Baleen whale acoustic ecology with focus on minke whales (*Balaenoptera acutorostrata*) and reference to anthropogenic noise

Photo: AM Friedlaender.

Baleen whale acoustic ecology with focus on minke whales (*Balaenoptera acutorostrata*) and reference to anthropogenic noise

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Der Dekan

The earth has music for those who listen.

William Shakespeare

Für meine Eltern.

Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation selbständig von mir angefertigt wurde und in Inhalt und Form meine eigene Arbeit ist. Es wurden keine anderen als die angegebenen Hilfsmittel und Quellen verwendet. Die Arbeit wurde unter Einhaltung guter wissenschaftlicher Praxis entwickelt.
Diese Arbeit wurde weder ganz noch zum Teil schon einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein erster Promotionsversuch. Die Promotion soll im Fach Zoologie erfolgen. Für die Prüfung wird die Form der Disputation gewählt. Der Zulassung von Zuhörern bei der mündlichen Prüfung wird nicht widersprochen.

Kiel, den

Denise Risch

Summary

Passive acoustic approaches for studying marine mammals have developed substantially over the past decade. Advances in technology now allow data collection in remote areas and over extended timescales. The first two chapters of this thesis focused on the application of passive acoustics for monitoring migratory baleen whales in the Northwest Atlantic Ocean. The development and application of new localization algorithms showed how small-scale arrays can be used to obtain baseline data about the acoustic behavior of individuals, which will help to improve interpretation of long-term acoustic data sets. Acoustic monitoring in the Stellwagen Bank National Marine Sanctuary (SBNMS) revealed seasonal peaks of acoustic abundance for right (*Eubalaena glacialis*) and sei whales (*Balaenoptera borealis*) in spring and fall, respectively. Both species are primarily present during these two seasons and to a lesser extent in winter and summer, indicating the importance of this area as part of their migration route. Fin whales (*Balaenoptera physalus*) were acoustically present year-round, although song production was reduced during summer. While recorded on only a few days of the entire period, blue whale (*Balaenoptera musculus*) song was detected near SBNMS in three separate years.

There is considerable uncertainty concerning migration routes, winter calving habitats and thus population structure of North Atlantic minke whales (*Balaenoptera acutorostrata*). Given that this species is still being hunted across its summer range, this uncertainty has important conservation and management implications. In chapters III-V I used 3.5 years of acoustic array data from the Gulf of Maine to describe the species' vocal repertoire, examine individual calling behavior and provide first source level estimates. Based on these data, an automatic detector was developed and applied to year-round data from several sites along the US East coast and beyond to track minke whale migration. Minke whales produced three call categories at a mean source level of 165 ± 4 dB rms re 1 μPa. Individual whales combined calls in non-random order, leading to two distinct calling patterns. Unlike other baleen whales, animals sharing the same acoustic space used different patterns simultaneously, without switching. Analysis of seasonal occurrence patterns revealed peak acoustic presence in higher latitudes during summer and fall and in lower latitudes during winter. Migration appears to follow the general direction and location of the Gulf stream in the spring and occurs in more open waters in the fall. A higher abundance of calls at offshore recording sites, suggests that there is a winter habitat located in deeper waters off the Southeastern US.

Antarctic minke whales (*Balaenoptera bonaerensis*) have long been suggested as the likely source for the mysterious 'bioduck' signal, which is the predominant underwater sound in the Souther Ocean during austral winter. I analyzed data from the first two multi-sensor acoustic tags attached to Antarctic minke whales and was able to confirm the production of the bioduck by this species. This finding will allow the interpretation of a wealth of existing recordings, and thereby substantially improve our understanding of the distribution, abundance, and behavior of Antarctic minke whales. This is critical information for a species that lives in a rapidly changing polar environment and is subject of ongoing lethal sampling efforts.

The effects of widespread anthropogenic noise in the marine environment is of increasing concern. Most discussions have centered on highly visible and regulated activities, such as seismic airguns and naval sonar. In this last chapter we showed, that humpback whale (*Megaptera*

novaeangliae) song was reduced, concurrent with transmissions of an Ocean Acoustic Waveguide Remote Sensing (OAWRS) experiment approximately 200 km distant. This is the first time that active sonar used in fisheries science has been shown to have this effect, highlighting the importance to study and regulate the impact of all anthropogenic noise sources, including research applications.

In conclusion, this thesis highlighted the suitability of passive acoustic monitoring for an increased understanding of the spatio-temporal distribution patterns and behavior of highly mobile and little studied baleen whales. In particular, it considerably improved current knowledge about the acoustic ecology and spatio-temporal distribution of minke whales.

Zusammenfassung

Die Erforschung von Meeressäugern mittels passiv akustischer Methoden hat sich im letzten Jahrzehnt enorm weiterentwickelt. Technologische Fortschritte erlauben nun die Datensammlung in entlegenen Gebieten und über stark verlängerte Zeiträume. Die ersten zwei Kapitel dieser Studie sind der Anwendung passiv akustischer Methoden für die Beobachtung von Bartenwalen im Nordwestatlantik gewidmet. Die Entwicklung und Anwendung neuer Lokalisationsalgorithmen verdeutlicht in diesem Zusammenhang, wie kleinskalige Hydrophonanordnungen genutzt werden können, um fundamentale Daten über das akustische Verhalten von Individuen zu erfassen. Diese Daten liefern grundlegende Informationen für die weiterführende Interpretation akustischer Langzeitdaten. Das akustische Monitoring im Stellwagen Bank National Marine Sanctuary (SBNMS) ergab zwei deutliche saisonale Höhepunkte in der akustischen Präsenz von Glattwalen (*Eubalaena glacialis*) im Frühjahr und Seiwalen (*Balaenoptera borealis*) im Herbst in diesem Gebiet. Beide Arten sind besonders zu diesen beiden Jahreszeiten, und weniger häufig im Sommer und Winter, akustisch präsent. Dieses zeitliche Verteilungsmuster belegt die Bedeutung des Gebietes als Teil der saisonalen Wanderungsroute beider Arten. Finnwale (*Balaenoptera physalus*) waren ganzjährig akustisch präsent, wenngleich die Häufigkeit ihrer akustischen Signale im Sommer reduziert war. Blauwalgesang (*Balaenoptera musculus*) konnte zwar nur an wenigen Tagen, jedoch in drei verschiedenen Jahren in den akustischen Aufzeichnungen aus diesem Gebiet nachgewiesen werden.

Bezüglich der Wanderungsrouten und den Überwinterungs-, und Fortpflanzungsgebieten und demzufolge auch der Populationsstruktur des Nordatlantischen Zwergwals (*Balaenoptera acutorostrata*), existieren grosse Wissenslücken. Dieses fehlende Wissen hat besondere Bedeutung für den

Schutz und das Management einer Art, die in ihren Nahrungsgründen im Sommer noch immer bejagt wird. Basierend auf 3.5 Jahren akustischer Daten aus dem Gulf of Maine, beschreibe ich in den Kapiteln III-V das akustische Repertoire, untersuche individuelle Rufmuster und liefere erste Messungen für den akustischen Sendepegel diese Art. Auf diesen Daten aufbauend wurde ein automatischer Detektor entwickelt, welcher für die Analyse ganzjähriger Daten von verschiedenen Orten entlang der US-amerikanischen Ostküste eingesetzt wurde, um die jährliche Wanderung dieser Art zu untersuchen. Zwergwale produzieren 3 verschiedene Ruftypen mit einem Sendepegel von 165 ± 4 dB rms re 1 µPa. Dabei werden die Rufe nicht nach dem Zufallsprinzip kombiniert und es konnten zwei verschiedene Rufsequenzen identfiziert werden. Im Gegensatz zu anderen Bartenwalen, wurden beide Sequenzen simultan benutzt, wobei Individuen jedoch nicht das jeweilige Rufmuster änderten. Im Sommer waren Zwergwale in höheren Breitengraden und im Winter in eher tropischen und subtropischen Gebieten akustisch präsent. Im Frühjahr scheint die Wanderung der generellen Richtung und Position des Golfstroms zu folgen, während tiefere Gewässer auf der Wanderung in die Wintergründe bevorzugt werden. Ein erhöhtes Vorkommen von Rufen in tieferen Gewässern vor der Südostküste der USA legen die Existenz von Wintergründen in diesen Gebieten nahe.

Antarktische Zwergwale (*Balaenoptera bonaerensis*) wurden lange als die mögliche Quelle des 'bioduck' Signals, welches die dominante Schallquelle im Südpolarmeer im Winter darstellt, impliziert. Die Analyse der ersten Datevon von akustischen Tags, bestätigen diese Annahme. Diese Ergebnisse erlauben eine neue Interpretation von bereits vorhandenen akustischen Langzeitaufnahmen und werden das Wissen um die Verteilung, den Bestand und das Verhalten dieser Art enorm erweitern. Diese Informationen sind besonders kritisch im Hinblick auf dramatische Veränderungen im polaren Lebensraum dieser Art, die ebenfalls weiterhin

aktiv bejagt wird.

Die Auswirkungen von weit verbreitetem Unterwasserlärm werden mit immer grösserer Besorgnis betrachtet. Bisher beschränkten sich die meisten Diskussionen auf bereits regulierte Aktivitäten, wie seismische- und Navy Sonarsysteme. Im letzten Kapitel dieser Studie zeigen wir die Reduktion von Buckelwalgesang (*Megaptera novaeangliae*) in der Folge eines Ocean Acoustic Waveguide Remote Sensing (OAWRS) Experiments in 200 km Entfernung. Dies ist das erste Mal, dass aktive Sonarsysteme der Fischereiforschung im Hinblick auf mögliche Auswirkungen auf das Verhalten mariner Säuger untersucht wurden. Die Ergebnisse verdeutlichen die Wichtigkeit, die Auswirkungen aller anthropogenen Lärmquellen, inklusive von Sonarsystemen, die für die Forschung genutzt werden, zu untersuchen.

Zusammenfassend unterstreicht diese Studie die Eignung passiv akustischer Methoden für ein verbessertes Monitoring und die Vermehrung des Wissens über die raum-zeitlichen Verteilungsmuster und das Verhalten von weit wandernden, wenig erforschten Bartenwalarten. Im besonderen konnte die Studie grundlegende Fragen zur akustischen Ökologie und den saisonalen Verteilungsmustern von Zwergwalen klären.

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Individual scientific contributions to multiple-author papers

Curriculum Vitae (CV)

General Introduction

Baleen whales: An Overview

Baleen whales comprise one of the two extant suborders of the order *Cetacea*. The Latin name of this suborder – *Mysticeti* – is derived from the Greek *mustoketos*, and translated as the “mouse-whale” (Rice 1998). The name seems ironic, given the enormous size of most members of this group, which also includes the blue whale – the largest animal ever to have lived on earth. The main difference to the second suborder – *Odontoceti* (toothed whales) – is a lack of functional teeth in this group. Baleen whales are filter feeders. Structurally based on keratin, baleen plates are arranged in parallel rows and suspended from the whales' upper jaw (Utrecht 1965). This highly specialized structure enables baleen whales to sieve large volumes of water and trap extensive quantities of small prey (zooplankton or fish). In addition, baleen whales differ from toothed whales by the possession of a paired blowhole and symmetrical skull. Their ribs are not articulated with the sternum (Bannister 2009).

1 Phylogeny & diversity

Cetaceans diverged about 56-53 million years ago (Mya) from aquatic, even-toed ungulates (artiodactyls) and gradually adapted to a completely oceanic lifestyle (Thewissen et al. 2007). Extant cetaceans (*Neoceti*) first appeared around 36 Mya, dispersed widely in oceans and some large rivers and estuaries and separated into mysticetes and odontocetes early in their evolutionary history (Steeman et al. 2009, Slater et al. 2010).

The diversification of modern cetaceans has been described as a rapid adaptive radiation, facilitated by the evolution of larger brains, echolocation (odontocetes), baleen (mysticetes) and emerging ecological opportunities following the extinction of archaic whales (Slater et al. 2010). However, rapid speciation during the early evolution of modern species has been questioned based on missing evidence by time-calibrated molecular phylogeny (Steeman et al. 2009). An alternative hypothesis describes cetacean diversification as less 'rapid' but rather initiated by re-structuring of the oceans, following major paleogeographic changes (Steeman et al. 2009). Early records of baleen whale fossils coincide with the break-off of the southern continent Gondwana about 35 Mya, resulting in the formation of the Antarctic circumpolar current (ACC) (Jackson 2010). Morover, a major reorganization of the Southern Ocean plankton ecosystem occurred at the onset of Antarctic glacation in the early Oligocene (about 33.6 Mya), driving the establishment of seasonally productive environments and subsequent biotic evolution (Houben et al. 2013). The ACC and its interaction with strong winds force deep mixing of the Southern Ocean and increase surface concentrations of nutrients such as silicate and iron, which in turn are driving large, diatom dominated phytoplankton blooms during austral summer (Berger 2007). This enormous primary productivity supports a large number and diversity of top predators. Several authors have suggested the formation of this ecological system and the subsequent first Antarctic glaciation period as a trigger for early cetacean radiation and indicative of a high latitude, austral origin of baleen whales (Berger 2007, Steeman et al. 2009, Marx & Uhen 2010, Houben et al. 2013).

Although there is still discussion about the driving forces behind cetacean evolution, it is well established, that baleen whales form a monophyletic group. However, phylogenetic relationships within this group are still obscure, despite a surge in research, investigating molecular as well as fossil records, in recent years (Rychel et al. 2004, Sasaki et al. 2005, Hatch et al. 2006, Jackson et al. 2009, McGowen et al. 2009, Steeman et al. 2009, Marx & Uhen 2010, Dornburg et al. 2012, Churchill et al. 2012). Especially the placement of the gray whale (*Eschrichtiidae*) and relationships within the *Balaeonpteridae* – the rorqual whales – have yet to be conclusively resolved (Jackson 2010). It is unclear why the delineation of mysticetes phylogeny is so variable, depending on the type of analysis. Probable hypotheses include the accelerated diversification of a hypothesized *Balaeonpteridae* crown group

(Nikaido 2006, Deméré et al. 2008, Jackson et al. 2009), or continued hybridization between species (Spilliaert et al. 1991, Bérubé & Aguilar 1998, Lefèvre et al. 1999). The former would have resulted in incomplete lineage sorting of genes, while the latter could weaken existing phylogenetic signatures (Jackson 2010).

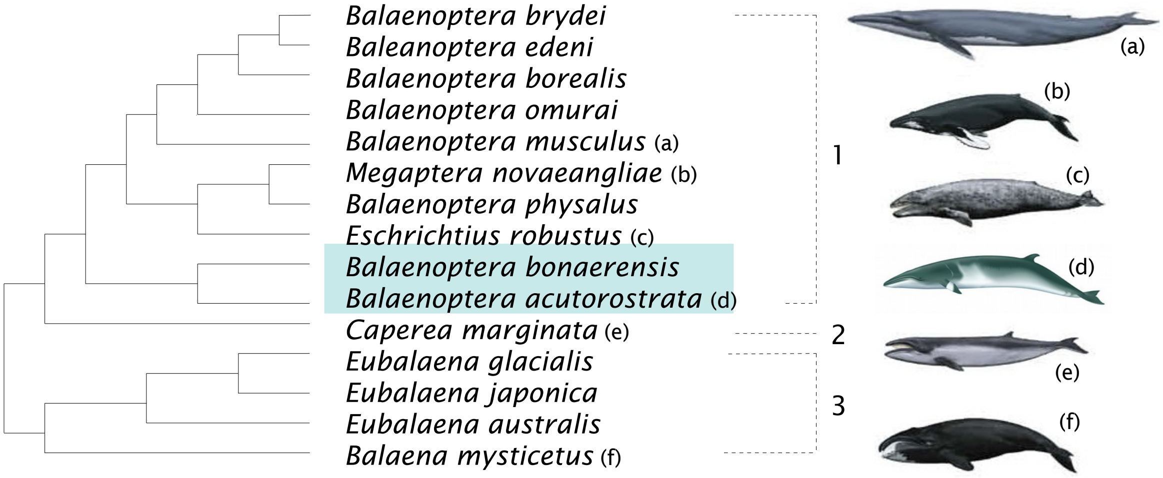

Figure 1: Phylogeny of baleen whales, following McGowen et al. 2009. 1=Balaenopteridae & Eschrichtiidae; 2=Neobalaenidae; 3=Balaenidae. The focus species of this thesis, the Common minke whale and its closest relative, the Antarctic minke whale are highlighted. Figure adapted from (McGowen et al. 2009); Artwork credit: Carl Buell & Uko Gorter.

Fourteen species of baleen whales, belonging to four families (*Balaenidae, Neobalaenidae, Eschrichtiidae, Balaenopteridae*) are currently recognized (Figure 1). The right whales (*Balaenidae*) comprise four species: the Arctic bowhead whale (*Balaena mysticetus*) and three species of right whales (*Eubalaena spp.*) (Rosenbaum et al. 2000, Churchill et al. 2012). The pygmy right whale (*Caperea marginata*; Family: *Neobalaenidae*) is recognized as a sister group to this family (Churchill et al. 2012).

As mentioned above, the phylogenetic placement of the gray whale

(*Eschrichtius robustus*; Family: *Eschrichtiidae*) is dubious. While most morphological (and some molecular) studies describe this species as a sister group to the rorqual whales (Deméré et al. 2008, Steeman et al. 2009), there is also molecular evidence to place it within this group (Rychel et al. 2004, McGowen et al. 2009).

The largest and least phylogenetically resolved family are the rorqual whales (*Balaenopteridae*). The following eight species are currently recognized by the Ad-Hoc Committe on Taxonomy of the Society of Marine Mammology: Common minke whale (*Baleanoptera acutorostrata*), Antarctic minke whale (*Balaenoptera bonaerensis*), sei whale (*Baleanoptera borealis*), Bryde's whale (*Baleanoptera edeni*)[1], Omura's whale (*Baleanoptera omurai*), blue whale (*Baleanoptera musculus*), fin whale (*Baleanoptera physalus*) and humpback whale (*Megaptera novaengliae*) (Committee on Taxonomy 2013).

2 Long migrations & fluid social systems

Marine environments are fundamentally different from terrestrial systems in that they are more 'open'. Currents, winds and waves create physical forces that transport nutrients, materials and organisms over large spatial scales with few barriers. Adapted to variable environments many marine organisms are relatively sedentary in their adult stage, but produce eggs, larvae or juveniles that disperse over large areas, extending their ability to survive when conditions change (Steele 1985, Shanks et al. 2003). Given more dynamic habitats, greater variability in available resources and their large body size, marine mammals require large home ranges and many species, especially the large, primarily pelagic baleen whales are significantly more mobile than terrestrial mammals (Whitehead 2001, Carr et al. 2003).

In many species, migrations develop as an adaptation to take advantage

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[1] Some researchers suggest to use *B. edeni* only for the small-form, coastal Bryde's whale of the Pacific and Indian Ocean, while using *B. brydei* for the larger, globally distributed oceanic form (see Sasaki et al. 2006).

of seasonal peaks in resource abundance, to avoid periods of resource shortage, escape inter-, and intraspecific competition or avoid predators and parasites (Alerstam et al. 2003). In contrast to many terrestrial species, where migration is often driven by food availability on either end of the migration path (Gauthreaux, Jr. 1982, Fryxell & Sinclair 1988), most species of baleen whales perform semi-annual, seasonal to-and-fro migrations (Dingle & Drake 2007) between productive high-latitude feeding and less productive low-latitude breeding grounds (Kellogg 1929, Norris 1967, Corkeron & Connor 1999).

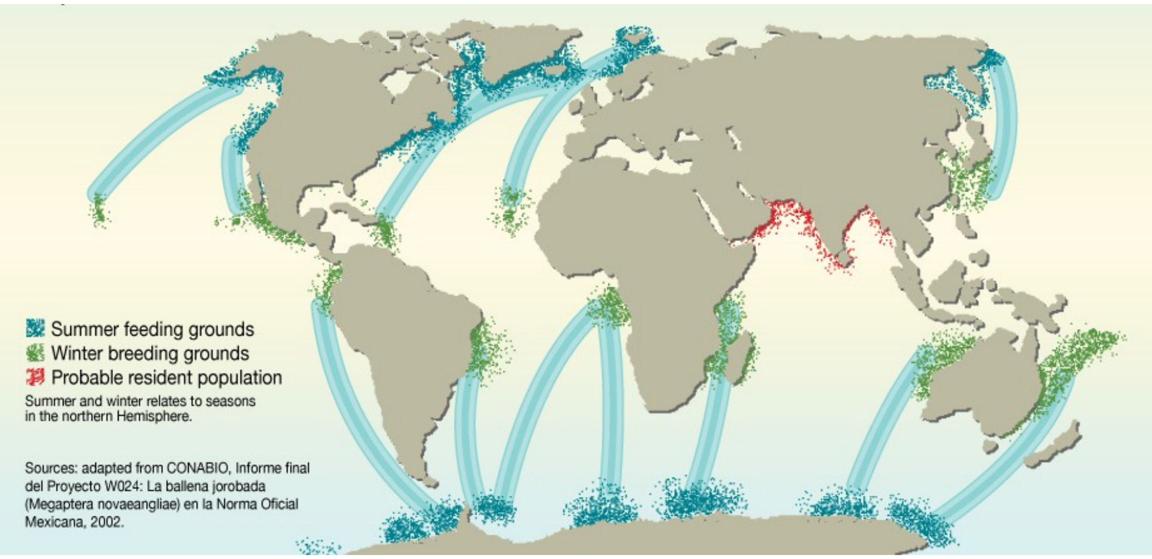

Figure 2. Annual worldwide humpback whale migrations. Figure adapted from Riccardo Pravettoni, UNEP/GRID-Arendal. (www.grida.no/graphicslib/detail/the-long-migration-of-the-humpback-whale_9cd5)

Humpback whales (*Megaptera novaeangliae*) currently hold the record both for the greatest absolute distance traveled between two sightings on different breeding grounds (9800 km; Stevick et al. 2011, Figure 2), as well as the greatest 'round-trip' migration distance (18,840 km; Robbins et al. 2011). They have also been shown to move with enormous directional precision, holding constant course for more than 200 km (Horton et al. 2011).

Next to those of humpback whales (Dawbin 1966, Clapham & Mead 1999, Calambokidis et al. 2001), migratory routes are well established for some populations of species, such as North and South Atlantic right whales(*Eubalaena spp.*) (Kraus et al. 1986, Mate et al. 2011) and gray whales (Pike 1962, Sumich & Show 2011). In addition, even though routes and destinations are less well understood, long longitudinal migrations have been suggested for blue whales (*Balaenoptera musculus*) (Mate et al. 1999, Reeves et al. 2004), fin whales (*Balaenoptera physalus*) (Širović et al. 2009, Mizroch et al. 2009), sei whales (*Balaenoptera borealis*) (Visser et al. 2011, Prieto et al. 2012) and minke whales (*Balaenoptera acutorostrata*) (Kasamatsu et al. 1995, Skaug et al. 2004). In ***Chapter V***, I show how the seasonal migration of western North Atlantic minke whales can be tracked by using large-scale networks of long-term passive acoustic recorders. Such comprehensively collected data can also be used in establishing the geographic extent of species-specific migration routes, providing critical information for marine spatial planning and informing attempts to mitigate adverse impacts of anthropogenic activities (Van Parijs et al. 2009, ***Chapter V***). In addition, I used long-term passive acoustic monitoring for baleen whales in Massachusetts Bay, a highly urbanized marine habitat in the Northeast United States, to show the importance of this region as part of the migration corridor and seasonal feeding ground for several large whale species (***Chapter II and III***).

Some baleen whale species do not follow seasonal migrations like those described above. Among the rorqual whales, the Bryde's whale appears to have a year-round tropical distribution (Best 1977, Kato & Perrin 2009). Similarly, bowhead whales perform latitudinal seasonal migrations (Heide-Jørgensen et al. 2006) but stay in Arctic waters year round (Víkingsson & Heide-Jørgensen 2013). There are also many reports of individuals, parts of or whole populations of traditionally migratory species, that do not migrate every year (Corkeron & Connor 1999). Prominent examples are humpback whales in the Arabian Sea (Mikhalev 1997) and fin whales in the Mediterranean Sea (Castellote et al. 2011).

In addition, recent passive acoustic data show a peak in singing activity in North Atlantic fin whales recorded in Davis Strait between Greenland and Canada, Massachusetts Bay and the New York Bight during boreal winter (Simon et al. 2010, Morano et al. 2012, ***Chapter II)***. Song in fin whales has been linked with mating behavior (Thompson et al. 1992, Croll et al. 2002). In the North Atlantic conception time in fin whales peaks in January (Lockyer 1984) and newborn calves have been observed off the coast of northern Norway during winter (Ingebrigtsen 1929 cited in Corkeron & Connor 1999). Together, these observations are convincing evidence for some mating and calving to occur in higher latitudes in fin whales (Corkeron & Connor 1999, Simon et al. 2010). Similar trends can be observed in other species. In ***Chapter VI*** of this thesis I provide unequivocal evidence for the Antarctic minke (*Balaenoptera bonaerensis*) whale to be the source of the mysterious 'bioduck' signal. One of the most pervasive animal-produced sounds of the Southern Ocean, the regular pulsed 'bioduck' signal has been recorded in Antarctic waters and contemporaneously in lower latitudes off the Australian west coast. This discordant seasonal occurrence pattern, indicates at a minimum a very widespread distribution of the species, or, more likely, a seasonal migration by one part of the population and year-round presence in Antarctic waters by another.

These examples give rise to the question of how well the current paradigm of semi-annual migrations between high-latitude 'feeding' and low-latitude 'breeding' grounds describes the actual movement, behavior and ecology of baleen whales. Baleen whales have been characterized as capital breeders, referring to the fact that in general they acquire and store energetic resources before reproduction (Lockyer 1984, Huang et al. 2008, 2011). This strategy appears beneficial especially in unpredictable systems with time-limited and discontinuous resource distributions (Houston et al. 2007). However, as described above, some baleen whale populations mate in higher latitudes, where they may be feeding at the same time. The degree and definition of capital breeding in this group might therefore be more variable and species might use more than one life-history strategy, depending on various factors such as sex, age-class or variable ecological parameters in different habitats (Alerstam & Hedenström 1998, Stephens et al. 2009). And partial or differential migration (Dingle & Drake 2007) might be more the norm than the exception in baleen whales. For example in right whales mainly pregnant females are migrating to warm waters in winter, while males and non-breeding females stay on higher latitude mating grounds (Kraus et al. 1986, Cole et al. 2013).

