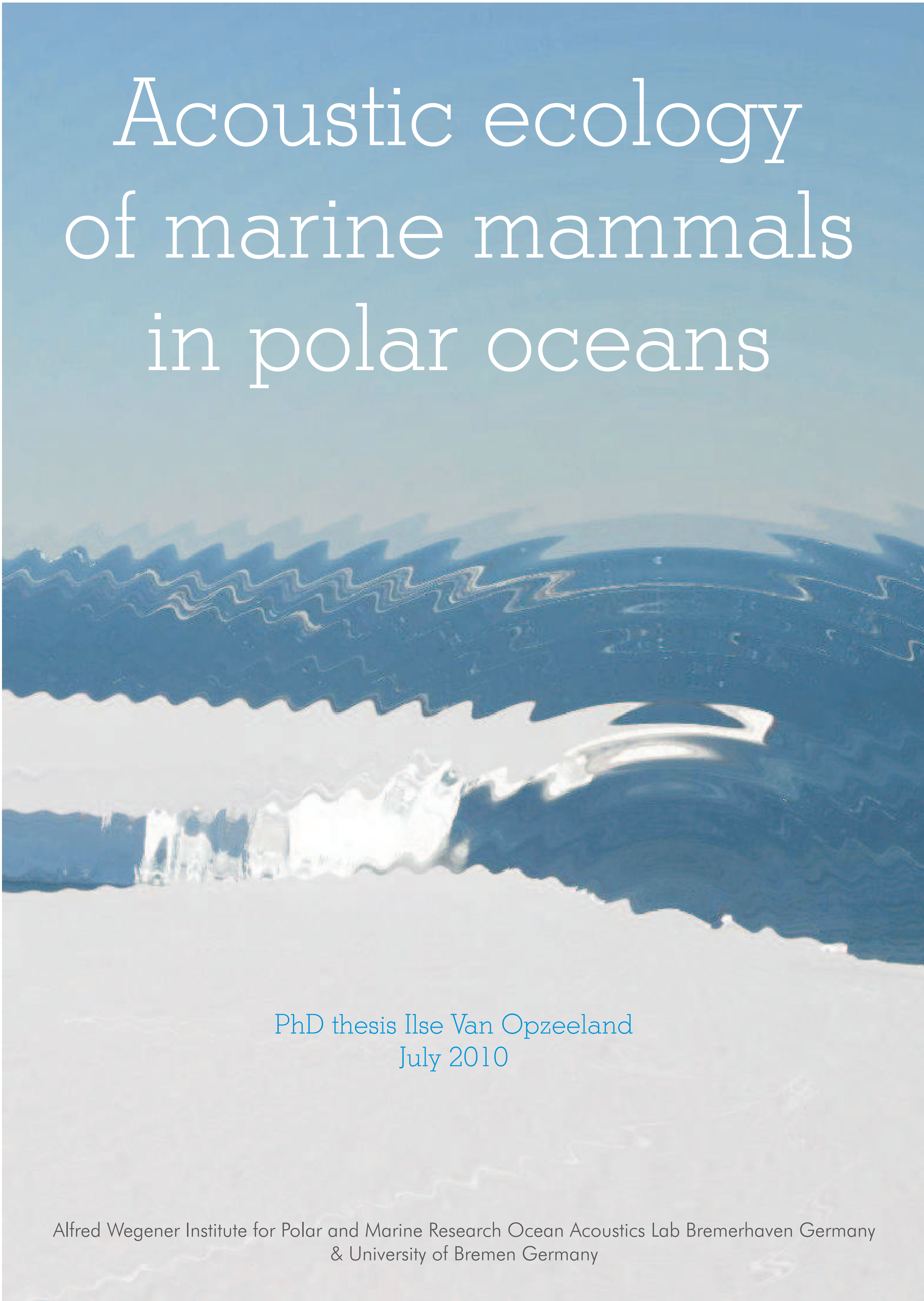

Acoustic ecology of marine mammals in polar oceans

PhD thesis Ilse Van Opzeeland
July 2010

Alfred Wegener Institute for Polar and Marine Research Ocean Acoustics Lab Bremerhaven Germany
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All things make music
with their lives.

John Muir

Witte morgen waarin de sporen van
wat vannacht is gebeurd.

Wit woud dat vannacht een huis
is geweest, maar nu.

Het is morgen geworden, er is
gekomen, geweest, gegaan.

Het sneeuwt door dak en muren naar
binnen, er zal niets zijn gebeurd.

Rutger Kopland

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Summary

In polar habitats, research on marine mammals – including studies of the possible ecological consequences of anthropogenic impact – is hampered by adverse climate conditions restricting human access to these regions. Marine mammals are known to produce sound in various behavioural contexts, rendering (hydro-)acoustic recording techniques, which are quasi-omnidirectional and independent of light and weather conditions, an apt tool for year round monitoring of marine mammal presence and behaviour in polar habitats. Acoustic behaviour is shaped by the species-specific behavioural ecology, as well as by abiotic, biotic and anthropogenic factors of the animal's living environment, a concept known as acoustic ecology. Acoustic ecology thereby describes the interaction between an animal and its environment as mediated through sound. An understanding of the acoustic ecology is important when interpreting acoustic data, as the acoustic ecology of a species determines if physical presence results in acoustic presence, on which temporal scale acoustic activity occurs and over which spatial scales acoustic presence can be detected.

This thesis comprises ten manuscripts/papers, which are based on acoustic data collected in the Southern and Arctic Oceans. All provide examples of how aspects of the acoustic ecology of the species shape acoustic behaviour. In addition, the majority of manuscripts/papers also illustrate how acoustic monitoring can provide information of physical presence of marine mammals in areas where prolonged visual observations are not possible.

The first two papers (I and II) provide an overview of acoustic monitoring techniques, describing their use on various spatial and temporal scales and discussing the suitability of various techniques for use and deployment in polar oceans.

Two further papers (VI and VII) investigate mother-pup interactions and the individuality of pup calls in one Arctic and one Antarctic phocid species (harp, *Pagophilus groenlandicus* and Weddell seal, *Leptonychotes weddellii*, respectively). For ice-breeding pinnipeds, differences in ice habitat are likely to lead to inter-specific differences in mother-pup behaviour, but might also explain behavioural differences between

populations of the same species. In harp seals, anthropogenic factors (hunting pressure) might explain the differences observed between two study populations.

To explore temporal patterns in underwater acoustic behaviour of marine mammals in the Southern Ocean, near-continuous, multi-year acoustic data from the PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA, 70°31'S 8°13'W, Ekström Ice Shelf), an ice shelf based, energetically autonomous recording station were analysed in papers III, IV,V,VIII, and IX.

Papers (III, IV and V) explore acoustic behaviour on various temporal scales in four Antarctic pinniped species: Weddell, leopard (*Hydrurga leptonyx*), Ross (*Ommatophoca rossii*) and crabeater seal (*Lobodon carcinophaga*) and interprets the findings in the context of species-specific acoustic ecology; Weddell seals were acoustically present year round, which likely relates to their behavioural ecology, *i.e.,* territorial mating strategy and potential advantages to males remaining in underwater territories almost year round.

Ross seals were never visually observed in the coastal area off PALAOA. Acoustic monitoring nevertheless showed that they are physically present from December to February. Leopard seal calls were recorded intermittently year round in three years, reflecting that some (potentially juvenile) leopard seals remain in coastal areas during austral winter.

Furthermore, the PALAOA data showed that humpback whales (*Megaptera novaeangliae*) were present during nine months of the year, reflecting the potential importance of coastal areas, such as the area off PALAOA, for animals wintering on the feeding grounds (manuscript VIII). Similarly, Antarctic blue whale (*Balaenoptera musculus intermedia*) calls were present year round, potentially reflecting that this species also relies on coastal areas with open water during austral winter (manuscript IX).

In addition, seasonal patterns in acoustic presence an unknown sound source, the bio-duck, were used to pose new hypotheses on the potential source of this signal.

The last paper (X) discusses the impact of anthropogenic noise on fish based on comparative evidence from other species. The comparative approach of this study reflects the idea that for animal taxa relying on sound for critical aspects of their behaviour, man-made noise likely forms an important aspect of acoustic ecology.

Acoustic ecology forms the overarching concept that braces these publications. Given the relatively sparse literature on this concept with respect to marine mammals, this synopsis includes a first detailed conceptual description of acoustic ecology for polar habitats. Particular emphasis thereby is given to the specific environmental conditions in polar habitats and the looming threats of climatic change and other anthropogenic influences.

Zusammenfassung

Das akustische Verhalten mariner Säuger ist Teil ihres natürlichen, artspezifischen Verhaltensrepertoires. Es wird durch biotische und abiotische Umweltfaktoren geprägt und kann auch durch anthropogene Faktoren beeinflusst werden. Die wissenschaftliche Untersuchung dieser Aspekte ist Gegenstand der akustischen Ökologie. Sie umfasst den Gesamtkomplex der über Schall erfolgenden Wechselwirkungen zwischen Tier und Umwelt und ist grundlegende Voraussetzung für die Interpretation akustischer Daten in einem artspezifischen Kontext. Aus ihrer Kenntnis lässt sich ableiten, ob sich die physikalische Präsenz einer Meeressäugerart in akustischer Präsenz widerspiegelt, auf welchen Zeitskalen akustische Aktivitäten stattfinden und über welche Entfernungen hinweg akustische Signaturen detektierbar sind.

Diese Dissertation umfasst zehn Publikationen (bzw. Manuskripte), die auf akustischen Daten aus dem Südpolarmeer und den arktischen Meeresregionen basieren. Sie alle stellen Beispiele dafür dar, wie einzelne Aspekte der akustischen Ökologie das akustische Verhalten der jeweiligen Art beeinflussen. Darüber hinaus illustrieren die meisten Manuskripte wie in Regionen, in denen längerfristige visuelle Beobachtungen nicht möglich sind, Informationen zum Vorkommen von marinen Säugern mittels akustischer Langzeitmessungen gewonnen werden können.

Die ersten beiden Publikationen (I und II) geben eine Übersicht über den Stand der Technik akustischer Datenerhebungsmethoden, beschreiben deren Einsatzmöglichkeiten auf unterschiedlichen Raum- und Zeitskalen, und diskutieren ihre Eignung für den Einsatz in polaren Meeren.

Zwei weitere Publikationen (VI und VII) untersuchen die Mutter-Jungtier Beziehung und die Individualität der Rufe von Jungtieren an jeweils einer arktischen und einer antarktischen Hundsrobbenart (Sattelrobbe, *Pagophilus groenlandicus* und Weddellrobbe, *Leptonychotes weddellii*). Die Ergebnisse des Vergleichs der Rufe beider Eisrobbenarten deuten darauf hin, dass sich artspezifische Unterschiede in den Vokalisationsmustern von Robbenmüttern und ihren Jungtieren ebenso wie Unterschiede in den akustischen Signaturen lokaler Populationen der gleichen Art auf variierende abiotische Faktoren wie Eis oder auch auf anthropogene Faktoren zurückführen lassen.

So könnte im Falle von Sattelrobben die Bejagung eine Erklärung für die beobachteten Unterschiede zwischen den zwei untersuchten Populationen darstellen.

Zur Untersuchung von zeitlichen Mustern im Vokalisationsverhalten mariner Säuger im Südpolarmeer wurden mehrjährige, quasi-kontinuierliche akustische Unterwasseraufnahmen der autonomen Horchstation PALAOA (PerenniAL Acoustic Observatory in the Antarctic Ocean, 70°31'S 8°13'W, Atka-Bucht, Ekström Schelfeis) analysiert (Publikationen III, IV, V, VIII und IX). In diese Studien gehen Aufzeichnungen des Observatoriums aus den Jahren 2006 bis 2009 ein.

Die Publikationen III, IV und V untersuchen auf unterschiedlichsten Zeitskalen das akustische Verhalten der vier antarktischen Eisrobbenarten Weddellrobbe (*Leptonychotes weddellii*), Seeleopard (*Hydrurga leptonyx*), Rossrobbe (*Ommatophoca rossii*) und Krabbenfresser (*Lobodon carcinophaga*), und interpretieren die Ergebnisse im jeweiligen artspezifischen akustisch-ökologischen Kontext. Weddellrobben sind in den akustischen Aufzeichnungen des Observatoriums ganzjährig präsent. Diese akustische Präsenz spiegelt sehr wahrscheinlich das territoriale Paarungsverhalten der männlichen Tiere wieder. Es wird vermutet, dass ein ganzjähriges Verbleiben im Bereich des Unterwasserterritoriums Vorteile bei der Partnerfindung mit sich bringt.

Bislang gab es keine Belege für Sichtungen von Rossrobben in der dem Observatorium vorgelagerten Meereisregion um die Akta-Bucht. Die akustischen Aufnahmen zeigen jedoch, dass sie sich dort regelmäßig von Dezember bis Februar einfinden. Rufe von Seeleoparden wurden in den drei Jahren mit Unterbrechungen jeweils ganzjährig aufgenommen, was darauf hindeutet, dass einige (möglicherweise juvenile) Seeleoparden während des Südwinters in den Küstenregionen der Antarktis verbleiben.

Des Weiteren wiesen die PALAOA Daten die Präsenz von Buckelwalen (*Megaptera novaeangliae*) während neun Monaten eines Jahres nach. Dies wird als Hinweis auf die mögliche Bedeutung der Küstenregionen für die Überwinterung interpretiert (Manuskript VIII). Gleichermaßen konnten akustische Signaturen von Antarktischen Blauwalen (*Balaenoptera musculus intermedia*) ganzjährig erfasst werden, was eine Nutzung küstennaher Polynjas auch während des Südwinters nahelegt (Manuskript IX). Zusätzlich wurden anhand des Jahresganges eines bestimmten akustischen Signals, das bislang generisch als “bio-duck” bezeichnet wird und noch keiner Tierart zugeordnet werden konnte, neue Hypothesen zu den möglichen Quellen dieses Signals aufgestellt.

Die letzte Publikation (X) diskutiert den Einfluss von anthropogenem Lärm auf Fische durch einen Vergleich mit entsprechenden Erkenntnissen von anderen Tierarten. Ein solch vergleichender Ansatz basiert auf der Annahme, dass anthropogener Lärm für alle Tierarten, die für kritische Aspekte ihres Verhaltens auf Schall angewiesen sind, einen gleichermaßen bedeutsamen Aspekt ihrer akustischen Ökologie bildet.

Der dieser Dissertation zugrunde liegende Arbeitsansatz stützt sich auf das Modell der akustischen Ökologie, die das verbindende Element der Publikationen dieser Doktorarbeit darstellt. Bislang wurde dieses Modell jedoch kaum auf marine Säuger in polaren Regionen angewandt. Die Synopse dieser Dissertation stellt die erste umfassende konzeptionelle Beschreibung der akustischen Ökologie antarktischer mariner Säuger dar, in der die spezifischen Umweltbedingungen der polaren Regionen ebenso wie die drohenden Gefahren des Klimawandels und weiterer anthropogener Einflüsse besondere Beachtung finden.

Samenvatting

Onderzoek naar mariene zeezoogdieren in poolgebieden – zoals studies naar de ecologische consequenties van antropogene invloeden – wordt belemmerd door de vijandige klimatologische omstandigheden die menselijke toegang tot deze gebieden beperken. Mariene zeezoogdieren produceren geluid in verschillende gedragscontexten, waardoor akoestische opname-technieken, die quasi-omnidirectioneel en onafhankelijk van licht en weersomstandigheden zijn, een geschikte methode bieden om de aanwezigheid en het gedrag van mariene zeezoogdieren in poolgebieden het hele jaar door te monitoren. Akoestisch gedrag van mariene zeezoogdieren wordt gevormd door de soort-specifieke gedragsecologie, maar ook door abiotische, biotische en antropogene factoren uit de leefomgeving van het dier, een concept dat bekend staat als akoestische ecologie. Akoestische ecologie beschrijft de interactie tussen een dier en zijn omgeving gemedieerd door geluid. Inzicht in de akoestische ecologie is belangrijk voor de interpretatie van akoestische gegevens, omdat de akoestische ecologie van een soort bepaalt of fysieke aanwezigheid van een dier ook resulteert in akoestische aanwezigheid, maar ook op welke tijdschaal een dier akoestisch actief is en over welke ruimtelijke schaal akoestische aanwezigheid van een dier kan worden gedetecteerd.

Deze dissertatie omvat tien manuscripten, die gebaseerd zijn op gegevens verzameld in de Zuidelijke en Arktische Oceanen. Allemaal verschaffen ze voorbeelden hoe aspecten van de soort-specifieke akoestische ecologie het akoestisch gedrag van een soort vormgeven. Daarnaast laat het meerendeel van de manuscripten zien hoe door middel van akoestisch monitoren informatie over de fysieke aanwezigheid van mariene zeezoogdieren kan worden verschaft in gebieden waar langdurige (visuele) observatie niet mogelijk is. De eerste twee manuscripten (I en II) bieden een overzicht van verschillende akoestische opname-technieken en beschrijven hoe deze op verschillende tijd en ruimte schalen in pool-oceanen kunnen worden ingezet.

Manuscripten VI en VII beschrijven het onderzoek naar moeder-pup interacties en de individualiteit van pup vocalisaties in een Arctische en Antarctische zeehondensoort uit de familie Phocidae (respectievelijk, de zadelrob, *Pagophilus groenlandicus* en de Weddell zeehond, *Leptonychotes weddellii*). Voor zeehondensoorten die ijs gebruiken als platform voor geboorte en zorg voor pups, verklaren verschillen in ijs habitat vermoedelijk de verschillen in het gedrag van moeder en pup, maar mogelijk ook de verschillen tussen populaties van dezelfde soort. Voor zadelrobben speelt mogelijk de jacht (antropogene factor) ook een rol in de verschillen die werden gevonden in gedrag tussen de beide studiepopulaties.

In manuscripten III, IV, V, VIII en IX werden de tijdspatronen in onderwater vocalisaties van mariene zeezoogdieren in de Zuidelijke Oceaan onderzocht middels semi-continue, meer-jarige akoestische opnamen van PALAOA, een energetisch zelf-voorzienend akoestisch observatorium op de Ekström Ice Shelf (70°31'S 8°13'W). Manuscripten III, IV en V onderzoeken het akoestisch gedrag over verschillende tijdsschalen van vier Antarctische zeehondsoorten: de Weddell zeehond, het zeeluipaard (*Hydrurga leptonyx*), de Rosszeehond (*Ommatophoca rossii*) en de krabbenrob (*Lobodon carcinophaga*). De bevindingen werden geinterpreteerd in de context van de soort-specifieke akoestische ecologie; Weddell zeehonden waren het hele jaar akoestisch aanwezig, hetgeen vermoedelijk is gerelateerd aan de gedragsecologie van deze soort. Weddell zeehonden hebben een territoriaal paarsysteem, waarbij het mogelijk voordelig is voor mannelijke dieren om het hele jaar in hun onderwater territorium aanwezig te blijven. Hoewel Rosszeehonden nooit werden waargenomen in het kustgebied nabij PALAOA, blijkt uit akoestische gegevens dat ze fysiek aanwezig zijn van December tot Februari. Zeeluipaard vocalisaties waren met tussenpozen het gehele jaar aanwezig in PALAOA opnamen (over drie jaar), hetgeen laat zien dat enkele (mogelijke juveniele) zeeluipaarden in de kustgebieden blijven gedurende de winter.

Verder tonen de PALAOA opnamen de aanwezigheid van bultrug walvissen (*Megaptera novaeangliae*) gedurende negen maanden van het jaar. Dit is mogelijk een indicatie voor het belang van kustgebieden, zoals het gebied nabij PALAOA, voor bultruggen die overwinteren in de Antarctische fourageergebieden (manuscript VIII). Vocalisaties van Antarctische blauwe vinvissen (*Balaenoptera musculus intermedia*) waren eveneens het gehele jaar aanwezig in de opnamen, wat er mogelijk op duidt dat de kustgebieden met open water ook van belang zijn voor deze soort (manuscript IX). Daarnaast werd de seizoensperiodiek in de aanwezigheid van een onbekend geluidssignaal, de 'bio-duck', gebruikt om nieuwe hypothesen te formuleren met betrekking tot de mogelijke bron van dit signaal.

In het laatste manuscript worden de invloeden van antropogeen onderwater geluid op vissen bediscussieerd gebaseerd op de bevindingen van vergelijkend onderzoek aan andere diersoorten. Deze vergelijkende benadering weerspiegelt het idee dat voor diergroepen die voor veel aspecten van hun gedrag afhankelijk zijn van geluid, menselijk lawaai vermoedelijk een belangrijk aspect vormt van de soort-specifieke akoestische ecologie.

Akoestische ecologie vormt het omvattende concept van deze verschillende manuscripten en publicaties. Gegeven de schaarse hoeveelheid literatuur over dit concept met betrekking tot mariene zeezoogdieren, is in de synopse ook een gedetailleerde conceptuele beschrijving van akoestische ecologie opgenomen. Bijzondere nadruk ligt daarbij op de specifieke omgevingsfactoren van poolgebieden en de dreiging van klimaatverandering en andere antropogene invloeden.

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1. Preface

The data for the work in the Antarctic presented in this thesis were collected adhering to the SCAR Code of Conduct. All necessary permits were obtained from the Umweltbundesamt (UBA, Germany) for construction and maintenance of the PALAOA acoustic observatory and to carry out the playback experiments on Weddell seals. For the data collected in the Arctic, a scientific permit was issued under the Marine Mammal Regulations (MMR, part of the Fisheries Act, USA) and the project was approved by the DFO (Canada) animal care committee.

This thesis is a cumulative work, consisting of 3 published, and 1 accepted paper(s) and 4 manuscripts that are still in preparation (2) or submitted (2) for publication (referred to as papers and manuscripts, respectively in the synopsis). Papers and manuscripts are presented as independent pieces of work (chapter 3 of the thesis). Among these papers, there is in some cases substantial cross-referencing and repetition of descriptions (*e.g.* with respect to the details on data collection by PALAOA), which is inevitable given the thesis format.

In the synopsis, I provide a motivation and background to the work presented in this thesis, as well as an overarching framework on acoustic ecology, how the findings can be interpreted in the context of acoustic ecology and the role of acoustic ecology in the interpretation of acoustic data in general. Furthermore, I present an outlook of questions emerging from the work presented in this thesis and future plans to address these.

2. Synopsis

1. Motivation: why study marine mammals in polar oceans?

The accumulating evidence of human impacts on marine mammals, such as commercial and subsistence hunting, environmental contaminants, overfishing, habitat destruction, climate change, marine debris and underwater noise, have raised the need for a better understanding of how these processes relate to consequences on individual and population levels. Such an understanding is urgently needed for the development of conservation and mitigation measures to manage and protect marine mammals and their habitats (*e.g.,* Reynolds *et al.,* 2009). Marine mammals can serve as sentinel species for aquatic ecosystem health (Bossart, 2006; Moore, 2008). Given their long life spans, high trophic level in the ecosystem and high fat stores that can serve as depots for anthropogenic toxins, their physical condition is a valuable indicator of many human-induced changes in the marine environment. Furthermore, environmental changes resulting in behavioural responses may directly be reflected in spatio-temporal changes in marine mammal distribution patterns.

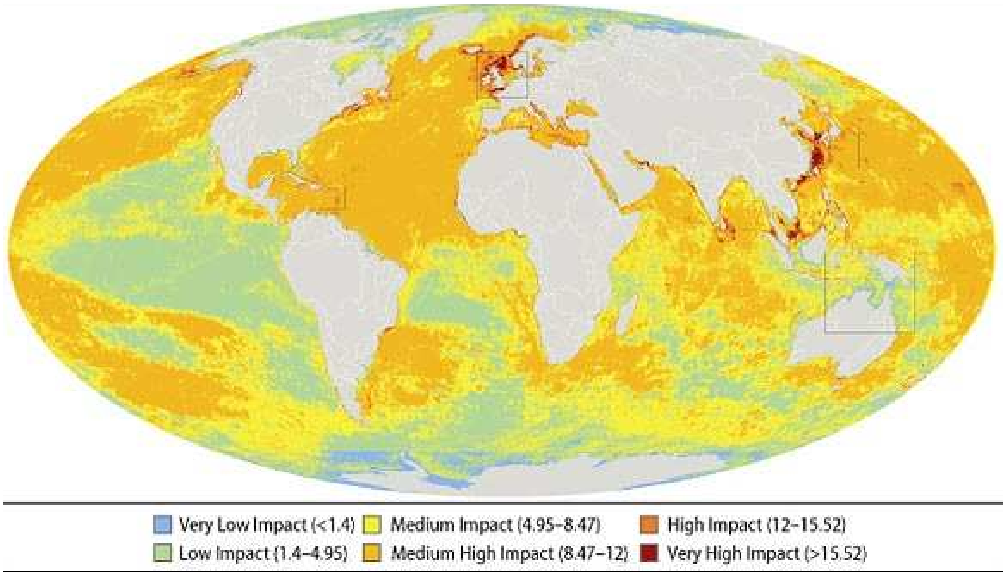


Figure 1. Global map of cumulative human impacts based on an ecosystem-specific, multi-scale spatial model. Analyses included 17 global data sets of anthropogenic drivers (*e.g.,* different types of fishing, presence of oil rigs, shipping traffic). Figure reproduced from Halpern *et al.,* 2008.

Figure 1 shows a map of estimated spatial variation in human impacts (*e.g.,* shipping, fishing, pollution) on marine ecosystems, reflecting that no area is unaffected by human influence, although areas of relatively low impact are associated particularly with high latitudes (Halpern *et al.,* 2008).

The threats for many marine mammal species in high latitude waters are nevertheless likely to be no less severe than those in temperate and tropical regions: the current gaps in knowledge on animals in their seasonal or permanent polar habitats, significantly impedes our understanding of possible consequences of human-induced changes. In polar areas, climatic conditions (seasonally) restrict human access; thereby complicating data collection aimed at investigating how marine mammal distribution relates to environmental factors and might be affected by *e.g.* climate-induced changes in ice conditions.

In particular polar species, such as ice-breeding seals, narwhals and beluga whales, are thought to be vulnerable to climate-induced perturbations affecting their permanent habitat (Tynan & DeMaster, 1997; Siniff *et al.,* 2008). Nevertheless, given the importance of polar waters as a feeding area for many seasonally present marine mammal species, the effect of human-induced changes to this habitat can affect marine mammal populations beyond the period they spend in polar oceans. Noting that climate-induced changes are believed to occur in polar regions at faster rates than elsewhere (*e.g.,* Clarke *et al.,* 2007), it is vital to accurately describe and understand the state and diversity of polar ecosystems in general, to reliably assess the extent of future changes and to carefully evaluate the possible consequences for their inhabitants.

In the Arctic, recent computer projections of the National Snow and Ice Data Center have indicated that the receding Arctic sea-ice will leave more and more areas partially or largely ice-free year-round within the near future (Johannessen *et al.,* 1999; Overpeck *et al.,* 2005). The ice-free areas open opportunities to re-route commercial vessel traffic between the Pacific and Atlantic Ocean to take advantage of the open Northwest and Northeast Passages. Alongside the ecological implications of changes in ice conditions for marine mammals with ice-associated habitats (*e.g.* Tynan & DeMaster, 1997), an increase in shipping activity and the year-round presence of vessels in these areas will lead to increased noise levels, possibly additionally affecting marine mammals that inhabit this area permanently or seasonally.

In the following sections, I provide a brief introduction to polar regions and polar marine mammals. Thereafter I discuss why newly emerging acoustic recording techniques are specifically suitable as a tool to collect data from these regions, the role of acoustic ecology and how knowledge based on acoustic observations can contribute to further our understanding of marine mammals in their polar habitats.

2. Polar oceans

The earth's polar oceans comprise the Southern Ocean, with the Antarctic Convergence being recognized as its natural northern boundary (CCMLAR, 1980), and the Arctic Ocean, *i.e.,* the ocean located within the Arctic Circle occupying the region around the North Pole (Fig 2). Although the two polar oceans are strikingly similar in many aspects of their overall ecology, dominated by cold conditions and the presence of sea-ice, both at the same time strongly differ in atmospheric, oceanographic and biological features.

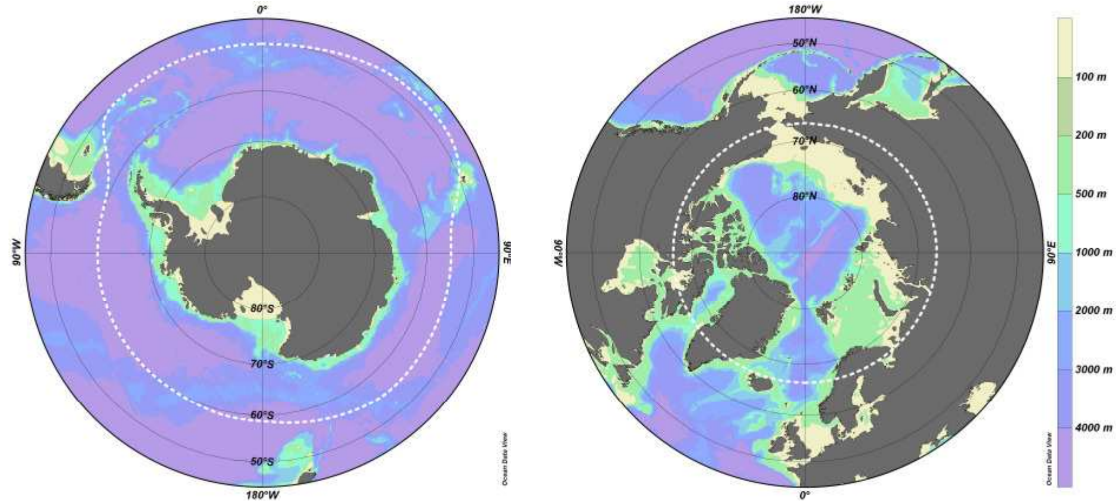
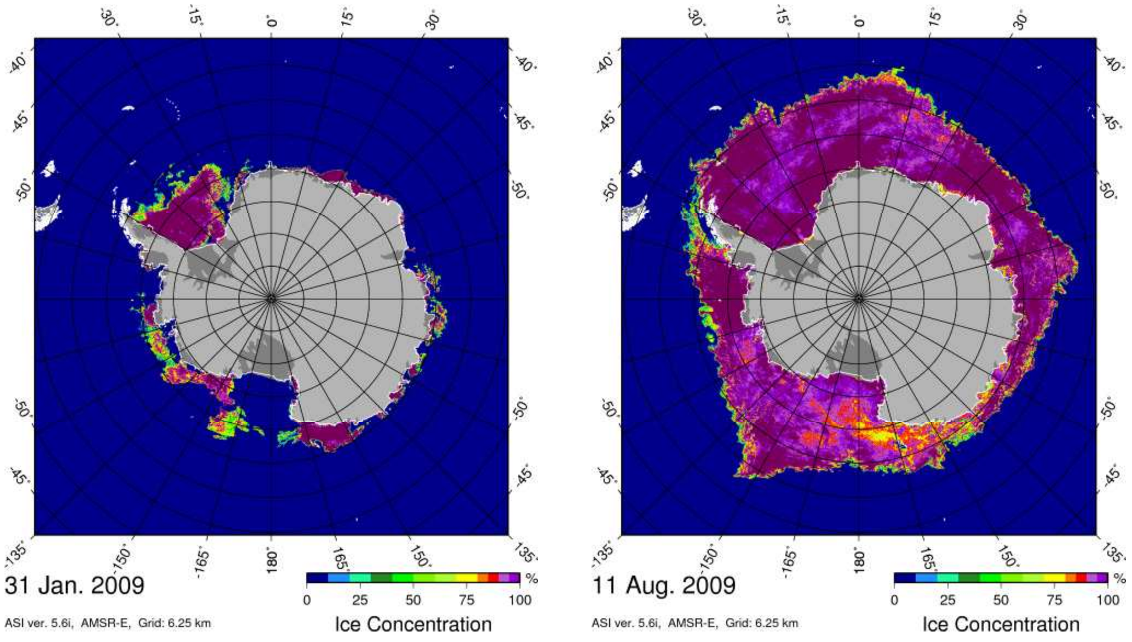


Figure 2. Maps of the earth's polar oceans. Left: the Southern Ocean, with the Antarctic Convergence (white dotted line, schematic representation of mean position of Antarctic Convergence) as its northern boundary; right: the Arctic Ocean and the Arctic Circle (white dotted line).

2.1 The Southern Ocean

The Antarctic consists of a continent forming ~10% of the earth's land surface. The continent is surrounded by a dynamic, open ocean and an unusually deep continental shelf, a side-effect of the weight of the ice sheet covering the continent (Knox, 2007). Apart from the northern part of the Antarctic Peninsula, most of the Antarctic continent lies south of the Antarctic Circle (66° 33'44 S), south of which continuous daylight prevails during austral summer, and continuous darkness during austral winter. The natural northern boundary of the Southern Ocean is formed by the Antarctic Convergence (or Polar Front), which forms a sharp temperature boundary between northern temperate waters and southern polar waters (Fig 2). The Southern Ocean's sea ice canopy offers substantial seasonal habitat heterogeneity, reaching up to $20x10^6$ km^2 during winter and receding to less than $4x10^6$ km^2 in austral summer (Knox 2007; Fig 3). Furthermore, the seasonal cycle of formation and melt of the circumantarctic sea ice is in itself of high significance to the Antarctic marine ecosystem, particularly for krill.



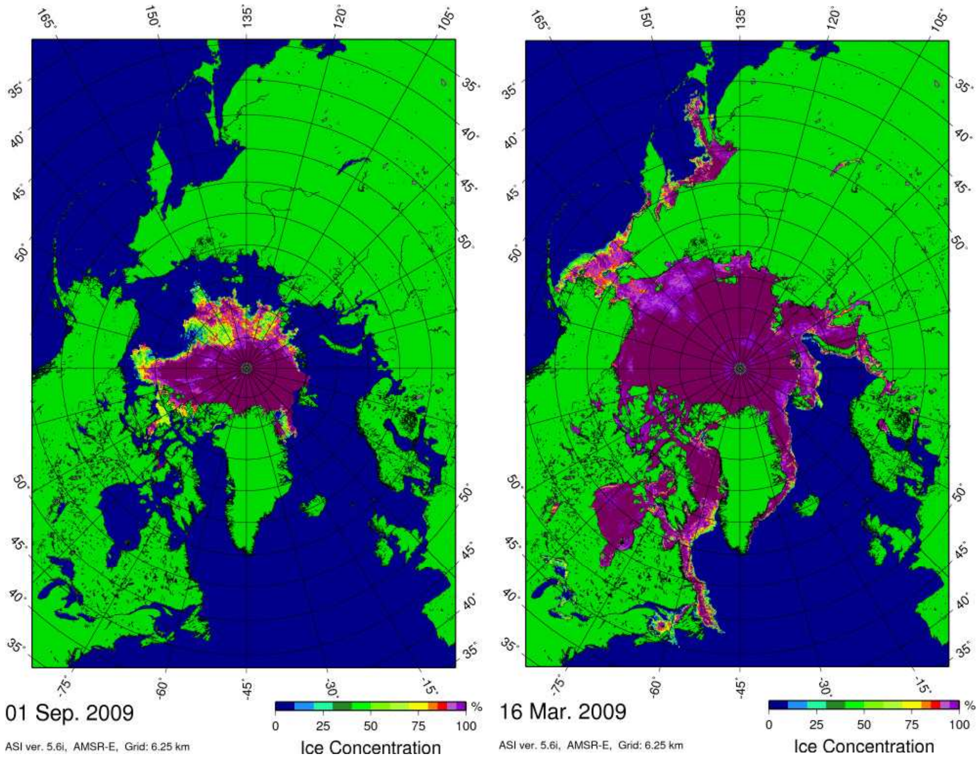
Austral summer **Austral winter**

Figure 3. Maps of the sea ice concentration in the Southern Ocean. Left: Example of a day with minimal sea ice extent (31 January 2009); Right: Example of a day with maximal sea ice extent (11 August 2009). Maps provided by www.seaice.de (Spreen *et al.,* 2008).

Krill, holding a central position in the Antarctic food web, provides the food base for a wide range of fish, squid, birds and marine mammals. Although many aspects of the relationship between krill abundance and sea ice are still under discussion (see Siegel, 2005 for a review), it is generally believed that ice-edge algal blooms form an important and predictable food source for krill, while under-ice biota provide krill protection from predators and a food source during austral winter and spring (Knox, 2007). Given its important role as the food base for many marine mammal species, krill is thought to be one of the important drivers behind marine mammal distribution.

2.2 The Arctic Ocean

The Arctic Ocean is characterized by extensive shallow shelf seas surrounding a largely land-locked ocean, influenced by seasonal air and freshwater fluxes from the surrounding continents. The Arctic Ocean has a permanent cover of slowly circulating multi-year ice floes surrounded by a zone of seasonal pack ice and a zone of land-fast ice (*e.g.,* Stonehouse, 1989; Fig 4). Sea ice coverage in the far North is relatively stable, with sea ice melt occurring primarily at the periphery. Consequently, a large part of the Arctic sea ice consists of multi-year ice. However, this situation may change rapidly within the next decades, as the Arctic sea ice recently showed substantial decreases in both extent and thickness in response to global warming (IPCC, 2007). In winter, maximum sea ice cover is 13.9x10^6 km^2, while in summer 6.2x10^6 km^2 of the Arctic Ocean is ice-covered (Johannessen *et al.,* 1999).



Boreal summer **Boreal winter**

Figure 4. Maps of the sea ice concentration in the Arctic. Left: Example of a day with minimal sea ice extent (1 September 2009); Right: Example of a day with maximal sea ice extent (16 March 2009). Maps provided by www.seaice.de (Spreen *et al.,* 2008).

Although the planktonic base of the food supply of marine predators such as fish, birds, pinnipeds and cetaceans is broadly similar across all latitudes, the key prey organisms differ between polar oceans. In the North, benthos and fish form the most important prey for marine mammals (*e.g.,* Smetacek & Nicol, 2005). Arctic cod (*Boreogadus saida*) is one of the pivotal fish species in the Arctic marine ecosystem occurring mainly in marginal ice zones (Andriashev, 1970; Ainley & DeMaster, 1990). The ice-edge habitat is critical for Arctic cod since the level of recruitment depends on the availability of the crustacean species on which cod larvae feed that in turn depend on ice-edge algal blooms (Drolet *et al*., 1991). In addition, benthic communities in coastal areas form an additional important food resource utilized by birds and marine mammals (Dayton *et al.,* 1994)

3. Polar oceans as a habitat for marine mammals

The highly productive polar waters attract many marine mammal species. Depending on the costs and benefits of movement, pinnipeds and cetaceans migrate between tropical or temperate marine regions and polar oceans, follow the seasonal waxing and waning of sea-ice or remain in their polar habitat year round. The pinniped species covered in this thesis live year round in close association with ice (Arctic: harp seal, *Pagophilus groenlandicus*; Antarctic: Weddell seal, *Leptonychotes weddellii*; leopard seal, *Hydrurga leptonyx*; Ross seal, *Ommatophoca rossii*; crabeater seal, *Lobodon carcinophaga*, Fig 5). The cetacean species covered in the chapters of this thesis are humpback (*Megaptera novaeangliae*) and Antarctic blue whales (*Balaenoptera musculus intermedia*) (Fig 6), which undertake seasonal migrations between feeding grounds in cold productive polar waters and breeding areas in tropical or temperate waters. Although some species covered in this thesis are thus only seasonal inhabitants of polar oceans, all species are considered true Arctic or Antarctic species, given that they depend either directly or indirectly on polar oceans for critical portions of their life histories (Boyd, 2002).

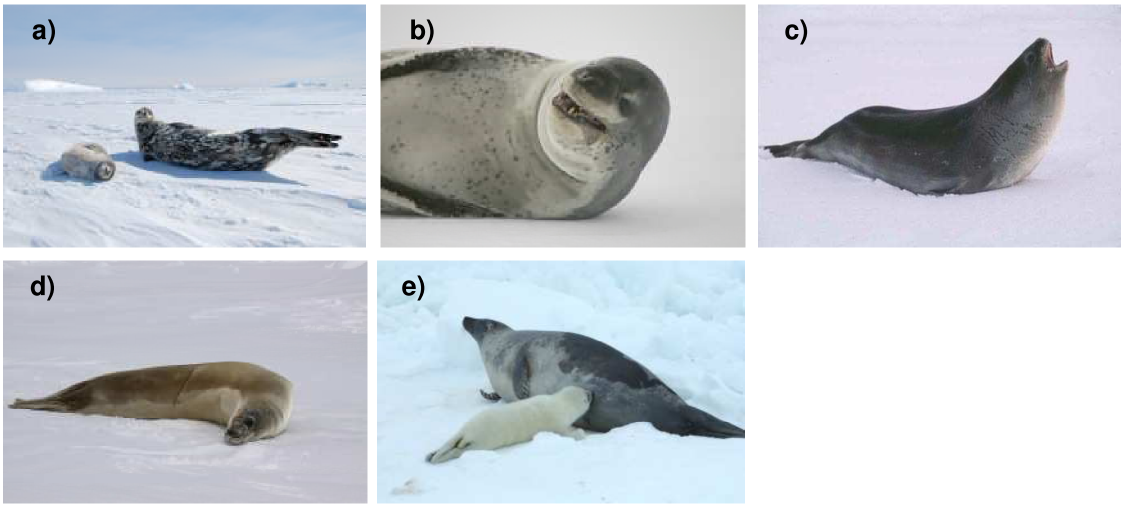


Figure 5. The five pinniped species covered in this thesis, a) the Antarctic Weddell seal (*Leptonychotes weddellii*), b) the Antarctic leopard seal (*Hydrurga leptonyx*), c) the Antarctic Ross seal (*Ommatophoca rossii*), d) the Antarctic crabeater seal (*Lobodon carcinophaga*), and e) the Arctic harp seal (*Pagophilus groenlandicus).* Pictures a, d and e by I. Van Opzeeland. Pictures b and c by J. Plötz.

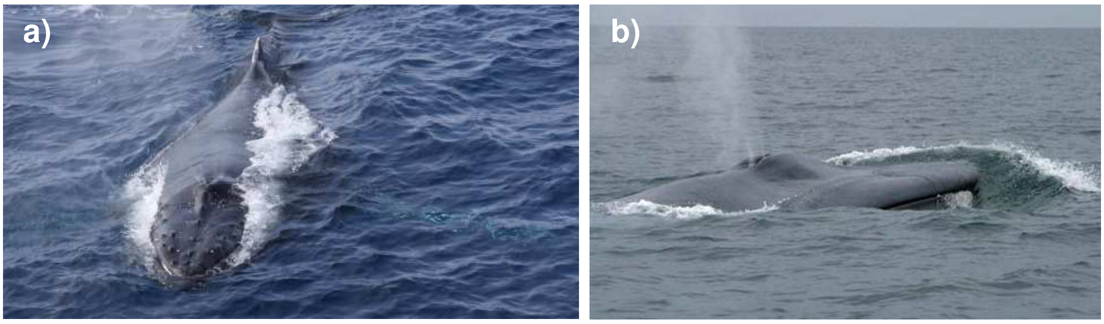


Figure 6. The two cetacean species covered in this thesis, a) the Southern Hemisphere humpback whale (*Megaptera novaeangliae*), picture by I. Van Opzeeland and b) the Antarctic blue whale (*Balaenoptera musculus intermedia*), picture by NOAA.

3.1 Pinnipeds

Dispersal of pinnipeds into polar areas is thought to have commenced with the evolution of large body size in ancestral pinnipeds (Costa, 1993). In Costa's (1993) model, early pinnipeds exhibited a primitive form of otariid breeding patterns, with females requiring numerous short-duration foraging trips to sustain lactation. The evolution towards a larger body size enabled females to separate foraging from lactation as females had increased maternal reserves to rely on. This temporal separation of foraging and breeding is thought to finally have enabled these basal phocids to inhabit and reproduce in seasonally less-productive areas, in relative absence of resource competitors. Upon reaching higher latitudes, development of a shortened lactation period would have pre-adapted these early phocids to breeding on unstable substrates, such as ice (Costa, 1993).

Apart from a number of physiological adaptations for life in ice-dominated environments, such as sharp and strong claws for locomotion on the ice, the lanugo fur of pups and thick subcutaneous blubber layers, polar pinnipeds also developed remarkable behavioural adaptations to life in their habitat. In temperate regions, the onset of parturition in terrestrial breeding pinnipeds is to a large extent determined by ambient temperature (Boyd, 1991). Polar pinnipeds, however, depend on ice for breeding. Consequently, parturition occurs in late winter and early spring, when snow accumulation is at a maximum and the ice is most extensive and stable, minimizing pup mortality as a result of ice breakup (Pierotti & Pierotti, 1980). As the period of optimal ice and foraging conditions is relatively short, pupping is generally synchronous within ice-breeding pinniped populations compared to pinnipeds breeding on land. Given that the lactation period is generally relatively short in phocids, lasting one to six weeks, depending on species, precociality of young is necessary so that pups can forage and defend themselves independently at an early age. The number of offspring produced per reproductive cycle in pinnipeds is typically limited to one, which is likely a consequence of the greater parental investment necessary to produce precocial young.

In some ice-breeding pinniped species, such as harp and Ross seals, spatial and temporal disparity in resources (*i.e.,* mates and/or food) leads to migratory movements between different areas of their home range, although the spatial scale of movement generally does not extend beyond the polar ocean (*e.g.,* Ridgway & Harrison, 1981). However, the scale and pattern of movement of many migratory species can differ between individuals, depending on sex, age and reproductive status (Ridgway & Harrison, 1981; Dingle & Drake, 2007). Other species are more stationary and remain in the breeding area year round (*e.g.,* Green & Burton 1988; Rouget *et al.,* 2007; paper III and IV), which might have beneficial consequences for mating success in territorial species such as Weddell seals (paper III).

Within the ice habitats of polar pinnipeds, there exists considerable variation which appears to influence behavioural patterns and the timing of behaviour (Trillmich 1996; Lydersen & Kovacs 1999). Variability in the temporal and structural stability of the haul-out platform, risk of predation, availability of food within the breeding habitat and access to the water are factors that are thought to have resulted in the evolution of *e.g.,* different mating systems (papers I and III) and maternal strategies (paper I, VI and manuscript VII) with each ice-breeding species filling its own niche within the polar ocean habitat.

3.2 Cetaceans

Only few cetacean species that occur in polar waters are exclusive to these regions. The narwahl (*Monodon monoceros*), bowhead (*Balaena mysticetus*) and beluga whale (*Delphinapterus leucas*) are strictly Arctic in their distribution, whereas exclusively polar species are absent in the Southern Hemisphere. The difference between both polar oceans in the evolution of cold water forms of marine mammals is thought to relate to bathymetric differences: the relatively closed basin of the Arctic Ocean hinders marine mammal movement to warmer waters, whereas the unconfined northern boundary of the Southern Ocean allows relatively unconstrained meridional migration (Davies, 1963). Cetaceans benefit from polar habitats through the association between prey availability and ice rather than from the direct needs of ice for breeding or resting like pinnipeds. Breeding in these cetacean species takes place at lower latitudes in temperate or tropical waters (Corkeron & Conner, 1999).

Evolution of cetacean presence in polar oceans is thought to be related to the gradual retreat of cold productive waters from lower to higher latitudinal regions in the interglacial (*i.e.,* warmer) periods (Stern, 2002). During the last glacial maximum (~20.000 years ago), the glacial ice sheet extended to much lower latitudes compared to the present situation. When the ice sheet retreated towards the poles in the interglacial period, the availability of sunlight for photosynthesis in cold water regions became more variable between seasons, leading to seasonal peaks in cold water primary productivity. Whale distribution is thought to have followed this retreat of cold productive water towards the poles, which has also been suggested one of the driving forces behind the bipolar (or anti-tropical) distribution of some cetacean species (*i.e.,* north-south species pairs *e.g., Berardius spp*, *Eubalaena spp*, Davies, 1963; Fordyce, 2002).

While odonocetes are generally more variable in their distribution patterns and migratory behavior, all baleen whale species, except bowhead (*Balaena mysticetus*) and Bryde's whales (*Balaenoptera edeni*)[1], undertake seasonal migrations between feeding grounds in cold productive polar waters and their breeding areas in relatively unproductive tropical or temperate waters. Corkeron & Conner (1999) revisited several hypotheses as to why baleen whales undertake these long-distance migrations to return to tropical or temperate waters for breeding. They concluded that the most likely hypotheses driving baleen whale migration are those related to calf growth and survival, *i.e.,* the benefits of the absence of killer whales in the wintering areas and the presence of calm water. However, there is

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[1] Bowhead and Brydes whales remain in polar and tropical waters, respectively.

substantial evidence for various baleen whale species that not all individuals of a population undertake the annual migration and that part of the population is present on the feeding grounds in winter, presumably to avoid the energetic demands of migration (manuscript VIII and IX).

Much of the current knowledge on cetaceans is based on directed and incidental takes or stranded animals. These offered the possibility to collect a suit of morphological and physiological data, although the potential of information that could be obtained from such material is often not maximally exploited (*e.g.,* Corkeron, 2009a). Large gaps still exist in what is known on cetacean stock structures and behavioural patterns, such as migration, and breeding strategies. Such information is essential to understand population status of marine mammals and the factors that threaten their persistence and/or population recovery over time. Commercial whaling severely depleted whale stocks, with many whale populations reduced to less than 10% of their original abundance (*e.g.,* Best, 1993). Humpback whales were in many cases the first species taken and frequently hunted to commercial extinction (Clapham *et al.,* 1999). Humpback whales in the Southern Hemisphere were target of illegal Soviet catches in the 1960s: while 2710 humpback whales were reported to have been landed, the actual total was more than 48 000 (Yablokov *et al.,* 1994). Overall, it is not unlikely that many humpback whale populations were reduced by more than 90% of their initial population sizes (Clapham *et al.,* 1999). Blue and fin whale populations in the Southern Hemisphere also were reduced to a fraction of their original abundance with over 350,000 and 700,000 whales killed, respectively (Clapham & Baker, 2002). Blue whales are now thought to number approximately 1% of their pre-exploitation abundance, increasing at an annual rate of 7.3% (though the confidence interval on this rate of increase is wide, 1.4-11.6%, Branch *et al.,* 2007). Even less is known about fin whales, with no recently accepted abundance estimates, and no currently accepted estimates of trends in abundance (NMFS, 2006).

4. The importance of sound for marine mammals

Sound plays an important role for marine mammals, as visibility underwater is often restricted and water has excellent sound transmission properties (see Box 2, page 2, paper X). Marine mammals use sound passively by exploiting sounds of biotic and abiotic origin as acoustic cues for *e.g.,* orientation and localization of prey, predators and conspecifics. In addition, marine mammals also actively produce sound in various behavioural contexts, which makes acoustic recording techniques a suitable tool to monitor their presence and study their behaviour. Two important aspects of the role of sound for marine mammals are sound reception and sound production, which will be briefly introduced in the next two subsections of this section. In addition, the last subsection of this section describes the possible effects of anthropogenic underwater noise on marine mammals.

4.1 Sound reception

Marine mammal ears generally resemble the ears of terrestrial animals, although the external ear is absent (except in otariids) and the middle ear is extensively modified (Southall *et al.,* 2007). Many of these modifications seem to have evolved in adaptation to hydrostatic pressure, hydrodynamics, and sound reception in water (*e.g.,* Au, 1993; Wartzok & Ketten, 1999). Within marine mammals, there is a great diversity between species in hearing range and sensitivity. However, for more than 80% of the marine mammal species hearing data is non-existent because of the limitations in obtaining experimental hearing data for these species (Rice, 1998; Southall *et al.,* 2007). For example, no baleen whale species has been tested to date for hearing sensitivity. Baleen whale hearing ranges are extrapolated from hearing data from terrestrial mammals in combination with mathematical models based on ear anatomy of stranded animals. Southall *et al.* (2007) divided cetaceans and pinnipeds into five functional hearing groups based on the frequencies that they have been measured or estimated to hear: low frequency cetaceans (mysticetes, hearing range 10 Hz – 10 kHz), mid-frequency cetaceans (dolphins and toothed whales, hearing range 150 Hz – 160 kHz), high frequency cetaceans (porpoises, some dolphin species, hearing range 200 Hz – 180 kHz), pinnipeds in water (hearing range 75 Hz – 75 kHz) and pinnipeds in air (hearing range 75

Hz – 30 kHz). The highest hearing sensitivities are usually in the animal's own sound production frequency range (Southall *et al.*, 2007).

The distance over which sound is detected by a receiver, the bioacoustic space, consists of multiple spatial scales over which sound can convey information to a receiver (Clark *et al.,* 2009). Examples of different bioacoustic space types are the range over which a listening animal detects sounds from a calling conspecific (communication space) and the range over which an animal can detect signals from other species (produced by *e.g.,* prey or predators) or abiotic sources such as oceanographic features (but see Table 1 for summary of different bioacoustic space types).

Receiver	***Sound Source***			
	Self	**Conspecific**	**Other species**	**Abiotic source**
Self	Echolocation (navigation, food finding)	Communication	Predator, Food finding	Navigation, Food finding
Conspecific	Communication	Eavesdropping, Bi-static navigation Bi-static food finding	NA	Bi-static navigation
Other species	Detection by predator	Bi-static food finding	Eavesdropping	NA

Table 1. Table providing an overview of the different types of acoustic spaces. NA: not applicable. Reprinted from Clark *et al.* 2009.

The size of a bioacoustic space is determined by physical factors such as local background noise levels and propagation properties of the medium in which the animal communicates (*i.e.*, water depth, sea-floor substrate), but also by receiver characteristics, such as hearing sensitivity. The calling animal (passively and to some extend actively, *e.g.,* Brumm & Slabbekoorn 2005) determines the range over which signals can be detected by the source level, directivity and frequency band (*i.e.,* low frequency sounds transmit over larger distances than high frequency sounds) of the sounds produced. Size and shape of any bioacoustic space can vary in space and time, depending on species and the factors mentioned above. Knowledge on the acoustic characteristics of communication signals can therefore reveal many aspects of behavioural ecology and the physical environment in which animals live and communicate.

4.2 Sound production

Along with many other marine animals, marine mammals use sound in social contexts, for orientation, prey detection and to respond to the presence of predators. A comprehensive summary that illustrates the many kinds of sounds with variable physical properties that are produced by marine mammals is provided by Richardson *et al*. (1995). Mysticete cetacean species (baleen whales) range and can communicate over micro (< 1 km^2) to synoptic (>2000 km^2, Orlanski, 1975) scales (Moore *et al.,* 2006). In some baleen whale species, low frequency calls are also thought to play a role in orientation (Clark & Ellison, 2004). Odontocete species (toothed whales, dolphins and porpoises) tend to range and communicate over micro- to mesoscale areas (1 - 2000 km^2, *e.g.* Tyack, 2000), producing sounds over a wider frequency range (*e.g.* Richardson *et al.,* 1995). Sounds within the human hearing range of these species are mostly social sounds (*e.g.,* whistles and pulsed calls), whereas high frequency clicks are used for echolocation. Pinnipeds produce sounds both in air and in water. Their sounds also cover a wide range of frequencies and play a role in mother-pup recognition, male-male competition, and for males to attract females during the breeding season (Insley *et al.,* 2003; Van Parijs, 2003; paper I). Pinnipeds are bound to land or ice for breeding and moulting; therefore, access to land or ice is a fixture of their life histories. Acoustic behaviour in pinnipeds ranges from local (<1 km) to mesoscales with communication occurring both in air and in the water near haul-out sites on transit routes and foraging grounds (paper II). Given that marine animals communicate acoustically across such widely differing spatial scales, inter-specific differences in communication scales have to be taken into account in both the study design and interpretation of the data (paper II), as will also be further discussed in paragraph 5.

4.3 Anthropogenic noise sources and their impact on marine mammals

Anthropogenic noise can affect marine mammals in various ways (Fig 7), depending on factors such as the behavioural context in which an animal is exposed to the sound, the hearing sensitivity of the receiving animal, the received sound exposure level and the duration and duty cycle of the sound source (see for reviews Richardson *et al*., 1995; NRC, 2003; Nowacek *et al*., 2007; Southall *et al*., 2007). Nevertheless, much of the mechanisms behind the effects of noise on marine mammals is still not understood, which is also illustrated by the body of literature in which no apparent effect is reported (*e.g.*, Richardson *et al.,* 1995; Southall *et al*., 2007). Here I only included studies describing an effect as this section merely serves to illustrate the range of impacts man-made noise can have on marine mammals.

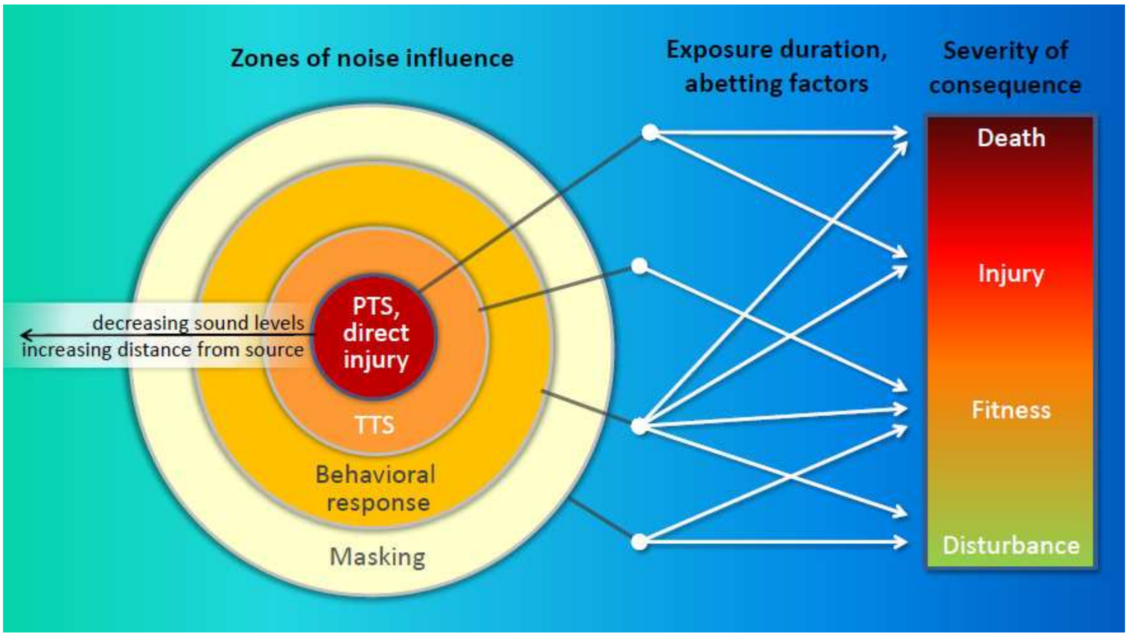

Figure 7. Schematic representation of noise zones and severity of potential consequences for marine mammals. Concentric circles (left) indicate zones of possible direct influence of sound on individual animals. Color bar (right) indicates range of potential consequences of acoustic exposure. White arrows symbolize the relation between direct influences to potential consequences, each standing for specific risk scenarios. The arrow from behavioral response to 'Death' specifically refers to scenarios discussed for beaked whale response to mid-frequency sonar (see section 4.3.5). Consequences of sound exposure depend on factors, such as exposure duration and additional abetting factors (*e.g.,* ocean temperature, health state of the exposed individual). Figure by O. Boebel.

4.3.1. Masking

The effects of masking of sounds (Fig 7) are mainly determined by the type of sound that is masked (*e.g.,* sounds produced by predators, prey) and the duration of the period that sounds are masked. Croll *et al.* (2002) suggested that the increased low frequency noise levels in the ocean, as a result of the increase in commercial shipping (Payne & Webb, 1971; McDonald *et al.,* 2006), may mask low frequency vocalizations and affect encounter rates between male and female fin whales, thereby potentially disrupting breeding behaviour. Fin whale (*Balaenoptera physalus*) males are thought to use low frequency reproductive advertisement displays to attract females over long distances (*i.e.,* ~100-200 km, Cummings & Thompson, 1971) for the purpose of mating (Croll *et al.*, 2002). A reduced communication range in combination with the typical separation of individuals during the breeding season, with possibly even larger inter-individual distances compared to pre-whaling population sizes, could impact populations that are still recovering from past overexploitation, such as blue and fin whales. In addition, masking might also affect the likelihood of detecting prey and potential predators (Richardson *et al.*, 1995).

4.3.2 Behavioural responses

Behavioural responses to anthropogenic sound sources are – with one notable exception discussed in section 4.3.5 – thought to be transient in nature and are therefore generally regarded as among the least severe in their impact, although impact severity is strongly dependent on behavioural context during which exposure occurs (*e.g.,* Southall *et al.,* 2007). Studies have reported animals to modify their vocal behaviour in response to the presence of noise sources. Beluga whales (*Delphinapterus leucas*), manatees (*Trichechus manatus*) and Northern right whales (*Eubalaena glacialis*) were found to increase vocal effort in response to elevated ambient noise conditions, known as the Lombard effect in humans (Scheifele *et al.*, 2005; Miksis-Olds & Tyack, 2009; Parks *et al.,* 2010). Miller *et al.* (2000) found that humpback whales lengthen their song in the presence of low-frequency active sonar, presumably to compensate for acoustic interference. Pacific humpback dolphins (*Sousa chinensis*) were found to increase the number of whistles in response to the passage of boats, suggesting that noise from transiting vessels affects dolphin group cohesion (Van Parijs & Corkeron, 2001). Blue whales were found to call more during periods within a seismic survey, possibly reflecting a similar effect as found in Pacific humpback dolphins (Di Iorio & Clark, 2009). Reduced call rates or complete cessation of vocalizations in response to the presence of anthropogenic sound have also been documented for various species (*e.g.,* Watkins & Schevill, 1975; Bowles *et al.,* 1994; Rendell & Gordon, 1999). Other behavioural reactions to human-made sound include avoidance reactions and deflections from migratory routes in response to industrial sounds (Malme *et al*., 1983; Richardson *et al*., 1985, but see Southall *et al.,* 2007 for a complete overview of behavioural responses).

4.3.3. Temporal threshold shifts (TTS)

In some cases, exposure to human-made sound can result in threshold shifts in hearing sensitivity that are temporal and reversible in nature (Fig 7). Depending on the severity of temporal hearing loss, the animal's ability to communicate with conspecifics, detect prey and potential predators is temporarily compromised (see Southall *et al.,* 2007 for a summarizing discussion).

4.3.4. Permanent threshold shifts (PTS)

When the sound source to which animals are exposed is sufficiently loud, this can result in a permanent threshold shift in hearing sensitivity. Permanent threshold shifts are considered an auditory injury and affect fitness and survival of the impacted individual permanently, impairing its ability to communicate with conspecifics, detect prey and potential predators (Southall *et al*., 2007).

4.3.5. Injury and death

Over the last decades a number of beaked whale (family Ziphiidae) mass strandings coincided with naval active sonar exercises (see Cox *et al*., 2006 for a review). This has raised concerns that certain sounds from naval mid-frequency sonars could directly or indirectly result in death of beaked whales and several mechanisms by which exposure to mid-frequency sonar may lead to strandings have been proposed (*e.g.,* Cox *et al*., 2006; Rommel *et al*., 2006). One of the hypotheses is that mid-frequency sonars generate an avoidance reaction involving repetitive shallow dives in an attempt to maximize the horizontal distance travelled away from the sound source (Zimmer & Tyack, 2007). Marine mammals have several adaptations to counter the effects of decompression sickness (DCS), such as alveolar collapse during deep dives which limits lung and blood gas exchange to shallow dive depths (Scholander, 1940). Zimmer and Tyack (2007) proposed that the gas-bubble lesions observed in many stranded beaked whales (*e.g.* Jepson *et al.*, 2003), may have been caused by the fact that these shallow avoidance dives do not exceed the depth of alveolar collapse, leading to DCS-like symptoms. The strength of the beaked whale avoidance reaction to mid-frequency sonar has been attributed to the similarity of the sonar sound to the calls of killer whales, the primary predator of beaked whales (Zimmer & Tyack, 2007). Although beaked whales appear particularly vulnerable to these noise sources, other species have also stranded following naval sonar exercises (see Weilgart, 2007).

4.3.6. Research needs: chronic noise exposure

There is a clear need for more information to better understand the effects of anthropogenic sound sources and how these affect marine mammal populations (NRC, 2003; 2005; ESF, 2008). Studies on the effects of noise on marine mammals have since long mainly focussed on injury and changes in behaviour as a result of short-term exposure to man-made sound (*i.e.,* sonar, seismic sources). However, the potential chronic impacts of rising noise levels in the ocean, such as the long-term effect of masking of vocalizations, is now also becoming topic of investigation (*e.g.,* Hatch *et al.*, 2008; Clark *et al.*, 2009). Nevertheless, unravelling the many aspects of the impact of long-term chronic noise exposure on marine mammals and the marine ecosystem (*i.e.,* prey species) is not straightforward. One of the key recommendations of reports on the impact of noise on marine mammals emphasizes the need to establish ‘noise budgets’, an accounting of the relative contributions of various sources to the total (local) noise field, for areas in the ocean (NRC, 2003). Information on noise budgets can be used to identify and characterize spatial and temporal patterns of noise sources and will aid in the development of models to predict how the presence of specific noise sources affects the various bioacoustic spaces of animals, *e.g.,* species-specific communication ranges (*e.g.,* Clark *et al.,* 2009). Such knowledge is a prerequisite for development of management strategies to protect the acoustic environment of marine habitats.

5. Acoustics as a research tool in polar oceans

Historically, visual surveying from ships, shore-stations, and aircraft is the standard method for taking a census of marine mammals (*e.g.,* Eberhardt *et al.,* 1979; Wilson *et al.,* 1996). When sighting data is collected systematically with surveys conducted along line transects, estimates on the total number of animals in a population can be obtained from the number of animals detected during the survey (*e.g.,* Anderson, 1979; Calambokidis & Barlow, 2004). Visual observations depend on favourable weather and light conditions and the presence of a team of observers on-site. Observer fatigue and the limited human visual field render a continuous effort and omnidirectional data collection difficult. In polar areas, weather conditions can be particularly adverse year round with heavy storms and fog. Outside the summer period, favourable sighting conditions are further restricted by limited daylight hours. In contrast to visual observation, acoustic recorders can be operated autonomously, are quasi-omnidirectional and independent of light and weather conditions, providing the option of studying animals at night and under conditions where visual observation is not possible (Table 2). Nevertheless, passive acoustic monitoring depends on marine mammals to produce sound; a precondition that cannot be taken for granted in all cases and something that should be taken into account in the interpretation of acoustic data (see also section 6).

Acoustic techniques only recently entered the range of easily accessible research tools, as significant advances in audio and computer technology now allow the acquisition and handling of large acoustic data sets. Acoustic techniques have become increasingly important as a tool for remote sensing the behaviour of various marine mammal species (*e.g.,* Stafford *et al*., 1998; McDonald & Fox, 1999; Janik, 2000; Johnson & Tyack, 2003; Mellinger *et al*., 2007). Passive acoustic recording techniques can be used to monitor responses of marine mammals to environmental change on various time and spatial scales. By coupling environmental data to recordings, it is possible to combine on-site measurements of acoustic activity with biological or oceanographic features (Stafford *et al.,* 2009). In addition, passive acoustic monitoring can be used to study anthropogenic impacts on marine mammals such as the presence of underwater noise sources (Di Iorio

Factor of influence	*Visual observations*	*Acoustic observations*
Sensitivity to light, weather, ice conditions	Yes	No
Cue	Surface (*e.g.,* blow, foot print, body part	Underwater (*e.g.,*calls, clicks)
Detection range	< 3 km	> 10 km
Directionality	Directional	Quasi-omnidirectioal
Personnel	Intensive	Extensive
Potential for bias	Subjective	Objective, Repeatable, Comparable
Identification of individuals and groups	Yes	Difficult
Counts of absolute number of animals in groups observed	Yes	No - Acoustic absence does not always mean physical absence
Potential to recount same individual	Yes	Yes

Table 2. Comparison of visual and acoustic observation. After Erbe 2000.

& Clark, 2009). Acoustic recordings can be used to identify stocks on the basis of regional dialects, providing information on movement and association patterns of animals *e.g.,* between different populations or areas (*e.g.,* Noad *et al.,* 2000; McDonald *et al.*, 2006). Furthermore, to monitor population recovery, acoustic data can be used for relative abundance estimations based on call density measurements at multiple geographic locations (McDonald & Fox, 1999; Marques *et al.,* 2009). Relative abundance estimates can be compared across different recording locations over multiple years to provide a measure of population growth, trends in distribution and seasonal presence over time (*e.g.,* Stafford *et al.,* 2009).

In the end, the research question or purpose determines which instrumentation features, such as the possibility of recording over longer time spans, the need for a vessel or on-site operators, or the access to real-time data, are required to collect the appropriate acoustic data. Paper II discusses how passive acoustic recording techniques can be applied over a range of spatial and temporal scales and provides examples of research and management applications. Figure 8a provides an overview of various types of acoustic instrumentation and compares spatial and temporal scales of observation. With the exception of acoustic tags (*i.e.,* small acoustic recorders that are temporarily attached to marine mammals), acoustic techniques can generally be concluded to collect data over larger temporal and spatial scales compared to visual surveys. When positional accuracy in relation to the number of individuals that can be monitored is compared, visual surveys, acoustic tags, ship-towed hydrophone arrays and arrays of 3 autonomous hydrophones provide much more accurate data on position and on a substantially larger number of individuals compared to other (*e.g.*, cables hydrophone arrays or a single autonomous hydrophone) monitoring techniques (Fig 8b).

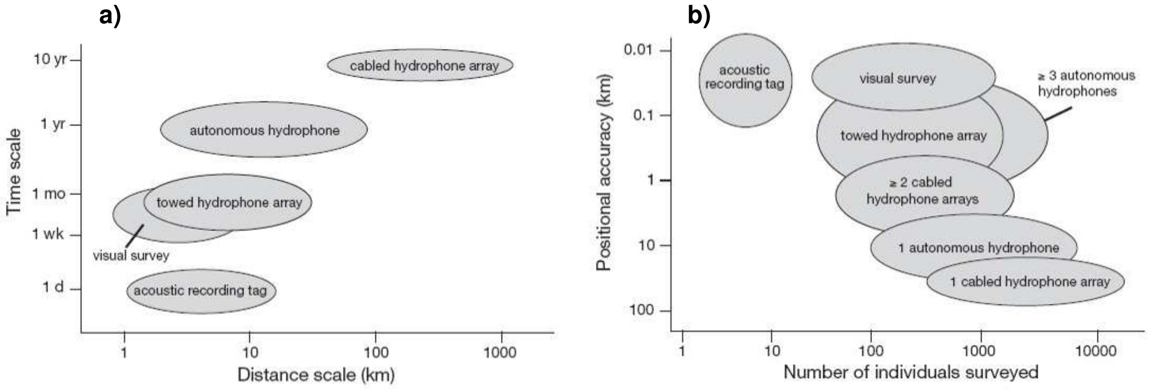

Figure 8. a) Approximate temporal and spatial scales over which acoustic data are collected using an acoustic recording tag on a single individual, an autonomous hydrophone, a vessel towed array or a bottom-mounted cabled hydrophone array, in comparison with the temporal and spatial scales of visual surveys. b) Approximate range of accuracy and number of individuals covered using an acoustic recording tag on an individual animal, a single autonomous hydrophone, a vessel towed array composed of 3 or more hydrophones, and 2 or more cabled hydrophone arrays. Figures by D.K. Mellinger, reprinted from paper II.

Nevertheless, not all acoustic techniques are equally well suited for collecting data in polar areas, as the specific physical conditions of polar environments complicate the use of certain acoustic instrumentation types. Paper I presents an overview of new and emerging passive acoustic recording techniques and discusses their suitability for use in polar environments. For example, ship-towed hydrophone arrays can be used in ice-covered areas, but high noise levels generated by icebreaker vessels towing the array mask the majority of animal vocalizations (Leaper & Scheidat, 1998). Autonomous acoustic recording devices can be used in polar environments, but only in areas deeper than 400 m so that drifting icebergs cannot cause damage to moored instruments. The presence of ice also complicates the use of acoustic tags when these come off under the ice or in areas that are not easily accessible, hampering retrieval of the tag. Cabled recording stations have the advantage that they can record continuously and over broad frequency bandwidths, allowing real-time monitoring and - in the case of a hydrophone array - localization of marine mammals, while having few restrictions to data storage, data access and power supply. However, in polar environments, acoustic monitoring using a network of hydrophones connected by cables to shore-based stations would require substantial cable length, increasing the chances of damage due to ice movements and cable melt-in. One exception represents the PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA), which features the advantages of a cabled system using an ice shelf based, energetically autonomous recording station, but uses a wireless local area network to transfer acoustic data to the nearby German Antarctic Neumayer Station III.

5.1. PALAOA

PALAOA is located at 70°31'S 8°13'W (Fig 9), on the Ekström Ice Shelf, located on the eastern Weddell Sea coast (Boebel *et al.*, 2006; Kindermann *et al.,* 2008; Klinck, 2008). The ice shelf here has a thickness of about 100 m, with about 160 m of water between the base of the ice shelf and the ocean bottom (Fig 10).

Acoustic recordings are made continuously year-round with two hydrophones suspended to about 80 m below the ice shelf. The hydrophones were lowered on their cables through two boreholes (separated by 300 m) and connected to the energetically autonomous PALAOA station (see Kindermann *et al.,* 2008 for more detailed information).

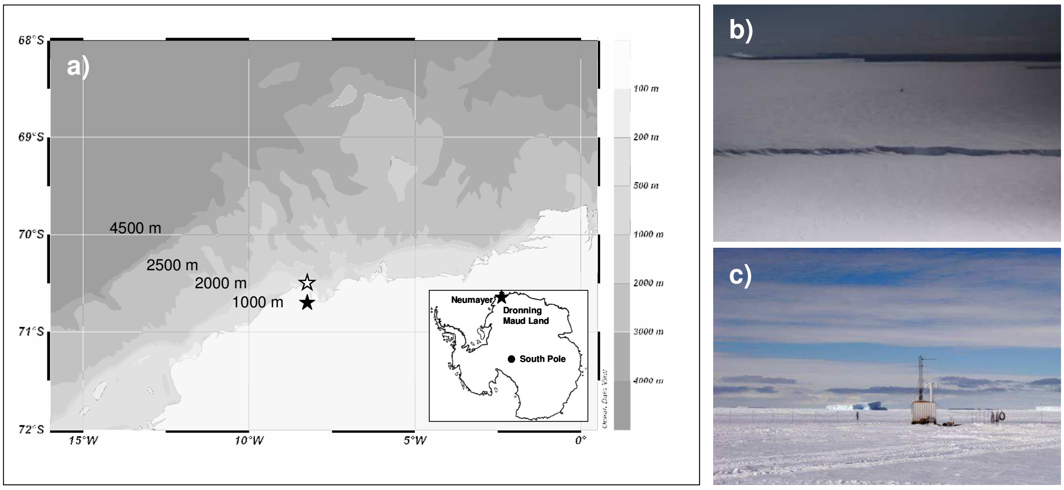

Figure 9. a) Bathymetry map showing the location of PALAOA on the Eckström Ice Shelf (white star) and the location of the German Antarctic Neumayer Station II (black star). Inset image: map of Antarctica showing the location of Neumayer Station II (black star). b) aerial picture of PALAOA on the ice shelf taken from the East (within Atka Bay), c) the PALAOA station on the ice shelf. Pictures: picture b by AWI Logistics Department, picture c by L. Kindermann.

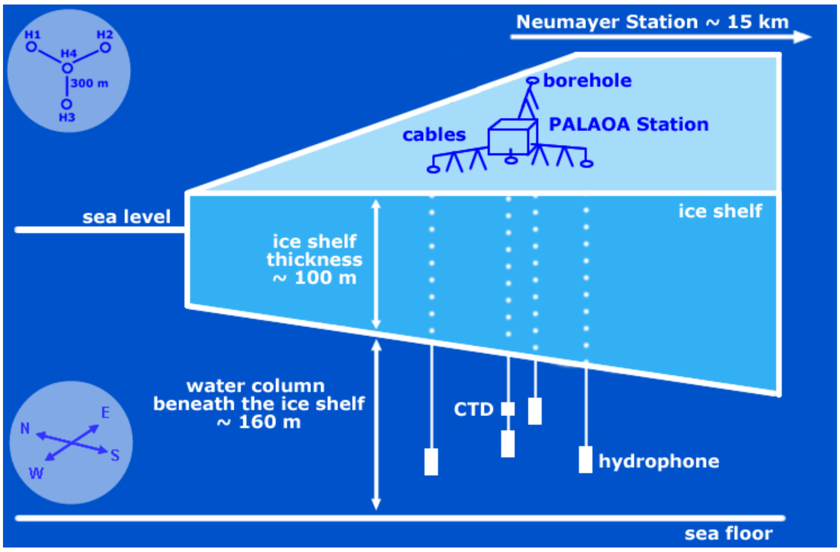

Figure 10. Schematic representation of the PALAOA array, with PALAOA station in the middle and four hydrophones extending from it. Since January 2006, only the central and the western hydrophone are operational. The central hydrophone location is equipped with a CTD sensor which simultaneously collects oceanographic data. Hydrophones were deployed through boreholes through the approximately 100m thick ice shelf and suspend approximately 80 m under the ice shelf. The distance between PALAOA and Neumayer Station II is ~15km (~21km to Neumayer Station III). Figure from Klinck 2008.

After conversion from analogue to digital signals, PALAOA uses a wireless local area network link to transmit acoustic data as a stream from PALAOA to the German Antarctic Neumayer Station III (Neumayer Station II until March 2009). At Neumayer Station, the stream is segmented into MP3 files of 1 minute duration, saved locally and transported to Bremerhaven, Germany, twice a year (Fig 11). High quality data can be buffered on request at PALAOA and Neumayer Station and downloaded through an FTP link for detailed analysis. For immediate processing, the audio is compressed and transmitted in near-real time from Neumayer Station to Bremerhaven via a satellite link. In Bremerhaven, the audio stream is also made publicly accessible (www.awi.de/acoustics).

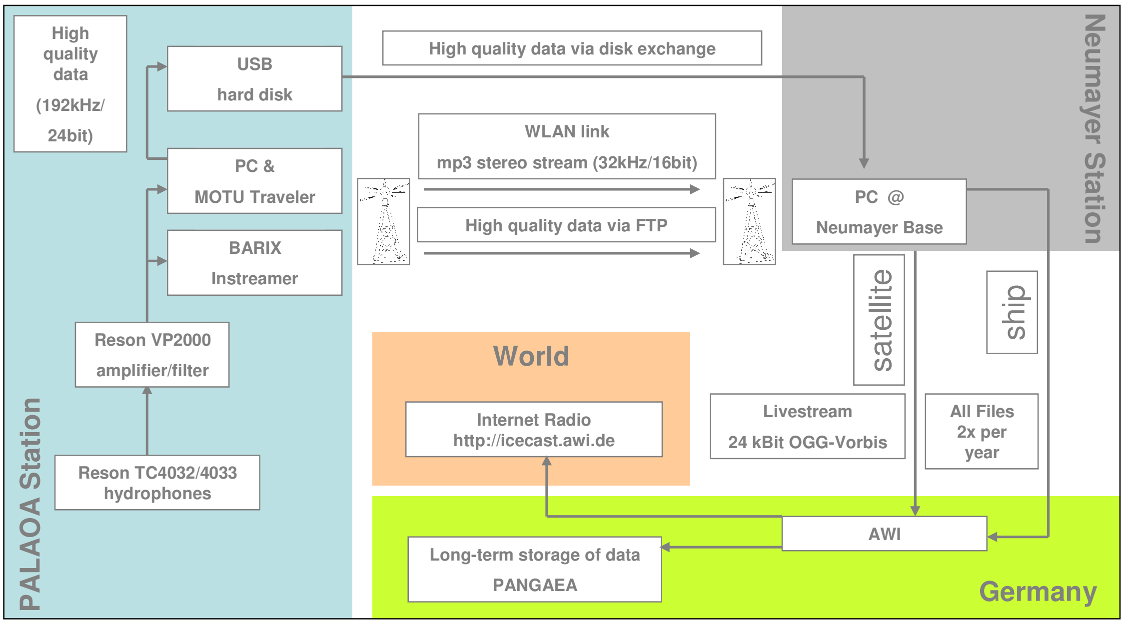

Figure 11. Data handling of acoustic data from PALAOA to Bremerhaven. Within PALAOA (blue background), acoustic recordings are streamed as 16 Bit, 32 kHz mp3 files and transferred to Neumayer Station through a WLAN link. High quality (*i.e.,* 24 bit 192 kHz) data can be stored locally on USB hard discs and transferred to Neumayer Station (grey background) through disc exchange or can be downloaded from PALAOA through FTP. At Neumayer Station, acoustic recordings are cut into 1-min files, compressed into ogg-vorbis, and transmitted in near-real time to Bremerhaven (green background) via satellite link. High quality data tapes are shipped to Bremerhaven. In Bremerhaven, real time data are stored and made publicly accessible via the internet (pink background) in near real time, while high quality acoustic data are archived in PANGAEA (Publishing Network for Geoscientific and Environmental Data).

To date (July 2010), PALAOA has overall covered almost a full year (99.7%) over the complete period that the observatory has been operational. Per year, PALAOA has covered 45, 65, 72 and 91% (in minutes recorded) of the year for 2006, 2007, 2008 and 2009, respectively. As to 2010, PALAOA has so far not had any major outages and covered 49% of the year (Fig 12).

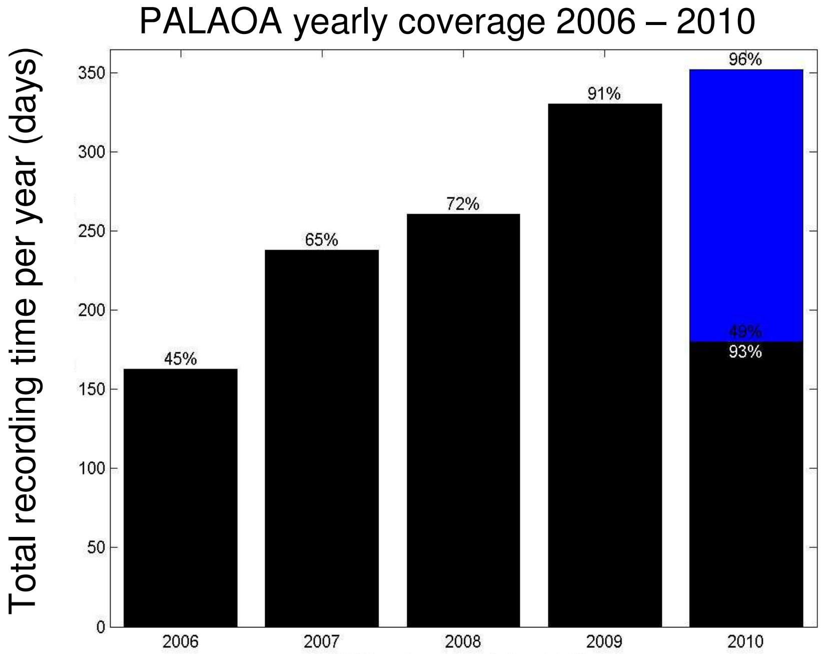

Figure 12. Overview of the yearly amount of time that PALAOA was operational over 2006-2010. Total recording time in days per year. Black bars indicate coverage for each year and in 2010 coverage until 16 July 2010 (46% relative to entire 2010, 93% relative to 16 July 2010). Blue bar represents an optimistic estimation of the PALAOA coverage over the whole of 2010. Figure by L. Kindermann.

5.1.1 PALAOA's spatial scale

The spatial scale over which PALAOA can record marine mammal vocalizations is largely dependent on the acoustic characteristics of calls; high frequency pinniped vocalizations are likely to be recorded only from animals vocalizing within a few tens of kilometers offshore of PALAOA, with leopard and Ross seal vocalizations propagating over larger distances than Weddell seal vocalizations[2]. Low frequency humpback whale calls were estimated to be detected within a range of 200 km off PALAOA (paper VIII). Sirovic *et al.* (2007) reported similar ranges for blue whale calls, which have been detected up to 200 km from acoustic bottom recorders deployed at ~3000m depth. A comparison of on- and off-shelf acoustic ranges for low-frequency air-gun signals shows no significant difference for these two depth regimes (Boebel *et al.,* 2009), suggesting that the acoustic ranges of blue whale calls reported by Sirovic *et al.* (2007) likely also apply to the PALAOA recordings from the shelf.

Given that PALAOA records with two spatially separated hydrophones, recordings can be used to determine the direction of a sound source. The determination of the position of a sound source, however, would require the deployment of additional autonomous recorders. In the outlook more detailed information is provided on such a planned spatial extension of the PALAOA recordings.

5.1.2 PALAOA's time scale

PALAOA has been recording since December 2005 (~4.5 years by now, Fig 12) with an expected additional life-span of another 1-3 years, primarily depending on stability of the ice shelf on which the observatory is located. This time frame allows investigation of research questions regarding processes at time scales ranging from seconds (*e.g.,* call characteristics) to interannual patterns in vocal behaviour (see also paper II).

The systematic mapping of the biological sound sources present in the PALAOA recordings and their temporal variation on different time scales was one of the primary goals of this PhD project and required a two-step process. First, by systematically hand-browsing one year of sub-sampled PALAOA recordings, information on the presence and monthly variation of vocal behaviour of various marine mammal species was obtained. For pinnipeds, PALAOA recordings from 2006[3] were sub-sampled (paper III), whereas

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[2] Measurements of the range over which PALAOA records pinniped calls are yet not available, but will be subject of experiments during the forthcoming field season.

[3] The PALAOA data from 2006 were used for this analysis because at the time when this PhD project started, in June 2007, the PALAOA data from 2006 was the only data set covering a complete year.

for low frequency baleen whale vocalizations, data from 2008 and 2009[4] were used (manuscript VIII.a and IX, respectively, Fig 13). This baseline knowledge on vocal behaviour was necessary to develop automated detection algorithms, which were then used to explore annual variability in vocal behaviour (manuscript IV and VIII).

