it for 14-20 days, and mates before returning to sea. The maternal attendance pattern on the pup is variable, however: some mothers attend the pup continuously, whereas others spend much time in the water (Twiss et al. in press).

Ad libitum behavioural observations and continuous-event sampling were carried out at three sites (Kaimes, Kirkhaven and Tarbet) during the 1997 breeding season. Tape recordings of pup vocalisations were obtained and playback experiments were carried out at Kaimes and Kirkhaven.

The breeding sites vary greatly in topography and in density of breeding females. Kaimes and Kirkhaven have been colonised by breeding grey seals only within the last few years. The former is a tidal gully and the latter has a sandy beach at the head of a rocky inlet that forms the island's main harbour; both experience limited human disturbance. Thirty hours of observations over 5 days were carried out at Kaimes, when female numbers fluctuated between 8 and 21, and pup numbers increased from 11 to 20. Eight hours of behavioural observations were carried out over 2 days at Kirkhaven. The third study site was at Tarbet, on a rocky slope that connects a channel leading to the open sea with the flat grassy top of the north island. Thirty pups and more than 40 females were observed there during 30 hours of behavioural observations over a period of 8 days.

Recordings and sound analysis of pup vocalisations

Pup calls were recorded at a range of 2-15 m using a Marantz CP430 tape recorder and a Sennheiser ME80 gun microphone with an integral windshield. Recordings were analysed with the RTS digital sound analysis system (Signal program; Engineering Design, Belmont, Massachusetts) (FFT size: 256, frequency resolution: 29 Hz, time resolution: 34.0 ms , weighting function: Hanning). Signals were filtered using a bandpass filter (<10 and >2700 Hz). All measurements of temporal and frequency parameters were made directly from the spectrograms on the screen (cursor error: ± 9 ms, ± 10 Hz).

Two hundred and sixteen clear vocalisations from 20 pups (3-37 calls per pup, 2-6 days of age) were analysed. For each call, total duration (DURTOT) (i) was the only temporal variable measured. Frequency variables measured on the first harmonic were: (ii) beginning frequency (BFREQ); (iii) ending frequency (EFREQ); (iv) maximal frequency (MAXFREQ); (v) minimal frequency (MINFREQ); and (vi) the frequency sweep (SWEEP), measured as the difference between the minimal and maximal frequency of the second harmonic. All frequency measurements were taken at the centre of the trace. To characterise the entire call, the following variables were used: (vii) number of call parts; (viii) presence or absence of broadband noise; (ix) presence or absence of rhythmic frequency modulation (FM); frequency trends at the (x) start and (xii) end of the call (flat, rising or falling); and (xii) spectral richness (SR) that reflects the spacing between harmonics as described by Miller and Murray (1995). Spectral richness was coded as 0 when broadband noise was present, as 1 when the separation between harmonics was greater than the width of a harmonic band, as 2 when the separation is equal to the width of a harmonic band, and as 3 when the harmonic bands are very close together. Figure 1 illustrates some of the acoustic parameters measured for each call.

Playback experiments

Sixteen mother-pup pairs were used for this part of the study. Pups and mothers were not marked, but natural markings including scars and pelage patterns, used in combination with location allowed for reliable identification. Recordings of pup vocalisations were made on day 1 of the study. Observations were made on day 2 to see whether a focal mother was still paired with her pup. If this was the case, then the pair was included in the playback experiments. A pairwise-comparison design was used. Two mother-pup pairs were matched such that the pups were of about equal age (± 2 days). Each test comprised of periods of behavioural observation and a minimum of two playbacks. Each playback involved either the calls of the mother's own pup or those of the non-filial pup (i.e. the other female's pup in the pairwise comparison).

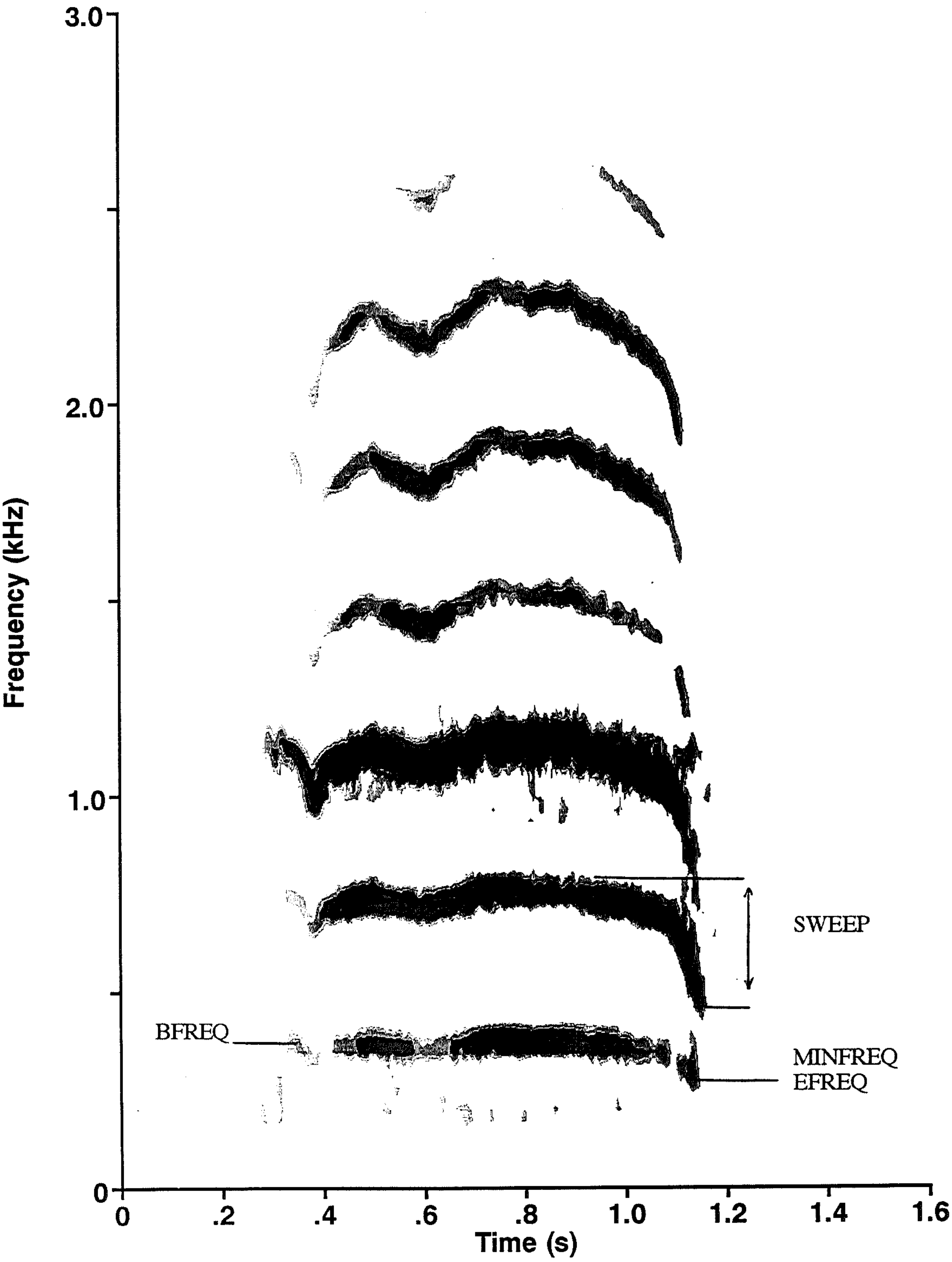

Figure 1. Sonagram illustrating some of the acoustic variables used.

Behaviour of the focal mother was recorded using a Sony video-camera for later analysis. Each test followed the pattern illustrated in Figure 2.

Figure 2. Schedule illustrating the periods of behavioural observations preceding and following the playback experiments:

Behavioural observations: BO <--->
Playback 1: pb1 ***
Playback 2: pb2 ###

BO pb1 BO pb2 BO
<-------------->***<-------------------------------->###<---------------->
0_________ 5-6 _________ 10 _________ 15-16 _________20 (Time in min)

The order of presentation of the playbacks was counterbalanced. Four pairs of females received the own pup playback first followed by the non-filial pup playback, and 4 received the non-filial pup playback first. Each playback consisted of a minute-long series of calls. The loudspeaker, a Nagra DSM with a 10-m coaxial lead, was placed as close to the mother as possible, which in practice was 5-10 m. All the equipment and the observer were concealed behind a stone wall and mother-pup pairs near this location were chosen for the playbacks to minimise disturbance.

Playbacks were separated by only 10 minutes to minimise possible changes in conditions (i.e. location of mother and pup, nursing stage of pup, interference from a male or neighbouring female). During analysis, movements towards and away from the loudspeaker were scored for 2 min prior to the onset of the playback (pre-trial period) and for 2 min following the onset of the playback (trial period). Three categories of maternal response to the playback stimulus were defined. Whole-body movement was considered a stronger response and given a score of 3, this required the female to move and change location. Stretched-neck posture, also referred to as "alert" (Haller et al. 1996; Tinker et al. 1995) was given a score of 2, this required the female to support herself on her foreflippers with her head and upper body elevated from the substrate and direct her head towards a particular area. Head turn was given a score of 1, this required the female to look and listen. Flippering and scratching and comfort movements of the female were also recorded, as were the location and activity of her pup and of other neighbouring females. Fogden (1971) described flippering as the action of "extending one of its foreflippers, flexing the digits and rapidly moving the flipper backwards and forwards in a scratching motion". Moreover, Ballard & Kovacs (1995) described comfort movements as "an animal prone and performing low-intensity activities including weight shifting, stretching, and scratching without changing location".