Beyond the question who is migrating, the related question why baleen whales migrate when they do is still a subject of debate. While it is easy to explain the presence of baleen whales on highly productive feeding grounds during summer, the driving forces behind migrations to warm, resource-poor breeding grounds are less clear. Theories that have been put forward include an evolutionary left-over behavior from when breeding and feeding grounds were spatially closer (Evans 1987), the optimization of energy budgets in warmer waters (Brodie 1975), resource tracking, i.e. following prey when resources decrease in higher latitudes during winter (Payne 1995), better calf survival in warm, calm waters with less demands towards thermo-regulation (Clapham 1996, 2001), as well as avoidance of killer whale predation (Corkeron & Connor 1999). There is insufficient data to fully support one or the other, but avoidance of killer whale predation and energy advantages for calves in warm, tropical waters seem to be the explanations favored by most authors (Clapham 2001, Connor & Corkeron 2001, Rasmussen et al. 2007, Mehta et al. 2007, Ford & Reeves 2008). However, both explanations have also been questioned. Energetic models show that neonates of most large whales are well able to tolerate temperatures in polar regions and that most species do not need to migrate to stay thermo-neutral (Watts et al. 1993). On the other hand, the importance of baleen whales as killer whale prey has been contested, by multi-year humpback whale sightings data, showing that most scars are acquired by young calves and that only few whales acquire new scars after their first sighting (Clapham 2001, Mehta et al. 2007).

Regardless of the underlying reasons for their movements, it is clear that many species of baleen whales range over very large distances. Generally, females disperse less than males. In a number of species, females in particular show philopatry and site fidelity to feeding and/or breeding grounds (Baker et al. 1990, Palsbøll et al. 1995, Rosenbaum et al. 2009, Valenzuela et al. 2009, Frasier et al. 2011, Costa-Urrutia et al. 2013), which together with co-migration of mother/offspring pairs during lactation, leads to a strong female influence on population structure (Hoelzel 1998, Tiedemann et al. 2000). Although baleen whale social organization is generally less complex and stable as compared to that of many toothed whale species (Connor et al. 1998), some data show evidence for long-term associations in the fission-fusion societies of humpback whales, particularly among females (Weinrich 1991, Ramp et al. 2010)

It has been argued that the mobility of cetaceans may be a primary reason for the development of their advanced social and communication systems, including the capacity for vocal learning (Connor et al. 1998, Rendell & Whitehead 2001). Vocal learning in turn is likely a prerequisite for more sophisticated social learning and both are highly adaptive in a fast changing and variable environment such as the open ocean. Among the baleen whales the continually evolving and horizontal transmission of humpback whale song across entire ocean basins provides a striking example for both: the capacity for vocal learning, as well as the existence of cetacean culture (Noad et al. 2000, Rendell & Whitehead 2001, Garland et al. 2011). In addition, further evidence for the evolution of culture in baleen whales was recently added by a long-term study of humpback whale foraging behavior. Similar to song in this species, the spread of a new and persistent feeding technique (lobtail feeding) through a population of humpback whales was shown to be driven by horizontal cultural transmission (Allen et al. 2013).

In conclusion, baleen whales live in large-scale, acoustically mediated (see also next paragraph), fluid social systems and the combination of advanced vocal and social learning has given rise to some unique and remarkable social behaviors, including the evolution of advanced cultures with multiple traditions.

3 Acoustic ecology & passive acoustic monitoring of baleen whales

Acoustic communication is highly adaptive in the marine environment, where light penetrates only the upper water layers and sound travels five times faster than in air. Given these favorable physical conditions, low frequencies and loud source levels (Širović et al. 2007, Samaran et al. 2010a), baleen whales probably live in one of the largest communication networks worldwide (Payne & Webb 1971). Like other cetaceans they rely on the production and perception of sounds for almost all aspects of their lives. They use sound for navigation, prey detection, maintaining social contact and cohesion, as well as advertising and defending resources for example in a mating context (Tyack & Clark 2000, Clark & Ellison 2004, Stimpert et al. 2007).

It has been shown that baleen whales respond to signals of conspecifics at a range of 10 km (Tyack & Whitehead 1983). However, their signals may be detected at scales of hundreds of kilometers (Clark 1995, Stafford et al. 1998). For example, blue whale sounds in the Southern Ocean have been detected at ranges of 200-300 km (Širović et al. 2007, Samaran et al. 2010b). Generally, low frequencies can travel further than higher frequencies, since less energy is being lost through absorption (Urick 1983). Apart from frequency, sound propagation in the sea is primarily dependent on depth and temperature. Sound speeds generally increase with depth and warmer temperatures. In addition to bottom and surface reflections and associated energy loss, water layers of diverse characteristics refract sounds in a variety of ways, leading to unique propagation paths at different depths, which animals may take advantage of.

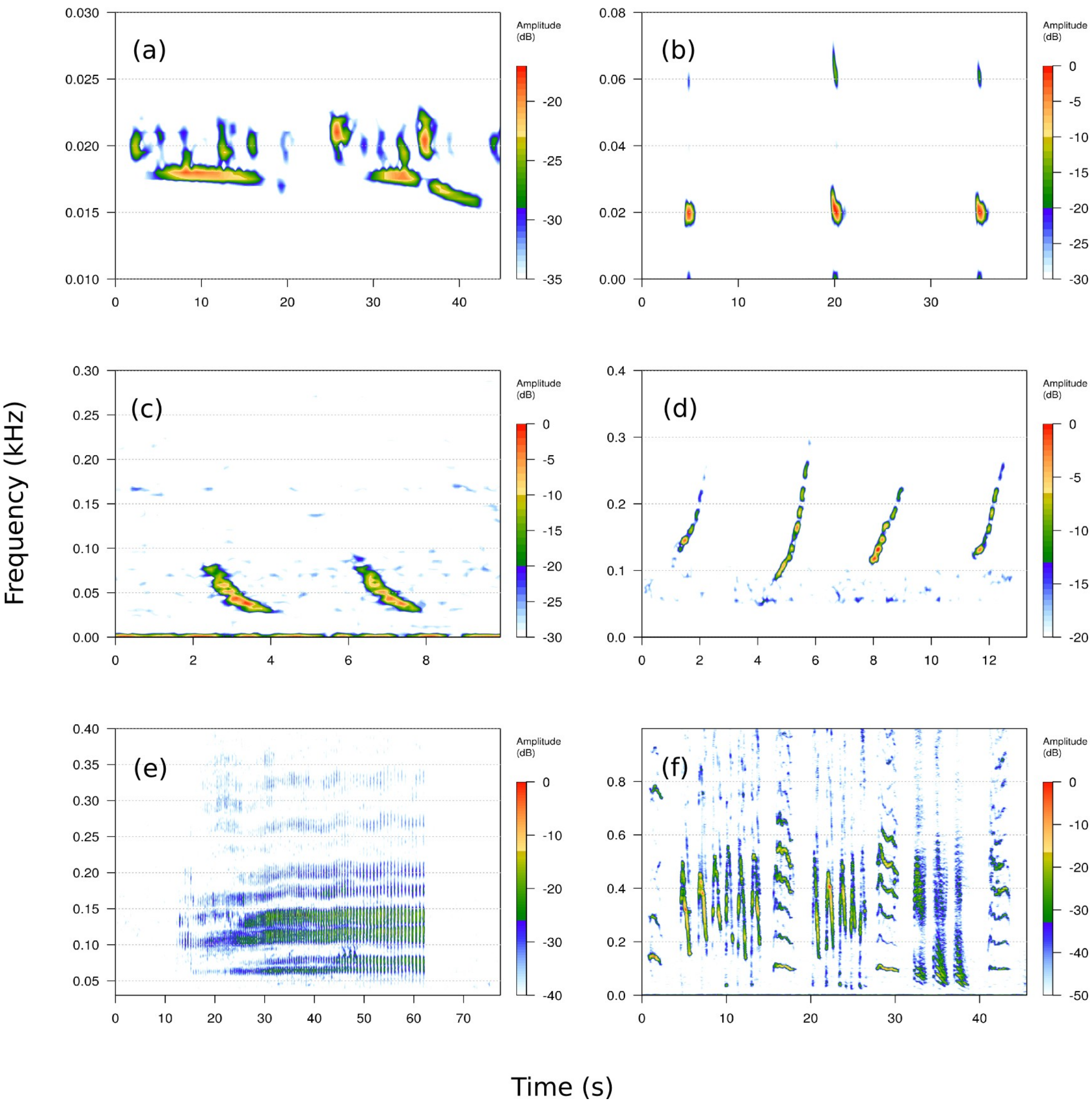

Figure 3. Example spectrograms of baleen whale vocalizations. (a) blue whale AB song, (b) fin whale 20 Hz song, (c) sei whale downsweeps, (d) right whale upcalls, (e) minke whale pulse train, (f) humpback whale song. Note different frequency and time scales of spectrograms. Spectrogram parameters: (a) Fast Fourier Transform (FFT) = 4096 pt, overlap (ovlp) = 95%, samplerate (SR) = 2000 Hz: frequency resolution (FR) = 0.5 Hz, time resolution (TR) = 100 ms; (b) FFT = 1024 pt, ovlp = 75%, SR = 2000 Hz: FR = 1.9 Hz, TR = 128 ms; (c) FFT = 4096 pt, ovlp = 75%, SR = 10,000 Hz: FR = 2.4 Hz, TR = 250 ms; (d) FFT = 512 pt, ovlp = 75%, SR = 2000 Hz: FR = 3.9 Hz, TR = 64 ms; (e) & (f) FFT = 1024 pt, ovlp = 75%, SR = 2000 Hz: FR = 1.9 Hz, TR = 128 ms.

One of the best described features of marine sound transmission is the deep sound or SOFAR (SOund Fixing and Ranging) channel. In this layer of minimum sound speed, which, depending on the environment is typically at a depth of between 600-1200 meters (shallower in Arctic waters), sound gets trapped and can travel over very long distances with little transmission loss. Whether baleen whales take advantage of these unique propagation characteristics at different depths is unknown, but it has been hypothesized that they may do so (Payne & Webb 1971). Regardless of the absolute distance, given probable signal detection at or just below background noise levels (Clark et al. 2009), low-frequency baleen whale vocalizations have a much larger active space than those of any other mammal. In ***Chapter VII*** of this thesis I show that humpback whales behaviorally respond to low-frequency signals of a new type of remote sensing technology (OAWRS) at a range of 200 km. The OAWRS source exhibits frequency characteristics similar to humpback whale vocalizations, indicating that whales are indeed able to hear and respond to sounds over such large ranges. This may be particularly true for signals that are novel or are similar to other biologically relevant signals or both (Ellison et al. 2011, Risch et al. 2012).

Thus, acoustic communication using long-range signals plays an important role in the fluid social systems of baleen whales, where individuals are often highly dispersed or out of sight. In such unstable, non-territorial social systems, acoustic signals may play a vital role in storing information about individual or group identity, behavioral state, as well as cues about the signaller's quality (Smith et al. 2008, Rehn et al. 2010, King & Janik 2013). Furthermore, the larger the communication range, the larger will be the potential audience. In the open ocean the acoustic space of groups and populations of the same or sympatric species will therefore often overlap, which has important implications for signal evolution, especially if signals serve in a reproductive context. In such large acoustic networks, individuals may also employ eavesdropping, which has been defined as 'extracting information from an interaction between other individuals' (McGregor & Dabelsteen 1996).

Although such behavior is generally difficult to demonstrate (Mccomb & Reby 2005), it may occur in the floating lek mating system of humpback whales (Clapham 1996), where females could listen to vocal interactions between competing males (Cholewiak 2008). In addition to true eavesdropping, it has been shown, that many mammals attend to vocalizations even if these are not aimed directly at them. For example elephant contact calls directed at immediate family members are often attended by members of the wider population, who adjust their behavior based on this information (McComb et al. 2000). Although detailed behavioral observations are often impossible in cetaceans, and in far roaming baleen whales in particular, it is conceivable that, similar to the large-scale networks of elephant societies, in baleen whales conspecifics and perhaps even heterospecifics sharing the same acoustic space attend to each other's calls possibly over very large distances.

Baleen whales include the largest species ever to have lived on earth. In general, body size (which is correlated to vocal tract size) is inversely related to an animal's optimal vocalization frequency, due to physiological constraints on signal evolution (Fletcher 2004). In cetaceans, there is strong evidence, that body size has constrained the evolution of minimum but not the maximum frequencies of tonal signals, which indicates that throughout cetacean evolution, low-frequency sounds have been selected for (May-Collado et al. 2007). A likely explanation for these patterns are the advantages of long-distance communication, as observed in many baleen whales and discussed earlier.

Baleen whales are generally very vocal and produce a range of different signals (Figure 3). Due to their large body size, most species are low-frequency specialists. However, the song of several species may contain a broad range of frequencies (Payne & Payne 1985, Tervo et al. 2012). Humpback and bowhead whales in particular, produce complex, hierarchically structured songs, which have been well studied (Payne & McVay 1971, Cholewiak et al. 2013, Stafford et al. 2008, Tervo et al. 2011). Blue and fin whales produce more stereotypic, high intensity song units at very low frequencies (~15-30 Hz) (McDonald et al. 2001, Croll et al. 2002). In humpback, fin and blue whales it has been shown, that only males produce songs (Glockner 1983, Croll et al. 2002, Oleson et al. 2007a). Thus, songs are thought to serve primarily in a reproductive context, functioning as male advertisement or to mediate interactions between competing males during the breeding season (Tyack 1981, Tyack & Whitehead 1983, Oleson et al. 2007a). However, increasing acoustic recording effort is beginning to show the occurrence of song outside the traditional breeding season, on summer feeding grounds and migration in all of these species (Stafford et al. 2007, Simon et al. 2010, Vu et al. 2012) and alternative functions of songs, such as navigation and prey detection have been suggested (Clark & Ellison 2004). In ***Chapter II*** of this thesis I show the persistent year-round presence of fin whale song in Massachusetts Bay, corroborating data from other studies in the Gulf of Maine and on Arctic feeding grounds, which have shown the presence of fin whales in higher latitudes during boreal winter (Simon et al. 2010, Morano et al. 2012).

In addition to song, most baleen whale species produce other call types in different behavioral contexts. Several species produce feeding-associated vocalizations, which compared to the elaborate reproductive song displays, are generally much simpler in structure (Cerchio & Dahlheim 2001, Oleson et al. 2007b, Širović et al. 2013a). Fin, blue and right whales use frequency modulated call-counter calls as contact calls to coordinate movement and maintain group cohesion (Clark 1982, Oleson et al. 2007b, Širović et al. 2013a). Finally, a variety of variable social calls have been been described for most species (Oleson et al. 2007a, Dunlop et al. 2008, Stafford et al. 2008, Stimpert et al. 2011, Parks et al. 2011a). Despite growing knowledge on the function of certain types of baleen whale vocalizations, there are still large gaps in our understanding of even the most basic parameters of baleen whale calling behavior. In many species the concentration on studying prevalent types of vocalizations in particular habitats has led to the neglect of other types of vocalizations and the appreciation of the full vocal repertoire. For example, although humpback whale song has been studied in detail on breeding grounds in many different ocean basins (Payne & McVay 1971, Noad et al. 2000, Cerchio et al. 2001), only recently have researchers begun to understand its extended presence on feeding grounds and on migration (Charif et al. 2001, Noad & Cato 2007, Stimpert et al. 2012, Vu et al. 2012) shown that, next to song, humpback whales produce a range of social and feeding related vocalizations, which need to be taken into account, when using PAM to infer seasonal presence of the species (Murray et al. 2013). This is true for vocalizations of all species of baleen whales, most of which are much less studied than the humpback whale.

Of the baleen whale species occurring in the North Atlantic, vocalizations of sei, Bryde's and minke whales are the least well described (Mellinger et al. 2000, Baumgartner et al. 2008, Širović et al. 2013b). This lack of knowledge on a widely distributed and still commercially exploited species such as the minke whale was the impetus for a large part of this thesis. In ***Chapters III-V*** I explore the suitability of using passive acoustic monitoring (PAM) to better describe the vocal repertoire of North Atlantic minke whales on migration (***Chapter III***), show differential call usage and non-random combinations of different call types (***Chapter IV***) and use these vocalizations to investigate minke whale large-scale seasonal and spatial distribution patterns in the western North Atlantic (***Chapters III & V***).

Marine mammal distribution and abundance have traditionally been monitored through visual sighting surveys (Jewell et al. 2012, Kaschner et al. 2012). However, visual methods are limited when monitoring animals that spend a large proportion of their lives submerged under water (Borchers et al. 2013, Thomson et al. 2013). Visual surveys are also restricted to daytime monitoring and dependent on good weather conditions. In addition, visual surveys are often spatially restricted to relatively coastal areas and thus can only provide a snapshot of the true distribution, particularly of far-ranging species such as baleen whales (Kaschner et al. 2012). As a result, knowledge on baleen whale distribution and abundance during boreal winter is generally sparse (Best et al. 2012). In ***Chapter V*** of this thesis I show how large-scale networks of acoustic recording units can be used to investigate migratory routes and unknown winter habitat of an understudied species such as the minke whale.

With current technological advances, especially the increased lifetime of batteries and enlarged storage capacity, PAM is increasingly being used to augment visual surveys (Clark et al. 2010, Gerrodette et al. 2011). This new technology is especially useful in remote areas, during nighttime or adverse weather conditions (Moore et al. 2006, Mellinger et al. 2007, Van Parijs et al. 2009). PAM can provide long-term records of seasonal occurrence and distribution patterns, providing valuable insights into how species utilize their habitat and when they are present in coastal areas and hence at higher risk of deleterious anthropogenic impacts (Gallus et al. 2012, Mussoline et al. 2012). Figure 4 (a) illustrates the increased temporal and spatial coverage of several

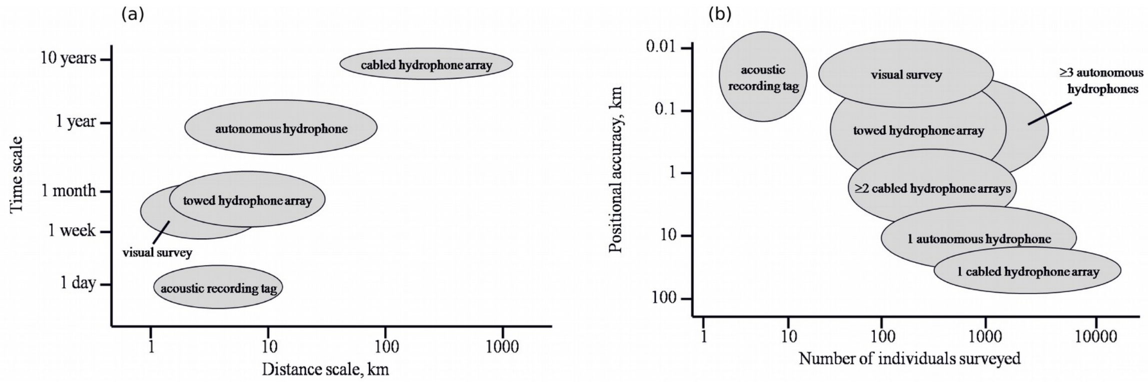

Figure 4. (a) Approximate temporal and spatial scales over which marine mammal survey data can be collected, comparing visual and acoustic techniques. (b) Location accuracy and number of individuals covered by different monitoring techniques. Figures courtesy D.K. Mellinger, reprinted from (Van Parijs et al. 2009).

types of acoustic monitoring devices as compared to visual surveys. Figure 4 (b) gives an overview of the number of individuals that can be monitored with the various methods, showing that with their higher spatial resolution, PAM can generally capture more individual animals, although most acoustic methods (with the exception of acoustic recording tags) provide a lesser amount of positional accuracy when compared to direct visual observation.

Despite the obvious advantages of PAM, there are limitations to this form of monitoring also. Firstly, marine mammals need to be vocalizing in order to be detected and therefore an absence of acoustic detections does not necessarily equal an absence of the monitored species. Secondly, for most baleen whale species only few call types have been described so far and apart from vocalizations related to reproduction and a few exceptions (Oleson et al. 2007a, Stimpert et al. 2007) behavioral context is largely missing. Related to behavioral changes, calling rates are often variable and most vocalizations show distinct seasonal and diel patterns of occurrence which vary with geographic location (***Chapter V***). Moreover, some call types are sex-specific and in those cases PAM can catch only the part of the population, which produces the vocalization. All of these factors need to be taken into account when interpreting results from PAM surveys.

Overall, the advantages of passive acoustic monitoring especially when used in tandem with visual observations (Barlow & Taylor 2005, Gerrodette et al. 2011) are increasingly being recognized and efforts are made to address data gaps concerning the vocal behavior of various species (Van Parijs et al. 2009). For example, it has been shown, that the monitoring of several call types with variable functions at different times of year can improve accuracy of spatio-temporal distribution patterns obtained by means of passive acoustic monitoring (PAM) (Oleson et al. 2007b, Širović et al. 2013a). Another convenience of PAM is that data can be collected remotely and largely independent of human observers. Also, data can be assembled opportunistically from a variety of different platforms (Figure 4). For example, widely spaced acoustic monitoring networks such as the array data from the IUSS Sound Surveillance System (SOSUS) deployed for military underwater surveillance have been used to investigate seasonality and large-scale distribution of baleen whales in the North Pacific and Atlantic Oceans (Stafford et al. 1998, Clark & Gagnon 2004).

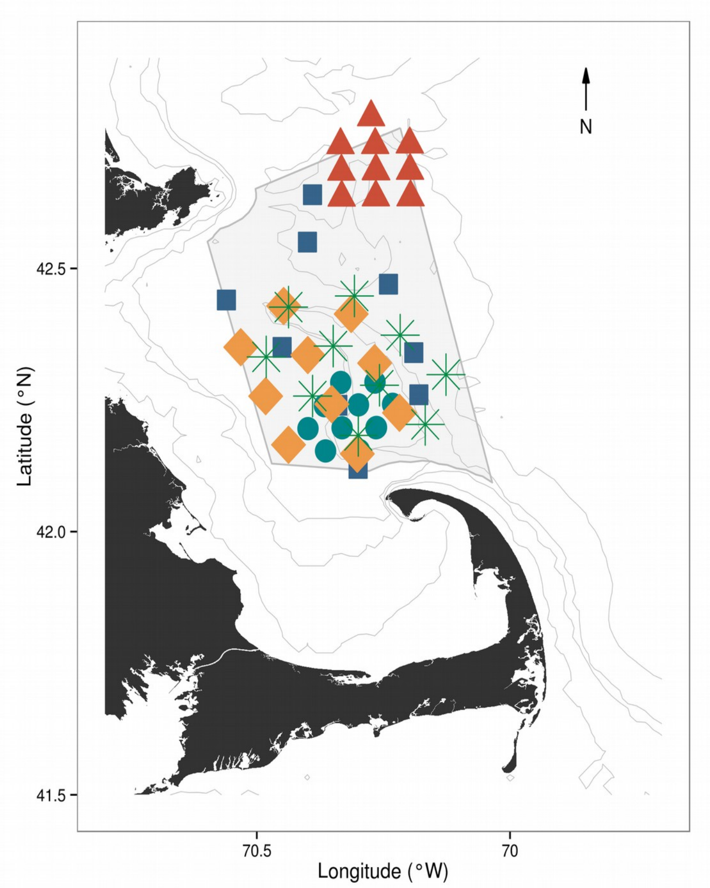

Figure 5. Map of the Stellwagen Bank National Marine Sanctuary (SBNMS) (grey shaded area). Symbols depict locations of arrays of acoustic recording units deployed from 2006-2010, which have been analyzed for baleen whale presence in this thesis. Map projection: Mercator.

Most data analyzed in this thesis (***Chapters I-V, VII***) was collected as part of a long-term ocean noise monitoring project (Clark et al. 2009, Hatch et al. 2012) in the Stellwagen Bank National Marine Sanctuary (SBNMS), located in Massachusetts Bay, USA (Figure 5). For 3.5 years passive acoustic data was collected almost continuously, using different configurations of acoustic arrays, typically consisting of 10 individual recording units (Figures 5 & 6). In ***Chapter II***, I show the utility of such long-term data for obtaining spatio-temporal distribution patterns, including the assessment of migration timing for a range of baleen whale species.

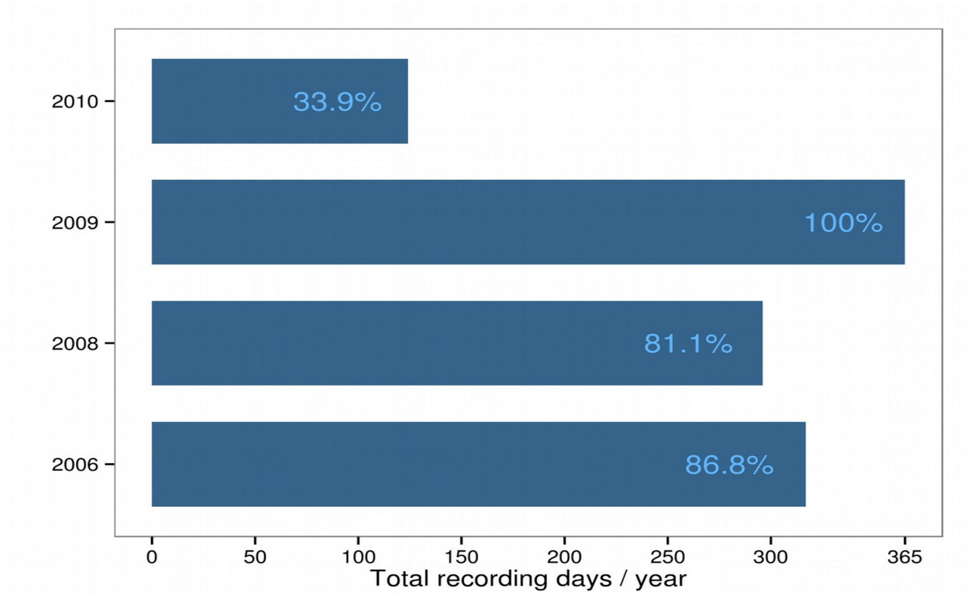

Figure 6. Yearly acoustic recording effort during 3.5 years of passive acoustic monitoring in the Stellwagen Bank National Marine Sanctuary (SBNMS).