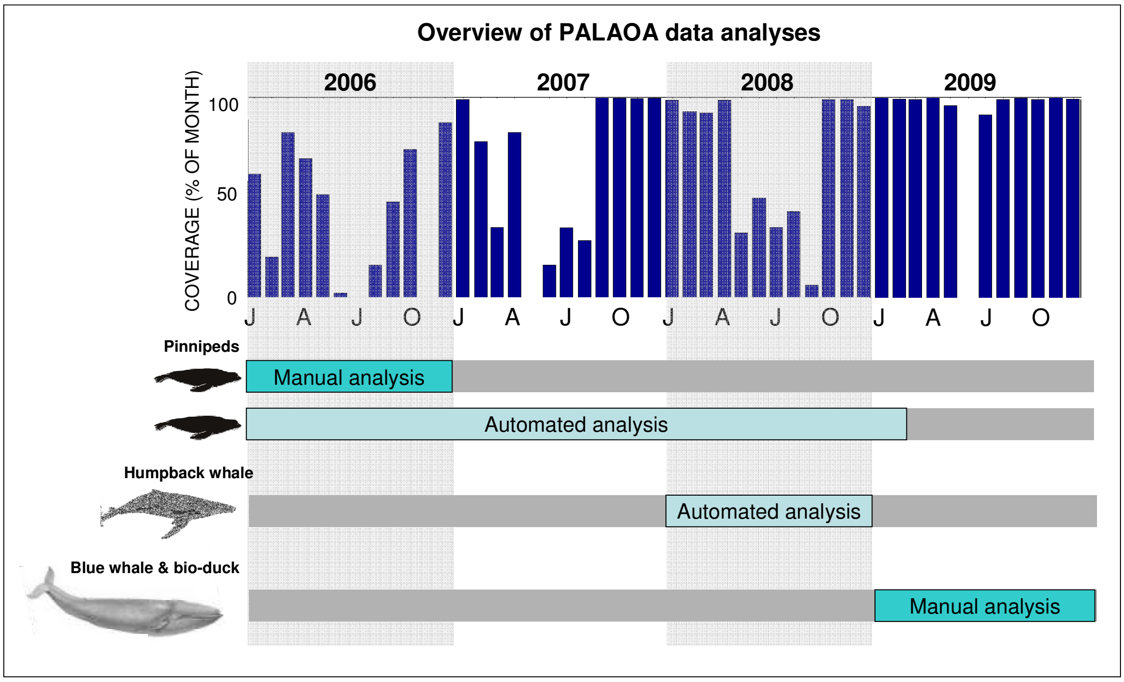

Figure 13. Monthly coverage of PALAOA data from 2006-2009 and overview of PALAOA data analyses of which the results are presented in this thesis. For pinnipeds, analyses comprised manual analysis over 2006 and automated analysis of PALAOA data from 2006, 2007, 2008 and the first two months of 2009. For humpback whales, automated detection analysis was performed on data from 2008. For blue whales and the bio-duck signal, analysis comprised manual analysis of 2009 data.

Alongside the investigation of acoustic behaviour on various time scales, PALAOA's perennial data set offers the unique opportunity to investigate the representativeness of sub-sampling strategies for manual acoustic analyses and autonomous acoustic recorders. Autonomous acoustic recorders can be set to a sub-sampling strategy that maximizes the chance of detecting the focal species while minimizing energetic and data storage requirements. Using sub-sampling strategies can significantly extend the operational

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[4] Analyses of the PALAOA data focusing on the low frequency part of the spectrum (<100Hz) were performed in 2010, which allowed selecting a year with minimum recording gaps, *i.e.,* 2009, during which 91% of the year was covered.

period of a recorder, which is also beneficial in terms of reducing the logistic effort of recorder retrieval (particularly in polar environments). Alternatively (or in addition), information on vocal repertoire can be used for automated detection algorithms incorporated in the firmware of the recording device to automatically start recording when specific calls or sounds are detected, while otherwise in remaining in sleep mode. This can save up to $^1/_2$ - $^2/_3$ of operation power (M. Motz, pers. comm.).

The findings presented in this thesis, as based on analyses of PALAOA data, provide baseline information on vocal behaviour of marine mammals in the high Antarctic. The current PALAOA recordings represent a relatively undisturbed[5] Antarctic soundscape. On a short time scale, it is possible to use the PALAOA data and baseline knowledge on the local soundscape to investigate impact of the presence of ships, occasional geophysical seismic activity and loud natural sound events such as iceberg collisions in the vicinity of the observatory. On a larger time scale, comparison of PALAOA data to future recordings from the same region enables investigation of how *e.g.,* climate-induced changes have influenced the local soundscape. Even if the recordings are interrupted for decades, future studies will be able to use the PALAOA data as a baseline reference to evaluate changes over long time spans.

The ecological scale on which a species interacts with its environment is a chief determinant in assessing which time scales are appropriate for investigation. Ecological scale is determined by the species' intrinsic life history characteristics and can vary in time from years to centuries in marine mammals (Moore, 2009). Frankham and Brook (2004) argued that to address conservation issues, *e.g.,* to investigate population recovery of large baleen whale species that were subject to whaling, observations at generational time scales are generally most appropriate. Although the PALAOA data set in itself is not suitable to address questions on generational time scales, when combined with other data sets it provides an important piece of the puzzle (see Outlook, section 8.1 – the SORP project).

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[5] With the exception of whaling; the large scale reduction of whale stocks is likely to have had substantial consequences for the soundscape in the Southern Ocean.

In conclusion, the PALAOA recordings allow the description of the vocal behaviour of marine mammals in a high Antarctic habitat on various time scales, which can be used to optimize sampling strategies for analysis and acoustic recorders, to develop automated detection algorithms. Furthermore, it allows studying the effects of short term human-induced changes in the local soundscape and comparison of the local soundscape over longer (*e.g.,* decadal) time scales to investigate the impact of changes in the ecosystem. Lastly, the PALAOA data also provide a first insight into the functioning of an ‘acoustic ecosystem’ in a - from the human perspective - remote region like the Antarctic. This aspect will be further discussed in the next section.

6. *Acoustic ecology*

Acoustic ecology describes the interaction between an animal and its environment as mediated through sound. Figure 14 represents the various factors that can influence acoustic behaviour of polar marine mammals[6]. Together, these factors form the acoustic ecology of a species. The behavioural ecology of a species influences vocal behaviour (arrow A). Behavioural ecology entails the evolutionary and ecological basis for animal behaviour and the role of behaviour in the adaptation of an animal to its living environment. Examples of behavioural ecological factors that can influence vocal behaviour are mating strategy, distribution patterns (*e.g.,* migratory behaviour and home range) and breeding system (*e.g.,* maternal strategies, length of the lactation period). In turn, behavioural ecology is influenced by abiotic and biotic factors from the environment (arrow B and C). The presence of prey and predators can for example affect marine mammal distribution patterns (arrow C), whereas ice conditions influence mating strategy (arrow B, *e.g.,* Van Parijs, *et al.* 2004; paper I). Biotic factors can influence acoustic behaviour for example when the presence of predators leads to reduced vocal activity (*e.g.,* Jefferson *et al.,* 1991) or when specific feeding calls are produced during foraging (*e.g.,* D'Vincent *et al.,* 1985; arrow D). Abiotic factors can influence vocal behaviour directly, for example when changes in local soundscape[7] result in changes in the source level of animal vocalizations (arrow E). Abiotic factors are also of influence on biotic factors (arrow F), *e.g.,* when ice conditions determine prey distribution. Finally, anthropogenic factors such as climate-driven changes and anthropogenic underwater noise can impact ice conditions and local soundscapes (arrow G and H), respectively, thereby having the potential to indirectly influence acoustic behaviour. Anthropogenic factors can also directly influence the behavioural ecology of a species (arrow I), for

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[6] Although the figure presents examples of abiotic factors specific to marine mammals in polar oceans (*e.g.,*'ice conditions'), the basic figure in principle applies to all animals relying on sound for critical aspects of their behaviour.

[7] Many elements producing the sounds within a soundscape are biotic in origin (*e.g.,* sounds produced by conspecifics, prey); nevertheless, I list soundscape as abiotic factor given its effect on *e.g.,* vocal behaviour (or any of the other factors) which is mediated through the sound (*i.e.,* physics) of the source, rather than the source's physical presence. Listing soundscape as abiotic factor also enables inclusion of abiotic sound sources (*e.g.,* glacier calving, iceberg collisions) which also form important aspects of the soundscape in large parts of polar oceans.

example by affecting behaviour or distribution patterns through hunt (*e.g.,* Branch *et al.*, 2007; Wirsing *et al.,* 2008).

Variation in acoustic behaviour *e.g.,* in temporal patterns of vocal activity, vocal repertoire size and composition, reflects inter-specific differences in the factors that shape this relationship. In analogy to ecology, each species might be thought of as filling its own acoustic ecological niche, shaped by internal and external factors and interactions between both. Without an understanding of the factors and processes that determine and influence the acoustic repertoire of a species, call patterning, individual and group calling behaviour as well as seasonal and regional variation in call usage, no coherent research or management question can be addressed using acoustic tools (paper II). It is the acoustic ecology of a species that determines if physical presence also results in acoustic presence, on what temporal scale acoustic activity takes place and over which spatial scales acoustic presence can be detected. A solid understanding of the acoustic ecology of marine mammals is also likely to contribute to further insights into the mechanism by which anthropogenic noise sources impact various aspects of the lives of marine mammals. Passive acoustic monitoring is only really useful when the results are interpreted in the context of the acoustic ecology of the animals and in a regionally and seasonally appropriate context (paper II).

As mentioned previously in section 5, acoustic monitoring of marine mammals relies on animals producing sounds. Acoustic data is therefore in many cases almost per definition ‘presence-only’ data. Nevertheless, once the understanding of the acoustic ecology of a species is sufficient, it is also possible to draw conclusions on absence of animals based on acoustic data. In the PALAOA data, year-round acoustic presence of Weddell seals, blue and humpback whales provides evidence for year-round physical presence of these species in the area off PALAOA (paper III and manuscripts IV, VIII, IX). A sudden absence of their calls over a certain period could therefore, but still not necessarily has to[8], indicate their physical absence. By contrast, the exclusively seasonal acoustic

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[8] Given that there is still much to be learned on the acoustic ecology of these species.

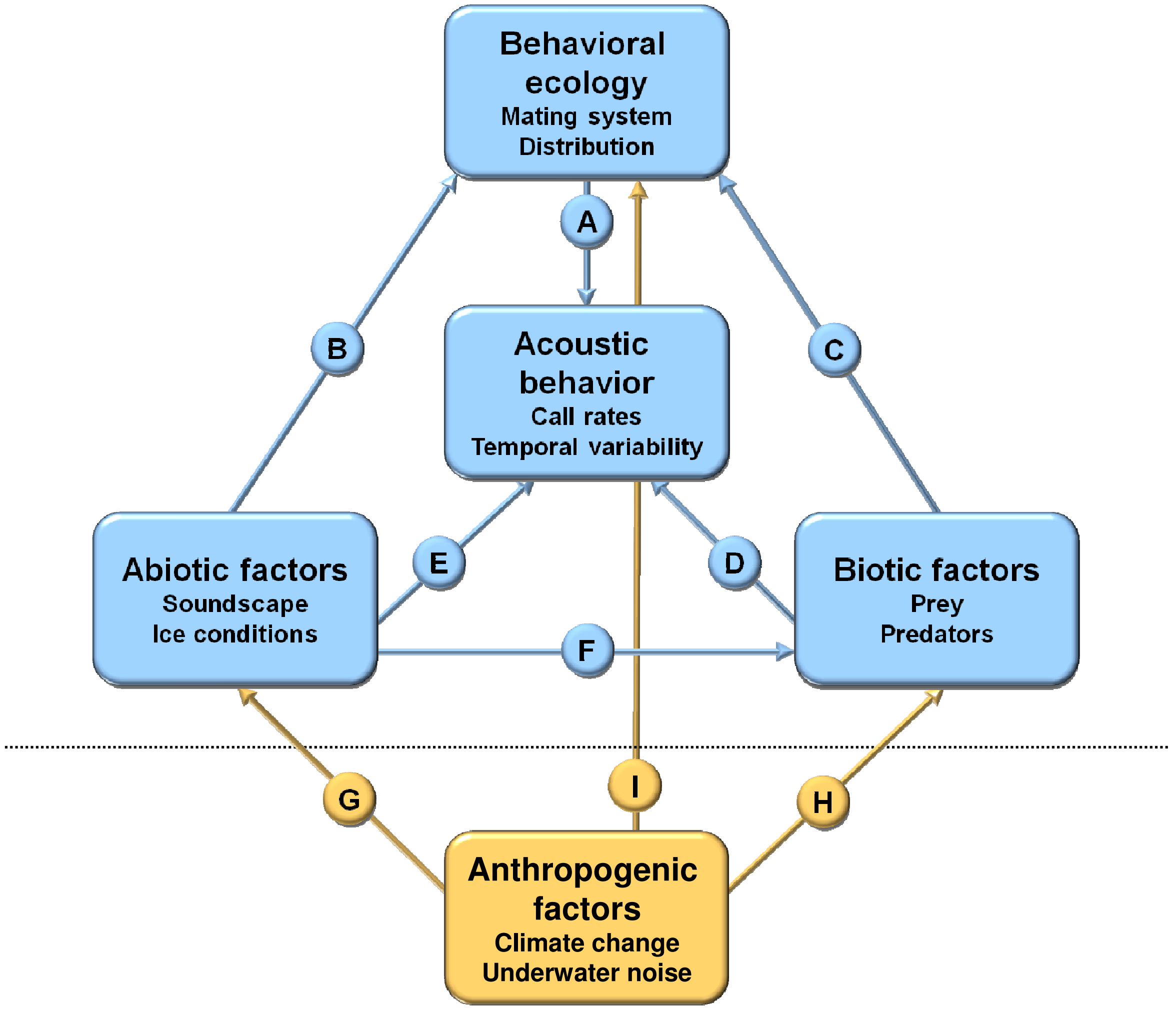

Figure 14. Schematic representation of the acoustic ecology of polar marine mammals, showing the interactions between behavioural ecology, biotic and abiotic factors as well as anthropogenic factors shaping acoustic behavior.

presence of Ross seals in austral summer demonstrates their seasonal presence, but does not necessarily imply their absence in austral winter. This could either imply their migration out of the coastal region or that they only vocalize during the mating season while remaining present but silent for the remainder of the year, in analogy to *e.g.,* harbour seals (*Phoca vitulina*, Van Parijs *et al.,* 1997). For pinnipeds, ‘out-of-season’ acoustic presence (*e.g.,* manuscript IV, and crabeater seal calls in the PALAOA recordings in April, I. Van Opzeeland pers. obs.) might indicate that animals do (occasionally) vocalize outside the mating season and that acoustic absence can be interpreted as an indicator for physical absence. Nevertheless, it is important to maintain caution when interpreting acoustic absence in terms of physical absence of animals, in particular when little in known on the factors that shape and determine acoustic behaviour. Figure 15 shows that acoustic observations can be used to assess physical presence of a species when its sounds are recorded, while whether or not physical presence of a species results in acoustic presence is mediated by its acoustic ecology.

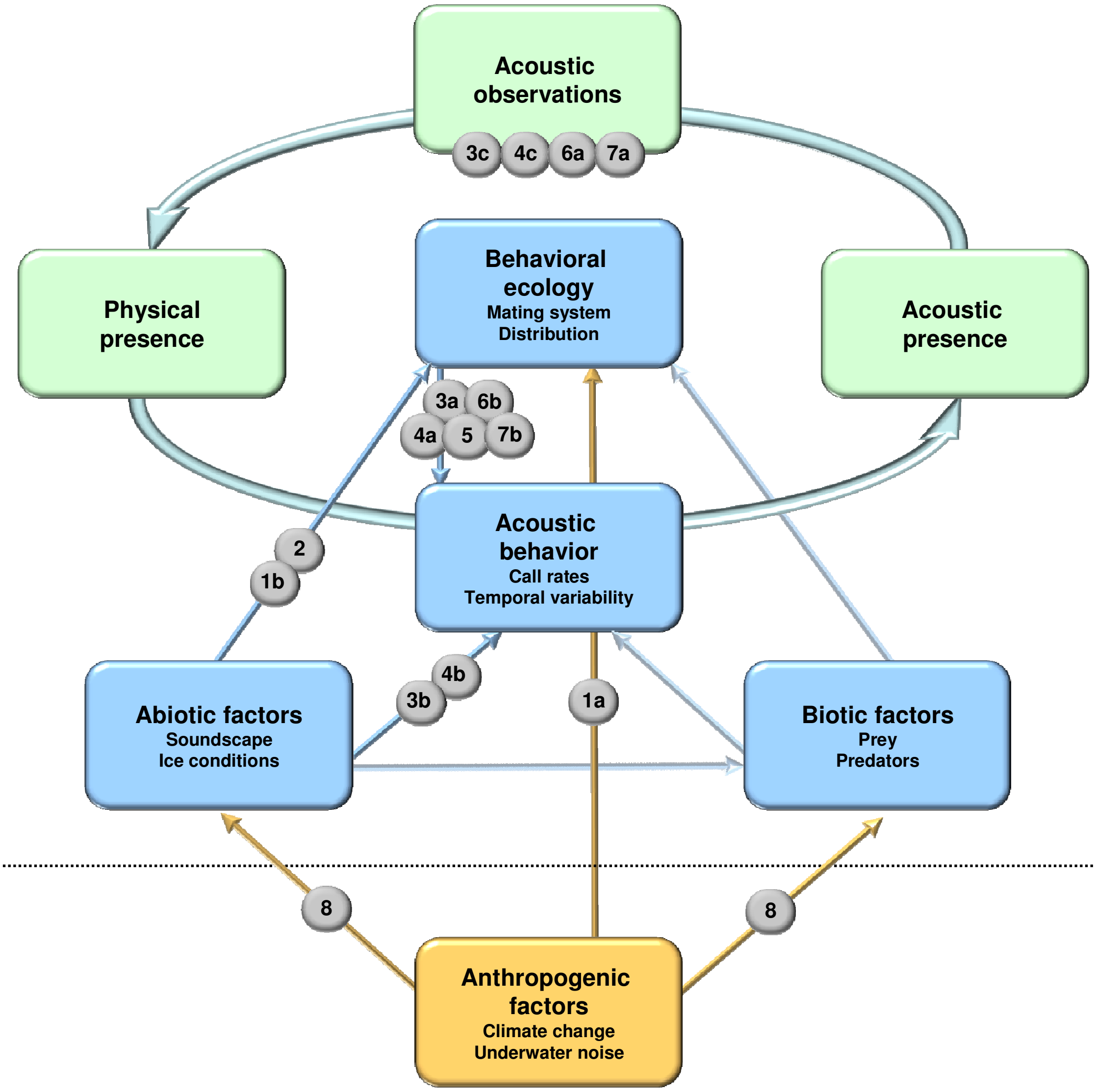

Figure 15. Schematic representation of interrelation between physical and acoustic presence. Numbers correspond to numbers in the first column of Table 3, which lists the main findings/hypotheses of each paper presented in this thesis.

Arrow number	Paper	Acoustic Ecology (main) factor	Information on physical presence from acoustic observation	Hypothesis/result
1a	Geographic variation harp seal mother-pup	Anthropogenic factor	NA	Commercial hunt may have resulted in changes in maternal behavior.
1b	Geographic variation harp seal mother-pup	Abiotic factor	NA	Differences in ice conditions between study locations may influence maternal behavior.
2	Absence maternal vocal recognition Weddell seal	Abiotic factor	NA	Breeding substrate may enable female breeding strategy in which other cues than acoustic cues are used for relocation of pups.
3a	Acoustic ecology Antarctic pinnipeds	Behavioural Ecology	NA	Mating strategy influences acoustic behavior.
3b	Acoustic ecology Antarctic pinnipeds	Abiotic factors	NA	Soundscape (inter-specific interference) and ice conditions may influence acoustic behavior.
3c	Acoustic ecology Antarctic pinnipeds	NA	Yes	Species-specific patterns in seasonal acoustic presence.
4a	Multi-year patterns in acoustic behavior Antarctic pinnipeds	Behavioural Ecology	NA	Mating strategy influences acoustic behavior.
4b	Multi-year patterns in acoustic behavior Antarctic pinnipeds	Abiotic factors	NA	Soundscape (inter-specific interference) and ice conditions may influence acoustic behavior.
4c	Multi-year patterns in acoustic behavior Antarctic pinnipeds	NA	Yes	Near year-round acoustic presence of leopard seals.
5	Variation in leopard seal vocalizations	Behavioural Ecology	NA	Distribution influences vocal behavior
6a	Humpback whale vocal presence	NA	Yes	Humpback whale presence in Antarctic coastal area during 9 months
6b	Humpback whale vocal repertoire (supplement)	Behavioural Ecology	NA	Humpback whale diel call activity patterns relate to social behaviour (?)
7a	Seasonal patterns in blue whale vocal behavior and acoustic presence of the bio-duck signal	NA	Yes	Year-round acoustic presence of blue whales in Antarctic coastal area, winter-presence of bio-duck
7b	Seasonal patterns in blue whale vocal behavior and acoustic presence of the bio-duck signal	Behavioural Ecology	NA	Seasonal difference in blue whale call repertoire composition
8	Impact of underwater sound on fish	Anthropogenic factor	NA	Underwater noise may impact fish in many ways

Table 3. Main findings/hypotheses of each paper presented in this thesis. The first column: arrow numbers relating to the numbers in figure 15. The second column: paper title. The third column: acoustic ecology factor that was hypothesized to be a main determinant of the finding (fifth column). The fourth column lists a ‘yes’ for papers in which acoustic observations provided information on acoustic presence. (NA: not applicable).

Acoustic ecology (or soundscape ecology) studies started in the late 1960s with R. Murray Schafer's World Soundscape Project. This project recorded and archived natural, village and city soundscapes from all over the world to preserve and draw attention to specific sound marks and dying sounds, ranging from foghorns to human accents and dialects. It also served to draw attention to (and find solutions for) noise pollution and the strained relationship between the human community and its sonic environment. The term 'soundscape' reflects the idea that the listener is part of a dynamic system of information exchange, in analogy to being part of a landscape. As also pointed out in the schematic representation of acoustic ecology discussed in the previous section, the soundscape concept recognizes that when an individual enters an environment it has an immediate interaction with the sounds within the environment (Truax, 2001). Acoustic ecology has since the World Soundscape Project developed into a broad multi-disciplinary research and art field, comprising 'phonographers' (exploring the world through sound), environmental music composers, bioacousticians and environmental health researchers and many other disciplines. In bioacoustics, a more holistic approach of the study of animal sound and the sound environment in which animals live is relatively recent (*e.g.,* Slabbekoorn & Bouton 2008; Barber *et al.*, 2009; Clark *et al.*, 2009), although concerns on the potential effects of human-induced changes to the sound environment were expressed during early studies (*e.g.,* Payne & Webb 1971). Thus, given that acoustic ecology is an emerging field particularly within marine mammal research, the results presented in the following papers, represent first steps exploring the acoustic ecology of marine mammals in polar habitats, providing baseline information while simultaneously opening up new research questions.

Acoustic ecology forms a central theme in this thesis, explaining how various factors shape vocal behaviour, but also functioning as a mediator determining the relation between physical and acoustic presence. The following sections provide a summary description of the papers presented in this thesis and an interpretation of the findings in the context of acoustic ecology.

6.1 Individuality of in-air pup calls in two ice-breeding pinniped species (paper VI and manuscript VII)

These two papers investigate the individuality of in-air pup vocalizations and their putative role in mother-pup reunions in two ice-breeding phocid species, the Arctic harp seal and the Antarctic Weddell seal. The lactation period lasts 2 and 6 weeks for harp and Weddell seals, respectively. During the lactation period, both harp and Weddell seal females leave their pup alone for periods of up to several hours to forage under the ice to sustain lactation (Reijnders *et al.,* 1990; Lydersen & Kovacs, 1999). Given that both species form breeding aggregations on the ice, consisting of tens (Weddell seal) to hundreds (harp seal) of animals, some mechanism for mother-pup recognition is required during the lactation period to avoid confusion over pup identity when the female returns from her foraging trip. While in otariid species vocalizations generally play an important role in mother-pup reunions (Insley *et al*., 2003), mother-pup recognition in phocids seems more variable and dependent on breeding strategy and stability of the ice type used for breeding, although only a limited number of species has been investigated to date (paper I). In paper VI, pup vocal and mother-pup behaviour were compared between the Northeast (Greenland Sea) and Northwest (Front) Atlantic harp seal populations. The level of pup call individuality and mother-pup behaviour was found to differ between populations. Mothers attended their pups on the ice more in the Front population compared to the Greenland Sea population, which might be explained by population differences in behavioural adaptation in response to commercial hunt. Given that the Greenland Sea population was reduced to a smaller proportion of its initial population size than the Front population, females in the Greenland Sea population might have evolved a behavioural tendency to maximize their time in the water, in response to hunting pressure (arrow 1a[9], Figure 16). Furthermore, differences in sea ice extent between years during which data were collected in the two areas might also have affected the behaviour of female harp seals with pups (arrow 1b, Figure 16). Possibly, differences in maternal behaviour either relating to ice conditions or commercial hunt indirectly affect pup vocal behaviour, for example when females spent less time on the ice with

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[9] In this case the anthropogenic factor influencing behavioural ecology is hunting pressure, which would be expected to work directly on behavioural ecology (*i.e.,* maternal strategies).

their pup. Multi-year data are needed to investigate if differences in pup vocal behaviour and mother-pup behaviour are merely due to interannual variability (*i.e.,* due to exceptional ice conditions during the season when this study was conducted) or are a more persistent difference in behaviour between these harp seal populations.

In Weddell seals, pup call individuality was investigated and playback experiments were conducted (manuscript VII). During the playback experiments, pup calls were played back to Weddell seal mothers to investigate if they responded differently to playbacks of own and alien pup calls. The level of call individuality differed between pups. Females were found not to respond differently to playbacks of own and other pup calls. A possible explanation might be the stationary nature of fast ice as a breeding substrate, reducing the importance for individual pups to be vocally distinctive, as the mother-pup pair can rely more on spatial cues for relocation (arrow 2, Figure 15). In addition, olfactory cues might be used for final confirmation of identity. Alternatively, the finding might be explained by vocal recognition not having been fully developed at the time during which this study was conducted, *i.e.*, when most pups were approximately two weeks old. Weddell seal females only start to forage under the ice after the first two weeks post-partum, so that there might be no need for vocal recognition (or response to pup calls by females) prior to the period that females start undertaking foraging trips.

Comparing both studies illustrates how similarities in the behavioural ecology of polar species, such as ice as a breeding substrate and the need for females to forage during the lactation period, have led to a largely parallel evolution of mother-pup behaviour in these (quasi-) antipodal species. Nevertheless, it also illustrates how differences within the ice habitat (*i.e.,* the stability and ice type, arrows 1b and 2, Figure 15) are likely to be of influence on (vocal) behaviour, leading to inter-specific differences as well as differences between populations of the same species.

6.2 Underwater vocal behaviour of Antarctic pinnipeds (Paper III and manuscripts IV, V)

These manuscripts and paper investigate aspects of the adult underwater vocal behaviour of the four Antarctic pinniped species, Weddell, leopard, Ross and crabeater seals. Paper

III is based on one year of hand-browsed PALAOA data and provides a first baseline description of temporal patterns in the vocal behaviour of Antarctic pinnipeds. Inter-specific variation in vocal behaviour is discussed in an acoustic ecological context, relating to species-specific behavioural ecology and interactions with abiotic and biotic factors from the environment. One of the most intriguing results of this paper is the distinct seasonality in the acoustic presence of each species and the sequential pattern in the timing of peak vocal activity of each species; Weddell seals calls were present year round, except in February (the month during which ice cover is lowest in Atka Bay), leopard seals were present from October to January, Ross seals from December to February and crabeater seals from August to January. In aquatic mating pinnipeds, calls are produced in a mating context (Van Parijs, 2003). In most species, the timing of the peak in call activity therefore reflects the period when mating takes place. The near year round acoustic presence of Weddell seals possibly reflects that males occupy underwater territories throughout winter (arrow 3a, Figure 15). In the other three species, vocal activity shows a strong seasonal peak, reflecting that vocal displays related to mating are likely to be strongly seasonal in these species and that timing of mating might be related to abiotic and biotic factors (arrow 3b, Figure 15).

Apart from detailed information on temporal patterns of acoustic behaviour of the four Antarctic pinnipeds, this paper also provided the first information on (acoustic) presence of these species in the area; Ross seals have never been visually observed in the area off PALAOA (arrow 3c).

Paper III provided the basis for manuscript IV, in which vocal behaviour of three[10] of these species is further investigated over 3+ years of PALAOA data (2006, 2007, 2008 and the first two 3 months of 2009). This paper shows that the overall pattern of seasonal acoustic activity of each species re-occurred over four austral summer seasons (arrow 4a, Figure 15). However, Weddell seal call activity was more variable between years as compared to the other species. Given that Weddell seals rely on leads in their fast ice

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[10] Paper IV used automated detection to analyse vocal behaviour over multiple years for Weddell, leopard and Ross seals. Based on the broadband character of crabeater seal vocalizations, these calls could not reliably be detected with the automated detection method used in this paper. Automated detection of the calls of this species will require development of other detection techniques which was beyond the scope of this thesis, but will form part of future analyses.

habitat for breathing, the inter-annual difference in the number of detected calls possibly reflects variability in local ice conditions between years (arrow 4b, Figure 15). Furthermore, leopard seal call activity was found to decrease rapidly with the onset of Ross seal call activity in all years. These findings are in accordance with our previous hypothesis (paper III) that temporal segregation of acoustic activity between species might be related to inter-specific acoustic interference. The 'acoustic plenitude' of Ross seals during the period that they are acoustically present (*i.e.,* the breadth of the frequency band and the temporal density of calls) might reduce the bioacoustic space of other species. Given the importance of underwater calling for mating, but also the energetic costs to produce calls, other species might time acoustic activity to prevent overlap with Ross seals.

In contrast to the manual analysis of the 2006 data (paper III), leopard seal calls were found present during winter of all years by the automated analysis (though only few in 2006, see discussion in manuscript IV). Some of the calls detected in the winter period were juvenile leopard seal calls. These findings suggest that juvenile leopard seals possibly remain in Antarctic coastal waters year round (arrow 4c, Figure 15). Manuscript IV is still in preparation. Further work will involve time-series analysis to explore annual patterns in call activity in relation to ice cover in greater detail (see manuscript IV for more details).

Manuscript V investigates the variation in the acoustic characteristics of one leopard seal call type ('high double trill', call type L3) between three Antarctic locations: Drescher Inlet, Atka Bay and Davis Sea. Previous genetic studies have shown that there is sufficient exchange of individuals between leopard seal breeding groups to prevent development of a genetic population structure (Davis *et al.,* 2008). The results of manuscript V show that overall there is little variation in the acoustic characteristics of call type L3 across the three recording locations, although acoustic parameters (*i.e.,* pulse repetition rate and call bandwidth) of calls from Drescher Inlet differed slightly from calls recorded at the other two locations. The overall similarity in acoustic characteristics of call type L3 seems to mirror the homogeneity of the genetic data, suggesting that there is exchange of individuals between breeding groups (arrow 5, Figure 15). This leaves it likely that subtle differences in leopard seal vocalizations are attributable to other factors (such as differences in local group composition when recordings were made) than geographic isolation of populations.

Together these manuscripts and paper provide insight into the internal and external factors that are likely to influence and shape the vocal behaviour of these four ice-breeding pinnipeds. Manuscripts IV and V thereby exemplify how further temporal and spatial extension of the acoustic data set enable investigation of hypotheses put forward in paper III. Behavioural ecological factors such as mating strategy are likely to be among the most important factors that shape vocal behaviour to optimize communication of breeding status or fitness to potential mating partners and/or competitors (3a, 4a, 5 Figure 15). Depending on the intended range of communication, the local soundscape (abiotic factor) might for species such as leopard and Ross seals be a further determinant of the timing of vocal activity (3b, 4b Figure 15). This aspect can be further investigated by comparing the timing of vocal activity to local signal-to-noise ratios or noise budgets over multiple years. Ice conditions are another relevant abiotic factor, the role of which has not been fully explored, yet. In this context, spatial expansion of recording sites will enable investigation of the role of ice in relation to pinniped vocal behaviour in near- and off-shore areas. Finally, paper III and manuscript IV provided insight on seasonal patterns in the physical presence of species in the area off PALAOA (3c, 4c, Figure 15).

6.3. Vocal behavior of cetaceans recorded by PALAOA (manuscripts VIII and IX)

In manuscript VIII, the occurrence of a specific humpback whale call type (‘moan’) over one year of PALAOA data was investigated. Humpback whale calls were present over nine months of the year, including 4 months during austral winter. Humpback whales are therefore likely to remain on the feeding grounds throughout austral winter and - in contrast to previous beliefs - enter ice-covered areas. The findings of this study suggest that humpback whale feeding grounds might extend further south towards the Antarctic continental shelf than previously assumed. This reflects the potential importance of coastal areas for humpback whales by providing food year-round and areas of open water where animals can surface to breathe.

This paper exemplifies how acoustic observations can be used to obtain information on physical presence of a species during periods and in an area where prolonged visual observations are not possible (arrow 6a, Fig 15).

With respect to acoustic ecology and the question how various factors shape acoustic behaviour, the supplementary material to this paper (manuscript VIII.a) allows the following additional consideration; To date only little is known on the context in which sounds are produced by humpback whales on the Southern Hemisphere feeding grounds. We can therefore only speculate on the function of calls. In the Northern Hemisphere, a large part of the sounds produced by humpback whales on the feeding grounds is related to coordinated foraging behaviour during which small prey are concentrated (Ingebrigtsen, 1929; Jurasz & Jurasz, 1979; D'Vincent *et al.*, 1985; Thompson *et al.,* 1986). Humpback whale foraging dives are known to reach up to 150 m depth (Dolphin *et al.,* 1995). Zooplankton exhibits diel vertical migration, ranging in depth between 50 and >300 m, depending on species and season (Cisewski *et al.,* 2010). In our study, diel call patterns are, when interpreted in a feeding context, somewhat contradictive; the decrease in overall humpback whale vocal activity in March and April coincides with the time at which zooplankton concentrations are at shallow depths. Feeding at shallow depth would be expected to have energetic benefits since transit time to shallower food resources is reduced (*e.g.,* Baumgartner *et al.,* 2003). Our finding of decreased call activity when most prey is at shallow depth might therefore reflect that calls are produced in a social rather than a feeding context (in that case, vocal behaviour could be mediated by social factors *i.e.,* behavioural ecology, arrow 6b, Figure 15). The supplementary material on humpback whale vocal behaviour presented in this thesis is in an early phase of preparation and will be extended with analyses of data from other years to investigate if this pattern persists across years.

Manuscript IX presents preliminary results on seasonal patterns in the usage of four call types by Antarctic blue whales (*Balaenoptera musculus intermedia*) and acoustic presence of the bio-duck signal. For blue whales, one year of PALAOA data (2009) was manually analyzed. Three Antarctic blue whale call types were present throughout the year (arrow 7a, Figure 15), among which the ‘Antarctic blue whale call’, which is usually referred to as blue whale song when produced in regular sequences. Although this will be subject of further analysis, song was present in all months (except June when only one day of data was available) and in some cases also consisted of sequences of other call types than the ‘Antarctic blue whale call’. One call type (S) occurred from January to June, reflecting that this call type might be produced in specific behavioral contexts (arrow 7b, Figure 15). Blue whales in Northern Hemisphere waters produce a call type similar to S, which possibly functions to maintain contact between foraging dives (Oleson *et al.,* 2007).

The bio-duck has been recorded at various locations in the Southern Ocean, but the origin of the signal remains unknown. Knowledge on the temporal patterns of occurrence of this signal might provide information on the source (arrow 7a, Figure 15). Analysis of acoustic presence of the bio-duck signal was based on PALAOA data from two years (2006 and 2009). In 2006, the signal was present from April until October (no data for November), while in 2009 it was present from May until December. The bio-duck signal has previously been suggested to be produced by minke whales (*Balaenoptera bonaerensis*). Their association with ice-covered areas, year-round presence in Antarctic waters as well as parallels between the bio-duck signal and the sounds produced by minke whales in Northern Hemisphere waters, are in support of this suggestion. Further work involves analyses of diel patterns in acoustic presence of blue whale call types and the bio-duck signal as well as further investigation of temporal patterns and structure of blue whale song in this data set.

Manuscripts VIII and IX clearly illustrate the importance of acoustic techniques as a monitoring tool in polar areas; both studies confirmed presence of cetaceans over a time span and in a period in which it would not have been possible to collect visual data (arrows 6a and 7a, Fig 15). Both studies also illustrate the seasonal differences in the calls that are detected by PALAOA. Whether this is due to a difference in the range over which different call types are detected (as is likely the case for humpback whale moans and high calls, manuscript VIII) or if these reflect actual differences in vocal repertoire composition (Antarctic blue whales, manuscript IX), it is important to take such information into account when using automated detection algorithms to investigate acoustic presence over multiple years.

The bio-duck signal provides an interesting example of how acoustic observations provide further information on the possible source of the sound through temporal patterns in acoustic activity and hypotheses on the acoustic ecology of the source (*e.g.*, in this case the possible relation of the bio-duck signal to months with ice-cover). Hopefully, further analyses of the PALAOA data (*e.g.,* diel patterns in acoustic presence, estimations of source level) provide further information that contributes to solve this mystery.

6.4 Fish and increasing underwater noise levels

Although paper X is beyond the realm of polar marine mammal research, it clearly illustrates how anthropogenic factors have the potential to interfere with acoustic behaviour, emphasizing the role of anthropogenic factors in the acoustic ecology of aquatic animals (arrows 8, Figure 15). The paper calls attention to the existing large gaps in our knowledge on the effects of man-made underwater noise on fish. The comparative approach of this study reflects the idea that for animal taxa relying on sound for critical aspects of their behaviour, man-made noise likely forms an important aspect of acoustic ecology. The main conclusion of this paper is that there is very little known on the effects of noise on fish, but that it is highly likely that underwater noise affects many aspects of the lives of fish. Although the immediate effects of short duration high intensity underwater sound on aquatic animals can have dramatic physiological consequences for nearby individuals (Fig 7), chronic noise exposure affects the acoustic ecology of a species, thereby affecting animals over much larger spatial and temporal scales, possibly affecting aquatic animals on population scales. The schematic representation of acoustic ecology (Fig 14) illustrates how anthropogenic noise can indirectly impact acoustic behaviour through changes in the local soundscape. Anthropogenic noise can however also affect distribution (behavioural ecology) as well as the distribution and behaviour of prey and predator species (biotic factors). The suit of factors through which chronic anthropogenic underwater noise can affect acoustic behaviour and behavioural ecology illustrates the complexity of the issue as well as the potential severity of its impact.

7. A broader perspective: the role of marine mammals in marine ecosystems

Previous sections have illustrated the potential of acoustic recording techniques as a unique research tool for marine mammals in polar oceans and interpreted acoustic data in the framework of acoustic ecology. Improving our understanding of marine mammals in polar habitats is essential from the perspective of species protection and conservation and from an ecosystem-based point of view. It is widely assumed that marine ecosystems are controlled by bottom-up processes: the supply of nutrients by sources of physical forcing such as currents, waves and upwelling and the conversion to organic matter by phytoplankton photosynthesis (*e.g.,* Smetacek & Nicol, 2005). Nevertheless, the role of marine mammals in (polar) marine ecosystems should not be underestimated. In a review, Bowen (1997) summarized the varying ways in which marine mammals influence their environment, recognizing that marine mammals can have both top-down (*e.g.,* marine mammal predator influencing prey behaviour and life history) and bottom-up effects (*e.g.,* their role in nutrient storage and recycling).

7.1 Bottom-up effects

7.1.1. Defecation

Depending on habitat type and species-specific feeding ecology, marine mammals contribute to the recycling and renewal of nutrients (Kanwisher & Ridgway, 1983; Lavery *et al.,* 2010; Fig 16). Much research effort with respect to nutrient recycling has recently been aimed at the Southern Ocean ecosystem and iron fertilization. In contrast to the Arctic Ocean, the Southern Ocean marine ecosystem is iron-limited due to *e.g.,* lack of river run-off, atmospheric, and sediment iron-input (the latter relating to the deeper continental shelf and hence relative absence of sediment as iron source, Tremblay & Smith, 2007). Iron is essential for phytoplankton, as it plays a role in electron transfer processes that form part of photosynthesis (*e.g.,* Nicol *et al.,* 2010). Krill feed on phytoplankton, store iron in their body tissue, but also excrete iron-rich faeces. Marine mammals and other diving marine vertebrates particularly require iron in their diet because of their elevated haemoglobin and myoglobin levels which are necessary for binding oxygen. Baleen whales and most of the Antarctic seal species feed on krill and contribute to the recycling of nutrients by defecating near the surface (which is related to the fact that they shut down non-crucial body functions during diving). In addition, marine mammal species that feed at depth and defecate in the euphotic zone, such as sperm whales, increase the standing stock of nutrients in the euphotic zone (Lavery *et al.*, 2010). Given that whales generally concentrate in areas of high productivity, defecation might create a positive feedback loop in which whales act as ‘gardeners’, promoting local primary productivity, thereby again ensuring the availability of prey in these areas. Furthermore, by enhancing new primary productivity, whales are thought to act as a carbon sink and have been estimated to remove significant amounts of CO_2 from the atmosphere (Lavery *et al.,* 2010).

The large scale removal of whales from the Southern Ocean during industrial whaling is thought to have had far-reaching impacts on the ecosystem by reducing nutrient input and recycling (*e.g.,* Butman *et al.,* 1996; Lavery *et al.,* 2010). Such alterations are likely to have reduced carbon export to the deep ocean and affected food web structure *e.g.,* in that larger whale populations would have enhanced primary productivity which in turn would have supported larger krill populations (Nicol *et al.,* 2010).

7.1.2. Whale falls

Another way in which marine mammals contribute to the input and recycling of nutrients is after their death, through their sinking carcasses which provide benthic communities with nutrients (Butman *et al*., 1996, Fig 16). Whale falls are thought to have a specific impact on biodiversity in that they provide isolated and distinct resource-rich patches supporting various organisms and communities. Butman *et al.* (1996) suggested that reduction in large baleen whale populations during 19th-century commercial whaling might therefore not only have had consequences for krill populations, but potentially also at the level of benthic habitat heterogeneity (and thereby biodiversity) that whale falls create.

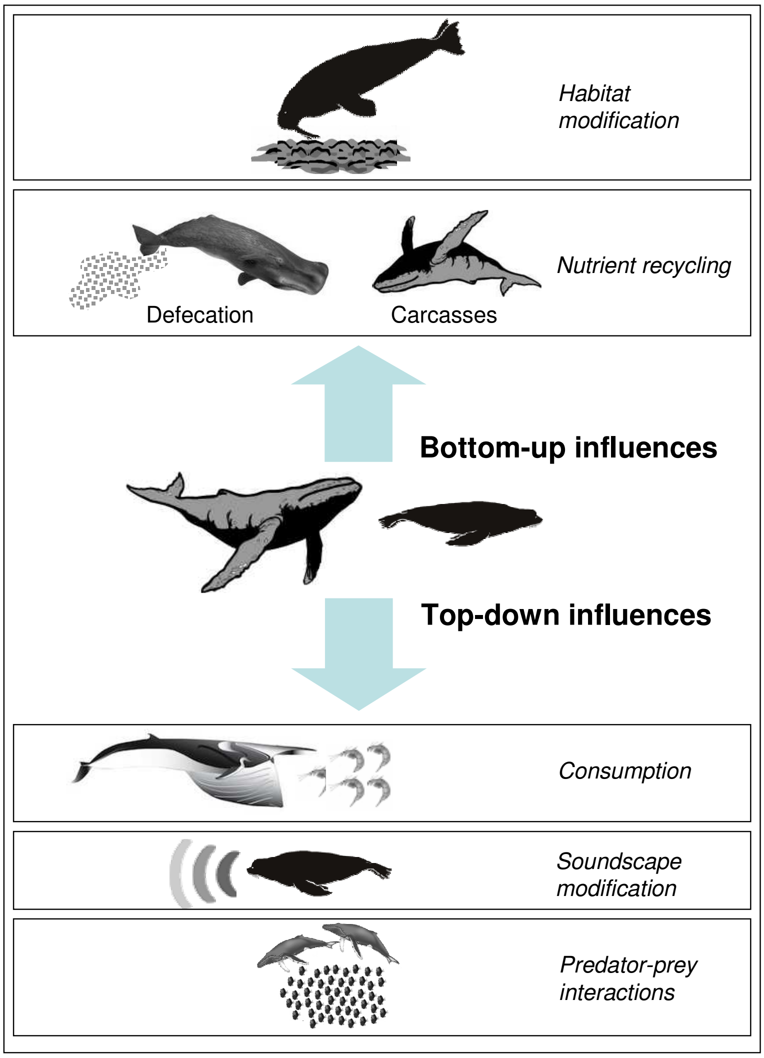

Figure 16. Various roles of marine mammals in the ecosystem: bottom-up influences (habitat modification and nutrient recycling) and top-down influences (consumption, soundscape modification, predator-prey interactions).

7.1.3. Habitat modification

Walruses (*Odobenus rosmarus*) and grey whales (*Eschrichtius robustus*) modify their habitat, for example while bottom-feeding, which offers opportunities to various invertebrate species to settle and/or feed on debris (Bowen, 1997). In some marine mammal species these modifications work to the advantage of the animal, for example when habitat modifications result in higher prey densities, *e.g.* when marine mammals create clearings suitable for larvae of prey species to settle or remove accumulated mud from the sea bottom which contributes to prey population health (Katona & Whitehead, 1988).

7.2 Top-down effects

7.2.1. Consumption

By consuming prey, marine mammals have a top-down effect on the marine ecosystem (Fig 16). This effect can be divided into aspects that concern the amount of biomass that flows through the marine mammal component of the marine ecosystem, but also the effect of consumption on community structure. Estimations of the amount of biomass that is consumed by marine mammals and the impact of consumption on food stocks is still the topic of on-going debates, especially when it concerns prey species of commercial interest, *e.g.*, cod (*Gadus morhua*) and capelin (*Mallotus villosus*) in the Arctic (*e.g.,* Lavigne, 1996). Corkeron (2009b) pointed out that Norway's current policy on marine mammal management (involving culling of marine mammals) is partly based on model results indicating that more harp seals and northern minke whales equate to less cod and herring (*Clupea harengus*), while more complex fish-fisheries-climate interactions leading to collapses of fish stocks are a much more plausible.

The effect of consumption on community structure is illustrated by the uncontrolled 'experiment' that resulted from the overexploitation of large baleen whales in the Southern Ocean during the 20th century. Given that the largest species were "harvested" first, cetacean biomass declined from an estimated 45 million to 9 million tonnes in this period (Laws, 1985). The amount of krill that was released from cetacean predation is thought to have been partly redistributed to minke whales, crabeater seals, Antarctic fur seals (*Arctocephalus gazella*) and various penguin species which have all increased in numbers (but see discussion in section 7.1.1. on the effects of whaling on prey populations). The complexity of the changes in interactions in the Southern Ocean food web is further illustrated by the fact that the increase in king penguin numbers might have resulted from the increase in krill-feeding squid which in turn is thought to have become more abundant as a result of the decrease in sperm whales (Laws, 1985). Hence, this once again illustrates how the reduction in the number of large whales is likely to have led to large scale changes in the community structure and ecosystem functioning of the Southern Ocean.

7.2.2. Soundscape modification

Modification of the biotic component of the soundscape, *e.g.,* through the presence of calls or echo-location clicks, can also be regarded as a top-down effect of marine mammals on the (acoustic) ecosystem. Nevertheless, acoustic presence may not solely affect the biotic soundscape, but also have actual ecological effects when calls cause marine mammal hotspots to be recognized by other individuals, attracting or repelling other species or conspecifics from such areas (Katona & Whitehead, 1988).

7.2.3. Predator-prey interactions

The co-evolution of predator and prey in many cases results in adaptations in the behaviour of prey to avoid predation and can therefore also be regarded as a modifying (top-down) effect that marine mammals have on their environment. Some prey species adapt their predator avoidance tactic to the type of predator by which they are attacked. For example, herring and krill can minimize the risk of predation by seabirds, seals and larger fish by forming tight schools, while when attacked by bulk-feeders, scattering is a more successful strategy (Bowen, 1997). Harbour seals were found to respond strongly (by moving away from the surface) to the calls of mammal-eating killer whales (*Orcinus orca*) and unfamiliar fish-eating killer whales, but not to the familiar calls of local fish-eating killer whale populations (Deecke *et al.,* 2002).

8. Outlook

Much of the work forthcoming from this thesis will be followed up by temporal and spatial extension of the scales on which data are collected. This will allow a more thorough investigation of various aspects of the acoustic ecology of polar marine mammals. Expanding the spatial scale enables comparison of the PALAOA data with other regions and marine ecosystems (*e.g.,* coastal versus offshore). This thesis has provided first insights into some aspects of the acoustic ecology of species occurring in the area near PALAOA, but the spatial scale of this 'acoustic ecosystem' is still unclear. The coastal ecosystem and ice conditions off PALAOA might provide a rather specific habitat, promoting high marine mammal species diversity and many specific (acoustic) interactions that do not occur in offshore areas. If this is the case, comparison of data from various recording locations might also shed light on the habitat characteristics that distinguish a coastal habitat from offshore habitat.

8.1. Spatial extension

An example of how the spatial scale of our research will be extended is the HAFOS project, which will commence this austral summer 2010/11. The HAFOS project involves deployment of 9 autonomous acoustic recorders in the Weddell Sea (Fig 17). The recorders will be deployed over 2-3 cruises and will be left to record for up to 3 years. Data from these recorders will, along with simultaneously collected oceanographic data, contribute to our understanding of acoustic ecology by facilitating a comparison of offshore data from the Weddell Sea and the PALAOA data from a coastal area, and providing information on the detection ranges of baleen whale sounds and whale movement patterns, also in relation to ice and prey.

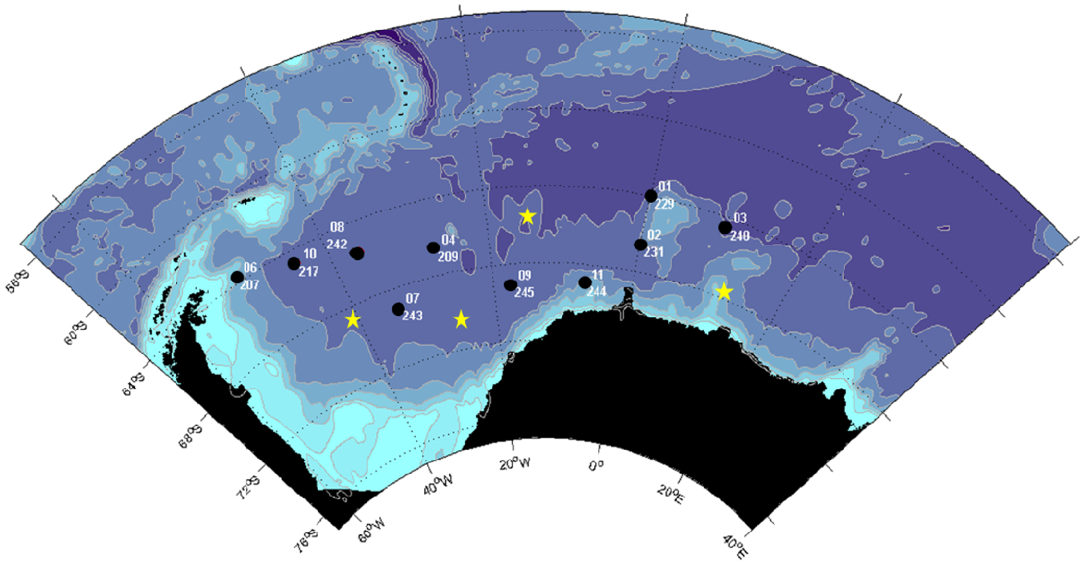

Figure 17. Deployment locations of acoustic recorders within the HAFOS project in the Weddell Sea. Black dots indicate existing moorings on which acoustic recorders will be attached. Stars indicate additional moorings planned for deployment within the next 3 years.

On a smaller scale, the PALAOA-S (PALAOA-Satellite, satellite station of PALAOA) recording units also render a spatial extension of the PALAOA data set (Fig 18) possible. The PALAOA-S units are portable autonomous acoustic recorders designed to collect continuous sound records up to 2 weeks. The PALAOA-S system consisted of an insulated metal box with two solar panels. The box contains a solar charger, 12V battery, solid state recorder, GPS and an acoustic encoder for the GPS-signal, which recorded on the second audio channel of the recorder. A hydrophone is connected to the solid state recorder through a long (50-100 m) cable. The metal box is placed on the ice (ice floe or fast ice) and the hydrophone is deployed through a drilled hole in the ice surface, through existing leads or seal breathing holes in the ice. Deployment of PALAOA-S recording units is planned within Atka Bay (east to south-east of PALAOA) during this austral summer 2010/11 to estimate the recording range of PALAOA. Autonomous recorders will be distributed on the fast ice at various distances from PALAOA. Synchronization of PALAOA and PALAOA-S recordings enables comparison of the sounds recorded on all or only a subset of these recorders, from which the detection range of various sounds can be determined. Insight into the call type-specific detection range of the sounds of the four pinniped species provides information on inter-specific differences in communication range. In addition, these PALAOA/PALAOA-S data sets permit localization and tracking of vocalizing marine mammals, which in the case of pinnipeds allows investigation of pinniped mating strategies (*e.g.,* use of underwater territories).

Figure 18. PALAOA-S recording unit recording on the fast ice in Atka Bay. The hydrophone is deployed through a lead in the fast ice (December 2008). Picture by I. Van Opzeeland.

Another aspect that can be addressed by spatial expansion of our data base, are estimates of relative abundance of marine mammals. Currently, our research group is involved in collaboration with various research institutes under the Southern Ocean Research Partnership (SORP), which will investigate acoustic trends in abundance, distribution and seasonal presence of blue and fin whales in the Southern Ocean. PALAOA forms one of the acoustic data sets that will be included in this project.

8.2. Temporal extension

A temporal extension of the data presented in this thesis will involve further analyses of PALAOA data from other years, for example the automated detection of humpback whale calls from 2006-2010. It is our hope that PALAOA will continue to record for a few more years. Nevertheless, the major impact of the collision of ice-berg (B-15K, H. Gernandt, 2010) on 11 February 2010 (Fig 19d) with the ice shelf tongue on which the observatory is located caused large cracks in the ice shelf tongue, rendering calving of this segment of the ice shelf possible. A possibility for succession of PALAOA by PALAOA II is yet undecided.

A change of the temporal scale at which the analysis of our existing PALAOA data set is performed, provides another possibility to further investigate acoustic interactions. Figure 20 shows four spectrograms (from PALAOA data), each comprising 24 hours, which illustrates how various biotic and abiotic events temporarily dominate the soundscape. Such long-term spectra and spectrograms (*i.e.,* spectrograms over days or weeks of data), reveal the frequency distribution of acoustic energy instead of the individual vocalizations, and allow assessing the acoustic contributions of biotic and abiotic acoustic sound sources, such as glacier calving events and iceberg collisions (Fig 20d), to the local noise budget and their respective interaction.

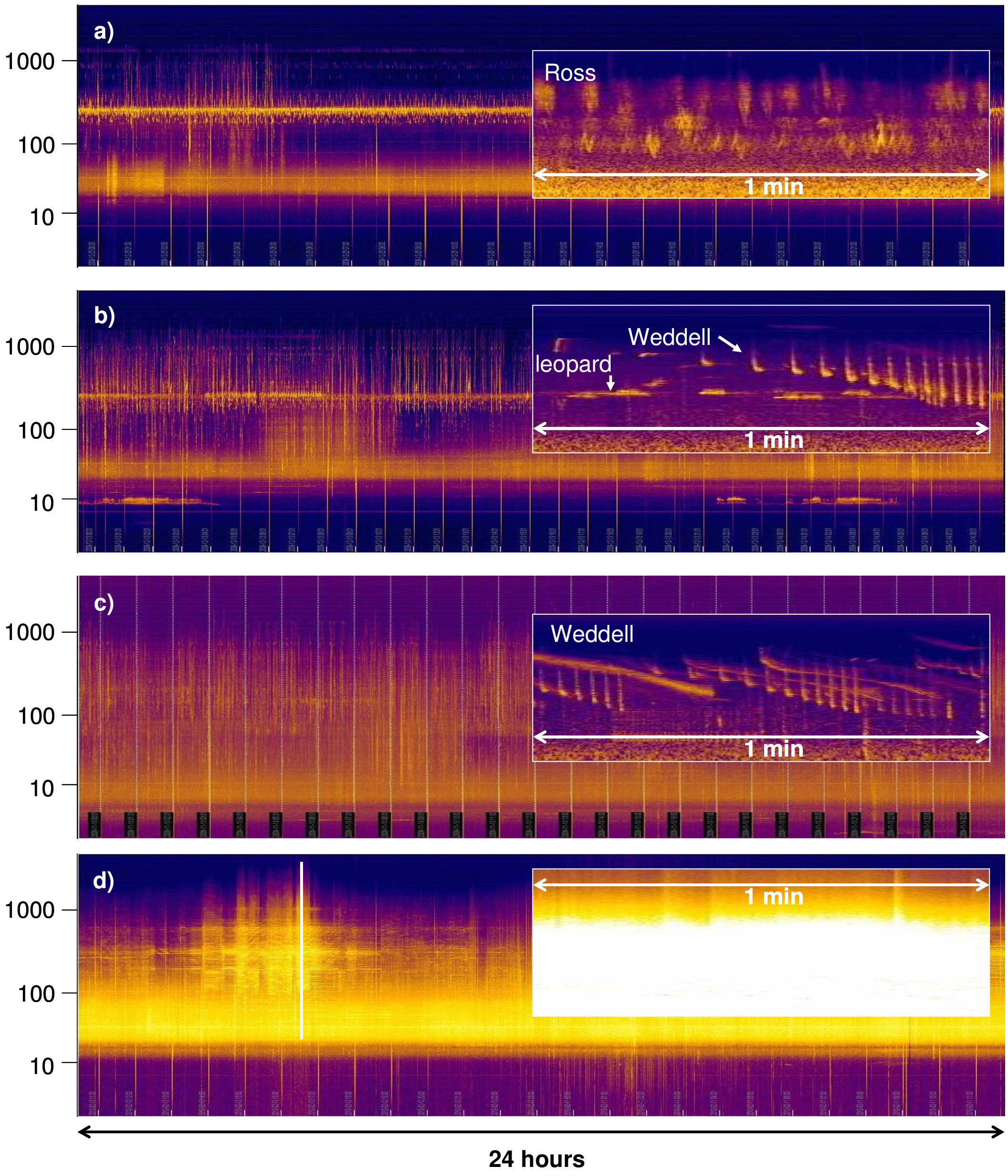

Figure 19. Four long-term spectrograms, each representing 24 hours of PALAOA recordings (hours indicated at the bottom of spectrograms), a) Day spectrogram (26 Dec 2009) with Ross seal vocal activity. The yellow band consists of calls shown in the inset image, b) leopard and Weddell seal calls on 14 Dec 2009, with an example of calls of both species in the inset image, c) Weddell seal vocal activity on 14 Nov 2009. The inset image shows an example of the trill and the falling chirp, d) the collision between ice berg B-15K and the PALAOA ice shelf tongue on 11 Feb 2010. Inset image corresponds to the point in time indicated by the white line.

9. Final note

Although conservation is not the main topic of my thesis, it has nevertheless formed a recurring theme in many sections, reflecting the critical status of various marine mammal species and populations. Scientific research is invaluable in providing the necessary information on which conservation measures protecting habitats and ecosystems can build. Nevertheless, "*conservation will be ineffective unless and until it acknowledges human impacts of all types and degrees, assumes a 'big picture' ecosystem perspective, and requires that all stakeholders acknowledge their responsibility and contribute to solutions. Deficiency of scientific information may therefore not be the primary problem with current or future conservation. Rather the primary issues have to do with human values and whether we, the human species, will be able to accept ourselves as only one element of a larger natural world, recognize and mitigate our impacts, impose a higher level of precaution with regard to other species, and strive to conserve the ecosystems upon which those species – and we – depend.*" (quote from Reynolds *et al.,* 2009, but see also Meadows *et al.,* 1972).

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3. Publications:

Contributions to publications

This listing comprises all publications and manuscripts that constitute this thesis and details my specific contributions to each of these writings.

Publication I

Van Opzeeland IC, Kindermann L, Boebel O, Van Parijs SM (2008) Insights into the acoustic behaviour of polar pinnipeds – current knowledge and emerging techniques of study. *Published: Animal Behavior: New Research.*

I conducted the literature research for this review paper, wrote the initial draft manuscript and all further versions which resulted from discussion with the other three authors.

Publication II

Van Parijs SM, Clark CW, Sousa-Lima RS, Parks SE, Rankin S, Risch D, Van Opzeeland IC (2009) Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales. *Published: Marine Ecology Progress Series.*

I analysed the data for section 'Real-time PAM of Antarctic pinnipeds and other marine mammals' and wrote the corresponding section (page 31). All other authors also each contributed sections. The first author wrote the initial draft manuscript and all further versions which resulted from discussion with all other authors.

Publication III

Van Opzeeland IC, Van Parijs SM, Bornemann H, Frickenhaus S, Kindermann L, Klinck H, Ploetz J, Boebel O. Acoustic ecology of Antarctic pinnipeds. *Accepted for publication: Marine Ecology Progress Series.*

I conducted all acoustic data analysis. Statistical analyses of the data were performed together with the fourth author. Acquisition and archiving of PALAOA recordings was accomplished by the fifth and sixth author. I wrote the initial draft manuscript and all further versions which resulted from discussion with the second, third, seventh and eighth author.

Publication IV

Van Opzeeland IC, Van Parijs SM, Kindermann L, Boebel O. Multi-year patterns in the acoustic behavior of Antarctic pinnipeds. *Manuscript in preparation.*

I conducted all acoustic data analysis. Ideas on development of automated detection of pinniped calls using the XBAT template detector were developed together with the second author. Acquisition and archiving of PALAOA recordings was accomplished by the third author. Ice data were prepared by the fourth author. I wrote this initial draft manuscript.

Publication V

Kreiss CM, Van Opzeeland IC, Klinck H, Bornemann H, Kindermann L, Figueroa H, Rogers TL, Ploetz J, Boebel O. Leopard seal (*Hydrurga leptonyx*) vocalizations from three Antarctic locations. *Manuscript in preparation.*

I supervised the first author (MA student from the University of Bremen) during the preparation of the manuscript. The first and third author conducted acoustic analysis of the data from all three locations. The third, fourth, fifth, sixth, seventh and eighth author all played a role in the collection of acoustic data at the three recording locations. Statistical analyses were performed by the sixth and ninth author together with the first author and me. I contributed to the preparation and writing of the initial draft and further versions of this manuscript. Further versions of the manuscript resulted from discussions with all other authors.

Publication VI

Van Opzeeland IC, Corkeron PJ, Risch D, Stenson G, Van Parijs SM (2009) Geographic variation in vocalizations of pups and mother-pup behavior of harp seals (*Pagophilus groenlandicus*). *Published: Aquatic Biology.*

I conducted all acoustic and statistical analysis of pup calls. Together with the second and fifth author I collected acoustic and behavioral data in the Greenland Sea population. The third author collected acoustic and behavioral data in the Front population. Data collection in the Front region was possible through support of the fourth author. Behavioral data were statistically analysed by the second author. I wrote the initial draft manuscript and all further versions which resulted from discussion with all other authors.

Publication VI

Van Opzeeland IC, Van Parijs SM, Kreiss CM, Boebel O. Individual variation in pup vocalizations and absence of behavioural signs of maternal vocal discrimination in Weddell seals (*Leptonychotes weddellii*). *Submitted to Marine Mammal Science.*

Playback experiments and acoustic data collection were conducted by me together with the third author (student assistant, University of Bremen). I designed the experimental set-up and coordinated the work in the field. I performed statistical analysis of the acoustic data and behavioral data (the latter with help of S. Frickenhaus, AWI). Acoustic measurements on a subset of Weddell seal pup calls were conducted by Antje Funcke (University of Bremen), a student assistant. I wrote the initial draft manuscript and all further versions which resulted from discussion with all other authors.

Publication VIII

Van Opzeeland IC, Van Parijs SM, Kindermann L, Boebel O. Seasonal patterns in Antarctic blue whale (*Balaenoptera musculus intermedia*) vocalizations and the bio-duck signal. *Manuscript in preparation.*

I conducted the acoustic analysis of the PALAOA data. Acquisition, archiving of PALAOA recordings as well as creating the spectrogram image file data base was accomplished by the third author. CTD data were also provided by the third author. I wrote this initial draft manuscript.

Publication IX

Van Opzeeland IC, Van Parijs SM, Kindermann L, Burkhardt E, Boebel O. Calling in the cold: pervasive acoustic presence of humpback whales (*Megaptera novaeangliae*) in Antarctic coastal waters. *Submitted to Biology Letters*

Humpback whale calls were identified in the PALAOA recordings by me. Ideas on development of automated detection of humpback whale calls using the XBAT template detector were developed together with the second author. I designed and tested the humpback whale moan detector, performed the automated detection analysis of the PALAOA data and reviewed all humpback whale moan detections. Taryn Overton (student assistant NOAA, Woods Hole) assisted in the processing of the detector output. Acquisition and archiving of PALAOA recordings was accomplished by the third author. The data on sea-ice were prepared by the fifth author. I wrote the initial draft manuscript and all further versions which resulted from discussion with all other authors.

Publication IX.a

Van Opzeeland IC, Van Parijs SM, Kindermann L, Burkhardt E, Boebel O. Supplement to paper IX: Vocal repertoire of humpback whales near the Eckström Ice Shelf. *Manuscript in preparation.*

I type-identified and counted humpback whale high calls and performed the CART analysis on the acoustic measurement data. Rosa Wilm, a student assistant (University of Munich), helped with the diel counts of humpback whale moans over the seven day period. Acoustic measurements on a subset of humpback whale calls were conducted by Svenja Zakrzewski (Hochschule Bremerhaven). Acquisition and archiving of PALAOA recordings was accomplished by the third author. I wrote this initial draft version of the manuscript.

Publication X

Slabbekoorn H, Bouton N, Van Opzeeland I, Coers A, Ten Cate C, Popper A (2010) A noisy spring: the impact of globally rising underwater sound levels on fish. *Published: Trends in Ecology and Evolution.*

This paper partly based on two publications on which I was first author, which were published in Dutch in 'De Levende Natuur' and 'Visionair' in 2007[1],- which both focus on the potential effects of noise on fish. For this paper, I contributed to these parts and provided information on noise impact on marine mammals. The first author wrote the initial draft manuscript and all further versions which resulted from discussion with all other authors.

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[1] Van Opzeeland IC, Slabbekoorn H, Andringa T, Ten Cate C (2007) Underwater racket: fish and noise pollution. De Levende Natuur 108: 39-43

Van Opzeeland, Slabbekoorn H, Andringa T, Ten Cate C (2007) Underwater noise pollustion: effects on fishes. Visionair 4: 11-13

Publication I

Insights into the acoustic behaviour of polar pinnipeds – current knowledge and emerging techniques of study

In: Animal Behavior: New Research
Editors: E. A. Weber, L. H. Krause

ISBN: 978-1-60456-782-3

Chapter 6

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

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ABSTRACT

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

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

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

To date, a range of different types of passive acoustic instruments are used, the choice of which depends largely on the purpose of the study. These instruments in addition to computer-based methods that have been developed for automated detection,

classification and localization of marine mammal sounds will be discussed. The autonomous PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA) is presented here as one example of such recording systems.

INTRODUCTION

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

POLAR HABITATS

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

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

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

PINNIPED ADAPTATIONS FOR LIFE ON ICE

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

ACOUSTIC BEHAVIOUR OF POLAR PINNIPED MOTHER-PUP PAIRS

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

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

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

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

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

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

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

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

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

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

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

ACOUSTIC BEHAVIOUR AND MATING STRATEGIES IN POLAR PINNIPEDS

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

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

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

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

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

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

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

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

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

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

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

POLAR PINNIPEDS AND ANTHROPOGENIC NOISE

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

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

ACOUSTIC DATA COLLECTION

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

ACOUSTIC INSTRUMENTATION

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

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

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

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

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

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

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

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

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

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

PALAOA

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

SOFTWARE TECHNOLOGIES

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

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

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

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

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

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

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

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

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

ACKNOWLEDGEMENTS

We thank Holger Klinck and Robert Huisman for providing constructive comments on this manuscript.

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Publication II

Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales

Vol. 395: 21–36, 2009
doi: 10.3354/meps08123

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published December 3

Contribution to the Theme Section 'Acoustics in marine ecology'

Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales

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ABSTRACT: Defining the appropriate scale over which to conduct a study in the marine environment is critical to achieving appropriate scientific, management, mitigation and conservation objectives. This paper focuses on applications of passive acoustic technologies over a range of spatial and temporal scales. It is divided into sections dealing with archival and real-time passive acoustic sensor applications. Each section assesses the principles behind using the respective technology and provides recent examples of research and management applications for marine mammals and fish. The section on archival sensors highlights the need for continued development of automated acoustic detectors to assess large data sets. Case studies are presented of detectors developed for determining seasonal occurrence and distribution of haddock sounds and humpback whale vocalizations. Also presented are studies of other applications using archival sensors: tracking singing humpback whales in Brazil, using vocalizations to assess the reproductive strategies of Arctic bearded seals and assessing regional variability in call patterns for North Atlantic right whales. The section on real-time passive acoustic sensors focuses on real-time buoys and towed arrays. Case studies presented include a real-time buoy system used for monitoring endangered North Atlantic right whales and a stationary autonomous array providing real-time access to Antarctic acoustic data. The value of using towed arrays for real-time applications is also assessed, and a case study is provided on the use of towed arrays to improve abundance estimates of North Pacific cetaceans and to better understand vocalization behaviors.

KEY WORDS: Passive acoustics · Mesoscale · Archival arrays · Real-time buoys · Towed arrays · Localization · Automated detection · Marine mammals · Fish

INTRODUCTION

The task of scientists, managers and mitigators alike is to use the right set of tools at the right spatial scale for the issue that needs addressing. To do this efficiently and effectively is no easy task, yet it is essential. Spatial scaling has long been an acknowledged driver defining research questions within the atmospheric and earth sciences. However, it is a more recent concept for ecologists, the value of which is increasingly becoming understood (Wiens 1989). Accurately describing and understanding the processes that deter-

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mine the distribution of organisms is a fundamental problem in ecology, with important conservation and management implications (Redfern et al. 2006). The terms 'synoptic' or large-scale, 'meso' or medium-scale and 'micro' or small-scale have most frequently been used in meteorology and oceanography, where descriptors of weather systems need to be provided at local, regional, continental and global scales (e.g. Capet et al. 2008). This terminology is also valuable when searching for meaningful spatial descriptors of the marine environment, particularly in relation to the movement patterns of biological entities that live within it. The terminology itself is somewhat arbitrary and needs to be taken in the context of each specific situation. Here we define synoptic scales for regional marine areas of >2000 km^2, mesoscale as areas between 1 and ~2000 km^2 in size and microscales as areas <1 km^2 (Orlanski 1975).

Marine animals live their lives and communicate acoustically across widely differing spatial scales. Large whales range and can communicate over micro- to synoptic scales (Moore et al. 2006), while smaller whales and dolphins tend to range and communicate over micro- to mesoscale areas (e.g. Tyack 2000). Pinnipeds are bound to land for breeding and moulting; therefore, access to land or ice is a fixture of their life histories. Acoustic behavior in pinnipeds has been shown to range from local (<1 km) to mesoscales with communication occurring both in air and in the water near haul-out sites on transit routes and foraging grounds (e.g. Insley et al. 2003, Van Parijs 2003). Sirenian vocalizations tend to be more localized than those of cetaceans and pinnipeds. Although movements of manatees may exceed 820 km (Reid et al. 1991), their communication range is short, with sounds limited to distress calls or to identify, locate or maintain proximity between mothers and calves (Sousa-Lima et al. 2002a, 2008). Dugongs may use their vocalizations at slightly longer distances while patrolling their territory (Anderson & Barclay 1995). Fish routinely produce sounds for long periods of time, allowing for seasonal and diurnal tracking of large shoals, and communicate over ranges of a few hundred meters up to 8 km (e.g. Saucier & Baltz 1993, Mann & Lobel 1995, Luczkovich et al. 1999, 2008, McCauley & Cato 2000).

Most marine management and conservation areas, zones, parks or sanctuaries tend to be micro- or mesoscale in size. Management areas rarely encompass the entire range of the biota and are generally targeted towards areas where important biological activities occur. Similarly, scientific studies are typically practical only at micro- or mesoscales, because studies conducted on ocean-basin scales remain logistically and financially prohibitive to most institutions (see Mellinger et al. 2007). These relatively small scalar approaches mean that little is still understood about how marine animals use the synoptic scale and how significant this scale is in terms of their management and conservation.

Passive acoustic monitoring (PAM) encompasses a functional suite of tools that can answer scientific questions and influence management and/or mitigation applications over all spatial scales. The tools that are available to acquire and analyze passive acoustic data have undergone a revolutionary change over the last decade, and have substantially increased our ability to collect acoustic information and use it as a functional management tool. Recent reviews of the passive acoustic technologies currently available concentrate both on cetaceans (Mellinger et al. 2007), pinnipeds (Van Opzeeland et al. 2008) and fish (Gannon 2008, Luczkovich et al. 2008). The present study focuses on the value of using bottom-mounted buoys, towed arrays and real-time acoustic sensors for both scientific and management applications with respect to acoustically active marine animals over a wide range of spatial scales. We divide this article into 2 sections based on available passive acoustic sensors: archival and real-time. Each section discusses the applications of these technologies and provides case studies related to the application. To date, the majority of applications of these technologies have focused on cetacean research, management and/or mitigation. However, the value of using similar applications for pinnipeds, sirenians and fish has yet to be fully realized. In the present study we provide case studies of applications for most taxa.

ARCHIVAL PASSIVE ACOUSTIC SENSORS

Mellinger et al. (2007) and Van Opzeeland et al. (2008) provide reviews of the types of archival marine acoustic recording units (ARUs) that are currently available for both science and management purposes. ARUs vary widely in type, from stationary units consisting of single or multiple hydrophones, a single hydrophone deployed on an individual animal, to multiple sensors on towed or bottom-mounted hydrophone arrays. Therefore, the spatial scale and breadth of coverage of acoustically active marine animals varies widely, depending on the type of sensor that is used (Fig. 1a).

As the technical capabilities of such units have improved and costs have decreased, it has become increasingly feasible to deploy multiple recorders in the form of acoustic arrays (≥3 ARUs). This, in turn, has enabled an increase in the accuracy of the data collected and the number of individuals surveyed (Fig. 1b). Collecting passive acoustic data on multiple channels makes it possible to detect, localize and track vocalizing fish and marine mammals. To do so accu-

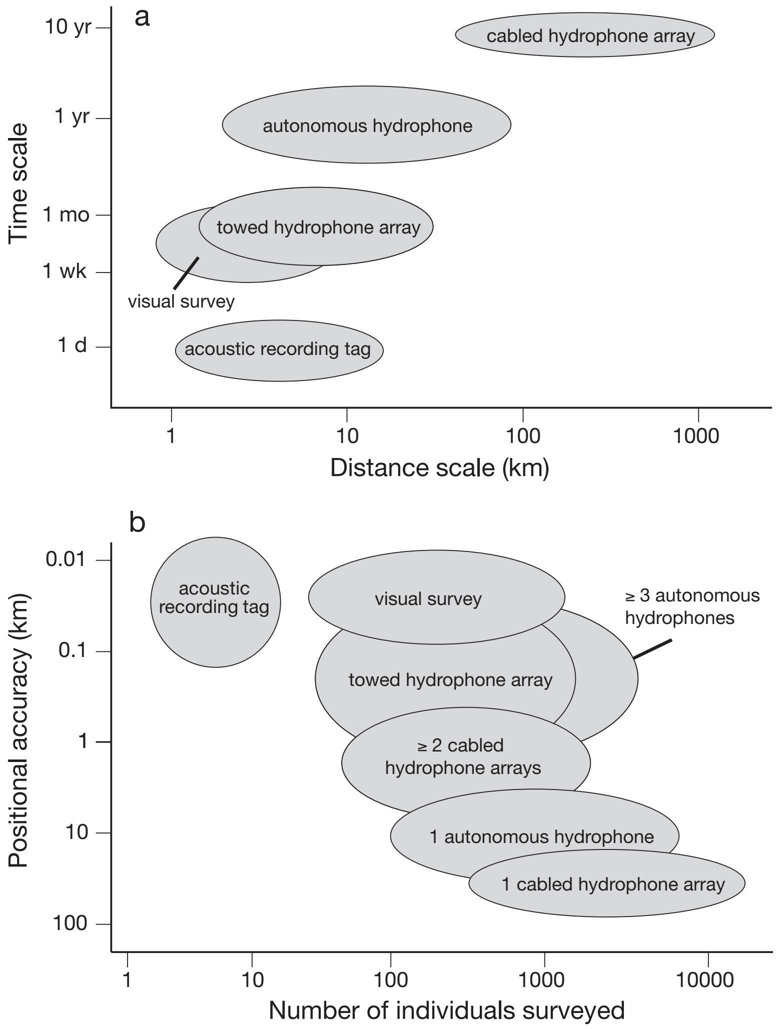

Fig. 1. (a) Approximate temporal and spatial scales over which data are collected using an acoustic recording tag on a single individual, an autonomous hydrophone, a vessel towed array and a bottom-mounted cabled hydrophone array. These acoustic techniques are compared with the temporal and spatial scope of visual surveys. (b) Approximate range of accuracy and number of individuals covered using an acoustic recording tag on an individual animal, an autonomous hydrophone, a vessel towed array composed of ≥3 hydrophones and ≥2 bottom-mounted cabled hydrophone arrays. Figures were provided courtesy of D. K. Mellinger

rately requires precise time synchronization of all the channels and can be logistically difficult when using separate sensors as opposed to systems such as towed arrays that simultaneously log multi-channel data. However, if done properly, acoustic arrays can improve understanding of species distributions and densities over varying temporal and spatial scales. Such arrays have been routinely used to study cetaceans (e.g. Moore et al. 2006, Mellinger et al. 2007). More recently, their utility has also been shown for investigating long-term behavioral strategies in pinnipeds (e.g. Van Parijs 2003, Van Opzeeland et al. 2008). However, the data collected by ARUs can easily run into multiple terabytes in size. Thus the first step to accessing data from both archival and real-time ARUs is to find the sounds of interest. It is logistically impossible to hand browse these types of data sets. Therefore, there is an increased need for suitable acoustic detection and recognition software to deal with this problem. Several valuable tools already exist to do this (e.g. Ishmael: Mellinger & Clark 2006, www.pmel.noaa.gov/vents/acoustics/whales/ishmael; Pamguard: Urazghildiiev & Clark 2006, www.pamguard.org; XBAT: Figueroa 2006, www.xbat.org); however, it is vital to realize that a solid understanding of the acoustic behavioral ecology of each species is imperative to using these tools appropriately. Without an understanding of a species' acoustic repertoire, call patterning, individual and group calling behavior as well as seasonal and regional variation in call usage, no clear or coherent research or management question can be addressed.

In the following we provide examples over a range of spatial scales of how archival acoustic sensors can be used to study the behavioral ecology of vocal marine animals. Our aim is to provide an understanding of the tools and methodologies that are currently available to address a range of ecological questions directed towards improving marine animal management, mitigation and conservation strategies.

Regional differences in North Atlantic right whale acoustic patterns and call types throughout the northwestern Atlantic Ocean

Collecting acoustic data over large spatial and temporal scales is becoming increasingly commonplace. The value of increased data collection over larger scales is indisputable in terms of understanding and managing populations more effectively. However, marine animal behavior varies considerably between seasons and over geographical areas. Therefore, it is no surprise that their acoustic behavior is equally variable, driven by varying life history parameters and experiences at the individual, population and species level. When using acoustics to implement management and mitigation strategies for a species it is imperative to understand their call repertoire and whether this varies regionally.

In the case of the endangered North Atlantic right whale *Eubalaena glacialis*, acoustic monitoring can be a valuable tool for both management and conservation. Ship strike is one of the main anthropogenic causes of mortality in this species (e.g. Silber & Bettridge 2006), and reducing the likelihood of strikes in high vessel traffic areas is of primary concern. Low reproductive rates are also a major factor limiting their recovery, although calf production has increased during the past 6 yr (Kraus et al. 2005). Identification and protection of the mating grounds for this species may also be an important step toward their conservation. However, the location of the majority of the population during the breeding season (presumed to peak in October–December) remains unknown (Weinrich et al. 2000, IWC 2001, Kraus & Hatch 2001). Passive acoustic monitoring can monitor areas of high risk and investigate remote inaccessible areas for the presence of right whales.

The upcall, or contact call, is typically the call type used for diagnostic detection of right whale species (Wade et al. 2006, Clark et al. 2007). This call is highly stereotypic making it ideal for species recognition. Studies of the behavioral function of sounds in the right whale repertoire have identified 2 additional classes of sounds, tonal calls and gunshot sounds, related to social and/or mating activity (Parks & Tyack 2005) and potential male reproductive signals (Parks et al. 2005). In order to develop an effective management or monitoring scheme and search large quantities of acoustic data for the presence of a given species, it is important to understand whether to use a single call type or a combination of several call types. To make this decision a good understanding of regional patterns and call type usage in the target species is needed.

In the present North Atlantic right whale study, bottom-mounted ARUs were deployed in 3 known right whale habitat areas (Cape Cod Bay, Massachusetts; the Great South Channel, approximately 50 nautical miles offshore from Massachusetts; and the Bay of Fundy; see habitat descriptions in Kraus & Kenney 1991, Brown et al. 1995) to determine whether regional differences existed in the vocal behavior of the whales. The first 2 habitats have been shown to be frequented by large numbers of right whales during the spring, and the latter is primarily used in summer months. Data were collected during a short period within each of these peak periods (8 d in Cape Cod Bay between 1 March and 10 April 2004, 5 d in the Great South Channel between 12 and 17 May 2004 and 8 d in the Bay of Fundy between 7 and 24 August 2004). The Cape Cod Bay array consisted of 4 units, while the Great South Channel and Bay of Fundy arrays consisted of 5 units each. ARUs were spaced 3 to 5 nautical miles apart to allow for maximal acoustic survey area with the ability to localize vocalizations within the array itself. Sampling rate was between 2 and 8 kHz. The recordings were inspected for right whale calls using XBAT and labeled as upcalls, other tonal calls or gunshot sounds. Analyses of the call types across the 3 habitat areas show a clear difference in the calling behavior of right whales in the spring versus the summer habitat areas (Fig. 2). Gunshots accounted for a significantly larger proportion of total detected sounds in the Bay of Fundy than in either Cape Cod Bay or the Great South Channel (ANOVA, $F_{2,\,19} = 54.9$, $p < 0.0001$). These results suggest that the social interactions of right whales change through the seasons, with an increase in gunshot sounds, thought to be related to reproduction, later in the year. The present study demonstrates the utility of using upcalls as a tool for monitoring the presence of right whales and managing ship strike throughout most regions of the western Atlantic. However, it also suggests that other call types, such as gunshots, may be more effective for indicating right whale presence in some regions, such as their foraging and breeding grounds. This then also begs the question as to how each of these call types is used on the calving grounds. To date, this research has not been undertaken but should be done to validate any management or mitigation strategy for this region. Overlap of call types between species is another concern when using acoustics for single-species management and mitigation. In the case of the North

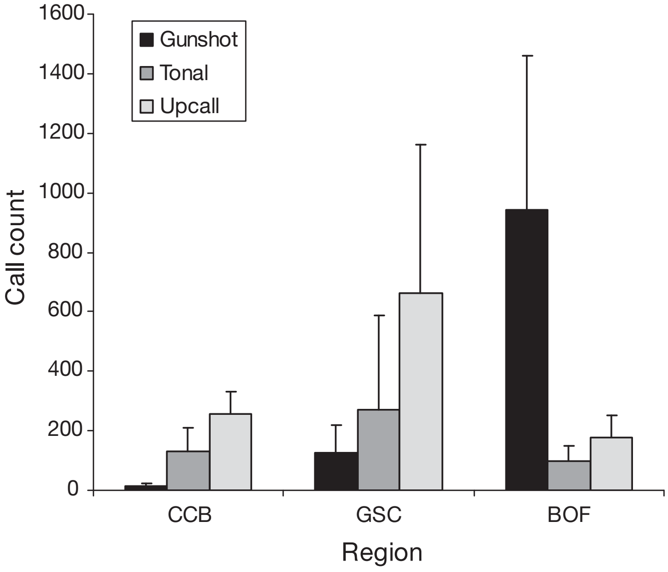

Fig. 2. Archival sea bed acoustic recording units (ARUs) were deployed in 3 North Atlantic right whale habitat areas off the northeast coast of the USA: Cape Cod Bay (CCB), the Great South Channel (GSC) and the Bay of Fundy (BOF). Bars represent the median (±SE) of daily call counts broken down by 3 call types (gunshot, tonal and upcall) for each habitat area

Atlantic right whale, humpback whales are capable of producing upcalls that closely resemble those of right whales. How significant this overlap really is and whether there is potential for differentiation should be explored further.