Statistical analysis

Pup vocalisations

Minitab 11.21 for Windows was used for the analysis of the pup vocalisations. To assess variation between pup calls, a one-way analysis of variance was conducted for each of the following variables: DURTOT, BFREQ, MAXFREQ, MINFREQ, and SWEEP. A stepwise, cross-validated discriminant function analysis (DFA) was performed to determine the probability of correctly assigning a vocalisation to a specific pup.

Playback experiments

All computations for this part of the study used Minitab 8.2. Movement scores were calculated as the difference between trial and pre-trial total number of movements towards the loudspeaker minus the equivalent for movements away from the loudspeaker. A Wilcoxon signed-ranks test was performed on the result of the two trials to test whether the response of the mother to her own's pup's call was greater in the trial versus the pretrial. To test for an order effect, a Mann-Whitney test between the 8 mothers with own pup first and the 8 with non-filial pup first was carried out. A chi-square goodness of fit test was used to test the effect of playback. The number of mothers that responded more during the playback than the pre-trial were compared to expected frequencies.

Results

Acoustic structure of pup calls

Descriptive statistics for the 216 vocalisations recorded from 20 grey seal pups are shown in Table I. The calls contained true harmonics and were sometimes spectrally complex. They varied in their beginning and ending frequency trends, with the majority flat at the start and falling in frequency at the end. In the example shown in Figure 1, BFREQ is the same as MAXFREQ and EFREQ is the same as MINFREQ. This call has a flat BFREQ, a falling EFREQ, no FM, no noise and SR equal to 1. Calls from two different pups are shown in Figure 3.

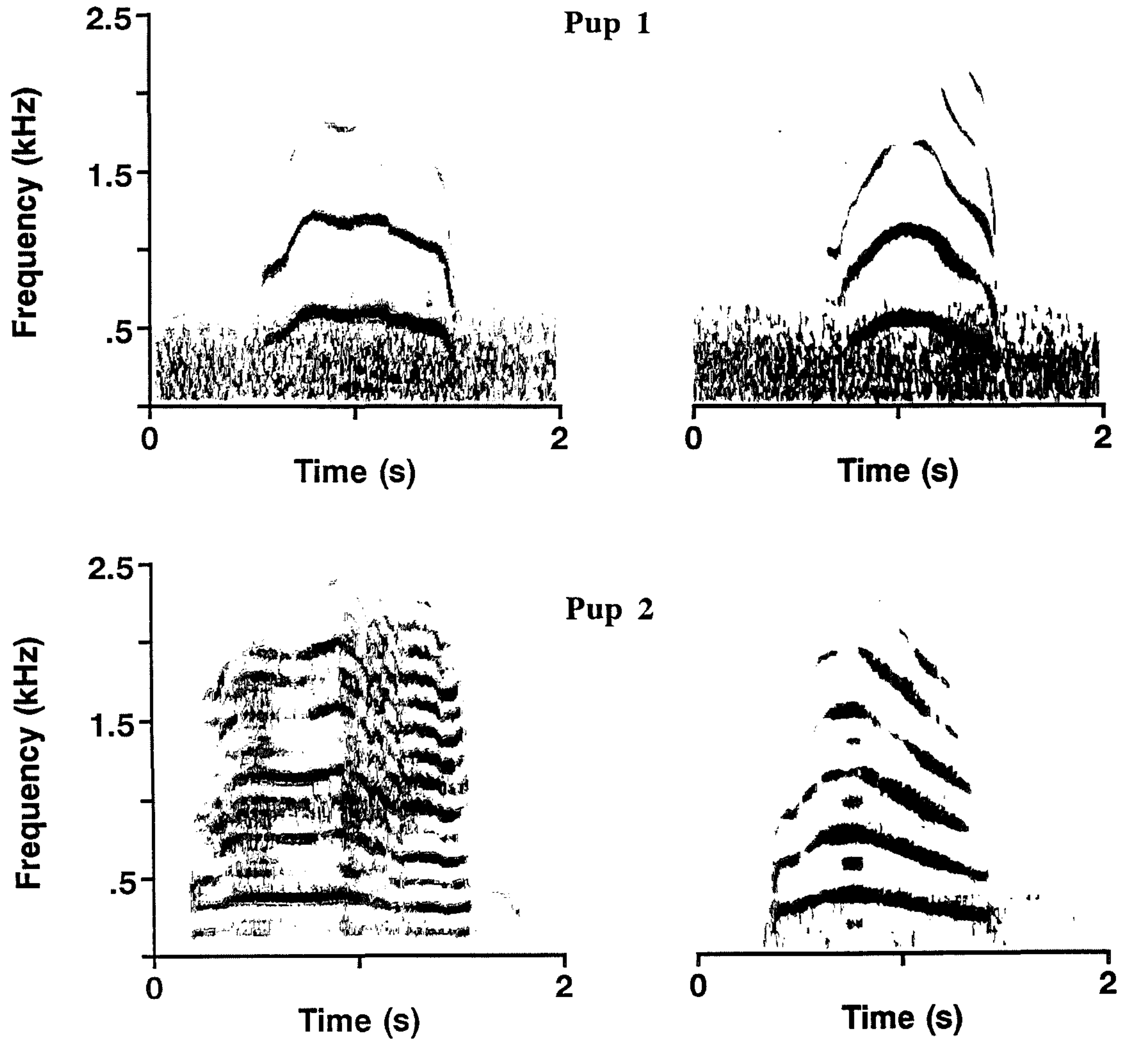

Figure 3. Illustration of between and within differences in grey seal pup vocalisations

Between pup variation of calls

One-way analysis of variance revealed significant differences between pups for all frequency and duration variables (Table I). The coefficients of variation (CV) based on the mean of pup means are shown in Table I. Discriminant function analysis (cross-validated) assigned individual vocalisations to the pup producing the call in 68 out of 216 cases (31.5%). To estimate the number expected at random, bootstrapping was used and 10,000 simulations were run in the program Resampling Stats (Arlington, Virginia). The average number of correct assignments expected at random was 16.9 (Figure 4). The 68 achieved through DFA was thus highly significant ($p<0.0001$). This was not due to differences in sample size between pups, as no correlation was found between sample size and the proportion of calls correctly classified (Pearson's correlation, $r = -0.193$, $N=18$, $p>0.05$). These results show that pup vocalisations have acoustic structures that allow for classification by DFA and that there is greater variation between rather than within pups.

Table I: Descriptive statistics on vocalisations from 20 grey seal pups (number of calls per pup 3-37), and results of analysis of variance.

Variable	Mean of pup means ± SD	CV	Anova	
			F	p
DURTOT (ms)	991 ± 399	40.3	5.8	0.001
BFREQ (Hz)	313 ± 85.1	35.8	9.1	0.001
EFREQ (Hz)	237 ± 51.6	21.7	*	*
MAXFREQ (Hz)	410 ± 97.6	23.8	28.4	0.001
MINFREQ (Hz)	252 ± 48.5	19.3	9.8	0.001
SWEEP (Hz)	292 ± 139	47.4	10.1	0.001
	Mean percentage of SR ± SD			
SR, level zero	6.4 ± 15.6			
SR, level one	78.6 ± 28.1			
SR, level two	13.9 ± 24.6			
SR, level three	1.1 ± 6.1			

* data could not be transformed

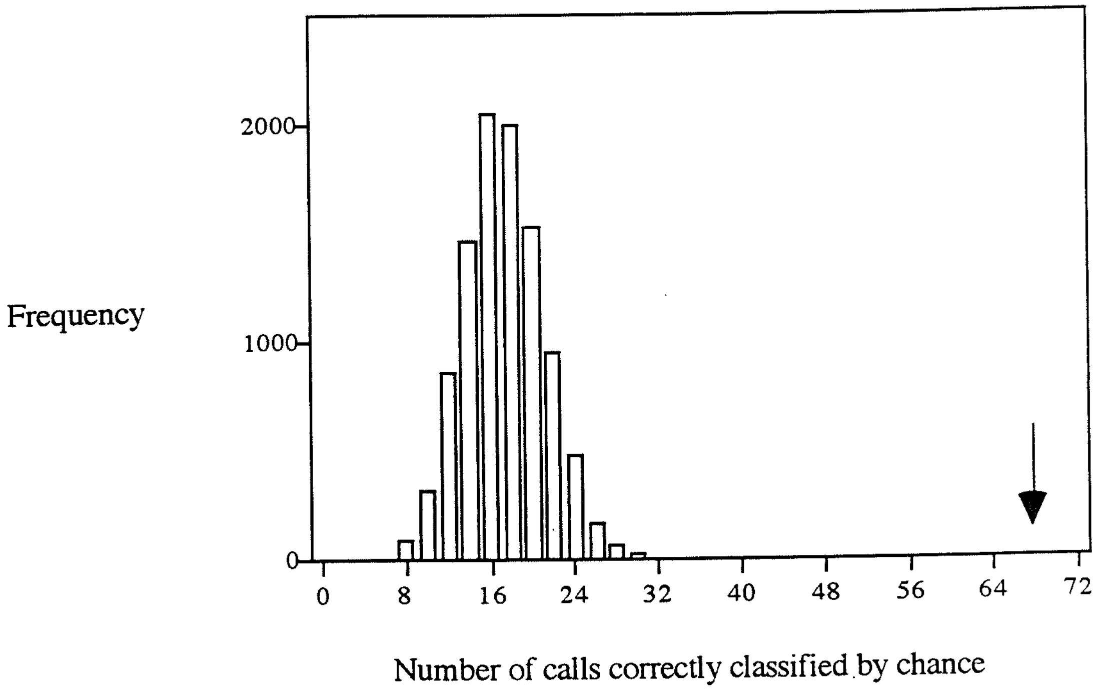

Figure 4. The expected number of calls correctly classified by chance is 16.9. The arrow shows the result achieved through DFA for 216 calls