Where detailed knowledge on the vocal behavior of species exists, PAM can be used effectively in density estimations (Lewis et al. 2007, Marques et al. 2011). These data can be essential when monitoring population status, population development or recovery, particularly of rare or endangered species (Li et al. 2010, Gerrodette et al. 2011). However, several parameters need to be known in order to convert call densities to estimates of animal abundance, the most important of which is a reliable estimate of cue rate (Marques et al. 2013). The rate with which animals vocalize may vary with call type, depth, sex of calling animal, behavioral state, season, location, group size and level of disturbance (Croll et al. 2002, Oleson et al. 2007a, Parks et al. 2011a, Risch et al. 2012: ***Chapter VII***). Thus, a better understanding of basic vocal behavior is necessary, to use PAM beyond species detection. While some parameters such as absolute calling rate can only be obtained through acoustic tag recordings or behavioral focal follow studies (Johnson et al. 2009, Parks et al. 2011a), some of these parameters can be estimated by carefully analyzing small-scale acoustic array data. In ***Chapters I & IV*** I show, how acoustic array recordings can be used to localize and track individual animals, providing data on calling rates of vocally active animals, source levels (and following: estimates of minimum detection distance) and call type usage.

Apart from population monitoring, PAM data can be used for exploring geographic variability in vocalizations (see ***Chapter V***), habitat use and environmental correlates (Baumgartner & Fratantoni 2008, Stafford et al. 2009) as well as for the study of behavior and the impact of anthropogenic activities such as the introduction of underwater noise (Di Iorio & Clark 2010, Melcón et al. 2012). While monitoring the soundscape of SBNMS in 2006, we incidentally recorded an Ocean Acoustic Waveguide Remote Sensing (OAWRS) experiment, which was carried out on Georges Bank, in the Gulf of Maine, roughly 200 km from our acoustic array location. Through careful analysis of humpback whale song recordings, we were able to show a behavioral response of singing humpback whales to this newly introduced low-frequency sound source (***Chapter VII***).

To date most passive acoustic monitoring of marine mammals has been concentrated on a single species approach. However, animal vocalizations are shaped by the biotic (including other vocal species) and abiotic environment that surrounds them. This concept is particularly important in the marine environment, where species primarily live and interact in a world of sounds and the visual sense plays a much smaller role than in terrestrial habitats. The acoustic ecology of a species, which describes the interactions of a species with various environmental factors that shape its behavioral ecology through the use and perception of sounds, is therefore important to consider (Clark et al. 2009, Van Opzeeland & Miksis-Olds 2012).

In terrestrial environments the idea of sound as an ecological property of a landscape was first expressed by the Canadian composer R.M. Schafer (1977), who in the early 1970ies established the World Soundscape Project (WSP) to record, characterize and preserve natural and urban soundscapes from around the world. The terms *biophony* to describe sounds made by living organisms and *geophony* for nonbiological ambient sounds, which together create all natural soundscapes, where first introduced by (Krause 1987) and can be extended by the term *anthrophony* for sounds made by humans (Pijanowski et al. 2011a). Since these early works, which focused on the study of natural sounds and how humans relate to them, soundscape ecology and the importance of protecting natural soundscapes has gotten renewed attention in recent years (see special issue on soundscape ecology: Pijanowski & Farina 2011). This new field of study is closely related to and has been proposed as a branch of landscape ecology and sets out to describe and measure relationships between biological, geophysical and anthropogenic sounds and their spatio-temporal variability (Pijanowski et al. 2011a).

In the marine environment, recent concerns about the increasing impact of anthropogenic noise, particularly of far-reaching and ubiquitous noise sources such as global shipping traffic or seismic surveying (see the last part of this Introduction), have also called for a more holistic approach to monitor marine soundscapes, and away from an entirely species-specific monitoring approach (Clark et al. 2009, Hatch & Fristrup 2009). From a conservation perspective such larger-scale monitoring is fundamental to the full characterization of human noise sources and their spatio-temporal effects on

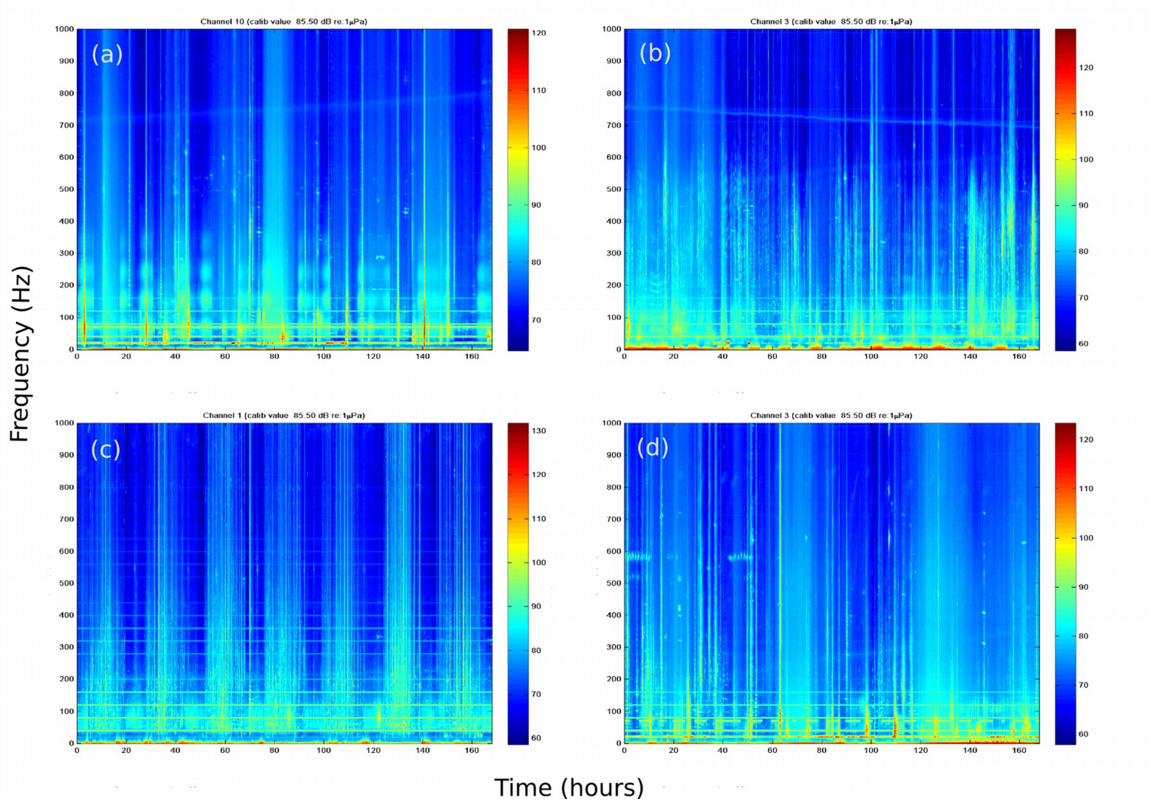

Figure 7. Long-term spectrograms showing aggregated data for one week of low-frequency sounds recorded in the Stellwagen Bank National Marine Sanctuary in 2009 for (a) winter (December-February), (b) spring (March-May), (c) summer (June-August) and (c) fall (September-November). The red band at the bottom of panels (a),(b) and (d) represents acoustic energy of fin whale song, which is not present during summer (c). Spectrogram parameters: Fast Fourier Transform (FFT) size: 1024 pt, Sample rate (SR): 2000 Hz, # of aggregated spectra: 200, Frequency resolution: 1.95 Hz, Time resolution: 102.4 s.

the marine environment including marine mammals (Clark et al. 2009, McWilliam & Hawkins 2013). In addition, the application of acoustic indexes (Farina et al. 2011, Sueur et al. 2012, Gasc et al. 2013) for monitoring and comparing species assemblages (rather than single species) at different sites and their development over time, may help to manage and interpret the vast amounts of acoustic data which are collected during long-term acoustic monitoring projects (Pijanowski et al. 2011b). If basic properties and contributors to a particular habitat's soundscape are understood, long-term spectrograms as shown in Figure 7 and acoustic diversity indexes may thus allow a quicker appreciation of possible changes in the overall health status of marine soundscapes. In ***Chapter II*** of this thesis I employ species-specific detectors to describe seasonal changes in the low-frequency soundscape of the Stellwagen Bank National Marine Sanctuary (SBNMS), driven by the presence of different migratory marine mammals species. In the future, these data will be compared to new approaches such as acoustic diversity indexes (Pieretti et al. 2011, Sueur et al. 2012) in order to explore their feasibility for monitoring multi-species presence and temporal changes in marine soundscapes.

One of the smallest: The minke whale

A group of Antarctic minke whales surfacing near the Antarctic peninsula
Photo: Ari M. Friedlaender

1 General Biology

Although minke whales are one of the most common and widely distributed large whale species, often found in coastal waters during summer, most populations have been surprisingly little studied. A true cosmopolitan, the species can be found in all oceans, inhabiting tropical as well as polar and even ice-covered habitats (Scheidat et al. 2011). The common minke whale (*Balaenoptera acutorostrata*) is a sister species to the Antarctic minke whale (*Balaenoptera bonaerensis*). For the common minke whale three subspecies have been suggested: *Balaenoptera acutorostrata acutorostrata* in the North Atlantic, *Balaenoptera acutorostrata scammoni* in the North Pacific and the dwarf minke whale, *unnamed subspecies*, in the Southern hemisphere (Reilly et al. 2008a). The exact placement of the dwarf minke whale is still unclear but genetic evidence suggests the existence of at least two different populations in the Southern Hemisphere, one in the western South Atlantic linking animals from Brazil, Chile and the Antarctic Peninsula, and one in the western South Pacific. The same study also found, that North Atlantic minke whales were more closely related to South Atlantic dwarf minke whales, than either are with dwarf minke whales from the South Pacific, indicating that the Southern hemisphere sub-species status of common minke whales needs to be revised (Pastene et al. 2010).

The smallest of the balaenopterid whales, minke whales are typically about 10 meters in size. A clearly defined white band on the pectoral flipper distinguishes the North Atlantic from the North Pacific subspecies, where this feature is less pronounced. In dwarf minke whales this patch extends into the shoulder region, and it is mostly absent in Antarctic minke whales. While in the Southern Hemisphere their diet consists primarily of krill (*Euphausiids*), small schooling fish such as capelin (*Mallotus villosus*), herring (*Clupea spp.*) and sandeel (*Ammodytes spp.*) are the preferred prey in the Northern hemisphere, although krill is taken, when abundant (Macleod et al. 2004, de Boer 2010, Anderwald et al. 2012a). Minke whales also appear to adjust to seasonal or regional differences in prey distribution (Anderwald et al. 2012a). During the summer feeding period their occurrence is closely related to the distribution of their prey (Macleod et al. 2004, Robinson et al. 2009, de Boer 2010) and individual animals may show highly specialized feeding strategies and strong site fidelity (Dorsey 1983, Kuker et al. 2005). Around the west coast of Scotland minke whales are commonly observed in association with seabirds feeding on the same prey (Anderwald et al. 2012b). Minke whales are typically sighted alone or in small groups and though inconspicuous in most areas, dwarf minke whales wintering at the Great Barrier Reef, Australia, are very inquisitive and regularly approach humans, leading to a vessel-based swim-with industry in the area with potentially adverse impacts to the animals (Mangott et al. 2011). With the exception of the population inhabiting the Sea of Japan, which breeds in the fall, conception and birth seem to occur in winter (Reilly et al. 2008a)

2 Distribution & abundance

Minke whales occur widely throughout all ocean basins. In the North Atlantic they range from Baffin Bay to the Caribbean in the Northwestern Atlantic and from the Barents Sea to the West African continental shelf in the Northeastern Atlantic (van Waerebeek et al. 1999, Reilly al. 2008a). While there is evidence that North Atlantic minke whales undergo seasonal migrations between high and low latitudes (Mitchell 1991, van Waerebeek et al. 1999, Skaug et al. 2004, Víkingsson & Heide-Jørgensen 2013), some individuals may also stay in temperate waters year-round (Macleod et al. 2004). Migrations in the North Atlantic seem to be segregated by sex, with females arriving earlier on northern feeding grounds and preferring higher latitudes (Laidre et al. 2009). In the eastern North Pacific acoustic recordings suggest migratory movements between Hawaii and the Chukchi Sea (Delarue et al. 2013), and a northward migration in summer has also been suggested for the western North Pacific (Reilly et al. 2008a). Some degree of sex segreation can also be observed in the western North Pacific, with females being found in more coastal areas, while especially immature males are found further offshore (Wade et al. 2010). In addition, similar to North Atlantic minke whales, a year-round population may exist off California in the eastern North Pacific. Dwarf minke whales in the South Atlantic seem to migrate between Brazil and the Antarctic Peninsula (Acevedo et al. 2010). In general, there is very little knowledge on minke whale winter distributions in any ocean basin, which is likely due to a primarily offshore distribution of the species in tropical waters near the equator at this time of year (Mitchell 1991, Felix & Haase 2013, Víkingsson & Heide-Jørgensen 2013). There is also evidence that parts of Antarctic as well as dwarf minke whale populations may stay in polar waters year-round (Acevedo et al. 2010, ***Chapter***

VI). In ***Chapter V*** of this thesis I confirm seasonal migratory movement of minke whales in the western North Atlantic and an offshore distribution of the species during boreal winter. The identification of the Antarctic minke whale as the source of the mysterious bioduck signal in ***Chapter VI***, confirms the presence of Antarctic minke whales in tropical Australian, as well as Antarctic waters during austral winter (McCauley 2004, Van Opzeeland 2010), adding further support to the idea, that not all individuals of a given population undertake yearly migrations.

Due to large-scale exploitation by whaling, several baleen whale populations are among the most critically endangered marine mammals in the world today (Baker & Clapham 2004). Due to its small size and fast movements, minke whales became a target of industrial whaling operations only after the demise of the larger whale species in the early 1970ies (Horwood 1990). Today, commercial and scientific whaling for this species still continues in the North Pacific, North Atlantic and in Antarctic waters. In the North Atlantic, common minke whales are currently listed as a species of least concern under the IUCN Red List (Reilly et al. 2008a). Latest 'best' estimates by the International Whaling Commission (IWC) for the eastern North Atlantic are 81,000; 40,000 for the Central Atlantic and 17,000 for West Greenland (www.iwcoffice.org, accessed October 1st, 2013). Current estimates for the North American east coast are 8,987 (CV=0.32) individuals (Waring et al. 2007). Anderwald et al. (2011) suggest that there may be two separate breeding populations in the North Atlantic. However to date, no breeding grounds have been identified. In ***Chapter V*** of this thesis I show how acoustics may help to identify important winter habitat for this species, where more directed genetic sampling may be possible in the future to resolve this important question with respect to minke whale population structure in the North Atlantic.

While abundance of minke whales in the eastern North Pacific has only been assessed for parts of the US coast (Reilly et al. 2008a), in the western

North Pacific at least two sub-populations are currently distinguished. While the sub-population, called 'J-stock' inhabits the Yellow Sea, East China Sea and the Sea of Japan, 'O-stock' inhabits more offshore waters of the Northwest Pacific and the Okhotsk Sea (Kato 1992). There has been concern and debate within the IWC about the status of 'J-stock', which next to being targeted by whaling operations, is also by-caught in fishing gear in considerable numbers (>200/year; Reilly et al. 2008a). The Convention on International Trade in Endangered Species (CITES) currently lists all common minke whale populations under Appendix I (threatened with extinction), with the exception of the West Greenland stock, which is listed under Appendix II (not currently threatened but trade needs to be strictly regulated).

Antarctic minke whales are listed as data deficient under the IUCN Red list and under Appendix I of CITES (Reilly et al. 2008b). There are currently no agreed upon abundance estimates for this species. While it has been suggested, that the species increased in population size after the decline of other large whales species due to extensive whaling operations in the Southern Ocean (Mori & Butterworth 2006), this claim has been discounted based on genetic analyses showing that current numbers are at or below hypothesized historical population sizes (Ruegg et al. 2010). In addition, the most recent circumpolar population surveys suggested a dramatic decline of the species (Branch & Butterworth 2001). However, the reasons for and the extent of this apparent downward shift in abundance are a subject of considerable debate within the IWC. The abundance of the dwarf form of the minke whale in the Southern Ocean has not been assessed to date since most sighting surveys do not distinguish it from the Antarctic minke whale at sea (Reilly et al. 2008a).

In addition to direct hunts, minke whales in all oceans are subject to indirect takes in fisheries (Benjamins et al. 2011) and exposed to a variety of other threats, including ship-strike, chemical and noise pollution, as well as degradation and loss of habitat (Halpern et al. 2008, Davidson et al. 2012).

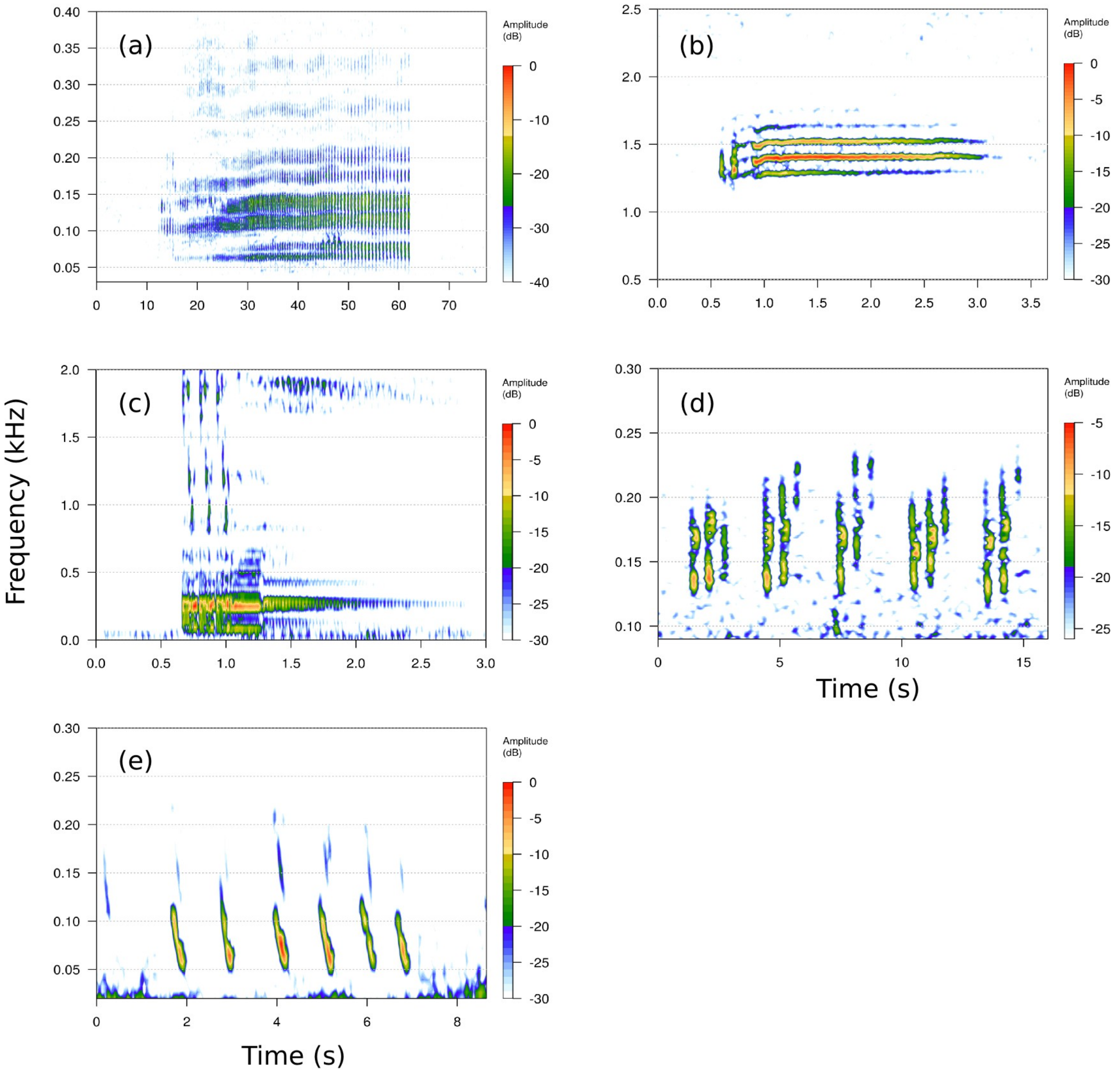

Figure 8. Spectrograms of known minke whale vocalizations from different ocean basins. (a) North Atlantic slow-down pulse trains, (b) North Pacific boing vocalization, (c) Australian dwarf minke whale 'star wars' vocalization, (d) Antactic bioduck, (e) Antarctic downsweeps.Note different time and frequency scales. Spectrogram parameters: (a) Fast Fourier Transform (FFT) = 1024 pt, overlap (ovlp) = 75%, samplerate (SR) = 2000 Hz: frequency resolution (FR) = 1.9 Hz, time resolution (TR) = 128 ms; (b) FFT = 512 pt, ovlp = 75%, SR = 8000 Hz: FR = 15.6 Hz, TR = 16 ms; (c) FFT = 512 pt, ovlp = 75%, SR = 16,000 Hz: FR = 31.5 Hz, TR = 8 ms; (d) FFT = 1024 pt, ovlp = 75%, SR = 4000 Hz: FR = 3.9 Hz, TR = 64 ms; (e) FFT = 4096 pt, ovlp = 75%, SR = 25,811 Hz: FR = 6.3 Hz, TR = 39 ms.

3 Acoustic behaviour of minke whales

Although their acoustic behavior has little been studied, minke whales are known to produce a variety of sounds across their geographic range. For example, low-frequency downsweeps, higher frequency clicks and a variety of other sounds have been reported from the Antarctic (Schevill & Watkins 1972, Leatherwood et al. 1981). More recently, Rankin & Barlow (2005) attributed the North Pacific 'boing' sounds to this species and Gedamke et al. (2001) described the distinct 'star wars' vocalization, produced by Australian dwarf minke whales (Figure 8). In the North Atlantic, Beamish & Mitchell (1973) attributed series of clicks in the 5-6 kHz range to this species and Edds-Walton (2000) recorded frequency-modulated downsweeps (118-80 Hz) in the Gulf of St Lawrence, Canada. Finally, in the Caribbean, Winn & Perkins (1976) and Mellinger et al. (2000) recorded low-frequency pulse trains with varying Inter-pulse interval (IPI) structure. The distribution of these different types of signals in different habitats and their functional significance in the minke whale acoustic ecology is largely unknown. This lack of knowledge of basic parameters of the minke whale vocal behavior inspired the idea to focus a large part of this thesis on the investigation of minke whale vocalizations. For example, in ***Chapters III and V*** of this thesis I explore seasonal and diel distribution patterns of North Atlantic minke whale pulse trains (Figure 8 a) and suggest, that they may serve as a male reproductive signal. This hypothesis is based on their increased occurrence at winter breeding grounds and absence from some female dominated northern feeding areas (***Chapter V***). However, more research is needed to conclusively confirm this hypothesis. In ***Chapter IV*** I show, that individual North Atlantic minke whales combine different types of pulse trains in non-random ways, but again the behavioral significance of these call sequences and whether they are produced in different habitat areas is unknown. Although some sounds of the Antarctic minke whale have been described since the 1970ies, it has long been hypothesized, that the mysterious 'bioduck signal', which has been recorded in the Southern Ocean for decades, may be produced by this species also. In ***Chapter VI*** I analyzed the first acoustic tag recordings from Antarctic minke whales and show the production of low-frequency downsweeps (Figure 8 e), as well as the bioduck signal by this species (Figure 8 d).

Increasing ocean noise: impacts on marine mammals

1 Sources of anthropogenic noise

Over the last decade anthropogenic ocean noise and its impacts on marine mammals have received increased awareness from scientists, conservationists and the general public alike. As outlined at the beginning of this Introduction, sound is the main modality with which marine mammals communicate, socialize, navigate, as well as find and handle prey. Sources of anthropogenic noise or the *anthrophony* of the marine soundscape are numerous and include underwater explosion (Finneran et al. 2000), construction and pile driving (Madsen et al. 2006), acoustic deterrent devices (Morton & Symonds 2002), scientific and military sonar systems (Frantzis 1998, Frankel & Clark 2000, Risch et al. 2012: ***Chapter VII***), as well as seismic airguns used in probing for oil and gas (Di Iorio & Clark 2010) and shipping (Hatch et al. 2008). Although the effects of noise on marine mammals have been recognized for over 40 years, concerns have been publicized more widely with the events of several mass strandings of marine mammals in relation to low-, and mid-frequency Navy sonar operations over the past 20 years (Frantzis 1998, Cox et al. 2006). These acute events with often lethal outcome have spurred a lot of research on the risks, extent and mechanisms behind anthropogenic noise pollution (Melcón et al. 2012, DeRuiter et al. 2013, Goldbogen et al. 2013).