Acoustic detection of haddock and humpback whale sounds: understanding seasonal distribution and occurrence

The next step to manage, mitigate and/or conserve a species regionally is to understand its seasonal distribution and occurrence. In order to do this, automated detectors targeting specific call types are needed.

The Gerry E. Studds Stellwagen Bank National Marine Sanctuary, situated in Massachusetts Bay on the northeast coast of the USA, is the research venue of an ambitious multi-year passive acoustic project aimed at developing a suite of tools to monitor and map ocean underwater noise over a mesoscale region (for more project details see Hatch & Fristrup 2009, this Theme Section). Ten archival ARUs were deployed in 2006 and will remain operational until late 2010[1]. By late 2010, more than 400 000 h of acoustic data will have been collected. Given recent technological advances, it is now fairly simple to collect a lot of continuous data over a long time scale. The tools with which to analyze this data are, however, not yet routine or well known. Among the primary tools that are becoming widely used are automated detectors. The present study provides an example of how these tools can be used.

As part of the present study, automated acoustic detection software ('detectors') is being developed to search for specific biological sounds produced by baleen whales and various fish species. Acoustic detectors were built using the automated data template detector tool available in XBAT (www.xbat.org, H. Figueroa). XBAT is an extensible sound analysis application which uses MATLAB as a platform for developing sound analysis tools. 'It is open-source, licensed under the General Public License. Users can access and visualize sounds, browse and search for salient events, and annotate and measure events. Developers can quickly create easy-to-use extensions with a powerful plug-in architecture'. The automated detectors operate using spectrogram cross-correlation of an example event (the template) and the sound file. Several templates can be arranged in presets.

In the present study, multi-species detectors were built for all large whale and fish species in the sanctuary. Here we describe the process of building detectors for 2 of these species. The first application was enumeration of haddock *Melanogrammus aeglefinus* spawning sounds. The objective in this case was to develop a detector to evaluate the seasonal occurrence and distribution of spawning haddock over multiple years within the study area. Stellwagen Bank Sanctuary forms one of the two primary spawning sites for haddock in the Gulf of Maine (Colton 1972). Thus this area plays an important role in the life-cycle of this species. Passive acoustics can help to gain a better understanding of haddock distribution and general reproductive behavior in this area, in order to better inform conservation and management of this species.

Haddock produce repetitive knocking sounds directly linked to their spawning behavior (Hawkins et al. 1967, Hawkins & Amorim 2000, Casaretto & Hawkins 2002). While these sounds are well described from laboratory experiments, little is known of sound production in wild haddock. These sounds comprise 3 types of calls: single, double and multiple knocks (Fig. 3a). All 3 call types were added to a preset. This preset was run against 10 randomly selected days of manually browsed data to estimate its accuracy at detecting spawning sounds. Multiple presets were constructed using different templates until the most accurate one was developed. The mixed call type preset was able to enumerate haddock knocks with an accuracy of 47%, while the accuracy of different templates was 75, 82, and 41%, respectively, for single, double and multiple knock calls.

This case study illustrates that the data template detector can be highly effective in enumerating sound events. The comparatively low accuracy of the template for multiple knock calls was due to a variable repetition rate of single pulses in different versions of this call type. It is therefore easy to perceive that the more stereotypic a vocalization, the better a detector based on cross-correlation will perform. As such, more variable sound types require different detection approaches. For example, rather than enumerating every single vocalization one might instead search for sound events.

Individual male humpback whales *Megaptera novaeangliae* produce long repetitive song sequences when attracting females and during male–male competition (e.g. Payne & McVay 1971, Winn & Winn 1978, Tyack 1981). Humpback whale song is gender-specific and has been shown to change over time scales of a year to several decades (e.g. Noad et al. 2000, Darling & Sousa-Lima 2005). Improving our understanding of song and how it is used seasonally, in the breeding and feeding grounds as well as along migration routes, will increase our comprehension of how this species uses

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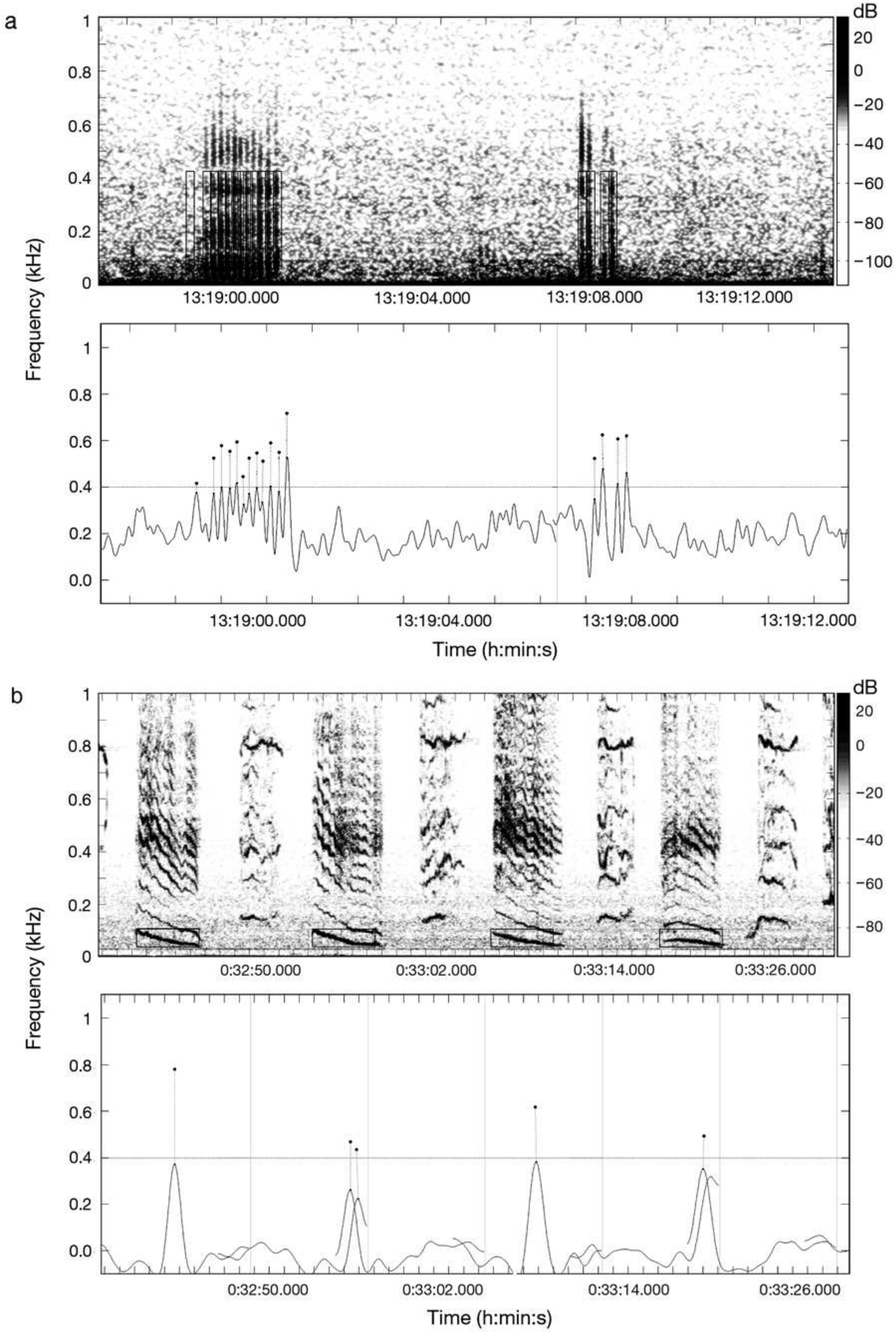
[1] All ARUs mentioned in this and subsequent studies were developed by the Bioacoustics Research Program of the Cornell Laboratory of Ornithology (BRP, www.birds.cornell.edu/brp/hardware/autonomous-recording-units)


a
b
Frequency (kHz)
dB
20
0
−20
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0.2
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1
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13:19:00.000
13:19:04.000
13:19:08.000
13:19:12.000
0:32:50.000
0:33:02.000
0:33:14.000
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Time (h:min:s)

each region as well as how its song evolves both temporally and spatially. Given the variability and length of humpback singing cycles, enumeration of each call type is difficult. However, it is possible to build acoustic detectors that identify song events. In this case, a single call type present in all humpback whale song in the study area during 2006 was selected to build a data preset (Fig. 3b). The resulting preset, based on 5 templates, proved highly effective in detecting hours with humpback whale song throughout 1 yr of acoustic data (89 % accuracy; based on comparison to 4 randomly selected days of hand-browsed data). In the present study, the presence of song within a given hour enabled the determination of song occurrence and distribution over a 12 mo period. Although different from enumeration, this approach is valuable for understanding patterns of sound production. In the case of humpbacks, however, it is important to revisit the efficacy of the detector every year, given that alterations in song may occur. Obviously, it is vital to understand the acoustic behavior of a species since this not only affects the effective operation of a detector but will determine the types of biological and management issues than can be addressed using passive acoustic data. Tools such as the data template detector or existing energy and contour detectors in XBAT and other platforms, which are easy and flexible to use, appear to be the way forward in developing tools and applications for processing acoustic data from multiple species.

Tracking behavioral changes in individual humpback whales and evaluating anthropogenic effects

Acoustic localization is a valuable tool for helping to understand the acoustic behavior of an individual or groups of animals. Once baseline individual and/or group behavior is understood, this tool can also be used to assess potential anthropogenic impacts on a species. A multiple year mesoscale study (Sousa-Lima 2007) was conducted at the Abrolhos National Marine Park located in the northeast portion of the Abrolhos Bank off the coast of Brazil (16° 40′ to 19° 30′ S). In this study an array of 4 bottom-mounted ARUs was used to detect (using similar XBAT sound event detectors as for the study described in the previous section), locate and track multiple singing male humpback whales, as well as to evaluate their behavioral responses to passing tourist boats. Singing whales were located using a custom built localization extension for XBAT (Source Locator version 2.2, K. A. Cortopassi & K. M. Fristrup unpubl. data). This tool estimates the location of a given signal by calculating the cross-correlation functions between different channels and searching for the best location estimate within a gridded search area. Temporal and spatial changes in the distribution of singing male humpback whales were determined by plotting estimated signal bearings and locations, thus building acoustic tracks of individual whales.

Tracked singers (Fig. 4) were enumerated at multiple points in time to determine whether the numbers of singers changed during periods of variable boat traffic (Sousa-Lima & Clark 2008). Singers were also acoustically tracked to evaluate whether their movements and vocal behavior changed during the approach of a boat (Sousa-Lima et al. 2002b, Sousa-Lima & Clark 2009). This study revealed that the scale of the disturbance created by boat traffic to the acoustic environment of humpback whales in the Abrolhos Park is much broader than previously thought. Bottom-mounted arrays are relatively unobtrusive to the animals, and data can be collected over larger spatial and temporal scales. This allows multiple focal individuals to be observed for extended periods of time before, during and after exposure to anthropogenic disturbances.

Understanding reproductive strategies and life history parameters by locating individual bearded seals over decades

PAM is most frequently thought of in terms of cetacean management and mitigation. However, pinnipeds have never seemed to be suitable candidates for PAM. This case study demonstrates how PAM can be used to provide detailed and long term insights into the reproductive strategies and life history of a pinniped species. The detail is so fine-scale that small-scale changes due to changing environmental conditions are also able to be detected.

Studies of pinniped reproductive strategies have largely concentrated on species which remain ashore during the entire breeding season. However, the Odobenidae and at least 15 of the 18 phocid species mate aquatically (Van Parijs 2003). The use of archival acoustic arrays has significantly advanced our understanding of the reproductive ecology of aquatic mating pinnipeds such as the harbor seal *Phoca vitulina* (e.g. Van Parijs et al. 2000), the bearded seal *Erignathus bar-*

←

Fig. 3. Example of acoustic detections using the data template detector in XBAT for (a) haddock pulsed calls and (b) humpback whale song notes. Lower sections of both examples show the cross-correlation functions. Dotted horizontal line at 0.4 indicates the detection threshold. Every correlation peak above threshold is saved in the detection log. Spectrograms were created with Hanning window. Fast Fourier transform algorithm size: (a) 512, (b) 1024; overlap: (a) 97 %, (b) 90 %

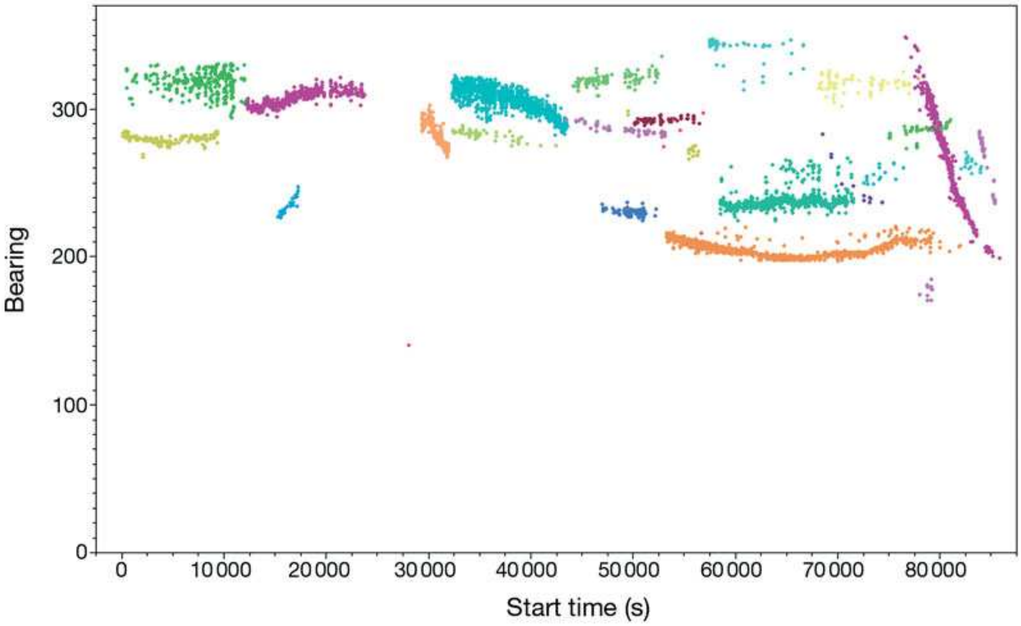

Fig. 4. A synchronized array consisting of 4 archival acoustic recording units was deployed in Abrolhos Park, Brazil. Humpback whale song was localized using XBAT software and the bearings of individuals were plotted. This figure represents plots from a 24 h sequence and shows the bearings of humpback whale sounds demonstrating how they can be used to make up tracks of multiple singers (distinguished by color)

batus (e.g. Van Parijs et al. 2003, 2004) and Weddell seal *Leptonychotes weddellii* (e.g. Harcourt et al. 2007).

Archival arrays of 3 to 5 buoys were used to record the trill vocalizations of male bearded seals at 2 Arctic sites, one in the Svalbard archipelago over 2 consecutive years, and one near Barrow, Alaska, over a 16 yr period. Males show stereotypical dive and vocal displays, with clear individual variation (Van Parijs et al. 2003). In Svalbard, acoustic localization provided at-sea locations for 17 males based on variation in trill parameters. Kernel home range analyses showed that 12 individuals displayed at fixed locations (95% kernels = 0.27 to 1.93 km^2), while 5 other males displayed over considerably larger areas (95% kernels = 5.31 to 12.5 km^2) (Fig. 5, Van Parijs et al. 2003). Movement patterns of males suggest that those with small areas patrolled aquatic territories, while those that used larger areas appeared to roam. These data thus provide evidence of alternative mating tactics in this species. In Alaska, acoustic localizations provided at-sea locations for 100 males based on variations in trill parameters, with 6 males being present over the entire 16 yr period (Van Parijs & Clark 2006). The acoustic data indicate that male mating tactics tend to show long-term stability in vocal characteristics, site fidelity and periods of tenure that cover a significant proportion of a male's adult life span. Ice cover was found to restrict the number of roaming males, whereas territorial males were present during all ice conditions, suggesting that varying ice conditions affect individual male strategies and reproductive success (Van Parijs et al. 2004).

Therefore, PAM can provide detailed and long-term information on pinniped species in key areas such as their mating grounds. This information can be so detailed that changes can be detected in individual area usage and behavior as a result of both intraspecific competition and varying environmental conditions.

REAL-TIME PASSIVE ACOUSTIC SENSORS

To date, discussions of real-time passive acoustic sensors have focused on cabled sea floor mounted hydrophones used mainly by government agencies in particular navies, such as the Sound Surveillance System of the US Navy (SOSUS), which provides real-time information. Mellinger et al. (2007) highlight the benefits of these systems in continuously providing near-real-time data, as well as in having hydrophones in pelagic areas where marine mammal surveys are rare. However, data access and recording bandwidth are usually severely restricted. In recent years, non-military real-time systems have markedly improved and are rapidly becoming a standard technology for use in both research and management. These non-military applications primarily consist of surface buoys or towed arrays; the former tend to consist of single units deployed remotely, while the latter depend on vessels for deployment. An increasing number of non-military acoustic observatories are now operational in coastal areas (e.g. the ALOHA Ocean Observatory Network, Petitt et al. 2002, Barnes et al. 2007). These systems (1) allow real-time monitoring and localization of marine animals; (2) record continuously over broad frequency bandwidths; and (3) have no restrictions on data storage, data access or power supply. Surface buoy and towed array applications are discussed in the following sections, and an example is presented of a non-military acoustic observatory.

Real-time surface buoy applications

Real-time surface buoys are acoustic recording packages anchored to the sea floor but which are connected to floats at the surface which transmit acoustic data via VHF, satellite or mobile phone signals (Fig. 6). The signals sent from these buoys can be transmitted to multiple recipients. The term near real-time is sometimes used in relation to these systems since certain logistical delays are involved in data processing. However, this tool is increasingly approaching real-time functionality.

While real-time buoys are useful tools for research applications, they are increasingly becoming invaluable for implementing management and mitigation strategies. The latter often require action to be taken in as close to real-time as possible for protection measures to be effective. For example, marine mammals can alter their distributions and movements daily, seasonally and annually. Often for management measures to be most effective, reliable real-time information on species distributions is needed. Examples of using real-time data from buoys for mitigation and management purposes include the Gulf of St. Lawrence, where real-time buoy information is being used to mitigate ship strikes of blue whales *Balaenoptera musculus* and fin whales *Balaenoptera physalus* (Simard et al. 2006), and along the northeast coast of the USA, where buoy data are being used to mitigate ship strikes of North Atlantic right whales (see following section).

Real-time acoustic monitoring of North Atlantic right whales

Ship strike mortality remains one of the two primary causes of anthropogenic mortality impeding the lack of recovery of the endangered North Atlantic right whale (e.g. Silber & Bettridge 2006). Ship strikes can be reduced by either separating vessels from whales or by decreasing the speed of the vessels (e.g. Vanderlaan & Taggart 2007). In 1999, NOAA's National Marine Fisheries Service (NMFS) and the US Coast Guard (USCG) established a reporting system that alerts mariners to the location of right whales throughout the East Coast of the US. When vessels greater than 300 gross tons enter these areas they must report to the USCG to receive current sighting information about right whales (Ward-Geiger et al. 2005). To extend the warning system to smaller vessels, the USCG developed another system, called the Auto-

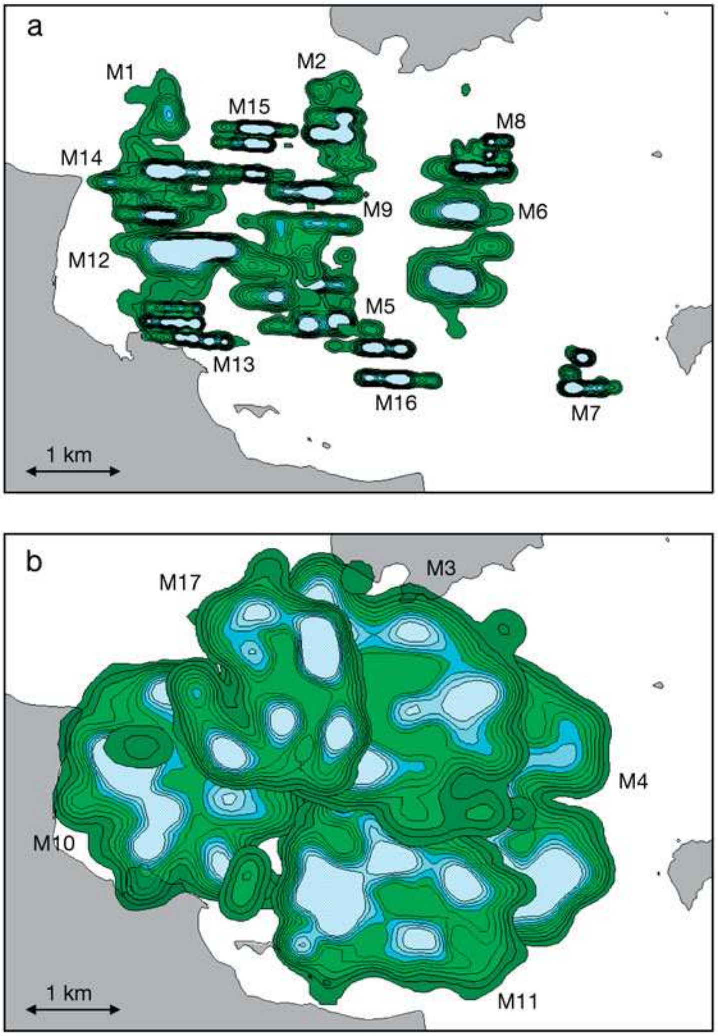

Fig. 5. Kernel home range plots of 50 to 95 % isopleths, represented by the different colour shades, for the trill locations, as calculated using 3 archival acoustic hydrophones, of (a) 12 individual territorial male bearded seals with small areas and (b) 5 roaming males with large areas in Svalbard, Norway 78° 55′ N, 11° 56′ E (reproduced from Van Parijs et al. 2004)

mated Identification System. In addition, the Northeast US Right Whale Sighting Advisory System (SAS) was created in 1996 to monitor right whale populations within the northeast waters of the United States (http://rwhalesightings.nefsc.noaa.gov/). The SAS provides sighting information from aerial and shipboard surveys to commercial ships and mariners. The positions and maps of right whale sightings are distributed through various means: faxes and verbal updates to commercial vessels, 24 h radio broadcasts and online postings to several web pages. Due to logistical and weather constraints, however, it is estimated that only 33 % of all whales are detected on a given day.

To improve the detection of right whales, Cornell University's Bioacoustics Research Program (BRP) developed a real-time passive acoustic buoy system that recognizes right whale upcalls using an automated detection program and relays these detections to the BRP (Fig. 7). Detections are then checked for accuracy, uploaded onto a web server and directly forwarded to the SAS and other parties for management and mitigation purposes (www.listenforwhales.org). The real-time buoy system continuously updates the presence of this species, and is a benchmark example of using passive acoustics for conservation purposes.

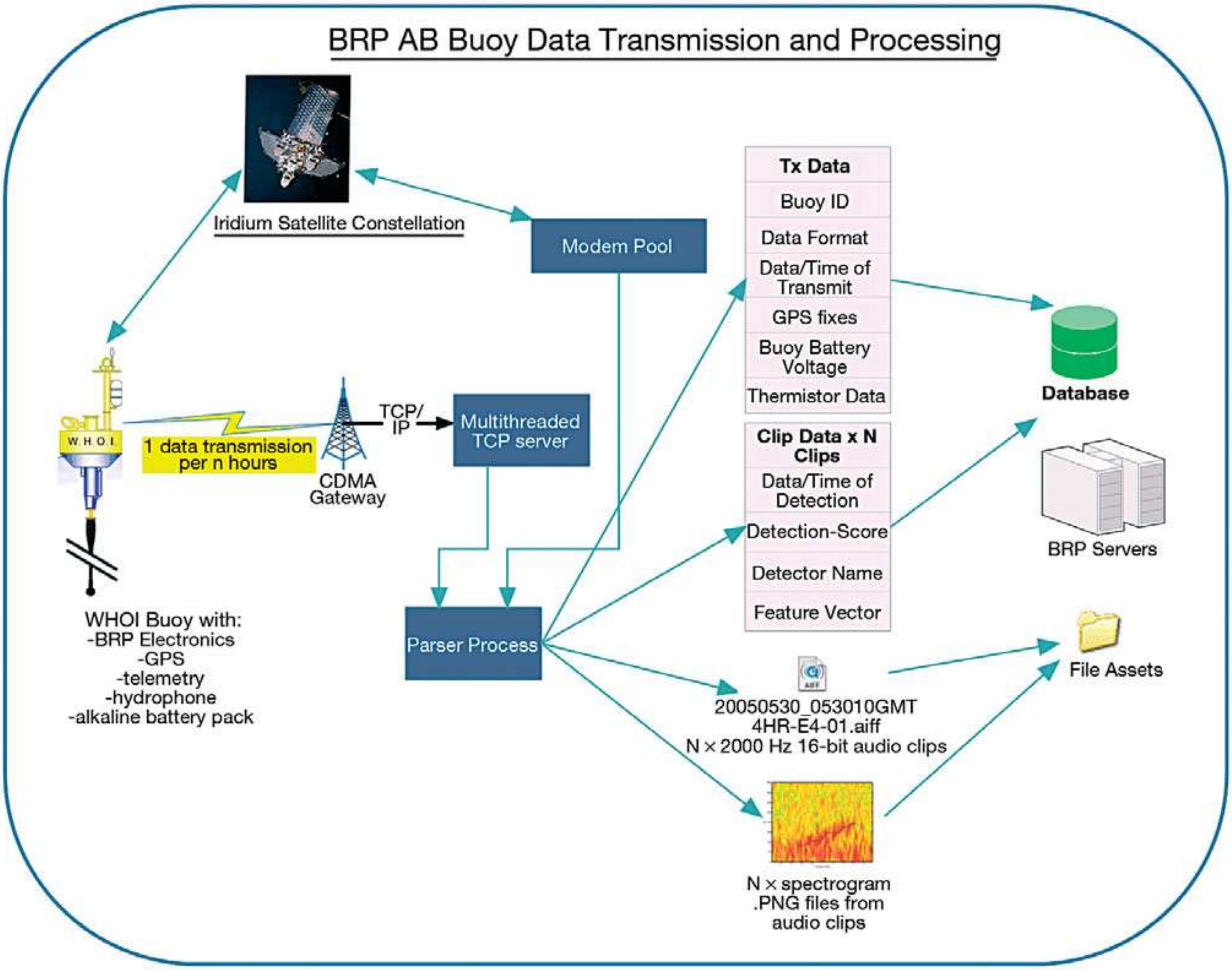

Fig. 6. Schematic diagram of an auto-buoy communications and server system that accepts and unwraps incoming data packets from multiple buoys via multiple cell phones and provides these data to a web server (see Fig. 7) that can be viewed over the internet. The auto-buoy hard ware was developed by Woods Hole Oceanographic Institute (WHOI), and contains electronics developed by the Bioacoustics Research Program at the Cornell University Laboratory of Ornithology (BRP), a global positioning system (GPS), a VHF telemetry receiver, an HTI hydrophone and an alkaline battery pack. Short sound clips of North Atlantic right whale up-call detections, with accompanying buoy information data such as buoy ID, location and voltage, are sent through GPS to an iridium satellite and via radio signal using a code division multiple channel access method (CDMA). The data then either pass through a modem pool or a multithreaded transmission control protocol (TCP) server. The data is subdivided into 2 categories separating sound clip data from the other data streams. These are then stored on a central data base and loaded onto a web server

Real-time PAM of Antarctic pinnipeds and other marine animals

Real-time passive acoustic arrays can provide valuable long-term acoustic monitoring data in remote areas such as the Arctic and Antarctic. The Perennial Acoustic Observatory in the Antarctic Ocean (PALAOA) is an example of a stationary autonomous listening station that continuously records underwater sound year-round. The PALAOA observatory is located at 70° 31′ S, 8° 13′ W, on the Ekström Ice Shelf, eastern Weddell Sea, 1 km from the ice shelf edge and 15 km from Neumayer Base (the German Antarctic research station). PALAOA consists of a 520 m baseline tetrahedral hydrophone array[2] deployed through boreholes underneath the 100 m-thick floating Antarctic ice shelf (Boebel et al. 2006, Klinck 2008). The observatory is energetically self-sustained utilizing solar and wind energy, and has operated since December 2005. The PALAOA system enables real-time acquisition of data which are subsequently transferred via live feed from the Neumayer Base to the Alfred Wegener Institute in Germany (www.awi.de/en/research/new_technologies/marine_observing_systems/ocean_acoustics/palaoa/palaoa_livestream). A main reason for incorporating real-time data transfer in the PALAOA system was to allow autonomous and continuous recording over long time spans without any limitation on onsite data storage (Boebel et al. 2006, Klinck 2008, Van Opzeeland et al. 2008).

The PALAOA recordings contain a variety of cetacean vocalizations, as well as vocalizations of 4 Antarctic pinniped species: Weddell *Leptonychotes weddellii*, Ross *Ommatophoca rossii*, crabeater *Lobodon carcinophaga* and leopard seals *Hydrurga leptonyx* (Fig. 8). The latter 3 species breed on pack-ice, and many aspects of the basic ecology of these species are still largely unknown due to the inaccessibility of their habitat. All 4 species exhibit species-specific vocal repertoires and have distinct patterns in their vocalization activity. Fig. 8 illustrates the call activity of all 4 species during 4 d in December 2006. Weddell seal call activity declined towards the end of December, which is near the end of the Weddell seal mating season (e.g. Bartsh et al. 1992, Harcourt et al. 1998, 2000). In contrast, Ross seal vocal activity started and increased throughout December. Crabeater seal call activity was very low, with calls only present in early December; higher call rates have been documented during October and November (Thomas & DeMaster 1982). Although Thomas & DeMaster (1982) reported that the peak underwater vocalization period for leopard seals coincided with that of crabeater seals, the PALAOA recordings show a relatively constant call rate in December for leopard seals. Acoustic analyses of PALAOA recordings over longer time spans are underway and will provide further insights into the acoustic behavior and ecology of all 4 pinniped species. The PALAOA recordings will also be used to develop an ocean noise budget and to monitor the effects of anthropogenic sounds (e.g. ice breakers, scientific sound sources) on marine mammal calling behavior.

Towed array applications

Real-time detection of cetaceans using passive acoustics is increasingly recognized as a potential tool for the mitigation of human impacts on the marine environment (Barlow & Gisiner 2006, Castellote 2007, Potter et al. 2007, Weir & Dolman 2007). The successful

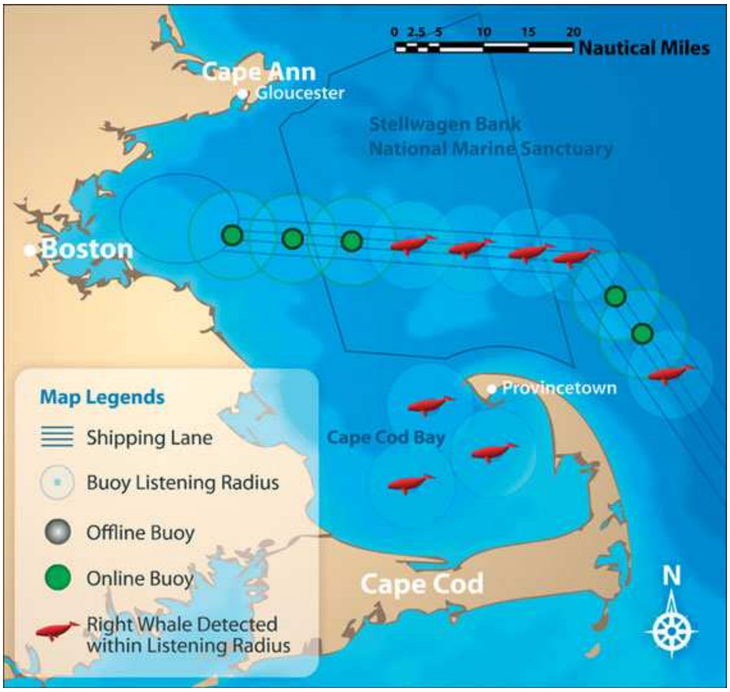

Fig. 7. Screen shot of the real-time auto buoy system that is operational off the northeast coast of the USA aimed at increasing the efficiency of the alerting system directed towards mariners entering into the area with the intention of reducing vessel speeds and thereby preventing ship strikes (see www.listenforwhales.org). Note that in this screen shot there are no offline buoys, indicating that at this point in time all buoys are functional and actively listening for North Atlantic right whale up-calls

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[2] Since mid-2006 the failure of 2 hydrophones has reduced the array to a 2-channel system

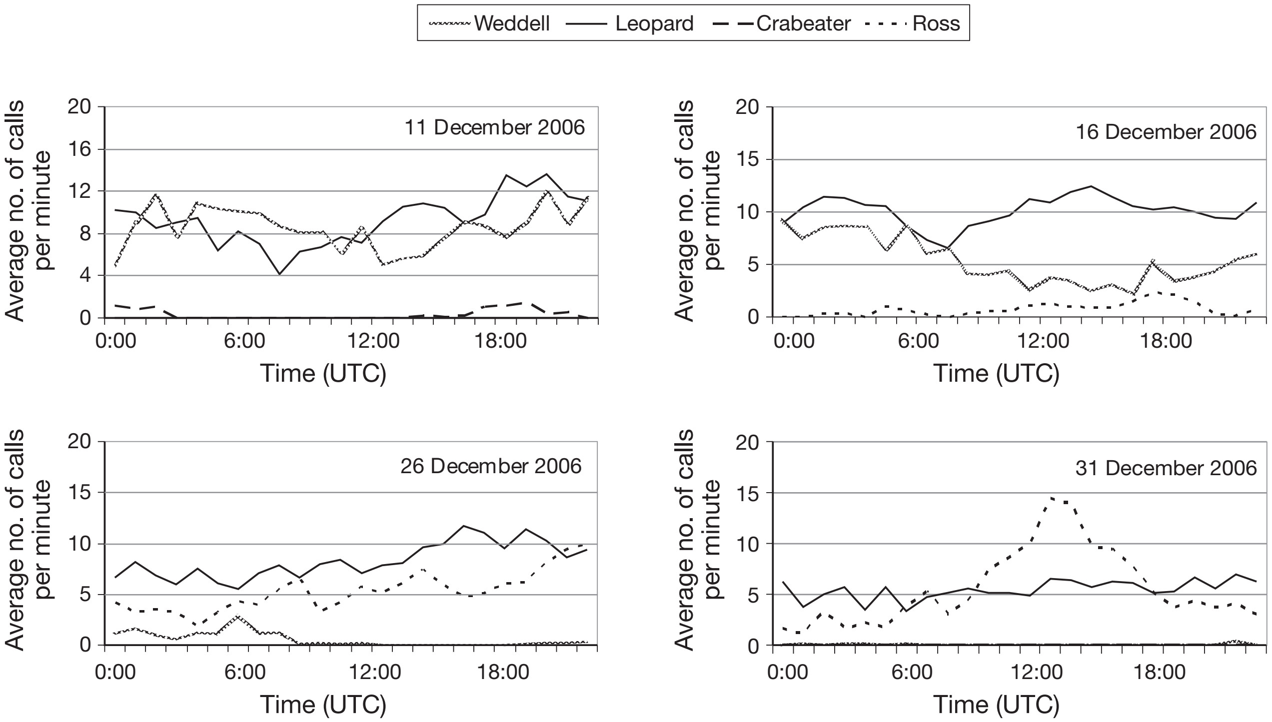

Fig. 8. Preliminary analyses of 4 days of real-time passive acoustic recordings made using the Perennial Acoustic Observatory in the Antarctic Ocean in December 2006. Results show different patterns of temporal variation in vocal activity of Weddell, leopard, crabeater and Ross seals. Average number of calls per minute is based on 10 min counts for each hour

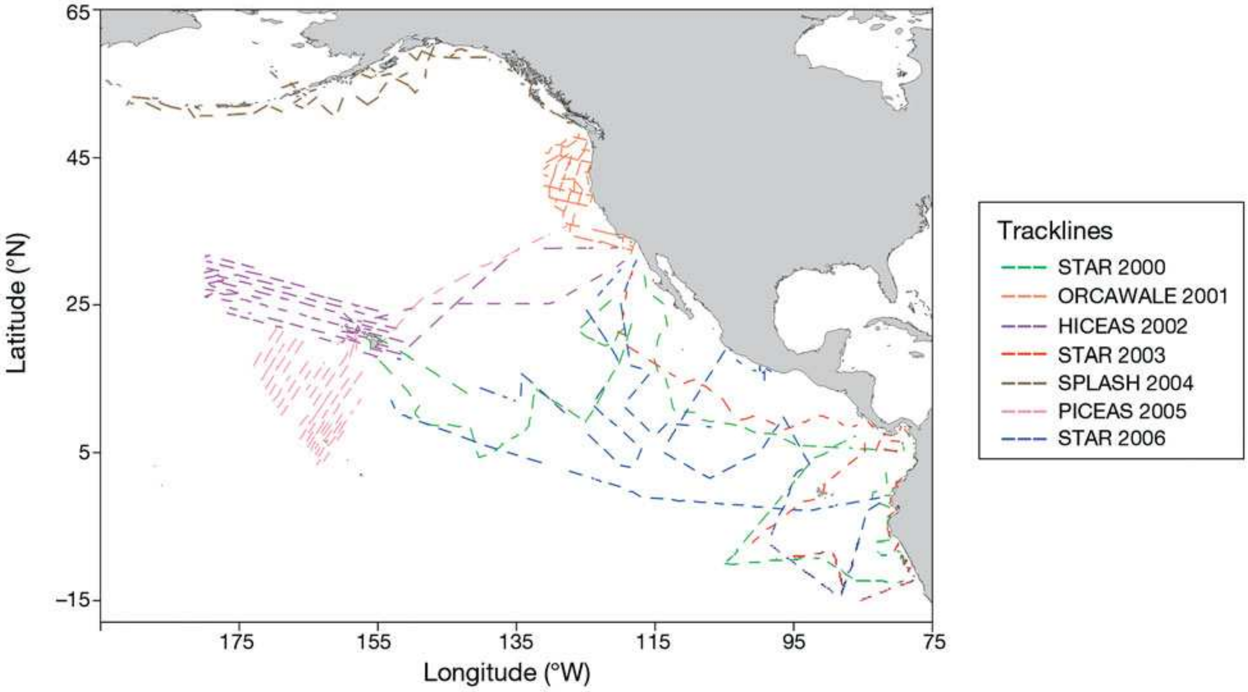

Fig. 9. Study area for 7 shipboard visual and acoustic cetacean surveys with tracklines of acoustic monitoring using a towed hydrophone array. Total distance surveyed for all tracklines combined is 46 370 km

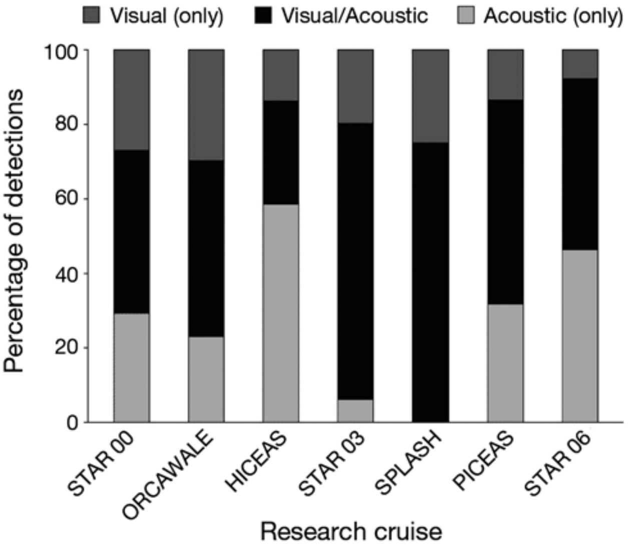

Fig. 10. Percentage of dolphin detections made by the visual observation team (dark gray), the acoustic detection team (light grey) and both the visual and acoustic detection teams (black) during 7 visual and acoustic cetacean surveys conducted by the Southwest Fisheries Science Center

use of towed arrays for this purpose requires that survey designs take account of the types of anthropogenic impacts, the range of detections and the vocal behaviors of animals. Ideally, such surveys should include pre-, during- and post-operation components (Castellote 2007). It is also important that complementary monitoring methods be used in such surveys — such as static acoustic monitoring (for increased temporal coverage) and visual observations (to account for biases due to silent animals).

A single towed hydrophone array consisting of at least 2 hydrophones can be used to obtain bearing angles to a sound source; convergence of bearing angles as the ship travels allows for localizations of the sound source with a left/right ambiguity. This ambiguity can be resolved by integration of a second array, offset from the first, or by a change in the direction of travel of the ship. While towed arrays have been used for detection of baleen whales (Clark & Fristrup 1997), dolphins (Rankin et al. 2008a) and porpoise (Akamatsu et al. 2001, Li et al. 2009), there are some limitations to its practical use. Several studies have shown that cetaceans respond to survey vessels, which may affect their vocal behavior (Au & Perryman 1982, Hewitt 1985). Also, a recent study has found a decrease in acoustic detection of dolphins forward of the vessel when using towed hydrophone arrays (Rankin et al. 2008b).

Passive acoustic detection of cetaceans using towed hydrophone arrays has yielded new insights into the acoustic behavior of several species. In 2002, passive acoustic detection and localization identified the mysterious 'boing' sound in the Pacific Ocean as emanating from minke whales (Gedamke et al. 2001, Rankin & Barlow 2005). The match of this sound to minke whales allowed researchers to gain additional understanding of the distribution, migration and stock structure of this species (Rankin & Barlow 2005).

Recent analyses of the vocal behavior of dolphins in the North Pacific have shown a strong correlation between group size, geographic range and vocal behavior (Rankin et al. 2008b). This correlation may indicate evolutionary changes that relate group size to vocal behavior. Since 2000, the NOAA's Southwest Fisheries Science Center has conducted combined visual and acoustic line-transect cetacean surveys covering a significant portion of the North Pacific Ocean (Fig. 9). The need to use towed hydrophone arrays in these population surveys was highlighted when it was recognized that a large number of dolphins were missed using only visual observations; for example, during the 2002 HICEAS survey, over 58% of the dolphin schools were only detected acoustically (Fig. 10, Table 1). However, the complex vocal behavior of dolphins has made species identification challenging. Nonetheless, recent improvements in the acoustic classification of dolphin whistles permitted

Table 1. Mean acoustic detection distances for single-species groups of dolphins, minke whales *Balaenoptera acutorostrata* and sperm whales *Physeter macrocephalus* for Southwest Fisheries Science Center research cruises years 2000–2007, inclusive

Taxon	Detection distance (nautical miles) Sample size	Mean	SD	Range
Lissodelphis borealis	5	0.58	0.67	0.1–1.5
Lagenorhynchus obliquidens	4	0.71	0.87	0.1–2
Orcinus orca	19	0.73	0.71	0.1–2.3
Grampus griseus	24	0.95	0.7	0.026–2.3
Lagenorhynchus obscurus	3	0.98	1.32	0.01–2.5
Feresa attenuata	2	1.00	1.05	0.26–1.75
Berardius bairdii	2	1.10	0.84	0.5–1.7
Steno bredanensis	28	1.53	1.19	0.01–4.5
Tursiops truncatus	53	1.79	1.33	0.08–6
Stenella attenuata	71	1.85	1.53	0.01–6
Lagenodelphis hosei	1	2.00	–	–
Delphinus spp.	112	2.22	1.6	0.1–6
Globicephala spp.	48	2.56	1.77	0.1–8.5
Stenella longirostris	35	2.61	1.55	0.1–6
Stenella coeruleoalba	136	2.63	1.84	0.1–10
Pseudorca crassidens	14	2.93	1.52	1–6
Balaenoptera acutorostrata	55	3.90	1.7	0.5–8
Physeter macrocephalus	231	5.90	4.2	0.7–21

the acoustic detection and localization of false killer whales *Pseudorca crassidens* during a recent survey dedicated to this species (Barlow & Rankin 2007, Oswald et al. 2007b). Future improvements in acoustic species classification will allow for continued integration of towed hydrophone arrays in shipboard surveys.

Not all species are difficult to identify based on their vocalizations. Because sperm whale vocalizations are easily identifiable and accurate group size estimates can also be obtained under most conditions, the use of towed hydrophone arrays has improved the estimation of total abundance for this species (Barlow & Taylor 2005). For species that are difficult to detect using traditional visual observation methods (such as minke whales), passive acoustics may be the only reasonable approach for population estimation (Rankin & Barlow 2005, Rankin et al. 2007b). Overall, the use of towed hydrophone arrays combined with visual observations has generated a large number of descriptions of vocalizations of various species which otherwise would not have been possible (Oswald et al. 2007a, Rankin et al. 2007a).

OUTLOOK

Passive acoustic technologies have been revolutionized during the last decade, in terms of both hardware and software. Archival and real-time passive acoustic arrays are now among the lowest cost approaches for mesoscale monitoring of marine areas and can be used to monitor vocal marine life in areas difficult to survey by traditional visual methods. Fixed autonomous passive acoustic arrays sample continuously for prolonged periods of time, allowing assessment of seasonal changes in distribution and acoustic behavior of individuals without introducing into the environment the types of disturbances generated by the presence of survey vessels or aircrafts. Unlike more traditional visual methods, passive acoustic technologies can survey in darkness and remain active during adverse weather conditions. Further, the ability to retrieve and redeploy archival ARUs provides a level of flexibility in data acquisition that is not available with other fixed long-term monitoring systems. Units can be deployed for short periods (days to weeks) or longer periods (months to years) with variable sampling rates. Real-time acoustic buoys, capable of relaying information almost instantaneously to a wide range of stakeholders, have recently shown their potential for enabling responsive management and mitigation of marine animals at the mesoscale level. Although these techniques have primarily been used with cetaceans, the potential now exists for studying many other marine animals such as pinnipeds, sirenians and fishes. However, there are still major hardware and software hurdles to overcome. Similarly, acoustic information can easily be misleading and interpreted incorrectly. PAM is only really useful when taken in the context of the acoustic behavioral ecology of the animals and applied in a regional and seasonally appropriate context. In order to improve PAM, more information is needed on individual, group, population and species sound level usage.

Acknowledgements. We thank B. Southall, D. Nowacek and H. Browman for the insight and innovation which made this theme section on passive acoustics possible. An immense number of people contributed to making the case studies in this manuscript happen. However, the hardware and software that were predominately used in these case studies was developed at the Bioacoustics Research Program at Cornell University, without which passive acoustics would not be what it is today. The hardware and software for the towed array studies are the result of a collaborative effort between J. Barlow, J. Oswald, D. K. Mellinger and S. Rankin. Funding for these case studies was received from Abrolhos National Marine Park, Animal Behavior Society, Brazilian Government (CAPES PhD Fellowship to R.S.S.L.), Brazilian Navy, Canon National Parks Science Scholars Program, Cornell University Lab of Ornithology, European Union Marie Curie Postdoctoral, Instituto Baleia Jubarte, Petróleo Brasileiro S.A. (PETROBRAS), Massachusetts Department of Marine Fisheries, NOAA National Marine Fisheries Service (NEFSC & SEFSC), Norwegian National Research Council, Norwegian Polar Institute, Ny- Alesund Large Scale Facility for Arctic Environmental Research and University Studies on Svalbard, US Navy and Alfred Wegener Institute for Polar and Marine Research. We also thank the 3 reviewers who struggled through a much rougher version of this manuscript and who we hope will find the end result a significant improvement as a result of their input.

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Submitted: June 3, 2008; Accepted: May 21, 2009

Proofs received from author(s): July 28, 2009

Publication III

Acoustic ecology of Antarctic pinnipeds

Vol. 414: 267–291, 2010
doi: 10.3354/meps08683

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 13

Acoustic ecology of Antarctic pinnipeds

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ABSTRACT: In aquatic-mating pinnipeds, acoustic communication plays an important role in male competition and mate attraction. Vocal repertoire size and composition during the breeding season varies between species and is presumed to be a product of interspecific differences in sexual selection. In this study, we examine seasonal and diel patterns in acoustic repertoire size, composition and call activity of 4 Antarctic pinniped species: Weddell seal *Leptonychotes weddellii*, leopard seal *Hydrurga leptonyx*, Ross seal *Ommatophoca rossii* and crabeater seal *Lobodon carcinophaga*. An 11 mo (Jan 2006 – Jan 2007, no recordings Jul and Nov 2006) near-continuous dataset was collected from the Perennial Acoustic Observatory in the Antarctic Ocean (PALAOA) located on the Ekström Iceshelf. The Weddell seal vocal repertoire consisted of 14 call types. Calls were present throughout the year except in February (11 mo), while repertoire composition varied considerably between months. The leopard seal vocal repertoire consisted of 7 call types. Calls were present between October and January (4 mo). All call types were used in a uniform manner throughout the entire call period. The Ross seal vocal repertoire consisted of 5 call types. Ross seal vocalizations were present from December until February (3 mo). Repertoire composition varied little between months. Crabeater seals produced one vocalization type, present from August to December (5 mo). Vocalizations in these species are likely produced in a breeding context. Inter-specific differences in behavioral ecology and interactions with abiotic and biotic environmental factors shape vocal behavior resulting in each species filling its own acoustic ecological niche.

KEY WORDS: Weddell seal · *Leptonychotes weddellii* · Leopard seal · *Hydrurga leptonyx* · Ross seal · *Ommatophoca rossii* · Crabeater seal · *Lobodon carcinophaga* · Vocal repertoire · Vocal activity · Aquatic mating · Acoustic ecology

INTRODUCTION

In many species acoustic communication plays an important role during the breeding season and serves a function in male–male competition and/or mate attraction (e.g. Ryan 1988, Heller & Von Helversen 2004, Catchpole & Slater 2008). Vocal repertoire size during the breeding season varies considerably between species and is presumed to be primarily a product of interspecific differences in factors that drive sexual selection (e.g. Searcy & Andersson 1986, Read & Weary 1992). In some species, the occurrence and composition of the vocal repertoire varies over the course of a breeding season, reflecting different stages in the breeding cycle (e.g. Emerson 1992, Roy et al. 1995, Slabbekoorn 2004). For example, female Bornean frog *Rana blythi* mating vocalizations occur exclusively when females have mature eggs and are involved in courtship (Emerson 1992, Roy et al. 1995). Several species of birds possess 2 acoustically distinct categories of song type that are specialized for use in intersexual and intrasexual communication (e.g. Staicer et al. 1996, Trillo & Vehrencamp 2005). In banded wrens *Thryothorus pleurostictus* songs produced by males during the dawn chorus play a role in aggressive male–male interactions, whereas songs

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used during the rest of the day differ in type and structure from the songs produced during the dawn chorus and presumably function solely to advertise the presence and location of a male to a mate (Trillo & Vehrencamp 2005).

In pinnipeds, the role of vocal behavior during the breeding season differs between land-breeding and aquatic-mating species. On land, the relative rarity of areas suitable for pupping and haul-out leads to the formation of dense female breeding aggregations, which enables males to defend harems and compete with other males for a place within the female breeding group (e.g. Bartholomew 1970). All land-breeding pinnipeds produce in-air vocalizations for the purpose of mother–pup recognition and male–male competition (e.g. Fernández-Juricic et al. 1999, Insley et al. 2003, Tripovich et al. 2008).

In aquatic-mating pinnipeds, females are much more dispersed during the breeding season, causing female movements to be both spatially and temporally less predictable (Van Parijs 2003). As a consequence, females can be less efficiently monopolized by males and therefore males must aim to attract females for the purpose of mating (e.g. Stirling & Thomas 2003, Harcourt et al. 2007). For those species of aquatic-mating pinnipeds where data are available, males are known to retain under water display areas using vocal and dive displays which are thought to function in male–male competition and/or male advertisement to females (see Van Parijs 2003 for a review). In some species, such as harp *Pagophilus groenlandicus*, Weddell *Leptonychotes weddellii* and ringed seals *Phoca hispida*, females are also known to produce underwater vocalizations (e.g. Kunnasranta et al. 1996, Serrano 2001, Oetelaar et al. 2003). However, in most aquatic-mating pinniped species only males produce vocalizations associated with mating behavior (see Van Opzeeland et al. 2008 for a review).

The underwater vocal repertoire of aquatic-mating pinnipeds has been described for the majority of species and varies considerably in size between species (Stirling & Thomas 2003). In a comparative review, Rogers (2003) examined the role of various behavioral and ecological factors on the size of the acoustic repertoire in aquatic-mating seals. Several factors such as the degree of sexual size dimorphism, stability of the pupping substrate, breeding colony density and the degree to which female distribution is predictable to males were shown to influence the size of the vocal repertoire. Based on the acoustic characteristics of the calls, the repertoire size and the function of vocal behavior, Rogers (2003) discriminates 3 groups of vocalization strategies in aquatic-mating seals. (1) The first group comprises hooded *Cystophora cristata*, grey *Halichoerus grypus* and crabeater seals *Lobodon carcinophaga*. The repertoire of these species is small and consists of short and broadband calls that are thought to be produced by males and have a function in agonistic interaction between males over relatively short distances. (2) Bearded *Erignathus barbatus*, ribbon *Histriophoca fasciata*, leopard *Hydrurga leptonyx* and Ross seals *Ommatophoca rossii* use stereotyped narrowband calls which are thought to function as signals to rival males and/or potential mates over long distances. These species have a moderately sized vocal repertoire. (3) The third group, consisting of harp, harbour *Phoca vitulina*, Weddell and ringed seals, has the largest vocal repertoire of the 3 groups, consisting of varied types of sounds that are thought to function in short-range mate attraction and/or territory defense.

As underwater acoustic behavior is in most cases assumed to have a dual function (i.e. male–male competition and mate attraction; e.g. Van Parijs 2003), the proportional usage of different call types could be expected to vary on a seasonal or daily scale reflecting different social contexts in which vocalizations are used. In addition, annual recordings can provide unique insights into how calling behavior is related to other behavioral and ecological variables. Van Parijs et al. (2004) showed that between-year fluctuations in ice cover affect 'territorial' and 'roaming' male bearded seals differently. Roaming males were not heard in years with increased ice cover, whereas territorial males were present during all ice conditions. In harp seals, vocalizations differ structurally during different parts of the year, suggesting that vocal behavior also plays an important role outside the breeding season, such as during herd migration (Serrano & Miller 2000). Nevertheless, as many aquatic-mating pinnipeds are ice-breeding species and occur at high latitudes, acoustic measurements are often only possible during restricted time periods (e.g. Thomas & DeMaster 1982, Cleator et al. 1989). In addition, studies on polar species that include recordings over multiple years are rare because of the logistic difficulties and costs of obtaining repeated recordings.

The PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA) is a stationary listening station at 70° 31′ S, 8° 13′ W (Fig. 1), on the Eckström Iceshelf near the eastern Weddell Sea coast. The PALAOA station is autonomous and allows continuous long-term acquisition of acoustic data. Recordings contain vocalizations of 4 Antarctic pinniped species: Weddell, leopard, Ross and crabeater seals. All 4 species differ substantially in their foraging and behavioral ecology as well as the ice type used for breeding and haul-out. Ecological differences between species as well as interspecific interactions might be reflected in acoustic behavior. Information on the presence of a certain species, mediated through their calls, might for example

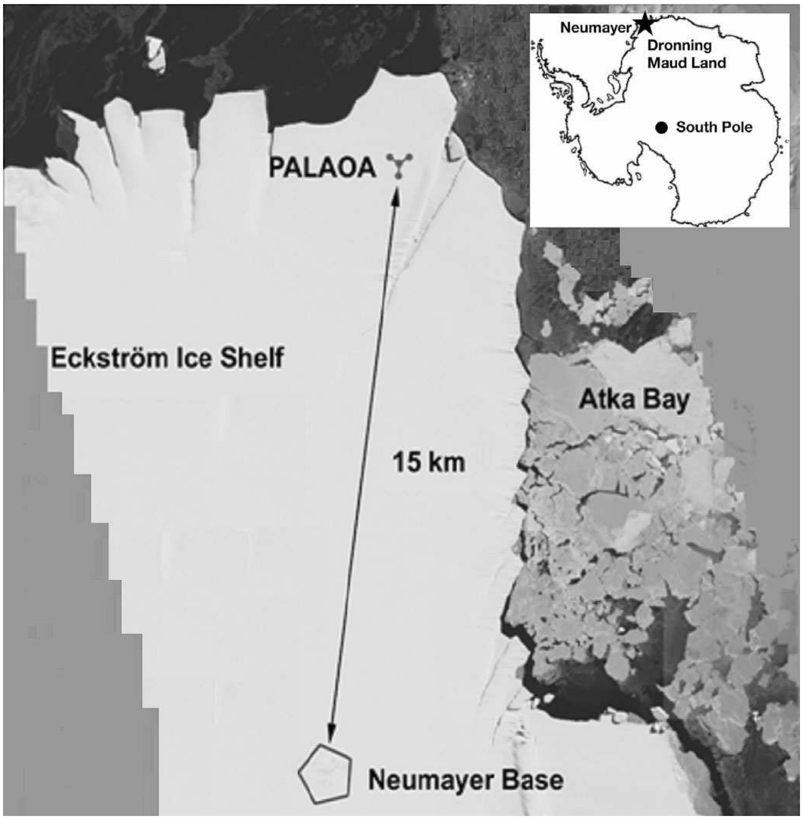

Fig. 1. IKONOS-2 satellite image from March 2004, showing the locations of the German Antarctic station Neumayer Base II and the PALAOA hydroacoustic observatory (70°31'S, 8°13'W). Inset image top right: Antarctica with the location of Neumayer Base II (★)

be used by and affect behavior of other seal species, e.g. in the case of a predator–prey relationship such as between leopard and crabeater seals.

As acoustic data are collected continuously, the PALAOA data offer the unique opportunity to investigate the calling behavior of these species to explore how acoustic behavior relates to breeding behavior, ecological variables and inter-specific interactions. Improving our knowledge on the fundamental ecology of Antarctic ice-breeding pinnipeds is vital as recent studies have shown that the climate driven changes and anthropogenic alteration of food webs are likely to affect these species (e.g. Learmonth et al. 2006, Cotté & Guinet 2007, Murphy et al. 2007). Long term acoustic datasets, such as the PALAOA database, require the use of automated detection and classification techniques as manual analysis becomes too time-consuming. However, elementary knowledge of the species-specific vocal repertoire and temporal patterns of call type usage is a fundamental requirement needed in order to build a comprehensive understanding of the acoustic behavioral ecology of the species in this area. This study provides a baseline description of the acoustic repertoire of all 4 ice-breeding Antarctic pinniped species — Weddell, Ross, leopard and crabeater seals — using an 11 mo data set obtained from the autonomous PALAOA station. Seasonal and diel patterns in the acoustic repertoire are examined from the perspective of multi-species call type variability on a monthly basis.

METHODS

Acoustic data. Underwater acoustic recordings were obtained from the autonomous PALAOA station. Recordings are made continuously year-round with 2 hydrophones deployed underneath the 100 m thick floating Antarctic ice shelf through boreholes spaced 300 m apart (Boebel et al. 2006, Klinck 2008). Water depth below the floating ice shelf is approximately 160 m. Both hydrophones are at a depth of 80 m below the floating ice shelf. The setup consists of a RESON TC4032 hydrophone (5 Hz to 120 kHz, sens. –170 dB re 1 V μPa^{-1}) connected to a RESON VP2000 amplifier (30 dB gain) and bandpass filter (10 Hz to 100 kHz), and a RESON TC4033 hydrophone (1 Hz to 160 kHz, sens. –203 dB re 1 V μPa^{-1}) connected to 2 RESON VP2000 amplifiers and bandpass filters. Both hydrophones are galvanically isolated through a Behringer HD400 isolation transformer to avoid picking up electromagnetic interference. The signals are digitized at 48 kHz/16 bit and encoded to a 192 kbit s^{-1} MP3 stream by a BARIX Instreamer device. The effective bandwidth of the recordings is 10 Hz to 15 kHz, dynamic range 60 dB to 150 dB re 1 μPa. This stream is transmitted from PALAOA to the German Antarctic Neumayer Station II (15 km) through wireless LAN. At Neumayer Station II, the stream is segmented into MP3 files of 1 min duration and saved locally. In addition, the audio is compressed to a 24 kbit s^{-1} OGG-Vorbis stream and transmitted in near-real time from Neumayer to Bremerhaven (Germany) via a 128 kbit s^{-1} satellite link, from where it is made publicly accessible (www.awi.de/acoustics; see also Kindermann et al. 2008). For this study only the MP3 data were used.

Weddell, Ross, leopard and crabeater seals are known to be present in this region. Every year Weddell seals form breeding groups in austral spring on the fast-ice in Atka Bay, near the PALAOA station (Plötz

1986). Crabeater seals have also been observed on the pack-ice bordering the ice shelf near PALAOA in austral summer (J. Plötz pers. obs.). Leopard seals and Ross seals have not been observed on the ice in the area near the observatory, but are known to occur in this part of the Weddell Sea (Erickson et al. 1983, Bester & Odendaal 2000).

Sampling regime. For this study we used data recorded between 4 January 2006 and 30 January 2007 (no recordings for July and November 2006), a total of 11 mo. No data were collected in July due to energy shortages at the PALAOA station. In November 2006 data collection was not possible due to temporary technical failure of the observatory. Within this period, data were sampled for analysis on every fifth day to provide a standardized sample across the year. For every fifth day, 10 consecutive minutes of each hour were analysed with the aim of obtaining a relatively balanced data set for monthly and seasonal comparisons across the year. In cases where it was not possible to sample the fifth day, the preceding day was analyzed instead.

Data were examined in 1 min sound files both aurally and visually using the spectrograms produced by Adobe Audition 2.0. Calls were counted and type-identified per species by using the overall spectrogram call shape. Catalogues of call types were constructed for each species based on previous studies (Weddell seal: Thomas & Kuechle 1982, Pahl et al. 1997; leopard seal: Rogers et al. 1995, 1996; Ross seal: Watkins & Ray 1985, Stacey 2006, Seibert 2007; crabeater seal: Stirling & Siniff 1979). Calls that were not identifiable from the call type catalogues, but were present twice or more, were assigned a new call type name and added to the call type catalogue. All call types produced by each of the 4 pinniped species differ considerably between species in structure and form. New call types could be attributed to one of the 4 species with certainty based on their overall call shape and were cross-validated by a second observer.

Data presentation. The number of calls counted per call type for the entire 11 mo data set is presented as a table for each species. The table shows the total number of calls that were counted per call type per month and the proportion of the overall vocal repertoire for each call type. Spectrograms and sound files of all call types described here are presented in Supplements 1 & 2, available at www.int-res.com/articles/suppl/m414p267_supp/.

Species-specific proportional call type usage per month was calculated only for those months in which at least 100 calls of this species were counted. This approach focused the analyses on months with peak calling activity. Calculating proportional call type usage allowed comparison of the vocal repertoire composition between months, independent of the number of samples analysed per month.

Seasonal patterns in overall call activity were obtained by summing all call types and calculating the average number of calls per minute for each day that was sampled.

Diel patterns in call type usage were calculated for each month by averaging the number of calls per call type counted per minute from the 10-min samples for each hour of the day. Calls were assigned to 1-h time windows of the hour in which they occurred (i.e. calls that occurred between 18:00 and 18:59 h were assigned to 18:00 h). Average diel call type-specific call rates were plotted only for months in which at least 100 calls of the species were counted. The local time at PALAOA is Coordinated Universal Time (UTC) – 33 min. In this study, time is therefore presented in UTC.

Statistical analyses. For all 4 species, changes in acoustic behavior were explored in relation to timing of pupping, mating and moult (phase in breeding cycle). Information on the timing of each of these phases was obtained from the literature (Weddell seal: Lugg 1966, Kaufman et al. 1975, Reijnders et al. 1990; leopard seal: Riedman 1990, Rogers et al. 1996, Southwell et al. 2003; Ross seal: King 1969, Thomas 2002, Southwell et al. 2003; crabeater seal: Siniff et al. 1979, Bengtson 2002, Southwell et al. 2003). Changes in the proportions of call type usage over weeks in relation to the different phases were explored using correspondence analysis (Greenacre 1984) in R version 2.9.2 (R Foundation for Statistical Computing, Vienna, www.R-project.org). Generally, correspondence analysis explores correspondence between the rows and columns of simple 2-way and multi-way tables (Greenacre 1984). For Weddell seals, a correspondence analysis was also performed to compare diel patterns in call type usage between months. For leopard, Ross and crabeater seals the periods during which they were vocally active were too short to compare diel patterns in acoustic behavior between months. See Supplement 3 for the full data set and R code for the correspondence analyses.

RESULTS

A total of 10730 min of PALAOA recordings composed of 1073 10-min samples over 11 mo were analyzed. The number of minutes sampled per month ranged between 310 and 1440 min due to gaps in the otherwise near-continuous data stream (Table 1). However, for all months, more than 300 1-min samples were analysed (average 975 1-min samples per month) and still allowed a balanced comparison of the vocal repertoire composition between months.

Table 1. *Leptonychotes weddellii*. Total number of Weddell seal calls per call type (W1–W14 with phonetic description) counted per month between January 2006 and January 2007. n = number of 1-min samples obtained

Call type	Description	Jan 06 (n = 1020)	Feb 06 (n = 340)	Mar 06 (n = 1360)	Apr 06 (n = 1050)	May 06 (n = 1240)	Jun 06 (n = 310)	Aug 06 (n = 350)	Sep 06 (n = 840)	Oct 06 (n = 1340)	Dec 06 (n = 1440)	Jan 07 (n = 1440)	Total (n = 10730)	Proportion of all calls (%)
W1	Trill	3	0	3	146	1500	608	574	1329	2042	1949	12	8166	20
W2	Falling chirps long	4	0	2	171	888	397	463	909	1321	1054	30	5239	13
W3	Falling chirps short	1	0	5	88	437	133	148	302	395	122	11	1642	4
W4	High-high-low sequence	0	0	0	56	287	72	54	183	113	2	3	770	2
W5	Single chirp high	1	0	0	176	1356	373	519	999	1062	614	6	5133	12
W6	Single chirp low	0	0	0	84	899	417	417	927	1561	1205	4	5514	13
W7	Chirp sequence	0	0	0	30	528	169	82	223	214	48	6	1300	3
W8	Oomp	0	0	0	0	43	162	751	1480	1765	658	0	5247	13
W9	Falling tone	0	0	0	80	516	110	152	182	273	36	13	1362	3
W10	Falling tone short	0	0	2	43	396	104	27	386	580	331	0	2059	5
W11	Rising tone	0	0	0	16	51	24	18	60	85	11	2	267	1
W12	Flat tone	0	0	0	9	41	25	11	11	22	19	0	138	0.3
W13	Warble	0	0	0	115	974	500	515	620	931	614	1	4270	10
W14	Pulse sequence	0	0	0	0	77	14	11	36	36	109	0	314	1
All calls		9	0	12	1014	8381	3108	3932	7647	10431	6799	88	41421	100

Overall call activity

Weddell seal call activity increased gradually from March to June showing a peak on 1 June 2006 (15 calls min^{-1}, Fig. 2). Over all days on which Weddell seal vocalizations were present and data was available, the average call rate was 5 ± 4.27 calls min^{-1} (mean ± average deviation) per minute. Leopard seal call activity showed a peak on 16 December 2006 (9 calls min^{-1}) and decreased again towards January 2007. The average call activity over all days that leopard seal calls were present is 3 ± 3.13 calls min^{-1}. Ross seal call activity increased sharply within the first part of January in both years to a peak on 10 January 2007 (35 calls min^{-1}). Average call activity over all days that Ross seal calls were present over January 2006, December 2006 and January 2007 was 11 ± 8.36 calls min^{-1}. Crabeater call activity showed a peak on 18 October 2006 (4 calls min^{-1}) and averaged 1 ± 1.00 calls min^{-1} over all days that crabeater vocalizations were present from August to December 2006. Data from November 2007 from Klinck et al. (2010) show that crabeater call activity is highest during the first half of November, with a peak of 6.5 calls min^{-1} on 4 November 2007.

Peaks in Weddell, leopard and Ross call activity showed a typical sequential pattern; decreased Weddell seal vocal activity was followed by an increase in leopard seal vocal activity and decreased leopard seal vocal activity was followed by an increase in Ross seal vocal activity. While the sequential pattern seemed present in both January 2006 and 2007, Weddell, leopard and Ross seal call activity was higher in January 2007, compared to call activity in January 2006.

Overall call repertoire

Weddell seals

For the Weddell seal a total of 41 421 calls was counted over the study period. The vocal repertoire consisted of 14 different call types (Fig. S1 in Supplement 1, Table 1). Over the study period, 6 call types (W1, W2, W5, W6, W8, W13) each contributed more than 10% to the total number of Weddell seal calls, while the other 8 call types (W3, W4, W7, W9, W10, W11, W12, W14) occurred less frequently, ranging between 0.3 to 5% of the total number of calls. Call type W4 has not been described previously, whereas the other call types have been described in numerous previous studies (Thomas & Kuechle 1982, Pahl et al. 1997, Moors & Terhune 2004, Terhune & Dell'Apa 2006). Call type W4 was associated with Weddell seals based on its acoustic similarity to call type W2 and W3 and similar pattern of occurrence.

Leopard seals

A total of 13 687 calls was counted for leopard seals. The leopard seal vocal repertoire consisted of 7 different call types (Fig. S2 in Supplement 1, Table 2). Call type L6 contributed more than 60% to the total number of calls. The other call types occurred less frequently, ranging between 3 and 10% of the total number of calls. All leopard seal call types recorded by PALAOA have been described previously (Stirling & Siniff 1979, Rogers et al. 1995, 1996). Stirling & Siniff (1979) and

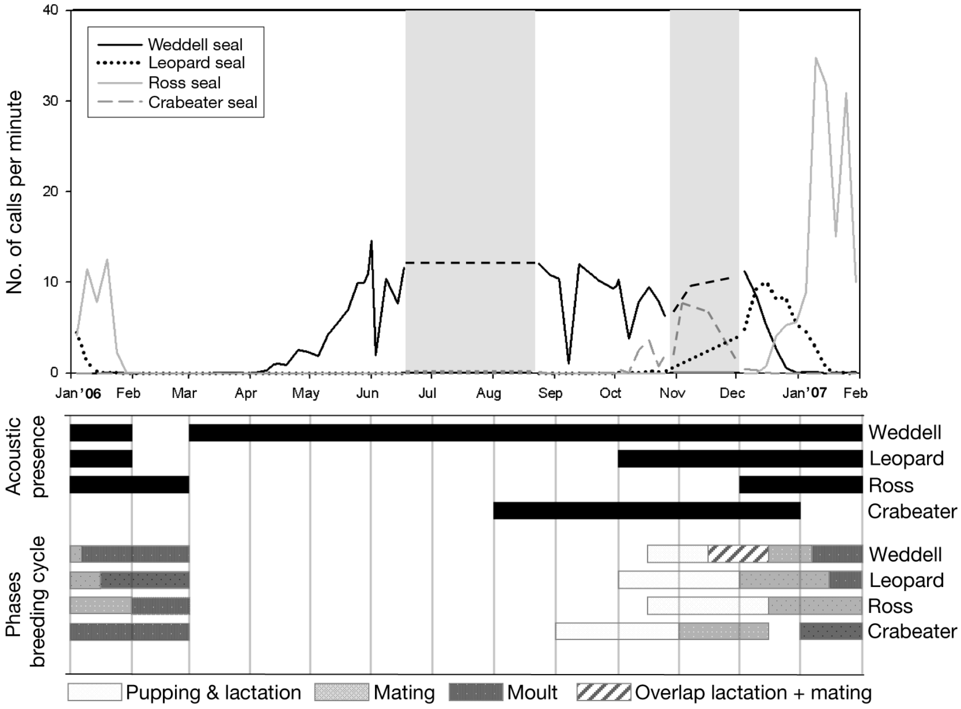

Fig. 2. Overall call activity for all 4 seal species in the period January 2006 to February 2007. The average number of calls per minute is calculated per day for all days that were included in the analyses. Call activity in the grey shaded areas represents counts of 1-min PALAOA samples from 2007 as recordings from these months were not available from 2006 (every fifth day, 2 min each sixth hour). For crabeater seals, call activity in November was based on PALAOA data from 2007 from Klinck et al. (2010). The lower schema shows acoustic presence for all 4 seal species and the timing of the pupping, mating and moulting periods for Weddell, leopard, Ross and crabeater seals based on literature (see 'Methods: Statistical analysis' for sources)

Rogers et al. (1996) discriminate 2 subtypes within call type L7: the 'mid double trill' and the 'mid single trill'. In this study all mid trills were lumped into call type L7. Both mid trill types are shown in Fig. S2.

Ross seals

A total of 42 231 calls was counted for Ross seals. The vocal repertoire consisted of 5 call types (Fig. S3 in Supplement 1, Table 3). Three call types (R1, R2 and R3) each contributed more than 20% to the total number of calls. Call types R4 and R5 occurred often in association; R4 is a tonal call, while R5 is a broadband sound (Fig. S3). These 2 call types occurred less frequently compared to the other call types, each contributing 6% to the total number of calls. Ross seal call types R1, R2, R3 and R5 have been described previously (Watkins & Schevill 1968, Stacey 2006, Gedamke & Robinson 2010). So far call type R4 has only been found present in the PALAOA recordings (Seibert 2007).

Crabeater seals

A total of 2126 crabeater seal moans were counted over the study period. For crabeater seals, we identified one call type in the PALAOA recordings, the moan vocalization (C1). The moan vocalization has been described in previous studies (Stirling & Siniff 1979, Thomas & DeMaster 1982). Klinck et al. (2010) identified another variety of this crabeater seal call type, the high moan. Both varieties of crabeater moans are depicted in Supplement 1, Fig. S4. However, in this study we did not discriminate between high and low moans and lumped all crabeater vocalizations into call type C1.

Monthly proportional call type usage

Weddell seals

Weddell seal calls were present in all months of 2006 for which data were available, except February (Fig. 2). Preliminary inspection of data from the following year (2007) showed that all call types were also present in July and November, the months for which no data were available in 2006. For the remaining months in 2006, the composition of the Weddell seal vocal repertoire varied and not all call types occurred in all months (Table 1). Call types W1, W2 and W3 were present in January 2006 and from March 2006 to January 2007. Call types W4, W5, W6, W7, W9, W11 and W13 occurred from April 2006 to January 2007, although W5 also occurred once in January 2006. Call type W12 was present from April to December. Call type W10 was present from March to December, whereas call types W8 and W14 occurred only between May and December.

Table 2. *Hydrurga leptonyx*. Total number of leopard seal calls per call type (L1–L7) counted per month between January 2006 and January 2007. n = number of 1-min samples obtained

Call type	Description	Jan 06 (n = 1020)	Feb 06 (n = 340)	Mar 06 (n = 1360)	Apr 06 (n = 1050)	May 06 (n = 1240)	Jun 06 (n = 310)	Aug 06 (n = 350)	Sep 06 (n = 840)	Oct 06 (n = 1340)	Dec 06 (n = 1440)	Jan 07 (n = 1440)	Total (n = 10730)	Proportion of all calls (%)
L1	Low ascending trill	27	0	0	0	0	0	0	0	1	601	54	683	5
L2	Low descending trill	38	0	0	0	0	0	0	0	3	587	84	712	5
L3	High double trill	39	0	0	0	0	0	0	0	5	1004	118	1166	9
L4	Hoot	19	0	0	0	0	0	0	0	0	360	35	414	3
L5	Hoot single trill	47	0	0	0	0	0	0	0	7	1253	129	1436	10
L6	Low double trill	425	0	0	0	0	0	0	0	64	6578	1420	8487	62
L7	Mid trill	31	0	0	0	0	0	0	0	6	692	60	789	6
All calls		626	0	0	0	0	0	0	0	86	11075	1900	13687	100

Proportional call type usage per month was calculated from April to December (Fig. 3). In April, call types W2 and W5 formed the largest part of the vocal repertoire, followed by W1 and W13. In May and June W1 was the most predominant call type, followed by W5 and W13, respectively. W8 was the most predominant call type in August and September, followed by W1 in both months. In October and December, proportional usage was highest for call type W1, followed by W8 and W6, respectively.

When the proportional composition of the repertoire was compared between months, the proportional usage of call types W1, W7, W10, W11, W12 and W14 was relatively constant from April to December. Proportional usage of call types W2 and W3 decreased towards December, although the proportional usage of call type W2 increased again to 16 % in December. Call types W4, W5 and W9 decreased in proportional usage from April to December. W13 showed a gradual decrease in proportional usage from June towards the pupping and mating period (October to December), whereas the proportional usage of W6 increased towards December. W8 showed a gradual increase in usage towards a peak in September (19 %), after which proportional usage decreased again. Furthermore, call types W4, W6, W7, W9, W11, and W13 were present in the recordings from January 2007, whereas these call types were not present in the January 2006 recordings (Table 1).

Fig. 4a shows the dissimilarity of Weddell seal repertoire composition based on a correspondence analysis of weekly call-type profiles. Call types W14 and W8 were clearly separated from the rest. The ordination in weeks (Fig. 4b) shows 3 groups of consecutive weeks (ellipses): winter (Weeks 16 to 24, W), spring (Weeks 34 to 43, Sp), and beginning of summer (S). In addition, the weekly call repertoire composition was separated through correspondence analysis according to the different phases, showing similarity in call repertoire composition between the mating phase (Ma) and the Lactation and Mating phase (LM) (Fig. 5a). Repertoire composition during the moult phase (Mo) was separated by the first discriminant axis, while Ma and LM were separated by the second discriminant axis (*y*-axis). The contribution of the call types (Fig. 5b) showed that call type W14 characterized the Ma and LM period, whereas Mo was characterized by an increased usage of W11 and reduction in usage of call type W12.

Table 3. *Ommatophoca rossi*. Total number of Ross seal calls per call type (R1–R5) counted per month between January 2006 and January 2007. n = number of 1-min samples obtained

Call type	Description	Jan 06 (n = 1020)	Feb 06 (n = 340)	Mar 06 (n = 1360)	Apr 06 (n = 1050)	May 06 (n = 1240)	Jun 06 (n = 310)	Aug 06 (n = 350)	Sep 06 (n = 840)	Oct 06 (n = 1340)	Dec 06 (n = 1440)	Jan 07 (n = 1440)	Total (n = 10730)	Proportion of all calls (%)
R1	High siren call	2149	7	0	0	0	0	0	0	0	564	9001	11721	28
R2	Mid siren call	1539	0	0	0	0	0	0	0	0	833	6477	8849	21
R3	Low siren call	2060	0	0	0	0	0	0	0	0	2259	12479	16798	40
R4	Tonal element	634	0	0	0	0	0	0	0	0	25	1692	2351	6
R5	Broadband element	520	0	0	0	0	0	0	0	0	73	1919	2512	6
All calls		6902	7	0	0	0	0	0	0	0	3754	31568	42231	100

Leopard seals

Leopard seal calls occur between October and January (Table 2). Preliminary inspection of PALAOA data from the following year showed that all leopard seal call types were present in November 2007, which was the month for which no data were available in 2006.

Call types L1, L2, L3, L5, L6 and L7 occurred from October to January, whereas L4 occurred in January and December, but did not occur in October. Proportional call type usage per month was calculated for January 2006, December 2006 and January 2007 (Fig. 6). Call type L6 was the most predominant call type in all 3 months. The proportional composition of the repertoire was relatively similar between December and January and did not differ largely between January 2006 and January 2007.

The correspondence analysis showed that leopard seal call repertoire composition differed between the pupping and lactation phase (PL) and moult phase (Mo) and were separated on the second discriminant axis (*y*-axis, Fig. S5a in Supplement 4). PL and Mo were characterized by a decrease in usage of call type L2 and L4, respectively (Fig. S5b).

Ross seals

Ross seal calls occurred between December and February (Table 3). The first Ross seal calls were recorded on December 16, 2006. Preliminary inspection of PALAOA data from the following year showed that no Ross seal calls were present in November 2007 (Seibert 2007), suggesting that Ross seal vocal activity

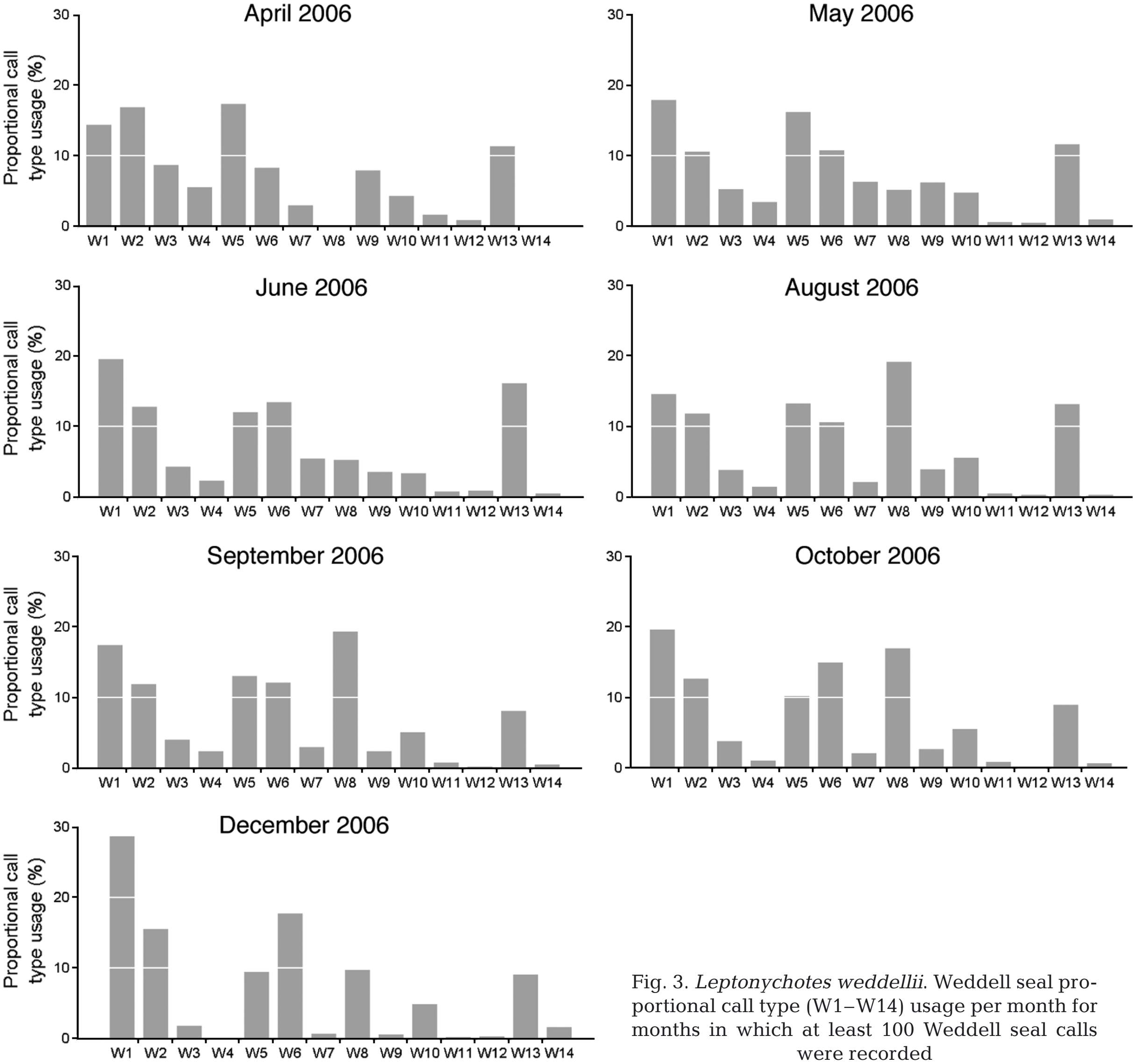

Fig. 3. *Leptonychotes weddellii*. Weddell seal proportional call type (W1–W14) usage per month for months in which at least 100 Weddell seal calls were recorded

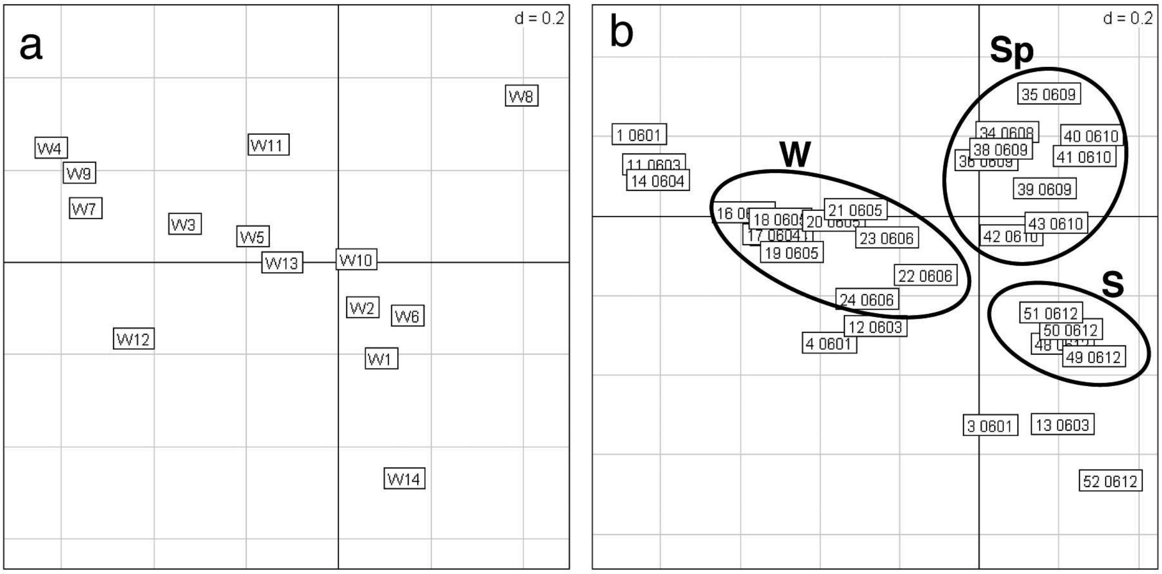

Fig. 4. 2D-Correspondence analysis call-type counts per week for Weddell seals. (a) Mapping of call-types, showing W8 and W14 as distinct from the rest. (b) Ordination of the weeks (format WW YYMM). Clusters of consecutive weeks are visualized by ellipses, corresponding to the seasons (W: winter; Sp: spring; S: summer)

starts in December. Of all call types, only R1 occurred in February. Proportional call type usage per month was calculated for January 2006, December 2006 and January 2007 (Fig. 7). Call type R1 was the most predominant call type in January 2006, followed by call type R3. In December 2006 and January 2007, call type R3 had the highest proportional usage, followed by R2 and R1, respectively. Call types R4 and R5 occurred in similar, relatively small proportions (<10%) and were used most often in January. All call types showed a similar pattern in proportional usage in January 2006 and 2007, although call type R3 formed a larger part of the vocal repertoire in January 2007 compared to January 2006.