Mother-pup recognition

Fourteen of 16 mothers showed more net movements towards the loudspeaker than away from it, suggesting that mothers responded to the playbacks. Movements of females are illustrated in Figure 5 for the 8 mothers that received the own pup playback first and for the 8 mothers that received the non-filial pup playback first. Order of presentation of playbacks showed no effect (Mann-Whitney: U=64.5, N_1= N_2= 8, p=0.49). The results of the two sequences were thus combined, and showed no significant difference in movement between the own-pup and non-filial-pup playback trials (Wilcoxon test: T=69.5, N=16, p=0.96). However, the overall number of movements did show an effect of playback (χ^2- test, χ^2=9.0, df=1, p=0.003), with more during playback than before it.

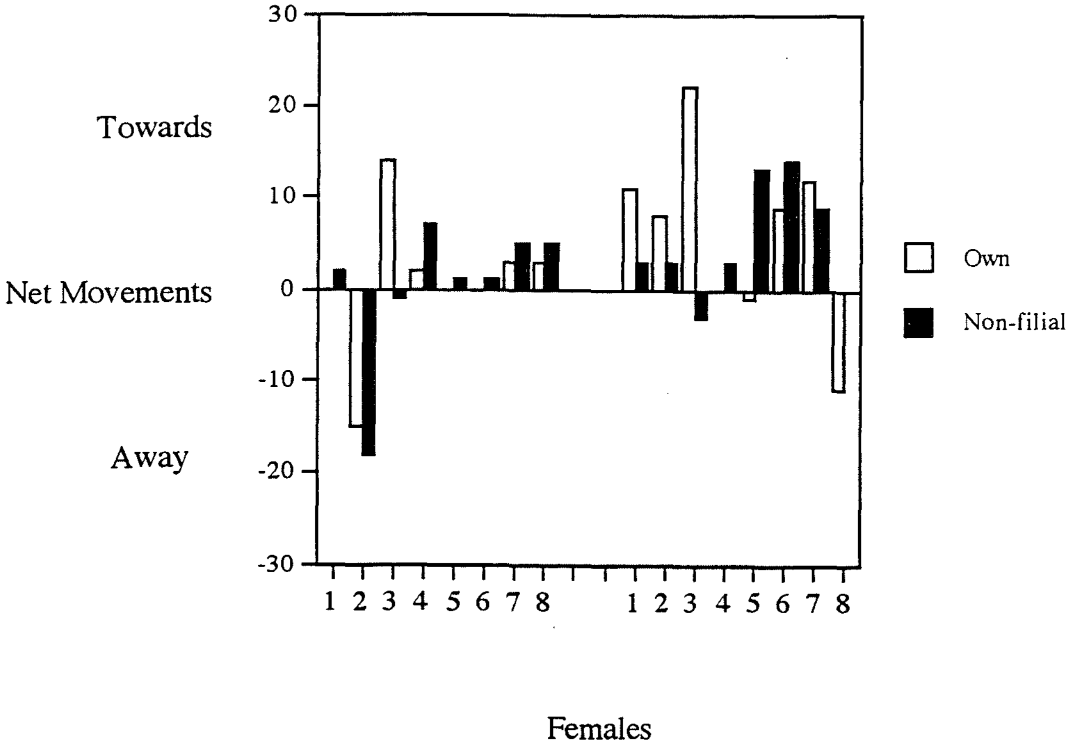

Figure 5. Difference between number of movements towards and away from speaker in mothers given own pup playback first (left) and those given non-filial pup playback first (right)

Fostering behaviour

Behavioural observations at all sites (n=15 days) revealed 17 cases of mothers nursing non-filial pups. At Kaimes there were 7 cases of such behaviour. The number of females present during the days of observation varied between 8 and 21. In one case, a mother nursed the same two pups indiscriminately for 4 out of the 5 days of observations. Six other mothers were seen to nurse two different pups on separate occasions. Two cases of mothers nursing non-filial pups were observed at Kirkhaven. In the first case, a mother nursed two different pups in quick succession. In the second case, a pup was seen to approach and start to suck from a female without her showing any of the smelling and nuzzling behaviour that mothers usually show towards their pups (Fogden 1968, 1971). It was then observed that the female was in the process of giving birth. The pup nursing was also very young and assumed to be non-filial. The first pup continued to suck and, after giving birth, the female attacked the newborn and swam away with the non-filial pup. Her own pup was never seen to feed and was assumed to have died. At Tarbet, five females were seen to nurse two different pups on separate occasions and one female nursed two pups at the same time. One female was seen feeding three pups in succession on 1 day, and then two different pups on the following 3 days. Another female fed a pup that had been weaned by its mother, followed by her own 3- to 4- day old pup, and later a third pup.

Discussion

It was found that pup vocalisations are stereotyped and individually distinctive, as necessary for individual recognition. However, the playback experiments detected no difference between responses of mothers to their own and non-filial pup's vocalisations. Furthermore, nursing of non-filial pups was found to be more widespread than reported previously (Kovacs 1995). Therefore, it appears that female grey seals in this study do not use all the information contained in pup vocalisations to discriminate pups.

Although our knowledge of the function of vocalisations remains limited, descriptions of acoustic repertoires are available for most pinnipeds (for review see Miller and Job 1992). Airborne vocalisations of grey seals have been anecdotally described during the breeding season in a few behavioural studies (pup begging call (Fogden 1971) and vocal displays from bulls (eg. Anderson 1978)). However, only three studies have given detailed descriptions and spectrograms of airborne sounds. Schneider (1974) described 7 call types (wail, moan, male roar, female warble, open-mouthed cough, snort and infant cry) recorded in wild and captive grey seals of the western Atlantic population. Boness and James (1979) recorded on Sable Island a pure tone call with a gradual onset that carries "sounds like the falsetto part of a yodel". This call has never been reported in any of the European colonies. Caudron et al. (1998) analysed the acoustic structure and individual variation of grey seal pup calls from a Barents sea colony and found pup calls to be individually distinctive. For a long time, grey seals were thought not to be very vocal underwater. However, recordings from Schevill et al. (1963), Schusterman et al. (1970), Schneider (1974) and more recently Asselin and Hammill (1993) have shown that grey seals are rather vocal underwater during the breeding season. Although a few studies have provided descriptions of some grey seal airborne and underwater vocalisations, the function of these calls remains speculative.

The difficulty in observing some species of pinnipeds has often led to the assumption that vocalisations are used in mate attraction and territorial defence. However, a few studies have investigated the function of specific calls in more detail. Shipley et al. (1981, 1986) suggested that male, northern elephant seal, stereotyped threat calls are used in individual recognition and dominance status. The Subantarctic, *Arctocephalus tropicalis*, the New Zealand, *A. forsteri*, and the south Australian, *A. pusillus doriferus* fur seals also use calls for individual recognition (Stirling and Warneke 1971; Roux and Jouventin 1987). Furthermore, Hanggi and Schusterman (1994) showed individual differences in male harbour seal underwater vocalisations and Renouf (1984; 1985) demonstrated how pup calls are used in mother-pup recognition. Therefore, it is not clear why grey seal pup calls are stereotyped and individually distinctive, but are not used in vocal recognition.

Riedman (1982) reviewed alloparental care and adoption in birds and mammals and put forward various hypotheses for its evolution. Environmental conditions such as unpredictable access to food, breeding sites and mates appear to create conditions that favour the communal rearing of young. Riedman suggested that this enhances inclusive fitness in species where there is high kinship between the foster parent and fostered young (e.g. lions, elephants, and baboons). A foster parent may gain valuable parental experience and the young one may benefit from increased chances of survival. However, benefits are not always mutual. Some adults exploit dependent young to temporarily increase their status (e.g. in macaques), while recognition errors are taken advantage of in other species (e.g. brood parasites). Boness (1990) and Riedman & LeBoeuf (1982) investigated fostering behaviour in the Hawaiian monk seal, and northern elephant seal, respectively. High levels of allo-suckling were observed in Hawaiian monk seals (Boness 1990). Pups that nursed from non-filial females were expected to have reduced suckling periods, be smaller at weaning and as a result have a lower survivorship to one year of age. However, no correlation was found between these measures of reproductive success and degree of fostering. Boness (1990) concluded that "high levels of fostering may be maintained in monk seals because they are not selected against". Riedman & LeBoeuf (1982) suggested that female northern elephant seals may even benefit from fostering by maintaining a regular reproductive cycle, through relatedness to fostered pups and increased maternal experience. Fogden (1971) even suggested that pups do not benefit from "inconsistent suckling partnerships" as feeding patterns become disrupted.