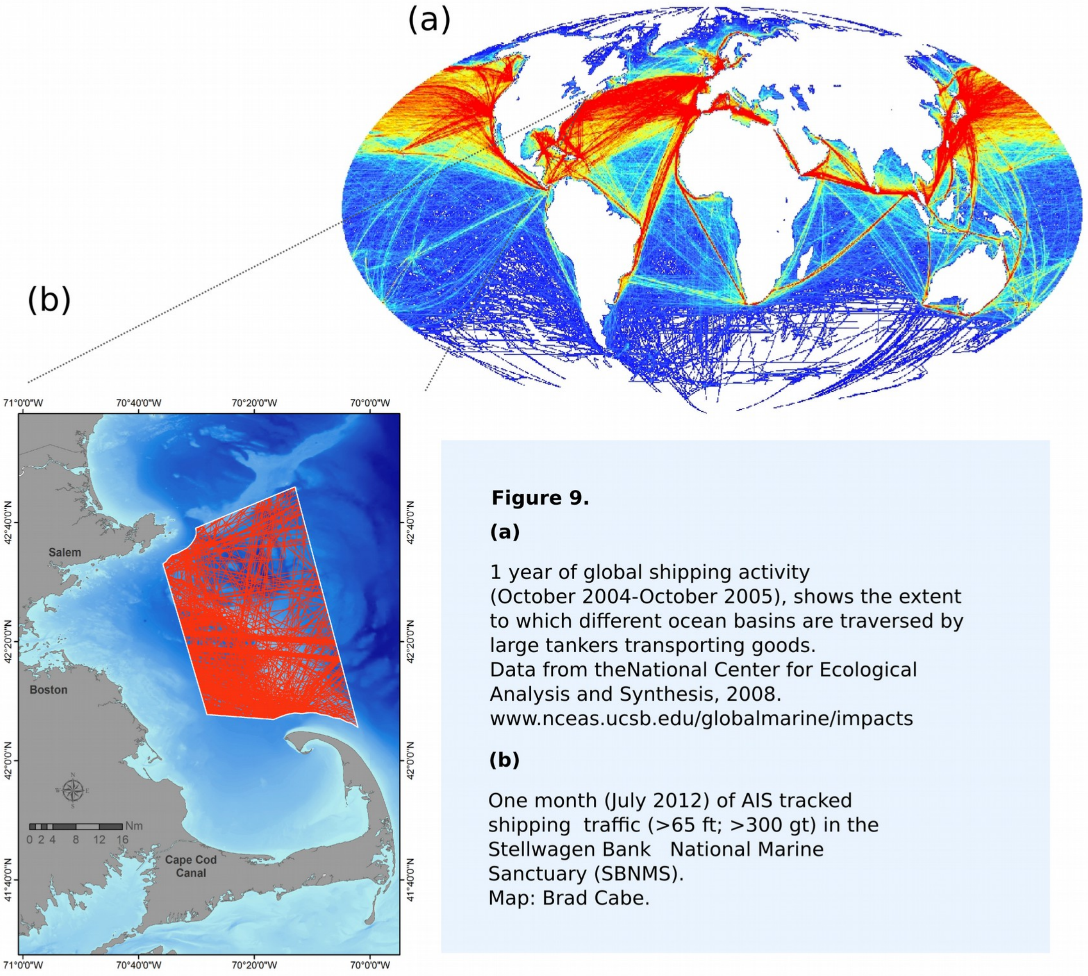

Figure 9.

(a)

1 year of global shipping activity (October 2004-October 2005), shows the extent to which different ocean basins are traversed by large tankers transporting goods.
Data from theNational Center for Ecological Analysis and Synthesis, 2008.
www.nceas.ucsb.edu/globalmarine/impacts

(b)

One month (July 2012) of AIS tracked shipping traffic (>65 ft; >300 gt) in the Stellwagen Bank National Marine Sanctuary (SBNMS).
Map: Brad Cabe.

Impacts of other acute sources such as seismic airgun surveys have also been assessed (DeRuiter et al. 2006, Castellote et al. 2012, Heide-Jørgensen et al. 2013). In some areas noise from seismic surveys has become so prolific however, that it can be considered a chronic noise source, adding to other ubiquitous, low-frequency noise sources such as global shipping. With most attention focused on describing and managing acute sources of noise, only recently have chronic sources of noise and their large-scale impact on the marine environment started to be considered, but to date these have hardly been incorporated into management frameworks (Ellison et al. 2011). With increasing numbers and size of commercial ships and tankers (Figure 9 a) and associated radiated noise, measurements in the North Pacific have shown, that low-frequency background noise has approximately doubled in each of the past four decades (Andrew et al. 2002, 2011, McDonald et al. 2006). In highly trafficked and developed coastal areas, that overlap with feeding areas and/or migration routes of endangered marine mammals the problem of chronic noise pollution is of particular concern. The Stellwagen Bank National Marine Sanctuary (SBNMS) is located just outside the busy port of Boston, Massachusettes, USA. Figure 9 b illustrates, the intensity of commercial shipping tracked by the US Coastguard's Automatic Identification System (AIS), criss-crossing this urban sanctuary every month. Shipping noise in SBNMS has been quantified to be at levels of high concern to marine mammals residing in these waters (Hatch et al. 2008). This concern initiated a long-term ocean noise project to determine the contribution of shipping traffic to the overall noise budget of the sanctuary and estimate the effects of such chronic noise exposure on marine mammals in terms of communication masking (Clark et al. 2009, Hatch et al. 2012). Most of the data analyzed in this thesis has been collected as part of this larger ocean noise project and the identification and characterization of seasonal and diel distribution patterns of marine mammals in this area (***Chapters II, III***) is an integral part towards the larger goals of this project.

2 Overview of impacts of noise on marine mammals

Anthropogenic noise can affect marine mammals in many different ways. Possible effects include lethal injuries, short-, or long-term hearing damage, and the disruption of normal behavior, including feeding, mating and communication (Southall et al. 2007, Nowacek et al. 2007). Disruption of communication behavior may include signal modifications, for example changes to signal duration, frequency or amplitude (Foote et al. 2004, Parks et al. 2007, Parks et al. 2011b), as well as changes in signal usage, repetition, or the cessation of signaling (Rendell & Gordon 1999, McCarthy et al. 2011). Changes in communication behavior have been demonstrated across several baleen whale species and in response to various noise sources (Croll et al. 2001, Di Iorio & Clark 2010). Traditionally, effects of noise have been assessed based on the 'zones of impact' concept (Richardson et al. 1995). This concept describes the severity of noise exposure effects as concentric regions around a noise

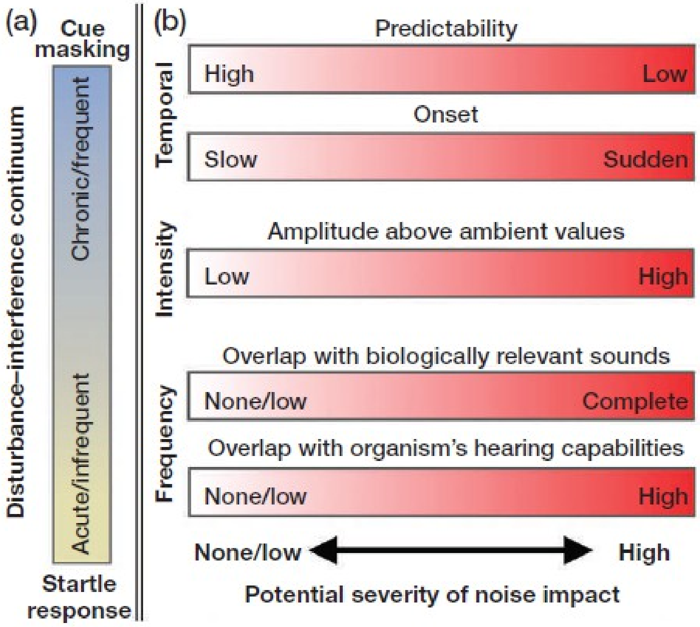

Figure 10. (a) Disturbance can range from acute to chronic with a range of responses from startle response to masking. (b) the severity of a noise impact is not just dependent on amplitude, but also depends on the temporal and frequency features of the stimulus. Figure reprinted from (Francis & Barber 2013).

source with effects diminishing with increasing spatial distance from the source. While this concept may help to visualize impacts of acute noise exposure, it fails to address questions of cumulative impact of ubiquitous chronic noise without a single source. In addition, this rather simplistic model is focusing entirely on the amplitude of a sound source, ignoring many other important factors, such as temporal predictability and persistence, behavioral context, novelty of a sound or frequency overlap with biologically important signals (Figure 10, Ellison et al. 2011, Francis & Barber 2013). In ***Chapter VII*** of this thesis I show the reduction of humpback whale song in response to a new kind of active fisheries sonar roughly 200 km distant. Although received levels in our recording area were just above background noise, whales changed their vocal behavior in response to this new stimulus, which showed similar time and frequency characteristics to their own signals. This study thus emphasizes the importance to consider other factors than just absolute received levels when studying noise impacts, since taking these into account, may reveal potentially important impacts that otherwise would be missed. New frameworks to assess and manage anthropogenic noise based on these more holistic approaches have recently been suggested for terrestrial as well as marine environments (Ellison et al. 2011, Francis & Barber 2013). In addition, the importance of considering chronic impacts of anthropogenic noise, such as the long-term effects of baleen whale vocalization masking (Figure 11) for example by shipping noise, is increasingly being recognized (Southall 2005, Hatch et al. 2008, Clark et al. 2009). Acoustic masking may act in a range of different ways, including the reduction of communication space, and the space over which important prey can be detected, as well as increasing annoyance levels and inducing anxiety and stress (Rolland et al. 2012). These responses to noise that are not always obvious or direct and easily measurable, may nonetheless carry severe direct or indirect costs to an animal's fitness, with possible subsequent population level effects (Wright et al. 2007, Francis & Barber 2013).

In conclusion, there is a clear need to better characterize anthropogenic noise sources, both as single sources, as well as with respect to their cumulative and spatio-temporal variability in the marine environment. This is underlined by recent efforts led by the National Oceanographic and Atmospheric Administration (NOAA) of the US, to quantify ocean noise budgets and map large-scale distributions of potentially impacted species and population (www.cetsound.noaa.gov). In addition, future research on the impact of anthropogenic noise on marine mammals needs to be placed in a more holistic framework, considering not only acute and highly visible impacts such as injury or habitat abandonment, but also lower level and longer-term effects, such as vocalization masking and health effects in relation to stress and chronic exposure.

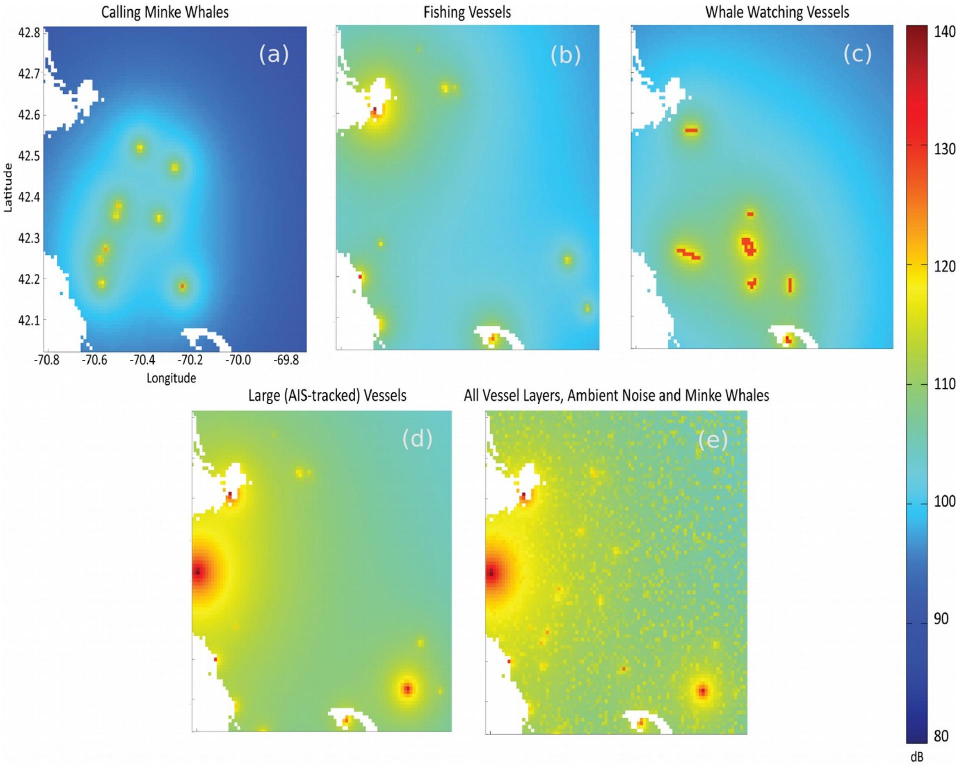

Figure 11. Acoustic footprints produced by (a) calling minke whales, (b) fishing, (c) whale watching vessels and (d) large tankers during one week in fall 2009 in the Stellwagen Bank National Marine Sanctuary. Panel (e) shows the combined footprint of minke whale calls, vessels and ambient noise, giving a snap shot illustration of the extent to which minke whale calls are masked by each of the contributing noise layers.

Thesis aims & outline

This thesis aims to achieve a better understanding of aspects of the acoustic ecology of baleen whales, in order to improve the feasibility of using passive acoustic monitoring to obtain data on their seasonal distribution and abundance. Such data is of major importance for conservation and management of these far ranging species, that are difficult to survey with other means. In addition, acoustic monitoring can also help to investigate impacts of increasing anthropogenic noise pollution, a topic of vital importance for marine mammals, which use sound as their main sensory modality. As part of a larger project aimed at characterizing the marine acoustic environment and the health of an urbanized, yet ecologically important marine region, the Stellwagen Bank National Marine Sanctuary (SBNMS), this thesis uses passive acoustic array data to investigate baleen whale acoustic ecology in this region and beyond, with a particular focus on the acoustic behavior of minke whales.

Chapter I

In order to use passive acoustic monitoring for marine mammals effectively, several parameters about a species' vocal behavior need to be known. In this first chapter we investigated new methodologies for using stationary and towed passive acoustic array data to address questions of animal abundance, behavior and occurrence. In particular, we show how passive acoustic arrays can be used to localize animals in 2D and 3D and how this data can be used to improve knowledge on call source levels, rates, depths and detectability as derived from these parameters.

Chapter II

In this chapter I used a multi-species detection approach to investigate the low-frequency component of the seasonally changing biotic component of the Stellwagen Bank National Marine Sanctuary (SBNMS) noise budget. I investigated the stability of seasonal patterns of blue, fin, sei and right whale vocalizations in

SBNMS across 3.5 years to evaluate the importance of this area as a migratory pathway and/or seasonal feeding ground for these four species. This manuscript is in an early phase of preparation and further analyses will involve the evaluation of diel patterns for all species. In addition, seasonal and diel patterns as assessed with the automated detector, will be compared to the experimental application of acoustic diversity indexes, in order to evaluate the usefulness of such new measures for assessing temporal changes in species diversity of a marine soundscape.

Chapter III-V

Little is known about the vocal behavior of North Atlantic minke whales. In chapters III & IV I used passive acoustic recordings from Massachusetts Bay to identify and describe different types of minke whale pulse trains, evaluate their relative occurrence and explore seasonal and diel patterns using an automated detector. In addition, minke whales were acoustically tracked, in order to estimate movement parameters, source levels and individual calling rates. Acoustic tracking data was used further to investigate repertoire usage and call type combinations on the level of the individual. In chapter V I use year-long recordings from different sites from across the North Atlantic Ocean to explore possible migration routes and winter distribution of minke whales based on their acoustic presence. In addition, I explored geographic differences in signal structure and diel patterns for the Northwest Atlantic Ocean.

Chapter VI

For decades, the regular pulsed 'bioduck' signal (Matthews et al. 2004) has been recorded in the Southern Ocean, but the animal producing this mysterious sound has remained unknown. In this chapter I analyzed data from the first multi-sensor acoustic tags attached to Antarctic minke whales (*Balaenoptera bonaerensis*), to explore the possibility that this species is the source of the bioduck signal, as has long been suggested.

Chapter VII

In fall 2006 acoustic recorders deployed in the Stellwagen Bank National Marine Sanctuary (SBNMS) low-frequency pulses produced by an Ocean Acoustic Waveguide Remote Sensing (OAWRS) experiment, roughly 200 km distant on Georges Bank during an experiment to image herring shoals over ecosystem scales (Makris et al. 2006). In this chapter we investigated the effect of OAWRS signals on the occurrence of humpback whale song recorded in SBNMS at the time of the Georges Bank experiment. In addition to the 2006 data, we collected recordings from approximately the same place, and at the same time, in 2008 and 2009, two years when an OAWRS experiment was not conducted. Thus, despite having what was initially observational data, we configured a design that allowed us to make planned comparisons from our data.

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PART A

Passive acoustic monitoring of baleen whales

Chapter I

Cholewiak D, **Risch D**, Valtierra R & Van Parijs SM (2013) Methods for passive acoustic tracking of marine mammals: estimating calling rates, depths and detection probability for density estimation. Chapter 6 – In: *Detection, Classification and Localization of Marine Mammals using passive acoustics.* (Adam O. & Samaran F. ed.), p. 107–145.

Marine Acoustic Recording Unit (MARU) floating at the surface after recovery.

CHAPTER 6

Methods for passive acoustic tracking of marine mammals: estimating calling rates, depths and detection probability for density estimation

Danielle CHOLEWIAK, Denise RISCH,
Robert VALTIERRA, and Sofie M. VAN PARIJS

1. Introduction

Anthropogenic activities and their impacts on marine ecosystems are steadily becoming an issue of global concern. From fisheries interactions to pollution, shipping and habitat degradation, human activities are driving ecosystem changes and are increasingly threatening the existence of numerous marine species (Davidson *et al*., 2012; Halpern *et al*., 2007; Kappel, 2005; Read, 2008). For scientists working within a management framework, effective and efficient means for assessing species distribution, abundance and their risk of impact by anthropogenic threats is of critical importance. Government agencies, such as the National Oceanic and Atmospheric Administration (NOAA) in the U.S., include within their mission the conservation, protection and recovery of marine species. This incorporates the evaluation of marine mammal abundance and occurrence, assessing the effects of sound on acoustic communication, hearing and behavior, monitoring interactions with fisheries, and evaluating the risk of vessel interactions (i.e. ship strikes).

Passive acoustic approaches for studying marine animal populations have expanded substantially in both depth and breadth over the past decade. Advances in hardware and software are now mature enough to allow data collection in remote areas as well as for species that are difficult to access using conventional approaches. More recently, new theoretical methodologies applied to acoustic data provide insightful ways of approaching large-scale ecological questions. These range from approaches that demonstrate the use of acoustic indices for monitoring biodiversity and species richness, to modeling (Clark *et al*., 2009) and measuring the effects of anthropogenic activities on marine animals. In this light, the use of passive acoustic methodologies to describe animal distribution, abundance and behavior are increasingly being recognized as a tool not only for basic research, but with clear applications for monitoring and mitigation to inform management and conservation strategies.

For management and research focused on cetaceans, surveys have traditionally been conducted visually, from either vessel or aerial platforms. However, it is recognized that these methodologies are affected by limitations in sighting conditions, particularly daylight and weather, as well as the amount of time the animals spend at the surface (i.e. 'sighting bias') (Clark *et al*., 2010). Recent passive acoustic studies have shown the extended occurrence and persistence of species beyond seasons and regions where they were previously documented through visual surveys (Morano *et al*., 2012; Mussoline *et al*., 2012; Vu *et al*., 2012). Therefore, it is becoming evident that whenever passive acoustic monitoring is applied to a region, the results show greater occurrence and persistence of species compared with visual survey data. These studies clearly demonstrate the fact that we are currently not collecting data in a way that fully describes the actual distribution, occurrence and abundance of marine mammals.

To enable managers and regulators to use passive acoustic monitoring effectively, either alone or in combination with visual surveys, several levels of acoustic information are needed. Characterization of species-specific call features in different contexts are necessary for baseline monitoring of seasonal and spatial species occurrence. Additionally, information on animal depth is important, as both the range over which vocalizations are detected, and the impacts to animals from anthropogenic activities may be heavily dependent on their location within the water column (Stafford *et al*., 2007; Thode, 2005; Vaage and Ursin, 1987).

Although still a young field, developments in statistical methodologies are enabling the incorporation of acoustic data into models to calculate animal density and abundance (Dawson and Efford, 2009; Efford *et al*., 2009). Marques *et al*. (2012) summarize the significant advances that are currently being made in the field of density estimation from passive acoustics. Their review highlights the essential need for baseline data on vocalization rates and group sizes in different behavioral contexts, by sex and age class, as well as the importance of collecting these data on different seasonal and spatial scales. These data are extremely scarce for most species. While the increasing availability of technologies such as digital recording tags has allowed for expanded studies that can provide information on individual calling rates, depth and underwater behavior (Baird *et al*., 2006; Oleson, Calambokidis, Burgess, *et al*., 2007; Parks *et al*., 2011; Wiley *et al*., 2011), the use of this technology is often constrained by cost, feasibility and effort needed to obtain adequate sample sizes. However, with the proliferation of fixed and towed hydrophone data, and new techniques for two- and three-dimensional localization and acoustic tracking, we have the opportunity to collect information that addresses these existing data gaps.

At NOAA's Northeast Fisheries Science Center, the Passive Acoustic Research Group is primarily working on collecting acoustic data in the western North Atlantic Ocean using a variety of fixed and mobile platforms. This work is focused on the acoustic ecology of marine mammals. We are part of a larger network of scientists conducting acoustic research throughout NOAA. Across the local, regional and federal government levels within the U.S., there is growing recognition that passive acoustic research is a vital component of future management strategies, however direct investment in research and infrastructure from NOAA is still lacking. Our work ties together long-term monitoring of marine species and mitigation of anthropogenic threats. Ultimately, our aim for these data is to improve broader marine management and conservation strategies.

In this chapter we present several pertinent approaches in analyses of passive acoustic data and discuss how they can improve our current modus operandi. We highlight two cases studies or 'applications', using data collected with both a towed array and bottom-mounted recorders. We demonstrate how these data can be used to address questions about animal abundance, behavior and occurrence. In turn, we discuss how this information can be applied to improving marine mammal management approaches for long-term occurrence, stock assessment and ship strike avoidance.

2. Application 1: Using acoustic arrays to create 2-D and 3-D tracks of North Atlantic right whales

Photo credit: Peter Duley / NOAA / NEFSC

Due to past exploitation and continuing pressure as a result of human-caused mortality, such as vessel strikes and entanglements, the North Atlantic right whale (*Eubalaena glacialis*) is one of the most critically endangered baleen whale species worldwide (Kraus *et al*., 2005). Although for the past two decades monitoring and management of this species have relied primarily on visual survey methodologies (Fujiwara and Caswell, 2001; Kraus, 1990) in recent years advances in technology and analysis tools have resulted in a wider appreciation of the use of passive acoustic monitoring (PAM) to augment traditional visual surveys and management frameworks (Van Parijs *et al*., 2009).

Several studies have investigated the vocal behavior of North Atlantic right whales (Mellinger, 2004; Morano *et al*., 2012; Mussoline *et al*., 2012; Vanderlaan *et al*., 2003). The two main call types produced by this species are 'up-calls', which are believed to serve as social contact calls and 'gunshot sounds', used in reproductive advertisement (Parks and Tyack, 2005; Parks *et al*., 2005). A few studies have started to investigate individual right whale vocal behavior to assess acoustic parameters such as calling rate, depth, temporal trends in vocalizations, as well as the frequency of occurrence of different call types. These data have been collected in short-term behavioral studies using a combination of dedicated focal follow approaches and the use of new technologies such as short-term recording tags (Matthews *et al*., 2001; Parks *et al*., 2011b). However, these approaches are generally both costly as well as limited in terms of sample size.

Since vocal behavior can be highly variable as a function of behavioral state, sex and age-class, and can vary by season and region (Van Parijs *et al*., 2009; Parks and Tyack, 2005; Parks *et al*., 2005), it is essential to collect data on right whale acoustic behavior on larger spatial and temporal scales, as well as across more individuals in order to better understand the detectability of right whales for passive acoustic monitoring applications. Longer term data sets collected with passive acoustic arrays and new analysis tools for detection and localization could help to start fill these gaps (Parks *et al*., 2012a). In addition, these data can provide valuable baseline information in relation to ship-strike management and mitigation of other anthropogenic impacts such as noise (Parks *et al*., 2011a, 2012b).

In this case study, we use a one-hour time series of PAM data and apply the 2-D localization method used by Parks *et al*. (2012), to demonstrate its feasibility for analyzing tracks of vocalizing right whales, as well as determine calling rates and other parameters of right whale calling behavior. In addition, we also provide background demonstrating a new method for 3-D localization and apply this technique for depth estimation of calling right whales using a single recording unit.

2.1 Methods

2.1.1 Data collection

Acoustic recordings of North Atlantic right whales were collected using an array of ten bottom-mounted archival recording units (MARUs) (Calupca *et al*., 2000). The array used for this application was placed in the southwest corner of the Stellwagen Bank National Marine Sanctuary (SBNMS) from March 28th to May 27th 2009 (fig. 1). This array forms part of a longer term near continuous data collection effort from 2006 to 2011 throughout SBNMS. For this effort, ten MARUs were placed for 3 month periods in areas with high baleen whale densities (see http://www.nefsc.noaa.gov/psb/acoustics/psbAcousticDeployments.html). SBNMS and Cape Cod Bay are well-known spring feeding habitats for North Atlantic right whales (Mussoline *et al*., 2012; Pendleton *et al*., 2012). Individual MARUs were spaced 3 nautical miles apart and placed in depths ranging from 28 to 82 m. The HTI-94-SSQ hydrophone of each MARU had a sensitivity of -168 dB re 1 V/μPa and was connected to a 23.5 dB preamplifier. The frequency response was flat (±1 dB) over the 10-585 Hz frequency range. MARUs were programmed to record continuously at a sampling rate of 2000 Hz with 12-bit resolution.