Ross seal calls were only recorded during the mating phase and therefore discrimination of call repertoire composition according to phase was not possible. The correspondence analysis showed that call repertoire composition varied little over the period that Ross seal calls were recorded (Fig. S6a in Supplement 4). The structure of call type usage showed that the first week during which Ross seal calls were recorded was characterized by increased usage of call type R3 (Fig. S6b).

Crabeater seals

Crabeater seal C1 calls were present between August and December 2006 (Fig. 2). Data from the following year showed that crabeater calls were also present and that call activity actually peaked in No-

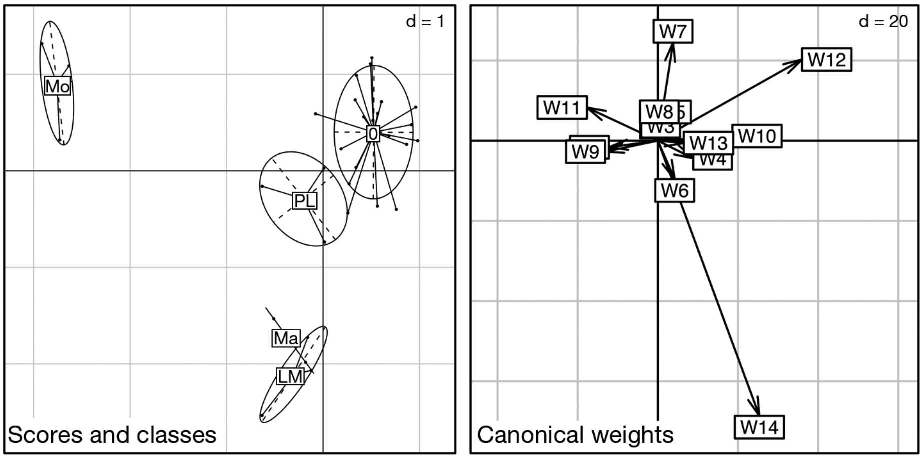

Fig. 5. Discriminating correspondence analysis of Weddell seal call-type profiles by weeks. (a) Plot of first 2 discriminant scores, with groups captured in ellipses. Mo: Moult; Ma: mating; LM: overlap of lactation and mating; PL: pupping and lactation; O: other weeks. (b) Plot of structure of call types: call type W14 dominates separation on the second discriminant (*y*-axis); call type W12 dominates the separation on the first discriminant (*x*-axis)

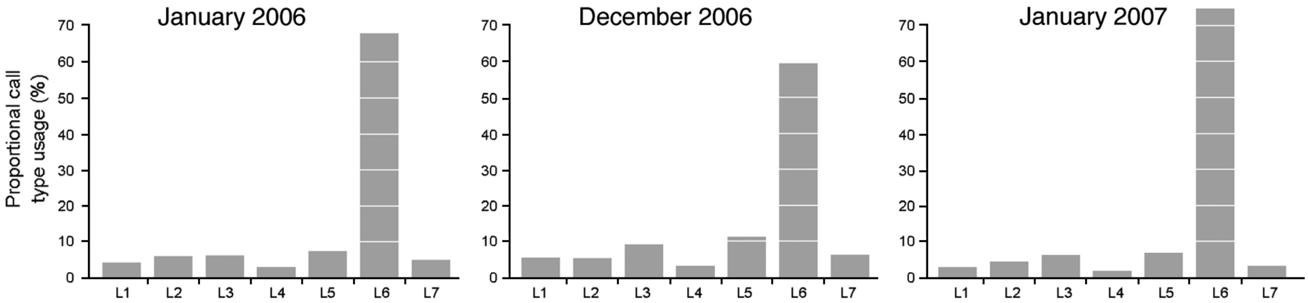

Fig. 6. *Hydrurga leptonyx.* Leopard seal proportional call type (L1–L7) usage per month for months during which at least 100 leopard seal calls were recorded

vember 2007. For 2006, the number of calls recorded by PALAOA was highest in October (Fig. 8).

Diel patterns in call type usage

Weddell seal

To determine the Weddell seal diel pattern in call type usage, only call types that contributed more than 10 % to the vocal repertoire were used (Call types W1, W2, W5, W6, W8 and W13). This approach excludes all call types that were rarely used when call type usage is compared on a diel scale. For all call types, the average number of calls per hour in April 2006 showed little variation over the day, with only a small peak occurring around 18:00 h UTC (Fig. 9a). In May, W1 was the most predominant call type. Overall the number of calls was highest around 7:00 and 16:00 h UTC, whereas there was only little calling activity between 10:00 and 14:00 h UTC. Due to a temporary energy shortage at the PALAOA station, no data were collected between 7:00 and 11:00, between 18:00 and 20:00 and between 22:00 and 23:00 h UTC in June 2006. Despite these gaps, the diel calling pattern in June resembled the 2-peak pattern in May 2006, but with call type W1 showing a sharp peak of 2 ± 0.64 calls min^{-1} (mean ± average deviation) around 16:00 h UTC. In August and September 2006 W8 was the most predominant call type, with an average of 2 ± 0.77 and 2 ± 0.45 calls $\text{min}^{-1}\ \text{h}^{-1}$ respectively. In August, the overall Weddell seal call activity showed peaks between 4:00 and 7:00 h UTC and 18:00 and 20:00 h UTC. In September the bimodal pattern in vocal activity was still visible (Fig. 9b). In October and December 2006 W1 was the most frequent call type, with an average of 2 ± 0.21 and 1 ± 0.22 calls $\text{min}^{-1}\ \text{h}^{-1}$ respectively. In these 2 months, the average number of calls $\text{min}^{-1}\ \text{h}^{-1}$ showed little variation over the day. When Weddell seal call usage patterns were compared for single days within each month, these generally reflected the average monthly pattern.

The biphasic pattern in Weddell seal diel call activity in May (Fig. 9a) can be partly resolved by a correspondence analysis. Fig. 10a shows the dissimilarity of W5, W8 and W9 from the other call types. The ordination of hours is shown in Fig. 10b and allows identification of the quiet phase between 10:00 and 12:00 h (first discriminant axis, *x*-axis). Vocal repertoire composition during the remaining time is grouped in 2 periods: morning+afternoon (upper part, 05:00 to 18:00 h) and evening+night (lower part, 19:00 to 04:00 h).

Leopard seal

Fig. 11 shows the diel calling pattern in January 2006, with 2 distinct peaks in L6 calling activity around

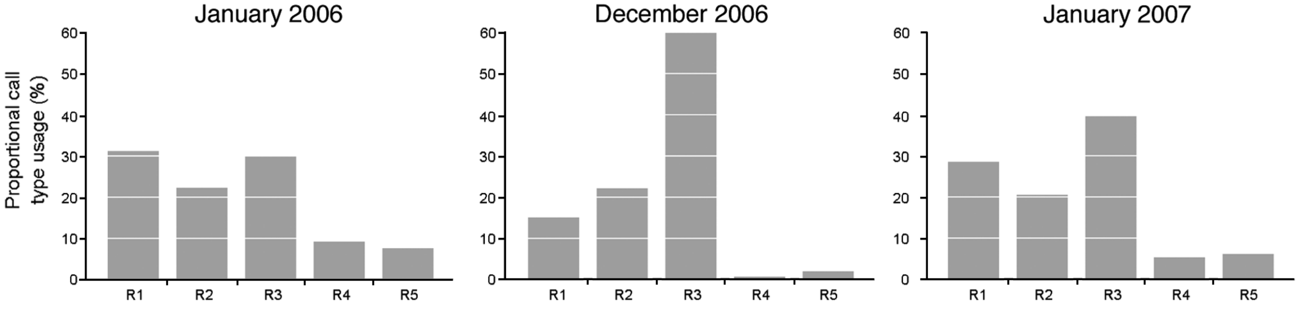

Fig. 7. *Ommatophoca rossi.* Ross seal proportional call type (R1–R5) usage per month for months in which at least 100 Ross seal calls were recorded

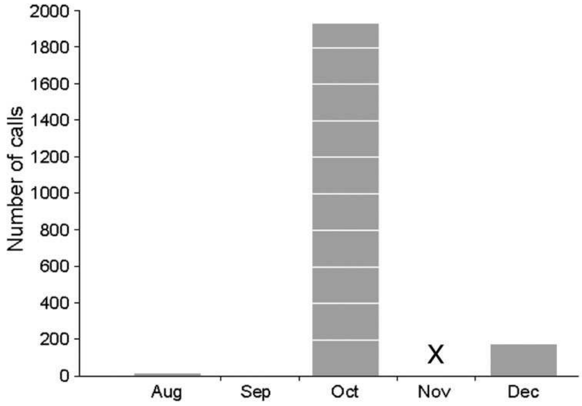

Fig. 8. *Lobodon carcinophaga.* Number of crabeater seal calls (type C1) recorded for all months in which crabeater calls were recorded, August to December 2006

8:00 (1 ± 0.98 calls min^{-1}, mean ± average deviation) and 20:00 h UTC (1 ± 1.13 calls min^{-1}). The call rates of the other call types also increased slightly during these hours, however, call rates were much lower compared to call type L6. In December, the number of L6 calls increased to 5 ± 0.33 calls min^{-1} h^{-1} and remained constant throughout the day. Call rates of the other call types also increased compared to January 2006 and 2007 and remained fairly constant throughout the day, ranging from 0.3 to 0.9 calls min^{-1} h^{-1}. The average number of L6 calls was 1 ± 0.25 calls min^{-1} h^{-1} in January 2007, and 0.4 ± 0.22 calls min^{-1} h^{-1} in January 2006. In contrast to the 2-peak pattern in call activity in January 2006, calling activity showed a 1-peak pattern in January 2007 with the peak occurring around midnight. Leopard seal call usage for single days within

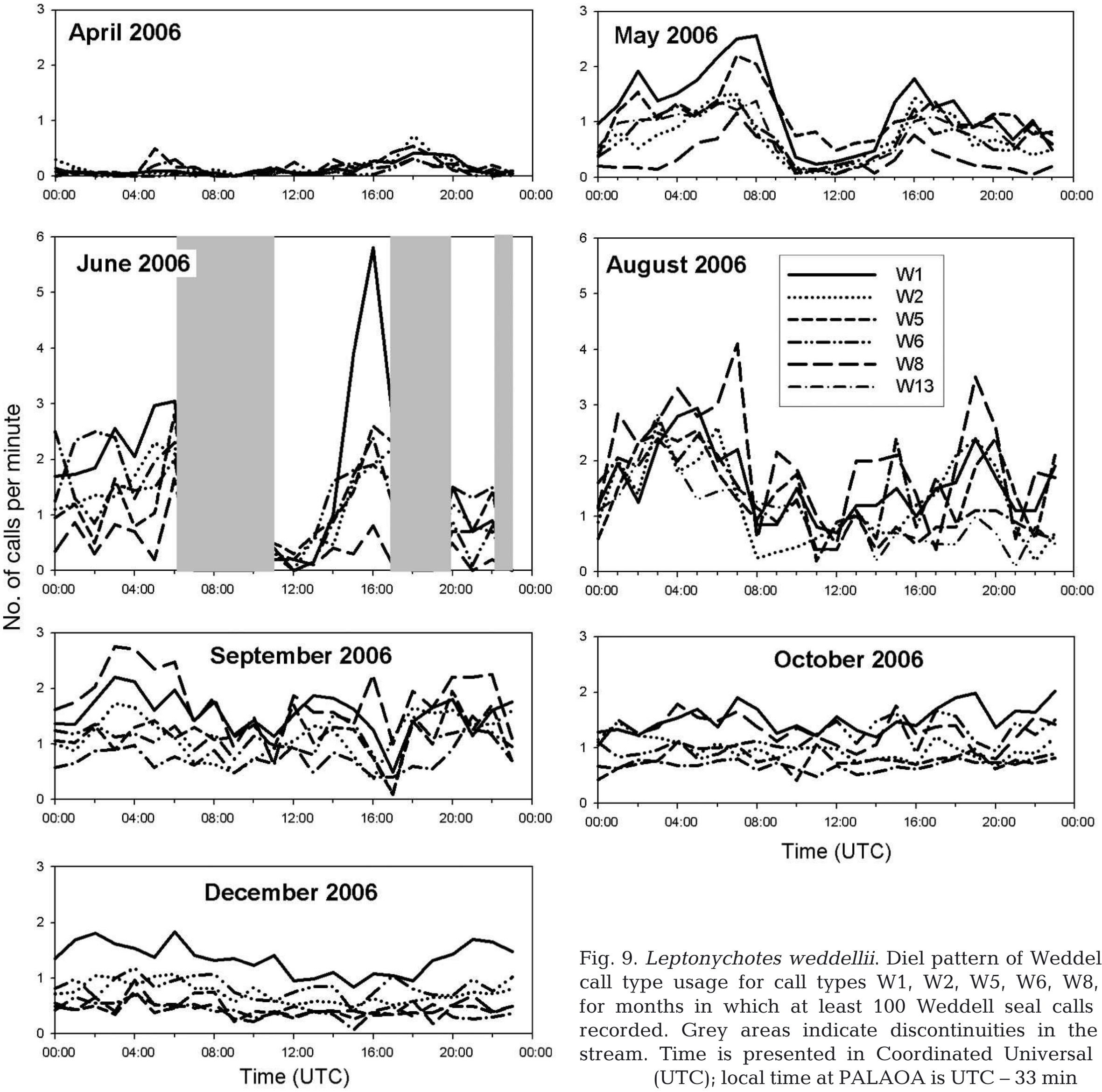

Fig. 9. *Leptonychotes weddellii*. Diel pattern of Weddell seal call type usage for call types W1, W2, W5, W6, W8, W13 for months in which at least 100 Weddell seal calls were recorded. Grey areas indicate discontinuities in the data stream. Time is presented in Coordinated Universal Time (UTC); local time at PALAOA is UTC – 33 min

each month showed relatively comparable patterns and reflected the monthly average patterns in call type usage and activity.

Ross seal

The diel calling pattern in January 2006 shows an increase in the number of calls for all call types between 12:00 and 19:00 h UTC (Fig. 12). R1 was the predominant call type in January 2006, with 2 ± 0.82 (mean ± average deviation) R1 calls min^{-1} h^{-1} in that month. In December, call rates increased during the second half of the day, with R3 being the most dominant call type in that month (2 ± 0.69 calls min^{-1} h^{-1}). In January 2007, R3 was also the predominant call type (9 ± 0.97 calls min^{-1} h^{-1}). Overall call rates in January 2007 were higher compared to January 2006 (7 ± 1.84 and 22 ± 2.28 calls min^{-1} h^{-1} for January 2006 and 2007 respectively). In January 2007, call rates were relatively constant over the day, with a short period of decreased call activity around 6:00 h UTC. However, when Ross seal call activity was compared between single days within a month, patterns in call activity varied considerably between days in January 2006 and January 2007. In addition, call types R1 and R3 were the most predominant call types when single days in January 2006 and January 2007 were compared (Fig. 13). In December the pattern in Ross seal call activity showed a more consistent pattern when single days were compared, with a period of low call activity occurring between 00:00 and 9:00 h UTC. Call type R3 was the most predominant call type on all days in December.

Crabeater seal

In October 2006, crabeater seal calling activity increased sharply between 16:00 and 19:00 h UTC and remained around 4 calls min^{-1} h^{-1} until 23:00 h UTC (Fig. 14). The average number of calls in October was 1 ± 0.94 (mean ± average deviation) calls min^{-1} h^{-1}. Fig. 12b shows considerable variability in the call activity pattern when comparing 2 separate days in October. In December 2006, the average number of calls in December was 0.1 ± 0.1 calls min^{-1} h^{-1}. The diel calling pattern showed 2 small peaks; one around 02:00 and one around 20:00 h UTC. This pattern is consistent with the pattern observed for separated days in December (Fig. 15).

DISCUSSION

The results of this study show that Weddell, leopard, Ross and crabeater seals exhibit substantial inter-specific variation in acoustic behavior, i.e. in temporal patterns of vocal activity, vocal repertoire size and composition. Variation in acoustic behavior can reflect inter-specific differences in the acoustic ecology of the species, the relationship between the organism and the environment mediated through sound. In analogy to ecology, each species might be thought of as filling its own acoustic ecological niche, shaped by internal and external factors and interactions between both (Fig. 16; Van Opzeeland 2010). Vocalizations are produced in a breeding context and consequently differences in behavioral ecology between species, such as distribution and mating system, are likely to shape

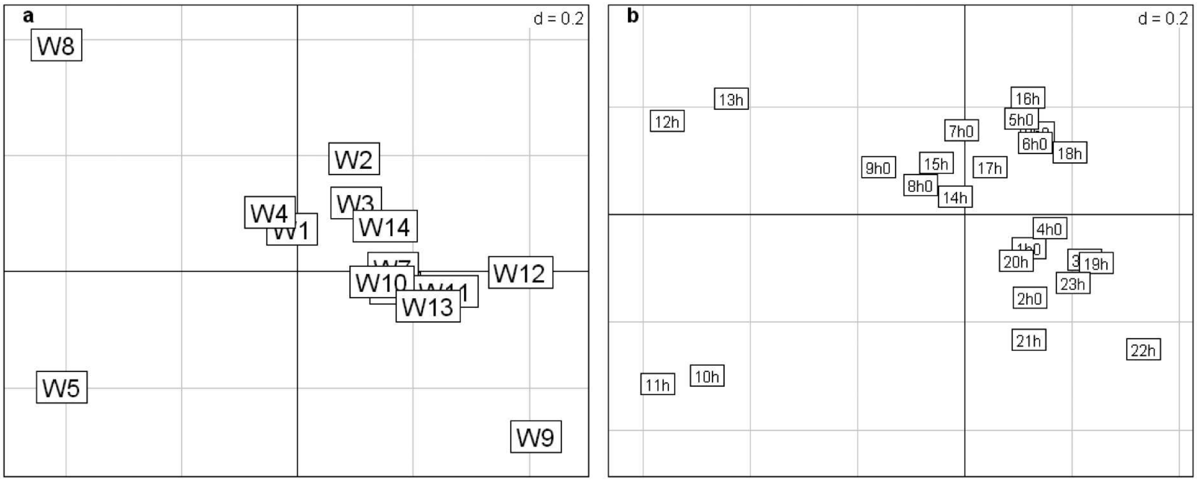

Fig. 10. 2D-correspondence analysis of hourly call-type counts of Weddell seals in May 2006. (a) Mapping of call types, showing W5, W8 and W9 as distinct from the rest. (b) Ordination of the hour bins, showing strong separation of the call patterns during 10:00–11:59 h and 12:00–13:59 h from the rest. Repertoire for the remaining time is grouped in two: lower part: evening and night (19:00–04:00 h); upper part: morning and afternoon (05:00–18:00 h)

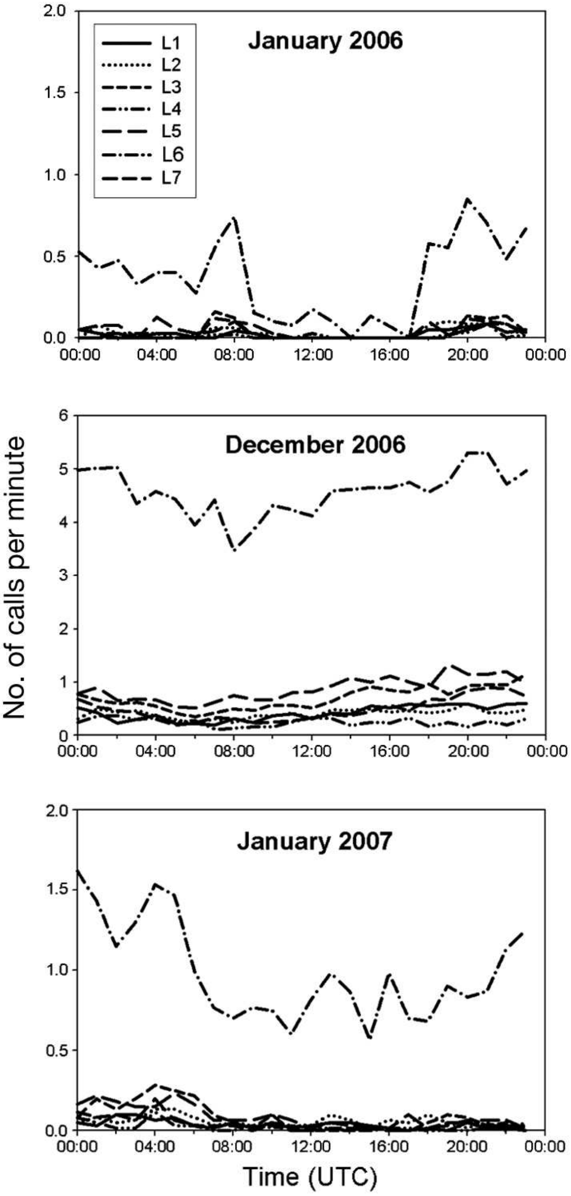

Fig. 11. *Hydrurga leptonyx*. Diel pattern of leopard seal call type usage (call types L1–L7) for months in which at least 100 leopard seal calls were recorded. Time is presented in Coordinated Universal Time (UTC); local time at PALAOA is UTC – 33 min

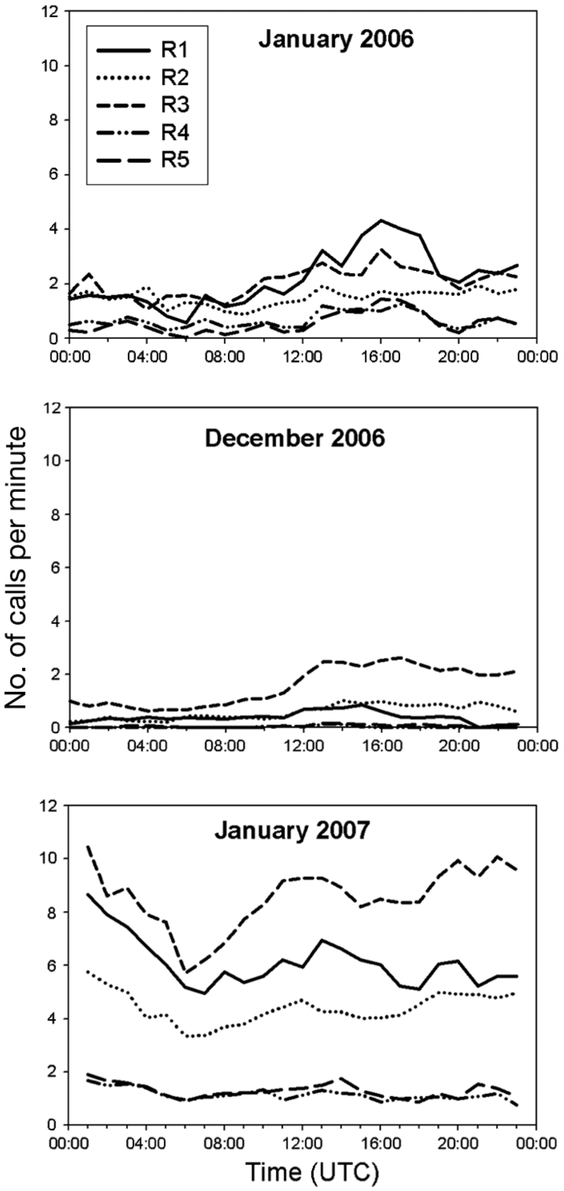

Fig. 12. *Ommatophoca rossi*. Diel pattern of Ross seal call type usage (call types R1–R5) for months in which at least 100 Ross seal calls were recorded. Time is presented in Coordinated Universal Time (UTC); local time at PALAOA is UTC – 33 min

vocal behavior. In addition, interactions with abiotic environmental factors, such as ice and the local soundscape, as well as biotic environmental factors, such as the distribution of prey and predators can also directly influence acoustic behavior. Interactions between abiotic factors and behavioral ecology (i.e. the influence of ice on mating strategy; Van Parijs et al. 2003) as well as between biotic factors and behavioral ecology (i.e. the effect of prey availability on distribution) can indirectly affect vocal behavior. Finally, anthropogenic factors such as climate driven changes and underwater noise can indirectly influence acoustic behavior, e.g. by affecting ice conditions and the local soundscape, respectively, and are therefore also a potentially important aspect of the acoustic ecology of Antarctic pinnipeds.

The results are discussed with respect to species-specific use of the acoustic environment based on the interactions shown in Fig. 16, recognizing that this is a non-exhaustive list while many of the factors mentioned are likely to act in concert and are of differing importance to each species.

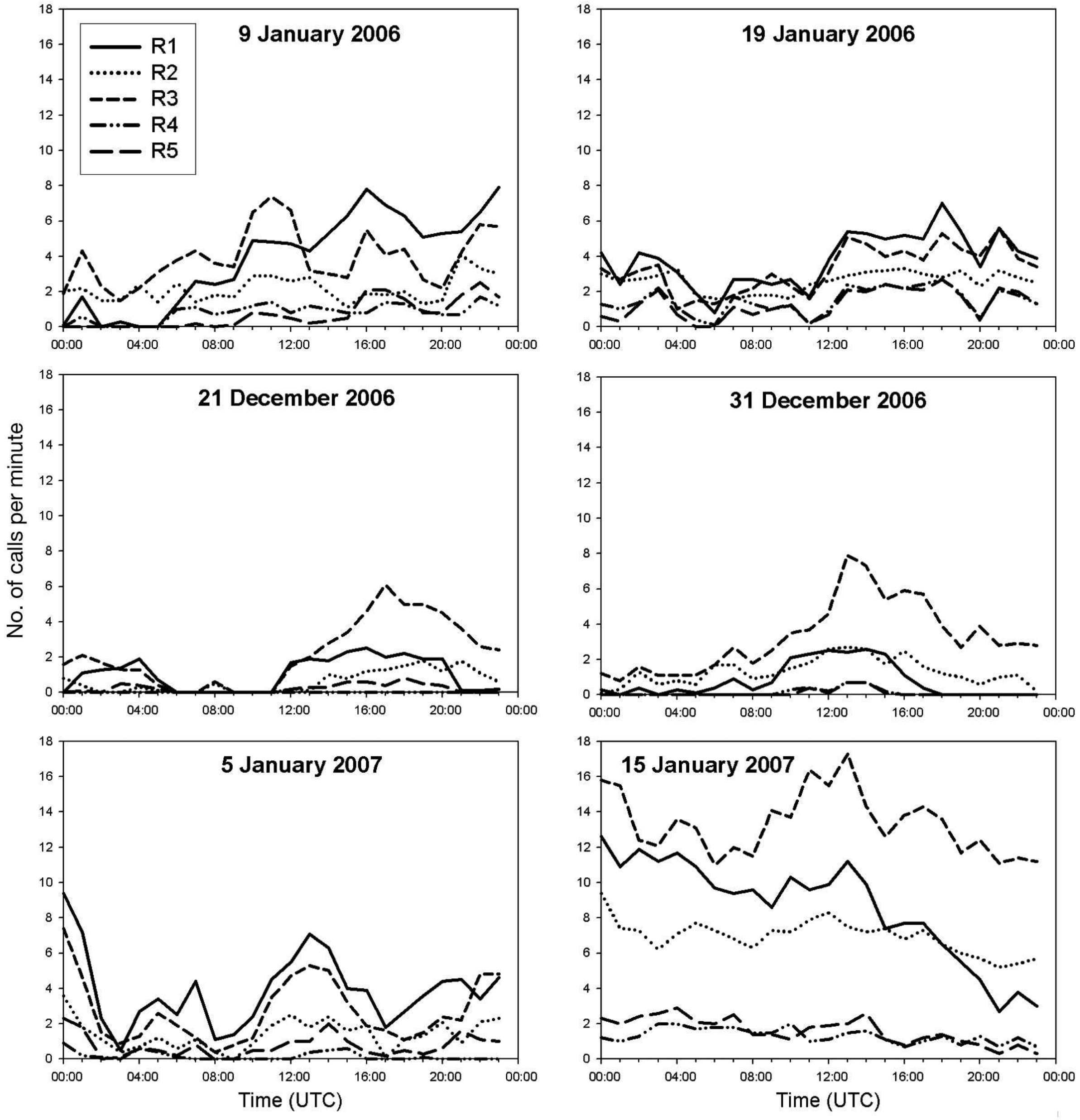

Fig. 13. *Ommatophoca rossi*. Diel pattern of Ross seal call activity on single days, chosen based on the variability in diel patterns, i.e. to illustrate the variation in vocal activity between days within the same month. Time is presented in Coordinated Universal Time (UTC); local time at PALAOA is UTC – 33 min

Behavioral ecology

Mating system

Vocal repertoire size and acoustic presence. Vocal repertoire size is largely determined by the function of vocal behavior and the distance between the vocalizing individual and the targeted audience (Rogers 2003). The large size of the Weddell seal vocal repertoire, the relative complexity and the subtle variations between call types reflect that calls might be used in inter- and intrasexual communication over short distances and are therefore not constrained by signal propagation needs. Weddell seal vocalizations have been suggested to serve a function for males in maintaining underwater territories below the Antarctic fast-ice (e.g. Bartsch et al. 1992, Stirling & Thomas 2003, Rouget et al. 2007). Nevertheless, as females move freely in this 3-dimensional underwater environment, males are unable to monopolize females and underwater territories might rather function as a display of male fitness for females and other males. This study showed that vocalizations

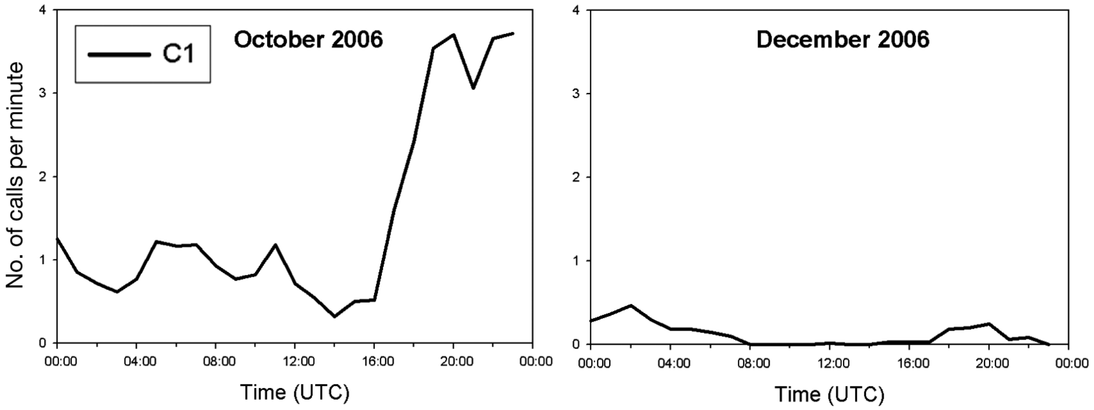

Fig. 14. *Lobodon carcinophaga.* Average diel pattern of crabeater seal call (type C1) usage for months in which at least 100 crabeater calls were recorded. Time is presented in Coordinated Universal Time (UTC); local time at PALAOA is UTC – 33 min

were recorded almost year-round, suggesting that a number of animals remain in the breeding area throughout the year. Males that occupy territories year-round might have an advantage over non-territorial males or males that move away in winter, in that they are already resident when females arrive at the breeding area (Harcourt et al. 2007, 2008). Their familiarity with the under-ice environment and neighbouring territorial males may reduce the cost of defending the breeding territory, which may eventually improve their mating success. The high Weddell seal vocal activity in winter and spring therefore suggests that males are actively engaged in acoustic displays in the breeding area for most of the year, and that the establishment and defense of underwater territories actually begins in winter, which is earlier than was previously assumed.

On the other hand, leopard and Ross seals are pack-ice breeders that migrate to and beyond the outer

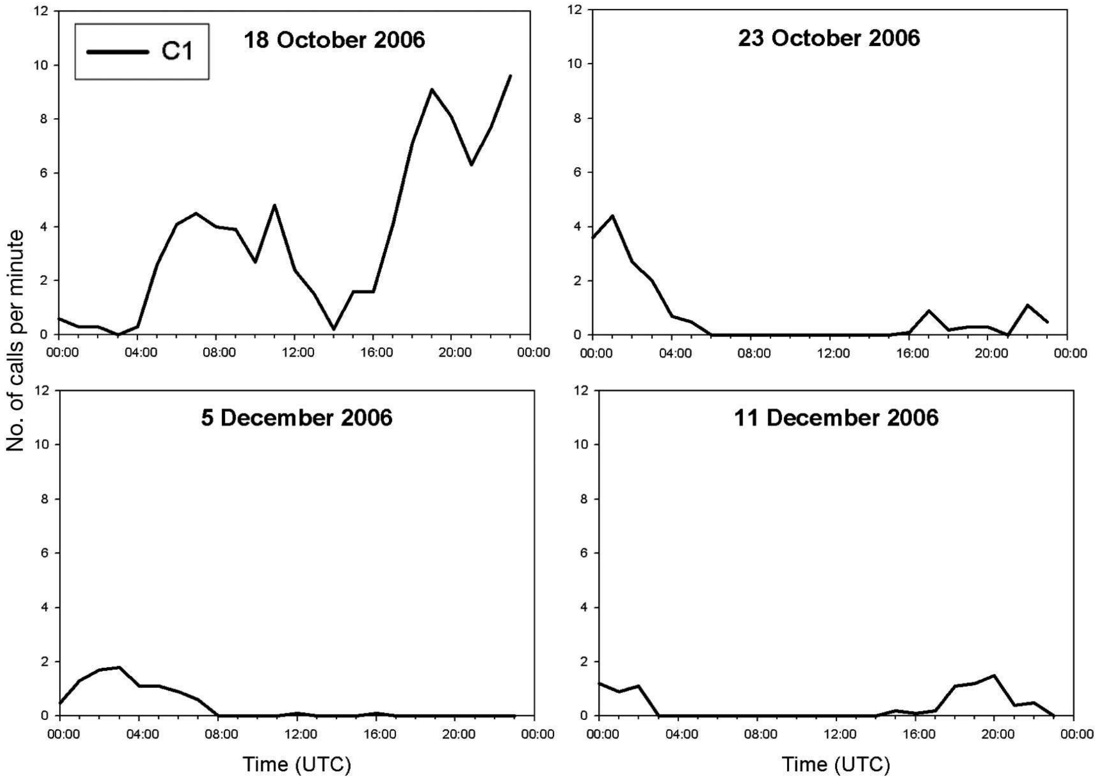

Fig. 15. *Lobodon carcinophaga.* Diel pattern of crabeater seal call activity on single days, chosen based on the variability in diel patterns, i.e. to illustrate the variation in vocal activity between days within the same month. Time is presented in Coordinated Universal Time (UTC); local time at PALAOA is UTC – 33 min

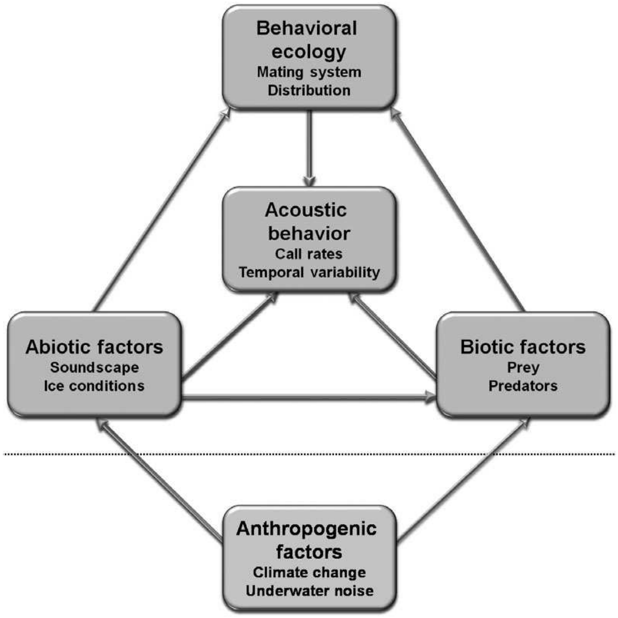

Fig. 16. Schematic representation of the acoustic ecology of Antarctic pinnipeds, showing how behavioral ecology, biotic factors and abiotic factors might interact to influence acoustic behavior of Antarctic pinnipeds

fringes of the Antarctic sea-ice in austral winter and move back into the inner pack-ice to breed in austral summer (Siniff & Stone 1985, Blix & Nordøy 2007). Females in these species are widely dispersed during the breeding season and calls are thought to function to attract mating partners over long distances. The medium-sized vocal repertoire of both species with highly stereotyped vocalizations may increase detectability of calls in spite of unfavorable propagation conditions and masking by background noise (Rogers 2003). In leopard seals, calls are produced by both sexes; females produce broadcast calls during the breeding season to signal their sexual receptivity, while leopard seal males call in search of mates (Rogers et al. 1995, 1996). Rogers & Cato (2002) suggested that in leopard seals, information related to the individual may be encoded in the vocalization sequences, rather than in the acoustic characteristics of call types, given that sequences may be less affected by signal degradation when communicating over long distances. In addition, the narrow frequency bandwidth of leopard seal calls and their long calling periods may also increase the chance that receivers recognize calls under poor signal-to-noise ratios.

For Ross seals, very little is known on mating behavior. Mating has been suggested to occur in December (King 1969) or around October–November immediately following pupping at the outer edge of the pack-ice zone (Thomas et al. 1980, Bengtson & Stewart 1997, Blix & Nordøy 2007). Based on the seasonal peak in Ross seal acoustic activity, we suggest that Ross seal mating in the Atka Bay region takes place relatively near the ice shelf region between December and January. Studies on several other aquatic mating pinnipeds have shown that seasonal peaks in vocal activity coincide with the period in which mating occurs (harbour seal: Van Parijs et al. 1999; leopard seal: Rogers et al. 1996; hooded seal: Ballard & Kovacs 1995; bearded seal: Van Parijs et al. 2001; grey seal: Asselin et al. 1993). Assuming that Ross seal mating occurs primarily in January, when the peak in vocal activity occurs, this also sheds new light on previous observations of changes in male Ross seal dive patterns in January (Southwell 2005, Blix & Nordøy 2007). Southwell (2005) noted that the male Ross seal dive pattern changed from longer presumably foraging dives in December to predominantly short dives with a modal duration of 1 to 2 min in January. These male Ross seal dive patterns in January are reminiscent of descriptions of typical male dive display behavior of other phocid species during the mating season (Van Parijs et al. 1997, 2003).

Crabeater seals only produce the moan (C1, comprising both the high and low moan variety; Klinck et al. 2010) in the PALAOA recordings. Crabeater seals breed on pack-ice and are serially monogamous (Siniff et al. 1979). The relatively simple acoustic display of crabeater seals consisting of short broadband calls is thought to function primarily in short-range underwater male–male competition (Shaughnessy & Kerry 1989, Rogers 2003). Crabeater seal males, in contrast to Weddell, leopard and Ross seal males, are able to monopolize females and haul out on ice floes to guard a female with her pup against intruder males until the pup is weaned and the female enters estrus. Once the pup is weaned and the female leaves the ice, the male is assumed to mate with the female. Rogers (2003) hypothesized that in crabeater seals a loud well-developed vocal display would likely attract males to the female that the male is defending, whereas the acoustic characteristics of the moan limit the signal to be received only by rival males in the vicinity. A recent study identified 4 additional crabeater seal call types which were recorded from a single animal of unknown sex and age in February 2007 (McCreery & Thomas 2009). The acoustic characteristics of these newly described crabeater seal call types and the month in which they were recorded, suggest that these calls serve as short-range communication and are not necessarily produced in a breeding context, comparable to the short-range call types that have been recorded from captive leopard seals (Rogers et al. 1996). The short-range call types described by McCreery & Thomas (2009) were not present in the PALAOA recordings analysed in this study. This suggests that the distance between the calling animals and PALAOA might simply have been too large to record these call types, rather than that these call types were absent from the vocal repertoire of the animals in the Atka Bay region.

Repertoire composition. In aquatic mating pinnipeds, competition between males is likely to become more intense towards the period that females enter estrus (see Van Parijs 2003 for examples). The intensification of male agonistic encounters could be reflected by the usage of specific call types. Some of the Weddell seal call types (e.g. W1, W9, W10, W13, W6) have in previous studies been described as territorial or threat calls functioning in male–male and male–female interactions during the breeding season (e.g. Watkins & Schevill 1968, Thomas et al. 1983, 1988). The highest monthly proportional usage of such proposed threat call types in this study occurred in June and December (W13 and W6 respectively) whereas call types W1 and W10 had a relatively constant proportional usage throughout the year. As Weddell seal vocalizations are thought to serve a function in maintaining underwater territories throughout the year (e.g. Bartsch et al. 1992, Rouget et al. 2007), this might explain why threat calls form such a consistent portion of the vocal repertoire during winter. Alternatively or in addition, these threat calls may also be produced in the context of gaining access to breathing holes in winter. During austral winter the number of open tidal cracks and leads in the fast ice is limited, with the presence of cracks being the major determinant of Weddell seal distribution in austral winter (Lake et al. 2005). This may result in competition between Weddell seals of both sexes for access to breathing holes. Several studies have observed both male and female Weddell seals to vocalize upon ascent to breathing holes, possibly to chase away other individuals from the hole (Watkins & Schevill 1968, Evans et al. 2004, Terhune & Dell'Apa 2006).

Weddell seal call type W8 was used only between May and December and showed a peak in proportional usage from August to October, the early onset of the breeding season. This call type has been described as the 'guttural glug' by Thomas et al. (1983) and Pahl et al. (1997) and is assumed to have a threat function. Most of the females are hauled out on the ice for extended periods in October to give birth and suckle their pups (e.g. Tedman & Bryden 1979 Thomas & DeMaster 1982, Reijnders et al. 1990) and call type W8 might therefore be used mainly or specifically by males, serving a function in male–male competition. The proportional usage of these calls decreases towards the peak mating period in November–December, possibly reflecting that calls used for mate attraction become more prominent in this period. Alternatively, males might also use fewer territorial calls in this period because males are settled in their territories. Injured males are often seen hauled out on the ice alongside whelping females (I. Van Opzeeland pers. obs.), possibly reflecting that contests for underwater territories might have subsided in this period. Call type W14 predominated during the mating (Ma) and mating+lactation (LM) period. This call type has been repeatedly observed to be produced in-air by female Weddell seals on the ice (I. Van Opzeeland pers. obs.) and possibly represents a call type that is produced mainly or exclusively by females. Given the period that these calls were most predominant, they could serve to signal female receptivity to males.

In contrast to Weddell seals, the vocal repertoire composition of the pack-ice breeding species remains relatively similar throughout their calling period, reflecting that the function of these vocalizations is potentially relatively uniform throughout the breeding season and that there are no stages within the mating season causing gradual change in repertoire composition as observed in Weddell seals.

For the pack-ice breeding species, their distance from the observatory might cause some calls to be too faint to be recorded, whereas such a bias is unlikely for Weddell seals which are located on the fast-ice within Atka Bay and just north of PALAOA. The precise location from which the pack-ice breeding seals vocalize is not known, but in austral summer the nearest pack-ice areas are located within 10 to 20 km off the fast-ice edge where PALAOA is located. In both the leopard and Ross seal vocal repertoire, low frequency calls L6 and R3 were the most predominant call types. These lower frequency calls are likely to transmit over longer distances than the other call types, increasing the chances of detecting these calls compared to other call types. Alternatively, the high proportion of these lower frequency call types in the vocal repertoire might be real, reflecting precisely that these calls are used most often because of their larger detection ranges. The vocal repertoire of captive leopard seals was dominated by call types L3, L4 and L6 supporting our observation that L6 forms one of the predominant call types of the leopard seal vocal repertoire (Rogers et al. 1996).

For crabeater seals, separate analysis of both varieties of moan showed that the low moan vocalization occurred from August to December, wheareas high moans occurred primarily in the first half of November (Klinck et al. 2010), which is the period in which most females enter estrus (e.g. Siniff et al. 1979, Shaughnessy & Kerry 1989). It is not known if female crabeater seals also produce underwater vocalizations and if the occurrence of the high moan could possibly be attributed to females advertising their sexual receptivity. Alternatively, the occurrence of the high moan in the first half of November might also link this call type to male crabeater seals in periods when intra-sexual competition for access to estrus females is strongest.

Diel call activity patterns. Weddell seal diel call activity patterns differed substantially between months and were in accordance with the patterns in call activity described by Rouget et al. (2007) who monitored Weddell seal underwater vocal activity from July to November. The low vocal activity during winter daytime hours is unlikely to be explained by haul-out behavior, as seals are rarely observed on the ice in this period (e.g. Sato et al. 2003, Rouget et al. 2007). Weddell seals are known to depend on visual cues for underwater orientation, hunting and location of breathing holes (Kooyman 1975, Wartzok et al. 1992, Burns et al. 1999, Davis et al. 1999). This led Rouget et al. (2007) to suggest that the daytime periods with low vocal activity in July–August could potentially be explained by the limited number of light hours in that period which seals might utilize for vision-dependent activities during which they vocalize less. However, we also observed this bimodal pattern in vocal activity in May and June when global radiation is low and the light–dark cycle is virtually absent at the site where this study was conducted (Koenig-Langlo & Herber 1996). This suggests that Weddell seals use an alternative cue to entrain their circadian rhythm in the period of constant darkness in winter. Bornemann et al. (1998) found a correlation between tidal rhythmicity and semi-circadian rhythm of Weddell seal underwater activity in summer; they suggested that in summer tidal movement might affect abundance and distribution of prey and that Weddell seals use the tide as a time cue to optimize foraging efficiency. However, Testa (1994) showed that Weddell seal dive depths in midwinter darkness lacked the diel pattern of autumn and spring dives. This leaves it unlikely that low vocal activity during winter daytime hours could be explained by Weddell seal foraging activity during which they would vocalize less or in deeper waters beyond recording range (e.g. Rouget et al. 2007). Alternatively, the observed diel rhythm in Weddell seal vocal activity might be entrained by social factors. Animals across various taxa inhabiting environments that lack time cues are known to socially and mutually synchronize circadian rhythms (e.g. Crowley & Bovet 1980, Marimuthu et al. 1981, Aschoff et al. 1983). Similarly, Weddell seals might use the vocalizations of conspecifics to synchronize their own vocal activity. In addition, all 6 call types that occurred frequently enough to be included in the diel pattern analyses have been described previously and are thought to have a territorial and/or threat function (Watkins & Schevill 1968, Thomas et al. 1983). Social synchronization of vocal activity might aid to maximize the effectiveness of signals used in male–male competition and female attraction. Towards September the diel rhythm becomes less pronounced, which might be explained by the fact that male–male competition becomes more intense and vocal interactions occur more continuously. Adult males, territorial males in particular, are known to rarely haul out from early October through mid December and spend most of the breeding season under the fast ice (Harcourt et al. 2007).

Similar to Weddell seals, leopard and Ross seals both exhibited continuous call activity in the months in which mating takes place which might on the one hand reflect the absence of factors constraining or influencing vocal activity and on the other hand the increased competition for mating partners promoting continuous vocal activity. These findings are in accordance with previous studies that found that most Ross seals haul out around solar midday in December, while haul-out patterns in January were more variable (Southwell et al. 2003, 2008).

For leopard seals, the continuous call activity observed in December could possibly be explained by a difference in male and female call strategies. Rogers et al. (1995) observed leopard seals in captivity and noted that the female called constantly for many days when she was sexually receptive, whereas males called throughout December and January. For males it might be more advantageous to advertise their presence over longer periods during the breeding season, which might introduce a trade-off between the hourly call rate and the total period over which a male can energetically afford to be vocally active. Males might therefore vocalize mainly during the hours that most females are in the water, whereas females might vocalize more continuously throughout the short period in December that they are in estrus. Given that previous studies found a clear diel pattern in leopard seal vocal activity in December (Thomas & DeMaster 1982, Rogers & Bryden 1997), a possible explanation for the observed difference might be the ratio of male and female callers at the different recording locations.

In addition, local ecological factors might also affect vocal behavior differently between recording locations. Van Parijs et al. (1999) found that harbour seal males adapted their temporal and spatial behavior to the periods when most females were in the water. Site-specific differences in ecological constraints on haul-out behavior of female harbour seals were therefore reflected in local variation in male display behavior. The absence of environmental factors such as prey availability constraining or influencing vocal activity at Atka Bay might therefore result in the continuous leopard seal vocal activity in December, whereas environmental factors might affect the vocal activity patterns in other areas differently.

In crabeater seals, the intensification of male–male competition might have a contrary effect on call activity compared to the other species. Competition between males for access to receptive females might force males to remain hauled out for extended periods during the day to defend the female against intruders. In November, periods of vocal activity might therefore be more restricted to the night and early morning hours, which is in accordance with the pattern in vocal activity observed in other studies (Thomas & DeMaster 1982, Klinck et al. 2010). The difference in call activity pattern in October and December might reflect that crabeater seal vocal behavior develops into a typical 2-peak pattern from start to peak mating season, resulting from such intensification in male–male competition.

Distribution

In contrast to leopard, Ross and crabeater seals, Weddell seals are relatively stationary, remaining in fast-ice areas where the presence of cracks and breathing holes determine their distribution (e.g. Stirling 1969, Lake et al. 2005). The species' sedentary nature is likely to explain the existence of geographical variation in vocal behavior on various spatial scales (Abgrall et al. 2003, Thomas & Stirling 1983). Trills and calls thought to have a function in territorial defense such as call type W6, were present at all sites, while all sites also had unique call types that were not shared with other breeding populations. This study identified 14 Weddell seal call types, 13 of which have been described previously. Nevertheless, the differences between call type representation, description and classification methods provided in a number of previous studies complicate the comparison of call types between study sites. In most cases call types recorded in this study exhibited subtle differences in acoustic structure compared to the call types recorded at other breeding populations, such as e.g. the different types of descending chirp sequences that have been described (Terhune et al. 1994, Moors & Terhune 2004, Hayes & Terhune 2007). However, none of these descriptions included the presence of a short ascending whistle, which in this study always preceded call type W2 and in some cases also W3, albeit in a less stereotyped form. Pahl et al. (1997) described this ascending whistle as a separate call type (call type DC202). Despite these differences, overall similarity in call characteristics and structure showed that all call types, with the exception of W4, could be classified into previously described call types. Call type W4 (Fig. S1) represents a strongly stereotyped chirp sequence that differed from the chirp sequences recorded at other sites. In contrast to the similar looking call types W2 and W3, call type W4 consists of 3 falling chirp segments followed by a low chirp. Call type W4 might therefore represent a site- or region-specific call for Atka Bay that is not used in other Weddell seal populations.

Leopard, Ross and crabeater seals move over much larger spatial scales, which might also be reflected in the absence of large differences in vocal repertoire composition. In accordance to our findings, previous studies report leopard seal call types L6 ('low double trill') and L3 ('high double trill') to be the most common call types (e.g. Stirling & Siniff 1979, Rogers & Cato 2002). However, call repertoire composition varies between different locations (e.g. Thomas & Golladay 1995, Rogers 2007). Most of the call types in the PALAOA recordings have also been recorded at Prydz Bay, except for call type L4 ('hoot'), which has only been recorded in captivity (Rogers et al. 1996). Rogers (2007) noted that call type L5 ('hoot with single trill') was only recorded at 2 opposing locations of the Antarctic continent, Prydz Bay and the South Shetland Islands, and not at any of the sites in between. However, we found call type L5 also to be present in the PALAOA recordings, which may suggest that there is movement of animals between the South Shetlands, Prydz Bay and Atka Bay. Differences between local vocal repertoires can be used to make inferences about potential movement and exchange patterns between populations (e.g. Perry & Terhune 1999, Cerchio et al. 2001). In leopard seals, this is particularly exciting as genetic studies have shown that there is sufficient gene flow between breeding groups to prevent development of population structure (Davis et al. 2008). Nevertheless, it has been suggested that the fact that there is geographic variation in vocal repertoires—despite the low genetic variability between animals from different regions—could indicate that some animals show site fidelity and that moving (potentially juvenile) leopard seals adapt their vocal repertoire to that of local breeding groups (Davis et al. 2008).

In our analyses, we did not discriminate between the 'mid double trill' and 'mid single trill' (Stirling & Siniff 1979, Rogers et al. 1996) and lumped all mid trills into call type L7 (Fig. S2). However, Klinck (2008) found that both mid trill types were present in the leopard seal vocal repertoire recorded at Atka Bay. The 'mid double trill' has so far only been recorded from animals in the South Shetlands (Rogers 2007), which could be an indication that there is movement of animals between the South Shetlands and Atka Bay, but not directly between Prydz Bay and the South Shetlands. However, further investigation is needed to gain insights into the relationship between leopard seal local vocal repertoires and movement patterns.

For Ross seals, 4 of 5 call types in the PALAOA recordings have been described previously (Watkins &

Ray 1985, Stacey 2006) while one was only present in the PALAOA recordings (Seibert 2007). Although Watkins & Ray (1985) and Stacey (2006) used different methods to categorize call types, their descriptions confirm that at least R1, R2 and R3 have also been recorded at other locations. Stacey (2006) also distinguishes a call type that looks similar to call type R5 in this study ('underwater call type B'). We found call type R5 to be almost always associated with R4, which is also reflected in the similar proportional usage of these call types within the repertoire. However, both call types also occurred independently, which is why we have assigned separate call type names. The absence of call type R4 in previous descriptions of the Ross seal repertoire could indicate that R4 is a region-specific call and that Ross seal call repertoires differ between areas.

Biotic factors

Prey availability

In many species, past experience with spatially and temporally predictable food sources might cause animals to return to and concentrate in these areas during periods that resources are abundant (Krebs & Davies 1993). The timing of the leopard seal mating period, following the weaning of pups after which both females and pups require extra food resources, might have evolved to coincide with the period when the sea ice breaks back towards the colonies and penguin fledglings and seal weanlings are compelled to leave the ice (Klinck 2008). Most leopard seal calls were recorded in December which coincides with the period in which mating occurs. In this period the presence of the emperor penguin *Aptenodytes forsteri* colony as well as the crabeater and Weddell seal breeding colonies in and around Atka Bay likely provide an attractive feeding spot for leopard seals. Given that leopard seals are solitary animals outside the breeding season, the presence of food sources that are reliably present in Atka Bay every year might also function to attract leopard seals to the breeding area and increase the likelihood of finding a mating partner. In addition to their own calls, the sounds from the penguin and seal colonies might also function as 'acoustic beacons' where many animals concentrate to mate and forage.

Presence of predators

For crabeater seals, the likelihood of encountering predators might be a factor influencing the timing of vocal activity. Vocalizing crabeater seals might provide location cues to leopard seals and might consequently increase their predation risk. Gilbert & Erickson (1977) suggested that crabeater seals might represent a more important leopard seal food source than krill or penguins. The peak in crabeater vocal activity in our data set occurred in October. The peak in crabeater call activity in November occurred when only few leopard seal calls were present in the recordings, suggesting that leopard seals might not yet be abundantly present at Atka Bay in this period. However, most crabeater seal body wounding by leopard seals has been suggested to occur between weaning and attaining maturity (Siniff & Bengtson 1977). If this reflects the main age class that is targeted by leopard seals, the majority of leopard seals might time their arrival in late November/ early December to coincide with the period when most crabeater seal pups are weaned.

The presence of leopard seals, in turn, might be restricted to the period that orcas *Orcinus orca* are absent. Although the extent remains unknown, Siniff & Bengtson (1977) found evidence for leopard seal predation by orcas. Preliminary analysis of the PALAOA data show that in subsequent years, orca echolocation clicks and vocalizations are present in the January recordings when leopard seal vocal activity decreases rapidly. However, further analyses of annual patterns in cetacean vocal behavior are underway and will provide further insight into such inter-specific relationships.

Abiotic factors

Soundscape: inter-specific acoustic niche partitioning

The observed differences between species in timing of acoustic behavior might reduce acoustic interference between calling individuals (i.e. jamming of signals) and increase the efficiency of signal propagation (e.g. Sueur 2002). Partitioning of the acoustic environment or sequencing of acoustic activity, either based on time, space or frequency bandwidth of signals, is referred to as acoustic niche forming (Latimer & Broughton 1984, Mossbridge & Thomas 1999, Sueur 2002, Brumm 2006, Boquimpani-Freitas et al. 2007) and has been observed to occur both intra-specifically and inter-specifically in orthopterans, amphibians and birds (e.g. Ficken & Hailma 1974, Gerhardt 1994). Harp seals are thought to overcome masking by calls of conspecifics by using frequency and temporal separation of call types (Serrano & Terhune 2002). Mossbridge & Thomas (1999) suggested that orcas modulate the frequency of their vocalizations as an adaptation to the presence of leopard seals during periods that both species exploit the same region. Particularly for species that rely on signal propagation over long distances to find a mating partner, such as leopard and Ross seals, acoustic niche forming might significantly reduce interspecific acoustic interference. Leopard and Ross seal calls dominate the soundscape during relatively short distinct periods in December and January respectively and might temporarily 'block' the acoustic space of other species. Such 'blocking' of acoustic space might occur through the relatively high amplitude of leopard seal calls (Rogers 2003) as well as the broad frequency bandwidth that is covered by Ross seal vocalizations, and might contribute to prevent inter-specific acoustic interference. Weddell and crabeater seals on the other hand, communicate over much shorter distances and might therefore not depend so much on efficient signal propagation. Complete separation of the period during which a species is vocally active might on the other hand not be possible because of other abiotic and biotic factors, such as the availability of prey, suitable ice and thermoregulation (haul out) which might further restrict the breadth of the acoustic niche of each species.

Ice conditions

The observed differences in the number of calls in January 2006 and January 2007 for Weddell, leopard and Ross seals suggests that a lower number of animals was present in the area around the observatory in 2006 compared to 2007. Despite the difference in the number of samples that were analysed in January 2006 and 2007, in both years samples were not biased towards certain times of day during which vocal activity was higher and such a sampling bias cannot therefore have influenced the results. Although Weddell, leopard and Ross seals depend on different ice types for breeding, they all rely on the large-scale reliability of sea-ice development. Previous studies found that inter-annual variability in sea-ice extent and composition affects behavior of ice-breeding pinnipeds: Siniff et al. (2008) observed fewer adult Weddell seals at the breeding area in McMurdo Sound in a year when ice closed off cracks that had reliably been open in previous years. In bearded seals, the number of displaying males was found to be restricted by between-year fluctuations in ice cover (Van Parijs et al. 2004). Not only differences in ice conditions between years might affect pinniped acoustic behavior, but seasonal availability of ice suitable for haul-out and pupping might also affect vocal behavior. The absence of Weddell seal vocalizations in the PALAOA recordings throughout February might reflect a short period during which seals might have moved (either actively or drifting passively on ice floes) out of Atka Bay to areas where suitable ice for haul-out was still present. Weddell seals aggregate along predictable annual tidal cracks in the fast ice close to the ice shelf edge of Atka Bay (J. Plötz pers. obs.). Seasonal fast-ice breakup in this area usually occurs in February, after which the ice sheet builds up again in March and April (G. König-Langlo pers. comm). Green & Burton (1988) also observed a very low number of Weddell seal calls in Long Fjord near Davis station (68° S, 78° E) between February and early April, followed by a period with a distinct lack of Weddell seal vocal activity in May and June during which no seals were sighted in the area. They suggested that the limited amount of ice available for seals to haul out on in addition to the potentially depleted food stocks in the pupping area might have caused seals to move out of the fjord. Alternatively, if calls play a role in Weddell seal territorial disputes throughout the year, as discussed previously, vocal activity might be linked exclusively to the presence of fast-ice being a prerequisite for the existence of underwater territories. In this case, seasonal fast-ice break-up in February would dissolve the underwater territorial system which might be reflected in the absence of Weddell seal vocalizations in this month.

Implications of a changing environment for Antarctic pinnipeds

All 4 species rely on different sea-ice habitats for most or at least critical portions of their life history and the effects of climate change are therefore likely to have differing impacts on each species. In Weddell seals, population dynamics have been linked to climatological cycles, mediated through changes in sea-ice extent and concentration (Testa et al. 1991, Siniff et al. 2008). Pup incidence was lower in years when sea-ice was more extensive, possibly related to decreased foraging success through the reduced amount of open water available for primary production ultimately affecting fish availability (Hadley et al. 2007). In crabeater seals, ice extent might also have an indirect impact given that sea-ice extent affects recruitment and abundance of krill, their primary prey (Siniff et al. 2008). Moreover, for pupping, crabeater seal females select ice floes based on floe size and physical characteristics (i.e. surface relief; Siniff et al. 1979) which offer protection from predation by leopard seals and orcas. Changes affecting the availability and duration of availability of such sea-ice types might also directly affect crabeater seal populations, e.g. through reduced reproductive success when floes melt before lactation is complete. Siniff et al. (2008) suggested that leopard and Ross seals might be less sensitive to changes in sea-ice given the fact that they are not philopatric with respect to breeding areas. However, this study and preliminary analyses of PALAOA data from following years show that calls of leopard and Ross seals reoccur each year and coincide with the mating period. Although information from Atka Bay on site-fidelity at an individual level is lacking, the PALAOA data suggest that at least on a species level animals return to the same breeding areas each year and might therefore be more philopatric than previously thought. Consequently, for these species local changes in ice conditions might also result in loss of site-specific breeding locations. Such changes might in turn also have consequences for other species, for example through shifts in timing of mating and the resulting changes in acoustic space. Acoustic techniques form an important tool to monitor such reponses to human-induced changes in environmental conditions (Laiolo 2010), particularly in remote areas such as the Antarctic.

Compared to other areas in the world, the Antarctic is still a relatively pristine area with respect to anthropogenic impact (Halpern et al. 2008). However, as in many other marine ecosystems, anthropogenic impact such as noise caused by e.g. vessels or seismic exploration can influence marine mammals in various ways (see Southall et al. 2007 for a review). Changes in the local soundscape as a result of anthropogenic activities can alter vocal behavior of species in affected areas or affect prey distribution (Southall et al. 2007) and are therefore also of potential influence on the acoustic ecology of Antarctic pinnipeds. To understand these impacts, knowledge on how species use acoustic space and the factors that shape acoustic behavior is indispensable.

Further investigation involves multi-year comparisons of vocal behavior of Antarctic pinnipeds and integration of the acoustic data in habitat models to contrast environmental attributes associated with seasonal occurrence and call rates. These approaches will contribute to improve our understanding of the fundamental ecology and acoustic ecology of Antarctic pinnipeds.

Acknowledgements. S. Riedel, D. Steinhage, A. Ziffer and the overwintering teams 2005 and 2006 (Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany), H. Schubert (Reederei F. Laeisz GmbH, Rostock, Germany), R. Verhoeven, J. Hoffmann and C. Müller (FIELAX Services for Marine Science and Technology mbH, Bremerhaven, Germany) all played crucial roles in setting up and/or maintaining PALAOA. The PALAOA project was partly funded by the Bremerhavener Gesellschaft für Innovationsförderung und Stadtentwicklung (BIS). We thank 4 anonymous referees for their constructive comments on our manuscript.

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Editorial responsibility: Hans Heinrich Janssen,
Oldendorf/Luhe, Germany

Submitted: July 27, 2009; Accepted: May 31, 2010
Proofs received from author(s): August 27, 2010

Publication IV

Multi-year patterns in the acoustic behavior of Antarctic pinnipeds

MULTI-YEAR PATTERNS IN THE ACOUSTIC BEHAVIOR OF ANTARCTIC PINNIPEDS

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Manuscript in preparation

ABSTRACT

In this study we investigate seasonal patterns in vocal activity of three Antarctic pinniped species, Weddell seal (*Leptonychotes weddellii*), leopard seal (*Hydrurga leptonyx*) and Ross seal (*Ommatophoca rossii*) over three years and two months (2006-2009) of near-continuous acoustic data from the PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA), 70°31'S, 8°13'W on the Eckström Iceshelf. For each species, one call type was selected to represent acoustic presence and used for development of automated detectors. Weddell seals calls were detected from April to December, while the number of calls varied between years, possibly reflecting a relation to local ice conditions in Atka Bay. Leopard seal calls were detected intermittently throughout the year, which might reflect that some (potentially juvenile) leopard seals remain in near-shore areas during austral winter. In all years, leopard seal call activity decreased rapidly with increasing Ross seal acoustic activity in December, possibly reflecting that leopard seals actively reduce call activity when Ross seals start to dominate the local soundscape. Peaks in Ross seal call activity corresponded to the coincidence of short duration changes in ice cover concentration, suggesting a relation between vocal activity and the presence of pack-ice in the area off PALAOA. This manuscript is still in preparation. Further analyses will involve 1) analysis to relate call detections to actual call rates and extract diel call patterns from automatically detected calls, 2) more detailed investigation with respect to the spatial scale of ice cover data from the area off PALAOA and its representativeness of specific pinniped ice habitats, 3) statistical analyses of the automated call detections to explore annual patterns involving time series analysis, 4) more detailed investigation of the temporal pattern of the occurrence of leopard seal call type variants (juvenile calls).

INTRODUCTION

In species that use vocalizations for intersexual display or intra-sexual competition, the timing, location and duration of acoustic behavior is expected to maximize the chances of obtaining a mate while minimizing the costs of display, both in terms of energy and predation risk (Krebs & Davies 1993; Bradbury & Vehrencamp 1998). To achieve this, animals often use, or in some cases depend on, biotic and/or abiotic cues from the environment. This results in temporally dynamic vocal behavior, linked directly or indirectly (*e.g.* through prey availability) to cycli in environmental factors such as light conditions and temperature (*e.g.* Blankenhorn 1972; Stafford *et al.* 2005). To cope with fluctuations in their living environment, vocal behavior often exhibits a certain level of plasticity *e.g.,* in the acoustic characteristics of communication signals or the timing of acoustic behavior (*e.g.* Miller *et al.* 2000; Fuller *et al.* 2007). For example, male song rate in pied flycatchers (*Ficedula hypoleuca)* during the breeding season is dependent on food resources and temperature (Gottlander 1987). In tawny owls (*Strix aluco*), rain fall substantially reduces territorial night-time call activity, presumably in response to the reduction in communication space caused by the increased ambient noise levels during rain (Lengagne & Slater 2002). The relationship between environmental fluctuations and temporal variation in vocal behavior can be used to gain insight into the factors that shape acoustic behavior and are therefore of specific relevance to the organism. Information on factors of influence can in turn be used to better understand the function of vocal behavior and the acoustic ecology of a species; the relationship between the organism and the environment mediated through sound.

Temporal variation in vocal behavior can be studied at various scales. However, in most cases cyclical patterns and fluctuations in acoustic behavior in response to environmental factors are best studied using multi-year data. These allow direct comparison of patterns on various temporal scales while avoiding temporal inter-dependency (*e.g.* seasonal variation in diel call activity). In this study, we investigate hypotheses on the acoustic ecology of Antarctic pinnipeds that have been proposed in a previous study (Van Opzeeland *et al.* 2010), using semi-continuous acoustic data from 3+ years.

In our previous study, several mechanisms were discussed as to which factors shape the timing of vocal behavior of four Antarctic pinniped species, Weddell seal (*Leptonychotes weddellii*), leopard seal (*Hydrurga leptonyx*), Ross seal (*Ommatophoca rossii*) and crabeater seal (*Lobodon carcinophaga*). All four species are aquatic mating and are thought to use vocalizations in male-male competition and/or male advertisement to females. Nevertheless, the mating system of each species differs substantially; Weddell seal males are thought to maintain underwater territories below the Antarctic fast-ice, whereas leopard seals are solitary with both males and females using calls to attract mating partners over long distances. Crabeater seal males guard females on the ice and are thought to use their calls for short-range underwater male-male competition. To date, only little is known on the mating system of Ross seals (but see Van Opzeeland *et al.* 2010). Given the difference in function of calls between all species, those species using calls to communicate over larger distances, such as leopard and Ross seals, were hypothesized to be more sensitive to acoustic interference by other species compared to those with shorter communication ranges. Leopard and Ross seals could therefore be expected to time their vocal activity during periods with little acoustic interference from other pinniped species. Furthermore, all species differ in the ice types used for breeding; while Weddell seals breed exclusively on fast-ice, leopard, Ross and crabeater seals all use different types of pack-ice for breeding (Siniff *et al.* 2008). Annual fluctuations in the availability and quality of each ice-type have been shown to affect pinniped behavior and vocal behavior (Van Parijs *et al*. 2004; Siniff *et al*. 2008) and might be expected to affect each species differently (Van Opzeeland *et al.* 2010).

The questions we address in this study are:

1) *How stable is the seasonal pattern in acoustic presence for all species when compared over multiple years?*
2) *Is there an interaction between local ice conditions and vocal behavior of Antarctic pinnipeds?*
3) *Is there evidence for inter-specific interactions based on the species-specific timing of acoustic activity?*

METHODS

Acoustic data

The PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA) is located at 70°31'S, 8°13'W on the Eckström Iceshelf, eastern Weddell Sea coast, Antarctica (Fig 1, Boebel *et al*. 2006; Klinck 2008). Recordings are made continuously year-round with two hydrophones deployed underneath the 100 m thick floating Antarctic ice shelf through bore-holes with an in-between distance of 300 m (see Kindermann *et al*. 2008 for further technical details). The effective bandwidth of the PALAOA recordings is 10 Hz to 15 kHz, dynamic range 60 dB to 150 dB re 1 µPa.

Signals are digitized at 48 kHz/16 bit and encoded to a 192 kBit MP3 stream by a BARIX Instreamer device. For this study data from January 2006 until February 2009 were used. Figure 2 shows the total recording time in days of PALAOA from 2006 to 2009. No recordings for July and November 2006 and May 2007 are available due to either technical failure or energy shortages at the observatory.

Detector development

Based on previous manual analyses of vocal repertoire composition and temporal variation in call type usage (Van Opzeeland *et al*. 2010), one call type for each species was selected to be automatically detected. To represent acoustic presence of the species throughout the year, only call types that composed a significant portion of the vocal repertoire showing relatively little temporal variation in usage were selected. In addition, call types were required to be sufficiently stereotyped or at least exhibit stereotyped parts to allow for automated detection. Pinniped calls were detected using the 'data template detector' in XBAT (Bioacoustics Research Program, Cornell Lab of Ornithology, www.xbat.org). The data template detector scans the recorded sound and compares it to selected spectrogram sections ('templates'), which are sections of sounds known to be produced by the target species. Acoustic similarity between the template and the acoustic events in the recording is quantified through spectrogram cross-correlation. Events for which the correlation value exceeds a specified threshold are detected and stored in 'logs' in XBAT.

Two to three different detectors each consisting of a different set of templates were created for each species. Using the 'Explain' function in XBAT, which shows correlation value between the template and the acoustic events in the recording, one detector was selected based on its specifity for target calls. To evaluate at which threshold settings the detector performed best, detector output at different threshold settings was compared to manual analysis of the same data. The manual counts were also performed in XBAT by manually detecting and selecting all target calls occuring on three randomly selected days and saving them in a manual log. Manual logs were created blind from detector output, *i.e.* without knowledge on which calls the detector would detect or miss. The days for which manual logs were created were randomly selected from three months between which vocal activity of each species was known to vary substantially based on previous analyses (*i.e.* one day in a month with peak vocal activity, one day in a month with little to no vocal activity; Van Opzeeland *et al*. 2010). For each species, manual logs were compared to the output of detector runs with detection thresholds from 0.05 to 0.55, in steps of 0.10. The purpose of automated detection in this study was to provide a reliable measure of acoustic presence for each species. The evaluation of detector performance therefore based on presence and absence of calls on an hourly basis, *i.e.* a match between manual and detector log was counted as 1, irrespective of the number of matches occurring within the same hour. False positive (FPR, FP/FP+TN) and true positive rates (TPR, TP/TP+FN) of the detector were calculated for all threshold settings and combined in a receiver operating characteristic (ROC) curve. For months during which calls were present in each hour, graphs show TPR at different threshold settings, whereas for months during which calls were absent in each hour, graphs show FPR at different threshold settings. This approach enabled the evaluation of which threshold optimized the TPR while minimizing FPR.

Detectors were developed for three species, Weddell, leopard and Ross seal. Calls of the fourth Antarctic pinniped species, the crabeater seal, were found to exhibit too few stereotyped features to use the template detection method and were therefore not analysed in this study.

Weddell seals

For Weddell seals, call type W2 was one of the most frequently used call types, composing 13% of the vocal repertoire. The manual analysis showed that call type W2 was a good indicator of Weddell seal vocal presence and showed least variation in usage between months (Fig 3). Call type W2 consists of a falling chirp sequence that is always precedented by an upsweeping whistle (Fig 4). The frequency and duration of the chirp sequence varies between call types, while the whistle part is very stereotyped and season-independent in its acoustic characteristics. Three different detectors were developed, each consisting of several data templates of different parts of the whistle. For the evaluation of the performance of each detector, one day for each month was randomly selected for January (low vocal activity), June (high vocal activity period in mid-winter) and November (high vocal activity and peak mating season). Figure 5 shows the performance of each detector at different threshold settings. For the detections runs a threshold of 0.4 was selected (spectrogram parameters: FFT size 4048 points, window size = 30s, max freq = 5000 Hz, window length = 1, window function = Hanning).

Leopard seals

For leopard seals, call type L6 is the call type that is most frequently used (62% of the vocal repertoire, Fig 6). The relative rarity of the other call types and the stereotyped nature of call type L6 made this call type the best representative of leopard seal acoustic presence. Call type L6 (‘low double trill’) consists of two nearly identical call parts, separated by a short pause (Fig 7). In many cases, the first call part of L6 is precedented by a short narrow-band tone. Data templates were created from parts of the two identical call parts as well as from the narrowband start tone. Three different detectors were developed and evaluated based on randomly selected days in January (moderate vocal activity), June (no vocal activity) and December (peak vocal activity). Based on detector evaluation (Fig 8), a threshold of 0.5 was selected for detector runs (spectrogram parameters: FFT size 4048 points, window size = 30s, max freq = 2000 Hz, window length = 1, window function = Hanning).

Ross seals

Call type R3 composed a stable 40% of the Ross seal vocal repertoire over the period that Ross seals were vocally present (Van Opzeeland *et al.* 2010, Fig 9). Call type R3 is a tonal V-shaped call, which in some cases is precedented or followed by an additional up- or down-sweep, respectively (Fig 10). Nevertheless, the V-shaped part is stereotyped in shape and always present. Three different detectors were developed and evaluated based on randomly selected days in January (peak vocal activity), June (no vocal activity) and December (moderate vocal activity). For the multi-year detection runs, a threshold of 0.5 was selected (Fig 11, spectrogram parameters: FFT size 4048 points, window size = 30s, max freq = 2000 Hz, window length = 1, window function = Hanning).

Local ice cover

The percentage of ice cover was calculated for the area within a 40 km radius off PALAOA from ENVISAT ice cover data with a 6.25 x 6.25 km resolution (Spreen *et al.* 2008). The 40 km radius was chosen based on preliminary estimations of the range over which pinniped calls are recorded by PALAOA.

To relate pinniped acoustic behavior to changes in local ice cover in a way that these are comparable between years, a measure for the time point of break-up of the fast-ice within a 40 km radius off PALAOA was sought. The timing of break-up was defined as the point in time at which the local ice concentration decreased below 80% followed by a minimum period of one month during which ice cover remains below 80%. This definition was partly based on field experience and perusal of satellite pictures of the area.

RESULTS

Annual pattern in call detections

Weddell seal calls were detected from April to December in 2006, from June to December in 2007 and from April to December in 2008 (Fig 12a). The number of calls that was detected was substantially lower in 2007 compared to the other years, with an average of 6 calls per recording hour for 2006 and 2008 and an average of 2 calls per recording hour in 2007. Most calls were detected in December 2006 (average of 12 calls per recording hour). Peak numbers of detected calls per recording hour occurred on 4 December 2006 (44 calls per recording hour) and 2 June 2008 (24 calls per recording hour). In 2007, the maximum number of calls per recording hour detected per day was 8 occurring on 11 and 23 November 2007 and 3, 4 and 7 December 2007.

Leopard seal calls were detected over eight months, in January and February and from May to Dec in 2006 (Fig 12b). In 2007, calls were detected over all months except March and August, totalling nine months, whereas in 2008 calls were present over 11 months (all months except February). Calls were detected outside the period during which they were expected to be present based on the manual analysis of the 2006 PALAOA data. To be sure that these calls were actual leopard seal calls all detections outside the period from October-January were manually reviewed. Although occassional false detections occurred (and were removed from the log), the majority of detections were actual leopard seal L6 calls. Based on overall call shape (Rogers 2007) these are likely juvenile calls (Fig 13). The average number of calls per recording hour did not differ much between years with 42 calls per recording hour detected in 2006, and 49 calls per recording hour in 2007 and 2008). Most calls were detected in December in all years, with an average of 265, 334 and 333 calls detected per recording hour for December 2006, 2007 and 2008 respectively. Peak numbers of detected calls per recording hour occurred on 12 December 2006 (583 calls per recording hour), 26 December 2007 (533 calls per recording hour) and 21 December 2008 (599 calls per recording hour). The number of calls detected during austral winter (April to September) was generally low, ranging from 1 to 14 calls per recording hour (average 0.59, 0.16 and 0.96 calls per recording hour for 2006, 2007 and 2008 respectively).

Ross seal calls were detected in January and December in all three years and in February in 2007 and 2008 (Fig 12c). The number of detected calls per recording hour over these three months varied substantially between months with 6 calls per recording hour in 2006 and 25 and 15 calls per recording hour in 2007 and 2008 respectively. The timing of the onset of Ross seal vocal activity is strikingly similar between years (17, 19 and 24

December in 2006, 2007 and 2008, respectively, noting that in 2008 the presence of a ship near PALAOA on 17 December might have affected the number of Ross seal call detections). In all four years, most calls were detected in January, with peaks occurring on 10 January 2006, 12 January 2007, 5 January 2008 and 19 January 2009 (58, 274, 138 and 183 calls per recording hour for 2006, 2007, 2008 and 2009, respectively).

Annual calling patterns and ice cover

Figure 14 shows the normalized number of calls detected per species and the ice concentration within a radius of 40 km off PALAOA for the entire period over which recordings were analyzed. The black dots mark the timing of ice break-up according our definition. The blue bars in the graph indicate the period from peak number of Weddell seal calls detected to the point where no calls were detected. In 2007 and 2008, this period coincides with ice break-up, whereas in 2009, ice break-up occurs well before the occurrence of the peak in vocal activity. Similary, the peak in the number of leopard seal call detections coincided with ice break-up in 2007 and 2008, whereas in 2009, the peak in call activity occurs around the same time as in other years and seems independent of the early occurrence of ice break-up. Ross seal call activity typically showed two peaks in all years (green dotted lines). In 2006, 2007 and 2009, peak call activity occurred after ice concentrations had increased again, presumably as a result of pack-ice drifting into the area. In 2008, the first peak in Ross call activity occurred earlier compared to other years and preceeded the temporal increase in ice cover.

Interspecific interactions

The timing of the first peak in Ross seal vocal activity coincides in all years with a dramatic decrease in the number of leopard seal call detections (Fig 14, red dotted lines).

DISCUSSION

Automated detection methods such as the template detection method used in this study, allow detailed and objective analyses of large acoustic data sets. In this study we used one call type as acoustic representative for each pinniped species and optimized detector performance to provide reliable information on the acoustic presence of each species on an hourly basis. This detector characteristic along with the fact that only one call type of each species is detected makes it difficult to translate the number of detections to actual call rates. Nevertheless, further analyses of the output of our detectors will explore how detection rates relate to actual call activity. Furthermore, patterns in hourly presence and absence of each pinniped species will also be investigated in more detail.

Annual pattern in call detections

Weddell seals

Our manual analysis showed that calls were present in all months of the year, except in February, whereas the automated analysis detected Weddell seal calls from April to December. In January and March calls were relatively faint and few in number (Van Opzeeland *et al.* 2010), which might explain why the data template detector did not detect any calls in these months. The near year-round presence of Weddell seal calls likely reflects their territorial mating strategy; males that occupy territories year-round might have an advantage over non-territorial males or males that move away in winter, in that they are already resident when females arrive at the breeding area. The fact that in all years many calls were detected in austral winter might reflect that males are actively engaged in acoustic displays in the breeding area for most of the year.

Overall, the number of detected Weddell seal calls was substantially lower in 2007 compared to the other years. Changes in local signal-to-noise ratios might influence the number of calls detected (see discussion leopard seal below). However, the number of detections was lower throughout the whole of 2007, whereas the number of calls detected for the other two species did not show similar differences between years. Manual perusal of the recordings from 2007 also suggests that the lower number of detections is unlikely related to differences in detector performance, but rather reflects an actual lower number of calls in this year. Environmental conditions of specific relevance to Weddell seals might therefore somehow have differed between years, resulting in either fewer animals present in Atka Bay or a change in the location of colonies, causing fewer calls to be recorded by PALAOA. Weddell seal colonies are located in the vicinity of fast-ice leads or cracks in the ice around icebergs within Atka Bay and just north of PALAOA. Changes in the position or number of icebergs can therefore affect the location where Weddell seal colonies form and thereby affect the number of animals within the recording range of PALAOA. Possibly, the sudded drop in ice cover in April 2007 (Fig 13) affected the settlement of Weddell seal colonies in Atka Bay in that year. While a more detailed investigation of local ice conditions in Atka Bay might provide some further information on interannual differences in ice cover and iceberg positions, data on Weddell seal colony sizes and locations are currently lacking. Future work involving localization of calling animals, will contribute to further our understanding of the relation between ice conditions and Weddell seal vocal behavior.

Leopard seals

Most leopard seal calls were detected during the leopard seal breeding season (October – January, Van Opzeeland *et al*. 2010), with a relatively stable number of detections in each year. The sudden decreases in leopard seal call detections in mid December 2007 and 2008 are likely explained by the presence of a ship in the area off PALAOA. Previous analysis showed that the template detector fails to detect leopard seal calls in the presence of ship noise, while an analyst can still reliably detect them under these noise conditions (Boebel & Van Opzeeland, unpublished data). Calls are therefore likely present, but fail to be detected by the template detector during the days that the ship is present. This will be subject of further study.

The detection of leopard seal calls outside the breeding season contrasted to the manual analysis of the 2006 PALAOA data (Van Opzeeland *et al.* 2010). The leopard seal calls that were automatically detected outside the breeding season were clearly recognizable as leopard seal calls and it is therefore highly unlikely that they were missed in the files that were manually analysed. Instead, the sampling regime that was used during manual analysis in combination to the relative rarity of leopard seal calls in this period is likely the reason why these calls were not present in any of the files that were manually analysed.

Interestingly, the leopard seal L6 call detector also detected incomplete L6 calls, which have been previously described by Rogers (2007) as juvenile variants of adult broadcast call types. These calls are thought to be produced by juveniles practicing adult vocalization types (Rogers 2007). Variants of call type L6 were mainly detected in September (but also in June and October) during distinct bouts of a few hours most often occuring at the end of the day. In most cases, L6 variants were present along with normal L6 calls. Rogers (2007) showed that juvenile leopard seals are often capable of producing both the variants and the adult version of call types. It is therefore difficult to draw conclusions on group composition, *i.e.* if both adult and juveniles or only juveniles were present outside the breeding season. However, temporal patterns of occurrence and the presence of other call type variants will be topic of further analyses of the data.

The presence of juvenile and adult leopard seal calls in austral winter suggests that leopard seal migratory behavior might be more variable than previously assumed. The majority of studies has found leopard seals to migrate north with the expansion of the pack-ice around April (*e.g.* Walker et al. 1998; Forcada & Robinson 2006; Nordøy & Blix 2009). Juvenile leopard seals often migrate even further north and the proportion of immature seals increases with decreasing latitude (*e.g.* Rounsevell & Pemberton 1994; Rogers *et al.* 2005). However, Rogers *et al.* (2005) found that tagged adult leopard seals did not reflect the usual northward migration and remained in relatively near-shore areas throughout austral winter. They suggested that it might be primarily younger animals that migrate north, while adult leopard seals are more sedentary. The presence of juvenile vocalizations in the PALAOA recordings nevertheless suggests that juveniles also remain in near-shore areas and that juvenile dispersal is not restricted to northern waters. Juvenile dispersal is often related to competition for resources (*i.e.* mates or food; Dobson 1982) and might therefore also be site-dependent. Krill is thought to be an important food source for leopard seals in winter (Øritsland 1977). The winter presence of humpback whales (*Megaptera novaeangliae*) in the area off PALAOA (Van Opzeeland *et al.* in prep) might reflect that there are sufficient food resources for animals to winter in this area.

Ross seals

Ross seal vocal presence was restricted to December, January and February, with most calls detected in January in all years. The strong seasonal pattern in acoustic presence might reflect either that the physical presence of Ross seals in the area off PALAOA is restricted to these months or that vocal activity only occurs in this period. To our knowledge there are no studies that have recorded Ross seal vocalizations outside these months (studies that have recorded Ross seal calls, other than PALAOA, are summarized in Stacey 2007), which might reflect that Ross seals only vocalize during the breeding season. Strongly seasonal vocal activity also occurs in harbor seals (*Phoca vitulina*), with males vocalizing only during the 40-day mating season (Van Parijs *et al.* 1999).