Although the costs of allo-suckling are unknown in grey seals, evidence of mate fidelity (Amos et al. 1993, 1995) and breeding-site fidelity (Twiss et al. 1994; Pomeroy et al. 1994) could point to high local levels of relatedness between grey seals in some locations. By implication, kin selection may be a factor in the maintenance of allo-suckling. However, the results of a DNA fingerprinting study by Perry et al. (1998) on grey seal fostering at Ramsey Island, Wales, did not support this hypothesis. Mean relatedness did not differ between filial-foster pup pairs and unrelated pup pairs on the same beaches. There was also no increased variation in relatedness in this small colony. Mothers at Ramsey Island suckled non-filial pups at random. Perry et al. (1998) concluded that in grey seals, fostering may not produce "any direct benefits that outweigh its costs but, rather, there are benefits to colonial breeding that compensate for the cost of fostering". Despite the cases of allo-suckling reported in this study, most females from all examined sites suckled their own pup exclusively, and attacked all non-filial pups. Allo-suckling remains the exception rather than the rule in grey seals. The occurrence of allo-suckling in this study was recorded from newly colonised sites around the periphery of the established breeding colony. It is likely that young and inexperienced females are more frequent here and it is these females that may be more likely to confuse pups (Pomeroy et al. in press).

This study has demonstrated that the acoustic structure of pup vocalisations would allow individual recognition. The frequent separations between females and pups, and the danger of injury to pups from non-filial females suggest that a system of recognition like that in otariids should occur.

Pre-weaning mortality in grey seal colonies varies substantially, mainly as a result of starvation and injuries arising as a consequence of separations and confusion over pup identity (Baker 1984; Baker and Baker 1988).

It remains to be seen whether the failure to discriminate between own and non-filial pup calls was due to factors such as female age and maternal experience, colony density and levels of disturbance or whether consistently accurate mother-pup recognition simply lacks costs. The direct cost, if any, of fostering and the many factors that may influence it need to be investigated further if we are to understand the selective forces acting on mother-pup recognition.

Chapter 5

Mother-pup vocal recognition in the grey seal (*Halichoerus grypus*) of Sable Island, Nova Scotia, Canada*

Abstract

Parental recognition of offspring would be expected to evolve among densely populated species in which parental investment is large, and separations of the mother-pup pair frequent. Although otariids present a well-developed system of mutual vocal recognition, evidence in phocids is weak. Furthermore, allo-suckling is prevalent in some species and may reflect confusion over the identity of pups. The vocalisations of grey seal, *Halichoerus grypus*, pups have been found to be stereotyped and individually distinctive on the Isle of May, Scotland. However, playback experiments showed that mothers fail to discriminate between the vocalisations of their pup and a non-filial pup. Moreover, allo-suckling was observed. In contrast, grey seals on Sable Island, Nova Scotia, a population reproductively isolated from that of the Isle of May, show very little allo-suckling. This may reflect the presence of a recognition system that does not appear to be present on the Isle of May. During the 1999 breeding season on Sable Island, vocalisations of grey seal pups were recorded and playback experiments carried out to determine whether female grey seals respond differently to the playback of vocalisations of their own pup, a familiar pup and an unfamiliar pup. Grey seal mothers were found to make significantly more head turns and body movements towards the loudspeaker during the playback of their own pup call than during the playback of a familiar or unfamiliar pup call. In addition, there was no evidence of an effect of pup age. This suggests that female grey seals can discriminate between pup calls using the stereotyped and individually distinctive vocalisations of their pup, and that different selective pressures may be in operation between the Sable Island and Isle of May colonies.

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Introduction

For individual recognition to occur, a signal containing identity information (a "signature"), needs to be emitted and a receiver must decode it ("recognition"). Furthermore, in order for an individual to use the signature in individual recognition, it needs to have greater among-individual variation than within-individual variation. Signature recognition has been demonstrated in a number of mammals, such as vervet monkeys, *Cercopithecus aethiops* (Cheney & Seyfarth, 1982), bottlenose dolphins, *Tursiops truncatus* (Sayigh et al. 1990) and free-tailed bats, *Tadarida brasiliensis mexicana* (Balcombe, 1990). Comparisons among species have shown how coloniality and different breeding systems affect the level of individual recognition.

Differences in pup rearing strategies between the Otariidae (eared seals) and the Phocidae (true seals) probably contribute to differences in mother-pup recognition behaviour. Otariid mothers come ashore to give birth to a single pup and then alternate between nursing bouts and trips at sea. These frequent separations during the long lactation period (4-36 months), and the need for a rapid and successful reunion upon arrival at the crowded rookery, has led to a well developed recognition system. Studies involving behavioural observations and playback experiments have demonstrated the importance of acoustic signalling in mother-pup reunions (Stirling & Warneke, 1971; Trillmich, 1981; Roux & Jouventin, 1987; Gisiner & Schusterman, 1991; Hanggi, 1992). These studies have led to a more detailed structural analysis of vocalisations involved in the recognition process. Schusterman, Hanggi & Gisiner (1992) found that inter-individual variability of Pup Attraction Calls in California sea lions, *Zalophus californianus*, was greater than intra-individual variability and thus provides a sufficient structural basis for a pup to recognise its mother as an individual. Furthermore, Philipps (1998) found that the calls of mother and pup South American fur seals, *Arctocephalus australis*, appear to exhibit sufficient stereotypy for recognition to occur. Finally, vocal playback experiments with free-ranging northern fur seals, *Callorhinus ursinus*, have shown that mother-pup recognition is both mutual (bi-directional) and can last beyond a single season (Insley, in prep.).

In contrast, females of most phocids have a relatively short lactation period (4-56 days) during which they remain with their pup, fasting or significantly reducing their food intake, although harbour seals, *Phoca vitulina*, show regular maternal foraging trips (Boness, Bowen & Oftedal, 1994). No evidence of maternal recognition was found in low density colonies of Hawaiian monk seals, *Monachus schauinslandi* (Boness, 1990; Job, Boness & Francis, 1995), hooded seals, *Cystophora cristata* (Ballard & Kovacs, 1995) and largha seals, *Phoca largha* (Burns et al., 1972). Interestingly, a captive harbour seal (Renouf, 1984) demonstrated that it could distinguish between different pup calls, suggesting that mothers have the capacity to recognise their pup's calls (Renouf, 1985). Furthermore, Petrinovich (1974), using playbacks, demonstrated individual recognition in northern elephant seals, *Mirounga angustirostris*. This could have evolved as a response to the trauma-starvation syndrome (Le Boeuf & Briggs, 1977) where pups become separated from their mothers due to altercations between adults in high density colonies, and subsequently die from no reunion. In McCulloch et al. (1999), pup vocalisations of grey seals, *Halichoerus grypus*, on the Isle of May, Scotland, were found to be stereotyped and individually distinctive, but playback experiments revealed a failure of mothers to respond more to their pup's call than to those of non-filial pups. Furthermore, 17 cases of allo-suckling were observed, suggesting that females do not use the information contained in pup calls to discriminate between pups.

Grey seals on Sable Island, Nova Scotia, Canada (45° 55' N; 60° 00' W), a population reproductively isolated from that of the Isle of May, show very little allo-suckling compared to the Isle of May and other UK colonies. This could reflect the presence of a recognition system that does not appear to be present in the Isle of May population.

The objective of this study was to determine, using playback experiments, whether female grey seals at Sable Island respond differently to the vocalisations of their own pup, a familiar pup and an unfamiliar pup. The relationship between pup calling behaviour and nursing was recorded by behavioural observations of mother-pup pairs. In addition, the effect of pup age and lactation stage on a mother's response to playbacks was investigated.

Methods

Study sites, animals and behavioural data collection

Sable Island is a crescent shaped, vegetated sandbar approximately 42 km long and 1.5 km wide, located 296 km south east of Halifax, Nova Scotia. A breeding colony of grey seals occupies the island from mid-December to early February. The Sable Island population in 1994 was estimated at 85 300 and a 1993 aerial photographic survey indicated that pup production continues to increase at a rate of 13% per year (Mohn & Bowen, 1996). The population was therefore estimated at 100 000 for 1999 with pup production of 25 000 (W. D. Bowen, personal communication).

A grey seal female at Sable Island typically comes ashore for a few days before selecting a site to give birth to her pup. She nurses it for an average of 15-17 days, during which mother and pup remain together and are relatively sedentary (Boness & James, 1979; Boness, Bowen & Iverson, 1995). At the end of lactation, the female weans her pup abruptly by departing the breeding grounds, but she mates before this. At this time males are defending loosely defined clusters of females.

Ad libitum behavioural observations and continuous-event sampling of mother-pup relationships (n=53) were carried out on Sable Island during January 1999. Four different locations were used. The mother's response to her pup calling was investigated. Variables recorded were as follows: time at which pup started calling, behaviour of pup (i.e. moving towards mother, moving away from mother, playing with flippers, sleeping), behaviour of mother (i.e. ignoring pup, presenting, flippering, interacting with other adults), whether or not the pup was fed, and time interval between calling and feeding.

Tape recordings of pup vocalisations and the playback experiments were carried out at 5 locations, 2 of which were the same as the behavioural observation sites. These sites were chosen for their low density and relatively long distance from the ocean, to minimise background noise from surf, calling pups and interactions between males and females.