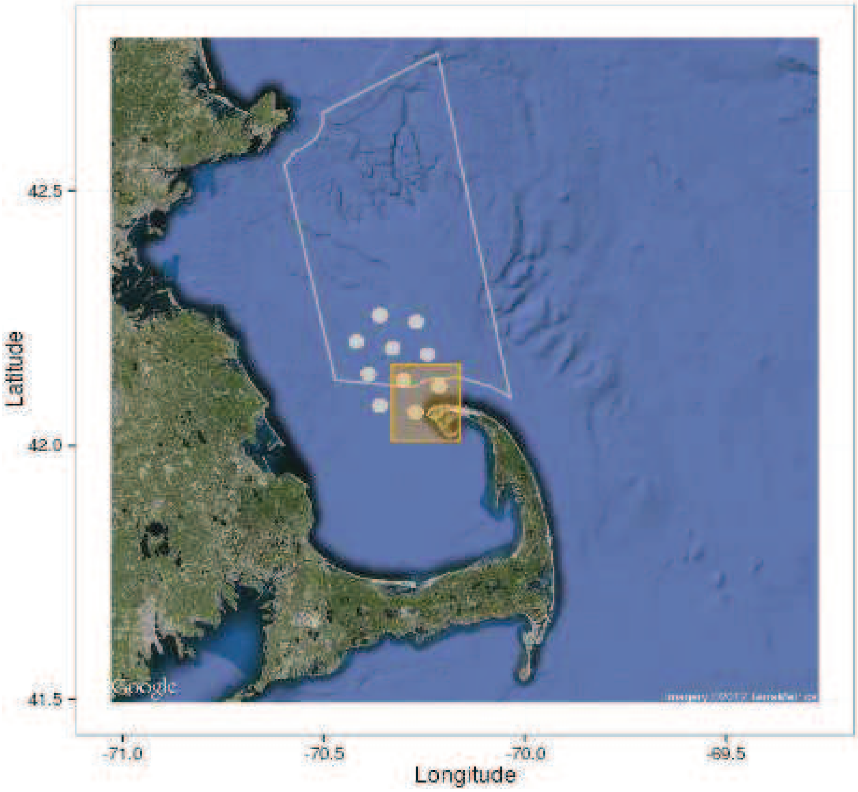


Figure 1: Map of the study region, north of Cape Cod, MA, USA. The white line indicates the Stellwagen Bank National Marine Sanctuary (SBNMS). Dots represent locations of marine autonomous recordings units (MARUs) and the yellow shaded area indicates the subarea plotted in Figure 6.

2.1.2 Two-Dimensional Tracking

For this study, the MARU recordings from the array mentioned above were time-synchronized and compiled into 10-channel data files. The Matlab-based (2010a, The MathWorks, Natick, MA, USA) sound analysis software XBAT (Figueroa and Robbins, 2008) was used for acoustic analysis and spectrogram generation (Hanning window, 1024 pt FFT). Right whale up-calls were detected by visual inspection of spectrograms and listening to sound files. One hour of data was selected for detailed analysis. Selection was based on review of the signal arrival patterns indicating the presence of clear, locatable right whale up-calls (Parks and Tyack, 2005), as well as the close proximity of several vocally active individuals to at least one recording unit. Three individual right whales were tracked for this analysis.

A two-dimensional (x, y) position was computed for each selection using the correlation sum location estimation (CSE) tool developed for XBAT (Cortopassi and Fristrup, 2005). The CSE algorithm calculates the sum of waveform cross-correlation values across all selected channel pairs for a grid of spatial points. The candidate location at which these values are maximized is selected as the most likely location. This method appears to be more robust to background noise than traditional localization methods that are based on hyperbolic fixing and rely on correlation peak picking. Each location was reviewed to ensure that the correct call was selected on all channels and that the estimated location agreed with observed arrival patterns across channels. Incorrect selections or location estimates were eliminated from the localization dataset.

A calibration experiment was conducted to empirically determine the localization error with this array configuration. 47 frequency-modulated tones were played at five known locations and depths within the array. Locations of these events were estimated using the CSE tool and location error in meters was calculated by subtracting the estimated position from the known location of the underwater speaker during transmission. Mean localization error was about 53.2 m (sd 30.8). To reduce the impact of localization error between calls, estimated tracks were smoothed using a moving average (MA) technique. The smoothed location at a specific point in time was calculated by averaging the surrounding five location estimates (Hen *et al*., 2004).

2.1.3 Calling rates

Calling rates were calculated for all three tracked right whales over the hour of analysis. Bouts of calling were separated using the bout criterion interval (BCI), as determined by plotting inter-call intervals (ICIs) on a logarithmic scale (Parks *et al*., 2011b; Slater and Lester, 1981). Mean and standard deviation for ICIs within bouts and inter-bout intervals (IBIs) were estimated based on the BCI.

2.1.4 Three-dimensional tracking and calling depths

Right whale calling depths were estimated with the multipath localization technique Direct-Reflected Time Difference of Arrival (DRTD). This method uses the direct path of an acoustic signal along with a varying combination of surface and/or bottom reflections (referred to multipath 'orders') of the signal to localize an animal (fig. 2). This method can be applied to multiple MARUs to resolve a three-dimensional source location, or to a single unit to resolve a two-dimensional (depth and radius) solution. In the case where MARUs are widely spaced, full three-dimensional localization with DRTD will not likely be possible due to radial limitations (see Results section below). However, three-dimensional localization can still be resolved when using DRTD as a supplement to TDOA, by applying TDOA to resolve 'in-plane' (x, y) localization, and DRTD for depth estimation. Solutions for the two methods can also be verified through comparison of the two estimated radial distances (using TDOA and DRTD) from the MARU channel to verify agreement.

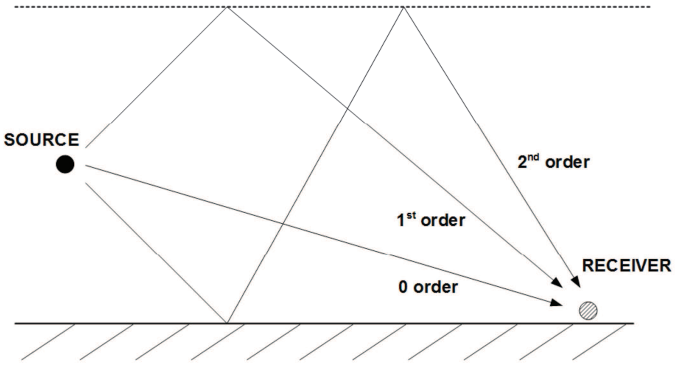
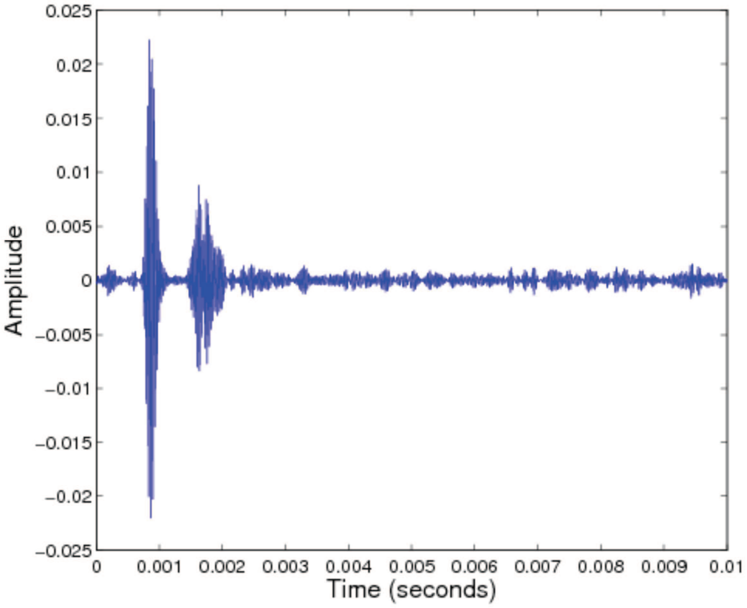


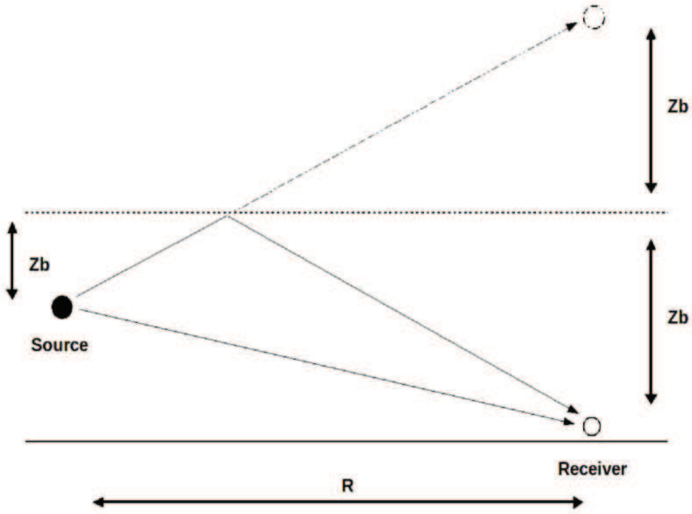
Figure 2: A diagram illustrating the multipath sound propagation from a source to the receiver (a bottom-mounted MARU).

2.1.4.1 Brief Background of the DRTD methodology

DRTD is a ray-based localization method, meaning that all signal paths are assumed to be straight line paths with the direction only changing as a result of either ocean surface or bottom reflections. Any effects due to sound stratification have been assumed to be negligible due to the relatively short path lengths and shallow depths of the sound channel in which the MARUs were placed. With DTRD, the time difference of arrival between the initially received 'direct-arrival' and a reflection of the signal are used to calculate the difference in path length between the two signals (fig. 3). By knowing the depth of the MARU and the time difference of arrival between the direct and reflected signal, a series of possible solutions for the source depth and radial distance from the MARU may be calculated.



(a)



(b)

Figure 3: (a) A time series with a pulsed signal and it's multipath surface reflection with a direct-reflected time difference of approximately 1ms. (b) Application of Lloyd's mirror to determine path lengths.

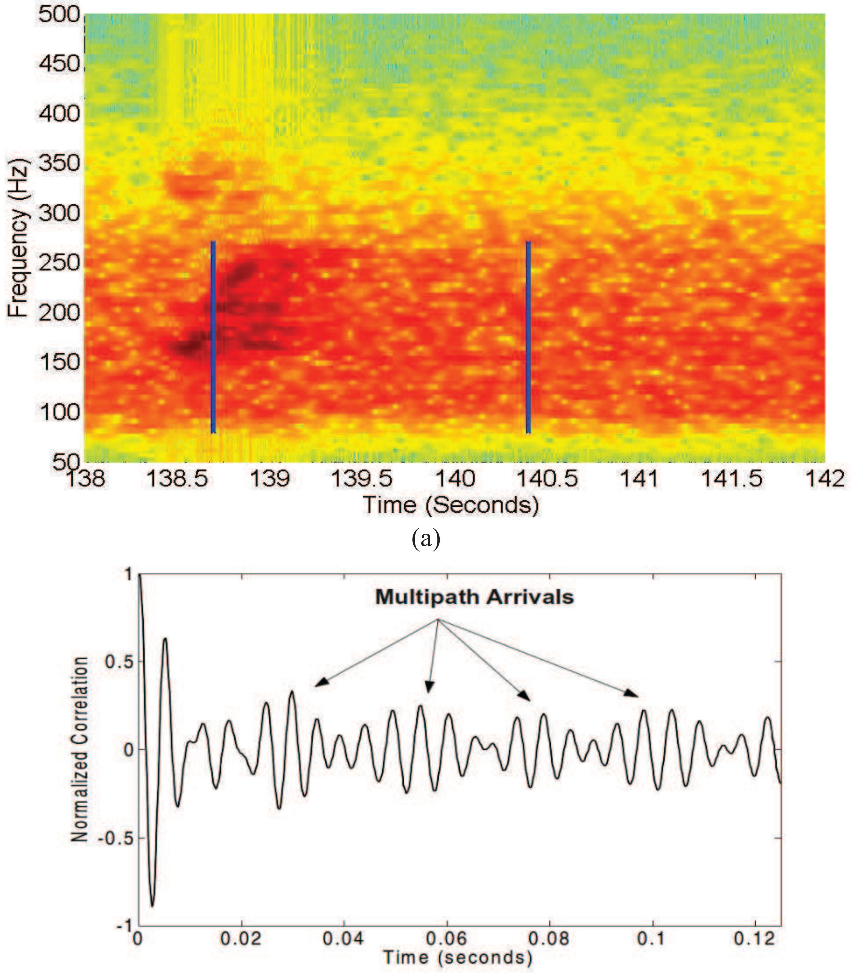
2.1.4.2 Application of the Autocorrelation method

Multipath time differences can vary from fractions of a millisecond to hundreds of milliseconds or more. Based on the depths of our study area (<100 m), measured time differences will be at most tens of milliseconds. Therefore, this creates a problem when attempting to apply standard multipath localization to a right whale: given signal periods of approximately one second for up-calls and the short time differences between multipath arrivals, overlap in the signals will make the task of distinguishing them very difficult.

This problem may be addressed through the application of an autocorrelation method, which takes advantage of the assumption that reflected signals are images of the direct signal and that the frequency is changing with time (like a reflected up-call)(Valtierra *et. al*., 2013). Using this method, knowledge of amplitude and phase is arbitrary and only the time-series of the direct-reflected signal is necessary for analysis. When the target signal is cross-correlated with itself, the time delay between multipath arrivals will be indicated by a series of local correlation peaks. The process is as follows: initially, an up-call is selected and windowed for autocorrelation (fig. 4a). The window is selected to include the most 'linear' part of the signal while leaving 'buffer' space beyond the signal. An autocorrelation is applied, and the time lag at which each correlation peak occurs corresponds to the time difference of arrival between the direct and reflected signal arrivals (fig. 4b).

2.1.4.3 Application of the forward method

In the application of DRTD, there are two unknowns: depth and radius. For a single direct-reflected time difference, there are several depth and radius combinations for the source that will result in the same time difference of arrival. This ambiguity can be overcome when there are several multipaths. By resolving several time differences between the direct arrival and a number of multipaths, several solution sets for depth and radius may be calculated, and successful localization is achieved if the solution sets converge at one unique point. This method can be called the 'forward method' because it directly uses the time difference measurements to calculate a set of location solutions. However, this method can be computationally intensive especially when using more than two solution sets for localization. A simpler approach may be taken through application of the 'backward method' coupled with a probability surface.



(a)

(b)

Figure 4: (a) A spectrogram of a windowed right whale up-call for autocorrelation analysis. FFT: 512 pts, bandpass filter 100-250 Hz. (b) Autocorrelation results of the up-call showing peaks corresponding to multipath arrivals.

2.1.4.4 Application of the backward method and probability surfaces

Unlike the forward method, where measured time differences are used to calculate a solution set of possible depth and radius pairs, the backward method considers every possible depth and radius within a defined space and resolution. This essentially works by the creation of a two-dimensional grid containing discrete points that correspond to possible source depths and radial distances. The simplicity lies in the comparison of the processed solution sets; where the forward method requires a multi-step algorithm capable of quickly sifting through multiple solution sets looking for a convergence point is computationally intensive, the backward method only requires the summation of probability surfaces and finding the point of highest probability of solution convergence.

In defining a solution space, the maximum depth may be determined by the depth of the recorder, and the radial distance and grid point spacings are determined by the practical limits relative to the minimum resolvable TDOA (see results below). The direct and multipath distances of each order to the MARU for all grid points may be calculated allowing for the time difference of arrival to be resolved by taking the difference in path lengths divided by the speed of sound. These results in a specific time difference of arrival assigned to each grid point for each multipath order. Using the geometric method, equations for the path lengths may be derived.

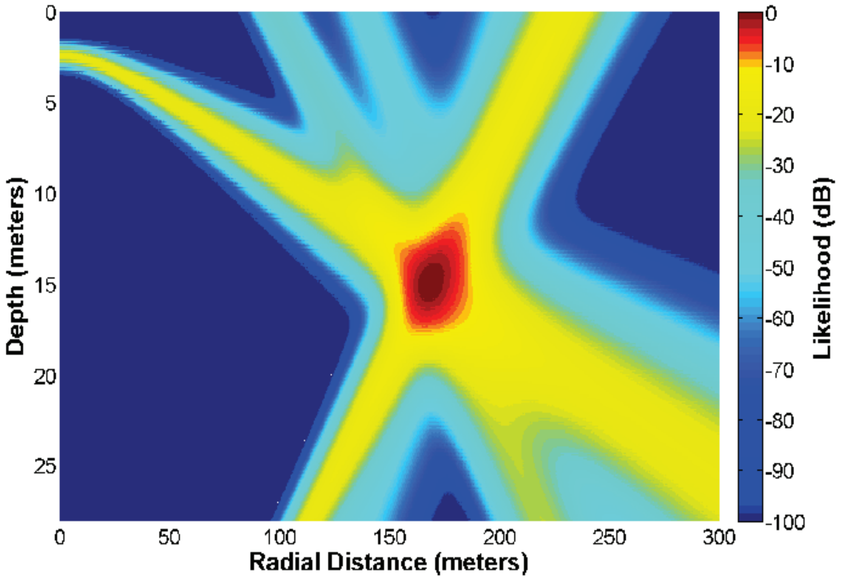


Figure 5: The sum of probability surfaces leads to a convergence at a unique point. This example is taken from the 2-D localization of a synthetic signal transmitted during an empirical calibration experiment. Radial distance refers to the distance from the MARU. (Valtierra *et al.*, in press)

After calculating the corresponding multipath time difference for each grid point, a probability surface may then be created by applying the probability density function (PDF) to each grid point. The PDF is assumed to have normal Gaussian distribution centered at the mean, or best estimate dte_n and standard deviation σ_n. The best estimate is the actual multipath TDOA measured through analysis of signal data recorded by the MARU. Using dte_n and σ_n, the PDF is then iterated over the entire grid using the time difference at each grid point to create a likelihood surface for each multipath order. The resulting likelihood surfaces contain areas of high probability corresponding to grid points where the calculated TDOA is close to the actual TDOA measured in the received acoustic signal (dte_n). The remaining outlying points had a low probability. The likelihood surfaces for every available multipath order are then summed together. Successful localization is achieved when the summed probabilities for all orders converge into a unique area of high likelihood (fig. 5).

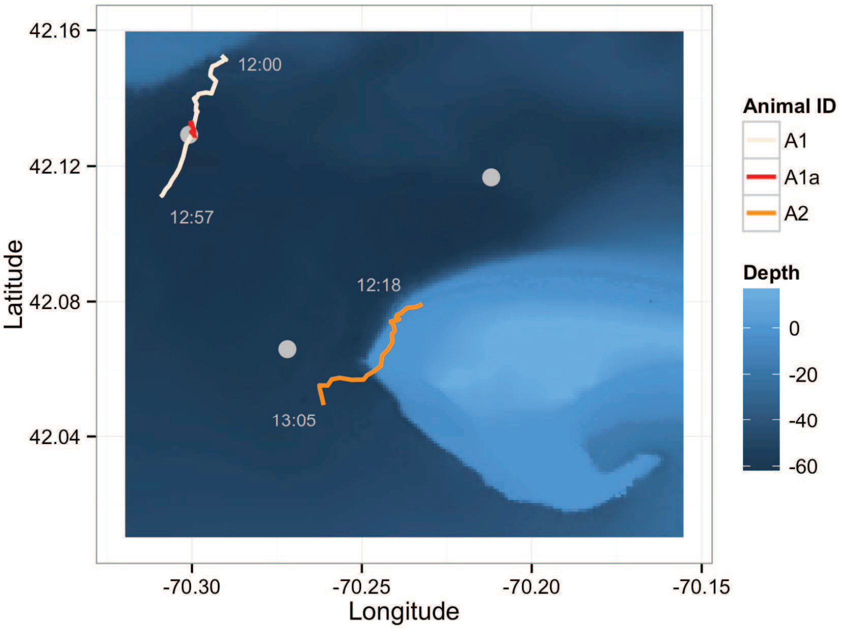


Figure 6: This figure represents a detailed map of the yellow shaded area in Figure 1. The figure shows the smoothed tracks of three North Atlantic right whales tracked using their up-calls during the one hour of analysis. Dots represent the MARUs used for localization and the lines represent tracks of calling animals, colored by Animal ID in the figure legend

2.2 Results and discussion

2.2.1 Two-Dimensional Tracking and Calling Rates

A total of 108 right whale up-calls made by three individual right whales were localized during the one hour time period (fig. 6). Over this period, calling rates averaged approximately one call per minute with inter-call intervals of 30 seconds (tab. 1). The bout criterion interval (BCI) determined from this analysis was 100 seconds and agreed with previously published values (Parks and Tyack, 2005; Parks *et al*., 2011b). Inter-bout intervals were approximately four minutes on average (tab 1).

Table 1: Estimates of North Atlantic right whale up-calling rates for each of the acoustically tracked individual whales (A1,A1a,A2) observed during the one hour analysis. ICI: inter-call interval (time between start times of successive calls from one individual within a calling bout); IBI: inter-bout interval (time between bouts of calling, defined by a bout criterion interval (BCI) of 100 s based on inspection of the log-survivorship curve of ICIs.

Animal ID	N calls	Track dur. (min)	Call rate (calls/min)	Mean ICI (s)	±SD ICI (s)	Mean IBI (min)	±SD IBI (min)
A1	62	60	1.0	18.7	20.8	4.3	2.5
A1a	19	20	1.4	22.9	27.4	4.0	1.9
A2	27	45	0.4	54.2	21.9	4.9	2.2
Mean **±SD**	**36** **±22.9**	**41.7** **±20.2**	**0.9** **±0.4**	**31.9** **±19.4**	**23.4** **±3.5**	**4.4** **±0.5**	**2.2** **±0.3**

2.2.2 Three-Dimensional Tracking and Calling Depths

Calling depths were estimated using the DRTD method and data from one bottom-mounted MARU for one of the three tracked right whales of the presented case study. The radial distance between right whale A1a and the closest MARU ranged from 100 to 500 m (fig. 6). Using 10 of 19 available calls, depth estimates for this individual whale ranged from 21 to 40 meters (fig. 7).

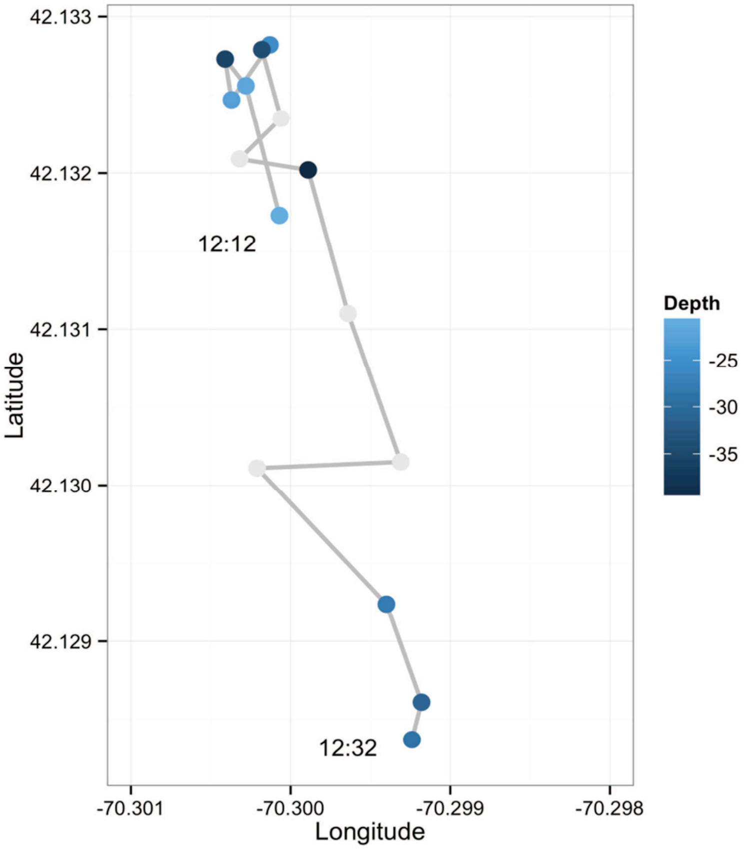


Figure 7: Detailed map of tracked North Atlantic right whale A1a, showing calling depth for calls that could be located using the DRTD method.

2.2.3 Limits to DRTD: Prediction of minimum time difference and maximum resolvable radial distance

The ability to apply DRTD to baleen whale vocalizations is inherently limited by the ability to resolve multipath arrivals in the acoustic signal, which is dependent on both source and recorder depth. As the sound source moves farther from the MARU or to very shallow depths, the direct reflected time difference of arrival decreases, and at a certain point the autocorrelation peaks overlap, making individual arrivals difficult to distinguish. This problem has the greatest effect on resolving the first order direct-reflected time difference and has the greatest impact on limiting the range over which this method may be applied. Predicting the minimum resolvable time difference between the direct and reflected signal arrivals can be used to estimate this limit.

The prediction may be made using a model for the autocorrelation solution of a right whale up-call (Valtierra *et al.*, in press). An equation was derived to predict the minimum time difference using call parameters (call length and sweep rate) typical for the animal of interest resulting in the following relationship of $dt_{min} = \pi / (2\beta T)$ where β is the up-call sweep rate (Hz/sec) and T is the call length. Using this method and the mean values for a right whale up-call of $T = 0.99$s and $\beta = 111$Hz/s (Parks and Tyack, 2005), the minimum time difference that can be resolved between the direct and reflected call was found to be 14.3 ms.

Based on the minimum resolvable time difference and the path length geometry, the maximum range under which DRTD may be applied to right whale up-calls may be calculated. Because the time difference of arrival is a function of both calling depth and radius, this maximum range will vary.

The relationship between depth and radius for the current case study is plotted in fig. 8, based on a bottom-mounted MARU depth of 100 m, a sound speed of 1480 m/s, and a time difference of arrival of 14.3 ms. As can be seen from the plot, as the source increases in depth, the maximum radius quickly increases due to the specific geometric nature of the multipaths.