Annual calling patterns and ice cover

In contrast to our expectations, the number of Weddell seal call detections seemed relatively independent of the timing of ice-break-up. Weddell seals breed on fast-ice and the transition of their stable breeding substrate to mobile pack-ice floes was expected to compromise the possibility for males to maintain underwater territories (Van Opzeeland *et al.* 2010). We therefore expected Weddell seal to be more reliant on ice-conditions and time their peak vocal activity in November (corresponding to the peak mating season, Van Opzeeland *et al.* 2010) accordingly. Given that ice coverage was calculated for a 40 km range off PALAOA, it cannot be excluded that ice cover shows strong local differences and that it is mainly the area north of Atka Bay where large scale transitions in ice type take place. As pointed out previously, further analyses of the data will investigate the relation between the number of Weddell seal call detections and local ice cover (*i.e.,* only Atka Bay) in more detail.

In leopard seals, the timing of vocal activity did not correspond to any specific feature in ice conditions, but rather seemed to correspond to a fixed time window between October and February. This apparent independence of ice conditions might be explained by a similar mismatch between the area over which mean ice cover was calculated and the area occupied by leopard seals as discussed in the context of Weddell seals. Alternatively, leopard seals might time their vocal behavior based on other environmental factors than ice. Leopard seals depend on ice during the period that females give birth to pups and suckle them on the ice. Mating in leopard seals is thought to not immediately follow the weaning of pups and has been suggested to be postponed, possibly by as much as a month (Siniff & Stone 1985). Calls are produced in a mating context during which both sexes vocalize underwater to attract mating partners over relatively long distances (Rogers *et al.* 1996). Ice conditions might therefore not be as important for leopard seals during the mating season. Instead, as hypothesized in our previous study, leopard seals might time their vocal activity to coincide with the presence of food sources such as penguin chicks and pinniped weanlings, the presence of which might depend less on the ice conditions within a 40 km range off PALAOA.

The number of Ross seal call detections was substantially lower in 2006 compared to the other years. A previous study showed Ross seal call activity in December 2005 to be much lower than in December 2006 (Seibert *et al.* 2007), reflecting that actual call activity was generally lower in the 2005-2006 season compared to other years. Much remains to be speculated with respect to Ross seal behavior, as so little is known on the biology of this species. The coincidence of the peaks in the number of Ross seals call detections and the short duration peaks in ice cover, suggest a relationship between vocal activity and the presence of pack-ice in the area off PALAOA. Possibly, Ross seals arrive (either actively swimming or passively drifting on floes) with the pack-ice in January. The substantially lower ice coverage in January 2006 might reflect that less pack-ice is present in the area in that year, resulting in a lower number of animals present.

Interspecific acoustic interactions

Interspecific acoustic interactions are likely to be of specific importance for the species that use their calls to communicate over long distances and rely mainly on vocalizations to find a mating partner, such as the leopard seal. In our previous study, we hypothesized that the temporal segregation in pinniped acoustic activity that we observed might have resulted from interspecific acoustic interference. The results of the automated detection of Ross and leopard seal calls seem to confirm our hypothesis and are in accordance with our manual analysis, showing that leopard seal call activity decrease rapidly with increasing Ross seal call activity. Manual inspection of the detector output confirmed that leopard seal call activity decreased as soon as Ross seal vocalizations became abundant, excluding the possibility that performance of the leopard seal L6 detector was influenced by the presence of Ross seal calls. Although the point in time in January at which no leopard seal calls were detected differs between years, it coincided in all years with the first peak in the number of Ross seal call detections. The 'acoustic plenitude' (*i.e.,* the breadth of the frequency band covered and the temporal density of calls) of Ross seals in the soundscape of Atka Bay is likely to leave little communication space for leopard seals. Given the high energetic costs of producing broadcast calls (Rogers 2003), it might be more advantageous for leopard seals to reduce call activity when Ross seals start to dominate the local soundscape.

Outlook

This manuscript is still in preparation. Further analyses are foreseen and will involve 1) analysis to relate call detections to actual call rates and if possible extract diel call patterns from the automatically detected calls, 2) more detailed investigation with respect to the spatial scale of ice cover data from the area off PALAOA and its representativeness of specific pinniped ice habitats, 3) statistical analyses of the automated call detections to explore annual patterns involving time series analysis, 4) more detailed investigation of the temporal pattern of the occurrence of leopard seal call type variants (juvenile calls).

ACKNOWLEDGEMENTS

S. Riedel, D. Steinhage, A. Ziffer and the overwintering teams 2005 and 2006 (Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany), H. Schubert, (Reederei F. Laeisz GmbH, Rostock, Germany), R. Verhoeven, J. Hoffmann and C. Müller (FIELAX Services for Marine Science and Technology mbH, Bremerhaven, Germany), all played a crucial role in setting up and/or maintaining PALAOA. The

PALAOA project was partly funded by the Bremerhavener Gesellschaft für Innovationsförderung und Stadtentwicklung (BIS).

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FIGURE LEGENDS

Figure 1. Bathymetry map showing the location of PALAOA (white star) and location of the German Neumayer Station II (black star). Inset image: map of Antarctica showing the location of Neumayer Station (black star).

Figure 2. PALAOA yearly coverage, showing the total recording time in days for each year from 2006 to 2009.

Figure 3. Occurrence of Weddell seal call types based on manual counts of calls over one year of PALAOA data from 2006 (Van Opzeeland *et al.* 2010). For each month the number of calls counted per call type is indicated. Call type W2 was one of the most reliable call types to represent Weddell seal acoustic presence over all months. No data were available for July and November 2006 due to temporary failure of the observatory.

Figure 4. Spectrogram of Weddell seal call type W2 with the stereotyped whistle part (zoom image) that was used for automated detection of this call type.

Figure 5. Performance of Weddell seal W2-call detector at different thresholds for one day for January (low vocal activity), June (high vocal activity period in mid-winter) and November (high vocal activity and peak mating season).

Figure 6. Occurrence of leopard seal call types based on manual counts of calls over one year of PALAOA data from 2006 (Van Opzeeland *et al.* 2010). For each month the number of calls counted per call type is indicated. Call type L6 was the most reliable call types to represent leopard seal acoustic presence over all months. No data were available for July and November 2006 due to temporary failure of the observatory.

Figure 7. Spectrogram of leopard seal call type L6. Parts of the start part of the call as well as parts of the two symmetrical call parts were used for automated detection of this call type.

Figure 8. Performance of leopard seal L6-call detector at different thresholds for one day for January (medium vocal activity), June (no vocal activity) and December (peak vocal activity and peak mating season).

Figure 9. Occurrence of Ross seal call types based on manual counts of calls over one year of PALAOA data from 2006 (Van Opzeeland *et al.* 2010). For each month the number of calls counted per call type is indicated. Call type R3 was the most reliable call types to represent Ross seal acoustic presence over all months. No data were available for July and November 2006 due to temporary failure of the observatory.

Figure 10. Spectrogram of Ross seal call type R3.

Figure 11. Performance of Ross seal R3-call detector at different thresholds for one day for January (peak vocal activity), June (no vocal activity) and December (moderate vocal activity).

Figure 12. Number of detections (real numbers) per recording hour for a) Weddell (blue), b) leopard (red) and c) Ross seals (green) from January 2006 to March 2009. Acoustic presence (AP) is indicated by the upper colored bar (bar present = calls have been detected). The grey bar (PAL) indicates the recording status of PALAOA (bar present = observatory is recording).

Figure 13. Spectrogram of a leopard seal calls: a) LDT recorded on 13 June 2007, b) possible juvenile variant of ascending trill, recorded on 14 June 2007.

Figure 14. Number of detections per recording hour in relation to percentage ice cover for the area 40 km off PALAOA. Upper plot shows the normalized number of call detections for all three species from January 2006 to March 2009. The lower graph shows percentage ice cover for the area within a 40km range off PALAOA from January 2006 to March 2009. Black dots indicate the timing of ice break-up: the point in time at which the local ice concentration decreased below 80% followed by a minimum period of one

month during which ice cover remains below 80%. Blue bars indicate period from peak number of Weddell seal calls detected to no calls were detected. Red dotted line indicates first day after leopard seal calling period on which no leopard seal calls were detected. Green dotted lines indicate the timing of the two peaks in the number of Ross seal calls detected.

Figure 15. Twentyfour-hour spectrogram of PALAOA recordings from 26 December 2009, illustrating how Ross seals temporarily dominate the soundscape at PALAOA. Inset image: 1-minute spectrogram of Ross seal calls, which cover a broad frequency range (~100 – 4000 Hz) and occur frequently in time.

FIGURES

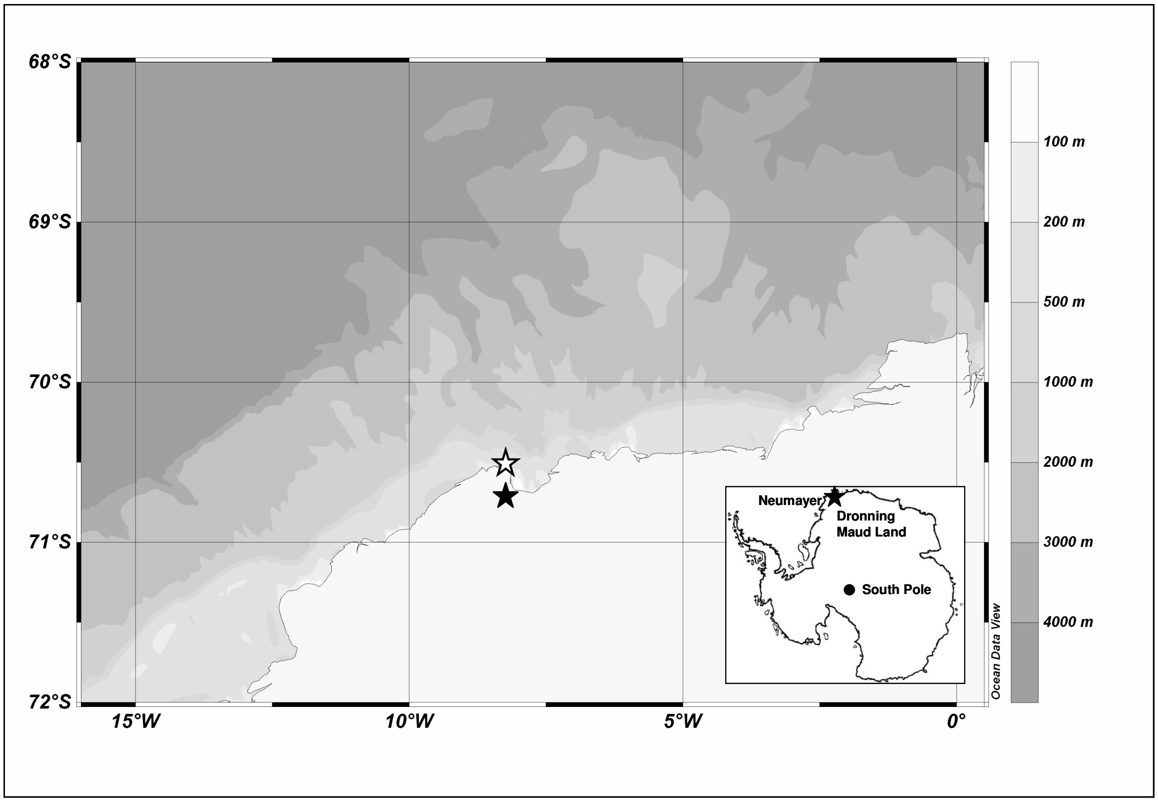


Fig 1

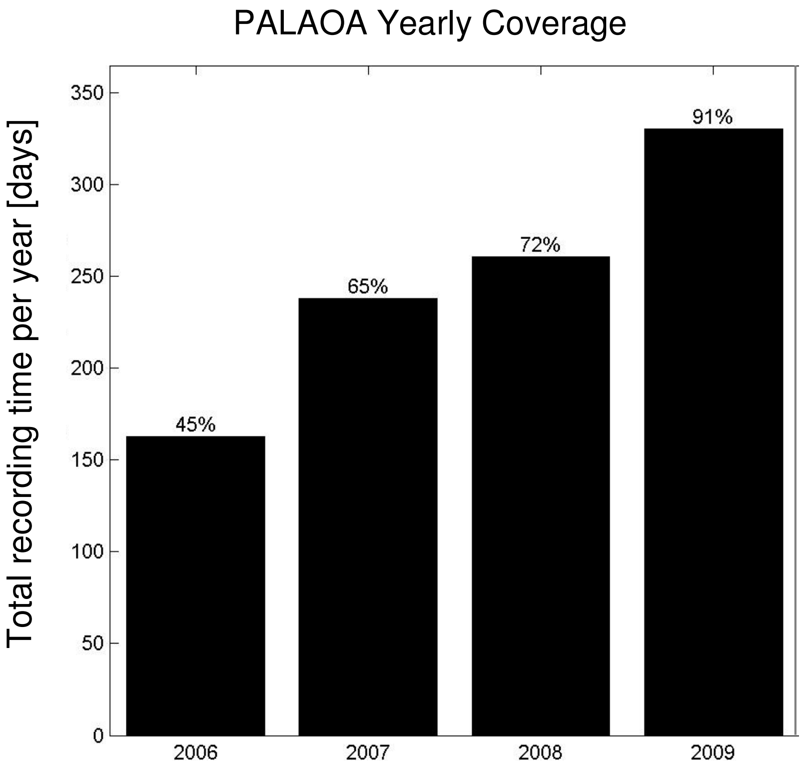

PALAOA Yearly Coverage
Total recording time per year [days]
350
300
250
200
150
100
50
0
45%
65%
72%
91%
2006
2007
2008
2009

Fig 2.

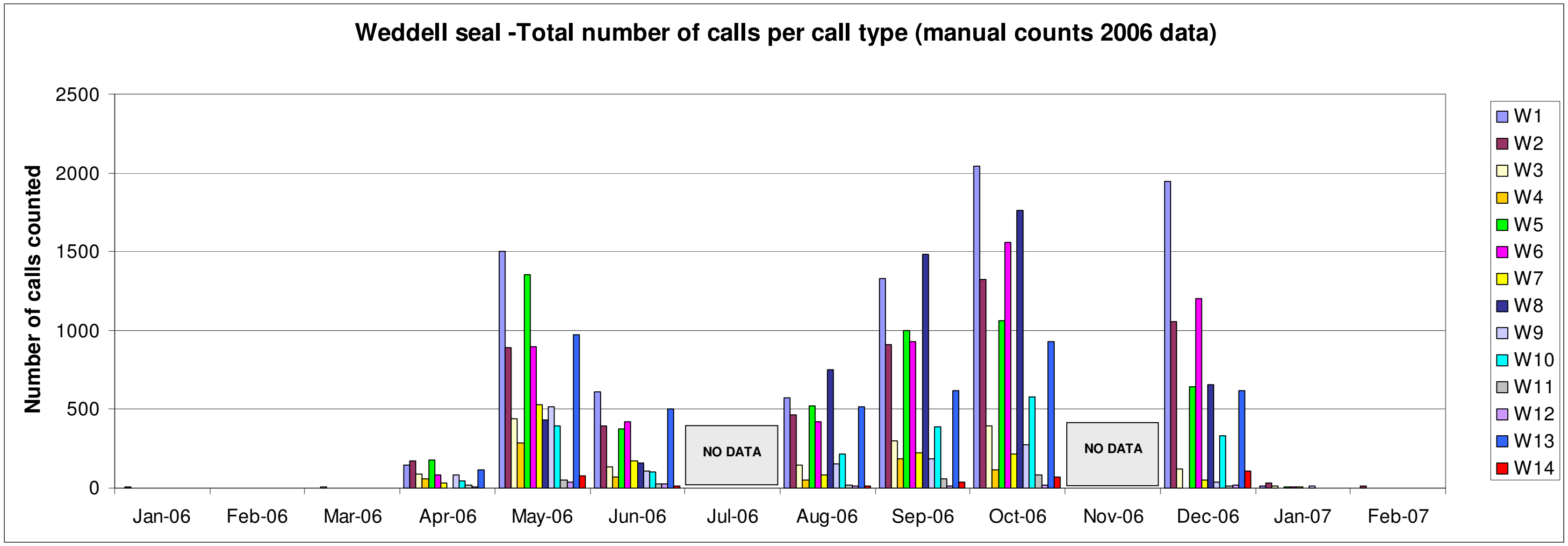

Weddell seal -Total number of calls per call type (manual counts 2006 data)
Number of calls counted
0
500
1000
1500
2000
2500
Jan-06
Feb-06
Mar-06
Apr-06
May-06
Jun-06
Jul-06
Aug-06
Sep-06
Oct-06
Nov-06
Dec-06
Jan-07
Feb-07
NO DATA
NO DATA
W1
W2
W3
W4
W5
W6
W7
W8
W9
W10
W11
W12
W13
W14

Fig 3.

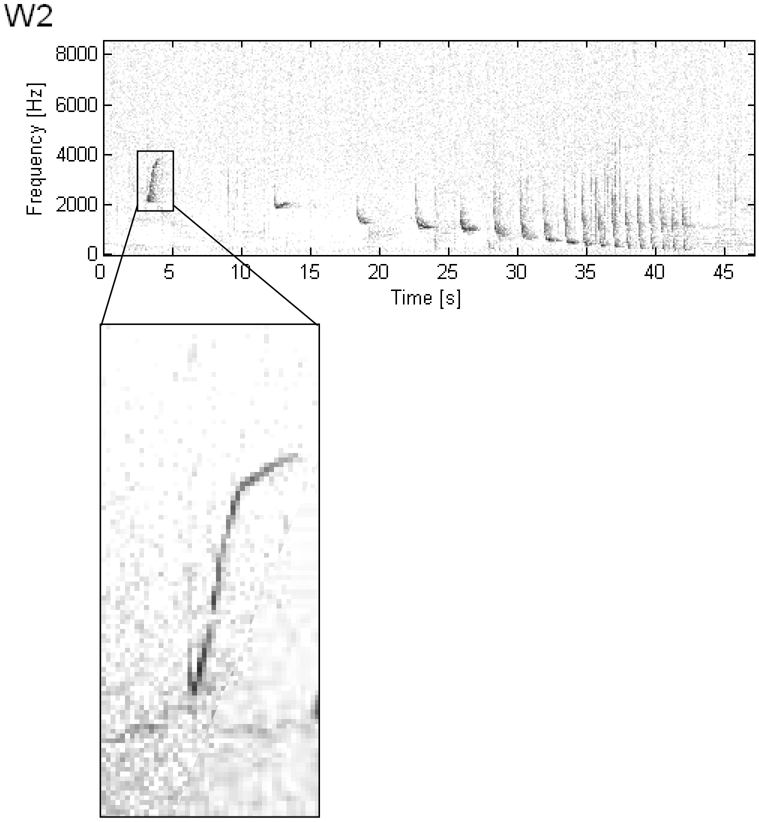

W2
Frequency [Hz]
0
2000
4000
6000
8000
Time [s]
0
5
10
15
20
25
30
35
40
45

Fig 4.

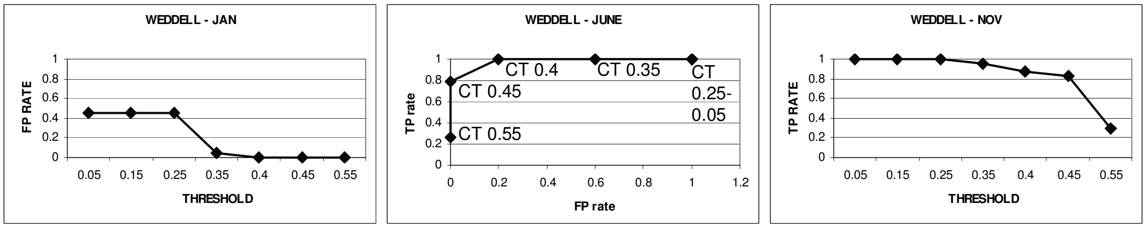
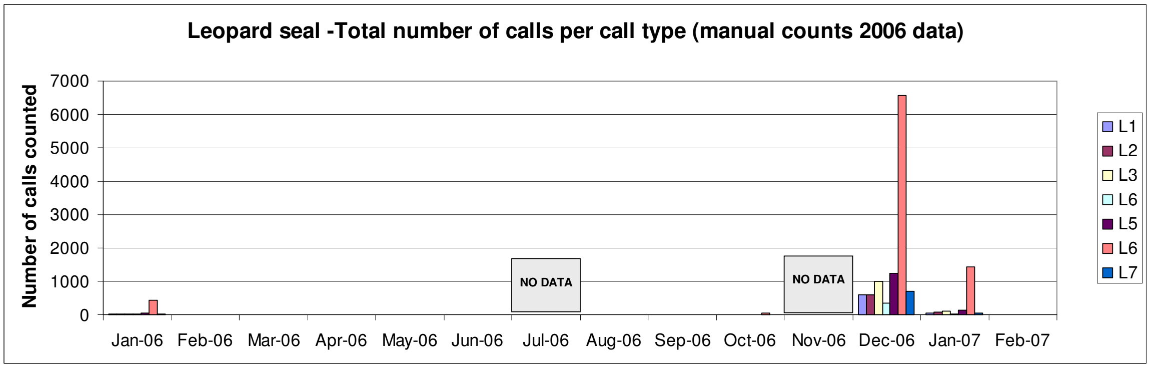

WEDDELL - JAN
FP RATE
1
0.8
0.6
0.4
0.2
0
0.05
0.15
0.25
0.35
0.4
0.45
0.55
THRESHOLD
WEDDELL - JUNE
TP rate
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
1.2
FP rate
CT 0.4
CT 0.35
CT 0.25-0.05
CT 0.45
CT 0.55
WEDDELL - NOV
TP RATE
1
0.8
0.6
0.4
0.2
0
0.05
0.15
0.25
0.35
0.4
0.45
0.55
THRESHOLD

Fig 5.


Leopard seal -Total number of calls per call type (manual counts 2006 data)
Number of calls counted
7000
6000
5000
4000
3000
2000
1000
0
NO DATA
NO DATA
Jan-06
Feb-06
Mar-06
Apr-06
May-06
Jun-06
Jul-06
Aug-06
Sep-06
Oct-06
Nov-06
Dec-06
Jan-07
Feb-07
L1
L2
L3
L6
L5
L6
L7

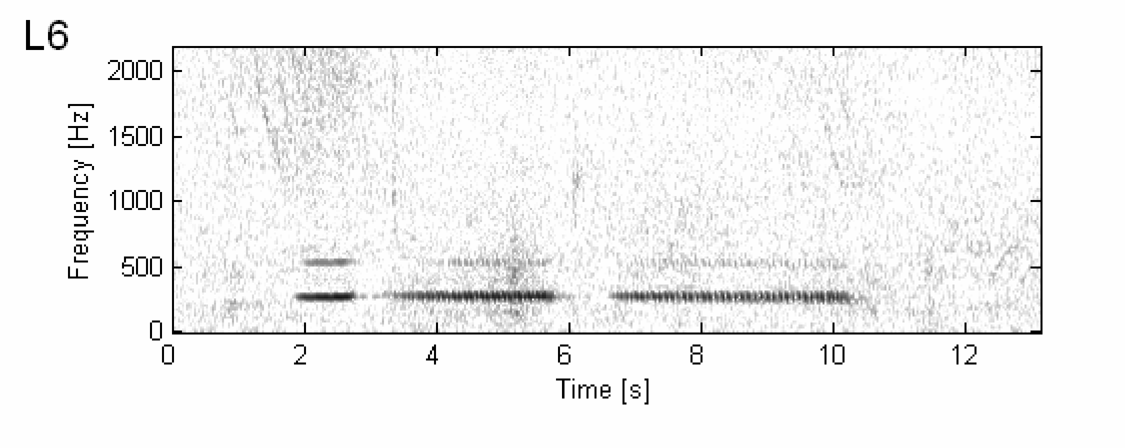

L6
Frequency [Hz]
2000
1500
1000
500
0
0
2
4
6
8
10
12
Time [s]

Fig 7.

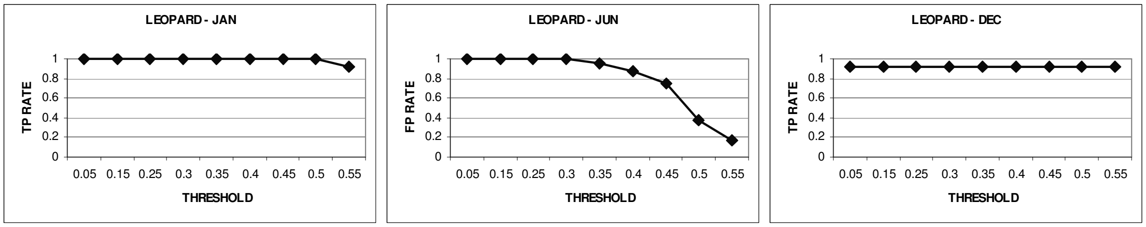

LEOPARD - JAN
TP RATE
1
0.8
0.6
0.4
0.2
0
0.05
0.15
0.25
0.3
0.35
0.4
0.45
0.5
0.55
THRESHOLD
LEOPARD - JUN
FP RATE
1
0.8
0.6
0.4
0.2
0
0.05
0.15
0.25
0.3
0.35
0.4
0.45
0.5
0.55
THRESHOLD
LEOPARD - DEC
TP RATE
1
0.8
0.6
0.4
0.2
0
0.05
0.15
0.25
0.3
0.35
0.4
0.45
0.5
0.55
THRESHOLD

Fig 8.

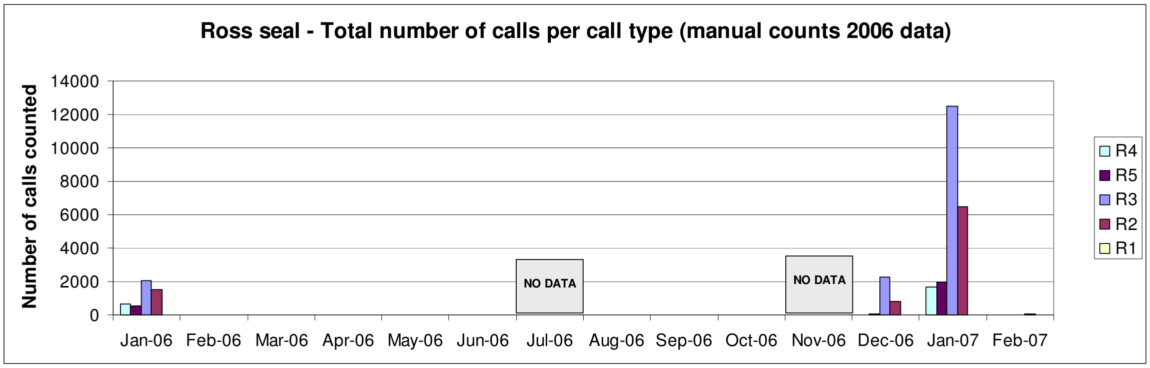


Fig 9.

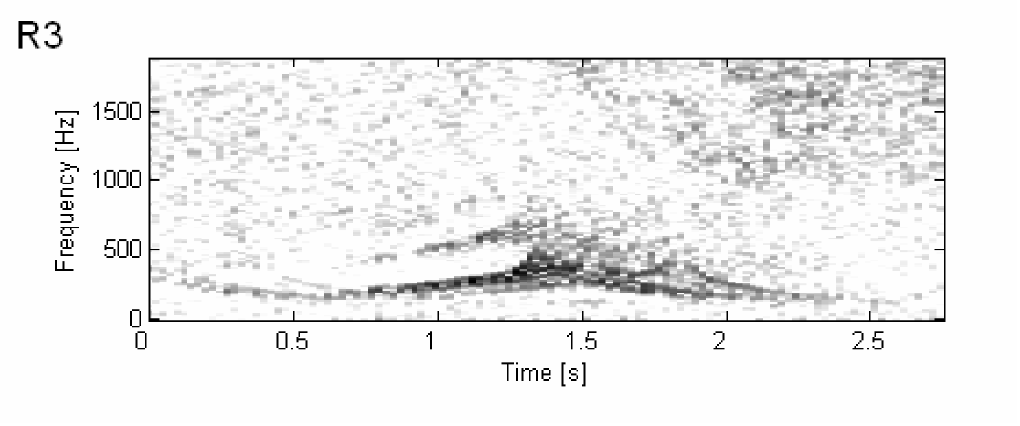


Fig 10.

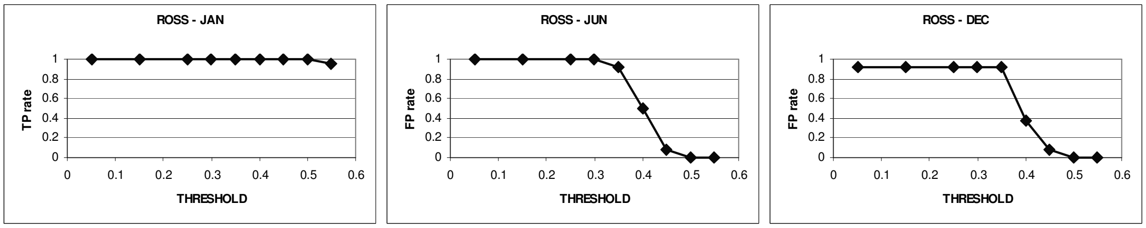


Fig 11.

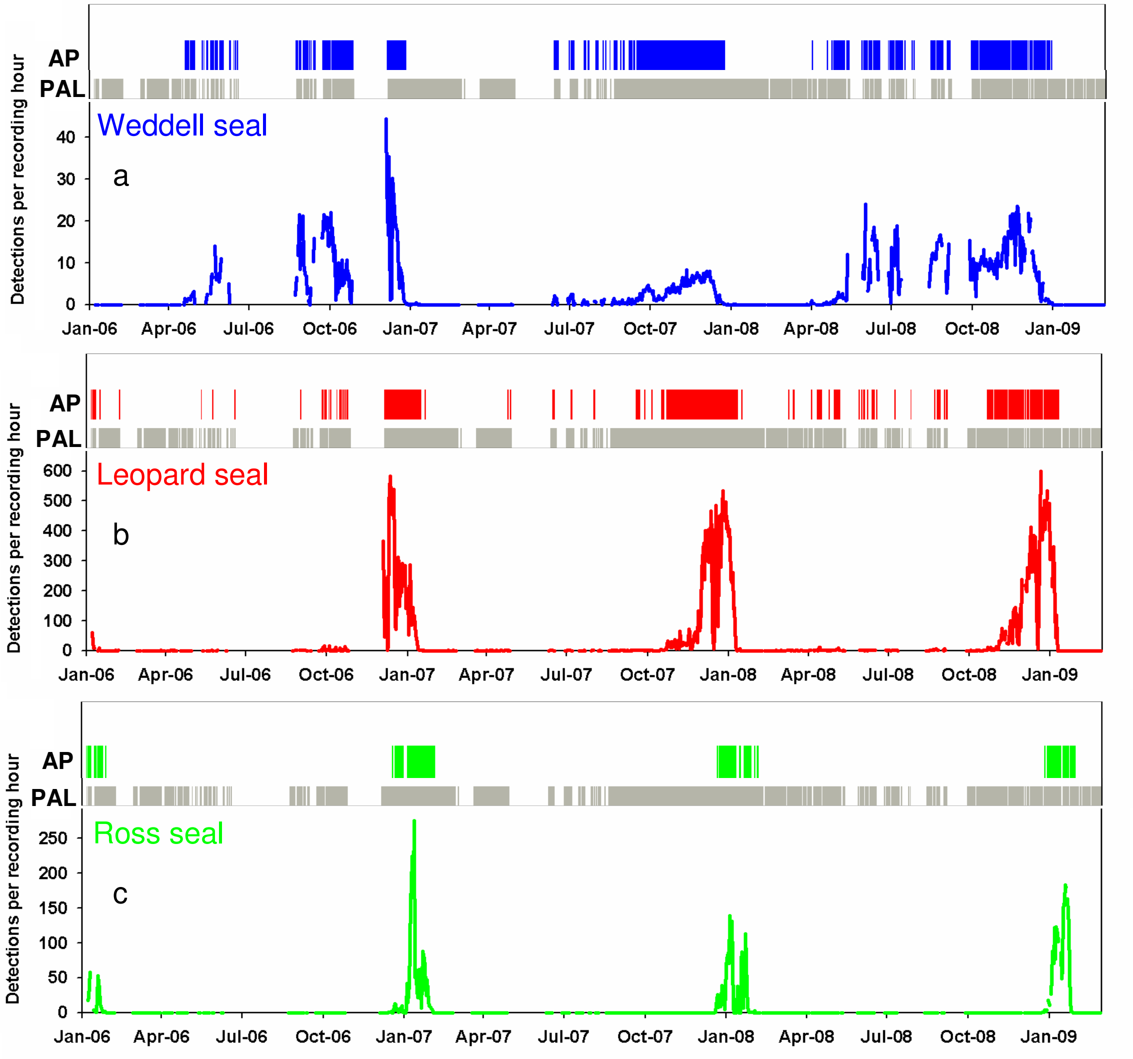

AP
PAL
Weddell seal
a
Detections per recording hour
0
10
20
30
40
Jan-06
Apr-06
Jul-06
Oct-06
Jan-07
Apr-07
Jul-07
Oct-07
Jan-08
Apr-08
Jul-08
Oct-08
Jan-09
AP
PAL
Leopard seal
b
Detections per recording hour
0
100
200
300
400
500
600
Jan-06
Apr-06
Jul-06
Oct-06
Jan-07
Apr-07
Jul-07
Oct-07
Jan-08
Apr-08
Jul-08
Oct-08
Jan-09
AP
PAL
Ross seal
c
Detections per recording hour
0
50
100
150
200
250
Jan-06
Apr-06
Jul-06
Oct-06
Jan-07
Apr-07
Jul-07
Oct-07
Jan-08
Apr-08
Jul-08
Oct-08
Jan-09

Fig 12a-c.

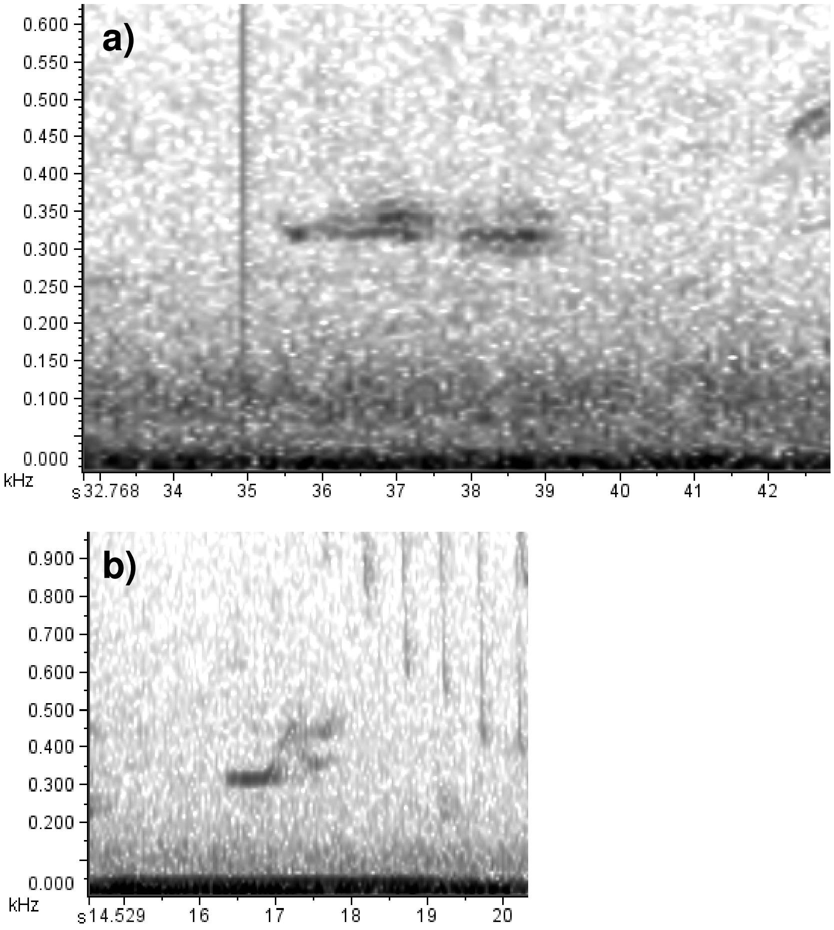

a)
0.600
0.550
0.500
0.450
0.400
0.350
0.300
0.250
0.200
0.150
0.100
0.000
kHz
s 32.768
34
35
36
37
38
39
40
41
42
b)
0.900
0.800
0.700
0.600
0.500
0.400
0.300
0.200
0.000
kHz
s 14.529
16
17
18
19
20

Fig 13.

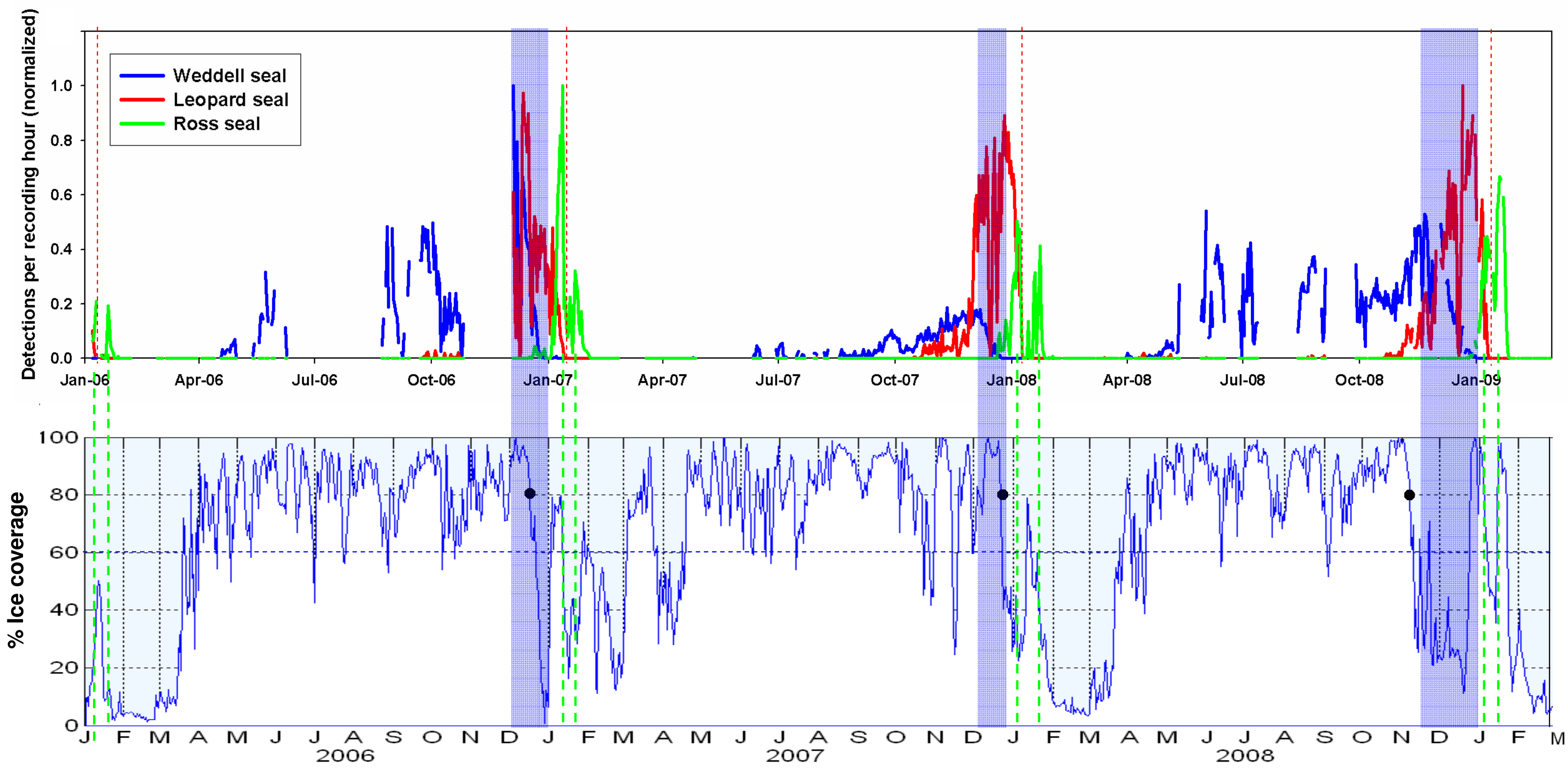

Detections per recording hour (normalized)
1.0
0.8
0.6
0.4
0.2
0.0
Weddell seal
Leopard seal
Ross seal
Jan-06
Apr-06
Jul-06
Oct-06
Jan-07
Apr-07
Jul-07
Oct-07
Jan-08
Apr-08
Jul-08
Oct-08
Jan-09
% Ice coverage
100
80
60
40
20
0
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M
2006
2007
2008

Fig 14.

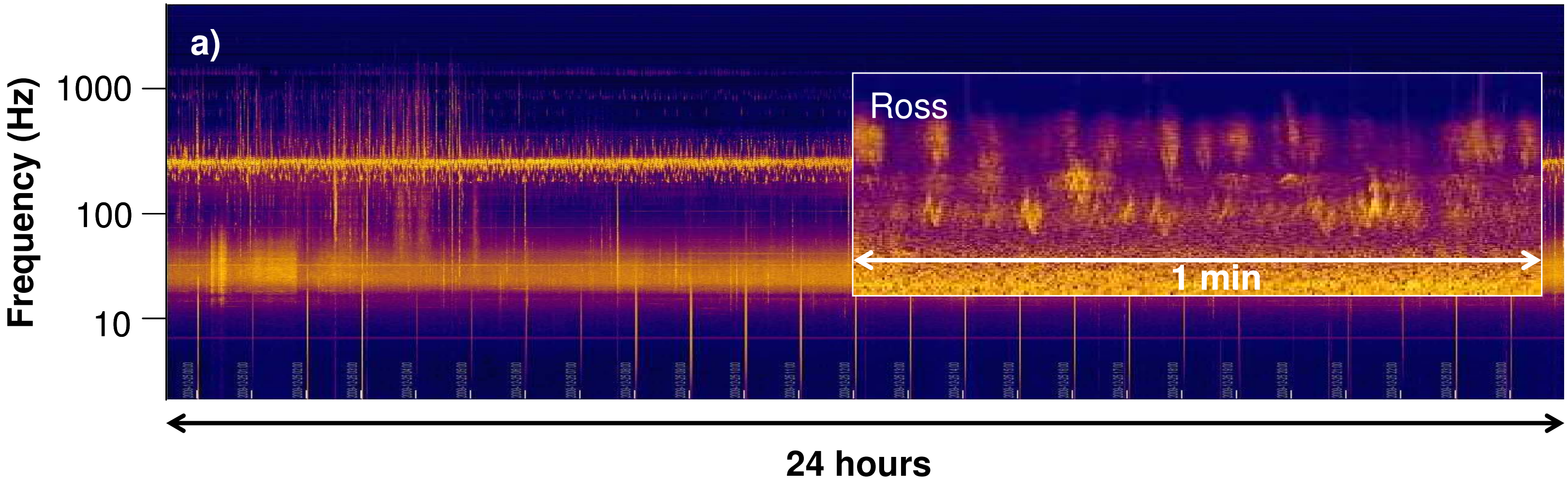


Fig 15.

Publication V

Leopard seal (Hydrurga leptonyx) vocalizations from three Antarctic locations

LEOPARD SEAL (*HYDRURGA LEPTONYX*) VOCALIZATIONS FROM THREE ANTARCTIC LOCATIONS

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Manuscript in preparation

ABSTRACT

Leopard seals (*Hydrurga leptonyx*) are known to produce underwater vocalizations during the breeding season in austral summer. This study investigated whether the acoustic characteristics o leopard seal high double trills (HDT) differed between three Antarctic locations (DI - Drescher Inlet (72°52'S – 19°26'W), AB - Atka Bay (70°31'S 8°13'W) and DS - Davis Sea (65°S 90°E)). The results showed some identifiable differences between DI versus AB and DS, although most acoustic parameters of HDTs did not differ largely between the three recording locations. HDTs recorded at DI had lower pulse repetition rates and narrower bandwidths compared to HDTs recorded at AB and DS. Principal Component Analysis showed a separation for HDTs originating from DI from HDTs recorded at AB and DS. Calls from AB and DS were less separable and showed partly overlapping clusters. Previous studies suggested that there is sufficient exchange of individuals between leopard seal breeding groups to prevent the development of genetic population structure. Our results support genetic studies and demonstrate a high level of similarity in leopard seal vocalizations between recording locations. Subtle site variation in calls from different recording locations might be attributed to differences in local social or environmental factors.

KEYWORDS

leopard seal, *Hydrurga leptonyx*, underwater vocalization, high double trill, geographic variation

INTRODUCTION

Geographic variation in vocal patterns can be found within a wide variety of taxa and may occur for several reasons including genetic variation, founder effects, social learning, or as an adaptation to environmental conditions (*e.g.,* Hunter & Krebs 1979, Catchpole & Slater 1995, Van Parijs *et al.* 2003). In non-migratory species or species that show site fidelity, geographic variation in vocal behaviour in some cases reflects distinct breeding populations or subpopulations (*e.g.,* Nelson *et al.* 2001, Stafford *et al.* 2001, Abgrall *et al.* 2003).

Several pinniped species exhibit geographic variation in their vocal behaviour, which in most species has been attributed to reproductive isolation of populations (*e.g.,* Le Boeuf & Peterson 1969, Thomas & Stirling 1983, Perry & Terhune 1999, Van Parijs *et al.* 2003, Risch *et al.* 2006, Terhune *et al.* 2008). Perry and Terhune (1999) compared harp seal (*Pagophilus groenlandicus*) underwater vocalizations between three North Atlantic breeding locations (‘Gulf’, ‘Front’ and Jan Mayen) and found the call repertoire and proportional call type usage in Gulf and Front to differ in a similar manner from the more distant Jan Mayen breeding group. These findings are supported by tagging studies, which showed that the Gulf and Front herd interbreed and are reproductively isolated from the Jan Mayen herd. In Weddell seals, both the call repertoire and the acoustic characteristics of call types were found to differ on a mesogeographic (600-2000 km) and macrogeographic level (>2000 km), suggesting that breeding groups were unlikely to mix over these distances (Abgrall *et al.* 2003; Thomas & Stirling 1983). However, on a microgeographic scale (150 km) no consistent differences existed in call repertoire and call characteristics between breeding groups (Pahl *et al.* 1997). These findings were also supported by tagging data, indicating that animals exhibited pronounced breeding site fidelity and were only likely to move between nearby breeding groups (Stirling 1974, Pahl *et al.* 1997, Cameron *et al.* 2007).

For leopard seals, knowledge of breeding populations, their mixing and distribution is only sparse. Slip *et al.* (1994) and Davis *et al.* (2008) found the genetic diversity in leopard seals sampled at six circumpolar locations to be low, suggesting that there is at least sufficient gene flow between breeding groups to prevent the development of genetic differentiation between populations. Nevertheless, Thomas and Golladay (1995) compared leopard seal underwater vocalizations between McMurdo Sound and Palmer Peninsula (*ca.* 5000 km distance), and found significant differences in call repertoire and call characteristics. They suggested that repertoires are likely to vary slightly between adjacent areas, and be more distinctive between distant regions, reflecting the low probability of encounter between geographically separated breeding groups. Hence, insights into the patterns of geographic variation of vocal behavior could potentially reveal more about the discreteness of leopard seal groups and the pattern of mixing between populations or breeding groups. In this study we therefore compare leopard seal vocal behavior between three Antarctic locations: Atka Bay, Drescher Inlet and Davis Sea (Fig. 1). These study sites allow comparisons on two different spatial scales. Atka Bay and Drescher Inlet have an along-shelf-ice distance of approximately 500 km, whereas the distance between Atka Bay and Davis Sea is about 4300 km. Drescher Inlet and Davis Sea have an along-ice-shelf distance of 4800 km.

To date, leopard seals are known to produce at least 13 different underwater vocalization types, which have been recorded during the breeding season from November to January (Stirling & Siniff 1979, Rogers *et al.* 1996, Thomas & Golladay 1995). The leopard seal call repertoire consists of short-distance “local calls” as well as long-distance “broadcast calls” (Rogers *et al.* 1996). Broadcast call types that have been recorded from free-ranging leopard seals at various recording sites are: the high, medium and low double trill, medium single trill, hoot and hoot with single trill, as well as the low ascending and descending trill (Stirling and Siniff 1979, Thomas and Golladay 1995, Rogers *et al.* 1996, Klinck 2008). The relatively similar vocal repertoire composition of leopard seals throughout their calling period, suggests that the function of their broadcast calls is relatively uniform (Rogers *et al.* 1996, Van Opzeeland *et al.* 2010), allowing selection of one broadcast call type to represent leopard seal vocal behavior. We selected one call type, the high double trill (HDT), to investigate geographic variation in leopard seal vocal behavior as based on the following reasons: 1) the HDT was found to occur at all leopard seal breeding sites (Stirling & Siniff 1979, Thomas & Golladay 1995, Rogers *et al.* 1996, Klinck 2008), 2) this call type can be used as a representative of overall leopard seal calling activity over the period in which leopard seals are acoustically present (Van Opzeeland *et al*. 2010), 3) in contrast to the low double trill, which forms a larger portion of the vocal repertoire than the HDT, the acoustic characteristics of the HDT allow reliable detection of this call type, even at higher background noise levels (Klinck 2008).

METHODS

Data collection

Atka Bay (PALAOA) data

Underwater recordings from Atka Bay (AB) were obtained from the PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA). PALAOA is an autonomous listening station located at 70°31'S, 8°13W on the Ekström Ice Shelf, 15 km north of the German Antarctic station Neumayer II (Fig 1). The Eckström iceshelf is a floating ice shelf which spreads into a typical finger-like structure (Boebel *et al.,* 2006). The North Pier, on which the observatory is located, is surrounded by the ocean on the north-west, north and east side. AB is located at the east to south-east side of the observatory. The depth of the seafloor inside AB ranges from 275 m in the inner section of the bay to 100 – 200 m near the shelf-ice edge and 900 m at the mouth of the bay (Wegner 1981). AB is covered with fast-ice from March to January. Recordings are made with a RESON TC4032 and a TC4033 hydrophone at a distance of 300 m from each other. The hydrophones are deployed through boreholes underneath the 100 m thick floating Eckström Ice Shelf, 80 m below the ice shelf (Boebel *et al.* 2006, Klinck 2008). The stereo-signal is amplified and digitized by a *BARIX Instreamer* at 16 Bit/48 kHz and transmitted wirelessly as a 192 kBits/s MP3 stream to the Neumayer Base, where it is stored on hard disk (see Kindermann *et al.* 2008 for more details). Effective bandwidth of the recordings is 10 Hz to 16 kHz, dynamic range 60 dB to 150 dB re 1 μPa.

Drescher Inlet (DIPS) data

During the Drescher Inlet Pilot Study (DIPS) acoustic recordings were made from 17 December 2003 to 2 January 2004 in the Drescher Inlet (DI) located at 72°50'S, 19°02'W (Fig. 1). DI is a 25 km long and up to 2 km wide crack in the Riiser Larsen Ice Shelf. The sea bed under the ice shelf extends over 100 km to the nearest grounding line of Dronning Maud Land (Schenke *et al.* 1998). According to bathymetric surveys of RV "Polarstern" (Graffe & Niederjasper 1997), the depth of the seafloor inside the inlet ranges from 430 m in the inner section to 380 m over a central 6-km-wide bank, and to 520 m at the inlet mouth. The depth outside the inlet gradually increases, reaching the 600 m isobath about 2 km distant from the inlet mouth. The fast-ice environment is characterised and strongly influenced by the seasonal ice break-up, particularly during late summer.

The recording setup was placed on solid sea ice at distance of about 6 km from the sea ice edge. Three RESON TC4032 hydrophones were deployed through boreholes in a 100 m baseline triangle at 100 m water depth. The system recorded three channels with a National Instruments DAQPad 6052E at 48 kHz/16 bit to wav files on a computer using the Ishmael software (Mellinger 2001). Effective bandwidth of the recordings is 10 Hz to 24 kHz.

Davis Sea data

Acoustic data from Davis Sea (DS, Fig. 1) were collected during an acoustic survey of the RV *Aurora Australis V4*. Recordings were made on 13 - 14 December 1997 on six locations between 62°S, 93°E and 63°S, 90°E. Water depth at these locations ranged from 3600 – 4000 m and ice cover at these locations varied between 4 – 8 / 10ths.

Recordings were made remotely using a sonobuoy (Sparton Electronics AN/SSQ-57A: frequency response 10 Hz - 20 kHz). Hydrophones were lowered to a depth of 18 m below the water surface. Signals with a custom-built receiver and recorded onto a Sony Digital Audio Tape recorder (TCD-D8: frequency response 10 Hz - 22 kHz).

Data analysis

Previous analysis of the PALAOA data showed a peak in leopard seal calling activity towards the end of December (Van Opzeeland *et al.,* 2010) which has also been reported by previous studies (Thomas and DeMaster 1982, Rogers *et al.,* 1996). Therefore, only acoustic recordings made in December were included in our analyses. For AB, recordings from 21 - 27 December 2006 were included (156 hours), for Drescher Inlet the recordings from 21 - 25 December 2003 (86 hours) and for DS the recordings made on 13 - 14 December 1997 (12 hours). Due to maintenance activities within the PALAOA observatory only one hydrophone (TC4032) was active in this period.

For each location 150 HDTs (Fig 2a) with a band-limited (1.5 - 4.5 kHz) signal-to-noise ratio > 15 dB, were selected for further analyses. In total 63 acoustic parameters were measured for all 450 HDT samples and investigated for geographic differences. Using OSPREY, noise-robust MATLAB™-based analysis software, 29 acoustic parameters were extracted from each of the two parts of the HDT calls. In brief, a spectrogram of the acoustic data is computed and displayed, and an analyst designates a time/frequency box around a call of interest, the *annotation box*. OSPREY then calculates a smaller *feature box* from which the acoustic parameters are automatically extracted and written to a logfile. For this analysis the following spectrogram parameters were used: frame size and FFT size 4096 samples (0.085 s), overlap 50% (0.043 s), and Hamming window, for a spectrum filter bandwidth of 47.6 Hz. A detailed description of how OSPREY determines the *feature box* as well as a detailed description of all 29 parameters and how they are calculated are given by Mellinger and Bradbury (2007).

The remaining 5 acoustic parameters describe the temporal evolution of the pulse repetition rate (PRR). The PRR is the rate of amplitude modulation of the signal, which appears as sidebands of the carrier frequency in the spectrogram (Klinck *et al.* 2008). Parameters of the PRR measured were (Fig. 2b): PRR start frequency of call part 1 (30), PRR maximum frequency of call part 1 (31), PRR envelope and frequency of call part 1 (32), PRR envelope start frequency of call part 2 (33), PRR envelope end frequency of call part 2 (34). For a more detailed description of how the PRR parameters were measured, see Klinck *et al.,* 2008.

To visualize the distribution of each acoustic parameter, we used the Matlab Statistics toolbox to produce estimates of probability density functions (PDFs) of all parameters independently for each geographic location. First, the parameter space (min to max) was linearly interpolated to 100 steps separately for each location. Second, probability density functions were calculated using the Matlab™ function „*ksdensity*“, employing a normal kernel distribution of optimized width (default settings, see Matlab™ function description). Figure 3 exemplifies the results for the parameters call duration, bandwidth, pulse repetition rate and signal-to-noise-ratio of call part 1. By screening the full set of parameter PDFs, relevant parameters were then selected for further analysis by Principal Component Analysis (PCA) on the basis of the visual separability of the three locations within each plot.

RESULTS

The mean duration of call part 1 was 1.10 ± 0.53 s for DS and 1.22 ± 0.61 s for AB, while the recordings from DI showed an intermediate median duration of 1.17 ± 0.48 s (Table 1). Call part 2 showed a corresponding pattern in mean duration for the three study sites, but had generally shorter durations compared to call part 1.

Kernel density estimations for the durations of leopard seal HDTs at the three study sites show partially overlapping distributions for call part 1 (Fig 3a). The curves are positively skewed, showing a peak for short call durations and an elongated tail towards longer call durations.

For lower and upper frequencies of the HDT, calls from DI had substantially higher values for lower frequencies and lower values in upper frequencies compared to the other two sites. The mean lower frequency of call part 1 for DI was approximately 100 Hz higher compared to AB and 80 Hz higher compared to DS (Table 1). The means for upper frequencies of call part 1 were approximately 600 Hz lower for high double trills recorded at DI compared to DS and more then 100 Hz lower as for HDTs recorded at AB. The resulting mean bandwidth of the calls at DI was substantially narrower than those of HDTs recorded at AB and DS (Table 1). Interestingly, the kernel density estimations showed bimodal distributions of the mean bandwidth of call part 1 for AB and DS, overlapping partly with DI (Fig. 3b). The results for call part 2 showed a corresponding pattern for the means of lower and upper frequencies between the three locations, though with smaller differences between locations than call part 1.

All PRR values measured for HDTs recorded at DI were lower than PRR values of calls recorded at AB and DS, respectively (Table 1). The distributions of the five pulse repetition rate parameters clearly separated DI from AB and DS calls. Calls from DI generally tended towards lower PRR which was most distinctive in the PRR start (parameter 30) of call part 1 (Fig 3c). PRR values measured for call part 2 showed a similar trend as call part 1, although differences between DI and the other two locations were less pronounced.

Signal-to-noise-ratios were lowest at DI compared to the other study sites (Fig. 3d, Table 1).

To explore if calls could be separated according to recording location, we performed a Principal Component Analysis (PCA). As described previously, only a subset of relevant acoustic parameters was included in the PCA, being all five PRR parameters, the lower and upper frequency and the duration of call part 1 and 2. The first two principal components of the PCA explained 67 % of the variance (Table 2) and revealed a clear separation of the HDTs originating from DI from those recorded at the other two study sites (Fig. 4). Component 1 represents mainly the contribution of the PRR parameters, whereas component 2 reflects the importance of the upper frequency of both call parts as well as the duration of call part 1 in distinguishing locations (Table 1).

DISCUSSION

1. Variation between recording sites

The results of our study demonstrate some identifiable differences in leopard seal HDTs recorded at different sites; interestingly more difference was observed between the closest sites (DI versus AB, 500 km apart) and the least, between the most disparate sites (AB and DS, 4300 km). The bandwidth and pulse repetition rates of calls recorded at DI differed from calls recorded at AB and DS, whereas calls recorded at the latter two locations were not clearly separable according to recording site. However, overall the observed pattern reflects a remarkable similarity in the acoustic characteristics of leopard seal HDTs across the three recording locations. While other species, such as harp and Weddell seals, exhibit considerable variation in their vocal behavior between breeding groups on varying spatial scales (*e.g.* Perry and Terhune 1999, Abgrall *et al*. 2003), our measurements show that leopard seal HDTs exhibit substantial acoustic similarity up to spatial scales larger than 4000 km. This leaves it likely that there is exchange or at least contact between individuals from the three different recording locations and that subtle site differences are attributable to other factors than geographic isolation of populations. Our findings correspond to the study by Davis *et al.*, (2008) who found no genetic differentiation between leopard seal populations across the Antarctic and suggested that there is sufficient gene flow between breeding groups to prevent development of population structure. Information on movement patterns from tagged leopard seals also not excludes exchange or contact between individuals from different breeding locations, although the range of movement varies largely between individuals (Rogers *et al.* 2005; Nordøy & Blix 2009).

Below we further discuss various aspects that might explain the observed differences in call characteristics between DI versus AB and DS, recognizing that these might also act in concert.

1.1. Differences in local group composition

In our study there was no information on the number of individuals sampled so that a relatively small subset of individuals may have been used to describe the total population variation for each location. However, adult male leopard seals within a region show little difference between acoustic characteristics for specific calls and this includes the HDT call (Rogers and Cato 2002). There was also no information on the sex or age class of callers, consequently it is not known to what extent differences in group composition between the three localities may have influenced the results; the HDT is known to be produced by both sexes and by juvenile and adult leopard seals, with substantial differences in the acoustic characteristics of HDTs produced by different age classes (Rogers *et al.* 1996, Rogers 2007). In our data, HDT bandwidth of calls recorded at AB and DS has a bimodal distribution, possibly reflecting two ‘types’ of HDTs produced by different age classes and/or sexes. In addition, the absence of this bimodal pattern and partial overlap of distributions of AB and DS with DI suggests calls are more homogeneous at the latter location. It cannot be excluded that the differences in leopard seal call repertoire and call characteristics between Palmer Peninsula and McMurdo Sound reported by Thomas and Golladay (1995) can be attributed to differences in local group composition, given that in their study no information on the individuals that produced the calls was collected.

The lack of information on the age and sex of the individuals that produced the HDTs in our study is an aspect of our data which we share with many other studies investigating the underwater vocalizations of marine mammals (*e.g.,* Perry & Terhune 1999; Stafford *et al.* 2001; Abgrall *et al.* 2003; Rossi-Santos & Podos 2006; May-Collado & Wartzok 2008). Although in many cases such information can simply not be collected, awareness of this potential bias can overcome overinterpretation of site variation in vocalizations. Particularly in territorial species (*i.e.,* species that defend geographic underwater areas against rival individuals), acoustic sampling should be conducted with caution, *e.g.,* by recording at several locations to ensure that calls of a sufficiently large number of individuals are sampled.

1.2. Local environmental conditions

Recordings from DI had smallest signal-to-noise-ratio of all three sites. Leopard seals use their calls to attract mating partners over relatively long distances (Rogers *et al.*, 1996) and might therefore adapt their calls in response to local ambient noise conditions to increase calling range. Calls recorded at DI had a substantially narrower bandwidth compared to the other two study sites. Narrowing the bandwidth of a call and concentrating the acoustic energy of the call in a part of the spectrum with little environmental noise is a strategy in various animal taxa to increase the range of communication in noisy environments (Ryan and Brenowitz 1985, Morton 1975, Bertelli and Tubaro 2002). Pulse repetition rate also differed between DI vs AB and DS which might reflect a similar adaptation to local ambient noise conditions. Several studies have found pulse repetition rate to be the acoustic variable that differs between groups or populations of animals in a wide range of species, although the reason for these differences remains unclear (Nevo *et al.* 1987; Rotenberry *et al.* 1996; Rankin & Barlow 2005). In this case the vocal characteristics of leopard seals recorded at DI could reflect either a short-term adaptation (*i.e.,* vocal plasticity in response to environmental conditions) or a learned vocal characteristic.

2. Call duration

The results for HDT duration at all three study sites showed similar distributions for the majority of HDTs. However, at all sites the skewed distribution of the duration of call part 1 revealed that while few call parts were shorter in duration than the mode, a significant proportion of the first call part had longer durations. Rogers (2003) noted that leopard seal vocalizations are potentially energetically very costly calls for the animals to produce and might therefore function to signal fitness to potential mating partners or a competitive response to other vocalizing individuals. Weddell seals have also been found to lengthen many of their underwater calls in response to overlapping vocalizations of conspecifics, thereby increasing the detectability of their calls and potentially indicating fitness of the calling individual (Terhune *et al.* 1994). Lengthening of calls in leopard seals may serve a similar function, although the number of calls with increased duration might be more restricted by the high energetic costs associated with the production of these calls.

3. Conclusion

In conclusion, our study has demonstrated that leopard seal HDTs exhibit large scale similarity across recording locations and that acoustic similarity is not related to geographic distance. We suggest that differences in local social factors, such as differences in group composition or local abiotic factors might explain the observed differences between recording locations.

ACKNOWLEDGEMENTS

The installation and operation of PALAOA would not have been possible without continuous support of AWI logistics, FIELAX and the overwintering teams. Recordings from the Davis Sea, thanks to the crew and staff of the Australian Antarctic Division that assisted with the acoustic surveys from the *Aurora Australis* special mention to the ship's captains, Murray Elis and Peter Pearson who were extremely helpful in ensuring the ship didn't drive backwards, over sonobuoys, at the time of the survey.

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TABLES

Table 1. Descriptive statistics of the acoustic parameters measured for leopard seal high double trills (HDT) recorded at AB, DI and DS (n=150 for each location).

	AB		DI		DS	
Parameter	**Mean**	**av. Deviation**	**Mean**	**av. Deviation**	**Mean**	**av. Deviation**
Lower frequency part 1 [Hz]	2807.08	41.58	2919.11	34.92	2836.89	33.85
Upper frequency part 1 [Hz]	3391.99	264.15	3264.62	74.70	3889.36	301.26
Bandwidth part 1[Hz]	584.91	252.95	345.51	88.76	1052.47	291.21
Lower frequency part 2 [Hz]	2741.7	35.0	2849.7	42.5	2794.4	30.5
Upper frequency part 2 [Hz]	3220.9	196.9	3192.0	75.8	3557.1	324.5
Duration part 1 [s]	1.22	0.61	1.17	0.48	1.10	0.53
Duration part 2 [s]	1.03	0.20	1.01	0.23	0.93	0.25
Signal-to-noise-ratio part 1 [Hz]	17.8	1.2	11.4	0.9	13.1	1.1
PRR start part 1 [Hz]	70.92	0.98	63.84	1.43	72.15	1.38
PRR max. part 1 [Hz]	74.93	0.65	68.55	0.89	76.00	1.40
PRR end part 1 [Hz]	70.53	1.63	62.82	1.66	72.04	2.12
PRR start part 2 [Hz]	64.45	2.66	57.21	2.01	63.68	2.75
PRR end part 2 [Hz]	72.25	0.88	66.68	1.40	70.37	1.40

Table 2. Component loadings from Principal Component Analysis parameters measured for HDTs recorded at AB, DI and DS (n=150 for each location).

HDT parameter	PC1 [49%]	PC2 [18%]	PC3 [11%]
PRR start part 1	0.40	-0.01	0.14
PRR max part 1	0.40	0.00	0.17
PRR end part 1	0.40	0.13	-0.08
PRR start part 2	0.37	0.00	-0.32
PRR end part 2	0.36	-0.20	-0.06
Lower frequency part 1	-0.32	0.32	0.02
Upper frequency part 1	0.20	0.49	0.33
Duration part 1	-0.07	-0.40	0.56
Lower frequency part 2	-0.28	0.35	-0.11
Upper frequency part 2	0.14	0.53	0.38
Duration part 2	-0.10	-0.21	0.50

FIGURE LEGENDS

Figure 1: Map of Antarctica showing the three study sites: DI = Drescher Inlet; AB = Atka Bay; DS = Davis Sea.

Figure 2 a) Spectrogram of the high double trill b) Spectrogram showing the high double trill modulation frequencies: 11= PRR start frequency call part 1; 12 = PRR maximum frequency call part 1; 13 =PRR end frequency call part 1; 14 = PRR start frequency call part 2; 15 = PRR end frequency call part 2.

Figures 3: Kernel density estimations for a) duration, b) bandwidth, c) pulse repetition rate and d) signal-to-noise-ratio of call part 1 of high double trills recorded at AB (green), DI (red) and DS (blue).

Figure 4: Scatterplot of the first two principal components of a PCA applied on all pulse repetition rate parameters, upper and lower frequency and duration of both call parts extracted from 450 HDTs recorded at DI (red), AB (blue) and DS (green).

FIGURES

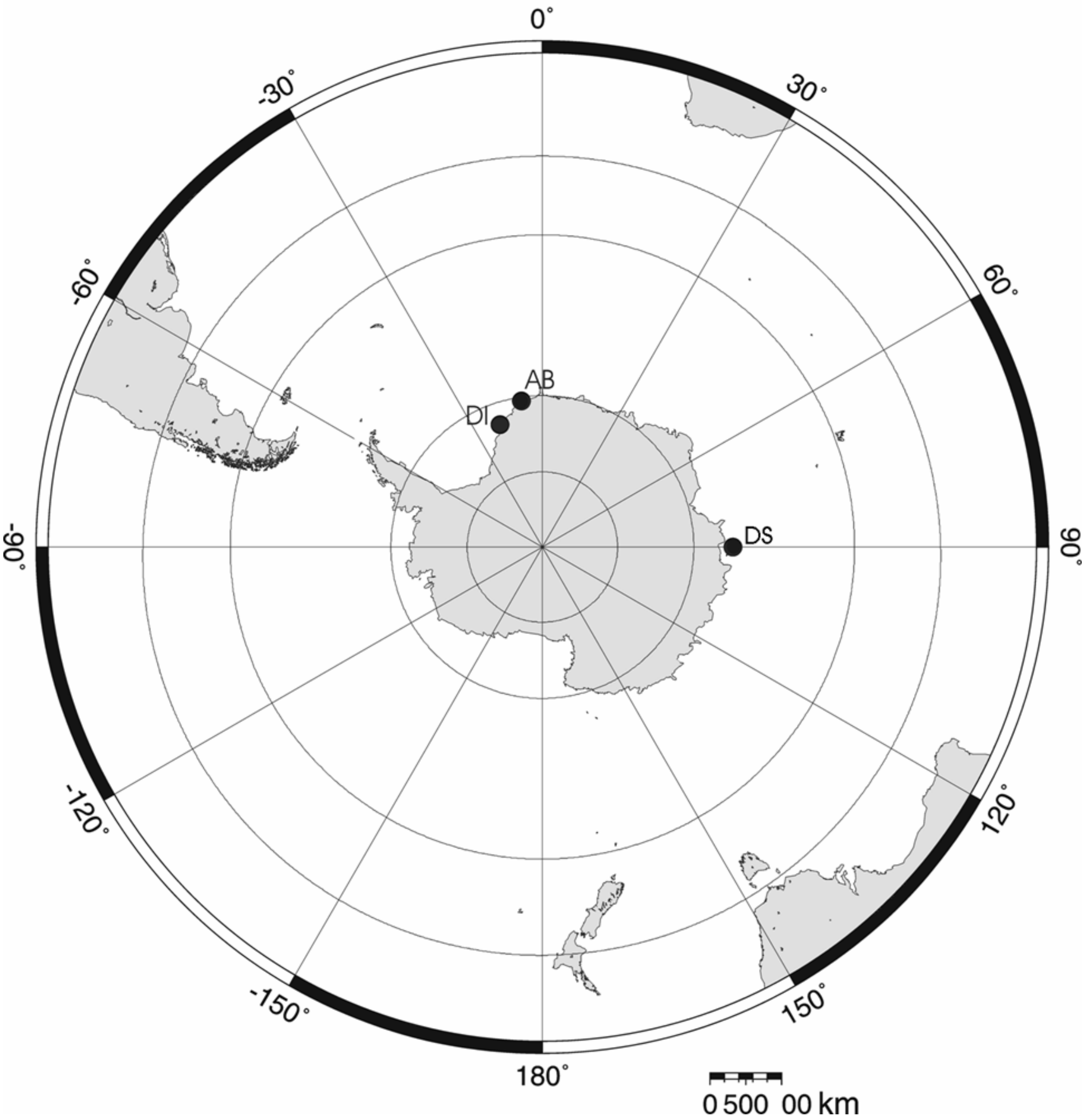
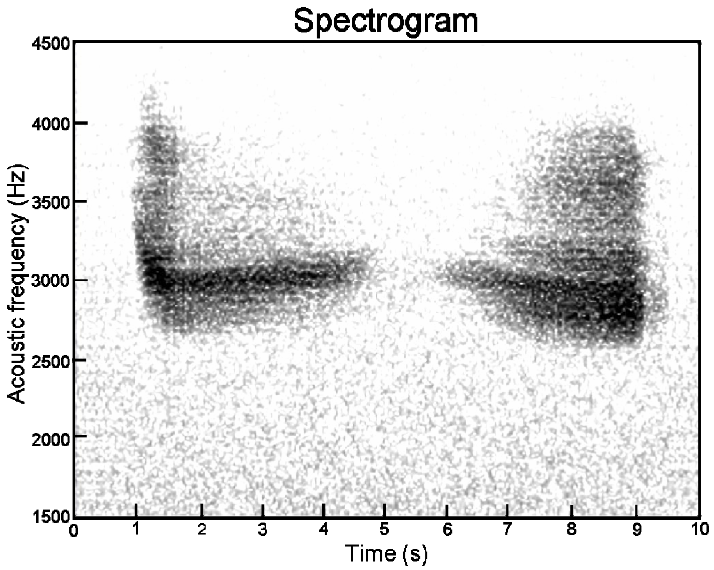
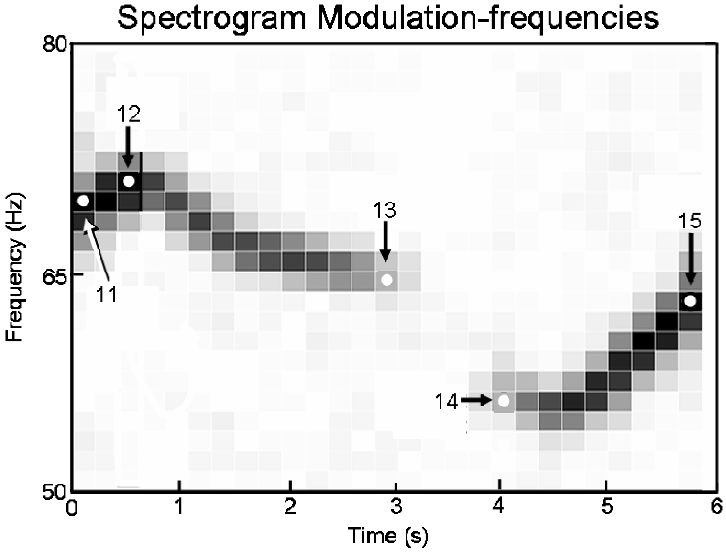


Fig. 1

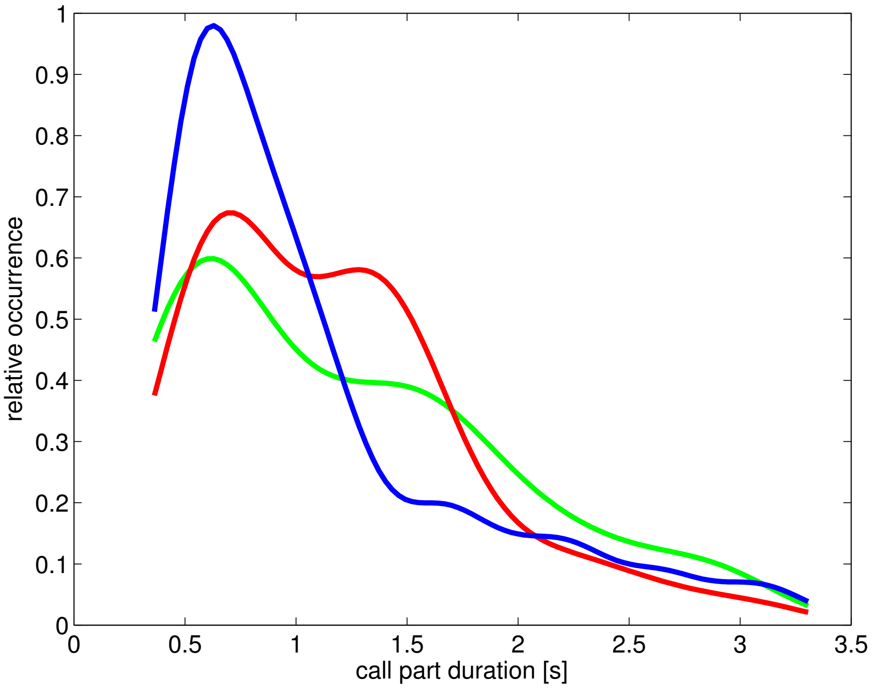

Spectrogram
Acoustic frequency (Hz)
4500
4000
3500
3000
2500
2000
1500
0
1
2
3
4
5
6
7
8
9
10
Time (s)

a)

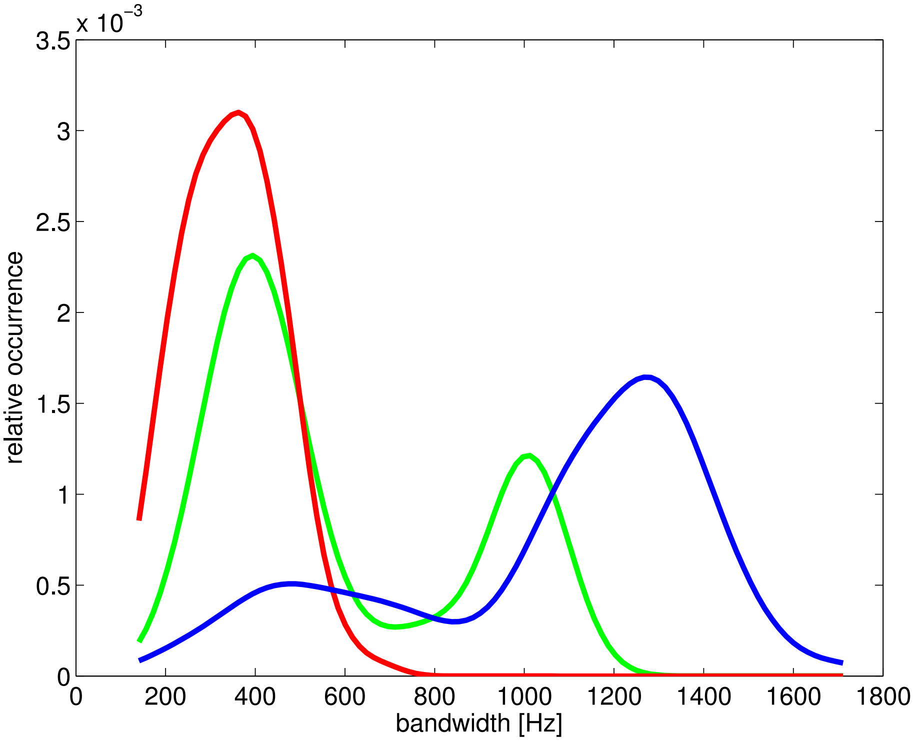

Spectrogram Modulation-frequencies
Frequency (Hz)
80
65
50
0
1
2
3
4
5
6
Time (s)
11
12
13
14
15

b)

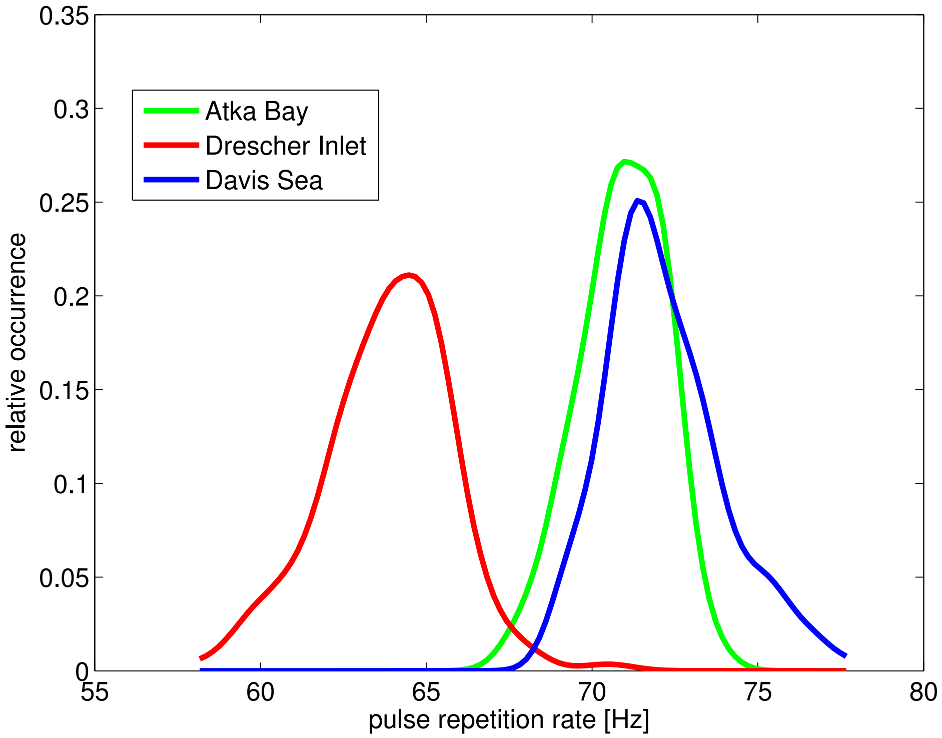
Fig. 2a & b


relative occurrence
call part duration [s]
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
0.5
1
1.5
2
2.5
3
3.5

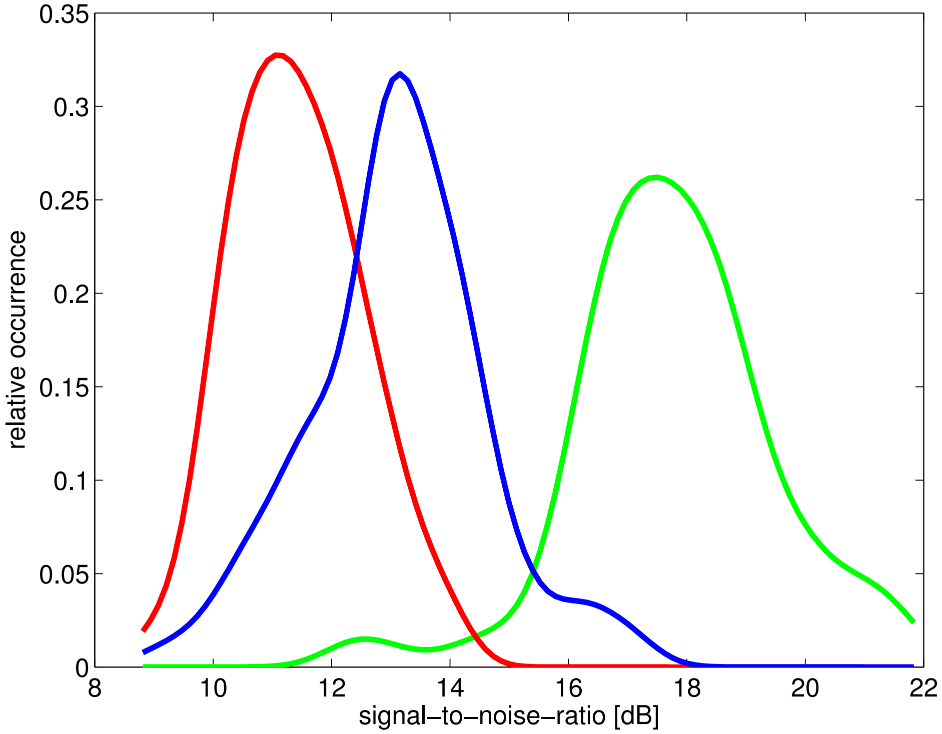
a)


x 10^-3
relative occurrence
bandwidth [Hz]
0
0.5
1
1.5
2
2.5
3
3.5
0
200
400
600
800
1000
1200
1400
1600
1800

b)


Atka Bay
Drescher Inlet
Davis Sea
relative occurrence
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
55
60
65
70
75
80
pulse repetition rate [Hz]

c)


relative occurrence
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
8
10
12
14
16
18
20
22
signal–to–noise–ratio [dB]

d)

Fig 3 a-d

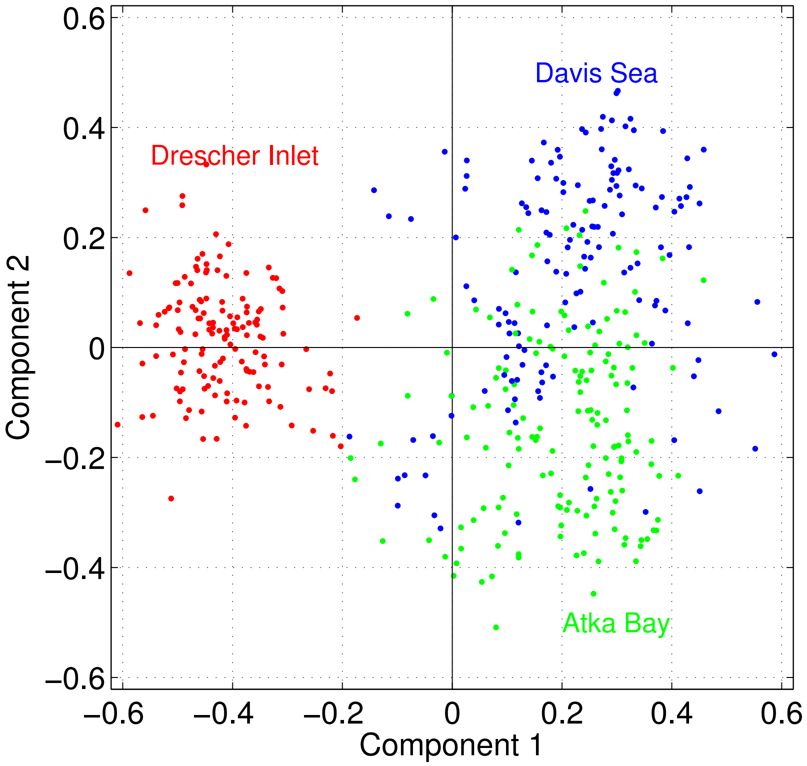

Davis Sea
Drescher Inlet
Atka Bay
Component 1
Component 2
0.6
0.4
0.2
0
−0.2
−0.4
−0.6
−0.6
−0.4
−0.2
0
0.2
0.4
0.6

Fig. 4

Publication VI

Geographic variation in vocalizations of pups and mother-pup behavior of harp seals (Pagophilus groenlandicus)

Vol. 6: 109–120, 2009
doi: 10.3354/ab00170

AQUATIC BIOLOGY
Aquat Biol

Geographic variation in vocalizations of pups and mother-pup behavior of harp seals *Pagophilus groenlandicus*

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ABSTRACT: All harp seal populations form breeding aggregations on the Arctic pack ice. However, pack ice conditions vary spatially and temporally among these aggregations with variation in environmental and oceanographic conditions, which may affect the behavioral interactions between mothers and their newborn pups. We investigated the variation in mother-pup behavior between harp seal breeding aggregations in the NE (Greenland Sea) and NW Atlantic coastal shelf region (Front). Acoustic cues provided by the pups are thought to be important in facilitating reunions with their mothers. Consequently, we measured variation in vocal parameters among seals to investigate geographic differences in pup vocalizations. Classification trees showed a distinctive split between Front and Greenland Sea pup vocalizations. There were no clear differences between male and female pups at the Front, where 42% of male and 38% of female pup calls could be attributed to a given individual. This contrasts with the Greenland Sea, where 55% of vocalizations of female pups were attributed to individuals compared with only 8% for males. Analyses of behavioral observations of mother-pup pairs made in the afternoon and evening showed that pups in the Greenland Sea suckled more and were more alert than pups in the Front. Further, mother-pup attendance patterns differed between sites. Mothers at the Front attended their pups 85.1% of the time, whereas mothers in the Greenland Sea attended their pups 52.2% of the time. These substantial differences between sites might be related to evolutionary changes in behavior resulting from commercial hunting or variable environmental conditions.