Recordings of pup vocalisations

Pup calls were recorded at 1-5 m range using a Marantz CP430 tape recorder and a Sennheiser ME80 gun microphone. Pups or mothers did not show any sign of disturbance due to the presence of the experimenter. Due to constant 25-knot winds, a two-core windshield made of silk and 3/4 inch wire mesh was used in addition to the microphone's integral windshield.

Playback experiments

Twenty-eight mother-pup pairs were used for this part of the study. Mothers were paint marked on the day before the playback experiments were carried out to allow for reliable identification. Marking was done using a paintbrush attached to a long wooden pole to minimise disturbance. Paint marks were temporary and usually lasted about 2-3 weeks. Pups were not marked because the areas used had small groups such that natural variation in size of pups and coat colour allowed individuals to be distinguished. There was also little movement of females and pups in contrast to some European colonies of grey seals (e.g. Isle of May, Scotland, UK, Table 1; Twiss et al. in press).

Recordings of pup vocalisations were made on day 1 of the study. Three mother-pup pairs of the same age-class were used to investigate the effects of pup age on recognition. Since the exact ages of pups were not known, I used the age-classification scheme described by Kovacs & Lavigne (1986) (Table 2). On day 2, each mother was subjected to three tests, each comprising a two-minute behavioural observation period followed by a playback. Three different playbacks were given: a playback of her own pup's call ("own call"), a playback of a familiar (i.e. neighbouring) pup's call ("familiar call") and a playback of an unfamiliar pup's call (i.e. from another study area; "unfamiliar call"). The order of presentation was counterbalanced such that 14 mothers received the own call condition followed by the familiar and unfamiliar calls, and 14 different mothers received the unfamiliar call followed by the familiar and own calls. Playbacks consisted of a series of calls played through a Nagra DSM loudspeaker with a 10-meter coaxial lead. The loudspeaker was placed within a 10-m range of the focal female before the beginning of observations for the pre-playback control period.

Table 1. Differences between the Sable Island and Isle of May populations of grey seals

	Sable Island	**Isle of May**
Location	West Atlantic, Nova Scotia	East Atlantic, Scotland
Population size (estimated)	100 000 in 1999 [1]	4 500 [2]
Topography	Sandbar, unrestricted access	Rocky island, limited access
Pup production (estimated)	25 000 in 1999 [1]	1 770 in 1997 [3]
Pupping season	January- mid-February	October-November
Mother fasts	Yes	Yes
Mother remains with pup	Yes	Some separations (see text)
Instances of allo-suckling	No, this study; infrequent [5]	17 cases in 1997 [4]
Mother-pup vocal recognition	Yes, this study	No [4]

[1] Bowen (pers. comm.), [2] Hiby et al. (1996), [3] SMRU (pers. comm.), [4] McCulloch et al. (1999), [5] Perry et al. 1998

Because the positioning of the loudspeaker caused some disturbance females were given time to settle before the start of the experiment. The presence of the loudspeaker per se did not appear to affect female behaviour. The placement of the loudspeaker and camera in respect to the mother and pup was such that head orientation towards either one was unambiguous. The three tests were separated by only 10 minutes to avoid any major change in contextual conditions (e.g. interference due to males and females or pup lactation stage). Maternal response to the playback stimulus was recorded using a Hi-8 Sony video camera. Head turns and body movements of the mother towards her pup were scored for a two-minute period immediately prior to the onset of the playback (pre-trial period, baseline score) and for the two minutes immediately following the onset of the playback (trial period). This was then repeated for movements towards the loudspeaker. Two-minute periods were chosen because responses to playbacks were expected to occur shortly after the playback. Using a longer period would have increased the difficulty of inferring that an increase was due to the playback or may have diluted the effect of the playback. I deliberately chose the pre-playback control period to be of comparable duration to the post-playback period.

Table 2. Ages (days) of grey seals pups, in descriptive age categories (From Kovacs & Lavigne 1986)

Age-class	Description	Age, days (Mean±SD)
I	Yellow tint to pelage; lacking coordination; neck, hips and ribs clearly visible; umbilicus present	2.4±4.4
II	Pelage white; improved coordination, shoulder to hip region filled out; ribs covered by a layer of blubber; umbilicus nor present	4.8±3.1
III	Pelage white to light grey; fat sheath extends posteriorly from neck; body barrel shaped; lanugo intact except for slight loss in the facial region toward the end of stage	12.1±2.9
IV	Lanugo being shed, exposing the juvenile pelage	16.0±3.0
V	Moulted pup, less than ~5% of the body surface still retaining lanugo	>21

Statistical analysis

Playback experiments

All computations were performed using Statview 4.5 (Abacus Concepts, Inc., Berkeley, CA, 1995). Orientation scores were calculated as the difference between the number of movements and head turns towards the pup or loudspeaker during the trial and pre-trial periods. A Wilcoxon Signed Rank test was used to test this difference and determine if mothers responded to each of the three playback conditions. Each statistical analysis was performed separately for the pup and loudspeaker directions. The expectation was that if females recognised their pup's vocalisation, they would orient towards their pup, the speaker or both more often in response to the pup call than to the unfamiliar or familiar pup calls. Kruskal-Wallis tests were performed to test these hypotheses. The effect of presentation order was determined using a Mann-Whitney test on the orientation scores for the two playback situations (own/familiar/unfamiliar and unfamiliar/familiar/own). The age-class of pups in this study was variable. The effect of pup age on a mother's response to the playbacks was assessed by performing a Kruskal-Wallis test on orientation scores by pup age-class for each of the three pup call types separately.

Results

Behavioural observations

Behavioural observations of mother-pup pairs (n=53) revealed that mothers may sometimes ignore their calling pup. Two types of calling bouts were observed: active (n=37) and passive (n=16). During active bouts, pups would call frequently and vigorously, orienting towards their mother and actively solicit suckling by approaching her. Thirty-six pups were fed following a bout of active calling with a mean time of 1.92 minutes (± 0.28 SE) between the first call and suckling. Only one pup actively called and was not subsequently fed. In this case, the mother was disturbed by a neighbouring female and moved away from the pup which then stopped calling. Sixteen pups were involved in passive calling. Although their calls were similar to the active-calling pups, passive-calling pups did not move or orient towards their mother. They often laid on their backs, scratching and playing with their flippers, or played with the sand. None of these pups were fed within 20 minutes of calling. Based on these observations, only calls that had lead to a nursing bout were used in playbacks.

Mother-pup recognition

Response to the playbacks

Mothers performed more head turns and body movements towards their pup following the playback of their own pup's call (Wilcoxon test: Z= -2.48, N=28, p<0.01) than during the pre-trial (Figure 1a). This was, however, not the case for the familiar (Z= -0.23, N=28, p=0.82) and unfamiliar pup calls (Z= -0.88, N=28, p=0.38).

Mothers performed more movements towards the loudspeaker during the trial than during the pre-trial, irrespective of playback condition (Wilcoxon test: Own: Z= -4.20, N=28, p<0.01;

Familiar: Z= -3.35, N=28, $p<0.01$; Unfamiliar: Z= -3.77, N=28, $p<0.01$), suggesting that mothers respond to the playbacks by orienting towards the loudspeaker (Figure 1b).

Effect of playback type

Orientation scores towards the pup were not significantly different among playback conditions (Kruskal-Wallis test: H=3.24, df=2, p=0.20), i.e. mothers did not orient more towards their pup during playback of their pup's call than during the familiar or unfamiliar pup's call. However, females responded significantly more towards the loudspeaker during their own pup's call than during the familiar or unfamiliar pup calls (H=7.22, df=2, $p<0.05$).

Effect of order of presentation

Order of presentation of playbacks did not affect the orientation of females towards their pup (Mann-Whitney: Z= -0.43, $N_1=N_2=42$, p=0.67), nor did they affect orientation towards the loudspeaker (Mann-Whitney: Z= -0.38, N1=N2=42, p=0.70, Table 3).