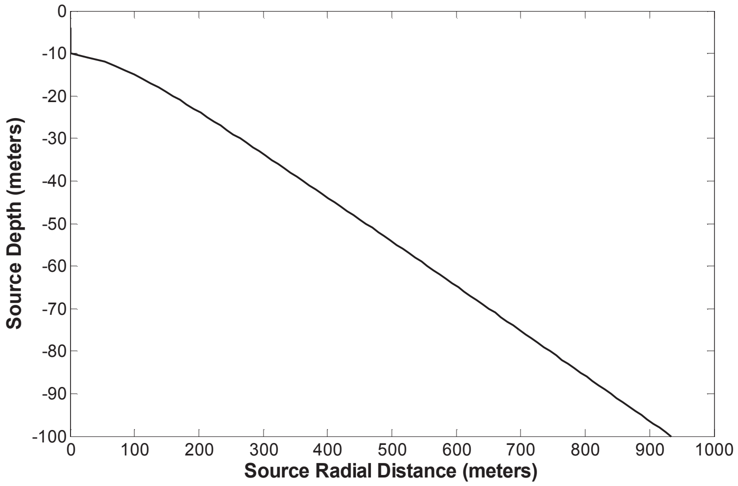


Figure 8: The depth relation for a first order direct-reflected time difference of 14.3 ms, assuming a bottom mounted MARU at a depth of 100 m with a sound speed of 1480 m/s.

Thus, in very shallow water, the application of the DRTD method is most likely impractical unless the source is very close to the MARU. For moderate source depths (greater than 100m) however, this method can localize animals at radial distances approaching one kilometer. Given the scale over which individual units in a fixed array may be placed, this method may be more practical as a supplement rather than a replacement to TDOA. However, when an animal is localized to within the range of DRTD, it is possible to obtain calling depth, using only one MARU. Given the large amounts of available PAM data sets, this method has the potential to significantly increase currently available data on calling depths for right whales and other baleen whale species. Moreover this information can be obtained without the need for improved equipment, and further the method is compatible with currently available and historic data sets.

3. Application 2: Using towed hydrophone arrays for 2-D and 3-D localization of beaked whales

Photo credit: NOAA/NEFSC

Beaked whales are notoriously difficult to detect via visual surveys, due to the fact that they spend long periods of time under water and tend to be relatively inconspicuous when at the surface. Visual detections of beaked whales during broad-scale cetacean surveys may decrease by an order of magnitude as sea state conditions change from Beaufort 1 to Beaufort 5

(Barlow *et al*., 2006), and less than 50% of individuals of some species are detected visually even under excellent sighting conditions (Barlow, 1999). Incorporating passive acoustic methodologies into visual surveys is therefore of critical importance for improving detections of these challenging species.

Little was previously known about the life history and social dynamics of most beaked whale species. However, research over the last decade has started to provide information about the characteristics of the vocalizations for many species. Visual encounters using boat-based surveys, short-term digital recording tags (DTAGs; (Johnson and Tyack, 2003)) (Dawson and Ljungblad, 1998; Gillespie *et al*., 2009; Hooker and Whitehead, 2002; Johnson *et al*., 2004; Rankin and Barlow, 2007; Rankin *et al*., 2011; Zimmer *et al*., 2005), and bottom-mounted recorders (Baumann-Pickering *et al*., 2010, 2012; McDonald *et al*., 2009), have enabled the description of species-specific vocalizations for over ten species. In addition, vocalizations of several species have been recorded from live- stranded or captive animals (Caldwell and Caldwell, 1991; Lynn and Reiss, 1992; Marten, 2000). Taken together, these data are beginning to form a solid foundation for incorporating passive acoustics into the methodologies used to detect and estimate the abundance of beaked whales.

Recently, intensive efforts centered on the occurrence of Blainville's beaked whales (*Mesoplodon densirostris*) in the Bahamas have helped to develop methodologies for density estimation using a combination of visual sightings, dense numbers of bottom-mounted hydrophones on a naval training range and DTAGs (Küsel *et al*., 2011; Marques *et al*., 2009; Moretti *et al*., 2010). However, for most researchers these extensive data acquisition methods are neither available nor practicable. To facilitate the evaluation of density and abundance of beaked whales on a broad scale, methodological approaches need to be married with other more standard data collection mechanisms, including incorporating acoustic data into traditional line-transect surveys.

Marques *et al*. (2012) describe a number of variables that need to be well-defined in order to incorporate acoustic data into density estimation frameworks. These include cue rate, the probability of detection, and detection distance. In the traditional line-transect framework, the observed distribution of sighting distances to animals or groups of animals is modeled to develop a detection function and determine the area for the survey (Buckland *et al*., 2001). For deep-diving animals, however, this presents a complication as the two-dimensional localization obtained through usual means (time difference of arrival or target-motion analysis) actually represents a slant distance to the vocalizing animal, not a perpendicular distance. Errors in measuring the distance to animals will affect the shape and precision of the detection function, which may lead to biases in the resulting abundance estimates or confidence intervals that are too narrow (Borchers *et al*., 2010).

To date this issue has been addressed in only one study on sperm whales (Barlow and Taylor, 2005a). In this case, the depth of the animals was found to have negligible impact on the overall density estimates, as the range of detection (on the order of several to many kilometers) was much greater than the modeled hypothetical depth of 500 m. For beaked whales, however, overall detection ranges are much shorter. For Cuvier's beaked whales, Zimmer *et al*. (2008) found that probably of detection was highest at distances of 700 m or less, with a maximum range of 4 km. For these species, the effect of the animal's depth may therefore have a relatively greater impact on error in 2-D range estimation. For example, consider an animal for which standard two-dimensional acoustic localization provides a (slant) distance of 300 m. If this animal is vocalizing at a depth of 200 m, the actual perpendicular distance to that individual would be 224 m, or 25% less than estimated by 2-D methods alone. Several species of beaked whales are thought to only produce sounds during deep (>200m) foraging dives (Tyack *et al*., 2006), and Yack *et al*. (2011) noted that most bearings obtained during a towed-array survey likely represented slant distances for animals at depth.

For most species we do not yet have the relevant data to assess the depths at which animals are vocally active, but increased application of three-dimensional localization methodologies can be used to address this issue. Several techniques have been established in previous studies, ranging from using more well-known methods like TDOA (Giraudet and Glotin, 2006) to methods which take advantage of multipath signal arrivals such as Direct Reflected Time Difference of Arrival (DRTD; (Nosal and Frazer, 2006; Thode, 2005)). Additionally, DRTD has also been applied to single hydrophone data to resolve depth and radius information even though latitude and longitude information may not be available (Aubauer *et al*., 2000; Mouy *et al*., 2012). In cases where multipath information is not available, modal or “group velocity” methods have been shown to provide a rough estimate for calling depths (Munger *et al*., 2011; Wiggins *et al*., 2004).

Currently, most efforts to estimate the abundance of beaked whales have primarily taken place only during cetacean surveys that were focused on other species (Barlow *et al*., 2006). Because individual species identification is challenging, these abundance estimates often lump several beaked whale species together (Waring *et al*., 2009). However, dedicated surveys in areas of known occurrence such as the Southern California Bight have demonstrated that the incorporation of acoustic methodologies for specific species can significantly improve upon detection rates using conventional visual observations (Yack *et al*., 2011). These results highlight the importance of increasing coordinated visual and acoustic efforts on abundance surveys.

In this application, we utilize data collected on a recent NOAA cetacean line-transect survey to demonstrate the application of analysis techniques for beaked whales. This survey enabled the characterization of the echolocation characteristics of Sowerby's beaked whales (*Mesoplodon bidens*) and improved the application of automated detectors to facilitate two-dimensional tracking. Here, we add to the single species approach discussed above and demonstrate the application of three-dimensional localization techniques to quantify the depths at which several animals were vocalizing.

3.1 Methods

3.1.1 Data Collection

In 2011, one half of the Atlantic Marine Assessment Program for Protected Species (AMAPPS) survey was conducted from the NOAA R/V Bigelow, throughout the western North Atlantic covering approximately 36°N to 42°N (fig. 9). Visual observations and acoustic recordings were collected simultaneously. Information on acoustic detections was not transmitted to visual observers in real-time. Visual sighting data were collected during daylight hours from approximately 06:00-18:00 EDT when sea conditions were less than sea state Beaufort 6, by two teams of trained observers operating from two different decks of the ship. In each team, two observers utilized high-powered "big-eye" binoculars (Fujinon, 25x150) to scan from the bow of the ship to 90° port or starboard, while one observer scanned the track line using hand-held binoculars and naked eye.

Acoustic recordings were collected using a three-element oil-filled hydrophone array (Benthos AQ-4 elements: -201dBV re: 1µPa), towed 300 m behind the ship, at approximately 12 m depth. Acoustic data were routed to a desktop computer via a Magrec HP/27ST monitor box (http://ecologicuk.co.uk, 80 Hz high-pass filter, 30 dB gain) and an external Fireface 400 sound card, with data recorded continuously at a sampling rate of 192 kHz utilizing the software package Pamguard (http://www.pamguard.org). Two-channel data were also routed to a second set of computers via an internal M-Audio soundcard, sampling at 44 kHz, for real-time detection and tracking of vocal animals utilizing the software packages WhalTrak and Ishmael. Survey speed averaged 10 knots.

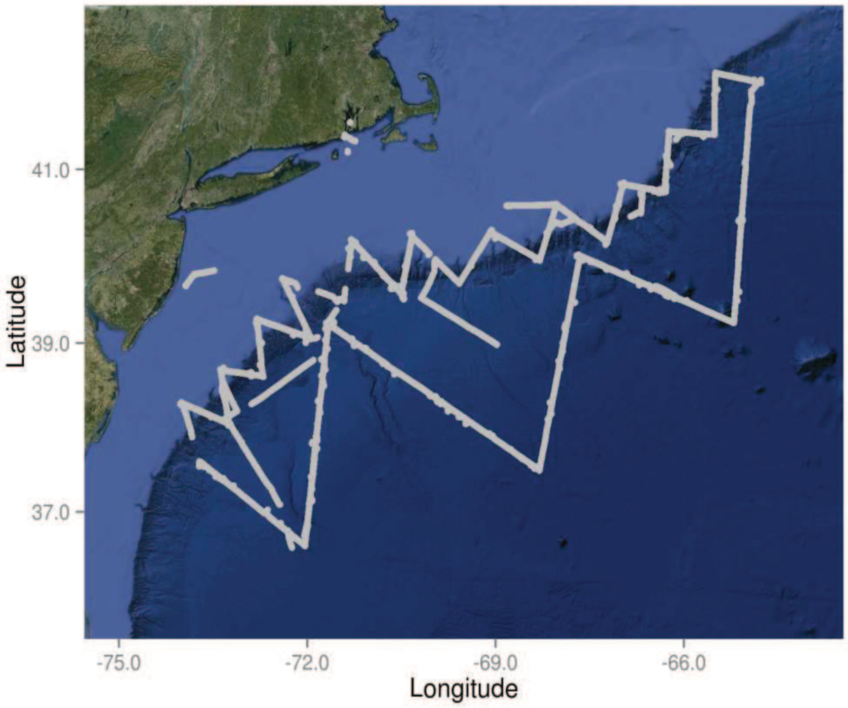


Figure 9: Area surveyed during the Atlantic Marine Assessment Program for Protected Species during the summer of 2011. Gray lines represent the actual vessel tracklines.

3.1.2 Acoustic analyses

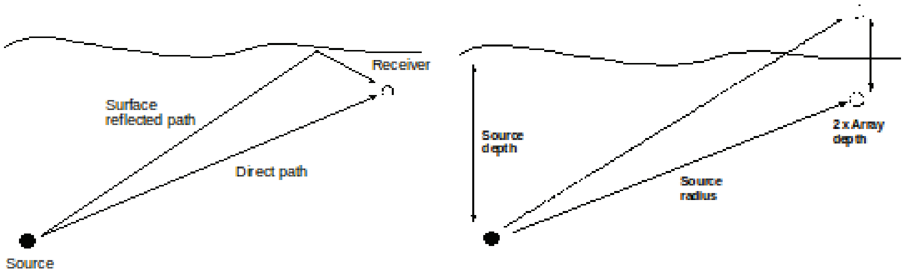
Acoustic data were post-processed using the software packages Raven (Charif *et al.*, 2004) and Pamguard (Gillespie, 2008), as well as custom-written Matlab scripts. Data analyses took place in three stages: 1) identification and characterization of echolocation clicks, 2) development and application of automated click detectors, 3) two-dimensional and three-dimensional localization of individual click trains. The first stage of data analysis was previously described (Cholewiak *et al.*, submitted). The second and third stages are described below.

3.1.3 Automated click detectors

The Pamguard software allows for the application and customization of an algorithm for the detection of transient acoustic signals, such as echolocation clicks. For the general detection of clicks, the user defines a set of parameters, including the signal threshold, the minimum number of samples between clicks, and the maximum length of clicks. By defining an additional set of criteria specific to the target signal, an automated classifier can be defined and applied as well. These additional criteria may include the signal's primary energy band, the peak and mean frequency, and the number of zero crossing.

3.1.4 Two-dimensional and three-dimensional localization

Pamguard Beta v1.11.02 currently allows for the application of target-motion analysis to compute two-dimensional locations of calling animals, using one of several algorithms (Gillespie *et al*., 2008). This method is capable of resolving the relative bearing and radial distance of a given sound source at a specific moment in time. At any instant in time, the relative bearing of the source relative to the array can be calculated using a pair of hydrophones. Over multiple vocalizations (e.g. echolocation clicks in a click train), changes in the bearing of the source relative to the array result in a set of intersecting bearing lines which correspond to the target location (Barlow and Taylor, 2005a; Gillespie, 1997). This methodology makes the assumption that the source is stationary relative to the vessel, which is reasonable in many cases given that survey speeds are often faster than the speed at which animals are traveling. However, given that the radial distance is independent of the source depth relative to the array, this method only provides a means for two-dimensional localization.



(a) (b)

Figure 10: (a) The direct and reflected signal path from the source to array (b) A multipath model using virtual receiver to estimate the bearing of a multipath signal

Full three-dimensional localization can be accomplished by combining two techniques, intersecting bearing estimates and multipath signal arrivals, in a manner similar to work previously conducted on sperm whale surveys (Barlow and Taylor, 2005a; Gillespie, 1997; Thode, 2005). In general, this is accomplished by finding the time difference between the direct signal arrival and surface reflections to the array (fig. 10a). By treating the surface reflection like a signal traveling to a 'virtual receiver', an additional bearing estimate may be made, resulting in a vertical bearing (fig. 10b). Knowing the additional vertical bearing along with the radial distance of the source, the depth of the source can then be resolved. Custom Matlab scripts were used to perform both time-series and autocorrelation analysis to measure the direct and surface reflected time difference of arrival. The time difference of arrival was then used to calculate the vertical bearing relative to the array, allowing for the source depth estimation using basic trigonometry. This can be accomplished through application of bearing estimation in a manner similar to that of array applications, however in this application rather than estimating a bearing based on a time difference of arrival between two hydrophones, the time difference is between a single hydrophone and the “virtual receiver” illustrated in fig. 10b. In this application, the time difference dt is the direct reflected time difference of arrival, and the distance between hydrophones, is two times the array depth. Knowing the bearing angle the source depth may then be calculated with the target radius originally estimated using target motion analysis being treated as the hypotenuse of a triangle, and the remaining triangle sides being the horizontal distance and depth.

3.2 Results and discussion

On 4 July 2011, at approximately 07:40 EDT, the R/V Bigelow encountered several small groups of Sowerby’s beaked whales at 40.78˚N, 60.6˚W, just off the continental shelf of the eastern United States, near Georges Bank. Over a period of approximately 25 minutes, at least three groups of animals were sighted, including a singleton, a pair, and a group of four individuals. The groups were distributed over several kilometers. As the ship passed through the area, several animals crossed the survey track line, and were approximately 300 m distant at their closest point of approach. Simultaneous with this encounter, multiple series of high-frequency echolocation clicks were detected by the acoustic team. Thirty minutes of continuous acoustic data encompassing and following the period of the visual encounter were included in subsequent analyses.

Analyses of echolocation characteristics from over 4000 clicks revealed that the majority of clicks had a median peak frequency of 33 kHz, with a -3dB bandwidth of 6 kHz, and an inter-click interval of 96 ms (Cholewiak *et al*. submitted, fig. 11). In Pamguard, an automated click detector was subsequently applied to the acoustic data. The classification algorithm with frequency sweep was customized to identify clicks containing greater energy in a test band (30 – 37 kHz), compared to two control bands (15 – 18 kHz and 85 – 95 kHz), and to identify clicks containing a peak frequency between 29 – 37 kHz.

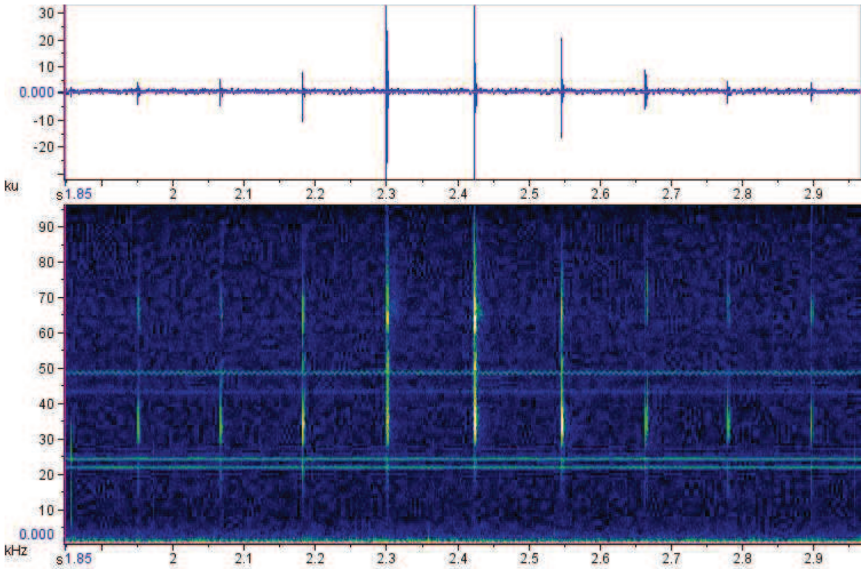


Figure 11: Example of waveform (top panel) and spectrogram (bottom panel) of a series of clicks from an individual Sowerby's beaked whale. (FFT: 512 pts, 50% overlap, Hann window)

Detected clicks were manually assigned to series of click trains (fig. 12) based on simultaneous comparison of spectrograms of the acoustic data and the bearing patterns as determined by Pamguard. Target-motion analysis was conducted for thirteen click trains, resulting in two-dimensional localizations for animals ranging from 82 – 456 m from the trackline. Based on relative locations, these click trains appeared to be produced by 3 – 5 individuals.

Click train series from three individuals were chosen for application of 3-D analysis (tab. 2). These individuals were estimated to be at radial distances of 192-250 m from the array. Click waveforms were visually evaluated to confirm the presence of multipath arrivals. For each click train, the time difference of arrival for direct and surface-reflected signals was compared for up to 5 different clicks and across three channels. The 2-D localization results from Pamguard were used as range inputs. Three-dimensional localization for these three individuals revealed vocalization depths ranging from 6 – 36 m.

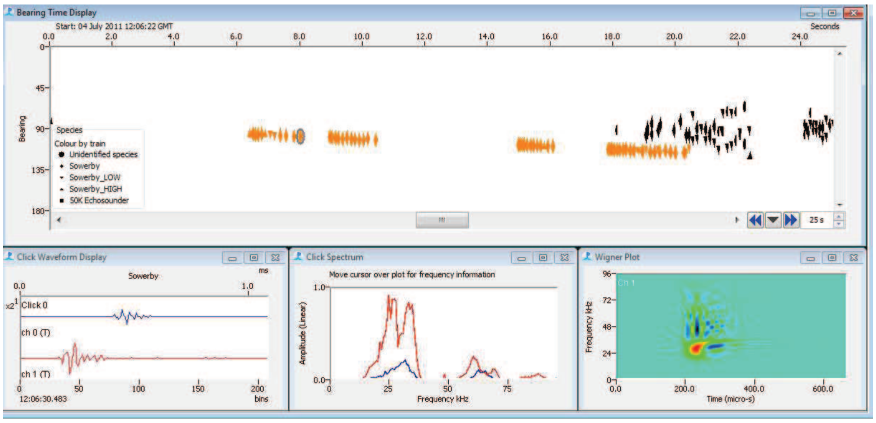


Figure 12: Top: Bearing-time display in Pamguard. Detected clicks are indicated by triangles. Orange triangles indicate clicks that were manually assigned to one click train series; black triangles represent clicks that are unassigned to individuals. Bottom (from left to right): The waveform display of one selected click (indicated by the gray circle in the top panel), the frequency spectrum, and Wigner plot.

Table 2: Data for three series of click trains representing three animals. Clicks were manually assigned to series based on simultaneous spectrogram and bearing-time review. Radial distances were approximations obtained from two-dimensional localization in Pamguard. Source depths were averaged over a series of clicks from multiple channels. Array depth was 12 m, ocean bottom depth was approximately 1000 m in area of encounter.

Individual	# Clicks Assigned to Click Train	Mean time difference (ms) between direct & reflected arrivals	Radial Distance (m)	Mean Depth (m)
1	57	0.44	192	**5.9 ±1.3**
2	88	0.9	247	**13.7 ±9.7**
3	96	2.31	250	**35.8 ±1.3**

The depths of the three individuals that were localized in 3-D are substantially less than those obtained from tagged individuals of both Cuvier's and Blainville's beaked whales, suggesting that the vocal behavior of Sowerby's beaked whales may differ from other ziphiids. The difference between the slant distance and the perpendicular distance estimated by traditional methods is minor for these individuals, given the shallow depths at which they were vocalizing. However, broader application of this methodology across multiple encounters is needed to characterize the average depths at which this species is detected. Further investigations may reveal whether the differences in depths at which different species vocalize are context-driven or species-specific.

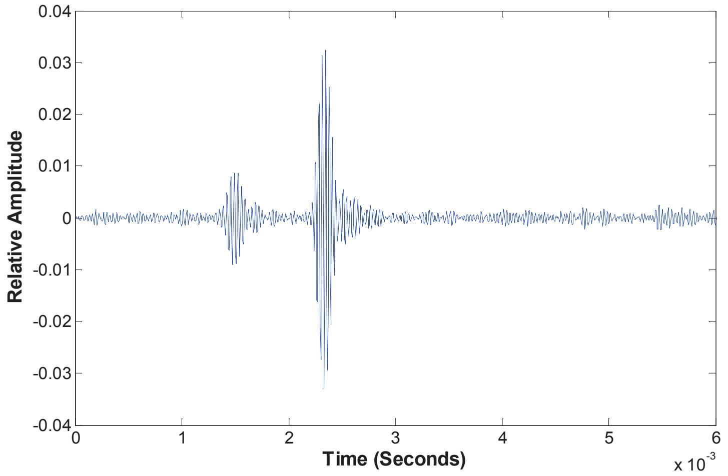


Figure 13: An example of beam focusing taken from an echolocation click recorded during the encounter with Sowerby's beaked whales. Note that the second arrival is of higher amplitude than the direct path.

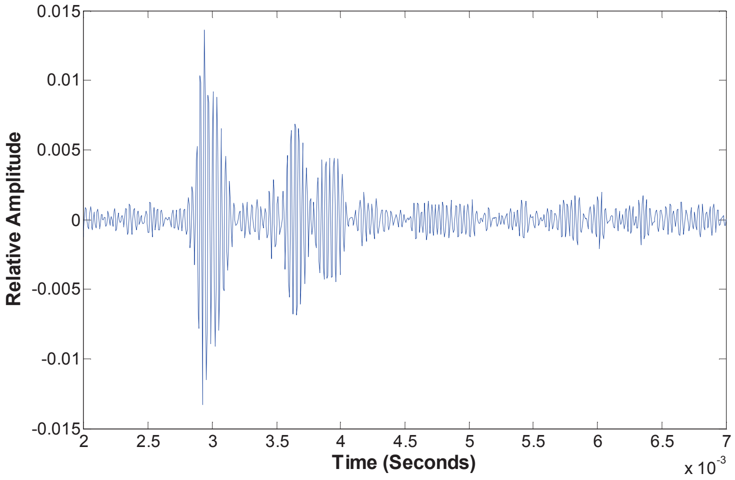


Figure 14: An example of a direct signal followed by a double surface reflection, recorded during the encounter with Sowerby's beaked whales.

Application of three-dimensional localization methods to high-frequency signals such as these is complicated by the effects of sea surface conditions. Depending on the sea state, when the wavelength of the signal is short compared to that of waves on the sea surface, propagation effects such as beam focusing or multiple reflections may occur adding difficulty to resolving time difference of arrival. These effects were observed in our towed array data, as well in similar experiments focusing on signal processing (Preisig and Deane 2004). In the case of beam focusing, (fig. 13) the received reflection will appear to have a greater amplitude than the direct signal. This is caused by the concave shape of a surface wave creating an acoustic focal point for reflections near the array. Multiple surface reflections (fig. 14) result in two or more first order reflections and can cause confusion when attempting to resolve the correct time difference of arrival required for bearing estimation. Additionally, because the recordings are being made in a dynamic environment, these effects will change continuously over time adding additional complication. It is assumed that these effects will have a greater significance at shallow depths, however additional work must be done to verify this and to resolve what the true time difference of arrival should be in the case of a perfectly flat sea surface.

4. Discussion

Passive acoustic monitoring (PAM) is a rapidly growing field in marine ecological research. For many species, these new PAM applications and the ensuing increase in temporal and spatial monitoring coverage have resulted in new knowledge on seasonal and regional distribution patterns (e.g., Lammers *et al*., 2011; McDonald *et al*., 2009; Mussoline *et al*., 2012; Simon *et al*., 2010). In addition, analyses of acoustic data have allowed us to gain new insights into species-specific behaviors (Baumgartner and Fratantoni, 2008; Jensen *et al*., 2011), as well as to elucidate behavioral changes due to acoustic disturbance (Holt *et al*., 2009; Melcon *et al*., 2012; Parks *et al*., 2011a; Risch *et al*., 2012).

One main aspect of measuring the effects of disturbance is to asses changes in the distribution and density of species or populations inhabiting the impacted area. For species of high risk and low densities, such as the Baltic harbor porpoise or the North Pacific right whale (Kyhn *et al*., 2012; Marques *et al*., 2011), this is especially important. Since visual density estimation is difficult in these cases, acoustics might be particularly useful to augment traditional methods of assessing changes in abundance.