KEY WORDS: Harp seal · *Pagophilus groenlandicus* · Pup vocalizations · Mother-pup behavior · Geographic variation · Climate change

INTRODUCTION

Geographic variation in behavioral traits offers opportunities to make inferences about selective pressures that may influence behavior and the degree of differentiation among populations. Geographic variation in behavioral traits is common to a variety of taxa and has been described in various behavioral contexts ranging from dietary preferences in garter snakes *Thamnophis elegans* to migratory routes in blackcaps *Sylvia atricapilla* and antipredator behavior in ground squirrels *Spermophilus beecheyi* (see Foster 1999 for a review). Research efforts into geographic variation in behavioral traits have, however, largely focused on variation in behavior of adults within populations. Less is known about differences in the behavior of young and juveniles.

In pinnipeds, geographic variation in behavioral traits such as mother–offspring interactions and male display behavior has been documented in a number of species (Terhune 1994, McCulloch & Boness 2000, Van Parijs et al. 2000). Several studies have also reported geographic variation in the vocalizations of pinniped species. In harbour seals *Phoca vitulina*, variation in

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vocal behavior occurs between genetically isolated populations. However, site-specific vocalizations are also present between genetically mixed groups, suggesting site-specific selection for changes in certain vocal parameters that may be driven by local ecology or climate or both (Van Parijs et al. 2000, 2003, 2004).

In many pinniped species vocal behavior is important in female recognition of offspring during the lactation period (Insley et al. 2003). Insley (1992) suggested that although many pinniped species exhibit individually stereotyped vocalizations, the degree to which selection has favoured development of a vocal recognition system may vary with the reproductive environment of different species. Female grey seals in 2 reproductively isolated populations were found to respond differently to playbacks of vocalizations of their own pups (McCulloch & Boness 2000). Females on Sable Island, Nova Scotia, were found to discriminate between calls of their own and non-filial pups, while on the Isle of May, females failed to recognize the calls of their own pup (McCulloch et al. 1999). The fact that allo-suckling (i.e. non-offspring nursing) was more frequently observed in pups on the Isle of May than on Sable Island may also indicate differences in pup behavior between the 2 colonies.

In ice-breeding seals, females form dispersed aggregations on the ice during the breeding season (Lydersen & Kovacs 1999, Van Parijs et al. 2001). In most species, females may have to forage to sustain late lactation, leaving their pup alone on the ice (e.g. Testa et al. 1989, Lydersen & Kovacs 1999). The relocation process is often complicated by hourly or daily movements of the ice, causing pups to drift away from where they were when their mothers left. However, the stability of the breeding substrate used can differ substantially between different species and sites, ranging from large stable ice floes with breathing holes through which females return to their young, to small mobile ice floes or pack ice, the location and size of which is often heavily influenced by currents and weather conditions (Terhune et al. 1979, Lydersen & Kovacs 1993). To date, little is known about which, and how, factors such as the role of ice conditions influence mother-pup reunions in most ice-breeding seals.

Harp seals *Pagophilus groenlandicus* are ice-breeding seals and the most abundant pinnipeds in the North Atlantic. There are 3 populations: (1) the White Sea/Barents Sea population, (2) the NW Atlantic population, subdivided into a Gulf of St Lawrence ('Gulf') component and a coastal shelf component off NE Newfoundland and/or southern Labrador ('Front'), and (3) the Greenland Sea (NE Atlantic) population, which breeds on the pack ice between eastern Greenland and Jan Mayen (Sergeant 1991). Several studies have found genetic separation between NE and NW Atlantic harp seals (Meisfjord & Sundt 1996, Perry et al. 2000).

All harp seal populations form large breeding aggregations on the ice. The whelping period varies somewhat between populations, but is strongly synchronous within populations, with the majority of pups in an aggregation born within a very short (3 to 4 d) period. Nursing lasts around 10 to 12 d (Sergeant 1991). During this period females spend a few hours each day in the water, leaving their pups alone on the ice. Alongside visual, olfactory and spatial cues, acoustic cues provided by the pup are likely to play an important role in the relocation process. Ice conditions, such as the rate of ice drift, the type of ice that is used for breeding and ice concentration, vary annually and between the different breeding locations of populations (Wilkinson & Wadhams 2005, Friedlaender et al. 2007). The breeding substrate in the Gulf of St. Lawrence consists of large stable ice planes with breathing holes. It is thought that this substrate enables the female to predominantly use spatial cues during the relocation of her pup (Kovacs 1995). In contrast to the situation in the Gulf, the ice pack encountered off Newfoundland (Front) is usually made up of small mobile seasonal (first-year) ice floes (G. Stenson pers. obs.). In the NE Atlantic, the ice pack encountered in the Greenland Sea mainly consists of perennial (multi-year) ice floes. Each of these ice types has distinctive physical (e.g. thickness, albedo and roughness) and biological characteristics (Snack-Schiel 2003).

Our aims in this study were to investigate (1) whether vocal characteristics of harp seal pups vary geographically, and (2) whether behaviors of mothers and their pups differ between the breeding areas in the Front and the Greenland Sea.

MATERIALS AND METHODS

Data collection. We recorded vocalizations and behavior of suckling harp seal pups and female attendance patterns during 2 study periods at 4 breeding sites, 2 in the Greenland Sea and 2 off southern Labrador-northeast coast of Newfoundland (Front). Because of the difference in timing of whelping in the 2 areas, the study in the Greenland Sea was carried out from 18 to 30 March 2002 and the study in the Front was conducted from 10 to 22 March 2004 to ensure that pups of similar age were present.

Data collection for the Greenland Sea and the Front were carried out in conjunction with harp seal abundance surveys run by the Institute of Marine Research in Norway and the Department of Fisheries and Oceans in Canada (see Haug et al. 2006 and Stenson et al. 2005 for descriptions of the surveys). Once breeding aggregations were located, data collection on mothers and pups was carried out from ice-strengthened vessels either directly or as a base for helicopters.

The breeding aggregations in the Greenland Sea were situated in the pack ice areas northeast of Jan Mayen, centred around 72° 14′ N, 12° 43′ W (Patch GS-A) and 72° 10′ N, 13° 10′ W (Patch GS-B, Fig. 1). These correspond to patches A and B in Haug et al. (2006). At the Front, the patches were situated off the coast of southern Labrador around 50° 46′ N, 55° 19′ W (F-A) and 51° 28′ N, 55° 07′ W (F-B, Fig. 1). These were referred to as the Cartwright and Belle Isle concentrations, respectively, by Stenson et al. (2005). The estimate of the number of pups in patch GS-A was 4700 and in patch GS-B was 82 600 (Haug et al. 2006); the estimate in patch F-A was 368 705 and in patch F-B was 272 074 pups (Stenson et al. 2005).

Pup vocalizations. We chose groups of pups to record based on safe access by helicopter or vessel to ice floes where several pups were within walking distance. The helicopter landed within a few meters of the nearest mother-pup pair. Landings and lift-offs were as short as possible in order to minimize disturbance. Helicopter landings frequently caused the nearest pups to start vocalizing, while mothers sometimes left the ice. However, mothers and pups were usually reunited within minutes of the helicopter taking off. In the case that females and their pups were noticeably disturbed by the helicopter landing and take off, we concentrated on recording pups that showed no disturbance or waited until behavior of disturbed animals had returned to normal before recording. In the Greenland Sea herd we caught all pups that we recorded and tagged them with a Dalton roto-tag in the webbing of the right rear flipper. This tag has been developed for long-term identification of domestic sheep and goats. Studies on a variety of species have shown that piercing caused by the insertion of the roto-tag heals quickly, with no apparent detrimental effect on the behavior of the individuals or apparent change in behavior of other individuals towards tagged individuals (Testa & Rothery 1992). In harp seals, the wound caused by insertion of the roto-tag caused little to no bleeding and had healed cleanly in all pups that were revisited on subsequent days. During the tagging and recording procedures, mothers left their pups and watched from a distance either from another flow or from the water. For all pups tagged during this study, reunion between mother and pup occurred within minutes after the observers left the pup. At the Front, study areas were marked with dye and visited only once to make acoustic recordings of individual pups. Within each study area recordings were made of 5 to 10 ind. and the recorder was therefore able to visually identify which pups had been recorded.

We determined the sex and approximate age (based on pelage-specific developmental stages; see Table 2 in Kovacs 1987) of each pup in both areas.

We used an MD 421-II microphone (Sennheiser; sensitivity 170 dB, frequency bandwidth 36 Hz to 17 kHz ± 3 dB) connected to a TCD-D8 digital audiotape recorder (Sony; frequency response 5 Hz to 22 kHz) to record pup vocalizations. The microphone was held 0.1 to 0.3 m from the vocalizing pup. Recordings were made for about 5 min for each pup and included 51 calls, on average, for each pup in both areas. The responses to our presence varied among pups, but overall they showed little or no reaction when we approached closely to record. Recording techniques were similar at each site to minimize variation in pup response to the recordings. The recordings were re-sampled (sampling frequency 22 kHz, dynamic range 170 dB; the highest frequencies within pup vocalizations were below 11 kHz) and spectrographic analyses (fast Fourier transformations — time resolution: 10 ms; frequency resolution: 102 Hz; FFT size: 512) were conducted using the sound analysis program Raven 1.2 (Bioacoustics Research Program, Cornell Lab of Ornithology). Calls for which one or more of the vari-

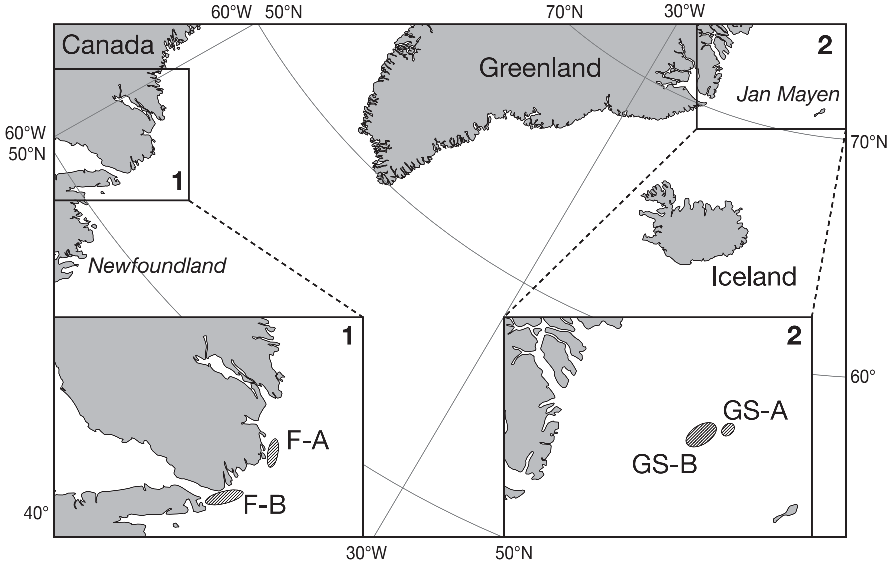

Fig. 1. *Pagophilus groenlandicus.* Study sites where vocalizations and behavioral observations of harp seal mother-pup pairs were made: the Front (1) and the Atlantic Greenland Sea (2). The insets show the whelping patches for the Front (F-A and F-B) and the Greenland Sea (GS-A and GS-B) where the data were collected

ables could not be measured were omitted from the analyses.

Using overall call shape, each signal was assigned a signal type (i.e. tonal call, pulsed call or a combination of the 2; see Miller & Murray 1995, Fig. 2 in Van Opzeeland & Van Parijs 2004). Tonal calls typically had a harmonic structure. Pulsed calls were characterized by a pulsed signal, lacking harmonic structure. As several acoustic variables could not be measured from the pulsed and combination vocalizations, these signal types were not included in subsequent analyses. Therefore we only used tonal calls in these analyses. Our recordings were consistent with the observations of Kovacs (1987), that tonal vocalizations were primarily associated with nursing, whereas pulsed signals were clearly related to situations in which pups felt threatened by the presence of the recorder or other seals nearby and were not considered to be pure mother attraction calls. Individuals with fewer than 15 recorded tonal vocalizations were excluded from analyses.

For the Front, we measured 10 vocal parameters for each tonal call (Fig. 2): (1) call duration (DURN); (2 to 4) three harmonics of greatest amplitude (PF1 to PF3); (5) the number of harmonics (HARM); (6) the maximum frequency of the lower harmonic (SH1); (7) the maximum frequency of the second harmonic (EH1); (8) the duration of the ascending part of the call (DURASC); (9) the duration of the plateau part (DURPLAT); and (10) the duration of the descending part of the call (DURDESC). In an earlier study on harp seal pup vocal behavior (Van Opzeeland & Van Parijs 2004), these parameters were measured for a subset of the data from the Greenland Sea (10 randomly selected individuals: N = 5 males and 5 females) to explore which parameters were important in individual variation. Seven vocal parameters (1 to 7) were highlighted as important. Therefore for the Greenland Sea data set, further analysis of the whole data set of tonal calls was carried out on only 7 of the vocal parameters (see Van Opzeeland & Van Parijs 2004 for more details).

Because of wind noise during recordings made at the Front we could not make good counts for HARM values in many cases. Consequently, we removed this parameter (i.e. HARM) from the Front data set. We included 9 vocal parameters in further analyses of the Front data.

We assessed variation in vocal parameters among pups using classification trees (CART). The data did not follow a normal distribution and were therefore log-transformed. Analyses were carried out in R (R Development Core Team 2007, version 2.5.1, www.R-project.org), running under MS Windows; and the RPART library (v.3.1-36, Therneau & Atkinson 2004) for CARTs. As opposed to other multivariate techniques such as discriminant analyses and principal component analyses, CART analyses provide a useful technique for exploring multivariate nonparametric data. Furthermore, CART analyses produce a result that is readily visually accessible (see Risch et al. 2007 for a detailed explanation of this analysis). We used 9 vocal parameters for analyses of Front data except when comparing them with data from the Greenland Sea, when we used only the 7 vocal parameters obtained from both areas in the comparative analyses.

Mother-pup behavior. Visual observations of mother-pup behavior were made from the ship drifting within the whelping aggregations using 7 × 50 binoculars (Zeiss) over 10 d in the Front and 13 d in the Greenland Sea. Behavioral observations in both areas

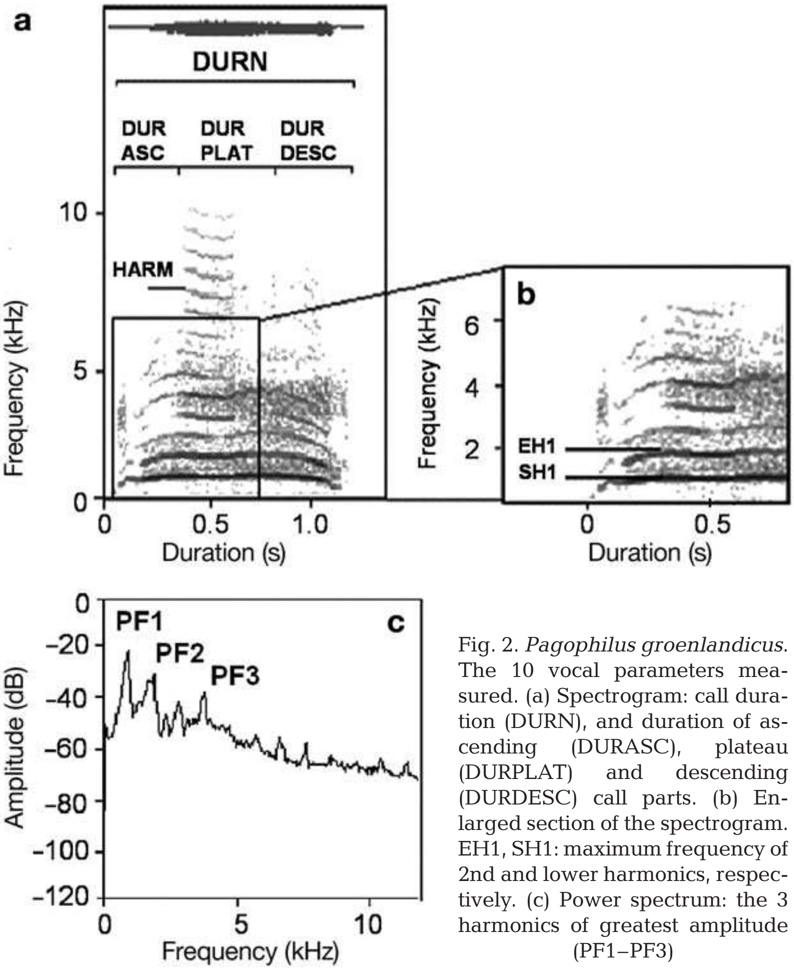

Fig. 2. *Pagophilus groenlandicus*. The 10 vocal parameters measured. (a) Spectrogram: call duration (DURN), and duration of ascending (DURASC), plateau (DURPLAT) and descending (DURDESC) call parts. (b) Enlarged section of the spectrogram. EH1, SH1: maximum frequency of 2nd and lower harmonics, respectively. (c) Power spectrum: the 3 harmonics of greatest amplitude (PF1–PF3)

were made when no persons were on the ice. We recorded behaviors of pups and female attendance patterns in 30 min blocks using scan sampling of mother-pup pairs at 30 s intervals (according to the methods used by Kovacs 1987 in the Gulf of St. Lawrence). Because of the relatively large distance between the observer and the mother-pup pairs we were not able to determine the sex of the pups observed from the ship.

We defined female attendance as the time spent by the female on the ice in the same area as her pup, regardless of her behavioral state (Kovacs 1987). There is a diurnal pattern to these attendance patterns with attendance increasing in the late afternoon and evening (Kovacs 1987). In the Greenland Sea behavior was recorded between 16:00 and 19:30 h. A few observations were also made before 16:00 h, but there were too few to include in the analyses. At the Front we made observations between 07:00 and 17:00 h. Because of latitudinal differences between the 2 study sites (Fig 1), time prior to local sunset differed between the 2 sites. Therefore, analyzing the data between 16:00 and 17:00 h, when data collection overlapped between the 2 sites, would not completely preclude some time-of-day effect. Therefore, we restricted the analyses to data collected after 16:00 h.

We observed 3 to 6 mother-pup pairs simultaneously; the developmental stage of each pup and behavioral state was determined for each seal under observation on each scan. Behavioral states were defined according to Kovacs 1987 (Table 1). Although Kovacs (1987) identified 18 behaviors, we did not observe all of the behaviors in either the Greenland Sea or the Front. Four of the behaviors (sexual, low threat, high threat, and fighting) were not observed in either study area. Four others (presentation, check pup, foreign social, and pup agonistic) were seen only in the Greenland Sea. Behavioral states for which there were <2 observations were eliminated from the set. Eight units of behavior (idle, comfort movements, nursing, nosing, locomotion, swimming, exploration, and alert) were observed often enough for analyses.

In line with Kovacs (1987), we selected pups opportunistically during scanning sessions, without reference to maternal presence or absence. Each observation session lasted 30 min, after which a new set of mother-pup pairs was selected and a new session started. Because the research vessel was drifting through the ice pack, 30 min was a conservative limit during which all pairs clearly remained within visual range. No pairs were sampled for more than 1 session. A linear model tested for the effects of site, pup stage and site–stage inter-

Table 1. *Pagophilus groenlandicus*. Behavioral criteria used to define behavioral states recorded during scanning sessions (from Kovacs 1987, their Table 1)

Behavioral state	Criteria
Idle	Resting motionless in a prone position on the ice (eyes open or closed)
Comfort movements	In a prone position performing low intensity activities, including weight shifting, stretching, etc., and in the case of pups, 'wriggling' without changing location, and shivering for young pups
Nursing	Female lying quiescent on her side, nipples exposed, pup in oral contact with the nipples (time spent moving between nipples was included as part of the nursing sequence)
Presentation	Female postures such that the nipples are accessible to the pup, often accompanied by gentle motions of the female's foreflipper that was furthest from the surface
Nosing	Non-nursing physical contact between a mother and her pup, consisting of naso-nasal or naso-body contact
Check pup	Female makes visual contact with her pup, turning her head if necessary
Foreign social	Non-agonistic, non-sexual physical contact outside the mother-pup pair
Sexual	Attempted mounting or copulatory behavior
Low threat	Female on ventum with head elevated from the ice, neck extended, mouth open and vibrissae erect, often accompanied by low growling vocalizations
High threat	Female on ventum with entire upper body elevated from the ice, nose held vertically, vibrissae held erect, often accompanied by a 'warbling' vocalization and rapid clawing of the ice with a foreflipper
Fighting	Female makes physical contact with another adult animal, biting, clawing or pushing
Attack pup	Female biting or clawing a pup
Pup agonistic	Pup growling accompanied by a variety of 'alert' body positions or lunging directed toward another animal
Locomotion	Changing topographical location on the ice
Swimming	Time spent by a pup in the water, whether or not it appeared to change location
Exploration	Pup investigating or manipulating an object or another pup, using its vibrissae, nose, mouth or foreflippers
Play	Repeated, exaggerated, jerky or 'wriggling' body movements, often accompanied by loud growling directed toward ice or skyward
Alert	Head and upper body elevated from the ice surface, eyes open, animal frequently on ventrum with foreflippers gripping the ice

action. We tested whether the suite of behaviors displayed by pups varied by site, pup stage class, and the interaction between these. We did this using the matrix of behavior with pups as rows, behaviors as columns. Behavioral matrices were compared using the function Adonis in vegan R-package (v. 1.8-8, Oksanen et al. 2007), running what is functionally a nonparametric MANOVA (Anderson 2001). This technique partitions sums of squares of a multivariate data set, thus allowing hypothesis testing. It differs from MANOVA (but is similar to AMOVA, Excoffier et al. 1992) in using the outer product matrix of the response matrix (MANOVA uses the inner product matrix). By doing so, semi-metric or metric distance matrices can be tested (Anderson 2001, Oksanen et al. 2007). Significance testing is achieved through permutations of raw data (Oksanen et al. 2007).

The matrix was row-standardized so that the analysis was of the proportions of different units of behavior exhibited by individual seal pups. As the data were proportions of unbalanced count data, we used Horn's modification of Morisita's index (Oksanen et al. 2007) to generate a distance matrix from the standardized behavioral matrix. Testing of the linear model was based on 1000 permutations.

In addition, we tested whether there was a site effect on female attendance. As the data were binomial (females present or absent) and over-dispersed (mean 39.9, variance 512.98), we ran a quasi-binomial generalized linear model (Venables & Ripley 2002) with logistic link function. This analysis was carried out using R (v.2.5.1) and the MASS library (v.7.2-36, Venables & Ripley 2002). Where significance was tested for, we accepted an α value of 0.05 as significant.

RESULTS

Vocal behavior of pups

After quality selection of the Front data set, 984 calls from 25 pups (12 males, 13 females) were suitable for further analyses (Tables 2 & 3).

An initial 33-node classification tree was pruned with cross-validation. The 1-SE rule (i.e. the smallest tree for which the cross-validated relative error rate is within 1 SE of the minimum; De'ath & Fabricius 2000) suggested that the appropriate descriptive tree was one with 11 nodes (Fig. 3). The analysis correctly classified 32% (315 out of 984) of calls according to individual for the Front data set (Fig. 3). The first major split was based on PF1. The next 2 splits occurred at SH1 and at other values of PF1, followed by splits based on DURN and SH1. Of the 13 female pups, 38% were classified correctly according to individual. For the 12 males, 42% were correctly classified. For the Greenland Sea data set, 43% of calls were correctly classified according to individual. The first major split was based on PF3 and separated male and female pups. Of the 42 female pups, 55% were classified correctly according to individual, whereas 8% of 49 male pups were correctly classified.

Table 2. *Pagophilus groenlandicus*. Descriptive statistics of the 9 mother–pup call parameters measured for 12 male (M) and 13 female (F) harp seal pups recorded in the Front. DURN: duration (ms); PF1–PF3: 1st, 2nd and 3rd peak frequency (kHz); SH1, EH1: maximum frequency of the lower and 2nd harmonic, respectively (Hz); duration of ascending (DURASC), plateau (DURPLAT) and descending (DURDESC) call parts, respectively (ms)

Vocal parameters	Sex	N	Mean ± SD	CV (%)
DURN	F	512	833.3 ± 282.9	34
	M	472	907.1 ± 333.3	37
PF1	F	512	1.4 ± 0.6	40
	M	472	1.2 ± 0.4	36
PF2	F	512	1.8 ± 0.8	43
	M	472	1.7 ± 0.6	38
PF3	F	512	2.5 ± 1.2	47
	M	472	2.5 ± 1.0	39
SH1	F	512	859.2 ± 181.3	21
	M	472	876.2 ± 154.5	18
EH1	F	512	1680.1 ± 333.5	20
	M	472	1707.3 ± 290.6	17
DURASC	F	382	0.2 ± 0.1	47
	M	347	0.2 ± 0.1	56
DURPLAT	F	401	0.7 ± 0.3	40
	M	372	0.7 ± 0.3	43
DURDESC	F	336	0.1 ± 0.1	64
	M	294	0.1 ± 0.1	58

Table 3. *Pagophilus groenlandicus*. Descriptive statistics of the vocalizations of 49 male (M) and 42 female (F) harp seal pups recorded in the Greenland Sea (from Van Opzeeland & Van Parijs 2004). HARM: number of harmonics; all other abbreviations as in Table 2

Vocal parameters	Sex	N	Mean ± SD	CV (%)
DURN	F	1173	871.2 ± 276.2	32
	M	1188	855.8 ± 595.7	70
PF1	F	1173	1.2 ± 0.4	32
	M	1188	1.1 ± 0.4	32
PF2	F	1173	2.1 ± 0.6	31
	M	1188	1.9 ± 0.8	40
PF3	F	1173	3.1 ± 0.7	23
	M	1188	2.8 ± 1.1	39
HARM	F	1173	10.9 ± 6.1	56
	M	1188	11.8 ± 7.0	60
SH1	F	1173	1042.7 ± 282.1	27
	M	1188	1016.4 ± 274.6	27
EH1	F	1173	1675.5 ± 451.9	27
	M	1188	1586.5 ± 454.5	29

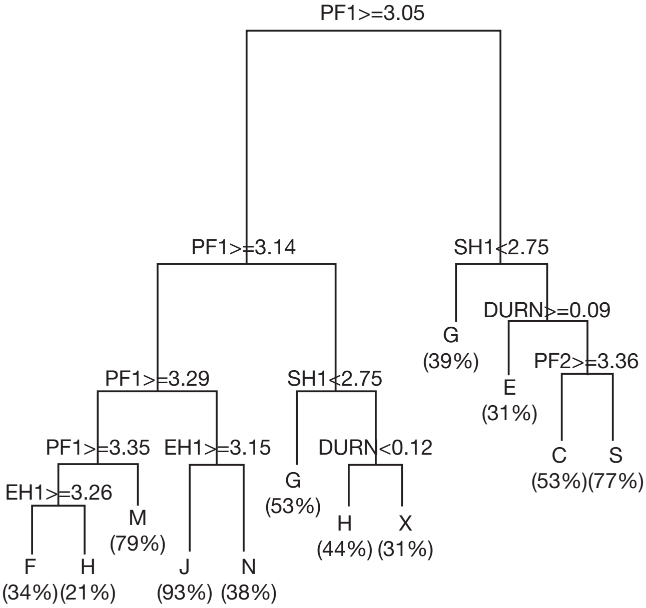

Fig. 3. *Pagophilus groenlandicus.* An 11-node classification tree showing how vocalizations from 25 harp seal pups recorded in the Canadian Front split, based on log-transformed data of 12 measured vocal parameters: call duration (DURN), 3 harmonics of greatest amplitude (PF1–PF3), the maximum frequency of the lower and 2nd harmonic (SH1, EH1, respectively). Letters at the bottom of the tree represent individual pups. Percentages indicate the percentage of calls that were classified correctly according to individual for the individual pups. Twelve of the 25 ind. were extracted by this analysis, explaining 52% of the total variation. The vertical depth of each split explains the proportion of total variation explained by that split. Splits early in the tree (i.e. near the top of the page) account for more variability in the data than those lower down in the tree

In order to compare pup vocal behavior between the Greenland Sea and the Front, a CART was run, using site as response variable. With no misclassifications, 100% of the variation in pup calls was explained in the first split, demonstrating a clear difference between pup vocal characteristics and site. DURN was found to be the vocal parameter driving the split between pup calls recorded in the Greenland Sea and pup calls recorded in the Front. Pups from the Greenland Sea had calls that were longer in duration (greater than 1.2 s) compared with Front pups. Table 4 summarizes the results of the CARTs for individual and sex differences within vocalizations recorded in the Greenland Sea and the Front.

Mother-pup behavior

A total of 46 h of scan samples were collected and a total of 91 mother-pup pairs were observed in the Greenland Sea (N = 4941 observations). In the Front, 85 h of scan samples were collected and a total of 180 pairs (N = 10 657 observations) were observed. After discarding data collected before 16:00 h, there were data on 136 pups (58 Front, 78 Greenland Sea). Kovacs's (1987) units of behavior were used (Table 1). As data were collected on only 2 Stage 4 pups at either site, these were concatenated with Stage 3 pups into a Stage 3+ category. There was a significant Site effect, but no effect of Stage or Site × Stage interaction (Table 5).

Review of the raw data (Fig. 4) suggested that pups in the Front spent more time idle, whereas Greenland Sea pups suckled more and were more alert than pups at the Front. We tested whether there was a site effect on female attendance using a quasi-binomial generalized linear model (GLM) with log link (Venables & Ripley 2002). This demonstrated a significant effect of site on female attendance. Females in the Greenland Sea were less likely to be present on the ice with their pups than those at the Front (Table 6). In late afternoon and evening, females in the Greenland Sea were with their pups around half the time (average time in attendance = 52.2 ± 38.69%, mean ± SD). At the Front, females were in attendance most of the time (85.1 ± 28.69%).

Table 4. *Pagophilus groenlandicus*. Results of the classification trees (CARTs) exploring individual and sex differences within harp seal pup vocalizations recorded in the Atlantic Greenland Sea and the Front

	No. of ind.	No. of calls	First major CART split	Pups correctly identified (%)	No. of female pups	Females correctly identified (%)	Misclassified female calls (%)	No. of male pups	Males correctly identified (%)	Misclassified male calls (%)
Greenland Sea	91	4075	3rd peak frequency (PF3)	43	42	55	14	47	8	86
Front	25	984	1st peak frequency (PF1)	32	13	38	66	12	42	34

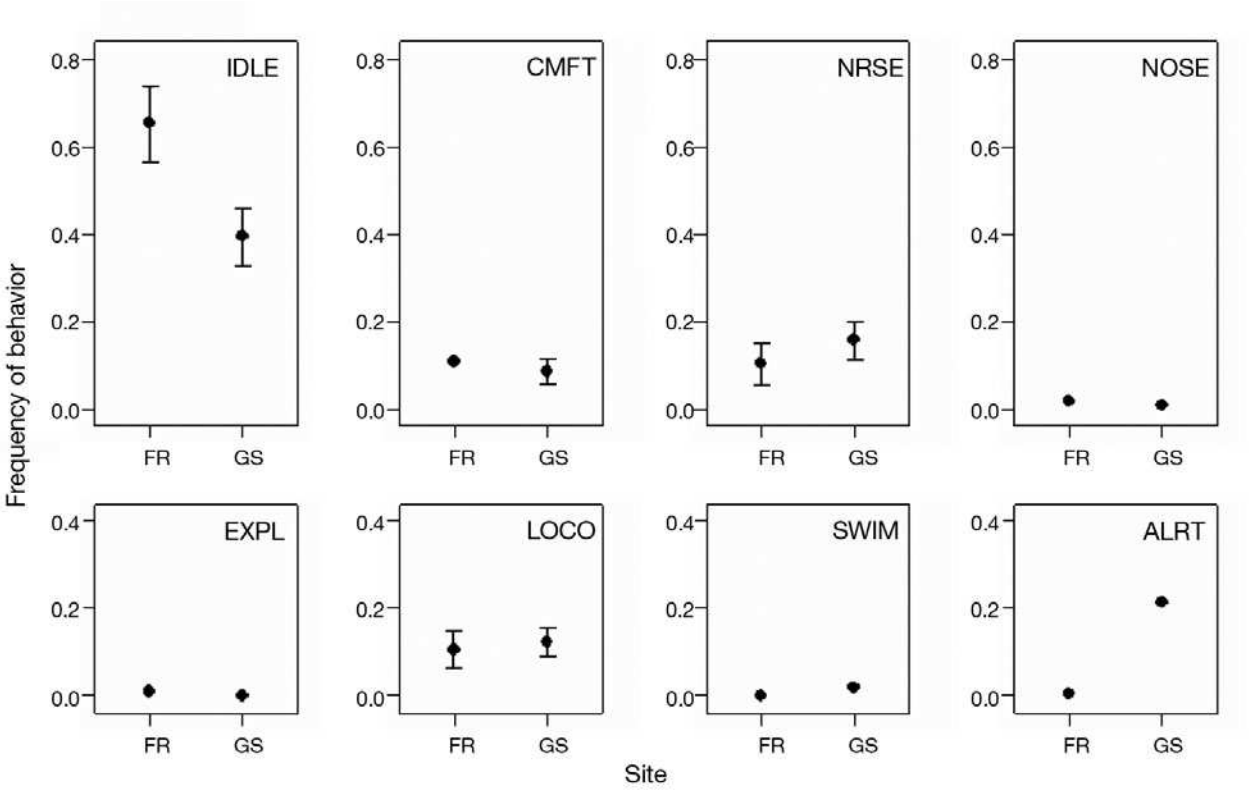

Fig. 4. *Pagophilus groenlandicus*. Mean ± SD for the 8 observed behaviors: idle (IDLE), comfort movements (CMFT), nursing (NRSE), nosing (NOSE), exploration (EXPL), locomotion (LOCO), swimming (SWIM) and alert (ALRT), for harp seal pups at the Front (FR, n = 58) and the Greenland Sea (GS, n = 78)

Table 5. *Pagophilus groenlandicus*. Nonparametric MANOVA (Anderson 2001) testing for effects of site (Greenland Sea or Newfoundland) and harp seal pup stage (1, 2, 3+, see 'Material and methods' for details of staging) and site–stage interaction. Eight units of behavior — idle, comfort movements, nursing, nosing, locomotion, swimming, exploration, and alert — were included in the analysis. Note that the *F*-values are pseudo-*F* values (see Anderson 2001 for details) rather than Fisher's *F*-ratio

	df	SS	MS	F_{Model}	R^2	p
Site	1	2.952	2.952	27.044	0.167	<0.001
PupStage	2	0.603	0.301	2.762	0.034	0.113
Site × PupStage	2	0.040	0.020	0.185	0.002	0.993
Residuals	130	14.191	0.109	0.798		
Total	135	17.786			1.000	

Table 6. *Pagophilus groenlandicus*. Quasi-binomial generalized linear model testing the effect of site (Greenland Sea, Front) on pup attendance by female harp seals. **Significant at $p < 0.05$

	Estimate	SE	*t*	p
Intercept	1.7771	0.2936	6.052	$1.35 \times 10^{-8**}$
Site (Greenland Sea compared to Front)	−1.5225	0.3454	−4.408	$2.12 \times 10^{-5**}$

DISCUSSION

Pup vocal behavior

We investigated the vocal behavior of harp seal pups in the Front by exploring a range of acoustic parameters, most of which have been shown to be important for recognition between mothers and pups in other pinnipeds (Insley 1992, Charrier et al. 2002, Insley et al. 2003). There was low variation (~40%) among pups at the Front, perhaps owing to confounding factors, such as age and sex. Nonetheless, we think that this low variation suggests that vocal recognition may not be the sole means of recognition between mother and pup harp seal pairs in the Front. Other studies of the Canadian harp seal population in the Gulf of St. Lawrence reached similar conclusions and suggested that olfaction and the use of spatial memory were likely important cues for the relocation and recognition of pups by females (Terhune et al. 1979, Kovacs 1987, 1995).

Our analyses of vocal behavior of harp seal pups from the Greenland Sea showed a significantly higher proportion of correctly classified vocalizations for female pups than for male pups, suggesting that vocalizations of female pups are considerably more distinct than those of male pups (Van Opzeeland & Van Parijs 2004). Similar analyses of harp seal pup vocal behavior in the Front, however, showed no significant differences between the proportion of correctly classified vocalizations for female and male pups. For the Greenland Sea it was suggested that female harp seal pup individuality may serve a function during later developmental age classes (Van Opzeeland & Van Parijs 2004). Adult female harp seals are evidently faithful to particular locations (Sergeant 1991, Perry et al. 2000), which may lead to selection for distinctive vocalizations among related females. However, unless females exhibit population level differences in their behavior patterns, this hypothesis would not explain the similar proportions of correctly classified vocalizations observed between males and female pups at the Front.

The duration of vocalizations of pups was the acoustic parameter that separated calls of pups according to location. Pup calls recorded in the Greenland Sea were longer than calls recorded in the Front. Several studies have suggested that lengthening of calls may be a response to reduce overlap with conspecific calls, which may occur in dense aggregations of animals (Watkins & Schevill 1968, Terhune et al. 1994). However, the sizes of the Greenland Sea breeding patches were smaller compared to the Front breeding patches (4700 and 82 600 pups in the Greenland Sea vs. 368 705 and 272 074 pups in the Front). Although we do not have detailed breeding patch density estimations, we do not think that a difference in density of the 2 harp seal breeding aggregations can explain the observed differences in durations of calls of pups.

Perry & Terhune (1999) reported variation in underwater vocalizations of adult harp seals among different breeding locations. Vocalizations obtained from the Gulf and Front components did not differ from each other, but did differ from the underwater vocalizations from the Greenland Sea herd (Perry & Terhune 1999). Similarly, we found evidence for geographic variation in vocal behavior of harp seal pups, perhaps owing to several factors though the reasons for these differences are not clear.

Mother-pup behavior

Female attendance differed significantly between the 2 sites; the age of the pup was not a significant factor to explain these differences. In the Greenland Sea, mothers attended pups for fewer hours in the afternoon and evening, and nursed their pups for longer periods, compared to mothers in the Front. There are several possible explanations for what may be driving the behavioral and acoustic differences between these populations, some of which may act in combination.

Females may have adjusted their behavior in response to hunting by humans to maximize their time in the water. We do not think that the risk of predation by polar bears can explain these differences, as very few bears evidently travel out as far as the northern Greenland ice, compared with significant polar bear presence at the Front (Wiig et al. 2003). However, harp seals have been harvested commercially since the 1700s, with the Canadian hunt starting earlier than the Greenland Sea hunt (Haug et al. 2006, Skaug et al 2007). Although the current hunt in the Greenland Sea is almost 2 orders of magnitude smaller than the Canadian hunt, the Greenland Sea population has been reduced to a smaller proportion of its initial population size than the Canadian population (Hammill & Stenson 2007, Skaug et al. 2007) and current pup production in the Greenland Sea is approximately an order of magnitude smaller than that in Canadian waters (Haug et al. 2006). Harvesting might have evolutionary consequences depending on the intensity of the hunt and the age classes targeted (Coltman 2008, Wirsing et al. 2008).

Geographic location and density might also affect maternal behavior as there was a large difference in the sizes of the Greenland Sea and Front breeding patches. Previous studies report varying effects of population density on maternal behavior (e.g. Boness et al. 1998, Bradshaw et al. 2000). However, more data, including detailed density estimations, behavioral observations on mothers and estimates of pup condition, are necessary to investigate the potential effect of whelping patch density on harp seal mother-pup behavior.

Some phocids might adjust their diving behavior and the timing of foraging in response to prey availability and movements (Kooyman 1975, Burns et al. 2008). Female harp seals leave their pups during the lactation period to forage under the ice. Therefore, site-specific differences in temporal patterns of prey behavior may also influence female attendance patterns.

Environmental conditions such as ice thickness, weather (i.e. wind speed, air temperature), or both, fluctuate substantially among sites and years. Weather conditions have been suggested to influence haul out patterns of females with pups in several ice-breeding seal species (Finley 1979, Thomas & DeMaster 1983). The observed differences in mother-pup behavior could therefore be related to geographic differences in environmental conditions.

Recent climatic variations have resulted in changes in the dynamics of ice and thaw, increasing the unpredictability of ice cover in all Arctic areas (Tynan & DeMaster 1997, Serreze et al. 2003). Serreze et al.

(2003) reported a record minimum Arctic sea ice extent in 2002, the year during which the behavioral and acoustic data were collected in the Greenland Sea. In addition, several studies suggest that the largest decreases in sea ice extent as a result of climate change occur in areas with multi-year ice (e.g. Serreze et al. 2003, Nghiem et al. 2007). To examine whether the ice extent and composition in 2002 in the Greenland Sea differed from other years, we used data from the Center for Satellite Exploitation and Research (CERSAT, http://cersat.ifremer.fr) database to plot the backscatter coefficients and sea ice concentration for March for both study areas over a period of 6 yr. Sea ice concentration indicates the sea ice extent (areas with <15% ice concentration represent open water). The backscatter coefficient provides information on the sea-ice age: low backscatter coefficients indicate pure first-year ice, whereas high backscatter coefficients indicate pure multi-year ice that has survived the melt period and is less saline than first-year ice. Intermediate coefficient values represent mixed ice types. When we compared backscatter and sea-ice concentration data from March 2000 to 2006 for both areas, the plots did not show a clear difference in ice type composition within areas over this 6 yr period; multi-year ice was consistently the predominant ice type in the Greenland Sea, whereas the Front was made up of first-year ice (Fig. 5). Sea ice concentration data also did not show clear differences between years within both areas. Nevertheless, when the ice extent within areas where whelping patches were located were compared between years, the ice extent in the Front area was low in 2004 compared to the other years, whereas it remained fairly constant over 2000 to 2006 in the Greenland Sea whelping patch area (Fig. 5). Friedlaender et al. (2007) reported the sea ice cover in the Front to have been below average ice cover in the period 1996 to 2006 and suggested that lack of solid ice may result in reduced reproductive success of adult harp and hooded seal females, increased pup mortality and changes in food availability. The observed differences in harp seal mother-pup behavior between the 2 sites could therefore be a result of the low sea ice extent in 2004 in the Front area, suggesting that the observed differences are a mere year-effect and potentially differ from years with average sea ice cover extent. However, as sea ice

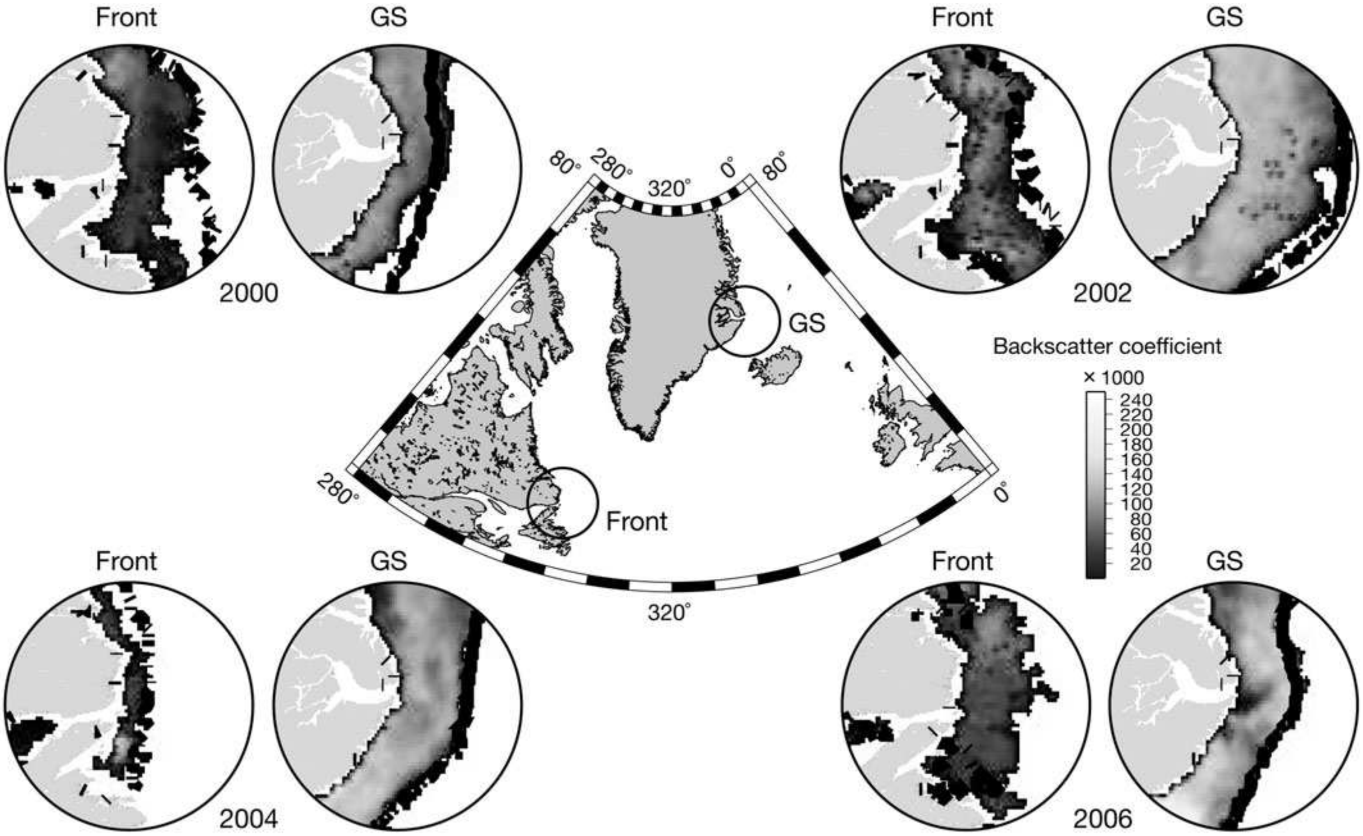

Fig. 5. Backscatter plot based on satellite imaging data from the CERSAT database showing March ice composition and extent for both study areas. High backscatter coefficients (white) indicate pure perennial (multi-year) ice, whereas low backscatter coefficients (black) indicate pure seasonal (first-year) ice. Black line (visible in some panels): boundary of 15% ice concentration; GS: Greenland Sea

extent has been below average for several years in this area (Friedlaender et al. 2007), differences in harp seal mother-pup behavior in the Front area may also reflect the effects of persistent changes in ice extent. In bearded seals, it has been shown that fluctuations in ice cover can affect the number of displaying males and their display behavior (Van Parijs et al. 2004). It is plausible that changing ice conditions also influence female behavior.

A number of plausible hypotheses exist that may explain the behavioral and acoustic variability observed in female harp seals and their pups within this study. However, the one conclusion that can be drawn from this study is that there is still little understanding with regards to the behavioral ecology of these populations and the drivers behind the decision-making processes for this species. The results of this study indicate that in addition to the traditional methods of studying population dynamics and ecology, behavioral studies can provide further insights into differentiation of populations and the potential effects of changing environments on populations. Given drastic climatic changes facing the Arctic, the current lack of data is likely to impede us in understanding the effects of habitat loss on harp seal populations world wide.

Acknowledgements. We thank T. Haug for providing us the opportunity to carry out our field work in the Greenland Sea during the 2002 harp seal cruise. C. Duck, D. McKinnon, D. Wakeham, L. Lindblom, P. Abgrall, S. Tucker and I. Stenhouse helped with aspects of the field work. L. Rabenstein kindly helped with handling the CERSAT ice data. We did not need permits or licenses to collect behavioral or acoustic data in the Greenland Sea. For data collection in the Front, a scientific permit issued under the Marine Mammal Regulations (MMR, part of the Fisheries Act) was obtained and the project was approved by the DFO animal care committee. Funding was provided by the Amundsen Center for Arctic Research and the Faculty of Science of the University of Groningen.

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Editorial responsibility: Brent Stewart,
San Diego, California, USA

Submitted: August 27, 2008; Accepted: June 9, 2009
Proofs received from author(s): July 13, 2009

Publication VII

Individual variation in pup vocalizations and absence of behavioural signs of maternal vocal discrimination in Weddell seals (Leptonychotes weddellii)

INDIVIDUAL VARIATION IN PUP VOCALIZATIONS AND ABSENCE OF BEHAVIORAL SIGNS OF MATERNAL VOCAL RECOGNITION IN WEDDELL SEALS (*LEPTONYCHOTES WEDDELLII*)

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Submitted to Marine Mammal Science (June 2010)

ABSTRACT

Individually stereotyped vocalizations often play an important role in relocation of offspring in gregarious breeders. In phocids, females often alternate between foraging at sea and attending their pup. Pup calls have been found to be individually distinctive in various phocid species. However, experimental evidence for maternal recognition is rare. In this study we recorded Weddell seal (*Leptonychotes weddellii*) pup vocalizations of 27 individuals at two whelping patches in Atka Bay, Antarctica. We explored individual vocal variation based on eight vocal parameters. Fifty-eight percent of all calls were correctly classified according to individual. For males (n=12) and females (n=9), respectively, 75% and 78% were correctly identified based on their vocal parameters. To investigate whether females respond differently to calls of familiar versus unfamiliar pups, we conducted playback experiments with 21 mothers. Maternal behavior did not differ between playbacks of own, familiar and unfamiliar pup calls. Our results suggest Weddell seal pup calls may not need to be individually distinctive because mothers in this colony rely primarily on spatial and/or olfactorial cues to relocate their pup. However, it cannot be excluded that differing environmental factors between colonies affects pup acoustic behavior and the role of acoustic cues in the relocation process.

KEYWORDS: maternal vocal recognition, vocal individuality, pup calls, playback experiments, Weddell seal, *Leptonychotes weddelli*

INTRODUCTION

In pinnipeds, the majority of species congregate to form breeding aggregations during the pupping season. Typically, otariids form large terrestrial breeding colonies. Lactation can last several months and females alternate between nursing their pup and foraging periods at sea, during which the pup can be alone for 3-15 days (*e.g.,* Trillmich, 1996). In many otariid species, vocal signalling has been shown to play an important role in successful mother-pup reunions (Insley *et al.,* 2003). In phocids, breeding systems are more variable and the lactation period is shorter (Lydersen & Kovacs, 1999). Some species are solitary breeders, such as hooded (*Cystophora cristata*) and crabeater (*Lobodon carcinophaga*) seals, and attend their pup continuously throughout the lactation period so that there is little opportunity for the pair to become separated (see Van Opzeeland *et al.,* 2008 for a review). However, the majority of phocid species breed gregariously and mothers leave their pup alone on the ice during short periods to forage at sea in order to sustain lactation. Although aggreagtions on ice are generally less dense than on land, hourly or daily movements of the ice, causing the pup to drift away from the herd, can complicate the relocation process. Phocid mothers are thought to use spatial and olfactory, but also vocal cues in the relocation and identification process of pups (Insley *et al.,* 2003).

Individually distinctive vocalizations, a prerequisite for vocal recognition, have been found in various phocid species: harbor (*Phoca vitulina*), harp (*Pagophilus groenlandicus*), monk (*Monachus schauinslandi*), northern elephant (*Mirounga angustirostris*), Weddell (*Leptonychotes weddellii*) and grey seal (*Halichoerus grypus*) pups (Renouf, 1984; Job *et al.,* 1995; McCulloch *et al.*, 1999; Van Opzeeland & Van Parijs, 2004; Collins *et al.*, 2006). However, the presence of individually distinctive vocal cues does not necessarily imply that there is vocal recognition (*e.g*. Job *et al.* 1995).

To date, experimental evidence through playback recordings investigating maternal vocal recognition in phocid mother-pup pairs is available for only three species: grey, Hawaiian monk and northern elephant seals (Petrinovich, 1974; Job *et al.* 1995; McCulloch & Boness, 2000). Northern elephant seal mothers were found to respond more to the playback of their own pup vocalizations than to the playback of vocalizations of an unfamiliar pup (Petrinovich, 1974). In Hawaiian monk seals, Job *et al.* (1995) found no evidence for vocal recognition of own pup calls by mothers, in spite of the fact that pup calls exhibited significant individual variation. In grey seals, individual recognition varied between sites, with mothers able to recognize their own pups calls at one colony (McCulloch & Boness, 2000), whereas this ability appeared absent at another grey seal colony (McCulloch *et al.*, 1999).

In this study we investigate if there is individual vocal recognition of the pup by Weddell seal mothers through playback experiments. Weddell seals form moderate-sized breeding colonies in fast-ice areas where ice cracks provide access to the water (Tedman & Bryden, 1979). The lactation period lasts 5-7 weeks (Reijnders *et al.*, 1990). Females rarely leave their pup during the first two weeks post-partum (Tedman & Bryden, 1979). After this initial period, they start to leave the ice regularly, presumably to forage to sustain lactation (Hindell *et al.*, 2002). Pups also enter the water during this period. Mother-pup pairs perform synchronous shallow dives, which are thought to serve towards the development of pup diving and swimming skills (Sato *et al.*, 2003). Weddell seal mothers and pups are known to vocalize while on the ice and the vocalizations of both female and pup have been shown to be moderately individually distinctive (Collins *et al.*, 2005; 2006). Based on behavioral observations of Weddell seal mother-pup pairs, it has been suggested that mother-pup vocal recognition might facilitate mother-pup reunions (Collins *et al.*, 2005; 2006).

The objectives of this study were to 1) examine whether Weddell seal pup calls are individually distinctive in the Atka Bay breeding colony 2) determine whether female behavioral responses differ between playbacks of their own pups calls, familiar pup calls (calls from a pup from the same colony) and unfamiliar pup calls (calls from a pup from another distant colony).

METHODS

Recording pup calls

This study was carried out during the Weddell seal pupping season from 14 - 21 December 2008. All necessary permits to work on the ice within the Weddell seal colonies in Atka Bay were obtained (UBA permit nr 94003-3/221). Vocalizations of suckling individual Weddell seal pups were recorded in two Weddell seal whelping patches located on the fast-ice within Atka Bay (patch I 70°34’S 08°04’W, patch II 70°36’S 08°03’W, Fig 1). These two whelping patches were chosen based on the relatively large number of animals that were present at both sites (approximate estimate of the number of animals in patch I 30 animals, in patch II 20 animals) as well as ice conditions permitting access on foot to mother-pup pairs. During the period that the experiments were conducted, we did not observe any movements of individuals between these two colonies.

Pups were caught and restrained in a canvas catching bag and tagged with Dalton rototags through the webbing of their left hind flipper. The sex of all pups that were tagged was determined. The piercing tip of the rototag was blunted prior to tagging to prevent the sharp tip from damaging the flipper during movement. To apply the tag, the webbing of the flipper was pierced with a scalpel. The tag (4x1 cm) was inserted into the left hind flipper of the seal pup with a custom-made rototag applicator. Rototags have been developed for long-term identification of domestic sheep and goats and are able to rotate a full 360° out of trouble. Studies have shown that piercing caused by the insertion of a rototag heals quickly, with no apparent detrimental effect on the behavior or apparent change in the behavior of others towards tagged individuals (Testa & Rothery, 1992). In all tagged Weddell seal pups, the wound caused by piercing the flipper caused little bleeding and had healed cleanly in all pups that were revisited on subsequent days. During the tagging procedure, mothers watched from a distance either on the ice or from the water. For all pups tagged during this study, reunion between mother-pup pairs occurred within minutes after the tagging procedure.

For the recordings, priority was given to easily accessible and vocalizing individuals. Recordings were made both prior to and after tagging. Recordings were made with a Sennheiser microphone (K6P Powering module with a ME64 microphone head: frequency response: 40 Hz – 20 kHz ± 2.5 dB) connected to an M-Audio Microtrack II solid state recorder (frequency response: 20 Hz – 20 kHz ± 0.5 dB). Calls were recorded in wav format (sampling rate of 44.1 kHz, 16 bit) onto 32 Gb flash memory cards. A microphone basket windshield and fur cover was used to reduce the background noise on the recordings caused by wind. The microphone was held 0.1-0.3 m from the vocalizing pup. Individuals showed varying responses to our presence, but overall showed little or no reaction when approached closely during recordings. Recording sessions were terminated if the pup started to nurse, the female became aggressive towards the recordist or the pair moved away from the recordist. For each pup, the mean duration of a recording was 6.5 min during which a mean of 19 calls was recorded for each individual.

A spectrographic analysis of the calls was conducted in Raven Pro 1.3 (Bioacoustics research Program, Cornell Lab of Ornithology). Pups produced only tonal calls (Fig 2a-c). Based on the vocal parameters that have been found to encode pinniped vocal individuality in previous studies (*e.g.,,* Charrier *et al.*, 2002; Van Opzeeland & Van Parijs, 2004; Collins *et al.*, 2006), ten vocal parameters were measured from the Weddell seal pup calls: (1) total duration of the call (TOTDUR), (2) start frequency of the call (SFRQ), (3) end frequency of the call (EFRQ), (4-6) maximum frequency of the first, second and third harmonic (MAXF1,2,3), (7) frequency of greatest amplitude measured over the whole call (PFW), (8-10) first, second and third frequency of greatest amplitude measured over the middle 0.25 s of the call (PF1,2,3). PF2 and 3 were reliably measurable for only a small number of individuals and were therefore not included in further analyses. Only calls for which all eight vocal parameters could be measured were included in the analyses. Pups with fewer than 10 vocalizations were excluded from the dataset.

Playback experiment

Playback experiments took place between 10:00 -16:00, the period during which most pairs are known to haul out on the ice (Lake *et al.*, 1997). To allow for reliable identification of the mother-pup pair, mothers were bleach-marked (Glynt Platinum Blond, 6% H_2O_2) with individually distinctive signs at least one day before the experiments were carried out. Only pairs of which both the pup was tagged and the female was bleach-marked were included in the playback experiments. The exact ages of the pups included in the playback experiments were not known as pups were already born when we started our experiments. (In contrast to harp and grey seals (Stewart & Lavigne, 1980), the age of Weddell seal pups cannot be reliably estimated based on moulting pattern) Based on knowledge of the period in which most births occur in Atka Bay and the size and behavior of the pups, all pups included in the playback experiments were estimated between 5 and 12 days old. During this study, only one pup was observed entering the water.

Playback experiments took place one or two days after the pup calls had been recorded. We found that removing the pup during the playback experiment caused a strong disturbance reaction and searching response in mothers. Therefore, we left the pair as undisturbed as possible during the playback experiment. Pups were lying within one body length of their mother during all playback trials.

We defined eight behavioral states for Weddell seal mothers (Table 1). Mothers were subjected to 3 playbacks, each comprising a playback, lasting approximately 30 seconds, and a 2-min observation following the onset of the playback (trial period). Before the onset of the tests, female behavior was recorded for 2 minutes to obtain a pre-trial period baseline score (Fig 3). We chose 2-min observation periods since test experiments showed that responses to the playback occurred shortly after the playback, also corresponding to the observation period of playback studies on other phocid species (*e.g.* McCulloch & Boness 2000). We waited until the mother's behavior was calm (motionless and silent) before starting a new trial, which usually lasted 1-2 minutes. The interval between playbacks was deliberately chosen to be relatively short to minimize possible changes in conditions between the pair (*i.e.,* female starting to nurse her pup) and in the colony (*e.g.,* movement of neighbouring mother-pup pairs).

The tree different playbacks to which females were subjected were: 1) a playback of the mother's own pup vocalizations (own pup call), 2) a playback of calls from a pup from the same colony (familiar pup call) and 3) a playback of calls from a pup from the other colony (unfamiliar pup call). Seven mothers received their own pup's call first, 7 mothers received familiar pup calls first and 8 mothers received the unfamiliar pup calls first. Playbacks consisted of sequences of 6 calls with natural silences between the calls, lasting approximately 30 seconds per call sequence. Calls were played at natural sound pressure levels through a Minivox loudspeaker (frequency range 100 Hz - 15 kHz) connected to the M-audio II solid-state recorder through a 10-m cable. The loudspeaker was placed within a 6-m range from the focal mother before beginning the observations for the pre-trial control period. The positioning of the loudspeaker sometimes caused some disturbance to the female. In these cases, we waited until behavior of the focal mother turned quiet again before starting the experiment. The playback experiment was performed blind, *i.e.,*, the observer did not know whether the call sequence that was played back was the female's own pup or a familiar or unfamiliar pup. Each mother was tested only once with each of the 3 given playback types.

Statistical analyses

Variation in vocal parameters across individuals was investigated using classification tree analyses (CART, Venables & Ripley, 1999; De'ath & Fabricius, 2000). Both the classification tree analyses and the statistical analyses of the playback experiment were carried out in R (The R Foundation for Statistical Computing, 2009, version 2.9.2., www.R-project.org), running under MS Windows and the RPART library (v.3.1-36, Therneau & Atkinson, 2004) for CARTs.

For the analysis of the playback experiment, we introduced behavioral scores to test for the difference in female response to own, familiar and unfamiliar pup calls.

Behavioral scores were defined as the difference in mean between pre-trial and trial total number of behavioral changes (*i.e.,*, transitions from 0 to 1 and 1 to 0 in the behavioral count data). To prevent pseudoreplication when comparing each trial to the same pre-trial (since there was only one pre-trial observation period for each playback session), we pooled all pre-trial observations of all females and randomly drew pre-trial observations to compare to each trial. We used a Kruskal-Wallis test to test whether the behavioral scores of females differed between pre-trials and trials. Subsequently, we used an Exact-Wilcoxon-Signed-Rank test to pair-wise test for behavior-specific differences between pre-trials and trials.

RESULTS

Vocal behavior of Weddell seal pups

Recordings were made from 27 individuals. After excluding individuals for which less than 10 calls were recorded, 21 individuals were suitable for use in the classification tree analysis. Table 2 lists descriptive statistics for female and male pups for all eight vocal parameters. A total of 336 pup calls were included in the CART analysis. Of these 21 individuals, 12 were male (IDs C,D,E,F,H,I,J,K,Q,R,S,T) and 9 were female (IDs A,B,G,L,M,N,O,P,U).

The initial 3425-node classification tree with individual as response variable was pruned with cross-validation. The 1-SE rule (*i.e.,*, the smallest tree for which the cross-validated relative error rate is within 1-SE of the minimum; De'ath & Fabricius, 2000) suggested that the appropriate descriptive tree was one with 19 nodes (Fig 3). The classification tree analysis correctly classified 58% of all calls (194 of 336 calls) according to individual. The first major split was based on the MAXF3, while the next two splits occurred at MAXF1 and other values of MAXF3. Of 12 males, 75% were correctly classified based on their vocal parameters. For the 9 females, 78% was correctly classified based on their vocal parameters.

Playback experiments

Playback experiments were conducted on 22 Weddell seal mothers. One female was excluded from further analyses because her pup vocalized repeatedly during trials. Twenty-one mothers were included in the statistical analyses. Behavioral scores including all eight female behavioral states were found not to differ when pre-trials and trials were compared (Fig 4, Kruskal-Wallis H: 17.02, df 15, P=0.32).

To compare behavior-specific differences between pre-trials and trials, we only included behavioral states for which there were more than 10 observations, these were: “head raise” (n=153), “check pup” (n=102) and “vocalize” (n=73). We found no significant differences when female behavioral scores between pre-trials and trials were compared for each of these three behavioral states (Fig 5a-c).

DISCUSSION

This study showed that Weddell seal pup calls are individually distinctive, which corresponds to the findings of Collins *et al.* (2006) that 52% of pup calls were correctly classified according to individual. Despite the apparent similarity to the percentage of correctly classified calls in this study (58%), both are based on completely different classification methods (discriminant function analysis vs classification trees) and are therefore not directly comparable. Collins *et al.* (2006) were able to obtain precise estimates of pup ages and found that the number of calls that was correctly classified according to individual was higher in older pups (>14 days) compared to younger pups. They concluded that pups develop more individually distinctive calls after the first two weeks post-partum when both the female and the pup start to periodically leave the ice to forage and vocal recognition might become more important for successful mother-pup reunions. However, our results showed that in some cases, calls of pups younger than 14 days also exhibit substantial individual stereotypy. The percentage of calls correctly classified varied substantially between individuals; for some individuals, no calls could be correctly classified, whereas for others, percentages varied between 33 and 100%. These differences were independent of pup sex. Pup age estimates in this study were less precise compared to the age estimates by Collins *et al.* (2006) and were based on size and behavior of pups as well as on experience from previous years with respect to the period in which most births occur in Atka Bay (J. Ploetz pers comm). Repeated visits to the colonies observed that by the third week of December most pups on the ice were fully moulted and alone, and presumably had been weaned. This observation confirmed our estimate that pups were 1-2 weeks old when this study was conducted. Our results suggest that the level of individual stereotypy in pup calls differs between individuals and is not necessarily linked to age or sex of the pup. Differences in pup individual call stereotypy might reflect an absence of the need for individual pups to be vocally distinctive as mothers in this colony might rely primarily on other cues (*i.e.* spatial and/or olfactorial) to relocate their pup. However, differing environmental factors between colonies such as local ice conditions or breeding colony density can affect pup acoustic behavior and the role of acoustic cues for successful mother-pup reunions (McCulloch & Boness, 2000; Van Opzeeland *et al.*, 2009).

In previous playback experiments with otariids, pups were temporarily removed from their mothers and placed out of sight from the female to evoke a stronger response to pup call playbacks (*e.g.,* Charrier *et al.*, 2002). However, since this caused a strong disturbance reaction in Weddell seal mothers, we did not separate mother-pup pairs during playback trials. Except for one pair, which was not included in the analyses, pups did not vocalize and generally were idle during the experiment, lying within one body length of their mother. One of the most prominent behavioral reactions of females to playbacks (irrespective of the identity of the pup of which calls were played back) that we observed was to briefly check their pup. Given that female behavioral scores for this behavior did not differ between playbacks of own and non-filial pup calls, it is unlikely that the presence of the pup during the playback experiments affected female response to the playbacks. These observations are also in accordance with previous playback experiments on a phocid species which found strong female behavioral reactions to playback of pup calls while the pup remained with its mother (McCulloch & Boness, 2000).

Female Weddell seals did not respond differently to playbacks of their own, familiar or unfamiliar pup calls. One possible interpretation of our findings is that the female is unable to discriminate between her own pup calls and calls of non-filial pups. This could imply that pup calls do not exhibit sufficient individual call stereotypy for the mother to vocally recognize her own pup. Overall, Weddell seal pup call classification rates (this study and Collins *et al.*, 2006) are well within the range of classification rates that signify vocal individuality reported in other studies (*e.g.,* Phillips & Stirling, 2000; Van Opzeeland & Van Parijs, 2004). However, our CART analyses also showed that for some individuals no calls could be correctly classified according to individual. The variability in individual stereotypy of pup calls might reflect that vocal cues might not be the primary cue on which the pair relies for recognition. Naso-naso contact between mother-pup pairs was often observed during this study and has previously been suggested to be the final method of mother-pup recognition (Kaufman *et al.*, 1975). Given the relative stability of the breeding substrate in Atka Bay, Weddell seal mother-pup pairs might adapt their behavior to minimize the chances of separation using olfactory cues as confirmation of identity. Observations suggest that Weddell seal mother-pup pairs primarily remain in relatively close spatial association (Tedman & Bryden, 1979), even during the period that both mother and pup start to leave the ice to forage, (Sato *et al.*, 2003), although females are also known to perform solo dives (Sato *et al.*, 2002). In addition, Weddell seal colonies are generally not very dense (minimum approximate inter-pair distance 4 m, pers obs. I. Van Opzeeland; Kaufman *et al.*, 1975) and mothers have been observed to avoid other seals during the first two to three weeks (Kaufman *et al.*, 1975). The potential importance of olfactory cues in mother-pup recognition is also reflected in the observations of Kaufman *et al.* (1975) that “females often left their pups to make nose to nose contact with bleating pups and pups often left their mothers to make nose to nose contact with bawling females”. In our study, females vocalized relatively often in response to playbacks of pup calls, irrespective of the identity of the pup of which calls were played back (although there was a non-significant tendency for females to call more often in response to own pup calls). In Weddell seals, calls may therefore function for both female and pup to induce individuals in the vicinity of the caller to respond, which may be used as directional cue (Kaufman *et al.*, 1975) while olfactory cues provide the final confirmation of identity.

Playback experiments with mothers were only conducted during the first two weeks of the lactation period. It can therefore not be excluded that vocal individuality and vocal recognition develop gradually during later phases of the lactation period, when the pair enters the water more frequently and the behavior of the pair becomes less synchronized. Females might well have recognized the call of their own pup against non-filial pup calls, but responded to them similarly given that there is no immediate need for a vocal recognition system during the initial period when the pair is on the ice together almost continuously. A similar development of vocal recognition during the lactation period towards the female's first foraging trip has been observed to occur in subantarctic fur seals (*Arctocephalus tropicalis*, Charrier *et al.*, 2001). Further study is needed to investigate the ontogeny of vocal individuality in Weddell seal pup calls as well as the role of vocal cues for mother-pup recognition in later phases of the lactation period.

ACKNOWLEDGEMENTS

We thank Stephan Frickenhaus, Joachim Ploetz, Horst Bornemann, Daniel Zitterbart, Lars Kindermann, Elke Burkhardt, Antje Funcke, the Neumayer overwintering team 2008-2009 and the AWI Logistics department.

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TABLES

Table 1. Behavioral criteria used to define behavioral states during playback experiments.

Behavioral state	Criteria
No response	Female is resting motionless in a prone position on the ice (eyes open or closed)
Head raise	Head and/or upper body of the female elevated from the ice surface, eyes open
Check pup	Female makes visual contact with her pup, turning head if necessary
Vocalize	Female produces vocal sound(s)
Move away from speaker	Female changes topographical position on the ice and moves away from the playback speaker
Approach speaker	Female changes topographical position on the ice and moves towards the playback speaker
Move towards pup	Female changes topographical position on the ice and moves towards her own pup
Presentation	Female postures so that the nipples are accessible to the pup

Table 2. Descriptive statistics of the eight vocal parameters that were measured for 12 male (M) and 9 female (F) Weddell seal pups in Atka Bay: TOTDUR: total call duration (ms), SFRQ: start frequency of the call (Hz), EFRQ: end frequency of the call (Hz), MAXF1-MAXF3: maximum frequency of the first, second and third harmonic (Hz), PFW: frequency with peak energy measured over the whole call (Hz), PF1: frequency with peak energy measured over the center 0.25s of the call (Hz)

Vocal parameters	Sex	N	Mean ± Sd
TOTDUR	M	172	0.55 ± 0.25
TOTDUR	F	164	0.62 ± 0.28
SFRQ	M	172	232.84 ± 67.62
SFRQ	F	164	244.55 ± 68.59
EFRQ	M	172	172.03 ± 68.68
EFRQ	F	164	164.93 ± 60.67
MAXF1	M	172	413.36 ± 72.59
MAXF1	F	164	368.92 ± 71.38
MAXF2	M	172	752.43 ± 138.05
MAXF2	F	164	669.23 ± 134.79
MAXF3	M	172	1093.02 ± 201.61
MAXF3	F	164	964.40 ± 203.84
PFW	M	172	467.69 ± 181.11
PFW	F	164	450.90 ± 268.60
PF1	M	172	480.73 ± 186.78
PF1	F	164	460.90 ± 268.22

FIGURE LEGENDS

Figure 1. Map showing the two Weddell seal breeding patch locations within Atka Bay (AB), near the Eckström Iceshelf, patch I: 70°34'S 08°04'W and patch II: 70°36'S 08°03'W. The location of the German Antarctic station Neumayer Base II is indicated by a black star. Inset image: Antarctica with the location of Neumayer Base (black star)

Figure 2. The eight vocal parameters measured (a) Spectrogram: call duration (TOTDUR). Enlarged section of the spectrogram: maximum frequency of the first, second and third harmonic (MAXF1-MAXF3) and start (SFRQ) and end frequency (EFRQ) of the call. (b) Power spectrum: the frequency of greatest amplitude measured over the whole call (PFW). (c) Spectrogram showing the center 0.25 s (shaded grey) and the corresponding power spectrum: the frequency of greatest amplitude measured over the center 0.25 s of the call (PF1)

Figure 3. Scheme of the playback procedure. Playback experiments consisted of a 2 minute baseline observation period, followed by three playbacks, each separated by a 1-2 minute pause. Females were subjected to three playbacks (in varying order): 1) a playback of the mother's own pup vocalizations (own pup call), 2) a playback of calls from a pup from the same colony (familiar pup call) and 3) a playback of calls from a pup from the other colony (unfamiliar pup call).

Figure 4. A 19-node classification tree showing how vocalizations of 21 Weddell seal pups split with individual as response variable based on 8 vocal parameters: TOTDUR: total call duration (ms), SFRQ: start frequency of the call (Hz), EFRQ: end frequency of the call (Hz), MAXF1-MAXF3: maximum frequency of the first, second and third harmonic (Hz), PFW: frequency of greatest amplitude measured over the whole call (Hz), PF1: frequency of greatest amplitude measured over the center 0.25s of the call (Hz). Letters at the bottom indicate individuals. Percentages indicate the percentage of calls that was correctly classified according to individual for individual pups. Sixteen individuals were extracted by this analysis, explaining 58% of the total variation (194 of

336 calls). The vertical depth of each split explains the proportion of variation explained by that split. Splits early in the tree (*i.e.,* near the root node) account for more variability in the data than those lower down in the tree.

Figure 5. Boxplots showing the behavioral scores for all eight female behavioral states. Behavioral scores were defined as the difference in mean between pre-trial and trial total number of behavioral changes (*i.e.,*, transitions from 0 to 1 and 1 to 0 in the behavioral count data) of Weddell seal mothers (n=22) in response to playback of calls of their own pup (own), calls from a non-filial pup from the same colony (familiar) and calls from a non-filial pup from the other colony (unfamiliar). Behavioral scores were found not to differ when pre-trials and trials were compared (Kruskal-Wallis H: 17.02, df 15, P=0.32).

Figure 6. Boxplots showing the behavioral scores for three female behavioral states: "head raise" (n=153), "check pup" (n=102) and "vocalize" (n=73). Behavioral scores were defined as the difference in mean between pre-trial and trial total number of behavioral changes (*i.e.,*, transitions from 0 to 1 and 1 to 0 in the behavioral count data) of Weddell seal mothers (n=22) in response to playback of calls of their own pup (own), calls from a non-filial pup from the same colony (familiar) and calls from a non-filial pup from the other colony (unfamiliar). (a) "head raise", Wilcoxon own vs familiar (V=88.8, P=0.45), own vs unfamiliar (V=86.5, P=0.33), (b) "check pup", Wilcoxon own vs familiar: (V=76.5, P=0.65), own vs unfamiliar (V=86.5, P=0.49), (c) "vocalization", Wilcoxon own vs familiar (V=42.0, P=0.43), own vs unfamiliar (V=44.0, P=0.55).

FIGURES

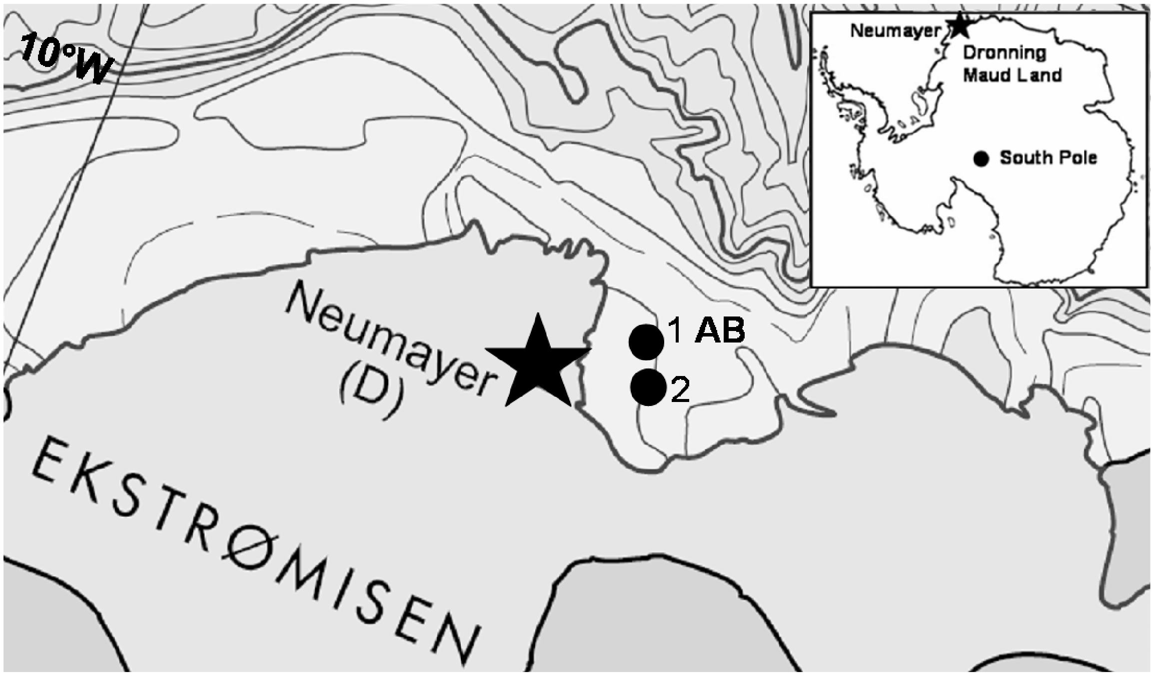

Fig 1.

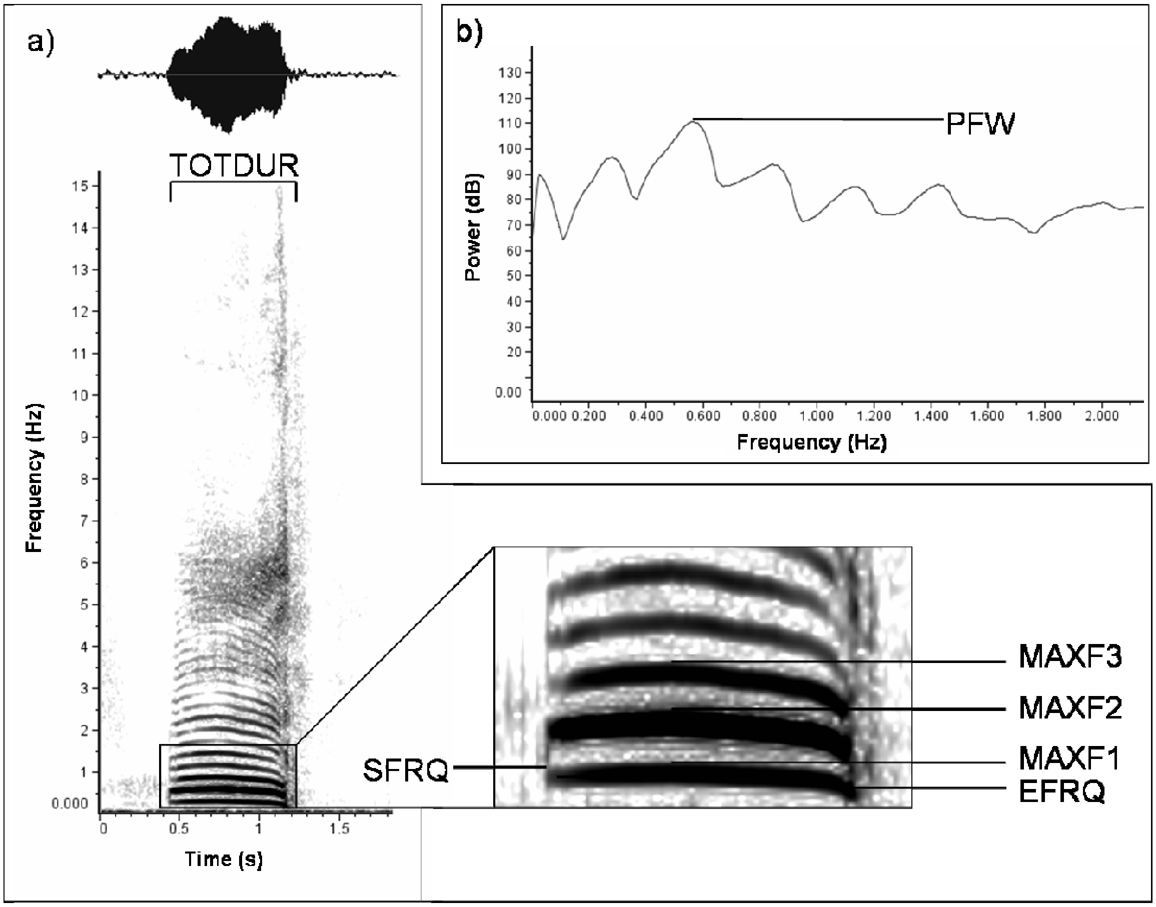
a)
TOTDUR
Frequency (Hz)
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0.000
0
0.5
1
1.5
Time (s)
SFRQ
MAXF3
MAXF2
MAXF1
EFRQ
b)
PFW
Power (dB)
130
120
110
100
90
80
70
60
50
40
30
20
0.00
0.000
0.200
0.400
0.600
0.800
1.000
1.200
1.400
1.600
1.800
2.000
Frequency (Hz)

Fig 2 a & b

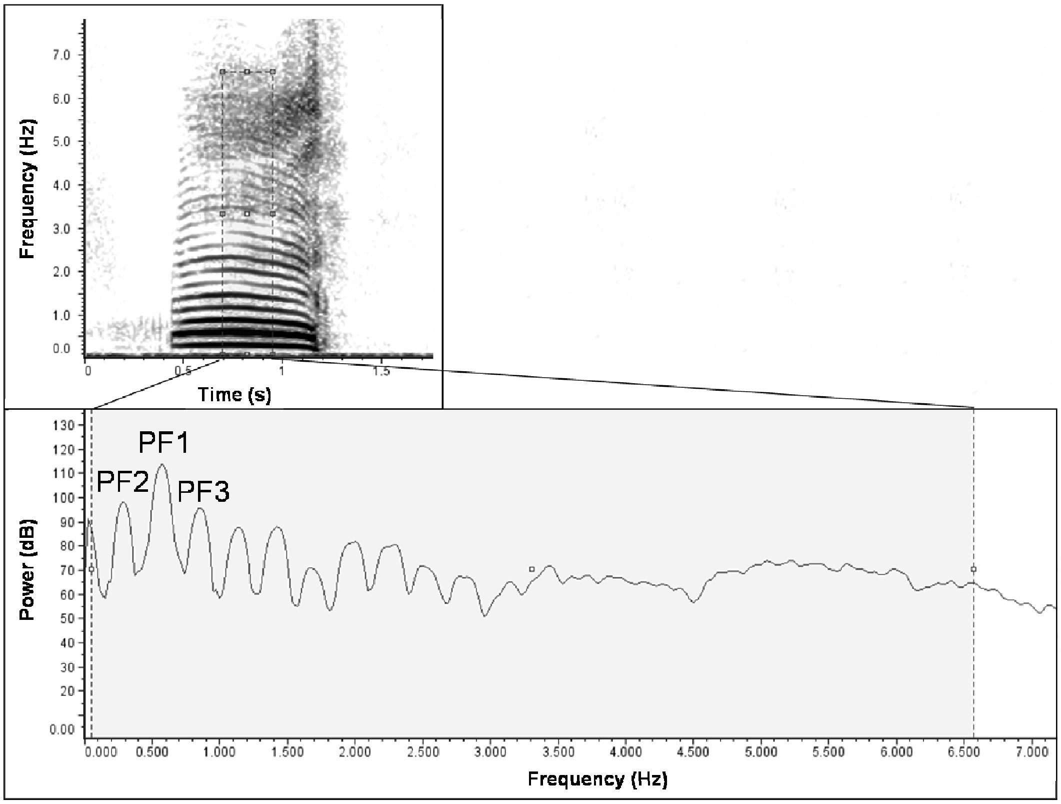

Fig 2 c

Pre-trial observation 2 min	Playback 1 + 2 min observation	Pause 1-2 min	Playback 2 + 2 min observation	Pause 1-2 min	Playback 3 + 2 min observation

Fig 3

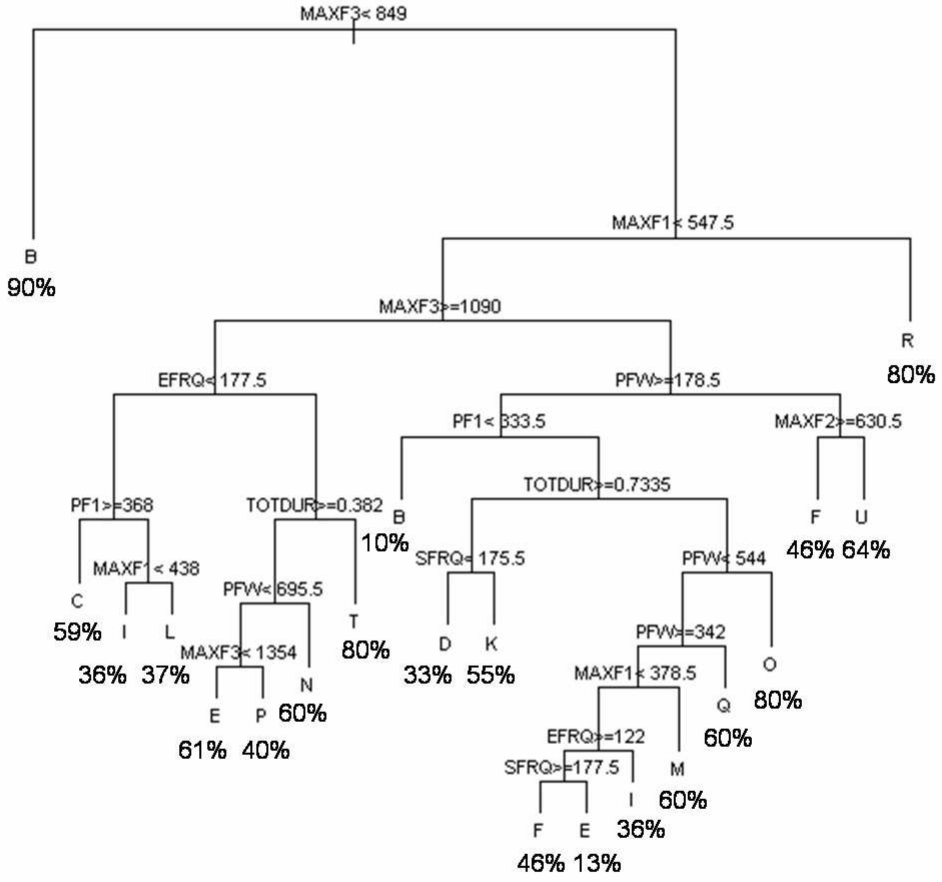
MAXF3< 849
B
90%
MAXF1< 547.5
R
80%
MAXF3>=1090
EFRQ< 177.5
PFW>=178.5
PF1< 333.5
MAXF2>=630.5
PF1>=368
TOTDUR>=0.382
TOTDUR>=0.7335
B
10%
F
U
46%
64%
MAXF1 < 438
C
59%
I
L
36%
37%
PFW< 695.5
MAXF3< 1354
T
80%
N
60%
E
P
61%
40%
SFRQ< 175.5
D
K
33%
55%
PFW< 544
PFW>=342
O
80%
MAXF1< 378.5
Q
60%
EFRQ>=122
SFRQ>=177.5
M
60%
I
36%
F
E
46%
13%

Fig 4.