Table 3. Effect of order of presentation of playbacks

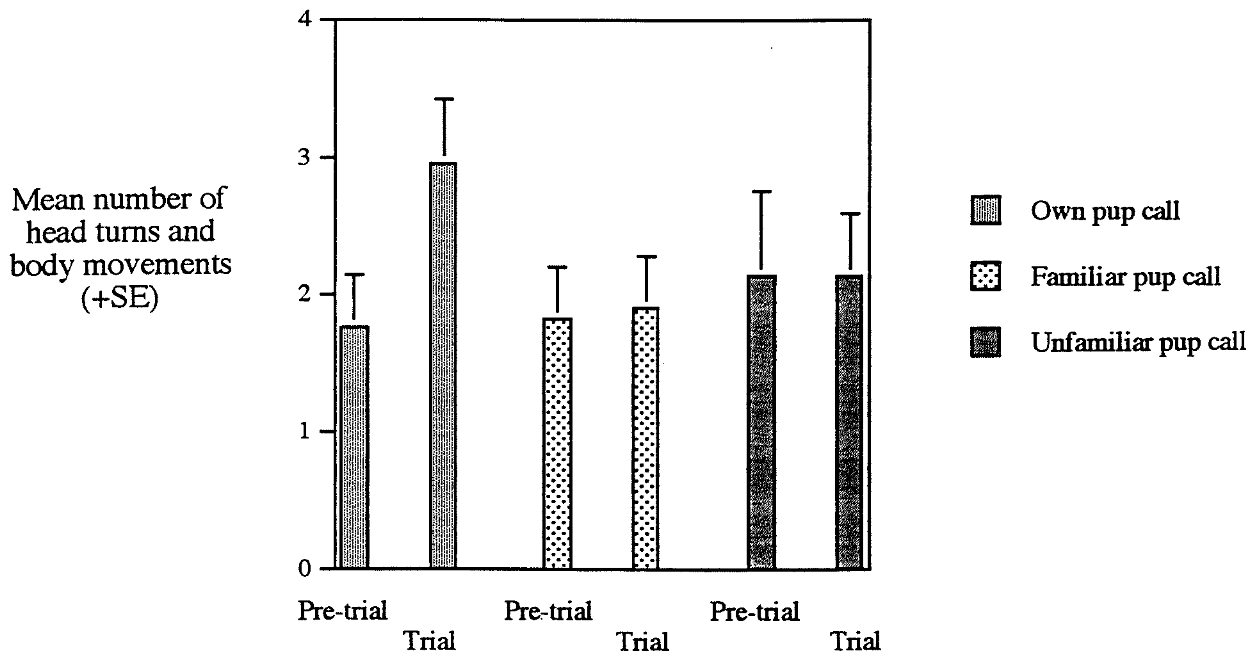
	Towards pup		Towards speaker	
	Mean	**SE**	**Mean**	**SE**
Condition 1	0.74	0.29	1.88	0.284
Condition 2	0.12	0.47	2.36	0.456
Mann-Whitney	Z=-0.43 ($N_1=N_2=42$, p =0.67)		Z= -0.38 ($N_1=N_2=42$, p=0.70)	

Condition 1= own/familiar/unfamiliar; Condition 2= unfamiliar/familiar/own

Effect of pup age

There was no evidence of an age effect. No difference was found in females responses to own, familiar, or unfamiliar pup calls in relation to pup age class (Figure 2a) for either orientation towards her pup (Kruskal-Wallis: Own: H=3.31, df=2, p=0.19; Familiar: H=0.11, df=2, p=0.94; Unfamiliar: H=3.31, df=2, p=0.19), or towards the loudspeaker orientation (Kruskal-

(a) towards her own pup



(b) towards the speaker

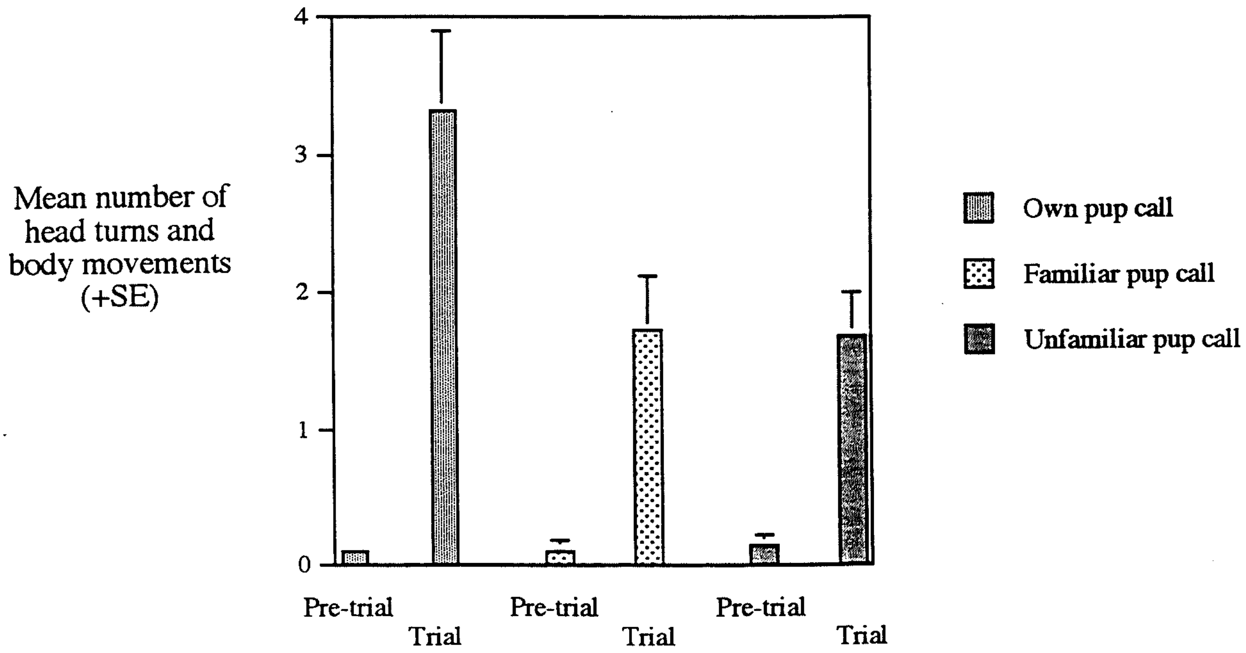
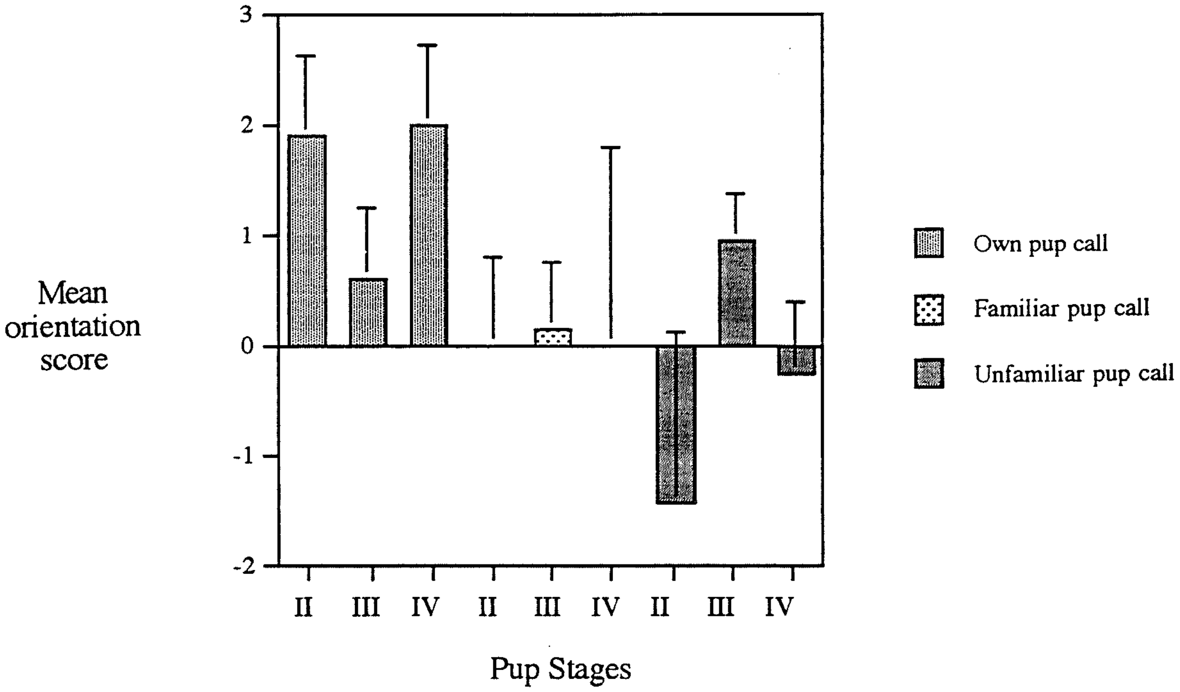


Figure 1. Mean number of head turns and body movements (a) towards her own pup and (b) towards the speaker during the pre-trial and trial periods (n= 28 females, + 1 SE).

(a) towards her own pup



(b) towards the speaker

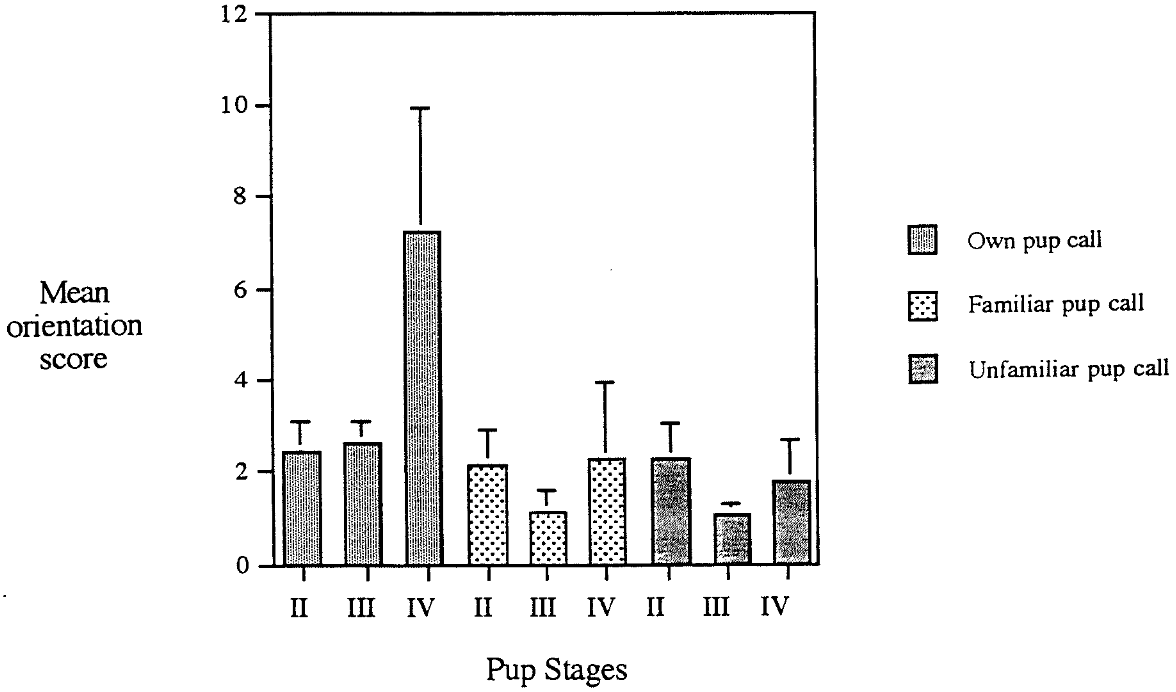


Figure 2. Mean orientation score (a) towards her own pup and (b) towards the speaker in response to the three playback types for females with pups in different age groups (± 1 SE). Orientation scores were calculated as the difference between the number of movements and head turns towards the pup or loudspeaker during the trial and pre-trial periods. Negative orientation scores mean that the mother performed more head movements during the pre-trial than the trial.