For successful density estimation from acoustic data, it is essential to obtain cue rates in different behavioral contexts and as a function of time, season, region and life-history parameters such as age and sex (see Marques *et al*., 2012). PAM can be used to localize and track vocal animals. Thus, some of these parameters, such as minimum group sizes, calling rates, as well as source level and detectability under different background noise scenarios can be estimated using these data.

The two case studies presented in the current chapter were selected to highlight the feasibility of using data from bottom-mounted recording units and towed hydrophone arrays to estimate some of these parameters. The 2-D localization of right whale up-calls and the tracking of several individuals in the first case study demonstrated the relative ease with which passive acoustic analyses can be used to estimate minimum group size and individual calling rates. Despite applying it to only one hour of data, call rates and bout lengths found in this analysis were similar to previously published data collected from archival recording tags (Parks *et al*., 2011b). This demonstrates that bottom-mounted recorder data, when synchronized into a time-aligned array, can be used to supplement other data collection methodologies on a broader scale.

Species-specific automatic detectors (e.g., ISRAT (Urazghildiiev and Clark, 2006)) and semi-automated localization algorithms can be applied to quickly access large quantities of data, facilitating analyses of datasets covering spatial and temporal scales important for conservation and management. The biggest advantage of large data sets, like those provided by long-term PAM is the ability to address questions of high variability in behavior as found in smaller, more controlled studies (Parks *et al*., 2011b). To date, few studies (e.g., Parks *et al*., 2012; Širović *et al*., 2004) have used passive acoustic data and localization techniques to estimate calling rates and minimum group size of baleen whales on a larger scale. In addition, PAM data can provide source level estimates for individual animals (Munger *et al*., 2011; Samaran *et al*., 2010; Stafford *et al*., 2007; Širović *et al*., 2007). If coupled with acoustic propagation models, robust source level information can then be applied to estimate detection ranges of species-specific calls.

Currently, more studies have used 2-D localization approaches as part of towed array surveys (Barlow and Taylor, 2005a; Lewis *et al*., 2007; Li *et al*., 2009). In our second case study, we utilized the freely available software package Pamguard (Gillespie *et al*., 2008) to detect and track beaked whale clicks from towed array data. In the context of towed array recordings, the estimation of distance to the survey trackline, species identification and minimum number of animals by passive acoustic tracking can improve simultaneously collected visual data by providing context to the visual encounter, aiding in species identification, as well as augmenting traditional density estimates. In the current example, the simultaneous collection of visual and acoustic data allowed for the description of the previously unknown acoustic signature of an understudied species (Cholewiak *et al*., submitted).

Estimating the depth ranges at which marine mammals are vocalizing can provide important behavioral information and help interpret PAM datasets. Although in theory the standard method of localization using 'Time Difference of Arrival' (TDOA) is capable of localizing animals in three dimensions, in practicality, for fixed arrays, this method is generally suitable for only two-dimensional or planar applications. If recorders are separated by several kilometers or more, then the change in absolute path length (the length as a function of both depths an horizontal distance) is negligible with a change in calling depth unless the difference in depth between the vocalizing animal and recorder is very large. For applications where the animal's depth is small compared to path length, the resulting changes in time difference of arrival between recorders as a function of depth will likely be beyond the resolution achievable when considering limits such as sampling rate and synchronization error. Limitations to depth estimations and three dimensional localization with fixed arrays can be overcome through the application of the Direct-Reflected Time Difference of Arrival (DRTD), as demonstrated for localizing right whales in the first case study. Only a few studies have used PAM data for 3-D localization of vocalizing animals (Newhall *et al*., 2012; Wiggins *et al*., 2004). However, with the application of methods such as the DRTD (Aubauer *et al*., 2000; Mouy *et al*., 2012; Nosal and Frazer, 2006; Valtierra *et al*., submitted), PAM data can be used to augment and significantly increase the availability of data on baleen whale calling depths, which have so far been collected mainly from tagged animals (Oleson *et al*., 2007b; Parks *et al*., 2011b).

Three-dimensional localization techniques have more frequently been conducted using odontocete signals (e.g., Giraudet and Glotin, 2006; Thode, 2005). Incorporating these techniques into towed array surveys has been done with sperm whales (Barlow and Taylor, 2005), but has not been applied to other species. For some deep-diving species such as beaked whales, much of what we know of their underwater behavior comes from tagging studies of few species in limited contexts. Case study 2 shows how the DRTD method of 3-D localization can be combined with 2-D localization of towed array data to obtain depth of vocalizing animals. This may have implications for improving distance estimation, which will ultimately result in an improved detection function for density estimation.

Obtaining depth estimates for calling individuals is important for improving our knowledge of basic calling behavior and the implications of such on density estimation, as well as in a context of management and mitigation. Under certain sound speed profile conditions, modeling the range over which calls propagate may be heavily dependent on the animal's location within the water column (Stafford *et al*., 2007; Thode, 2005). Moreover animals might be actively choosing a certain calling depth in order to increase signal strength of their calls (Oleson *et al*., 2007b). Thus, knowledge on preferred depths for vocalizing animals is crucial in order to estimate detection probability of species-specific calls from PAM data. In addition, the received levels of directional sound sources such as seismic arrays may be much greater for animals at depth than at the surface (Thode, 2005). In addition, animals that spend significant amounts of time in shallow depths will be more vulnerable to ship-strike (Parks *et al*., 2012b). In the case of vocalizing animals, PAM data can elucidate these behavioral patterns and supplement data which have traditionally been obtained with short-term recording tags (Jensen *et al*., 2011; Oleson *et al*., 2007b; Parks *et al*., 2011b).

In recent years, there has been a surge in the development of offshore industries, including oil and gas, as well as emerging alternative energy projects such as tidal turbines, wave energy or windfarms (Simmonds and Brown, 2010). In this context, successful species management and conservation is dependent upon accurate knowledge of temporal and spatial distribution patterns and population densities of a given species. As a result we have seen an increased effort, both spatially and temporally, of using PAM for monitoring and mitigation. Examples are large-scale projects such as for monitoring ocean noise in the Stellwagen Bank National Marine Sanctuary (Hatch *et al*., 2012), extensive acoustic monitoring in the Arctic ocean for mitigating seismic exploration (Moore *et al*., 2012), or the SAMBAH project (http://www.sambah.org/) to assess harbor porpoise density in the Baltic Sea.

In this chapter, we highlighted how combining PAM data with two- and three-dimensional localization and tracking techniques can be used to expand baseline vocalization data, extracting critical information such as animal depth and calling rate. Expanded application of these tools to fixed and towed array data will enable more detailed analyses of the inherent variability in species-specific calling behaviors. This knowledge in turn will facilitate the direct application of acoustic data to abundance estimation, ultimately improving marine mammal management.

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Chapter II

Risch D, Baumgartner M, Brady SP, Cholewiak DM, Clark CW, Davis G, Hatch LT, Thompson MA, Wiley D & Van Parijs SM (manuscript) Multi-year seasonal occurrence patterns of four species of baleen whales in Massachusetts Bay. (Drafted for *Marine Ecology Progress Series*).

Photos: D. Risch, D. Cholewiak & NOAA/NEFSC

Fin, sei, right and blue whale (upper left to lower right).

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Multi-year seasonal occurrence patterns of four species of baleen whales in Massachusetts Bay

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Abstract

Due to difficulties in gathering large-scale data especially in offshore marine habitats, little is known about seasonal distribution and long-distance migrations of most baleen whale species. With its ability to survey remote areas over extended timescales, it has been shown that passive acoustic monitoring (PAM) can elucidate some of these open questions. This study investigated the seasonal patterns in vocal activity and occurrence of four species of baleen whales; fin whales (*Balaenoptera physalus*), right whales (*Eubalaena glacialis*), sei whales (*Balaenoptera borealis*) and blue whales (*Balaenoptera musculus*) in Massachusetts Bay over three years and five months (2006, 2008-2010). One or two representative call types (fin whale 20 Hz note, right whale up-call, sei whale downsweep and blue whale AB song notes) were chosen per species and a low-frequency automated detection and classification system (LFDCS) was trained and run for their detection and classification in the multi-year data set. Fin whale song was detected in all months of the year with persistent seasonal patterns across all years. Song detection was lowest during May and June and occurred on over 75% of all sampled days from August to April. From September to March fin whales were vocally present for over 16 hours per day. These data suggest year-round presence

of fin whales in this area and confirm winter song in higher latitudes. Right whale up-calls and sei whale downsweeps showed a bimodal distribution of peak detection periods in spring and autumn, indicating that both species traverse this area during migration. However, right whale detections peaked in April and May, and were less common in the autumn, while sei whale detections showed a clear peak in occurrence in October in two of the recording years. Although the general patterns were similar, peak timing and extent varied between years. Blue whale song was detected on only 12 days of the entire recording period, occurring mostly in January and suggesting a general offshore distribution of this species with occasional visits to inshore waters during winter.

Introduction

Over the past decades, humans have altered the marine environment substantially. Increasing impacts of anthropogenic activities on cetaceans as part of the marine ecosystem include overfishing (Halpern et al. 2008), fisheries by-catch (Moore et al. 2009), ship-strikes (Redfern et al. 2013), chemical and noise pollution (Fossi et al. 2012, Moore et al. 2012), as well as the multitude of effects of global warming, such as ocean acidification and changes in sea ice distribution (Hoegh-Guldberg & Bruno 2010). In addition, with fast expanding technology, construction of alternative energy projects (Madsen et al. 2006), as well as the continued exploration for and extraction of oil and gas (Heide-Jørgensen et al. 2013) is reaching further and further offshore. All these threats are cumulative, especially in highly populated and industrialized coastal areas, where the footprints of different projects often overlap. The latter makes it particularly important to monitor and describe the extent and reach of these activities in order to better mitigate their effects (McKenna et al. 2012). Similarly, since the best way to mitigate or reduce human impact on marine fauna, is the physical separation of the two (Vanderlaan et al. 2008, van der Hoop et al. 2014), knowledge of year-round spatio-temporal distribution patterns of marine mammals is of critical importance (Best et al. 2012). However, due to the difficulties of collecting data in open ocean regions, especially during winter, large data gaps exist in particular for long-distance migrants such as most baleen whale species.

Seasonal to-and-fro migrations between productive high-latitude feeding and less productive low-latitude breeding grounds have long been described for a range of baleen whale species (Kellogg 1929, Norris 1967), although it is also becoming more obvious that partial or differential migration (Dingle & Drake 2007) might be more the norm than the exception in this group. In addition, the driving factors for these migrations are still debated (Corkeron & Connor 1999). However, it is well understood that many species of baleen whales range over very large distances throughout the year, while their seasonal destinations or the migratory pathways are often unclear. In the North Atlantic Ocean migratory routes are best established for humpback whales (Clapham & Mead 1999), and North Atlantic right whales (*Eubalaena glacialis*) (Kraus et al. 1986), but large gaps with respect to migration routes, timing and winter distribution exist for most other species.

At different times of the year, blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*) and right whales are sympatric in the Gulf of Maine, located in the western North Atlantic. All of these species have been shown to produce low-frequency vocalizations in different behavioural contexts. While blue and fin whale song are typically produced in a reproductive context, right whale up-calls and sei whale downsweeps are likely produced to maintain contact over large distances (Watkins et al. 1987, Mellinger & Clark 2003, Baumgartner et al. 2008, Parks et al. 2011). These vocalizations can be used to infer seasonal presence as well as large-scale movements using autonomous acoustic recorders (Clark & Gagnon 2004, Nieukirk et al. 2004, Simon et al. 2010, Morano, Salisbury, et al. 2012, Mussoline et al. 2012). Passive acoustic monitoring (PAM) allows data collection in remote areas, over extended timescales and largely independent of human observers (Mellinger et al. 2007, Van Parijs et al. 2009). For example, widely spaced acoustic monitoring networks such as the array data from the IUSS Sound Surveillance System (SOSUS), have been used to investigate seasonality and large-scale distribution patterns of baleen whales in the North Atlantic (Clark & Gagnon 2004). In addition, coupled with autonomous, mobile platforms their spatial reach can be enhanced even further (Baumgartner et al. 2013, 2014)

So far, most PAM approaches have focused on individual species assessment. The accurate and manual analysis of large amounts of bio-acoustic data in such contexts can be costly both in terms of time and processing power (Baumgartner & Mussoline 2011). With the drawback of decreased accuracy, the development of automated detection methods can reduce this effort to some extent and substantial advances in the field of bio-acoustic signal processing have been made in recent years (Urazghildiiev & Clark 2007, Gillespie et al. 2009, Baumgartner & Mussoline 2011, Popescu et al. 2013). Where the goal of analysis is the long-term assessment of large-scale species occurrence, rather than the detection of every call, automated methods can usually provide sufficient detail for conservation and management applications (Van Parijs et al. 2009).

In larger-scale management applications, where the need is to provide comprehensive data to assess the impact of a planned anthropogenic activity on the marine environment, the focus on single species is often too small and species by species analysis may prove prohibitive, both in terms of cost and effort. In these cases multi-species analysis approaches will greatly enhance efficiency. In addition, the analysis of multi-species vocal activity patterns might also reveal important ecological interactions between different species and their natural environment which may improve their use as sentinels of ecosystem change (Moore 2008). For example, with respect to the impacts of underwater noise, species with similar vocalization frequencies, may be impacted in similar ways by communication masking or distraction from vital life functions (Clark et al. 2009, Chan & Blumstein 2011, Hatch et al. 2012). Assessments from a multi-species perspective can therefore not only save time but also unravel important dynamics and relationships between the acoustic ecology of sympatric species and the effects of human activities in their marine habitat. Further, the importance of describing and evaluating noise budgets, including both anthropogenic, as well as biological sources is increasingly being recognized as an important conservation tool (Hatch & Fristrup 2009, Gervaise et al. 2012, McKenna et al. 2012, Francis & Barber 2013).

In this study we aim to show the applicability of a generalized automated detection system (LFDCS) to analyze the seasonal occurrence patterns of four sympatric baleen whale species (right, sei, blue and fin whales) by detecting their low-frequency vocalizations (Figure 2). We evaluate the stability of these patterns across multiple years and explore similarities and differences between occurrence patterns of these different species in our study area.

Materials and Methods

Data collection

Multi-year acoustic data were collected as part of two long-term monitoring projects carried out in 2006 and from December 2007 to May 2010 in the Stellwagen Bank National Marine Sanctuary (SBNMS) and surrounding waters, located in the Gulf of Maine (Figure 1; Hatch et al. 2008, 2012). Recordings were made using arrays of 9-10 Marine Autonomous Recording Units (MARUs) (Calupca et al. 2000), sampling continuously at a rate of 2000 Hz and 12 bit resolution. MARU frequency response was approximately -151.2 dB re: 1 µPa (± 1 dB) from 10-585 Hz. MARUs were typically deployed at 1-2 m above the sea floor in depths ranging from 20-100 m and for 3 consecutive months at a time.

Detection approach

Multi-year data were examined with a generalized low-frequency detection and classification system (LFDCS; Baumgartner & Mussoline 2011). In short, this detection system accounts for continuous narrowband and transient broadband noise, employs pitch-tracking to detect signals of interest and classifies detected calls using quadratic discriminant function analysis (QDFA). Detection and classification follow a multi-stage process consisting of spectrogram smoothing, noise reduction, pitch-tracking, attribute extraction and classification by comparing extracted features against an existing call library, using discriminant function analysis. The algorithms for each of these steps are described in detail in Baumgartner & Mussoline (2011) and will therefore only be described briefly here.

At the start of analysis, spectrograms of all data were created using a fast Fourier transform (FFT). For the right and sei whale analysis audio data sampled at 2000 Hz were processed with a sample frame size of 512, Hanning window and frame overlap of 128 samples (75%), resulting in a temporal resolution of 64 ms and a frequency resolution of 3.9 Hz. To analyze the lower frequency calls of blue and fin whales, the audio data was first re-sampled to 128 Hz, FFT frame size was set to 512 samples and the overlap between frames to 64 samples (87.5%), resulting in a temporal resolution of 0.5 s and a frequency resolution of 0.3 Hz. The resulting spectrograms were smoothed with a 3 x 3 smoothing kernel and equalized to account for noise (see Baumgartner & Mussoline 2011 & Baumgartner et al. 2013 for details)*.*The LFDCS then characterizes the fundamental frequency of dominant sounds using a contour tracing algorithm. To classify resulting pitch tracks, several attributes (e.g., start frequency, end frequency, frequency range, duration and slope of frequency variation) are extracted from each contour. These features and known species-specific example calls of a prior established call library are used in a quadratic discriminant function analysis (QDFA) for final call classification. For this analysis we used two narrow-band call libraries, which were specific to the two sets of acoustic data with differing sample rates. The call library for classifying right and sei whale calls contained 5 variants of right whale up-calls with 254 individual call examplars (Clark 1983, Parks & Tyack 2005; Figure 2 d) and 3 of sei whale downsweeps (217 exemplars) (Baumgartner et al. 2008; Figure 2 c)*.* A second call library was built for the lower sampled data set, containing 1 variant of the more stereotypic fin whale 20 Hz song notes (171 exemplars) (Watkins et al. 1987; Figure 2 b) and 1 variant for A and B note examples of blue whale song (115 exemplars)

(Mellinger & Clark 2003; Figure 2 a). Exemplars for the call libraries were manually extracted from various data sets collected in the Northwest Atlantic Ocean.

QDFA assesses the quality of a classification using the Mahalanobis distance (MD). MD measures the distance between the attribute vector of the unknown call to the mean attribute vector of a given classification category. MD will be small for well classified calls and high for outliers. In this analysis we used a maximum MD threshold equal to 3 for fin, sei and right whale calls, which Baumgartner & Mussoline (2011) showed to be conservative. A maximum threshold of 5 was chosen for blue whale song, since initial data perusal had shown a very low occurrence of these signals in our data. Choosing a higher threshold therefore retained more lower quality calls and ensured that fewer calls were missed at the cost of a higher false detection rate. However, due to the low number of overall detections for this species, detections were manually verified, and all false detections were removed from the dataset. While such post-processing of data is feasible for small data sets or, like in our case, rare call types or species, it is prohibitive for long-term data of highly vocal and/or abundant species. The choice of the MD threshold is therefore dependent on the analysis goal and expendable effort.

In order to accurately present seasonal distribution patterns and reduce the missed call rate, we chose a more conservative MD threshold for fin, right and sei whales. To account for some of the resulting false classifications, without post-processing the whole data set for these three species in the same manner as was done for blue whales, we instead followed a logistic regression approach as suggested by Baumgartner et al. (2013). This method determines the minimum number of detections (N_{min}) that are necessary to accurately predict the presence of a species within a given time period. For this long-term dataset and due to our interest in large-scale seasonal patterns, we chose hourly presence as a sufficient granularity for analysis. To estimate N_{min}, we initially evaluated species occurrence (i.e. presence/absence) for every third hour in 3 days of every month in the 2006 and 2009 detection data. However, due to relatively low calling rates of right and sei whales and in order to increase the true positive sample for these species, we extended this analysis by evaluating every third hour for 3 days in April and November 2008 and 2010 data for these two species. In a last step, additional hours were evaluated opportunistically, until a target of at least 60 positive hours were reached for each species and year. Subsequently, a logistic regression model was fitted to the data, in order to relate species occurrence to the number of species-specific calls detected in each hour of analysis. Using the intercept and slope of the fitted model, N_{min} was then estimated for a range of probabilities (70-95%) to accurately predict species presence. A range of N_{min} values were calculated in order to compare the effect of choosing a particular prediction probability on the resulting seasonal detection patterns. Finally, the overall detector output was binned by hour and species, and only hours with N detected calls >= N_{min} for 90% correct prediction probability (Table 3), were taken into account as true positive detections. All analyses were carried out in R v 3.1.1 (available at www.R-project.org).

Detection range estimation

Since variations in underwater ambient noise levels (NL) over time can have a profound impact on the detection probability of acoustic signals (Helble, D'Spain, Hildebrand, et al. 2013), an exploratory seasonal ambient noise analysis was conducted. LTSpec, a custom-written MATLAB script (LTSpec, Cortopassi 2007) was used to extract absolute root-mean-square (RMS) received levels (RL) in dB re 1 µPa/Hz. Seasonal week-long data (Table 1) were aggregated over a time period of ΔT = 600 s. Spectrograms were created using a sampling rate of 2000 Hz, a FFT size of 2048, and a Hanning window function, resulting in a frequency resolution of 1 Hz. Results were averaged by hour and 1/3rd octave frequency bands centered around 25 and 200 Hz to represent fin and blue whale, and right and sei whale call frequencies, respectively. These calculated ambient noise levels (NL) were then used to estimate seasonal variation in maximum detection ranges of species-specific vocalizations in the Stellwagen Bank area.

In order to model signal propagation an assumption of source and receiver depths of 20 and 50 m, respectively, was made and propagation was modeled for an omni-directional source over 8 horizontal radii and for all four seasons, using a BELLHOP acoustic simulation model implemented in ESME (Mountain et al. 2013), and environmental databases provided by the Oceanographic and Atmospheric Master Library (OAML) (available at http://esme.bu.edu/). For right whale up-calls we used an average source level of 172 dB (Hatch et al. 2012), a frequency of 200 Hz and a signal length of 0.1 s as input variables. In the absence of empirical source level data for sei whale downsweeps we used the same parameters as for right whales. For fin whales, propagation was modeled for a 20 Hz signal of 0.1 s duration and an approximate source level of 189 dB (Weirathmueller et al. 2013), while for blue whales a signal of 15 Hz and 0.1 s duration was modeled at 189 dB (Širović et al. 2007). The maximum propagation radius was selected for each model run and compared to all measured ambient noise levels. The maximum detection range was then estimated as the point at which signal-to-noise ratio (SNR=RL-NL) equaled 10 dB. Calculated ranges will thus give a rough estimate of maximum detection ranges for these species, as well as relative differences in detection range based on seasonal variation in ambient noise in the SBNMS study area.

Seasonal vocalization patterns

In order to avoid detection of the same call on multiple units, one channel of each multichannel data set was selected to explore seasonality using the described detection approach. Channels were selected with the aim to maximize recording time, while keeping a consistent recording location. However, due to varying study designs over the years and MARU loss due to trawling, the latter was not always possible. Overall the mean ± SE distance between 19 different recording locations was 26 ± 16 km (n=171) (Table 2). Hourly presence data for fin, right and sei whales were plotted as the sum of hours with detections per day. For blue whales, all detected calls were summed by day and plotted against day of occurrence.

Results

Detector evaluation

A total of 73, 131, 136 days and 582, 1085, 1176 hours of data were evaluated for the logistic regression analysis for fin, right and sei whales, respectively. The relative probability of occurrence of calling whales was strongly related to the total number of detected calls for fin whale song, right whale up-calls and sei whale downsweeps ($p < 0.0001$) (Figure 3). For accurate detection probabilities from 70-95%, the minimum number of detected calls (N_{min}) ranged from 18-34 calls per hour for fin whales, 15-25 for right whales and 2-4 for sei whales (Table 3). Since seasonality changed only in relative numbers of detected hours, while the overall pattern was consistent between these different levels of confidence, we chose a probability of 90% accuracy for all data presentation. Choosing this probability, the minimum number of detections for fin whales was N_{min}= 28, 21 for right whales and 4 for sei whales (Table 3, Figure 3). Using a confidence value of 90%, occurrence was falsely predicted in less than 5% of all hours and less than 3% of all days evaluated for all three species. In contrast, occurrence was missed in 30% of hours and 15% of days with manually detected fin whale song. Missed detection rate was especially high for right whale up-calls, with 94% of hours and 45% of days with manually verified detections missed when applying the logistic regression approach to the raw detector output. For sei whale downsweeps missed occurrence rate was 59% for all hours and 25% of all days with detections (Table 4).

Detection ranges

Average ambient noise levels in the selected 1/3rd octave bands (centered at 25 and 200 Hz) were similar across seasons, ranging from 88-99 dB re 1µPa. However, for both frequency bands ambient noise levels measured during winter were 5-7 dB higher than during the rest of the year (Table 5). Calculated detection ranges also varied seasonally, as well as by species (Table 5). While blue and fin whale call detection distances were estimated at maximum ranges of over 80 km, maximum detection range estimates for right whale up-calls ranged from 8-21 km. Shortest detection ranges (57 km) for low-frequency blue and fin whale calls were estimated for summer propagation conditions. For right whale up-calls shortest detection ranges were estimated for the winter period analyzed (Table 5).

Seasonality

From January 2006 to May 2010 a total of 1165 recordings days and 26,448 hours of single channel data recorded in the Stellwagen Bank National Marine Sanctuary (SBNMS) were analyzed for the occurrence of fin and blue whale song, right whale up-calls and sei whale downsweeps. Data was available for 317 days (86%) in 2006, for 296 (81%) days in 2008 and all days in 2009. For 2010, 124 (34%) days were available, while in 2007 only 63 (17%) days had recording effort. Except for blue whale song, all data will be summarized for 2006 and from 2008-2010, omitting data from 2007 due to the low and discontinuous recording effort during that year.

(a) Fin whale 20 Hz song

The most common signal in the data by far were 20 Hz fin whale song notes (Figure 4). Fin whale song was detected in each month of the year for all four years. In addition, song was present on 929 (80%) of all available recording days. Occurrence was similar in all years, ranging from 70-83% of days with detections per year. The lowest number of days with detections were recorded in May and June (Figure 4). During these months fin whale song was detected on 26% and 24% of available recording days, compared to over 80% of vocal presence in all other months, except July (68%) and December (75%). May and June also showed the lowest number of hours with song, with an average of 2-3 hours of song per day. In contrast, an average of 16-21 hours of song per day were detected from September to March (Figure 4).

(b) Right whale up-calls

Right whale up-calls were detected on 132 (11%) of all available recording days and were detected in all months, except for August (Figure 5). However, there was considerable variability in detections between months and years. In general, most detections were made in April and May, with on average 2-5 hours with detections per day. In these two months whales were detected on 43% and 28% of sampled days, respectively. A second peak in detections occurred from October to November with about 2 hours of detections per day (Figure 5). In November whales were vocally present on 16% of all sampled days. Although the general pattern of seasonality did not change between years, the relative amount and the timing of peaks in detections changed between years. Most days with detections were recorded in April 2009 and 2010, with 20 and 22 days with detections respectively.