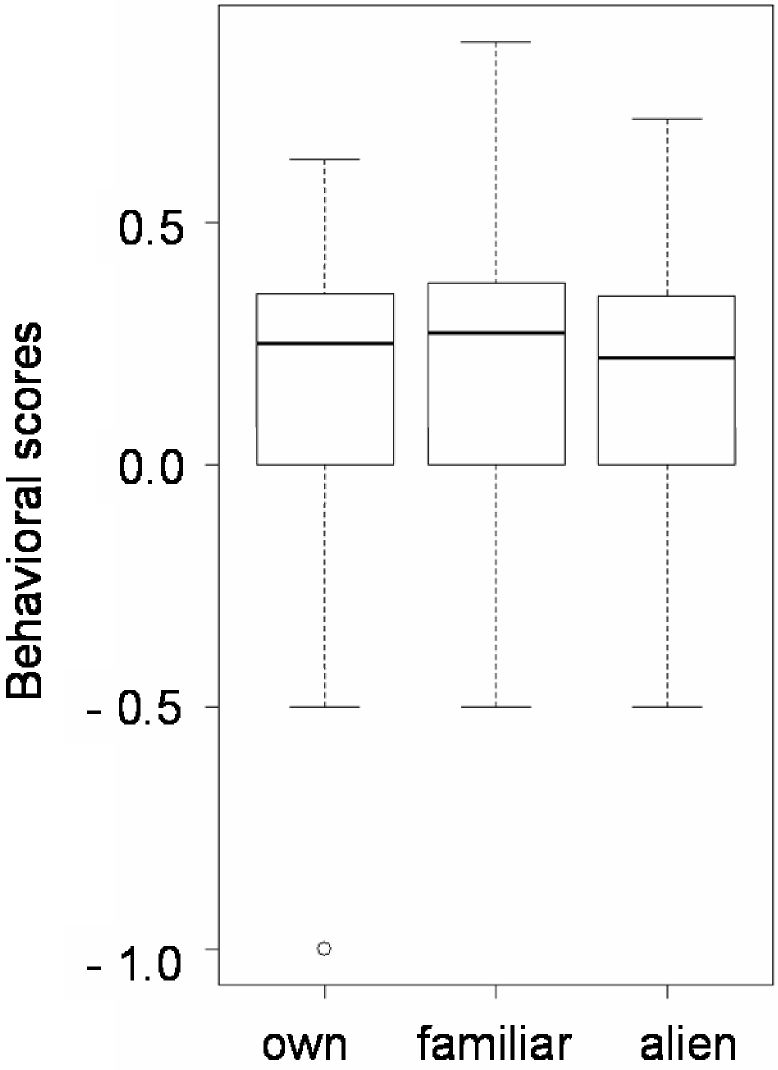

Fig 5.

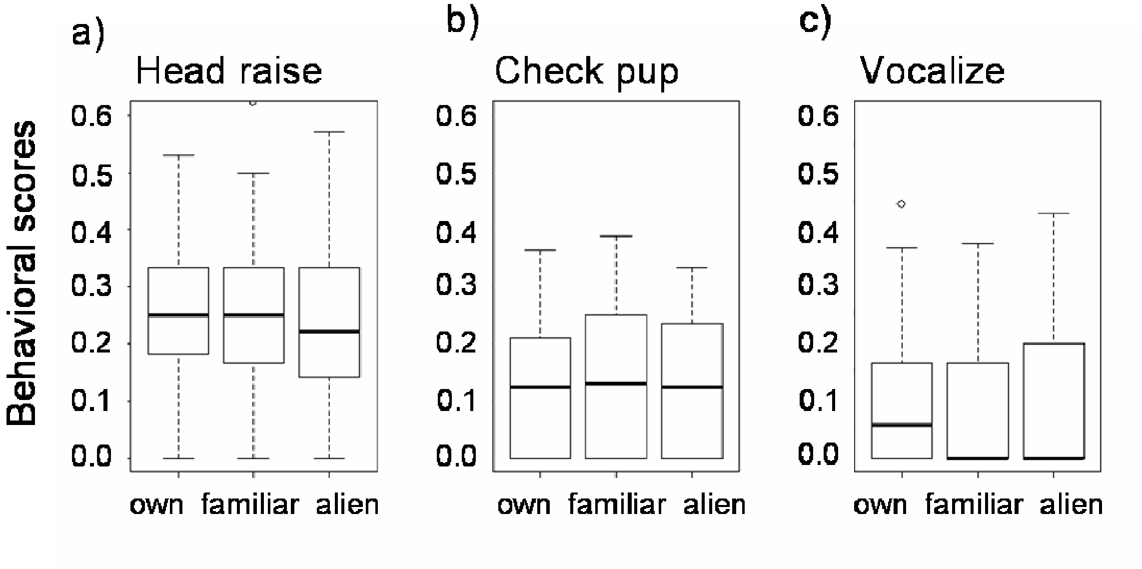
a)
Head raise
b)
Check pup
c)
Vocalize
Behavioral scores
0.0
0.1
0.2
0.3
0.4
0.5
0.6
own
familiar
alien

Fig 6 a-c.

Publication VIII

Seasonal patterns in Antarctic blue whale (Balaenoptera musculus intermedia) vocalizations and the bio-duck signal

SEASONAL PATTERNS IN ANTARCTIC BLUE WHALE (*BALAENOPTERA MUSCULUS INTERMEDIA*) VOCALIZATIONS AND THE BIO-DUCK SIGNAL

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Manuscript in preparation

ABSTRACT

Here we present preliminary results on seasonal patterns in acoustic presence of Antarctic blue whales (*Balaenoptera musculus intermedia*) and the bio-duck signal based on one year (2009) of near-continuous data from the PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA, Eckström Ice Shelf, 70°31'S, 8°13'W). Three Antarctic blue whale call types occurred throughout the year: call types A ('Antarctic blue whale call'), B and C. These calls were present as singular calls and regular sequences of calls, suggesting that Antarctic blue whale song varies and does not always consist of call type A. One call type (S) occurred from January to June, reflecting that this call type might be produced in specific behavioral contexts. Blue whales in Northern Hemisphere waters produce a call type similar to S, which possibly functions to maintain contact between foraging dives. The bio-duck has been recorded at various locations in the Southern Ocean, but the origin of the signal remains unknown. Knowledge on temporal patterns of occurrence might provide information on the source. Acoustic presence of the bio-duck signal was analysed for two years (2006 and 2009). In 2006, the signal was present from April until October (no data for November), while in 2009 it was present from May until December. The bio-duck signal has previously been suggested to be produced by minke whales (*Balaenoptera bonaerensis*). Their association with ice-covered areas, year-round presence in Antarctic waters as well as parallels between the bio-duck signal and the sounds produced by minke whales in Northern Hemisphere waters, are in support of this suggestion. Further work involves analyses of diel patterns in acoustic presence of blue whale call types and the bio-duck signal and further investigation of blue whale song in this data set.

INTRODUCTION

Blue whales

In the Southern Ocean, large baleen whale populations have been severely depleted during 20th century commercial whaling. Blue whale populations were reduced to a fraction of their original abundance with over 350,000 whales killed (Clapham *et al.* 1999). Blue whales are now thought to number approximately 1% of their pre-exploitation abundance, increasing at an annual rate of 7.3% (although the confidence interval on this rate of increase is wide, 1.4-11.6%, Branch *et al.* 2007). Passive acoustic monitoring is an important tool for monitoring populations, particularly in polar habitats where logistic contraints temporally and spatially restrict data collection. Relative abundance estimates (abundance estimations based on call density measurements) can be compared across different recording locations over many years and provide a measure of population growth, trends in distribution and seasonal presence over time (*e.g.,* McDonald & Fox 1999). However, to be able to use acoustic data to evaluate whale behavior, habitat and population status, an understanding of the acoustic ecology (*i.e.* the relationship between the animal and the environment mediated through sound) is required (*e.g.* Oleson *et al.* 2007a; Van Opzeeland 2010). The acoustic ecology determines vocal behavior through intrisic (the behavioral ecology of a species) and extrinsic factors (abiotic and biotic factors in the living evironment) and interactions between both, providing information on the factors that shape vocal behavior and are therefore of relevance to the animal. Knowledge on acoustic ecology is important in *e.g.* selecting the right time scale for acoustic monitoring and in the selection of acoustic signatures to assess acoustic presence.

So far, previous acoustic studies have focussed on the distribution of calling whales focussing on the occurrence of the Antarctic blue whale call type (Sirovic *et al.* 2004; Stafford *et al.* 2004; McDonald *et al.* 2006), without much attention for other call types in the vocal repertoire of Antarctic blue whales or temporal variation in the usage of different call types. Knowledge on temporal variability in usage of the various call types can convey information on the behavioral context in which calls are produced, but also the reliability of the Antarctic blue whale call type in comparison to other call types as an indicator of the acoustic presence of the species.

The Antarctic type blue whale call was first described by Ljungblad *et al.* (1998) and consists an 8-12s constant frequency (29-29 Hz) tone, followed by a 2s downsweep (28-20 Hz) that ends with a long (8-12s) constant frequency 19-20 Hz tone. Calls are usually produced in patterned sequences, with calls repeated approximately every 70-80s. The sequences are referred to as song: a limited number of stereotypic sound types in regular succession, forming a recognisable pattern in time. Other call types produced by Antarctic blue whales were described by Rankin *et al.* (2006) and include ‘high frequency downsweeps’, ‘high frequency upsweeps’, ‘variable high frequency downsweeps’ and the ‘concave vocalization’. Comparison of vocal repertoire composition over time was not possible in that study as recordings were made over a relatively short period (several days in January in 2002 and 2003). In this study we explore seasonal variation in repertoire composition of Antarctic blue whales using one year of near-continuous data from PALAOA.

The bio-duck

One of the largest still unresolved mysteries of the Southern Ocean, at least from the soundscape perspective, is the origin of the bio-duck sound. The name bio-duck originates from sonar operators on board old Oberon class submarines who often detected the signal and associated it with the sound of a duck. The bio-duck has been recorded by several researchers at various locations, throughout the Southern Ocean as shown in Figure 1: Perth Canyon (Matthews *et al.* 2004, McCauley *et al.* 2004), Ross Sea (Dolman *et al.* 2005), Cape Crozier, Ross Island (T.C. Poulter, 1964), Lazarev Sea (Klinck & Burkhardt 2008).

The bio-duck signal is characterised by its repetitive nature, consisting of regular down-sweeped pulses, with most energy located in the 50-300 Hz band, although for signals with higher intensity harmonics occur up to 1 kHz (Matthews *et al.* 2004; Klinck & Burkhardt 2008). Although some of the acoustic characteristics of the bio-duck seem to differ slightly between recordings made by different researchers (*e.g.* number of downsweeps and the presence of harmonics), the typical repetitive nature of the sound and the frequency band in of the signal are overall acoustic characteristics that allow reliable identification of the bio-duck signal.

The most common belief is that the sound is produced by minke whales (*Balaenoptera bonaerensis*, *e.g.,* Dolman *et al.* 2005) although fish sounds and submarine signals have also been proposed. However, to date no study has been able to attribute the bio-duck to any source. By combining localization of the sound and visual observations, previous studies have identified the source of other mysterious underwater sounds, such as the 'boing' in the North Pacific, found to be produced by minke whales, and the 'starwars sounds' near the Great Barrier Reef, attributed to dwarf minke whales (Gedamke *et al.* 2001; Rankin & Barlow 2005). Insight into the temporal patterns in acoustic presence of the signal provides information on the source and is also useful in the planning of surveys dedicated to identify the origin of the bio-duck signal. Previous studies recorded the bio-duck signal between late July and December (*e.g.* Klinck & Burkhardt 2008; Dolman *et al*. 2005), although only McCauley *et al.* 2004 recorded the signal over this entire period. The PALAOA recordings contain the bio-duck signal and allow year-round acoustic monitoring for the presence of the signal. Here we present data on bio-duck acoustic presence based on 2 years of near-continuous acoustic data from PALAOA.

METHODS

Acoustic data collection and sampling regime

One year of near-continuous acoustic recordings was obtained from the PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA, 70°31'S, 8°13'W, Eckström Ice Shelf, Fig 2, see Boebel *et al.* 2006; Kindermann *et al.* 2008; Klink 2008 for technical details). For this study, PALAOA data from 2009 were used, the year with highest annual coverage so far (operational 91% of the time). For June, 2% of the month was covered due to energy shortage within the observatory, whereas for the other months coverage was >90%.

Analysis of low frequency calls in the PALAOA recordings was performed visually by inspection of five-minute spectrograms created in Spectrum Lab 2.75 and saved as image files (1269 x 947 pixels). Images of five-minute spectrograms were sampled for analysis on every third day to provide a standardized sample across the year. For every third day, the first 3 consecutive 5-minute spectrograms of each hour (*i.e.,* three spectrograms representing fifteen minutes of recordings per hour) were inspected.

The analysis focused on low frequency sounds and therefore only calls occurring between 20 and 100 Hz were counted and type-identified (with the exception of the bio-duck signal, see below). Antarctic blue whale calls were type-identified based on previous studies (Ljungblad *et al.* 1998; Rankin *et al.,* 2006). In addition, a number of low frequency sounds presumed of biotic origin, could not be type-identified from literature and were assigned new call type names when present twice or more.

Occurrence of the bio-duck in the spectrograms was noted as present or absent for each 5-minute spectrogram for the 2009 data. In addition, data on bio-duck presence over 2006, collected during a previous study (Van Opzeeland *et al.,* 2010), are also presented here. In 2006, data were sampled following a different sampling regime: data were sampled for analysis every fifth day. For every fifth day, the first 10 consecutive minutes of each hour were analysed. For 2006, data were examined both aurally and visually in 1-minute sound files using the spectrograms produced by Audobe Audition 2.0.

Data presentation

Antarctic blue whale call counts were summed per call type per day to show seasonal patterns in daily call rates of each call type. This manuscript presents preliminary results on seasonal patterns in the occurrence of four blue whale call types and bio-duck presence. Analyses of diel patterns in blue whale call activity, acoustic signature description and temporal patterns of other low frequency sounds that were identified in the PALAOA recordings are currently in progress.

Bio-duck presence per month, for both 2006 and 2009, was expressed as the number of hours in which the bioduck was present as a fraction of the total number of hours analysed. Bio-duck presence in a given hour was determined by the presence of bio-duck signals in at least one of the spectrograms or sound files inspected of that hour. Analyses of diel patterns in bio-duck acoustic presence are in progress.

RESULTS

Over 2009, a total of 7,806 five-minute spectrograms over 12 months were analysed. Over all months spectrograms of 111 days were visually inspected. The number of five-minute spectrograms included per month was 45 for June and ranged between 576 and 792 for the remaining months. For 2006, a total of 9,300 minutes of PALAOA recordings (930 10-minute samples) over 10 months were analyzed. Over all months, 1-minute samples of 55 days were visually inspected. The number of minutes sampled per month in 2006 ranged between 310 and 1,440 minutes due to gaps in the otherwise near-continuous data stream.

Blue whales

Blue whale vocalization types

The four blue whale call types in the PALAOA recordings described here are call types A, B, C and S. These call types have previously been confirmed as Antarctic blue whale calls by Ljungblad *et al.* (1998) and Rankin *et al.,* (2006).

Call type A (Fig 3) corresponds to the Antarctic blue whale call type consisting of a 28 Hz tone followed by an inter-tone interval and a 20 Hz tone (Ljungblad *et al.* 1998; Rankin *et al.,* 2006). Given that spectrograms were cut-off at 20 Hz, no further differentiation of call type A based on variation in call characteristics was possible and calls consisting of only the 28 Hz component or both the 28 Hz and 19 Hz component were pooled into call type A. The reason for cutting the spectrograms at 20 Hz is the impact of the built-in hydrophone high-pass filter (at 10 Hz) to reduce low frequency system and cable noise in the recordings. Rankin *et al.,* (2006) concluded that the 28 Hz (27.7 Hz) component is the primary consistent feature of the 3-unit vocalization which is stable even over great distances, while the other call parts are often difficult to discriminate when calls are faint. The 28 Hz component, in many cases with a clear downsweeping tail (Fig 3), therefore allowed reliable identification of call type A. Call type A occurred in patterned sequences as well as in singular calls. Temporal variation in the occurrence of patterned and singular A calls will be explored during further analysis of the data.

Call type B and C (Fig 4 & 5) correspond to the 'high frequency upsweep' and the 'variable high frequency downsweep', repectively, described by Rankin *et al.* (2006). Call type B is a short-duration (~2 s) upsweep from 20 Hz to 40-60 Hz. Call type C is a steeply downsweeped call starting at 60-80 Hz and sweeping down to 20 Hz (duration ~ 1-2 s).

Call type S (Fig 6) corresponds to the 'high frequency downsweep' described in Rankin *et al.* (2006), starting at 80 Hz, sweeping down to 30-40 Hz (duration ~3s). Variants of call type S occurred, including the 'complex variation of the high-frequency downsweep' and 'amplitude modulated downsweep' (Rankin *et al.* 2006). Furthermore, the 'short high frequency downsweep' distinguished by Rankin *et al.* (2006) as a separate call type, was also pooled into call type S. The similarity of the 'short high frequency downsweep' to faint variants of call type S made reliable classification into a separate call type not possible.

Seasonal patterns

Blue whale call types A, B and C were detected over 12 months of the year[1], whereas call type S was only present from December to May.

The number of type A calls showed strong variation between months, in contrast to call types B and C (Fig 7). Most type A calls occurred in February (5719 calls), while the number of A calls varied between 119 and 3283 for the remaining months, except for June when only few data were available (5 calls). Most type B calls were detected in December (1105 calls), whereas the number of calls ranged between 370 and 760 for the remaining months, except for June, when 5 type B calls were detected. The number of type C calls ranged between 29 and 62 per month, for all months except June (1 type C call counted).

Call type S was present during 6 months of the year (December through May) with the number of calls counted per month ranging between 3 calls counted in May and 3086 calls counted in February.

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[1] For June, only one day of data was available for 2009. However, preliminary inspection of spectrograms from other years suggests that call type A, B and C are present throughout June.

Daily call rates (the total number of calls counted per day per call type) showed relatively large differences within months, in many cases reflecting a two- or three-peak pattern. Although this pattern was reflected strongest in the daily call rates of call type A, call type B and S also exhibited distinct differences in call rates within months.

The bio-duck

Acoustic signature

Analysis and description of the bioduck acoustic signature in the PALAOA recordings is currently in progress. Figure 8 is a five minute spectrogram with zoom of the bio-duck signal showing the regularity of the signal.

Seasonal patterns

The pattern of bio-duck acoustic presence differed between 2006 and 2009; in 2006 the bio-duck signal was present from April to October, whereas in 2009 it was present from May to December (Fig 9). The number of hours in which the bio-duck signal was detected also showed strong differences between years. In 2006, the bio-duck was present during most hours from April to June and in October. In 2009, the bio-duck was present during most hours from July to October. Furthermore, in August and September 2009 the bio-duck was present during all hours.

DISCUSSION

Blue whales

Temporal variation in the blue whale call repertoire

The seasonal separation between call types A, B, C versus call type S was apparent, suggesting that calls might be produced in different behavioral contexts. The presence of call type A throughout the year coincides with findings of previous studies on acoustic presence of Antarctic blue whales (Sirovic *et al.* 2004) as well as Northern Hemisphere blue whales (*e.g.* Stafford *et al.* 2001). Call type A occurs as singular calls, but is often also produced in regular sequences, referred to as song (Sirovic *et al.* 2004; McDonald *et*

al. 2006). Although the preliminary results presented here do not yet include a distinction in seasonal patterns of occurrence of singular type A calls and song, the PALAOA recordings of 2009 contain both song and singular type A calls in all months (except June when only one day of data was available).
The function of blue whale song is still poorly understood. Male blue whales are known to produce song (McDonald *et al.* 2001), but it remains unknown if females also sing. The fact that blue whale song is also produced on the feeding grounds has been suggested whales use calls reflecting off bathymetric structures as navigational cues (Clark & Ellison 2004). Alternatively, song on the feeding grounds might be a continued reproductive display, functioning as a low-cost opportunistic male advertisement to court females, as has been suggested for humpback whales (*Megaptera novaeangliae*, Clark & Clapham 2004). In humpback whales, vocal displays are thought to result in immediate matings, given that the occurrence of aseasonal births in humpback whales suggests that females conceive on the feeding grounds. Nevertheless, in blue whales, aseasonal births have not been reported and mating is therefore unlikely to occur on the feeding grounds. Oleson *et al.* (2007a) proposed that blue whale song on the feeding grounds might instead be produced in a slow- type of reproductive context, serving a function in long-term assessment and association prior to mating.

Interestingly, call type B and C were also produced year-round. In some months, call type B and C also occurred in regularly patterned sequences, suggesting that these call types also form part of song or a separate song type. More detailed analysis of the structure and temporal variation in occurrence of call type B and C sequences is currently in progress.

The strong seasonal pattern in acoustic presence of call type S suggests that this call type serves a function in seasonally-specific behavioral contexts. The presence of call type S coincides with the period of least ice cover in the vicinity of the observatory and potentially high prey availability in the marginal ice-edge zone close to the continent. Call type S might therefore be produced in a feeding context. The observatory is close to the shelf break (Fig 2), which is known to form important feeding habitat for both

Northern and Southern Hemisphere blue whales (*e.g.* Fiedler *et al.* 1998; Sirovic *et al.* 2004).

Northern Hemisphere blue whales are known to produce a call type that strongly resembles call type S (call type D, *e.g.* McDonald *et al.* 2001; Oleson *et al.* 2007b). Similar to our results, Oleson *et al.* (2007a) found a significant temporal segregation between the presence of call type D and other call types. Call type D was produced from April to November, whereas song and singular call types were produced from June to January. They suggested that call type D might serve a function in the localization of conspecifics and/or in maintaining group cohesion, given that frequency sweeps, in contrast to constant tones, can provide clues for binaural localization of a sound source. Type D calls were found to be produced by blue whales during shallow excursions between deep foraging dives, but were not directly associated to foraging events or cooperative feeding (Oleson *et al.* 2007a,b). Type D, and possibly also type S calls, might therefore serve to attract conspecifics to the area or to maintain contact with other individuals during foraging. The absence of call type S in austral winter in our study might reflect that the animals are in more distant areas and that type S calls can not be detected over larger distances. However, the signal-to-noise ratios of call type B and C in austral winter do not seem to reflect the whales to be further from the observatory. Alternatively, the absence of type S calls in austral winter could reflect that animals do not feed or feed only little in austral winter or that the amount of prey is not sufficient for wintering animals to attract conspecifics to share resources (Johnson *et al.* 2002). Baleen whales wintering on the feeding grounds are thought to skip migration to save energetic requirements of migration. However, if these animals continue feeding and how much prey is available to them during winter is unknown. Alternatively, seasonal differences in group composition might affect acoustic behavior and call type usage. In humpback whales, it is thought to be predominantly females that skip migration and remain on the feeding grounds during winter (Brown *et al.* 1995). If type S calls are produced by males during austral summer by means to attract females to areas with high prey densities, for example in the context of long-term association prior to mating, an absence of males in austral winter might explain the absence of type S calls. Nevertheless, this interpretation might be complicated by the observation that in blue whales in Northern Hemisphere waters both sexes produce call type D (Oleson *et al.* 2007b).

Blue whales in ice-covered waters?

The year-round presence of blue whale calls in the PALAOA recordings implies that whales enter ice-covered waters. Blue whales are known to associate with sea-ice (Kasamatsu *et al.* 1988; Mackintosh 1965). Sirovic *et al.* (2004) found a negative correlation between the blue whale calls and sea ice concentration and suggested that whales may have left the area when the sea-ice began to form. Our results might reflect that blue whales in the area off PALAOA might remain in the coastal polynya or other small areas of open water forming in response to *e.g.* winds or iceberg movements. Humpback whale calls were also detected in austral winter in the area off PALAOA and small patches of open water were found to be present within a 200 km area off the observatory in that year (Van Opzeeland *et al.* submitted). Automated detection of blue whale calls in the PALAOA data over multiple years will enable analysis of how blue whale acoustic presence relates to local ice cover.

Variation in the number of blue whale calls counted within months

The typical two or three peak pattern in each month that we observed in the number of calls counted, possibly relates to hydrophone depth (Fig 10). One of the hydrophones of PALAOA is equipped with a CTD sensor which measures pressure and hence is an indicator of hydrophone depth. The local minima in the number of calls counted per day frequently seem to match local minima in CTD pressure, which follow the well known fortnightly modulation of tidal strength. Tidal motion of the water underneath the ice shelf on which PALAOA is located results in variation of CTD and hydrophone depths due to the resulting drag force on the hydrophone cable, which extends approximately 80m below the ice shelf base. Possibly, the acoustic range and thereby the number of detectable calls varies with recording depth, *e.g.* due to acoustic interference processes under the ice shelf. Alternatively, increased tidal flow results in strumming noise, particularly at low frequencies, which might mask weaker calls from greater distances. This correlation between hydrophone depth and noise levels in connection with a decrease in number of calls detected needs further evaluation to be able to distinguish between any possibly natural variability and fluctuations introduced by the recording methods.

The bio-duck

Temporal variation in acoustic presence of the bio-duck: hints with respect to origin

The absence of the bio-duck signal from January until April in both years reflects that the source is present throughout austral winter and disappears again in austral summer. All previous bio-duck recordings have been made within this same period, although to our knowledge no study has recorded the signal before July. McCauley *et al.* (2006) suggested that the seasonal pattern of bio-duck presence in Perth Canyon (July until December) was consistent with an animal migrating back and forth between waters off Australia and the Antarctic, being present in the Canyon in austral winter and migrating to Antarctic waters in austral summer. Our results nevertheless, indicate the opposite: a source that is present in Antarctic waters only during austral winter and spring. Although some baleen whale species are present in Antarctic waters year-round (*e.g.* Stafford et al. 2001; Sirovic et al. 2004; this study), the seasonal patterns in acoustic presence and acoustic signatures of these species are hardly reconcilable with those of the bio-duck signal, leaving it unlikely that the sound is produced by blue, fin or humpback whales. Based on previous analyses of pinniped acoustic signatures and temporal patterns in call usage in the PALAOA recordings (Van Opzeeland *et al.* 2010), it is also highly unlikely that the bio-duck sound can be attributed to Weddell (*Leptonychotes weddellii*), leopard (*Hydrurga leptonyx*), Ross (*Ommatophoca rossii*) or crabeater seals (*Lobodon carcinophaga*). Nothing is known on the sounds produced by fish in Antarctic waters and we can therefore not exclude the possibility that the bio-duck signal is produced by fish.

Could the bio-duck be minke whale vocalizations?

To date, very little is known on the sounds produced by Antarctic minke whales, and their circumantarctic physical abundance is in stark contrast to their virtual acoustic absence. Available knowledge is based on a few short duration recordings of a limited number of animals of unknown age and sex. Schevill and Watkins (1972) recorded intense downsweeps from 130-115 Hz to 60 Hz. Leatherwood *et al.* (1981) also recorded this sound from

Antarctic minke whales along with a regular click sequences and four additional tonal sounds. In the North Atlantic, minke whales have been found to produce regular clicks (Beamish & Mitchell 1973), frequency modulated downsweeps (Eds-Walton 1999), gruntlike pulses and pulse trains (Winn & Perkins 1976; Mellinger *et al.* 2000). These sounds have in common with the bio-duck signals that they 1) are highly stereotyped sequence of frequency modulated short duration pulses, 2) occur throughout winter until spring, 3) occur in bouts lasting many hours.

Distribution patterns of Antarctic minke whales do not exclude the occurrence of the bio-duck signal in the same period off the Antarctic coast and in Antarctic waters; sighting data suggest a southbound movement starting in October from 10° - 20° S with most minke whales present in Antarctic waters in January, while some remain in temperate waters or on the feeding grounds throughout the year (Best 2007). The absence of the bio-duck signal in the PALAOA recordings in January could reflect minke whales remain in offshore waters until April or May, depending on feeding conditions and migrate south when the ice starts to form. It would be interesting to evaluate if the bio-duck signal is present in recordings made in off-shore areas between January and April.

Alternatively, the bio-duck signal might be produced only in season-specific behavioral contexts. In this case, the presence of the bio-duck signal in the period when ice cover is most severe suggests a link. Minke whales are known to associate with ice-covered areas and have been observed in fast-ice and dense pack-ice areas (*e.g.* Ribic *et al.* 1991; Thiele *et al.* 2004). The availability of open water where animals can breathe is nevertheless a prerequisite for marine mammals and observations suggest that the availability of breathing holes rather than the presence of ice restricts cetacean presence in ice-covered waters (Ribic *et al.* 1991; Gill & Thiele 1997). Antarctic minke whales have been observed creating breathing holes in ice-covered areas (Scheidat *et al.* 2008) which might reflect a behavioral adaptation to survive in heavy ice-covered areas. The production of regular patterned signals and their reflection off underwater structures such as the surface ice layer could provide navigational information to the animal, for example on the thickness of ice cover or the presence of leads or open water. Nevertheless, this hypothesis does not provide an explanation for the bio-duck signal recorded in Perth Canyon.

Further analyses of the diel patterns in presence of the bio-duck signal might provide more clues on the origin of the sound. In addition, an automated detection algorithm has been developed for the bio-duck signal which will also be used to explore acoustic presence across multiple years and relate bio-duck activity to seasonal and annual variation in ice cover.

Note

This manuscript is in an early phase of preparation and presents preliminary results and interpretations. Analyses are still in progress and include 1) description of acoustic signatures and temporal patterns of the other low frequency sounds that were identified in the PALAOA recordings, 2) diel patterns in vocal activity of blue whales, the bio-duck signal and other low frequency sounds and 3) seasonal patterns in the presence of blue whale song and the occurrence of other song types. The blue whale and the bio-duck will in a later stage likely form separate manuscripts.

ACKNOWLEDGEMENTS

The logistics department of the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany, Reederei F. Laeisz GmbH, Rostock, Germany, FIELAX Services for Marine Science and Technology mbH, Bremerhaven, Germany, all played a crucial role in setting up and/or maintaining PALAOA. The PALAOA project was partly funded by the Bremerhavener Gesellschaft für Innovationsförderung und Stadtentwicklung (BIS).

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FIGURE LEGENDS

Figure 1. Recording locations of the bio-duck signal: Perth Canyon (blue star), Ross Island, Cape Crozier (orange star), Lazarev Sea (grey star), Ekström Ice Shelf, PALAOA (green star). During the ANSLOPE survey sonobuoys were deployed on several occassions in the Ross Sea and further north toward New Zealand (blue dashed area), the bio-duck signal was present on most of the sonobuoy recordings.

Figure 2. Bathymetry map showing the location of PALAOA (white star) and location of the German Neumayer Base II (black star). Inset image: map of Antarctica showing the location of Neumayer Base (black star).

Figure 3. Five-minute spectrogram with several examples of Antarctic blue whale call type A. Inset image: zoom of call type A.

Figure 4. Five-minute spectrogram with several examples of Antarctic blue whale call type B. Inset image: zoom of call type B.

Figure 5. Five-minute spectrogram with Antarctic blue whale call type C. Inset image: zoom of call type C.

Figure 6. Five-minute spectrogram with several examples of Antarctic blue whale call type S. Inset image: zoom of call type S.

Figure 7. Seasonal presence of four Antarctic blue whale call types over 2009. Markers on graph lines indicate daily call rates (the total number of calls counted per call type per day) for: call type A (black line), call type B (green line), call type C (blue line), call type S (red line). For June only one day of data was available (1 June) due to power outages of the observatory (grey dashed area). Upper panel: bars indicate acoustic presence on a monthly basis for call types A,B and C (blue bar) and call type S (red bar).

Figure 8. Spectrogram of the bio-duck signal recorded by PALAOA: a) five-minute spectrogram, b) one-minute fragment showing the regularity of the signal.

Figure 9. Seasonal presence of the bio-duck signal. Vertical bars indicate the number of hours, as percentage of the total number of hours recorded, during which the bio-duck signal was present for each month for 2006 (black bars) and 2009 (grey bars). No data was available for July and November 2006 (grey dashed areas). For June 2009 (*), hours with bio-duck presence is bsed on one day of data. Upper panel: bars indicate acoustic presence of the bio-duck signal on a monthly basis for both years.

Figure 10. Seasonal variation in the number of type A calls counted per day (black line) and average CTD depth per day (blue line). Note that the number of type A calls in this graph should be multiplied by three for actual number of calls counted. CTD depth ranged between 134 and 157 m. Pink bars are drawn in by hand and indicate the pressure minima timing in hydrophone depth (*i.e.,* when there is high flow) and show the possible correlation to days with low call counts. For the period from mid-August until the end of October no pink bars were drawn, as no clear peaks in CTD depth were visible.

FIGURES

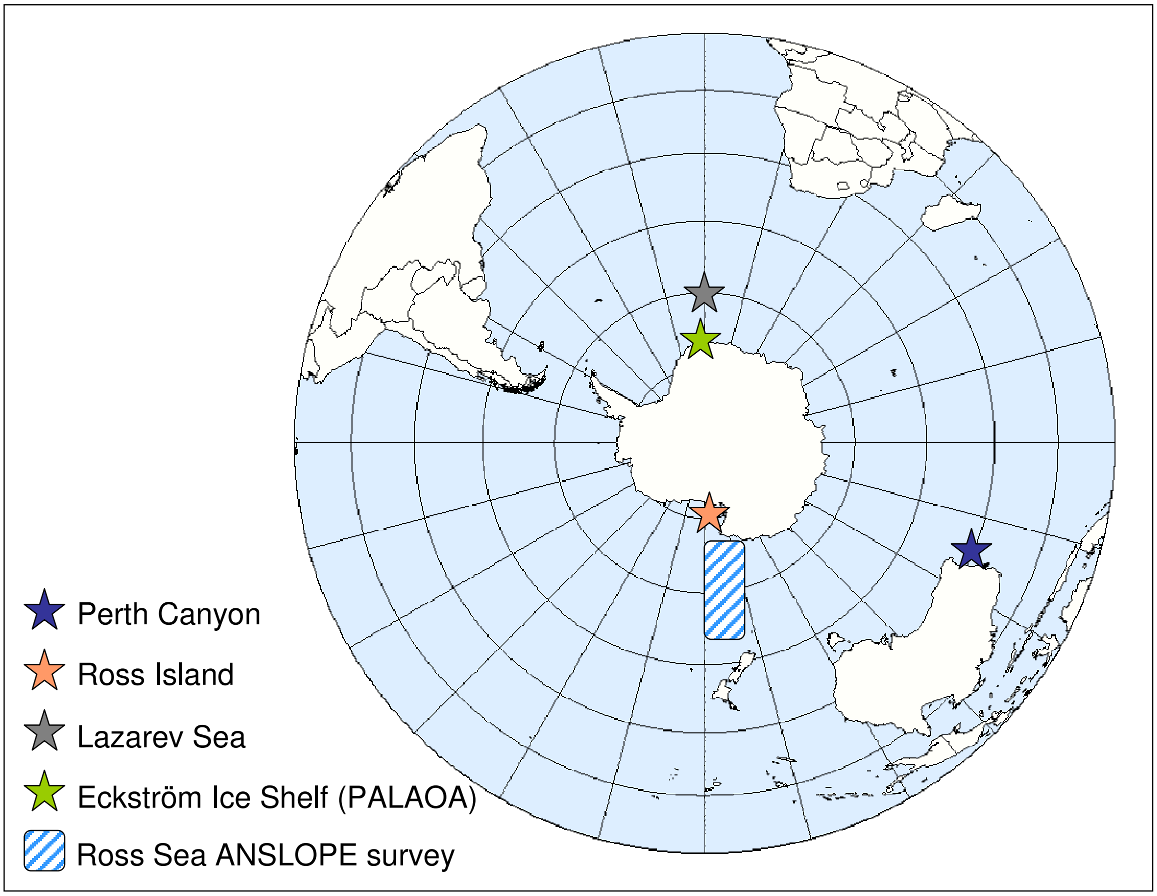


Fig 1.

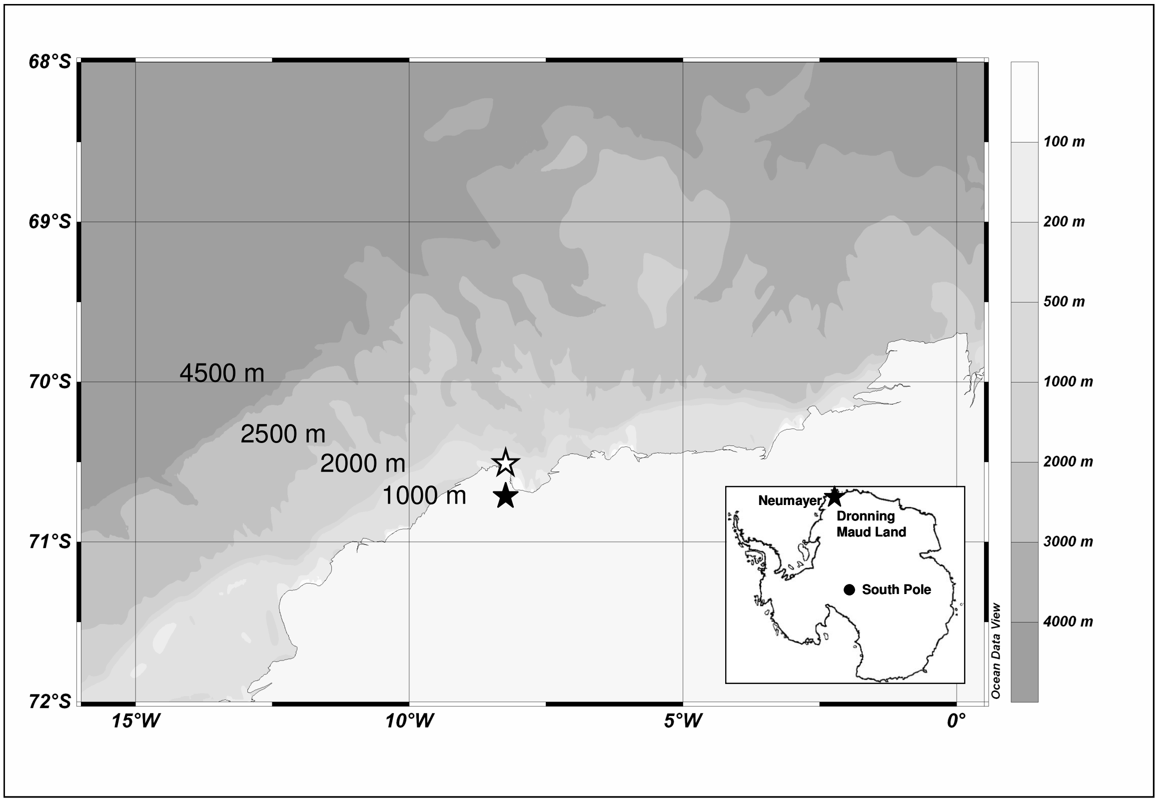

68°S
69°S
70°S
71°S
72°S
15°W
10°W
5°W
0°
4500 m
2500 m
2000 m
1000 m
Neumayer
Dronning Maud Land
South Pole
Ocean Data View
100 m
200 m
500 m
1000 m
2000 m
3000 m
4000 m

Fig 2.

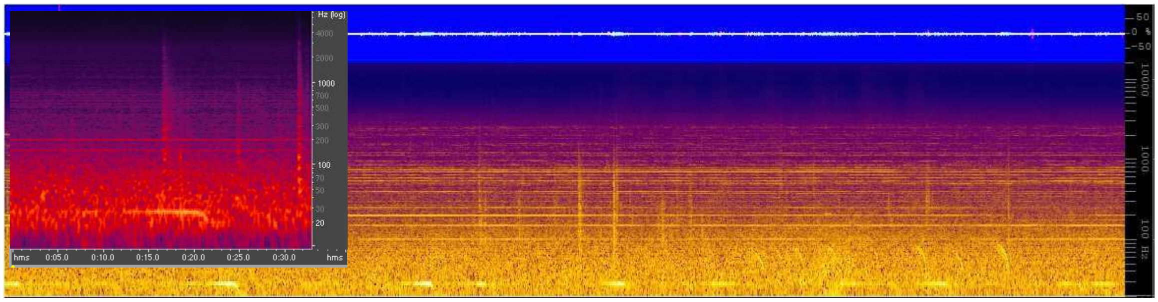

Hz (log)
4000
2000
1000
700
500
300
200
100
70
50
30
20
hms
0:05.0
0:10.0
0:15.0
0:20.0
0:25.0
0:30.0
hms
50
0 %
-50
10000
1000
100 Hz

Fig 3.

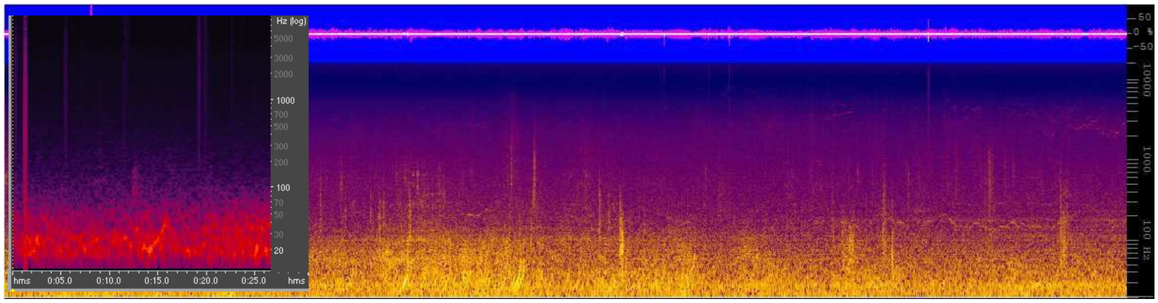


Fig 4.

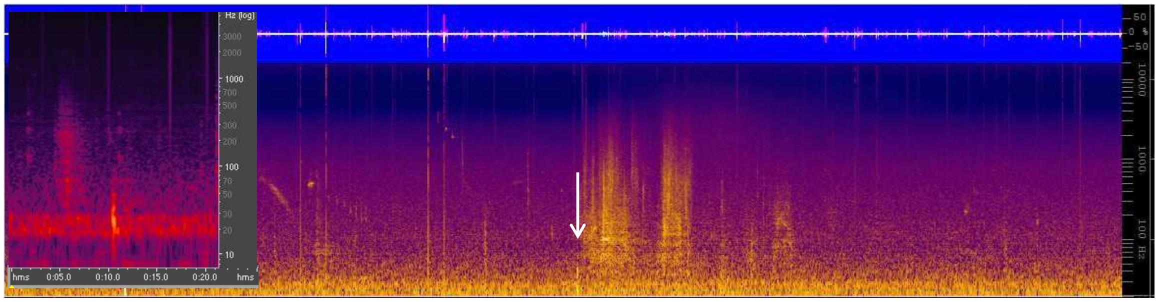


Fig 5.

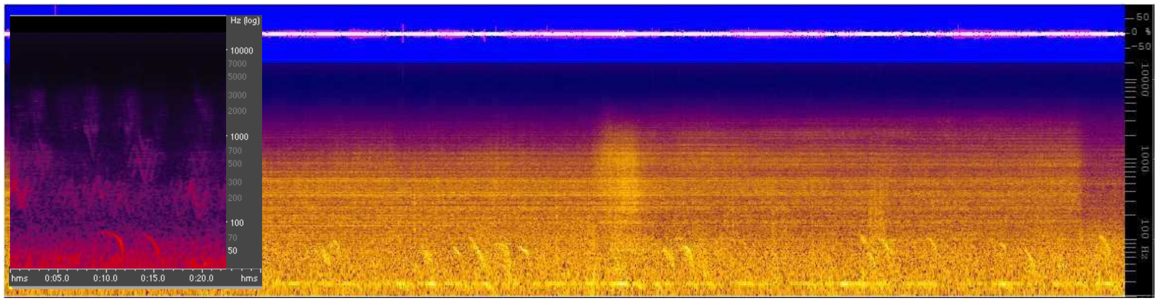


Fig 6.

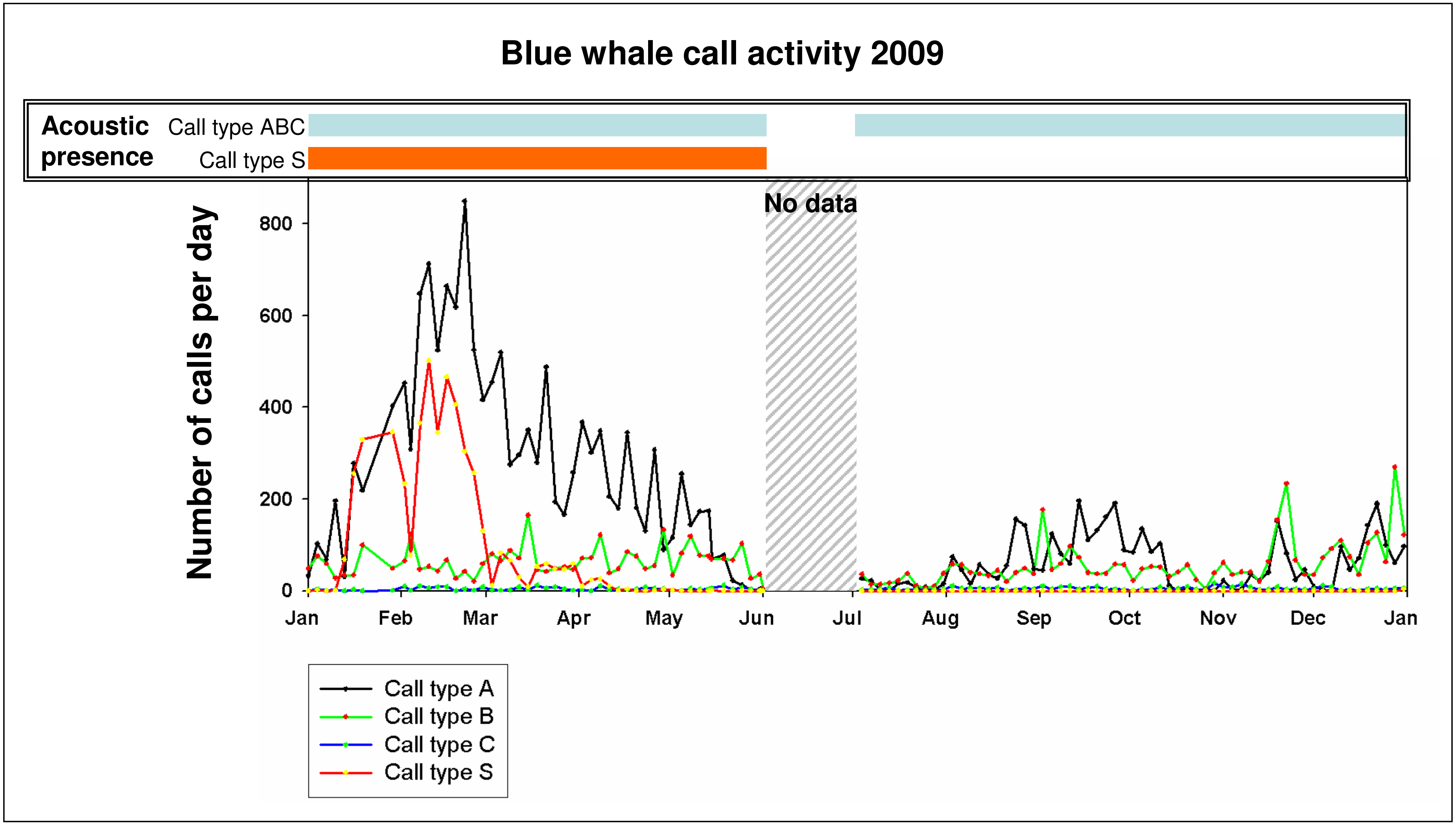

Blue whale call activity 2009
Acoustic presence
Call type ABC
Call type S
No data
Number of calls per day
0
200
400
600
800
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Call type A
Call type B
Call type C
Call type S

Fig 7.

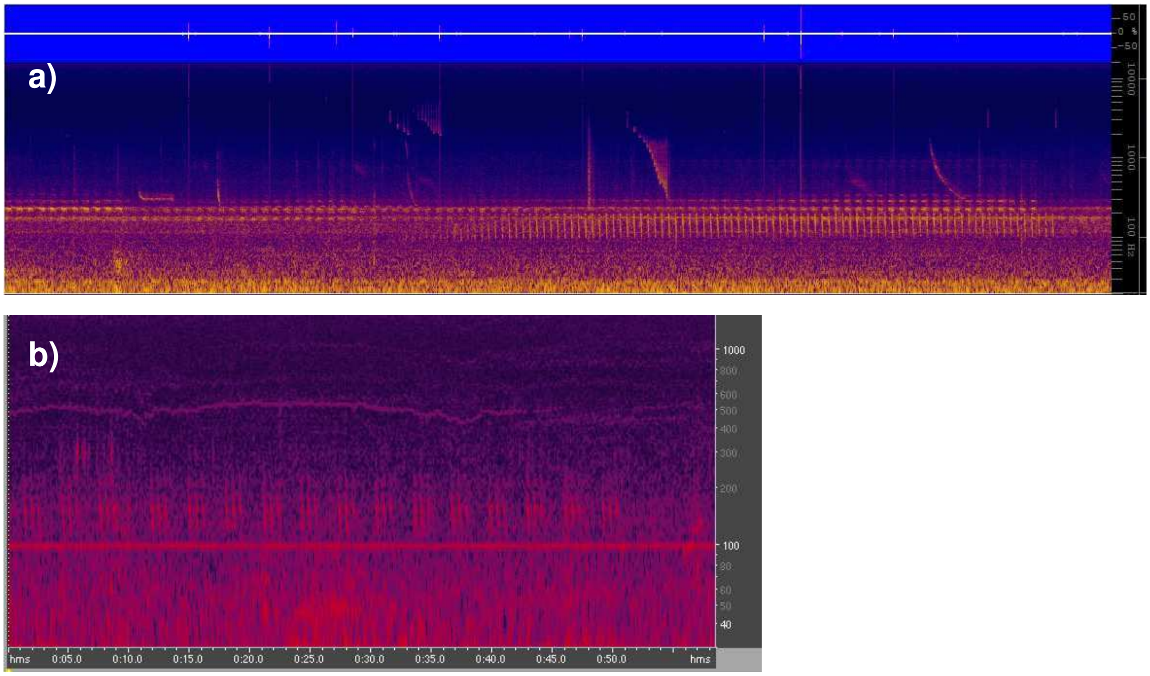

a)
50
0 %
-50
10000
1000
100 Hz
b)
1000
800
600
500
400
300
200
100
80
60
50
40
hms
0:05.0
0:10.0
0:15.0
0:20.0
0:25.0
0:30.0
0:35.0
0:40.0
0:45.0
0:50.0
hms

Fig 8 a & b.

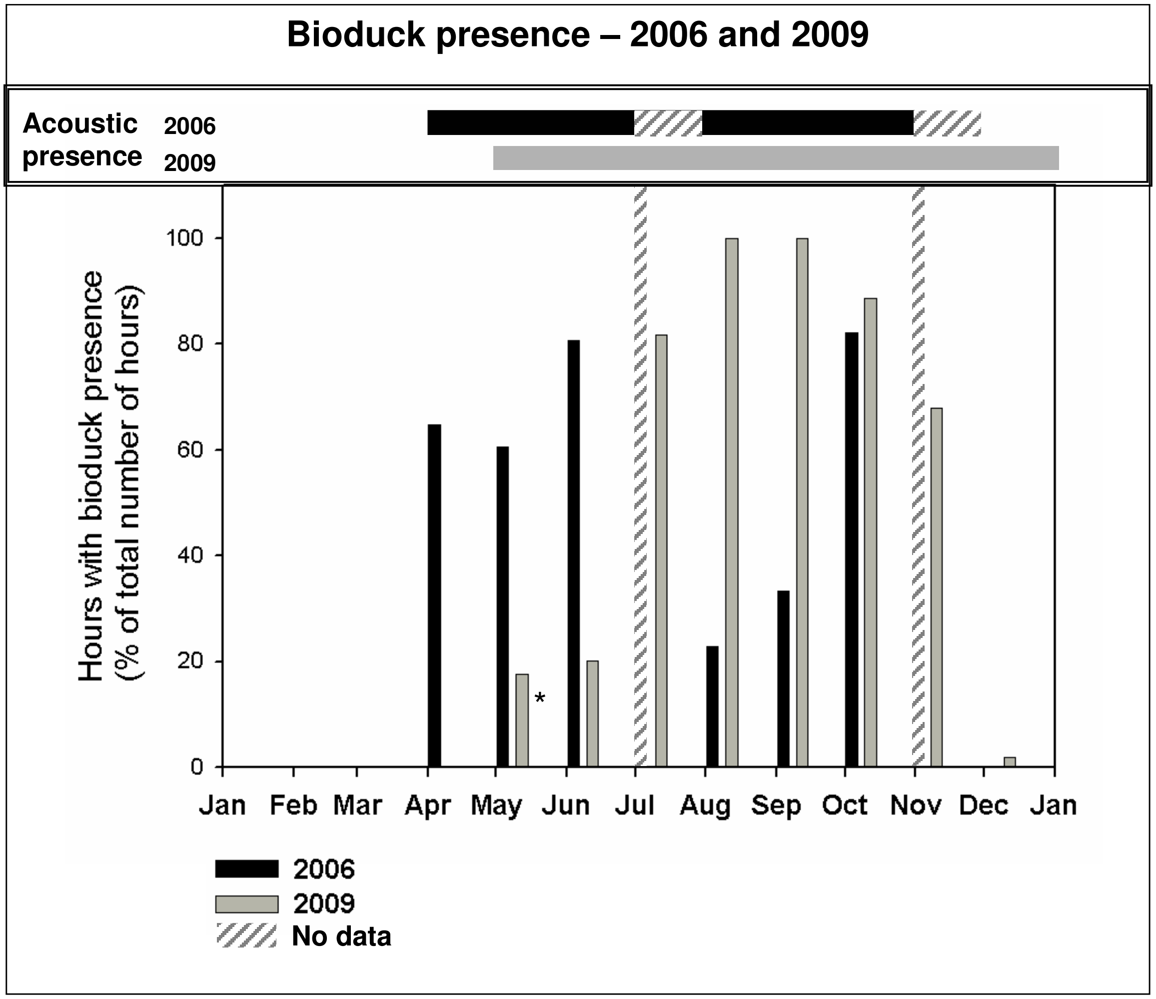
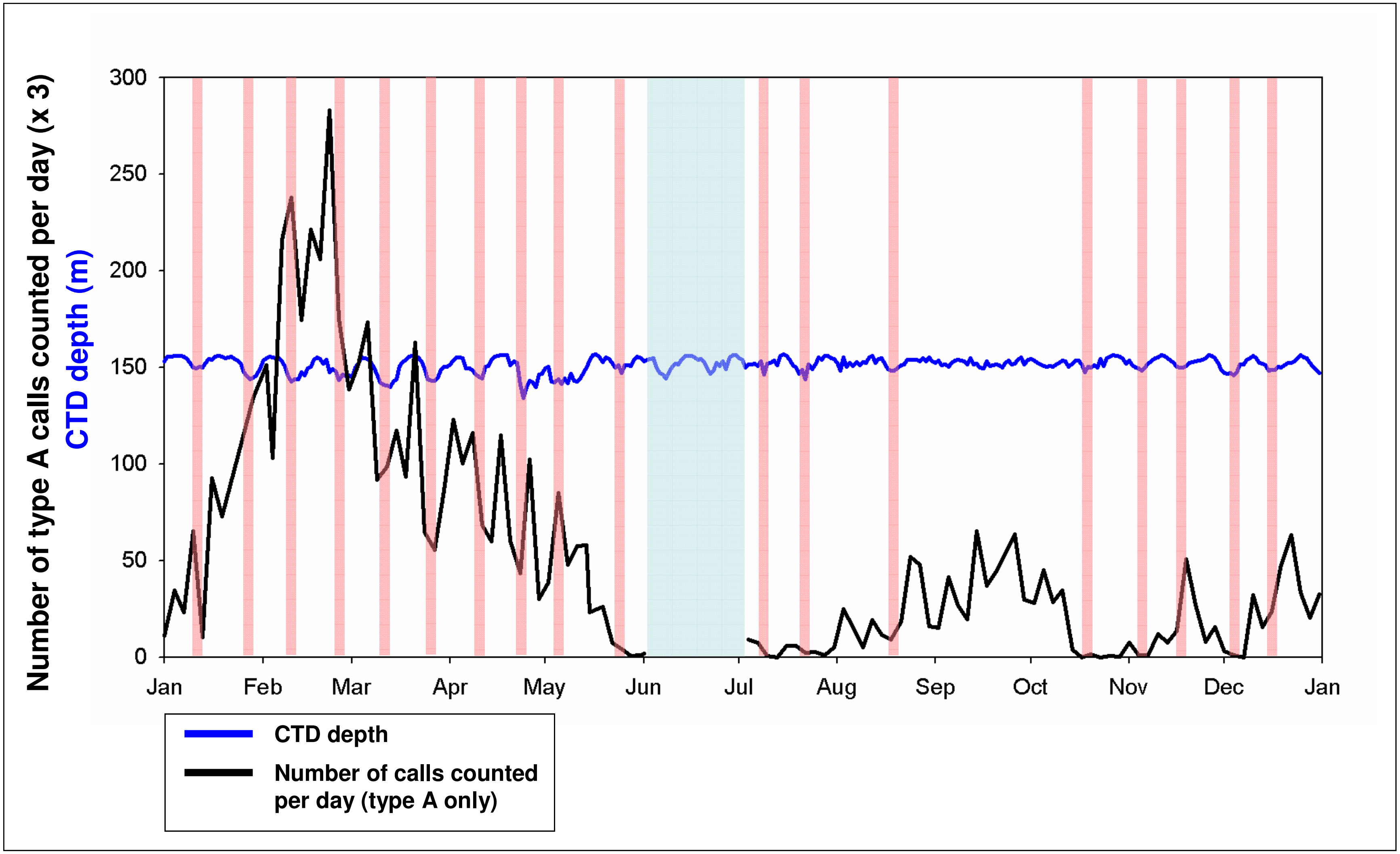

Bioduck presence – 2006 and 2009
Acoustic presence
2006
2009
Hours with bioduck presence (% of total number of hours)
100
80
60
40
20
0
*
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
2006
2009
No data

Fig 9.



Number of type A calls counted per day (x 3)
CTD depth (m)
300
250
200
150
100
50
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
CTD depth
Number of calls counted per day (type A only)

Fig 10.

Publication IX

Calling in the cold: pervasive acoustic presence of humpback whales (Megaptera novaeangliae) in Antarctic coastal waters

CALLING IN THE COLD: PERVASIVE ACOUSTIC PRESENCE OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) IN ANTARCTIC COASTAL WATERS

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Submitted to Biology Letters
July 2010

ABSTRACT

Humpback whales migrate between relatively unproductive breeding grounds and productive feeding areas. However, not all individuals of a population undertake the annual migration to the breeding grounds; instead some remain on the feeding grounds year-round, presumably to avoid the energetic demands of migration. In the Southern Hemisphere, ice and inclement weather conditions restrict investigations of humpback whale presence on feeding grounds as well as the extent of their southern range. In this study one year of near-continuous recordings from the PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA, Ekström Iceshelf, 70°31'S, 8°13'W) explores acoustic presence of humpback whales in an Antarctic coastal area. Humpback whale calls were present during nine months of 2008: January through April, June through August, November and December. Typically, calls occurred in bouts, ranging from 2 to 17 consecutive days with February, March and April having most daily presence of calls. Whales were within a 200 km radius off PALAOA. Calls were also present during austral winter when ice cover within this radius was >90%. These results demonstrate that Antarctic coastal areas are of greater importance to humpback whales than previously assumed, presumably providing food resources year-round and open water in winter where animals can breathe.

KEYWORDS: humpback whale, *Megaptera novaeangliae*, Antarctic coast, migration, acoustic presence, ice cover

INTRODUCTION

Baleen whales undertake annual migrations between tropical or temperate wintering areas where breeding takes place, and high latitude feeding grounds in summer [1]. In contrast to migrations undertaken by terrestrial species, which are primarily driven by nutritional resources at both locations [2,3], baleen whales migrate between relatively unproductive breeding grounds and productive feeding areas. Corkeron and Conner [4] revisited several hypotheses as to why baleen whales undertake these long-distance migrations and concluded that the most likely hypotheses driving baleen whale migration are those related to calf growth and survival, *i.e.,* the benefits of the absence of killer whales in the wintering areas and the presence of calm water. However, there is substantial evidence for various baleen whale species that not all individuals of a population undertake the annual migration and that part of the population is present on the feeding grounds in the winter [5,6,7,8]. Off the Alaskan coast, humpback whales (*Megaptera novaeangliae*) were present on the feeding grounds year-round [9]. Brown *et al.,* [10] found that the sex-ratio of humpback whales migrating from the feeding grounds in the Antarctic to the breeding areas near the east-Australian coast was highly skewed towards males, demonstrating that some females remain in the feeding area year-round.

Based on mark-recapture and historic catch data, most humpback whale feeding grounds in the Southern Hemisphere are believed to be located around 60°S [11,12]. However, this knowledge is primarily based on data collected off-shore during the austral summer and is limited in scope because of heavy ice conditions close to the continent as well as limited daylight and extensive ice cover in austral winter. Consequently, the extent of the southern range of humpback whale feeding areas is unknown. In the Northern Hemisphere, humpback whales show a strong affinity for coastal waters [13], which during the summer is thought to reflect the distribution of prey species [14]. Similarly, off the western Antarctic Peninsula, resource sites for humpback whales are mainly located in near-coastal areas [15,16], raising the question as to whether humpback whales off the Antarctic continent feed close to the ice-shelf edge. During Antarctic winter, vast areas of the Southern Ocean are ice covered while coastal polynyas within the ice-shelf edge region provide small areas of open water where minke whales and beaked whales have been observed [6]. Humpback whales are thought to avoid entering ice-covered areas [16], leaving the question as to where humpback whales remain on the feeding grounds during winter unresolved. Humpback whales are highly vocal and are known to produce sound on the breeding and feeding grounds as well as during migration [17,18,19]. Passive acoustic recording techniques therefore offer a suitable tool for monitoring humpback whale presence year-round in – from the human perspective – remote areas such as the Antarctic. In this study we investigate the year-round acoustic presence of humpback whales close to the ice-shelf edge using one year of continuous acoustic recordings obtained from the autonomous PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA).

METHODS

Acoustic recordings

The PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA) is located at 70°31'S, 8°13'W on the Eckström Iceshelf, eastern Weddell Sea coast, Antarctica (Fig 1). Recordings are made continuously year-round with two hydrophones deployed underneath the 100 m thick floating Antarctic ice shelf through bore-holes with an in-between distance of 300 m [20,21]. Signals are digitized at 48 kHz/16 bit and encoded to a 192 kBit MP3 stream by a BARIX Instreamer device. The effective bandwidth of the PALAOA recordings is 10 Hz to 15 kHz, dynamic range 60 dB to 150 dB re 1 μPa.

For this study we used recordings from 1 January through 31 December 2008. PALAOA records continuously year-round, however occasional gaps occur due to power outages. For recordings from January through April and October through December 2008 recordings covered at least 80% of the month. In the austral winter, from May through August 2008, more than 30% of each month was recorded, while for September 2008 only 9% of the month was covered.

Automated call detection

Previous analyses showed that two predominant humpback whale vocalization types were present in the PALAOA recordings: moans and high calls [22]. Both vocalization types were positively assigned to humpback whales based on previous evidence [19,23]. Moans are low frequency (~100 Hz) arch-shaped calls that are sufficiently stereotyped to allow for automated detection (Fig 2a & b). In contrast to high calls which were too variable to be useful for our automated detection method and were not included in the analysis in this study. Moans were automatically detected using the 'data template detector' in XBAT (Bioacoustics Research Program, Cornell Lab of Ornithology, www.xbat.org). Detections are based on acoustic similarity between a specified template and the acoustic events in the recording, quantified through spectrogram cross-correlation. Detections were run with one template of the moan (duration 1.1 s, bandwidth 240 Hz, detection correlation threshold 0.42, spectrogram parameters used for template development: FFT size 4048 points, window length = 1, window function = Hanning). All automated detections were visually and aurally reviewed and classified as false or true. Only verified detections were used to explore seasonal acoustic presence of humpback whales.

Ice cover

To compare humpback whale acoustic presence to local ice cover, percentage open water was calculated using ENVISAT ice cover data with a 6.25 x 6.25 km resolution [24]. Determination of the radius of the area off PALAOA for which percentage open water was calculated was based on estimations of the approximate distance of calling humpback whales recorded by PALAOA. This distance was estimated by comparing the received levels at PALAOA of humpback whale moans and an oceanographic RAFOS sound source with comparable acoustic propogation characteristics as humpback whale moans. The RAFOS sound source is located 191 km north of PALAOA (Fig 1) and produces a 80s sweep between 259 and 261 Hz at 180 dB_{rms} re 1 μPa. The RAFOS sound source was used to calculate the reduction in amplitude per unit distance and this was extrapolated to humpback whale moans, assuming moan source levels were 175 dB [23].

RESULTS

Seasonal presence

Humpback whale moans were present during nine months of the year in 2008: January through April, June through August and November and December. Most humpback whale moans were detected in March and April, *i.e.,* late austral summer. In May, October and September, no moans were detected.

Typically, moans occurred in bouts of a few days, ranging from 2 to 17 consecutive days, with only 13 single days (Fig 3). Of all months, February, March and April had most daily presence of humpback whale moans.

Ice cover

Moans were estimated to be produced by humpback whales at a distance between 135 and 170 km from the observatory. Figure 4 shows the percentage of open water for the area within a 200 km radius off PALAOA along with the days on which moans were detected (black triangles) and PALAOA recording status (black bar indicates the observatory was recording). Moans were present from February when open water dominated the area around PALAOA (> 90%) to the end of April when percentage of open water decreased to less than 30%. Further calls were detected in austral winter when percentage of open water was below 30% and in austral summer (November) approximately 2 weeks after seasonal sea-ice melt has started.

DISCUSSION

Humpback whale feeding grounds near the ice-shelf edge

The presence of humpback whale vocalizations in the PALAOA recordings from austral summer suggests that humpback whale feeding grounds in IWC areas II and III extend further south than previously assumed [12,25, Fig 5]. Tynan [26] proposed that humpback whale southbound migration and location of primary feeding areas is linked to the occurrence of predictably productive areas at the southern boundary of the Antarctic Circumpolar Current. With the receding pack-ice in austral summer, whales migrate south of the southern boundary, following the productive marginal ice-edge zone, approaching the continent by February-March [26]. In contrast to a more or less confined location of humpback whale feeding areas as proposed by the IWC [12], Tynan's [26] and our study suggest that feeding grounds in the Southern Hemisphere are more likely longitudinal regions through which the animals range in a southbound direction while foraging. Humpback whales are known to travel extensive distances on the feeding grounds as part of their foraging strategy [16]. The location of primary feeding areas might therefore not be static, but determined by seasonal sea-ice retreat, primary productivity and krill (*Euphasia superba*) abundance. Preliminary analyses show that humpback whale moans also occur in PALAOA recordings from previous years, suggesting that whales return to this area annually.

Winter presence

The results of our study show that Southern Hemisphere humpback whales are also present near the ice-shelf edge in the austral winter (Fig 5). Brown *et al.,* [10] suggested that females might avoid undertaking or completing the long-distance migration each year. Size rather than age is thought to be an important factor determining sexual maturity in humpback whale females [27] and it might therefore primarily be sexually or physically immature females that remain on the feeding grounds all year to maximize growth. These observations along with the relatively large number of Northern Hemisphere humpback whale populations in which individuals have been observed on the feeding grounds in winter [9,28,29,30,31], suggests that winter presence on the feeding grounds might be a feature to humpback whale populations in general, and possibly even a general characteristic of baleen whale migratory behavior [32].

The acoustic presence of humpback whales in the region off PALAOA in austral winter (June – August) implies that these whales overwinter in this area. Straley [9] found humpback whales present on Northern Hemisphere feeding grounds throughout winter, although no individual whales overwintered in the feeding area and whales were more likely to be irregular migrants departing late or arriving early on the feeding grounds. In our study, the extent of the Antarctic ice sheet in the mid-winter period with open water mainly occurring in coastal polynyas, excludes large scale north- or southbound migration of whales. This suggests that whales present on the feeding grounds in winter are more or less confined to these areas until the sea-ice recedes in austral spring.

Presence in ice-covered areas

The acoustic presence of humpback whales in April and in austral winter when sea ice cover in the area around PALAOA is pervasive contradicts previous suggestions that humpback whales avoid entering ice-covered areas [15,16,33]. Little is known about the presence of baleen whales in ice-covered areas, mainly because of the logistic difficulties of accessing these regions, particularly in the Antarctic. Nevertheless, observations of several studies suggest that the availability of breathing holes in the ice, rather than the ice itself restricts cetacean distribution to areas where polynyas or areas of open water reliably occur [6,34]. Sirovic *et al.,* [32] used passive acoustic techniques and found blue whale calls present in spring when sea ice cover was still substantial. Minke whales are known to associate with pack ice in winter and autumn [6] and have been observed creating breathing holes in ice [35]. Large groups of various cetacean species were observed being ‘entrapped’ in pools surrounded by vast ice-covered areas in winter [36,37,38]. In the Antarctic, the presence of open water and the formation of polynyas are variable and depend on catabatic and westerly winds transporting ice in northern directions [39], whereas easterly winds parallel to the coast transport ice towards the Antarctic continent. Furthermore, the presence of icebergs can affect the formation and size of polynyas as these often also tend to form on the lee side of (stranded) icebergs or glacier tongues [40]. Variability in the presence and size of areas with open water resulting from ice movements might temporarily limit access to certain areas, possibly explaining the temporal patchiness in the occurrence of humpback whale moans within and between months. In addition, humpback whale movements are likely also affected by krill distribution. In winter, krill is known to prefer under-ice habitat to open water, concentrating near specific sea-ice features such as ridges and polynya borders for feeding and shelter [41]. Although we do not know if humpback whales forage in the area off PALAOA, the coastal polynya likely offers plentiful food supply to humpback whales in winter.

Conclusions

Our results show that humpback whales may be much more plastic in their migratory behavior than previously assumed and that many aspects of their migration are still poorly understood [see also 42]. Acoustic recording techniques provide the possibility of monitoring acoustic presence on Antarctic feeding grounds year-round, but can also be used to gain insights to which breeding stock calling individuals belong [43,44]. Sounds recorded by PALAOA are likely produced by animals from breeding stock B, off the west-coast of South-Africa, which are thought to migrate to feeding areas between 20°W and 20°E [45]. Nevertheless, the lack of acoustic data on appropriate spatial and temporal scales currently impedes a comparison between vocal behavior on the breeding and feeding grounds or along migratory routes.

Commercial whaling and illegal hunting has drastically reduced humpback whale populations in the Southern Ocean [46]. As pointed out by Brown *et al.,* [10], improving knowledge on humpback whale migratory behavior is important given that incorrect assumptions on migratory behavior can significantly affect outcomes of population models and management decisions.

ACKNOWLEDGEMENTS

We thank Rosa Wilm, Svenja Zakrzewski and Taryn Overton for assistence with acoustic analyses. The logistics department of the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany, Reederei F. Laeisz GmbH, Rostock, Germany and FIELAX Services for Marine Science and Technology mbH, Bremerhaven, Germany all played a crucial role in setting up and/or maintaining PALAOA. Special thanks to overwinterer Max Goerler who maintained PALAOA during 2008. The PALAOA project was partly funded by the Bremerhavener Gesellschaft für Innovationsförderung und Stadtentwicklung (BIS).

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FIGURE LEGENDS

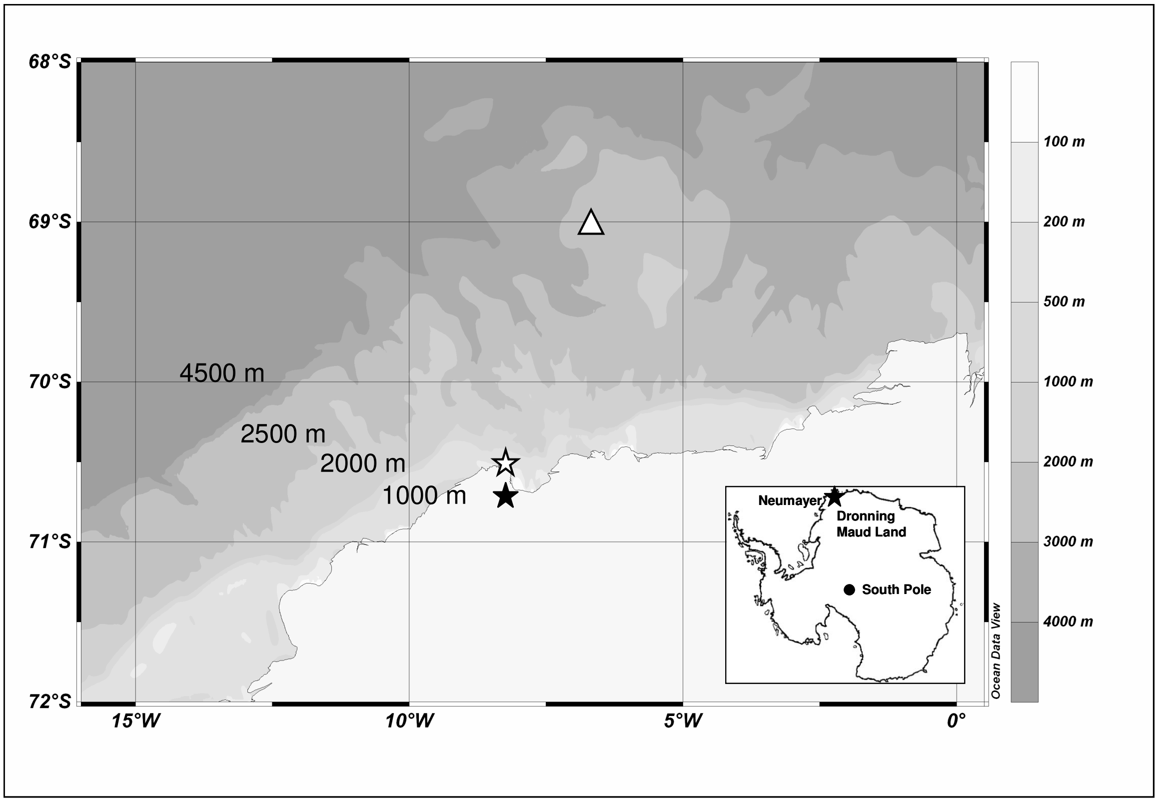
Figure 1. Bathymetry map showing the location of PALAOA (white star) and location of the German Neumayer Station II (black star). The white triangle indicates the location of a RAFOS sound source. Inset image: map of Antarctica showing the location of Neumayer Station (black star).

Figure 2. Spectrograms of humpback whale moans recorded by PALAOA: a) on 1 April 2008, b) on 6 July 2008.

Figure 3. Daily presence and absence, presented as 1 and 0, respectively, of humpback whale moans for all months in 2008. Crosses indicate that no recordings were available for that day.

Figure 4. Presence of humpback whale moans (black triangles) in relation to percentage of open water (area graph) within a 200 km range off PALAOA for all days in 2008. Recording status of PALAOA is indicated by the black bar below the acoustic presence indicators (station is recording = black bar present).

Figure 5. Seasonal humpback whale distribution between 20°W and 80°E, showing the summer (grey) and winter (white with black dots) concentrations. The white star indicates the location of PALAOA with the 200 km range (black half circle) in which humpback whales were acoustically present in austral summer and winter. The light grey and the diagonally striped areas represent the larger summer and winter ranges, respectively, as suggested in this study. Figure adapted from P. Best (2007). Reprinted and adapted by permission of the publisher.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South Pole
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2000 m
3000 m
4000 m
Ocean Data View

Fig 1.

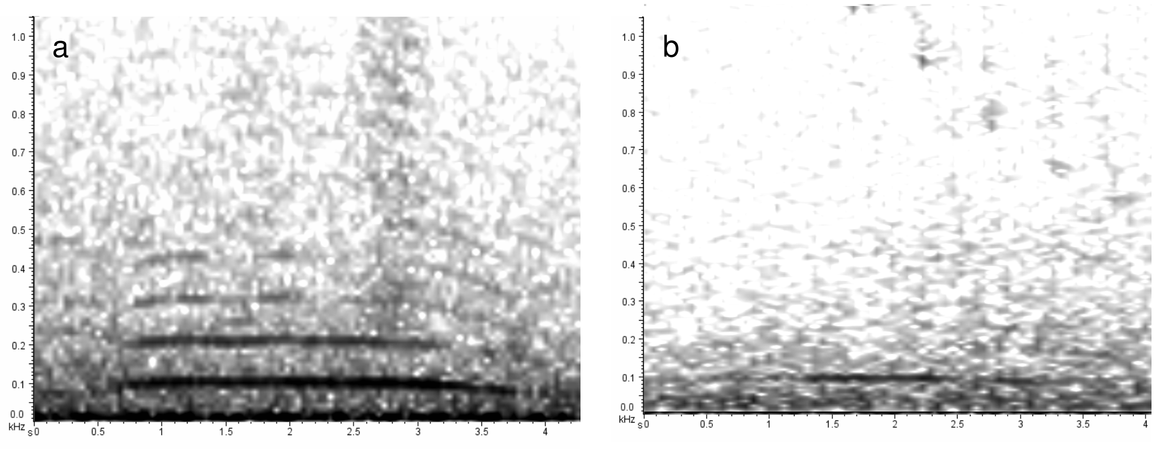
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Fig 2.

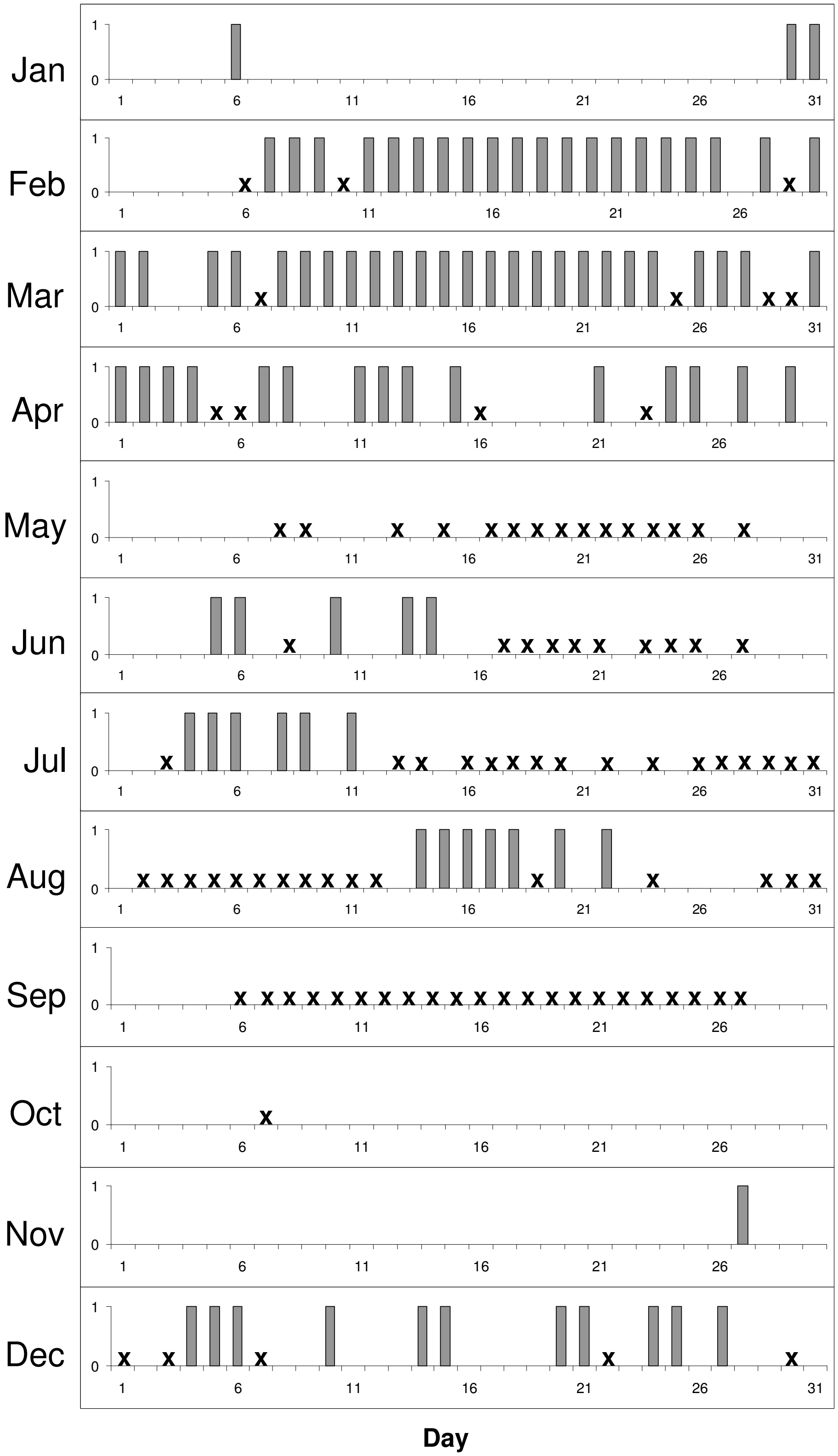

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Fig 3.