Wallis: Own: H=4.03, p=0.13; Familiar: H=2.08, p=0.35; Unfamiliar: H=1.4, p=0.49, Figure 2b).

Discussion

On Sable Island, grey seal mothers make significantly more head turns and body movements towards the loudspeaker during the playback of their own pup's call than during the playback of a familiar or unfamiliar pups' calls. Because there is no evidence of an effect of pup age, this suggests that female grey seals can discriminate between pup calls using the stereotyped and individually distinctive vocalisations of their pups (Caudron, Kondakov & Siryanov, 1998; McCulloch et al. 1999).

This finding is in contrast to a similar study at the Isle of May where no evidence of vocal maternal recognition was found despite the existence of individually distinctive pup vocalisations (McCulloch et al. 1999). Moreover, these differences seem paradoxical when one compares the behaviour of females and characteristics of the breeding colonies at these two sites (Table 1).

Sable Island is a large sandbar with unrestricted access from the sea. In the study areas, mothers remained with their pups throughout lactation. Although interactions do occur between mothers and neighbouring males and females, no confusion over pup identity was observed. Allo-suckling behaviour was absent in this study and has also been shown to be infrequent on Sable Island in earlier work (Perry, Boness & Fleischer, 1998).

By contrast, the Isle of May is a small rocky island, where females aggregate around a limited number of access gullies. Some mothers make frequent daily movements to the water, during which they interact aggressively with males and females. This causes pups to be separated from their mothers and is likely to be the reason for confusion over pup identity to arise, potentially leading to instances of allo-suckling (n=17, McCulloch et al. 1999). Lost pups risk injury from males and other females as they wander through the colony, and ultimately risk starvation if no reunion occurs (Baker, 1984; Baker & Baker, 1988).

The Isle of May with its frequent separations might be expected to show higher levels of recognition than Sable Island. However, both colonies might be expected to show some level of mother-pup recognition in response to colonial breeding and the consequences to pups of becoming separated (i.e. the "trauma-starvation syndrome", Le Boeuf & Briggs, 1977). We might, however, expect a difference in the level and intensity of recognition between the two sites, as found in Insley's (1992) comparison between elephant seals and fur seals. However, despite the existence of individually stereotyped pup vocalisations, which would permit discrimination between pup vocalisations, mothers on the Isle of May did not appear to recognise the calls of their offspring (McCulloch et al. 1999). Furthermore, high levels of allo-suckling were observed.

If allo-suckling on the Isle of May does not present any costs to the mother or the pup, then a strong selection for vocal recognition would not be required. Boness (1990) found fostering behaviour in Hawaiian monk seals to have no reproductive costs, and thus suggests an explanation for the apparent lack of vocal recognition in this species (Job et al., 1995). However, allo-suckling does seem to be costly in grey seals. Females do not simply switch pups as in monk seals. Instead, they continue to nurse their own pup as well as foster pups, reducing the amount of nursing time and milk allocated to their own pup (D. J. Boness, unpubl. Data). Although there is little empirical data on the cost of allo-suckling in grey seals, pre-weaning mortality levels (Baker, 1984; Baker & Baker, 1988) suggest that allo-suckling is not a successful substitute to maternal care on the Isle of May and that it occurs due to confusion over pup identity.

Breeding-site fidelity (Pomeroy et al., 1994; Twiss, Pomeroy & Anderson, 1994), and the resulting high local level of relatedness, has been suggested as an explanation for the occurrence of allo-suckling behaviour on the Isle of May. Perry et al. (1998) investigated the role of kin selection in fostering behaviour at Ramsey Island, Wales, a colony with similar characteristics to the Isle of May. Ramsey has isolated cliffbound beaches on which females give birth from September to December. Throughout lactation, females move from land to water during nursing bouts thus increasing the potential for allo-suckling. However, Perry et al. (1998) found that mothers did not preferentially foster related pups suggesting that kin recognition does not play an important role in the maintenance of fostering behaviour. Therefore, in a colony such as the Isle of May, mothers may be relying on location and olfactory cues to relocate their pup. The occurrence of allo-suckling could be explained by some pup movement and, possibly, mistakes by young inexperienced females.

An alternative, but not mutually exclusive, explanation for the absence of vocal recognition on the Isle of May is that there is a sensitive period (e.g. 4-12 hours in olfactory recognition in sheep, Lévy et al. 1996) during which females learn to recognise their pup's vocalisations. An early separation between the mother and the pup would lead to unsuccessful vocal recognition. Ultimately, recognition would fail completely if the mother failed to gain olfactory information. While one might expect selection to work against such a mechanism, the rarity of its failure may mean that this happened very slowly.

Because females remain with their pup throughout lactation on Sable island, perhaps they only need to recognise their pup at close range. This could easily be achieved through olfactory and location cues so that vocal recognition is not required. However, as shown above, mothers are able to discriminate between playbacks of their own pup and playbacks of familiar and unfamiliar pup calls. Another plausible hypothesis as to why vocal recognition occurs on Sable Island is that the behaviour is carried over from an ice-breeding ancestry, as was suggested for their mating system (Boness & James, 1979). Female grey seals that breed on land-fast ice around Amet Island (Haller, Kovacs & Hammill, 1996) and pack ice in the Gulf of St. Lawrence (K. M. Kovacs, personal communication) were found to spend a significant amount of time in the water, 12% and 19.8% respectively. Moreover, Haller et al. (1996) found that ice-breeding females spent more time engaged in maternal behaviours than land-breeding females. They suggested that mothers and pups had a higher risk of premature separation on the ice, and that this had led to a shorter and more intense lactation period (ice-breeding: 14± 1.4 days; land-breeding: 16-18 days). Therefore, vocal recognition may have evolved in response to these higher risks of separation and be carried over from an ice-breeding ancestry in the Sable Island colony. Since grey seals on Sable were probably hunted to extinction in the early 1900s, the colony there may have its origins in repopulation from ice-breeding seals. In the 1960s there were only about 250 grey seals on Sable Island. A few adult seals branded on Sable Island have been seen in the Gulf of St. Lawrence. However, no current empirical data exist on the interchange of individuals between Sable and ice breeding groups.

In conclusion, explanations for the discrepancy between the results of the Isle of May study (McCulloch et al. 1999) and the present study on Sable Island, remain elusive. Mother-pup vocal recognition is not found in the population that appears to show greater need for recognition. Vocal recognition on Sable Island may have evolved when grey seals were ice-breeders and there were higher risks of mother-pup separation. It may then have been maintained by their maternal pup rearing strategy, and/or never have been selected against.

Chapter 6

Conclusions

In-air and underwater repertoires

Grey seals have been found to be more vocal than previously thought, both in-air and underwater.

In the underwater repertoire, it is interesting to note how certain call types (1, 3, 5, 7 & 9) overlap with those of the ice-breeding grey seals of the Gulf of St. Lawrence, Canada. The absence of other call types in both places could be due to insufficient recording time or possible population differences as shown in many other species of pinnipeds (e.g. Weddell and leopard seals). This could be further investigated by comparing the recordings from these two places to vocalisations from the Baltic sea, where there is another reproductively isolated population of grey seals.

One of the major problems with recording underwater sounds is the difficulty in assigning the identity of the caller to a specific call type. Although, some behavioural observations can be made at the water surface, the murky waters and the efficient transmission of sound underwater makes it rather difficult to localise the emitter of the call. It was therefore with interest, that individuals were seen to produce calls on land (types A & B) very similar to ones heard underwater (types 1 & 5). From this, it was suggested that type 1 calls are produced by males and type call 5 by females. This contradicts with Asselin and Hammill (1993) who believe that both call types 1 and 5 are mostly produced by females as they were often recorded when only females were observed around the hydrophone. In this study, call type 1 was produced by males. Furthermore, no females were seen to produce this call. Captive seals could be used to see if any of these sounds are sex-specific. As males were seen to make wave-like body movements while producing type 1 calls, the clarity of water and size of an aquarium should allow good behavioural observations, making it possible to test the claim that these are produced by males.