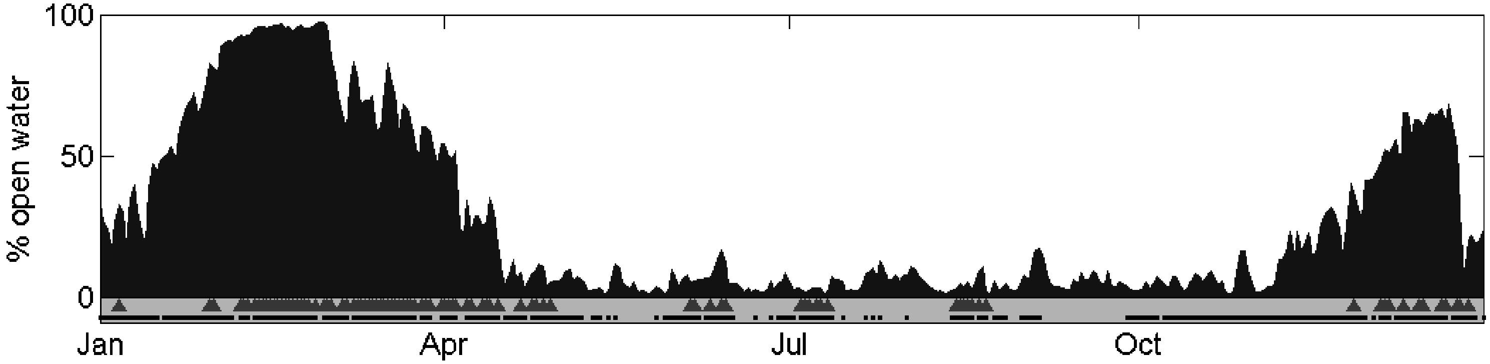
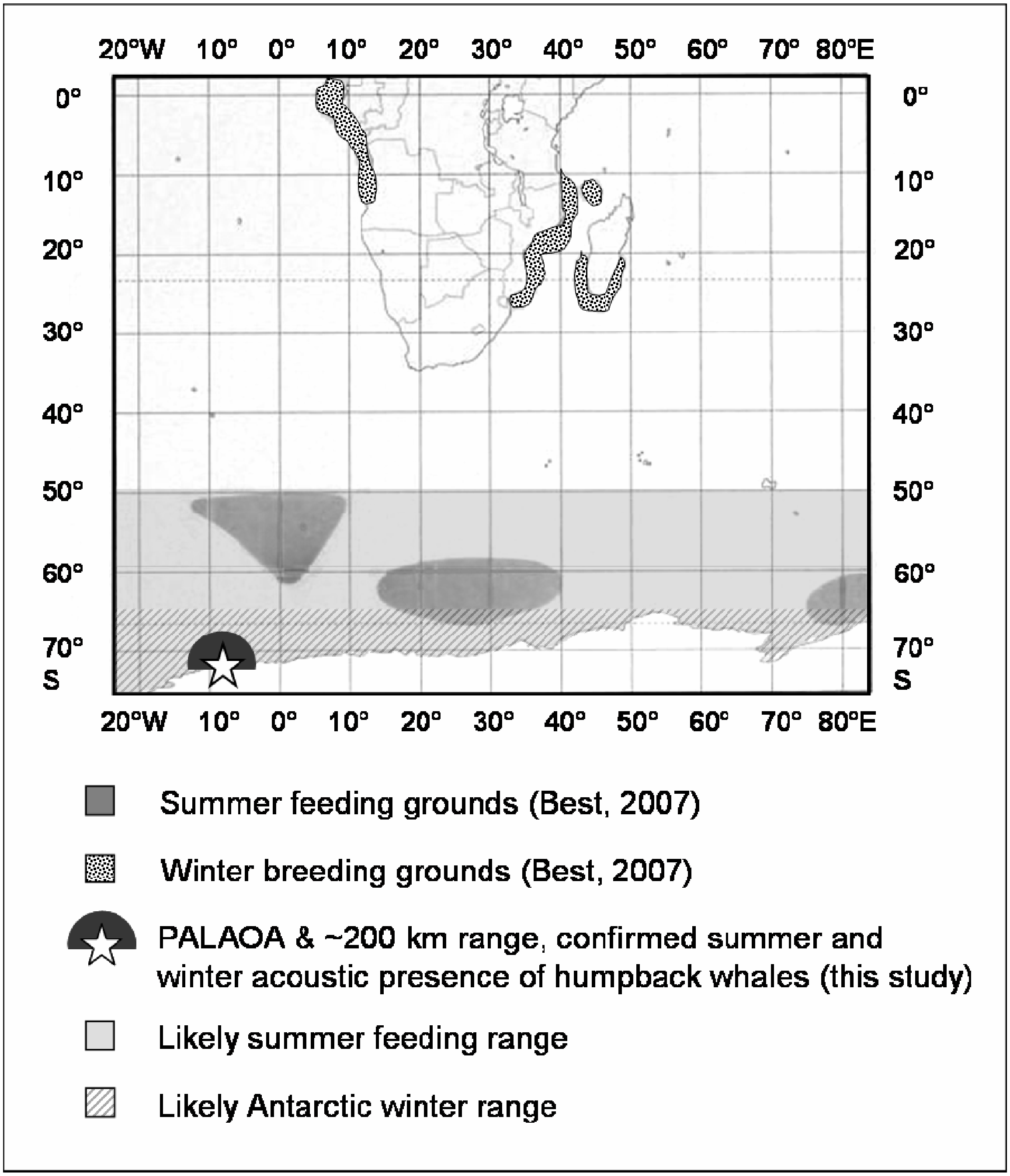


Fig 4.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Summer feeding grounds (Best, 2007)
Winter breeding grounds (Best, 2007)
PALAOA & ~200 km range, confirmed summer and winter acoustic presence of humpback whales (this study)
Likely summer feeding range
Likely Antarctic winter range

Fig 5.

Publication IX.a

Supplement to paper 9: *Vocal repertoire of humpback whales near the Eckström Ice Shelf*

SUPPLEMENT TO ‘CALLING IN THE COLD’

VOCAL REPERTOIRE OF HUMPBACK WHALES NEAR THE ECKSTRÖM ICE SHELF

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Manuscript in preparation

INTRODUCTION

Apart from the well-known highly structured song produced by males during migration and on the breeding grounds (Payne & McVay 1971), humpback whales also produce 'social sounds' (Payne 1978): separate surface-generated percussive sounds (i.e. breaches and tail-slaps) and social vocalizations. Social sounds are produced by both males and females (Dunlop *et al.* 2007), lack the complex structure of song and are the most common sounds recorded in the feeding areas, although also produced on the breeding grounds (*e.g.* Silber 1986; Thompson et al. 1986). In some populations, song has also been recorded on some feeding grounds (McSweeney 1989; Clapham 2000; Clark & Clapham 2004). Social sounds are thought to play a role in coordinated feeding behavior (Jurasz & Jurasz 1979; D'Vincent *et al.* 1985), inter- and intra-sexual social interactions (Tyack & Whitehead 1983; Silber 1986; Mobley *et al.* 1988) and during migration (Dunlop *et al.* 2007; 2008). In the southern hemsphere, humpback whale vocalizations have been recorded on the breeding grounds and during migration (Darling & Sousa-Lima 2005; Dunlop *et al.* 2007; 2008). Nevertheless, to our knowledge no study has described the humpback vocal repertoire on Antarctic feeding grounds. Aural monitoring of the PALAOA livestream revealed a seven-day period during which many different humpback whale vocalizations were present. Here we describe the humpback whale vocal repertoire composition, call characteristics and diel patterns in call type usage over this seven-day period. The analyses in their current form serve as a thesis-supplement to the manuscript 'Calling in the cold', but will be extended to other years in the near future and combined in a manuscript describing annual patterns in humpback whale vocal behavior in the area off PALAOA.

METHODS

Humpback whale vocalization types and diel call activity

By aurally monitoring the PALAOA live stream over the whole of 2008, occurrence and time of humpback whale acoustic activity was logged. Two classes of known humpback whale social vocalizations were identified in the PALAOA recordings: high calls and moan vocalizations (Thompson *et al.* 1986; Dunlop *et al.* 2007). No other call types were identified. High humpback whale high call and moan activity was was logged over a period of seven days between 24 March and 2 April 2008 (no recordings for 25, 29 and 30 March). Recordings from this seven-day period (total of 163 hours) were analysed in detail. Manual analysis entailed type-identification and counts per call type of all humpback whale calls within this seven-day period without subsampling the data.

1) High calls are highly variable (*e.g.* Dunlop *et al.* 2007) and were type-identified, partly based on call catalogues from literature (Thompson *et al.* 1986; Dunlop *et al.* 2007). However, given the variable nature of these calls, many high call types were different from the ones reported in literature. We therefore assigned new call type names to high calls that were not identifiable from existing call catalogues. A number of high calls could not be type-identified with certainty because of low signal-to-noise ratios. To be able to include these calls in the overall count of high calls, these were all type-identified as Z (n= 370).

2) Moans were stereotyped low frequency (~100 Hz) arch-shaped calls that could be assigned to humpback whales with certainty based on previous studies (*e.g.* "grumble" Dunlop *et al.* 2007). Moans were also included in the manual count of humpback whale calls during the seven-day period between 24 March and 2 April 2008.

To visualize diel call activity patterns over this seven-day period, all high call types were combined. High calls and moan calls were counted on an hourly basis and represented in a bar chart for each analysed day.

Acoustic characteristics of humpback whale vocalizations

For moans and all high call types that composed more than 5% of the high call vocal repertoire, (A, B, C, E, F, G, I, M and P), five acoustic parameters were measured (Fig 1): (1) start frequency (SF), (2) end frequency (EF), (3) minimum frequency (MINF), (4) maximum frequency (MAXF), (5) duration (DUR). From these five parameters, two additional parameters were calculated: (6) frequency range (MINF/MAXF) and (7) frequency trend (SF/EF). High calls occurred in both single and double variants of the same call type, repetitions of two single call types immediately following each other. For double variants, acoustic parameters were only measured from the first segment of the call. The choice of acoustic parameters was based on earlier work by Dunlop *et al.* (2007) which showed that these parameters were suitable to separate call types statistically.

A classification tree analysis (CART) was performed in R (The R Foundation for Statistical Computing, 2009, version 2.9.2., www.R-project.org) to explore if humpback whale vocalizations could also be classified into the various call types based on their acoustic parameters.

RESULTS

Repertoire composition and acoustic characteristics

Humpback whale vocalizations were type identified into 24 call types: the moan (Fig 2) and 23 high call types. Within the seven day period that was manually analysed, moans occurred more frequently than high calls (86% vs 14%). The 23 high call types consisted of 21 high call types (A-Q), composite calls (CC) and high calls that could not be type-identified (Z) (Fig 3). Most high call types, except high call type F, typically occurred in a single and double variant indicated with 1 and 2, respectively, with the double variant occurring more frequently for all call types except in call types A, B and C. High call types A, B, C, E, F, G, I, M and P (Fig 4a-j) each composed more than 5% of the humpback whale high call repertoire (single and double variants combined; Fig 4c-d shows an example of a double and a single variant for call type C, respectively). In addition, 11% of the high call repertoire consisted of composite calls: calls that consisted of combinations of other call types (Fig 5). Composite calls were highly variable in the type and number of elements that they consisted of and were not further type-identified. In addition, a number of broadband sounds could not be identified as vocal sounds, and appeared similar to surface percussive sounds reported by previous studies (*i.e.* “presumed underwater blow”, Dunlop *et al.* 2007). However, since these sounds were very similar to ice calving sounds and could not be visually confirmed to be produced by humpback whales, these sounds were not included in the count.

Calls were not produced in patterned sequences and therefore there was no evidence of humpback song in the recordings.

Acoustic parameters were measured for at least 20 calls for each call type (Table 1). Several call types showed overall similarity to call types described by Dunlop *et al.* (2007): call type P resembled the “wop” and “thwop” calls, moans resembled the “grumble”. However, the majority of call types described in this study differed substantially in overall structure from previous studies.

The CART showed that moans were clearly separable from all high call types based on their maximum frequency, which was below 145 Hz for 95% of the moans (Fig 8). All high call types except call type M and F, more than 50% of calls were correctly classified according to call type (Table 2).

Diel call activity

Manual analysis of the seven-day period from 24 March and 2 April showed that moan activity was highest on 1 April with an average of 5.1 moans per minute (Fig 7). Moan activity did not show a clear diel pattern, although on the days with highest moan activity the number of moans seemed to decrease in the evening hours; below 2 moans per min between 17:00 – 22:00 on 1 April and 20:00 – 23:00 on 2 April. On 31 March the number of moans per minute showed a peak around 11:00 and 23:00 hours. The number of high calls increased gradually from 24, 26 and 27 March, while no high calls were present on 28 March. The number of high calls was highest on 31 March with an average of 2 high calls per minute and thereafter decreased again towards an average of 0.1 high calls per minute on 2 April. Overall, when moans and high calls were combined, call activity was relatively constant on some days, whereas on other days call activity was clearly highest during the day, decreasing around 18:00 hours and increasing again around 22:00 hours (Fig 7-h).

DISCUSSION

Vocal repertoire composition and acoustic characteristics

Although the majority of high calls occurred within the seven day period that was analysed in this study, some faint high calls were also found to occur in January and July 2008. This suggests that the use of high calls is not restricted to March and April, but that high calls and moans are used throughout the year when humpback whales are present on the feeding grounds. Lower frequency moans are likely to propagate further than high calls. Movements in response to factors such as changes in ice cover or prey availability may possibly cause animals to move closer to the shelf in March and April explaining why high calls are mainly present in recordings from these months. Data from tagged individuals in Antarctic feeding areas also show that humpback whales do not stay in the same place for extended periods of time, but rather roam in fluid movements throughout the feeding area (Dalla-Rosa *et al.* 2008). In addition, the presence of ice in this period (see manuscript 'Calling in the cold') might also influence whale movements.

The double variants of high calls observed in this study, have to our knowledge not been described by previous studies. Instead, other studies found humpback whales to regularly produce repetitive series of calls during migration and synchronized feeding behavior (*e.g.* D'Vincent *et al.* 1985; Cerchio & Dalheim 2001; Dunlop *et al.* 2007). Such vocal behavior has been found to occur in humpback whales herding fish, but also while herding euphasids and is therefore unlikely to be explained by the prey-type that is herded. The double variants of high calls described in this study these differences might therefore reflect population-specific acoustic behavior. The social vocalization repertoire is known to contain population-specific call types (song-units) in some populations (Dunlop *et al.* 2008). Population-specific acoustic characteristics may provide cues to identify to which breeding population animals on the feeding ground belong (*e.g.* Darling & Sousa-Lima 2005). Currently, 8 geographically separated southern hemisphere humpback whale stocks with connections to feeding grounds in the Antarctic have been recognized by the IWC (breeding stocks A-G and X; Rosenbaum *et al*. 2009). However, to date information on movement patterns, migratory corridors and feeding destinations are largely lacking. Based on previous studies (*e.g.* Rosenbaum *et al.* 2009), we assume the sounds recorded near the PALAOA station are produced by animals from breeding stock B, off the west-coast of South-Africa, which are thought to migrate to feeding areas between 20°W and 20°E. However, mixing of different breeding stocks on the feeding grounds has been proposed as one of the possible explanations for genetic and acoustic similarities between breeding stocks A, B and C and feeding areas from different breeding stocks may therefore overlap (Mackintosh 1942; Darling & Sousa-Lima 2005; Rosenbaum *et al.* 2009; Razafindrakoto *et al*. 2009). Similarities in acoustic behavior on the feeding and breeding grounds, such as the presence of double variants of high calls, could provide information on humpback whale migratory behavior. However, too little is known on breeding stock B and C song and social vocalization repertoire characteristics from recent years to draw such comparisons.

Along with previous studies, this study shows that not only humpback whale song is highly diverse, but social vocalizations are also highly variable in structure. The CART showed that for the majority of call types most calls could be assigned to the correct call type based on their acoustic parameters, supporting the call type categorization used in this study. The relatively low percentage of correctly classified calls for call type F (29%) and M (42%) may be explained by the fact that the acoustic parameters used do not sufficiently represent the characteristics of these call types. Analyses of high call acoustic characteristics over multiple years will provide information on the stability of call types and their acoustic characteristics.

Diel patterns in call activity

Humpback whale vocal activity was found to decrease in the late afternoon and evening in March and April, which possibly is related to the behavior of Antarctic krill (*Euphausia superba*), their primary prey. Vertical migration of zooplankton[1] in March and April occurs within the upper 200 m of the water column and shows a distinct diel pattern in these months with zooplankton migrating to shallower water depth around 16:00-17:00 hours (Siegel 2005; Cisewski *et al*. 2010). The decrease in overall call activity coincides with the time at which zooplankton concentrations are at shallow depth. Our findings therefore potentially reflect that calls are produced in a social context rather than in a feeding context. Furthermore, the need and benefit of vocal behavior during foraging will be determined by prey type: fish-feeding humpback whales are thought vocalize during feeding to coordinate movements of group members, while North

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[1] Cisewski et al. (2010) suggested that the zooplankton community is likely to consist of multiple species, among which krill.

Atlantic right whales (*Eubalaena glacialis*) produce virtually no sounds while skim feeding on copepods (pers comm. S. Van Parijs). During further analyses we will use multi-year data from PALAOA to investigate diel call activity across years and in relation to seasonal variation of krill vertical migration.

ACKNOWLEDGEMENTS

Rosa Wilm and Svenja Zakrzewski assisted in acoustic analyses of humpback whale vocalizations.

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TABLES

Table 1. Descriptive statistics of high call types that composed more than 5% of the high call vocal repertoire, (A, B, C, E, F, G, I, M and P). The average and standard deviation (in % of average) if given for the five acoustic parameters that were measured: (1) start frequency (SF), (2) end frequency (EF), (3) minimum frequency (MINF), (4) maximum frequency (MAXF), (5) duration (DUR).

Call type	*A*	*B*	*C*	*E*	*F*	*G*	*I*	*M*	*P*	*Moan*
N	22	20	36	22	31	23	27	24	24	21
Parameter										
Start Freq [Hz]	396.41 (31%)	378.5 (44%)	575.81 (37%)	1070.36 (18%)	664.48 (40%)	546.39 (23%)	503.41 (37%)	412.83 (33%)	201.83 (37%)	95.71 (22%)
End Freq [Hz]	391.64 (30%)	471.5 (36%)	442 (35%)	1087.95 (17%)	789.81 (41%)	558.26 (24%)	276.70 (48%)	389.13 (34%)	200.71 (33%)	101.43 (27%)
Min Freq [Hz]	374.91 (29%)	378.5 (44%)	429.53 (36%)	982.41 (18%)	642.81 (36%)	515.48 (23%)	255.74 (39%)	292.33 (41%)	167.63 (41%)	83.43 (16%)
Max Freq [Hz]	405.86 (31%)	471.5 (36%)	575.81 (37%)	1105.82 (18%)	807.03 (41%)	577.57 (23%)	488.3 (38%)	424.46 (32%)	223.83 (30%)	115.24 (22%)
Duration [s]	0.96 (52%)	0.75 (36%)	0.38 (41%)	0.76 (38%)	0.62 (30%)	0.56 (31%)	0.98 (29%)	1.05 (29%)	0.55 (31%)	2.25 (37%)
Freq Range [ratio]	1.08 (8%)	1.28 (13%)	1.35 (13%)	1.13 (10%)	1.25 (15%)	1.12 (7%)	2.03 (36%)	1.5 (18%)	1.42 (25%)	1.4 (21%)
Freq Trend [ratio]	1.01 (7%)	0.79 (12%)	1.31 (13%)	0.99 (8%)	0.86 (17%)	0.99 (11%)	1.96 (33%)	1.08 (21%)	1.03 (30%)	1.0 (29%)

Table 2. Percentage and number of calls correctly classified by the classification tree analysis (CART) according to call type based on the acoustic parameters.

Call type	*N*	*Number of calls correctly classified*	*%*
A	22	13	59
B	20	12	60
C	36	21	58
E	22	22	100
F	31	9	29
G	23	21	91
I	27	19	70
M	24	10	42
P	24	21	88
Moan	21	20	95

FIGURE LEGENDS

Figure 1. The five acoustic parameters measured on all call types that composed more than 5% of the vocal repertoire: (1) start frequency (SF), (2) end frequency (EF), (3) minimum frequency (MINF), (4) maximum frequency (MAXF), (5) duration (DUR).

Figure 2. Spectrogram of a humpback whale moan vocalization.

Figure 3. Total number of calls counted per high call type for all 23 high call types identified in this study. Letters represent call types and numbers indicate the number of calls counted for single (*e.g.* A1) variety of call type or double variety (*e.g.* A2). Z are all calls that could not be type-identified and CC represent all composite calls.

Figure 4. Spectrograms of all high call types that composed more than 5% of the humpback whale vocal repertoire.

Figure 5. Spectrograms of two composite calls. Composite calls were not further type-identified and combined into ‘composite calls’ (CC).

Figure 6. Classification tree analysis with call type as a splitting variable. Maximum frequency (MAXFR) separated 95 % of the moans from high call types. For call types A, B, C, E, G, I and P more than 50% of calls was correctly classified based on the measured acoustic parameters.

Figure 7. Diel call activity for all seven days with the number of moans per hour represented in black bars and the number of high calls (all call types combined) per hour shown as grey bars (a-g). The last graph shows overall call activity (moans and high calls combined) for all days (h).

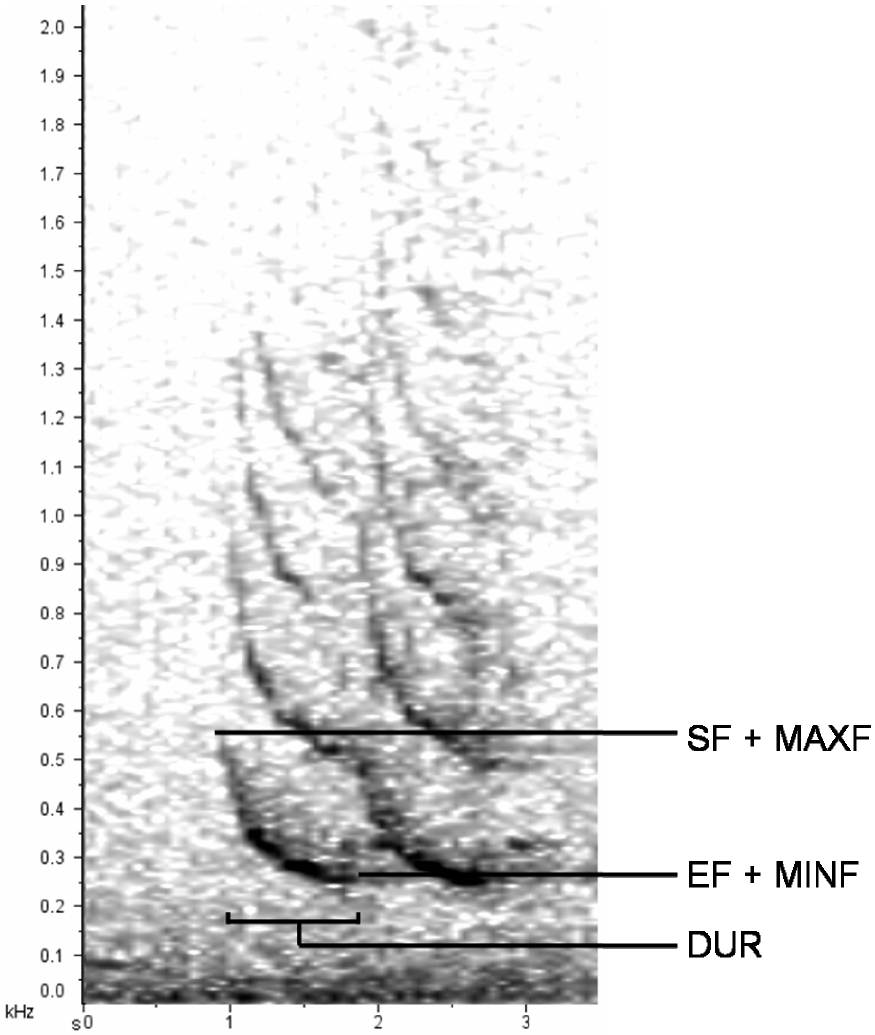

2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
kHz
s0
1
2
3
SF + MAXF
EF + MINF
DUR

Fig 1.

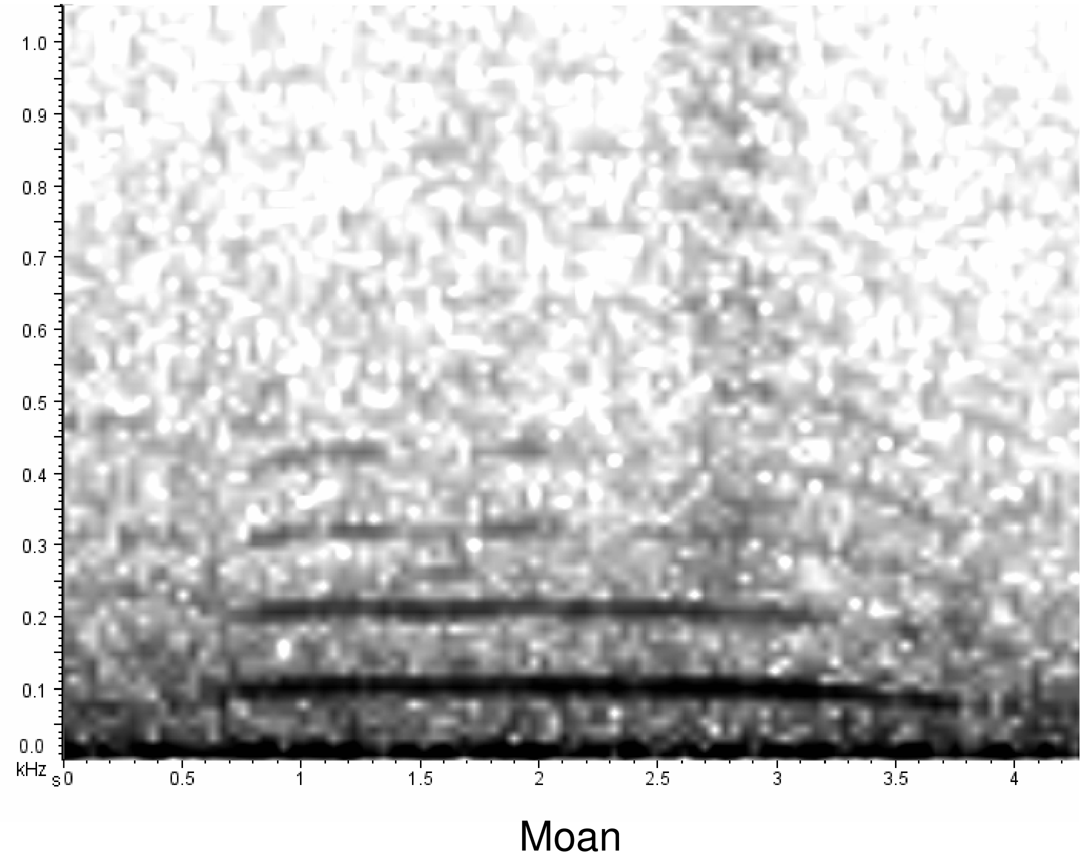


Fig 2.

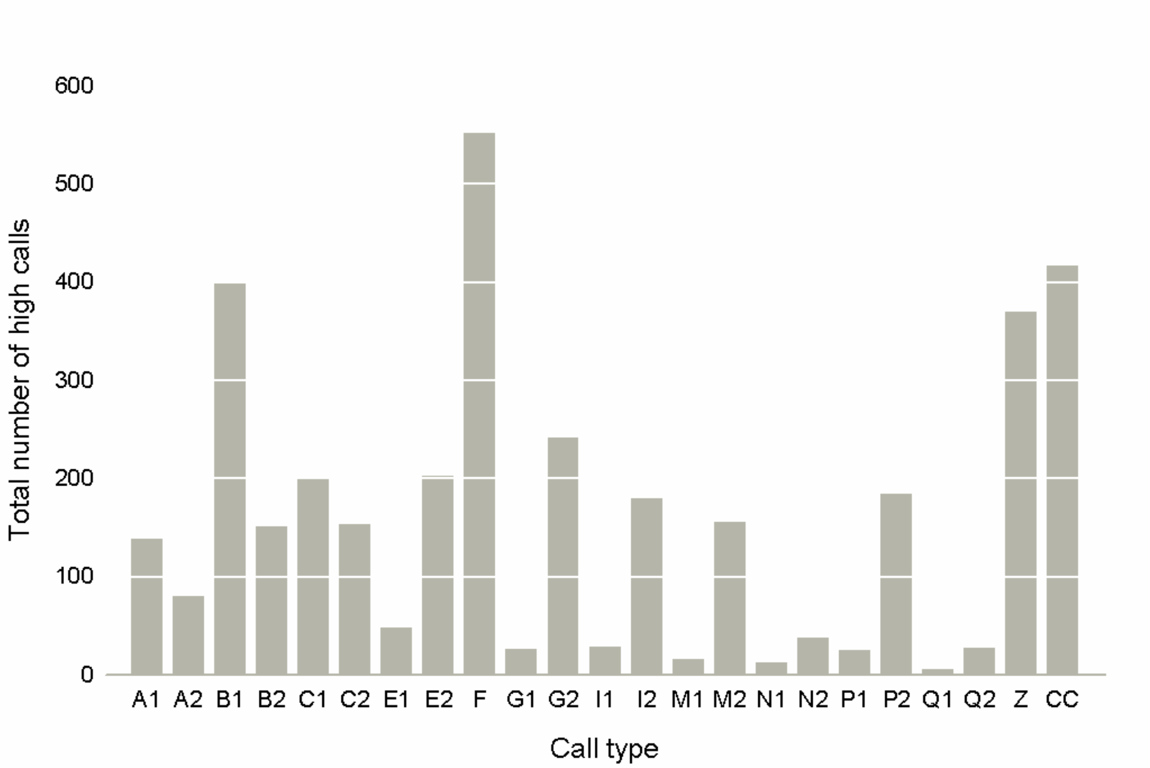
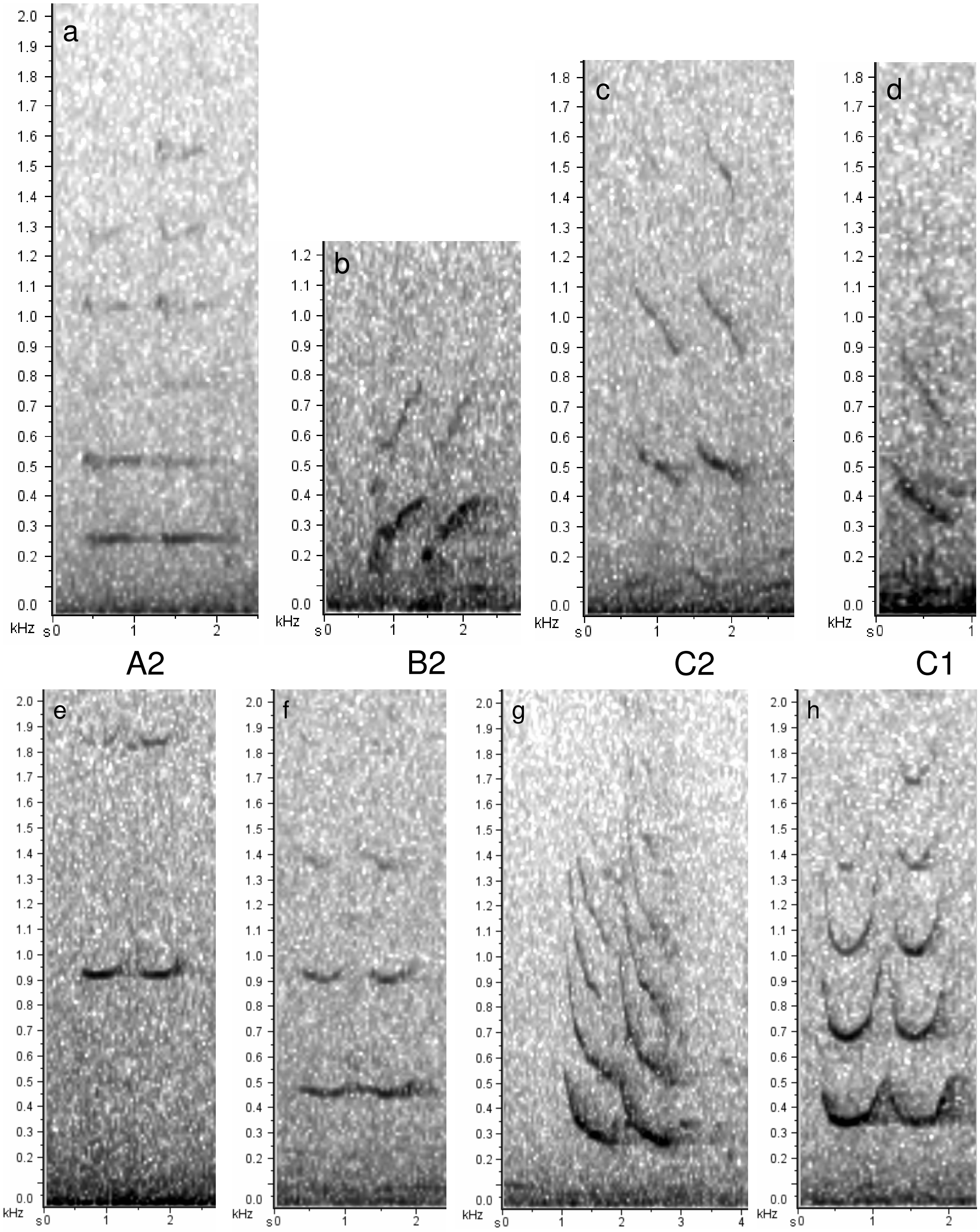
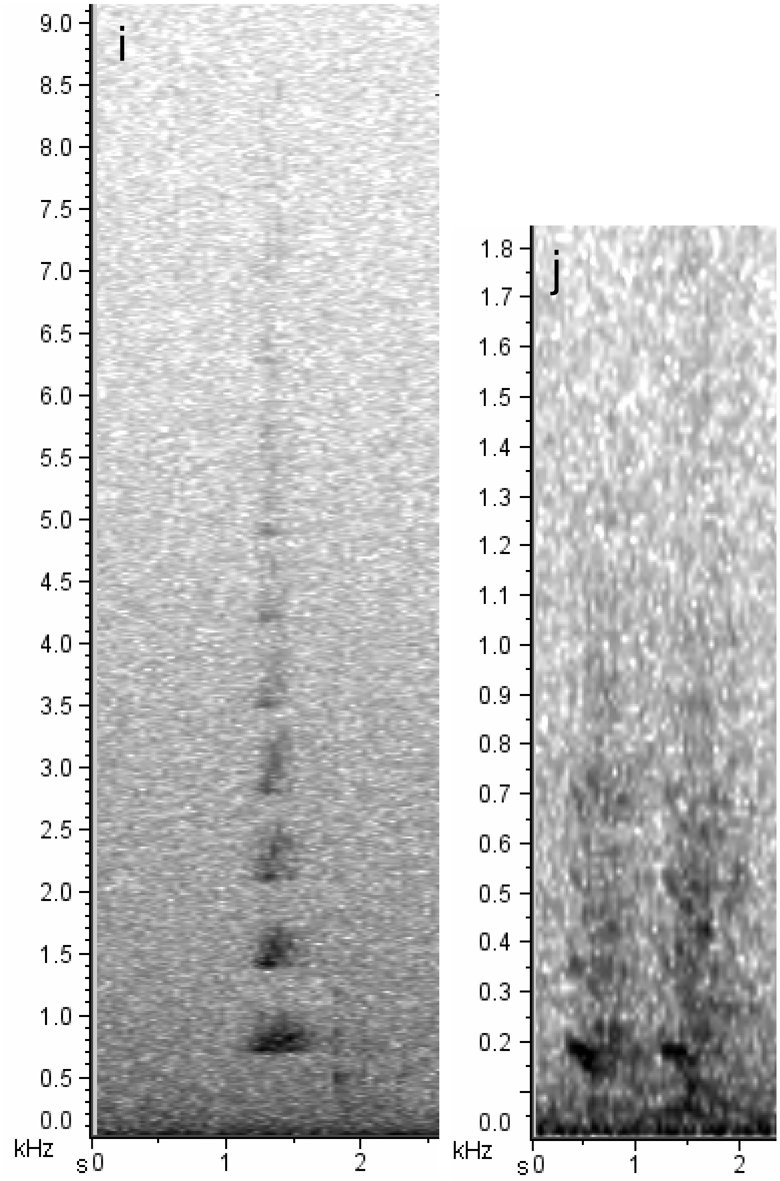

Total number of high calls
0
100
200
300
400
500
600
A1
A2
B1
B2
C1
C2
E1
E2
F
G1
G2
I1
I2
M1
M2
N1
N2
P1
P2
Q1
Q2
Z
CC
Call type

Fig 3.



A2 B2 C2 C1

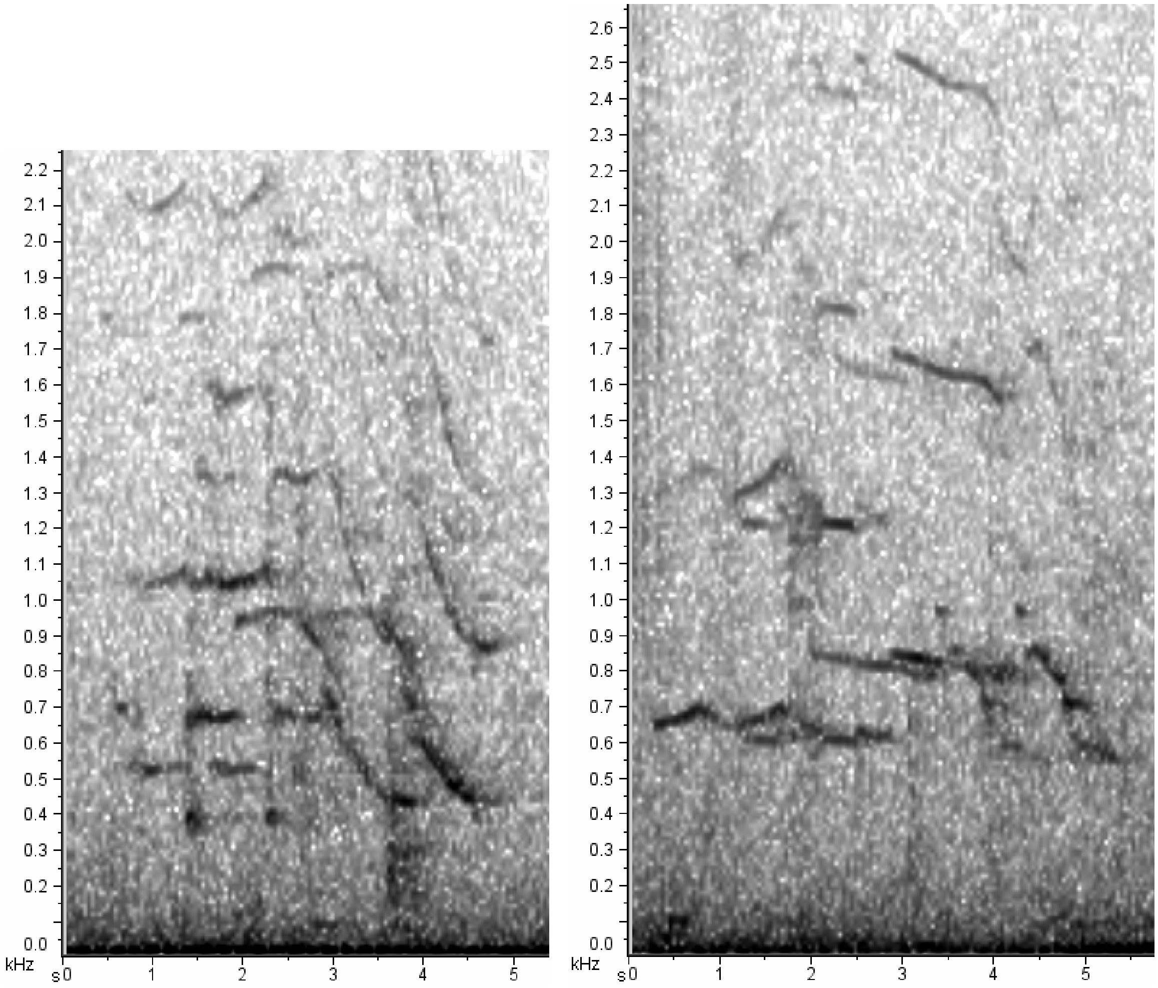
E2 G2 I2 M2


i
9.0
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
kHz
s 0
1
2
j
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.0
kHz
s 0
1
2

F

P2

Fig 4 a-j.



CC – example 1

CC – example 2

Fig 5.

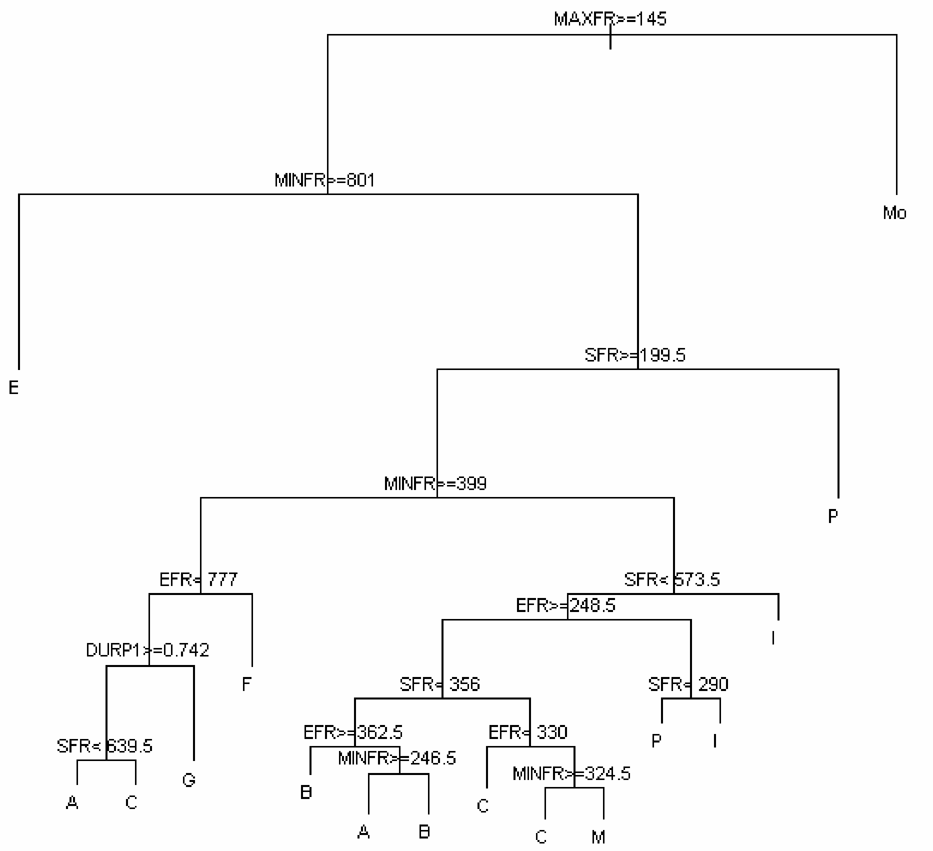

MAXFR>=145
MINFR>=801
Mo
E
SFR>=199.5
MINFR>=399
P
EFR< 777
SFR< 573.5
EFR>=248.5
I
DURP1>=0.742
F
SFR< 356
SFR< 290
EFR>=362.5
EFR< 330
P
I
SFR< 639.5
G
MINFR>=246.5
B
MINFR>=324.5
A
C
C
A
B
C
M

Fig 6.

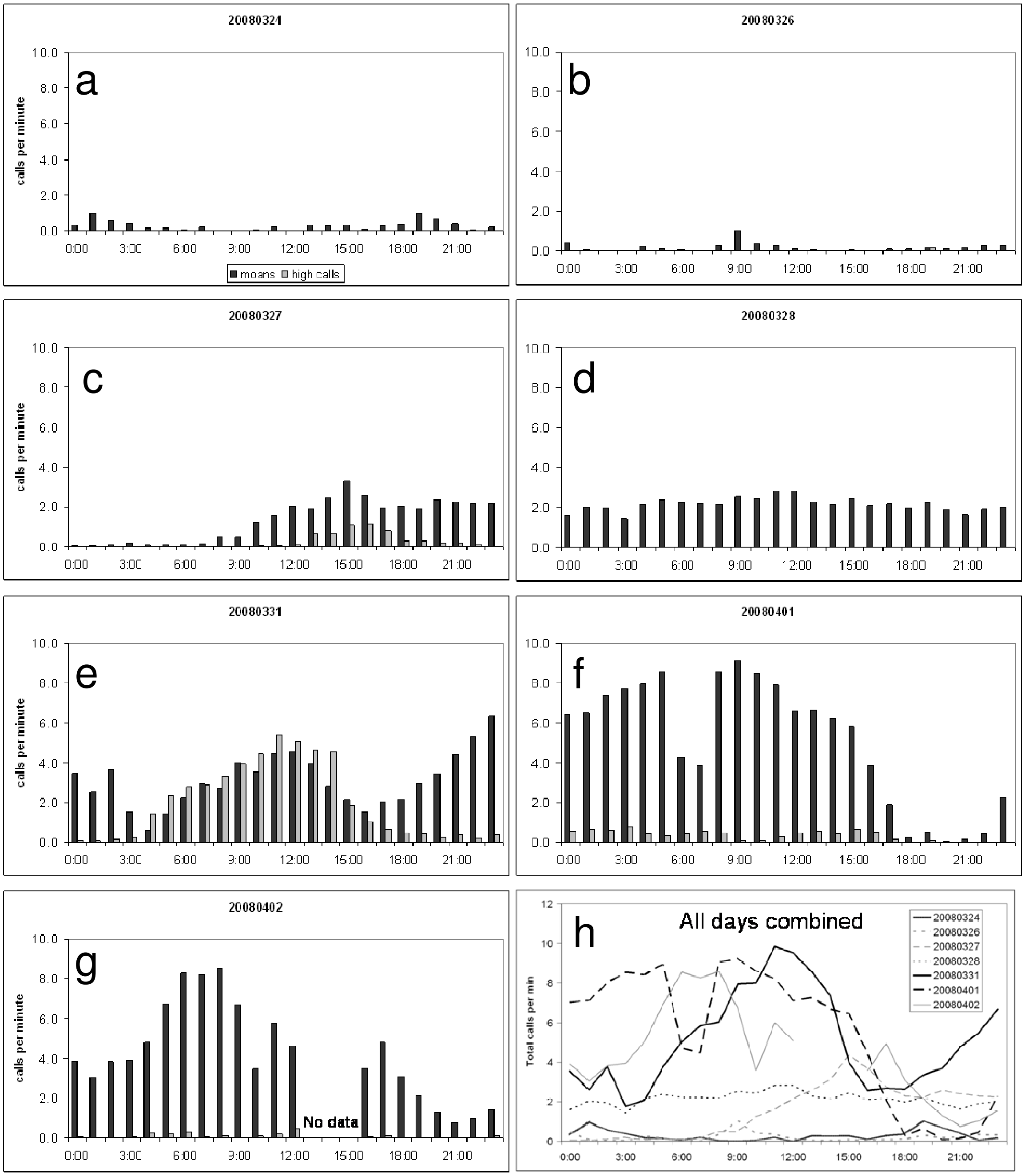
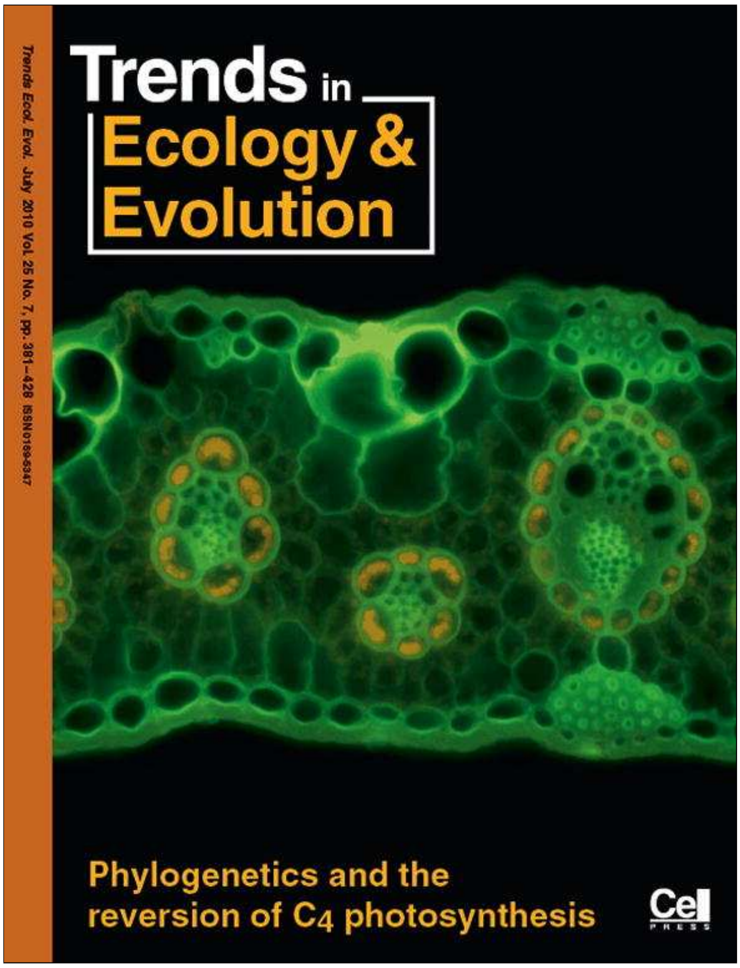

20080324
a
calls per minute
moans
high calls
20080326
b
20080327
c
20080328
d
20080331
e
20080401
f
20080402
g
No data
h
All days combined
Total calls per min
20080324
20080326
20080327
20080328
20080331
20080401
20080402
0.0
2.0
4.0
6.0
8.0
10.0
0:00
3:00
6:00
9:00
12:00
15:00
18:00
21:00

Fig 7 a-h.

Publication X

A noisy spring: the impact of globally rising underwater sound levels on fish


Trends Ecol. Evol. July 2010 Vol. 25 No. 7, pp. 381–428 ISSN 0169-5347
Trends in Ecology & Evolution
Phylogenetics and the reversion of C4 photosynthesis
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Review

A noisy spring: the impact of globally rising underwater sound levels on fish

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The underwater environment is filled with biotic and abiotic sounds, many of which can be important for the survival and reproduction of fish. Over the last century, human activities in and near the water have increasingly added artificial sounds to this environment. Very loud sounds of relatively short exposure, such as those produced during pile driving, can harm nearby fish. However, more moderate underwater noises of longer duration, such as those produced by vessels, could potentially impact much larger areas, and involve much larger numbers of fish. Here we call attention to the urgent need to study the role of sound in the lives of fish and to develop a better understanding of the ecological impact of anthropogenic noise.

The myth of a silent underwater world

In 1962, Rachel Carson wrote about a 'silent spring' in the context of the detrimental impact of the use of pesticides on singing birds. Here we call attention to a 'noisy spring', and the possible detrimental impact of increasing levels of anthropogenic noise on fishes[1] [1,2]. Fish populations have come under threat for a number of well-known reasons including fisheries [3], habitat degradation [4] and chemical pollution [5]. Human-generated underwater noise is potentially becoming another threat to fish, just as traffic noise has become a major concern in air with regard to birds and other terrestrial animals [6,7]. Although humans have engaged in all sorts of activities in, on, and near water bodies for a long time, only recently have these activities expanded in an increasingly noisy manner (Box 1). To date, underwater noise pollution has primarily attracted attention in the context of marine mammals [8–10], but it is increasingly recognized as a factor that may also have implications for fish [11–14].

In this review we focus on the need for behavioural and ecological studies on the impact of long-term anthropogenic noise on fishes. We take this approach since very large numbers of fish are exposed to moderate but widespread low-frequency noise, produced by vessels, offshore wind farms and other coastal activities, and yet we have the barest insight as to the nature and extent of the behavioural impact of such sounds on fishes (Figure 1). While data on fish behavioural responses to the increase in ambient sound are generally not available, we can use data derived from other vertebrates to suggest that anthropogenic noise may deter fish from important feeding and reproduction areas, interrupt critical activities, or cause stress-induced reduction in growth and reproductive output. The concern about wide-ranging effects is further heightened because sound is of critical importance in the lives of many fish species. Impeding the ability of fish to hear biologically relevant sounds might interfere with critical functions such as acoustic communication, predator avoidance and prey detection, and use of the 'acoustic scene' or 'soundscape' [15,16] to learn about the overall environment. Taken together, these potential effects could

Glossary

Active space: the distance from a sound-emitting animal over which the sound is detectable and recognizable by conspecifics. The active space is influenced by the source amplitude, receiver sensitivity, attenuation and degradation during transmission, and interference by ambient noise.

Anthropogenic noise: any sound generated by human activities, which has the potential to warn fish of the danger of approaching boats or risky water inlets. It may also be detrimental to fish through deterrence, interference and masking of biologically relevant sounds, or through physiological stress.

Auditory detection continuum: mechanistic scale of fish hearing, replacing the traditional and oversimplified categories of generalists and specialists. The scale ranges from fish species without a swim bladder or other air-filled body cavities and only able to detect particle motion (e.g. sharks) to fish species with a so-called otophysic connection between swim bladder and ear and able to detect motion as well as sound pressure (e.g. goldfish).

Auditory masking: the perceptual interference of one sound (often concerning a signal) by another (often referred to as noise). The masking impact occurring at the point of the receiver typically depends on the spectral overlap between and the amplitude ratio of the signal and the noise.

Cortisol: a corticosteroid hormone or glucocorticoid, often referred to as a stress hormone, due to its involvement in response to stress and anxiety. Cortisol serves to increase blood sugar levels, stores sugar in the liver as glycogen, and also suppresses the immune system.

Inner ear: the major structure in fish for detection of sound. The inner ear is located in the cranial cavity of fish and its basic structure is the same as the inner ears of sharks and all terrestrial vertebrates, including humans.

Lateral line system: a sense organ used to detect movement and vibration in fish. Lateral lines are usually visible as faint lines running lengthwise down each side of the body and sometimes as a faint network of dots on the head.

Swim bladder: an internal gas-filled organ found in most fish species (but for example not in sharks and rays amongst others) that contributes to the ability to control buoyancy control and allows a fish to stay at a particular water depth. The swim bladder can also serve as a resonating chamber and aid in sound production and sound perception.

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[1] Unless otherwise specifically noted, 'fish' in this paper refers to bony fishes of the Osteichthyes taxonomic subclass, the Actinopterygii (or ray-finned fishes)..

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Box 1. Human invasion of the underwater acoustic environment

Underwater sounds generated by human activities can be subdivided in two categories: sounds that are an unintentional by-product and sounds that are used as a measurement tool. Dominant in the first category are low-frequency noises from vessels for container shipping, public transport, fishing and recreational activities [1,2,67,68,88]. For example, >80% of global freight transport takes place over water by motorized shipping, while passenger crossing occurs on many rivers, lakes and seas, often on noisy ferries that shuttle between harbours at frequent intervals. Moreover, fishing vessels typically have strong and noisy motors for towing gear. Although the global fishing fleet has not grown much since the early 1990s it still includes about 1.2 million vessels. The number of recreational vessels is still on the rise, with a growing impact on coastal and in-shore waters [32,42,89]. Another significant source of anthropogenic noise of the first category is that associated with construction and exploitation of offshore platforms. The first submerged oil wells were drilled in a fresh water lake in Ohio (USA) around 1891, and five years later, the first marine oil wells were drilled near Santa Barbara, California (USA). Today, there are thousands of offshore oil and gas platforms worldwide. In addition, the more recent development of exploitation of renewable sources, such as wind, wave, tidal or current energy, also generates noise during construction and operational phases [90–92].

The second category of human-generated sounds for various types of underwater measurements involves both low and high frequencies. Underwater sound is used by navies, fisheries, the oil and gas industry, oceanographers, geologists, as well as meteorologists. The first time that sound was used by humans to locate objects underwater was shortly after the Titanic sank in 1912. After that, the use of mid- and later low-frequency sonar has become widespread for navigation and localization of submarines and other objects. In the context of fisheries, the first acoustic study concerned the localization of spawning cod at the Lofoten Islands in 1935 [93]. Then, by 1950, fish-finding echo sounders had become an essential aid to all commercial fishing vessels. Other acoustic measurement applications include seismic reflection profiling using high-intensity airguns to obtain information about the geological structures beneath the seafloor, and acoustic thermography of ocean climate (ATOC). The second of these was launched in the 1990 s using relatively high-intensity sound transmission for long periods to determine ocean temperature [9].

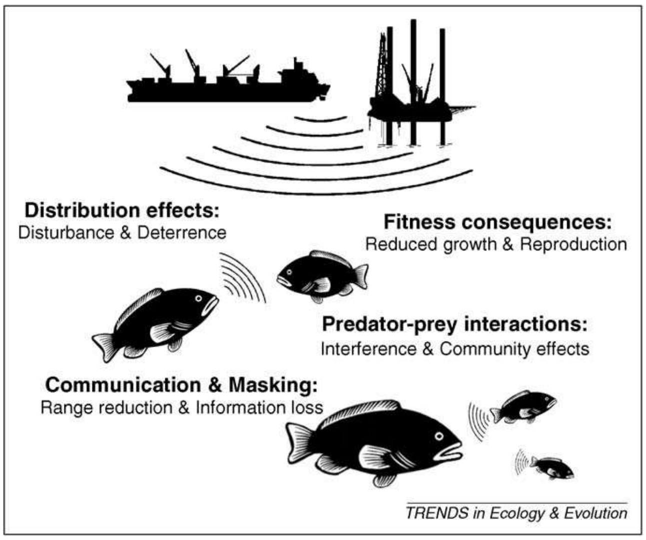

Figure 1. Four main domains of research to assess the potential impact of moderate but widespread anthropogenic noise conditions on fish (see Box 4).

have a significant impact on survival of individuals and populations and affect whole ecosystems.

It is important to make three points at the start of this review. First, our emphasis is on behavioural effects of human-generated sounds because these are likely to be the most significant for fish. At the same time we recognize that there is a great concern by many investigators, regulators and various industries about high impact sounds. Underwater explosions, pile driving, or seismic surveys, can all have dramatic effects on nearby fish, including physical damage and death. While not covered here, these immediate effects involving relatively few individual animals have recently been reviewed in great detail [14].

Second, we also emphasize in this review that researchers of the noise impact on fish can get valuable insights from investigations that have been concerned with similar issues in terrestrial animals and, to a lesser extent, marine mammals. In particular, studies on birds might provide guidance in experimental design and in asking questions that are the most useful in gaining a better understanding. Considering the striking similarities in the auditory system and perceptual abilities of all vertebrates [15], it would also not be surprising to find congruencies in the

Box 2. Underwater sound – an overview

The basic principles of sound propagation in air and in water are the same, but there are a number of features peculiar to underwater acoustics [94,95]. Water is an excellent medium for sound transmission because of its high molecular density. Sound travels about five times faster in water than in air (about 1500 vs. 300 m/s), and this means that wavelengths are about five times longer in water than in air (e.g. for a 100 Hz signal: 3 m in air, 15 m in water). Sound also attenuates less over the same distance in water than in air. As a consequence, sound travels much greater distances at higher amplitude levels in water compared to air, thereby enabling long-distance communication, but also a long-distance impact of noise on aquatic animals.

Sound levels or sound pressure levels (SPL) are referred to in decibels (dB). However, the dB is not an absolute unit with a physical dimension, but is instead a relative measure of sound pressure with the lower limit of human hearing corresponding to 0 dB in air. Underwater dB-levels are different from above water dB-levels [95]. Sound pressure levels above water are referenced to 20 µPa, while underwater they are referenced to 1 µPa. As a consequence, adding 25.5 dB to the airborne dB-level is required to get a comparable underwater dB-level. Furthermore, related to the much higher acoustic impedance of water compared to air, another 36 dB correction is required, making an airborne sound pressure level of 70 dB re 20 µPa comparable to an underwater 131.5 dB re 1 µPa.

Sound pressure levels are based on root-mean-square (RMS) measures averaged over time. They are useful for relatively long sounds but less effective for brief sounds such as pile-driving strikes and echolocation clicks of whales. Peak-to-peak values in the amplitude waveform provide an alternative measure, but comparisons between peak-to-peak and RMS levels are difficult [96]. Recently, investigators have adopted another so-called Sound Exposure Level (SEL), which is an alternative measure reflecting the total acoustic energy received by an organism [13,14]. A final issue of critical importance for understanding underwater sound as it relates to fish is the presence of a substantial particle motion component in the aquatic sound field, along with pressure. Since water is so dense, particle motion is a component of the sound field at all distances and fish are adapted to detect this component (see Box 3).

behavioural and physiological impact of human-generated sounds among very different vertebrate groups.

Third, it is important to stress that some fundamental insight into underwater acoustics is critical for a proper understanding of the problem with noise (Box 2). For example, the world of fish has been wrongly assumed to be quiet, as reflected by the title of Jacques Cousteau's 1956 movie *The Silent World*. The supposition that the underwater world is silent no doubt arose because sound transmission from water to air is poor, and because the air-adapted human ear is a relatively poor receiver underwater. In thinking about underwater acoustics, it is also important to realize that aquatic animals often live in a dark or turbid environment: even a few metres from the animal the use of vision to gather information becomes restricted. In contrast, sound is not restricted by low light levels or objects in the environment, while many aquatic animals, including all fish, have more or less advanced abilities to hear (Box 3).

Are there noise-dependent fish distributions?

If anthropogenic noise deters fish, or if noise is bad for fish survival and reproduction, one might predict lower fish diversity and density at noisy places. At the moment, however, there are few studies that indicate such negative correlations between the presence of noise and the presence of fish. Some studies report an effect of vessel noise on fish flight behaviour in the context of population assessments and catch rates for commercially important fish stocks. For example, horizontal and vertical movements away from vessels have been reported for Atlantic herring (*Clupea harengus*) and Atlantic cod (*Gadus morhua*) [17,18], presumably in response to ship noise. Another example concerns effects of nearby boating noise on blue-fin tuna (*Thunnus thynnus*) in large oceanic pens. In the presence of boat noise, tuna schools were less coherent than when the noise was not present and individual fish often swam independently towards the surface or the bottom [19]. Fish have also been reported to flee from seismic shooting areas as inferred from decreased catch

Box 3. Fish ears and hearing abilities

All fish studied to date are able to hear sounds [15,97,98]. They have two sensory systems for detection of water motions: the inner ear (there is no outer or middle ear) and the lateral line system. The ear serves to detect sound up to hundreds or even thousands of Hz (depending on the species), whereas the lateral line detects low-frequency sound (e.g. <100 Hz), but is generally considered to be primarily a detector of water motion relative to the body.

Sound can be thought of in terms of both particle motion and pressure fluctuations. Sensory hair cells in the inner ear and lateral line (both of which are very similar to those found in the mammalian ear) are stimulated by mechanisms that respond to particle motion and are responsible for converting these motions to electrical signals that stimulate the nervous system. The lateral line system is found along both sides of the body and typically spreads out over the head region where it plays a dominant role in the detection of water motion and low-frequency sound at short distances (one or two body lengths). In contrast, the inner ear also detects sounds of much higher frequencies and from greater distances (probably via acoustic pressure since particle motion declines with distance more rapidly).

Different fish species vary in absolute sensitivity and spectral range of hearing (Figure I), which relates to an auditory detection continuum based on presence or absence of specially evolved morphological structures [15,97,98]. Special features that improve the pressure-to-motion transduction from the swim bladder may involve gas-filled cavities reaching the inner ear. There may also be a direct mechanical connection between the swim bladder and the inner ear through a series of bones (the Weberian apparatus) such as in a large group of fish species (Otophysi) that includes goldfish (*Carassius auratus*) and catfish. Generally speaking, fish hear best within 30–1000 Hz, while species with special adaptations can detect sounds up to 3000–5000 Hz. Some exceptional species are sensitive to infrasound or ultrasound.

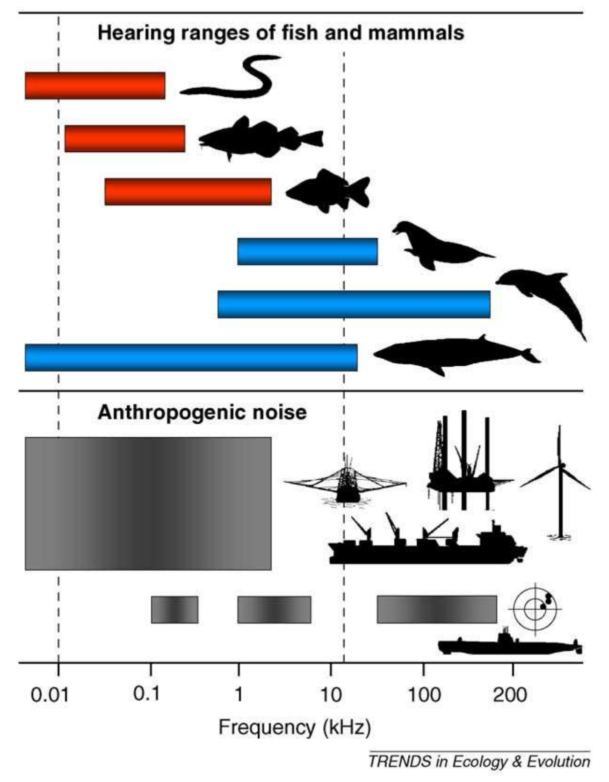

Figure I. Hearing ranges of selected fish and mammal species, reflecting some of the typical variety in these taxonomic groups (for reviews see Refs [10,15]). The vertical dashed lines demarcate the human hearing range in air. Each species has a more restricted range of peak sensitivity within the species-specific limits (not indicated). From top-to-bottom, red horizontal bars represent: European eel, a freshwater species spawning at sea with sensitivity to infrasound; Atlantic cod, a marine species with 'average' hearing abilities; and goldfish, representing many freshwater fishes with specially evolved hearing abilities. For mammals in blue, we included Californian sea lion (*Zalophus californianus*), bottlenose dolphin (*Tursiops truncatus*), and fin whale (*Balaenoptera physalus*). The anthropogenic noise ranges indicate where the majority of sound sources have most of their energy, although some human-generated sounds exceed these frequencies. At the bottom of the figure are frequency ranges of low-frequency (USA), mid-frequency and high-frequency sonar.

rates for both long lines and trawler fisheries [20,21]. However, there is also a study with direct observations on reef fish that remain close to their territories after exposure to seismic air-gun shooting [22].

In contrast to the little we know about effects of environmental sound on fish behaviour, a good deal is known about the potential impact of anthropogenic noise on bird behaviour. For a long time, declines in avian diversity and density associated with highways have been attributed at least partly to traffic noise [23]. The idea was supported by a study suggesting that a negative effect was dependent on the spectral overlap between traffic noise and birdsong [24] and by several studies showing spectral flexibility in bird species that do well under noisy conditions [6]. However, the best evidence for a negative impact of anthropogenic noise on birds comes from natural areas around extraction stations associated with the gas and oil industry [25,26]. Some extraction stations are noisy and others quiet, and this subdivision is independent of the above-ground variation in avian habitat characteristics. Consequently, and in contrast to traditional road-impact studies, the decline in bird breeding density and diversity found in these studies can be attributed solely to the impact of noise.

Whether similar results will be found for fish is not known, but the avian results are highly suggestive of questions that must be asked for fish, and they even suggest ways to explore and answer such questions. For example, it may be possible to investigate the impact of noise on fish diversity and density by making use of the maritime gas and oil industry. Similar to the above water situation with birds, there are offshore platforms that have high underwater noise levels due to compressor noise and human activity, while others serve as more silent satellites. Alternatively, freshwater systems, often being more accessible, can be explored experimentally by using artificial noise sources in some locations that can be compared to quiet, control locations. While data on sound conditions and fish behaviour at these control locations may provide insight into the potential for soundscape orientation [15,16], such an experimental set-up would allow for testing an impact on species community and relative densities dependent on artificial noise levels and specific noise features. The impact of anthropogenic noise on dispersal and passage of migratory fish can be tested in a similar way in canal and river systems [27,28].

Consequences for fish that remain in noisy waters

Notwithstanding the lack of proper monitoring data, fish sometimes congregate, seeking shelter or food, at places with artificially high noise levels. Anecdotal observations on fish under noisy bridges or near noisy vessels indicate that adverse effects are not necessarily overt and obvious, but they do not tell us whether fish experience any negative consequences related to the noise. For example, several studies in captive fish have shown an increase in secretion of the stress hormone cortisol during exposure to white noise or simulated boat noise [29,30, but see 31]. Other recent studies on potential indicators of stress in captive fish report noise-related rises in heart rate [32] and increased motility related to several blood parameters reflecting increased muscle metabolism [33]. Although one must be cautious in extrapolating to free-swimming fish that may be able to leave areas of high stress, these findings at least suggest that anthropogenic noise could be a stressor in natural water bodies.

Noise-dependent stress, like other environmental stressors, might affect growth and reproductive processes [34], but this has hardly been investigated. A relatively old study, in which the acoustics of the experiments were poorly controlled and calibrated, suggested lower egg viability and reduced larval growth rates in noisy fish tanks compared to more quiet control tanks [35]. A more recent and better study on rainbow trout (*Oncorhynchus mykiss*), exposed to realistic noise levels for fish tanks in an aquaculture facility [36] showed no impact on growth, survival, or susceptibility to disease, even over nine months of exposure [31]. However, given the very limited number of species investigated, it is not clear whether one can extrapolate from captive rainbow trout to other species that may differ in hearing ability and in the extent they depend on sound for natural activities.

In addition to an impact on growth or reproduction related to noise-determined physiological stress, anthropogenic noise may also affect populations in a more indirect way. Data on birds has shown that individuals that vary in reproductive abilities, related to age, experience, or size, may not be evenly distributed over noisy and quiet areas of otherwise suitable habitat [37,38]. The relative absence of more experienced and typically more productive males in noisy territories means that habitat productivity for these species diminished beyond the effect of a reduction in number of territory holders. These results may be relevant to fish since many species are territorial and have explicit age-dependent size classes varying in productivity [39]. However, so far we lack any study looking at distribution of size classes relative to noise levels.

Population productivity of noisy areas might not only be affected by lower numbers or lower-quality individuals, but might also decline due to lowered reproductive efficiency. Data on frogs has shown, for example, that anthropogenic noise may either increase or decrease calling activities [40,41], with possible fitness consequences related to increased energetic or predation costs or decreased mating success. While there are no similar data yet for free-living fish, a relatively old study reports on actual interruption of spawning in roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) by an approaching fast-moving powerboat [42]. Although obviously more data are required, it should be realized that the mere presence of fish in noisy waters does not necessarily mean that they are part of a reproductively active population. A better insight can be generated through studies on the impact of anthropogenic noise on the rate and nature of reproductive behaviour and acoustic signalling in free-living fish.

Masking of acoustic communication

A specific noise impact that could lead to lower reproductive efficiency for fish is masking of communicative sounds. Over 800 species from 109 families are known to produce sounds, while many more are suspected to do so [43–45]. The sounds that fish produce are, in most cases, broadband signals with most energy <500 Hz. Distinct variation in spectral and temporal characteristics can be related to species [46,47], populations [48], and gender [49]. Furthermore, graded variation in pitch and duration can be correlated with size [47,50,51] or seasonal fluctuations in motivation [52]. Such acoustic variation means that sounds can serve as information carriers in acoustic communication among fish [43,44,53]. That fish communicate acoustically becomes evident from the contexts in which the sounds are produced, such as during agonistic interaction in territorial fights, when competing for food, or when being attacked by a predator [54–57].

However, the most common context in which fish are known to produce sounds is in spawning aggregations [58,59] and courtship interactions [60,61]. Although often not explicitly demonstrated, sounds could serve in aggregating reproductive groups, in which they may contribute to synchronization of male and female gamete release [62]. At a more individual level, sounds could attract potential mates to a specific place for courtship or egg shedding [63]. Recent experimental evidence has unequivocally shown that sounds can modify mate choice decisions in fish. Female haplochromine cichlids (*Pundamilia nyererei*) provided with a choice between two males, matched in size and colour, preferred to interact with the male associated with playback of conspecific sounds [47]. An acoustic impact on sexual preferences was also inferred for Atlantic cod in which the male drumming muscle mass was correlated with mating success [64]. Although these examples strongly suggest acoustic communication occurs in fish, there is a substantial lack of insight into the distribution and nature of the phenomenon across species and across habitats (from shallow waters to the deep sea).

Clearly, however, if fish sounds serve a communicative function in a reproductive context, problems of detection and recognition due to the presence of anthropogenic noise [65–67] could have fitness consequences. It should be clear that fish have not evolved in a quiet environment, and natural noise levels can also become loud, for example during fish choruses [58,59]. Nevertheless, playback of field recordings under laboratory conditions, at natural spectral content and level, confirmed experimentally that noise generated by a cabin-cruiser type of boat can significantly increase detection threshold levels for conspecific sounds in both brown meagre drums (*Sciaena umbra*) and Mediterranean damselfish (*Chromis chromis*) [68]. Based

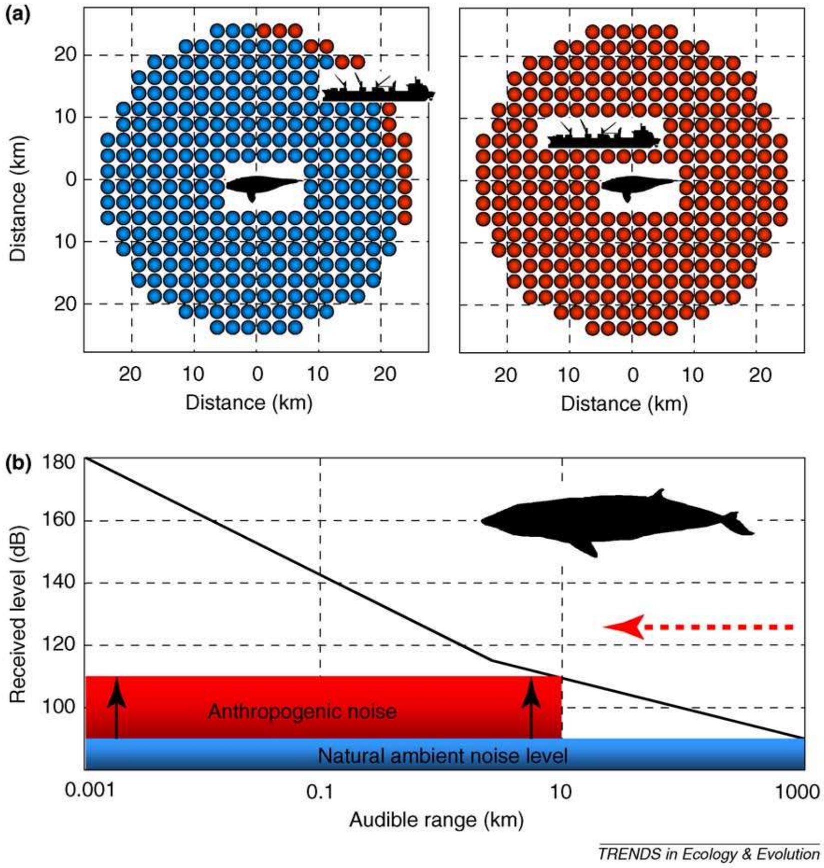

Figure 2. **(a)** Spatial distribution of sender communication space for uniformly distributed right whales listening to a 200 Hz conspecific call from a male individual in the centre of the space in the presence of noise from a ship with a source level of 172 dB re 1 μPa. Blue dots indicate receivers for which the whales are likely to detect the sound produced by the focal individual, while red dots indicate receivers for which the noise of the ship exceeds the signal beyond detectable levels. Left: the ship is approaching the calling whale from the northeast causing a 6% decrease in the sender's communication area. Right: the ship is within 2 km to the northwest of the caller causing a 97% decrease in the sender's communication area [87]. **(b)** Loss of communication range due to a rise in anthropogenic noise relative to historical conditions. Received sound levels for 20 Hz fin whale calls are depicted against a background of natural noise levels (in blue), yielding an audible range of 1000 km, and elevated noise levels due to anthropogenic influences (in red), leading to a reduced audible range of only 10 km. The graph is modified, with permission, after a model by Peter Tyack. He incorporated realistic signal attenuation during propagation through the ocean in his model and assumed a 90 dB re 1 μPa noise floor for the pre-industrial ocean, currently elevated by 20 dB from shipping (which is still a conservative estimate likely to be met at many places).

on these measurements, passing boats were inferred to reduce detection distances under field conditions by up to 100 times.

Masking leading to a reduction in detection distance, or the so-called active space, can lead to failure in mate attraction. Although we lack any empirical evidence demonstrating this for fish, data for birds and frogs can inform our views on the potential for masking effects. Male ovenbirds (*Seiurus aurocapillus*) near gas extraction stations experienced a decline in mate attraction rates when trying to convey their acoustic message in the presence of a noisy compressor [38]. Another consequence of masking could be that sexual signals are still detected, but that specific acoustic cues in the signals that are important for mate selection get lost. In fish, allometric correlations with acoustic features provide ample opportunity for female mate selection that targets male size [47,50,51]. Although no data are available yet on acoustic preferences of female fish for sounds of large males over sounds of small males, the phenomenon has been tested, confirmed and shown to be noise-level dependent in frogs [69,70]. Typically, large male frogs are acoustically more attractive to females than small ones, but this advantage seems to be lost under noisy conditions [71]. Apparently, noisy conditions can interfere with mate selection, while suboptimal pairing could negatively affect individual reproductive success and thereby affect whole populations.

It is not only essential to assess signal-to-noise threshold levels for an impact of anthropogenic noise on detection and recognition of relevant sounds. We also need insight into the potential scale of impact of such masking effects under natural conditions. Some calculations exist for active space shifts due to anthropogenic noise in frogs [72] and fish [68], and there are some especially insightful studies for marine mammals that may conceptually well apply to fish. For example, baleen whales (Mysticetes) produce low frequency sounds that may travel for hundreds of kilometres, and it has been suggested that these sounds may be used for communication and orientation [73,74]. Figure 2 illustrates at what distances such calls of North Atlantic right whales (*Eubalaena glacialis*) are still audible in the presence of anthropogenic noise from an approaching ship (a). Data are also shown for fin whales (*Balaenoptera physalus*) from historical to current ocean noise levels (b). It is important to realize that the active space may also be affected in a similar way for any sound in the auditory scene that may serve as a general orientation cue, for example in making settlement decisions such as suggested to be the case in coral reef fish [75] and crab larvae [76].

Noise-impact on predator–prey relationships

Hearing and localizing of sounds can also be advantageous for specific purposes such as locating prey and avoiding predators. For example, although sharks and other cartilaginous fishes probably have relatively poor hearing sensitivity compared to other fishes, they were reported to approach irregularly pulsed broadband sounds, which could be indicative for the presence of struggling prey [77]. Similarly, surface-feeding fish can localize prey accurately by listening to the surface waves produced when prey fall into the water [78]. Some bottom-feeding fish such as peacock cichlids (*Aulonocara*) are even able to sense the sound of prey submerged in the sediment [79]. In other species, broad hearing bandwidths have been correlated with predator avoidance. For example, some herring species (Clupeidae) of the genus *Alosa* are capable of detecting ultrasound (up to 180 kHz), which could allow detection and avoidance of echo-locating whales [80,81]. Field studies on European eel (*Anguilla anguilla*) and juvenile salmonids showed that they are able to detect and avoid infrasound (<20 Hz), which could allow them to sense the hydrodynamic noise generated by approaching predators [82,83]. Data are completely lacking in fish, but based on insight from very few and very different animal species, we believe that anthropogenic masking effects on predator–prey relationships could be widespread.

Predators that use sound for hunting (as might occur especially in dark or turbid environments) can be restricted by noisy conditions through lower availability of suitable foraging areas and a lower catching efficiency. An instructive mammalian example of this comes from a study on greater mouse-eared bats (*Myotis myotis*) which use subtle rustling sounds to locate their prey. Captive bats tended to avoid the noisy side of a two-compartment flight room, and also showed lower hunting efficiency when they did enter the noisy compartment [84]. Similarly, prey that use their ears to scan for predators can be negatively affected by anthropogenic noise. In a study on chaffinches (*Fringilla coelebs*), a species that is potential prey for cats and raptors, foraging birds increased the amount of time that they were upright and scanning visually for predators in high noise conditions compared to when it was quieter and they could listen for predators [85]. This finding was interpreted as a compromise on food intake rate to compensate for finches relying less on auditory detection of approaching predators. In line with this interpretation, a recent study on terrestrial hermit crabs (*Coenobita clypeatus*) reported a noise-dependent decrease in efficiency with respect to predator detection (represented by a walking person) [86]. These three experimental studies, while not for fish, clearly highlight the potential concerns for the effects of anthropogenic noise on predators as well as prey, and the need for parallel experiments with fish.

Conclusions

It has become clear that sound can be important to fish and that a rise in artificial noise levels underwater may have negative consequences for individuals as well as populations. Although sonar, piling and explosions typically attract most attention, it is reasonable to argue that the greater impact on fish will be from less intense sounds that are of longer duration and that can potentially affect whole ecosystems. Thus, our goal in this review has been to outline the potential impact of sound in four main areas related to moderate but widespread anthropogenic noise conditions (Box 4). The current lack of insight impedes our ability to make predictions about the effects of anthropogenic noise on fish and we have argued that we could gain such insight using data and methodology from studies on various terrestrial animals. We believe our review strongly suggests that the investigations needed most include those

Box 4. Major targets for future research

More field studies are needed on the role of sound in the life of fishes in general, especially with respect to the use of sounds for general orientation purposes (i.e. soundscape orientation [15,16]). Furthermore, while data are required on the effects of very high intensity, relatively transient sounds as well as on the effects of lower intensity, but more long-term sounds, the greatest impact on most fish clearly comes from the latter sources. Thus, studies of such sounds are most urgently needed. More specifically, the kinds of studies especially needed are those that focus on questions related to whether fish are affected behaviourally or physiologically by the global rise in noise levels or specific anthropogenic sounds and how mitigating measures could help to limit such impact. Insight showing that some species are affected by sounds but others are not, that some sounds are detrimental but others are not, or that noise causes trouble during some periods but not during others, are only some examples of how proper investigations may yield opportunities for mitigation with significant ecological implications at relatively low cost. We therefore advocate more studies in four main domains of research which are likely to provide critical insight into key questions raised in this article:

- **Noise-dependent fish distributions.** Are there differences in how fish are distributed in quiet and noisy environments, and how might these distributions vary depending on sound source, species, fish age, and other physical and biological factors?
- **Reproductive consequences of noisy conditions.** Is there a negative influence of anthropogenic noise on reproductive success, by causing physiological stress, by restricting mate finding, or by keeping fish from preferred spawning sites?
- **Masking effects on communicative sounds.** Does the presence of masking sounds of different types and intensities impact the ability of fish to communicate acoustically or use the acoustic 'soundscape' to learn about the environment?
- **Masking effects on predator–prey relationships.** Does the presence of masking noise affect the ability of fish to find prey (get food) or detect the presence of predators (become food)?

of noise-dependent distribution and reproduction as well as investigations of masking of sounds used for communication, orientation, or detection of predators and prey. Such studies in the aquatic environment are likely to be an order of magnitude harder than for similar studies in air, for example due to human observers having difficulty in seeing aquatic animals over large areas and localizing sounds underwater. Nevertheless, we expect experimental approaches in the laboratory and in the field to yield critical insights. There is no doubt that this will be a challenging and long-term enterprise, but studies on the impact of pesticides on birds and the conservation measures derived from these have also curbed the prophesy of a 'silent spring' for birds. We believe the investigations we have proposed could do the same for fish, and that these provide a better alternative to waiting to see what happens to fish in the dim future of a more and more 'noisy spring'.

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Acknowledgements

Much of the work presented in this thesis bases on data from the PALAOA acoustic observatory. I wish to thank Holger Klinck, the AWI logistics department, the Neumayer overwintering teams 2005-2010, FIELAX and Reederei Laeisz for their support in setting up and maintaining PALAOA. The XBAT software developed by Harold Figueroa (Bioacoustics Research Program, Cornell University) provided an indispensable tool for the automated analysis of the PALAOA data. Furthermore, I also thank Prof. Dr. Wilhelm Hagen from the University of Bremen for support throughout my PhD.

Many thanks to Olaf Boebel and Sofie Van Parijs for their continuous trust, inspiration, support and guidance throughout my PhD. Olaf, thanks for the many fruitful discussions we had, it is a pleasure working with you and to be part of the AWI's Ocean Acoustics Lab. I learned a lot from you and hope to continue to do so in the future. Sofie, thank you for being my 'eagle'[*], in scientific point of view, by being a supercoach teaching me so many things in bio-acoustic research, but also in being a friend, providing support and comfort when I most needed it.

Many thanks also to Lars Kindermann for his work and care for PALAOA, inspiring ideas, sharing enthusiasm and seemingly inexhaustible know-how on acoustics and for being a great colleague. Horst Bornemann was in my Phd committee and provided advice and support in Bremerhaven, but also during the work in the field. Horst, thanks for all your help and support, company, laughs, coffee and cake. With Joachim Ploetz I share his passion for nature and working in the field. I enjoyed our many conversations, sharing of ideas and the amazingly good (and 'politically correct') game (roe deer and wild boar) he brought me from the Harz. Many thanks also to Elke Burkhardt for support, maintaining a great marine mammal literature data base, and for relaxing coffee breaks. Daniel Zitterbart and Annette Bombosch, thanks for being great fellow-Phds and support during the last phase of my PhD. Daniel thanks also for your support and enthusiasm during the 2008/2009 field campaign. Cornelia Kreiss worked with me in the field conducting the

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[*] *How the wren became king,* Aesop 620-564 BC

playback experiments on Weddell seal mother-pup pairs and helped deploy and maintain the PALAOA-S recorders on the fast ice in Atka Bay. Thanks, Corni-copepodi for your great help in the field, moral support, company in our tiny orange living-container, delicious home-baked gluten-free cookies and for being a friend. Many thanks also to all the other students who helped with analyses of acoustic data: Rosa Wilm, Svenja Zakrzewski, Taryn Overton, Anna-Maria Seibert and Antje Funcke. I enjoyed your company and enthusiasm.

I furthermore would like to thank two people who are geographically more distant, but with whom I feel connected through work and thoughts. During my stay in Woods Hole in spring 2009, Denise Risch shared her house, car, computer and office with me. We already had a connection through Sofie and the harp seal work, but had never met until spring 2009. I much enjoyed the many discussions and conversations we had, figureing out the principles of automated sound detection, and our reflections on love and life in general, thanks for everything, Denise.

With Peter Corkeron (NOAA Woods Hole, USA) I worked during the harp seal project and an earlier killer whale project in Tysfjord, Norway. I enjoyed working with him a lot and admire him for his personality and work, the latter of which also provided an important scientific base for many aspects of this thesis. Thanks, Peter.

I thank my friends for support, laughs, visits to Bremerhaven and red wine when I needed it the most. Chris (Trierweiler) and Esther (Bouma), we met and became friends when we started our studies and will all finalize our PhD work this year – great timing and a good reason for a feestje! Chris, although the Arctic and Antarctic are amazing places to work, I'll never forget our first fieldwork-adventure on the isle of Schier in winter which sparked the love for (extreme..?) field work in both of us.

Manymany thanks for everything (and the design of the thesis cover!) to my parents, Rina Van Nuland and Jan Van Opzeeland who decided to move to the Arctic (65° 32′ N, 14° 8′ E) in 2007, a long way, but at least visits were great for thesis-inspiration and Robert and I never have to miss out on white Christmases anymore. Lastly, my love and thanks to Robert Huisman for being my muse and willow in the PhD-wind (or -storm, especially in the finalizing phase), thanks for everything, lief.

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