Chapters 2 and 3 suggested some possible functions for these vocalisations. Again, this proved difficult as surface interactions were often not clearly visible, and individuals are hard to distinguish in the field. Furthermore, half of the recordings were made at night, thus reducing the amount of behavioural data available. Yet again, captive seals could provide us with an insight into the possible functions of different call types. Indeed, the observation of female-male interactions and recordings of any associated vocalisations could indicate whether a particular call may be used for example in aggressive interactions or mating displays. For free-ranging seals, a useful technique would be to use triangulation. This method was used by Janik (1998) to investigate whistle interactions between wild bottlenose dolphin individuals. It involves the use of three hydrophones installed in a triangle to form a two-dimensional array. This technique localises the source of a sound on the basis of time difference with which a signal arrives at each pair of hydrophones. Each time delay corresponds to a hyperbola, and the point of intersection of the hyperbolas indicates the actual position of the calling animal. With the study of captive animals and the use of hydrophone arrays, it should be possible in the near future to identify the calling animal and investigate the role of that call in its social system.

Finally, the role of underwater vocalisations could be further investigated by using an underwater camera. Scientists at the National Geographic Society are currently developing a system called "Crittercam" (Boness D. J., personnal communication). It is an animal-borne video and data-logging system designed for studying the at-sea behaviour and ecology of large marine mammals. Over the past ten years, exploratory research using this method has been carried out on sea turtles, American alligators, sharks, sperm whales and a variety of pinnipeds. Crittercam is a powerful tool for studying the aquatic behaviour of marine mammals and has provided some fascinating insights into visual and vocal territorial displays, selective feeding and other unstudied behaviours (Boness D. J., personnal communication). By its small size, this system could easily, although expensively, be deployed on grey seals and provide information on their habitat and behaviour.

The Sable Island males produce an eerie "yodel" thought to be involved in advertising dominance status over a relatively long distance. My sample size of these calls was too small to allow further analysis. It would however be very interesting to investigate individual recognition in this call. Boness & James (1979) suggested this call could be individually distinctive as they could distinguish between individual bulls based on their yodel. The measurement of temporal and frequency features and subsequent multivariate tests need to be carried out to see what characteristics of the call is individually distinctive. Then, playback experiments could be performed to test if males can discriminate between individuals. If it is possible to establish their dominance status, then playbacks could be used to see how individual males respond to dominant and peripheral male calls.

Outside the breeding season, grey seals haul-out on sandbanks and isolated islands in large aggregations. These colonies are rather noisy during the rise and fall of the tide as individuals are disturbed by their neighbours as space becomes an issue. Their moaning has been described as a "song" by many fishermen and locals, and its eerie sound can be heard for miles in the still hours of dawn and dusk, and is therefore another sound produced by this species, though not studied here. In June 1997, I spent two weeks on the island of Sanday in Orkney, Scotland in an attempt to record this "song". The next step was going to be to study different colonies and investigate possible geographical differences in song and ultimately the existence of dialects. Unfortunately, clear recordings were not obtained due to the distance between animals and the recording equipment, bad weather conditions (rain and high winds) and the surprisingly low number of grey seals. I then went to Abertay Sands haul-out during the summer to attempt to record this same "song". Again, I was faced with recording problems as the animals were located half a mile offshore and the high number of individuals (500+) meant that calls overlapped each other at all times. As a result, I decided to concentrate on the underwater calls of grey seals and their in-air repertoire during the breeding season.

Mother-pup vocal recognition

The study of mother-pup vocal recognition on the Isle of May and on Sable Island provided some paradoxical results. Despite frequent separations and the pup calls being individually distinctive, mothers on the Isle of May failed to discriminate between the vocalisation of their own pup and that of a non-filial pup. Moreover, allo-suckling was widespread. In contrast, mothers on Sable Island can discriminate between pup calls using the stereotyped vocalisations of their pup despite the fact that they remain with their pup throughout lactation. The reasons for these differences were suggested to be that the mothers on the Isle of May were young inexperienced females in a newly colonised part of the island, and that vocal recognition on Sable Island is a relic from an ice-breeding ancestry when there were higher risks of premature separations. However, a few points should be raised on the validity of this comparison and arising conclusions.

First, there were differences in experimental protocol and in sample sizes. In the Isle of May study, 16 mother-pup pairs were used versus the 28 of Sable Island. Secondly, the number of playbacks given differed: 2 for the Isle of May study (Own vs Alien) and 3 for Sable Island (Own vs Familiar vs Unfamiliar). Although these methodological differences arose due to an improved experimental design on Sable Island, they nevertheless amount to confounding factors that need to be discussed. For example, although statistical tests showed that mothers on Sable Island are able to discriminate between pup calls, this significant difference is slight (females make 3 rather than 2 head or body turns following the playback of their own pup). It is therefore possible that a larger sample size might have brought different results to the Isle of May study. The absence of mother-pup vocal recognition on the Isle of May could be due to lack of statistical power rather than a true population difference.

Another point worth raising is at what level of difference a call should be considered to be individually distinctive? The statistical analyses of Chapter 4 showed that pup vocalisations are both stereotyped and individually distinctive. However, the discriminant function analysis was only able to correctly classify 68 out of the 216 vocalisations to the correct category. So, although the DFA performed better than random, 148 vocalisations were nevertheless assigned to the wrong category. Therefore, pup vocalisations seem to show greater between pup than within pup variation, but this variation might not be great enough for mothers to reliably discriminate them, and may therefore explain the absence of vocal recognition on the Isle of May. Another issue is that I assumed pup vocalisations would be as stereotyped and distinctive on Sable Island as on the Isle of May. As a result, I did not record random pup vocalisations to test for stereotypy. However, it is possible that pup vocalisations may vary between individuals more on Sable Island and this might explain why females there were able to identify their own pup. To examine this, it would be necessary to record pup vocalisations and carry out a one-way analysis of variance and a stepwise, cross-validated discriminant function analysis to determine the probability of correctly assigning a vocalisation to a specific pup.

In addition, given the possible age-related differences in the ability of females to identify their pups, and the unknown ages of the studied females, it is perhaps premature to conclude that there is a true population difference. Indeed the location, experience of females and proximity of pups to the speaker and/or mother were not taken into account due to the logistical circumstances (restricted area in which to do experiment, unknown age and experience of females) and all could have affected the data. Ideally, distances between pup and speaker, and pup and mother should have been kept constant, however this was not possible due to the topography and location of animals. For most playbacks, the location of the recording equipment was directly influenced by the proximity of other mother-pup pairs, by rocks or pools, and the need to avoid any unnecessary disturbance to the rest of the colony (i.e. the need to hide behind a wall). The use of branded animals could have provided the necessary information on age and experience. This was unfortunately not possible in the IoM study as it would have conflicted with other research occurring in the central area of the colony. Furthermore, on Sable Island, I did not have any motorised transport so was limited to areas near our field house. There were only 2 branded animals in my study site. The logical follow-up would be therefore to replicate both studies using the same experimental protocol and known-aged females. Once maternal experience is controlled for, playback experiments should demonstrate whether the differences between the two populations are genuine and not an artefact of sampling and analysing methods.

A further point concerns the behavioural observations of allo-suckling described in Chapter 4. The frequent separations between females and pups, and the danger of injury to pups from other adult females suggest that a system of vocal recognition would be advantageous. It was then observed that in certain situations, this vocal recognition process fails and leads to allo-suckling. Fogden (1971) found that a congested and disturbed beach presents a confused situation that deteriorates rapidly during the season until many of the mother-pup bonds break down, leading to even more confusion. She then suggested that the failure to discriminate between own and non-filial pup calls was due to factors such as female age and maternal experience, colony density and levels of disturbance, and that accurate vocal recognition simply lacks costs and maybe even benefits. However, if non-filial pups remain silent when stealing milk, then it may not be surprising that there has not been selection for better discrimination. Additional behavioural observations are therefore necessary to provide an indication of pup call rates during suckling.

Future playback experiments could be carried out to see if mothers react differently to the playbacks of their own pup and a non-filial pup at different stages of lactation. A pilot study suggested that mothers do not respond differently at different stages of lactation although they do seem to respond more to their own pup's call when their pup is approaching weaning age. A conflict of interests could occur between mother and pup at the time of weaning (Trivers 1974). Pups would gain from feeding longer while females would want to leave the colony to feed after the two weeks spent fasting.

Playback experiments could also be used to test if mothers are able to discriminate between the call of their pup, the call of their pup from the previous year and a non-filial pup. Behavioural observations from two Isle of May mothers suggest that females may respond more to their pup call of the previous year than to a non-filial call. It would be interesting to see whether pup calls of half-siblings (or full siblings if there is mate fidelity) are more similar in their acoustic structure to each other than to unrelated pup calls. This would require DNA fingerprinting to confirm maternity and determine paternity. If mate fidelity and site fidelity does exist as suggested by Amos et al. (1993, 1995), Twiss et al. (1994) and Pomeroy et al. (1994) determining maternity and paternity should be possible despite the large numbers of seals. Furthermore, if the calls of a mother's different offspring are similar, she may then only need to learn a certain template for vocal recognition.

Further research in this species is needed to answer some of the questions raised and not tackled in this thesis. The description of the in-air and underwater repertoires is a starting point for further comparative studies between the different populations of grey seals and the playback experiments bring into question the role and evolution of pup vocalisations. The use of new techniques such as the Crittercam system will soon provide us with some of the answers, which in turn will no doubt generate even more questions.

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