(c) Sei whale downsweeps

Sei whale downsweeps were detected on 209 (18%) of all available recording days (Figure 5). Sei whales were rarely detected during the winter months. There were no detections of sei whales in January in any of the recording years. In all years, sei whales were also largely vocally absent during summer, with no detections in June, and only one day with detections in August and two days in July. Sei whales were vocally most present in the autumn. October was the month with most detections, 53 days (25%) of all days with detections occurred during this month. During this month 56% of all sampled days showed vocal presence. September and November showed vocal presence on 27% and 31% of sampled days, respectively. With on average 8 hours with detections per day, October was also the month with the highest calling activity for this species. A smaller secondary peak in detections occurred during spring, with 39% and 26% of all sampled days showing vocal activity in April and May, respectively (Figure 5). There were significant differences in vocal presence between years. Most remarkably was the low number of days with detections in October 2009 (5 days) compared to a high of 24 days for both October 2006 and 2008. A peak in days with detections occurred in April 2009 (26 days), compared to 4-9 days of vocal presence for this month in all other years (Figure 5).

(d) Blue whale song

Blue whale song was detected on 13 days (1%) over the entire data set, 8 days of which were consecutive days from 12-19 January 2009 (Figure 6). Based on the fact, that no overlapping song sequences were detected during any of these days, this occurrence may represent the detection of a single animal in the proximity of our array. Other days with blue whale song were recorded on 25 March 2006, 4 September 2006, 17 January 2007 and 25 February 2009. No blue whale detections were made in 2008 or 2010.

Discussion

Detector performance and evaluation approach

The application of the LFDC system for multi-species detection in a long-term data set proved efficient and effective to accurately detect large-scale patterns of vocal occurrence for all four baleen whale species analyzed in this study. Compared to verifying detection data manually, time for post-processing of original detection results was significantly reduced by using the logistic regression approach suggested by Baumgartner et al. (2013). Thus, this approach enabled the efficient analysis of more than three years and five months of continuous sound data.

Evaluation of this combined approach for species-specific detection showed that although a large number of hours with detections were missed, daily presence could be predicted relatively reliably for fin and sei whales, with less than 25% days with detections missed and less than 3% falsely predicted days with detections for both species (Table 4). These results show that the proposed detection and logistic regression approach is applicable for fast data processing and detection of both species in long-term data sets. In contrast, right whale up-call detection results were relatively poor, with 94% of all hours and 45% of days with manually verified species presence within the evaluation data set missed by the combined automated detection and logistic regression approach. This result is likely related to low and irregular right whale calling rates (Parks et al. 2011), which hampers the successful application of the logistic regression approach as performed in this study, since it is reliant upon regular call production rates. Analysis of false detections for right whale up-calls, showed that, similar to results for the other species, only 3% of evaluated hours were falsely classified as containing right whale up-calls (Table 4). Therefore, due to this low misclassification rate, in the case of right whale up-calls, it may prove useful to manually post-process automated detection results rather than relying on the application of the logistic regression approach, in order to avoid high numbers of days with missed right whale presence.

In this study, the evaluation data set was pooled from different analysis years. However, it is important to note, that detector performance could change between analysis years. Detector performance and the calculation of N_{min} using the logistic regression approach may thus be better evaluated on a year to year basis. In particular, humpback whale song is prolific in our study area in spring and autumn (Vu et al. 2012). Although not analyzed in detail in this study, humpback whale song overlaps in time and frequency with right whale up-calls, as well as sei whale downsweeps, rendering it sometimes difficult to distinguish between the different signals, especially when analyzing acoustic data without visual context. In addition, the continually evolving nature of humpback whale song (Noad et al. 2000), may result in changing detector performance depending on the similarity of song phrases to species-specific signals of other species in a given year. In addition, although less likely, ambient noise conditions could change, for example in response to reduced shipping traffic after a recession (McKenna et al. 2012).

In future work detector performance should therefore always be analyzed per analysis year and the local call library and N_{min}, as estimated by logistic regression should be adjusted if necessary to increase accuracy and reduce missed call rates. Further, if data on calling behaviour suggests seasonal differences in call production rates, performance evaluation and logistic regression should be performed on even smaller time scales. The strength of the LFDCS detection approach is that such changes can easily be implemented, without having to change the underlying detection algorithm, making the system extremely flexible and adjustable for a range of different research questions (Baumgartner & Mussoline 2011, Baumgartner et al. 2013).

Detection ranges

The detectability of a species using passive acoustic monitoring (PAM) approaches is dependent on a variety of different parameters. Most importantly, call source levels, system sensitivity, as well as average background noise levels and propagation characteristics of a given area determine the detection radius for a specific call type. Results from the preliminary estimation of detection range based on local propagation, ambient noise conditions and species-specific call characteristics illustrate large differences in detection radii for the different species analyzed with the current multi-species detection approach. While low-frequency calls produced by fin and blue whales may be detected for over 80 km, detection radii for right whale up-calls ranged from 8-21 km in our study area. These differences in detection radius are important to keep in mind when interpreting the seasonal presence data presented in this study, since the difference in range of detection between the four species is at least 4-fold and means that in this study blue and fin whale song is detected at an entirely different spatial scale than right and sei whale vocalizations.

In addition, estimated detection radii in this study varied seasonally. For example, reduced detection radius for right whale up-call and sei whale downsweep signals during winter (Table 5) may be related to higher ambient noise levels within the critical frequency band for these species, driven by weather patterns (i.e. increased surface wave action due to winter storms). In contrast, a reduced detection radius for low-frequency fin and blue whale calls during summer (Table 5), may be related to differences in propagation characteristics, as here differences in ambient noise levels between seasons were less pronounced.

The complexity of inter-related effects and a general lack of knowledge of basic calling behaviour parameters often prohibits the correction of passive acoustic detection data (but see (Helble, D'Spain, Campbell, et al. 2013). However, the notion of seasonal variability in ambient noise levels or oceanographic parameters affecting propagation and detection radius of species-specific signals, warrants careful consideration when interpreting seasonal patterns in species occurrence based on PAM data alone.

Seasonality

(a) Blue and fin whales

The most common vocalization recorded throughout this study were 20 Hz song notes produced by fin whales. Fin whale song occurred on 80% of all recording days and was present in all months of every recording year. In contrast, blue whale song was recorded on only 13 days throughout the whole study period. While this disparity likely reflects a more offshore distribution of blue whales, who are also rarely sighted over the continental shelf (Wenzel et al. 1988), it may to some extent also reflect differences in relative numbers. Blue whales in the North Atlantic have been heavily exploited by historical whaling and there is little indication that the population is recovering. Populations estimates for the North Atlantic range from a couple of hundred to 2000 animals, although reliable abundance estimates are sparse (Clapham et al. 1999, Ramp et al. 2006)*.* In comparison, present estimates for fin whales in the North Atlantic indicate an abundance of about 35,000 (www.iwc.int/status, accessed November 4, 2013). A relatively greater abundance of fin whale, as compared to blue whale song has also been found in recordings from the mid-Atlantic Ocean and has been associated with relative numbers of individuals (Nieukirk et al. 2004).

The year-round detection of fin whale song in our study area corroborates data from other recent passive acoustic studies in an adjacent area in Massachusetts Bay and off Long Island, New York showing similar results (Morano, Salisbury, et al. 2012)*.* Similar to seasonal patterns found in the current study (Figure 4), Morano, Salisbury, et al. 2012 indicate a reduced abundance of fin whale 20 Hz notes during summer. They show that the reduction in absolute note abundance is related to an increase in inter-note interval (INI) during that time of year. Yet, the significant reduction of hours with detections during summer months in the current study cannot be explained with changes in INI exclusively. Instead, a change in absolute singing activity at this time of year and/or the relative number of singing individuals in the area are more likely causes for the observed seasonality patterns. The peak of singing activity during winter, which has also been shown in passive acoustic data from Davis Strait, Greenland (Simon et al. 2010), overlaps with the reproductive season which is thought to last from November to March in this species (Lockyer 1984). Since fin whale song is produced exclusively by males in a reproductive context (Croll et al. 2002), an increase of singing activity during autumn and extension of singing into winter may be explained by a switch from primarily feeding behaviour in the summer to reproductive behaviour later in the year. However, without more knowledge on fin whale distribution at different times of the year, the underlying causes for the observed changes cannot be conclusively resolved from PAM data alone. Overall, the data from this study indicate, that fin whales have a year-round presence in the Gulf of Maine and that seasonal migrations might be more flexible in this species than in other baleen whales.

(b) Right and Sei whales

Results for right and sei whales showed a bimodal peak in call detections during spring and autumn, which was repeated in several years (Figure 5) in both species. This seasonality likely reflects migratory movement and establishes Massachusetts Bay as an important area along spring and autumn migratory routes for both species. While similar results have been shown in other PAM studies from this area, targeting right whale up-calls (Morano, Rice, et al. 2012, Mussoline et al. 2012), this is the first long-term study representing sei whale migratory behaviour in this part of the western North Atlantic using passive acoustics. Sei whale downsweeps have only recently been described in detail (Baumgartner et al. 2008). While there is some overlap with similar downsweeps produced by fin whales in the North Atlantic (Castellote et al. 2012), we tested the LFDCS sei whale call library against 183 known fin whale downsweeps recorded in the Gulf of St Lawrence (Delarue, unpublished data) and determined a low misclassification rate of 6% (11 calls) (Risch, unpublished data). We are therefore confident, that most detected calls were correctly attributed to sei whales.

While both species showed peaks in detection in both spring and autumn and thus show some overlap in vocal and likely actual occurrence, it is interesting to note, that while right whale acoustic presence generally peaked in April, sei whale presence showed a distinct peak in October (Figure 5). The preferred prey of both species are euphasiids (Wishner et al. 1988, Schilling et al. 1992), and the different peaks of occurrence in the Stellwagen Bank Sanctuary might therefore be related to a separation of seasonal feeding habitats between these species. During spring, right whales spend considerable amounts of time feeding in Cape Cod Bay (Pendleton et al. 2012), and vocal occurrence in the Stellwagen Bank area during this time of year is likely related to movements in and out of Cape Cod Bay (Morano, Rice, et al. 2012). In contrast, sei whales do not seem to have a persistent presence in Cape Cod Bay during spring. However, both species seem to overlap in a nearby spring feeding ground, the Great South Channel, located between Cape Cod Bay and Georges Bank (Baumgartner & Fratantoni 2008). Differences in vocal peaks at different times of year, may thus indicate small-scale spatial niche separation in a common seasonal feeding habitat.

Although large-scale seasonal patterns were similar between years there were marked differences between years, most notably the absence of sei whale downsweeps in autumn 2009 (Figure 5). The data analyzed in this study were collected on one representative passive acoustic recorder per time period and while this study indicates, that larger scale seasonal patterns are well captured using this method, it is possible, that smaller scale movement patterns may be responsible for observed differences in acoustic detections between years. This interpretation is corroborated by comparing the seasonal patterns for right whale up-calls from our study to results from acoustic recordings from a 19 element acoustic array just to the west of our study area (Morano, Rice, et al. 2012). While the large-scale seasonal patterns, showing a spring peak in detections and a smaller peak during autumn, was the same in both studies, the differences in yearly detections are less pronounced than in our study. This potential difference in large-scale versus small-scale occurrence patterns highlights the importance of taking study design, location and number of available recorders into account, when interpreting results from PAM studies.

In conclusion, this study shows the suitability of using PAM and a generalized multi-species detection system for evaluating seasonal, multi-species occurrence patterns and elucidate large-scale patterns of overlap between different species. The concentration on one representative call type per species likely influenced the presented results with respect to species presence. Vocalization behaviour is likely dependent on general behaviour and using reproductive signals for some species (fin and blue whales) versus contact and/or feeding associated calls for another (right and sei whales) will therefore influence the results and need to be considered in the interpretation of the reported results. In future work more call types, such as gunshot calls or moans for right whales (Parks et al. 2012) or 40 Hz fin whale calls

(Širović et al. 2012), should be included in similar analyses to ensure a more comprehensive representation of each species' presence using PAM.

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Tables

Table 1. Summary of weeks analyzed for seasonal examples of ambient noise levels in the Stellwagen Bank National Marine Sanctuary (SBNMS) study area.

Season	*Analysis Week*	*MARU ID*	*Latitude*	*Longitude*
Winter	01/01/2009 - 01/07/2009	181	42.613	-70.239
Spring	04/01/2009 - 04/07/2009	211	42.243	-70.271
Summer	08/01/2009 - 08/07/2009	144	42.262	-70.232
Autumn	11/01/2009 - 11/07/2009	209	42.448	-70.307

Table 2. Summary of analysis start and end dates and locations of recorders for which data was analyzed in this study. See Figure 1 for a map of these locations.

Start Date	*End Date*	*MARU ID*	*Channel #*	*Latitude*	*Longitude*
01/06/2006	03/29/2006	82	3	42.470	-70.240
03/30/2006	05/24/2006	89	6	42.645	-70.374
06/29/2006	09/21/2006	79	5	42.470	-70.238
09/27/2006	10/15/2006	79	5	42.470	-70.236
10/16/2006	11/27/2006	81	6	42.338	-70.193
12/06/2006	02/21/2007	81	5	42.338	-70.193
12/20/2007	02/17/2008	136	10	42.635	-70.196
03/08/2008	05/30/2008	136	2	42.284	-70.267
05/30/2008	06/12/2008	139	1	42.283	-70.334
06/26/2008	07/14/2008	155	3	42.414	-70.314
07/14/2008	08/25/2008	153	7	42.165	-70.437
09/09/2008	11/24/2008	144	2	42.447	-70.308
12/19/2008	03/13/2009	181	10	42.613	-70.239
03/14/2009	03/28/2009	137	1	42.270	-70.443
03/28/2009	05/28/2009	211	3	42.243	-70.271
05/29/2009	07/16/2009	142	1	42.323	-70.439

07/16/2009	07/28/2009	207	6	42.413	-70.316
07/28/2009	10/02/2009	144	1	42.262	-70.232
10/03/2009	11/30/2009	209	3	42.448	-70.307
11/30/2009	12/16/2009	137	1	42.780	-70.163
12/16/2009	03/19/2010	214	10	42.613	-70.238
04/08/2010	05/23/2010	136	6	42.179	-70.242

Table 3. Summary of minimum number (N_{min}) of detected calls needed for a given species prediction probability based on logistic regression analysis. (BP: *Balaenoptera physalus* (fin whale); EG: *Eubalaena glacialis* (right whale); BB: *Balaenoptera borealis* (sei whale).

Pred. Accuracy	***N_{min} BP***	***N_{min} EG***	***N_{min}BB***
0.7	18	15	2
0.75	20	16	3
0.8	22	17	3
0.85	25	19	3
0.9	**28**	**21**	**4**
0.95	34	25	4

Table 4. Evaluation of LFDCS detection results after application of a 90% prediction accuracy threshold (N_{min}BP=28; N_{min}EG=21; N_{min}BB=4). Number of hours and days evaluated (h/eval and d/eval) and with manually verified detections (h/det and d/det) vs. total number and percentage of hours and days missed (h/missed and d/missed) and falsely predicted (h/false and d/false). (BP: *Balaenoptera physalus* (fin whale); EG: *Eubalaena glacialis* (right whale); BB: *Balaenoptera borealis* (sei whale)).

Species	***h/eval***	***h/det***	***h/missed***	***h/false***	***%missed h***	***% false h***
BP	582	403	121	4	30.02	0.99
EG	1085	178	169	6	94.94	3.37
BB	1176	201	119	9	59.20	4.48
	d/eval	***d/det***	***d/missed***	***d/false***	***%missed d***	***% false d***
BP	73	73	11	0	15.01	0
EG	131	131	59	2	45.04	1.53
BB	136	136	34	4	25.00	2.94

Table 5. Summary of median, 25th and 75th percentile ambient noise levels (NL) measured in the Stellwagen Bank study area, and presented as RMS pressure over ΔT = 1 h and 1/3d octave bands centered at 25 and 200 Hz to represent blue and fin whale (BP: *Balaenoptera physalus* (fin whale); BM: *Balaenoptera musculus* (blue whale)), as well as right and sei whale (EG: *Eubalaena glacialis* (right whale); BB: *Balaenoptera borealis* (sei whale)) call frequency bands, respectively. Estimated maximum detection ranges for the two species groups are based on a BELLHOP propagation model as implemented in ESME (Mountain et al. 2013), using their species-specific vocalizations, seasonal ambient noise level measurements and a detection threshold of 10 dB.

Species	***Season***	***NL (dB re 1µPa)***	***Max. Det. Range (km)***
BM/BP (25 Hz)	Winter	98.5 [97.8-99.3]	79
	Spring	88.3 [87.2-89.7]	>80
	Summer	93.8 [91.9-95.7]	57
	Autumn	93.8 [91.9-94.6]	>80
EG/BB (200 Hz)	Winter	97.1 [96.4-97.6]	8
	Spring	91.6 [90.3-93.1]	21
	Summer	89.1 [88.0-90.9]	19
	Autumn	90.1 [89.3-90.9]	20

Figures

Figure 1.

Map of the Stellwagen Bank National Marine Sanctuary (SBNMS) (grey shaded area). Symbols depict locations of single acoustic recording units deployed and analyzed for baleen whale presence in this study. Different colours represent different years (2006-2010). Map projection: Mercator.

Figure 2.

Example spectrograms of vocalizations of the four baleen whale species analyzed in this study. (a) blue whale AB song, (b) fin whale 20 Hz song, (c) sei whale downsweeps, (d) right whale up-calls. Note different frequency and time scales of the spectrograms. Spectrogram parameters: (a) Fast Fourier Transform (FFT) = 4096 pt, overlap (ovlp) = 95%, samplerate (SR) = 2000 Hz: frequency resolution (FR) = 0.5 Hz, time resolution (TR) = 100 ms; (b) FFT = 1024 pt, ovlp = 75%, SR = 2000 Hz: FR = 1.9 Hz, TR = 128 ms; (c) FFT = 4096 pt, ovlp = 75%, SR = 10,000 Hz: FR = 2.4 Hz, TR = 250 ms; (d) FFT = 512 pt, ovlp = 75%, SR = 2000 Hz: FR = 3.9 Hz, TR = 64 ms.

Figure 3.

Relationship between hourly call rate observed by the LFDCS detector and analyst observed presence for (a) fin whale song, (b) right whale up-calls and (c) sei whale downsweeps. Red line represent fitted logistic regression and N_{min}, represents the minimum number of calls necessary to achieve 90% probability of accurately predicting species presence based on the fitted model.

Figure 4.

Detections of fin whale 20 Hz song shown as hours per day with detections for data collected in 2006, and from 2008-2010. Red lines indicate periods with missing data.

Figure 5.

Detections of right whale up-calls and sei whale downsweeps, shown as hours per day with detections for data collected in 2006, and from 2008-2010. Red lines indicate periods with missing data.

Figure 6.

Detections of blue whale AB song, shown as number of detections per day for data collected in 2006, 2007 and 2009. No blue whales were detected in 2008 and 2010. Red lines indicate periods with missing data.

Figure 1.

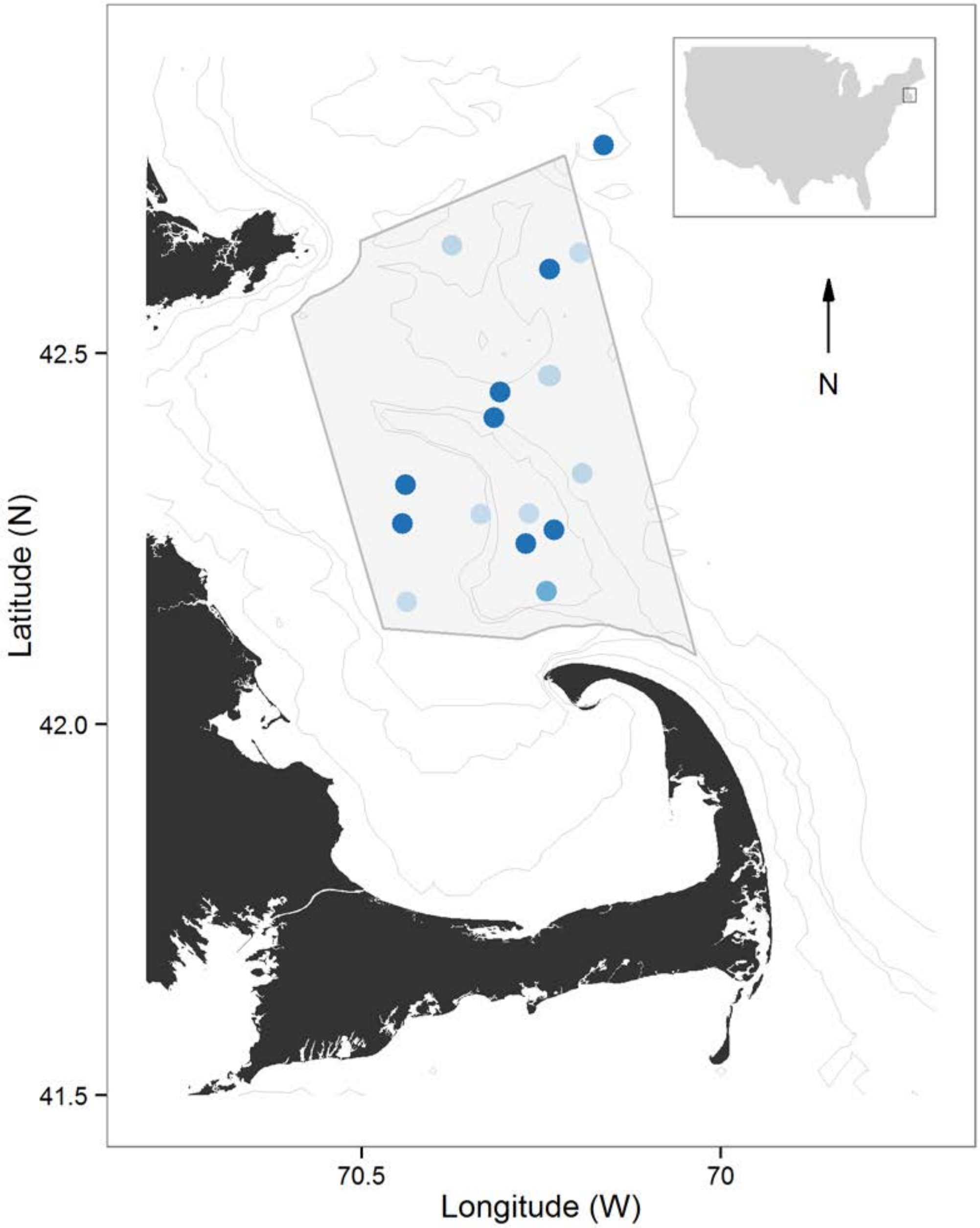


Figure 2.

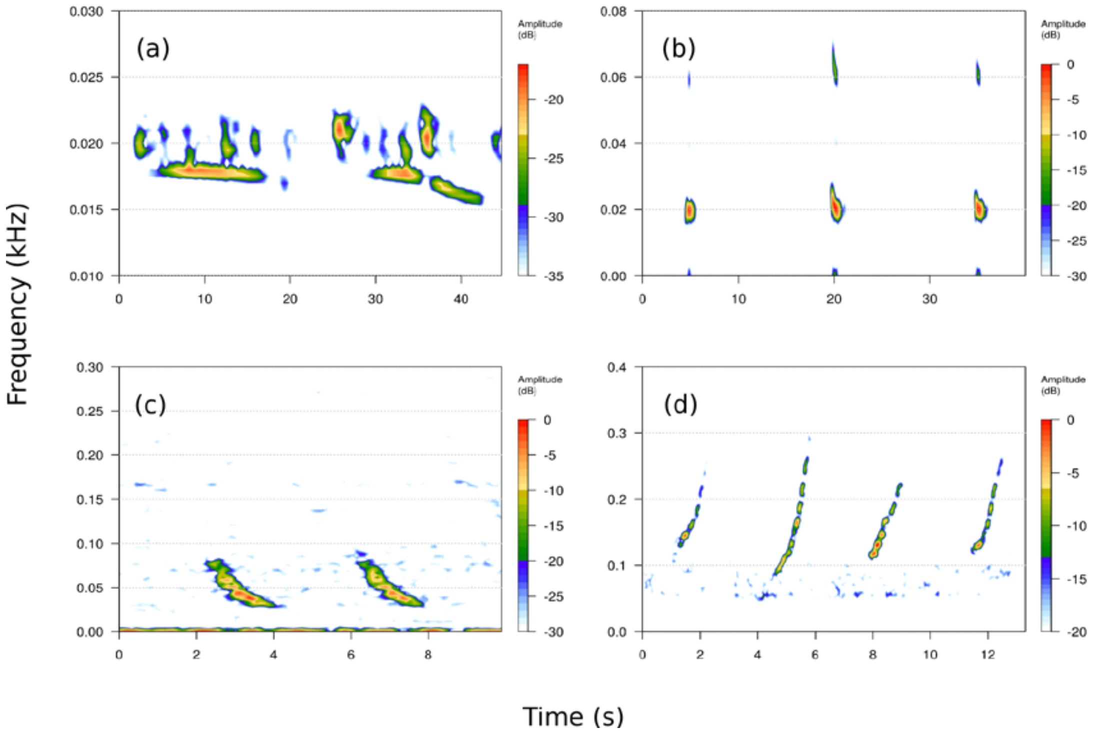

(a)
(b)
(c)
(d)
Frequency (kHz)
Time (s)
Amplitude (dB)
0.030
0.025
0.020
0.015
0.010
0
10
20
30
40
-20
-25
-30
-35
0.08
0.06
0.04
0.02
0.00
0
-5
-10
-15
-20
-25
-30
0.30
0.25
0.20
0.15
0.10
0.05
0.00
2
4
6
8
0.4
0.3
0.2
0.1
0.0
12

Figure 3.

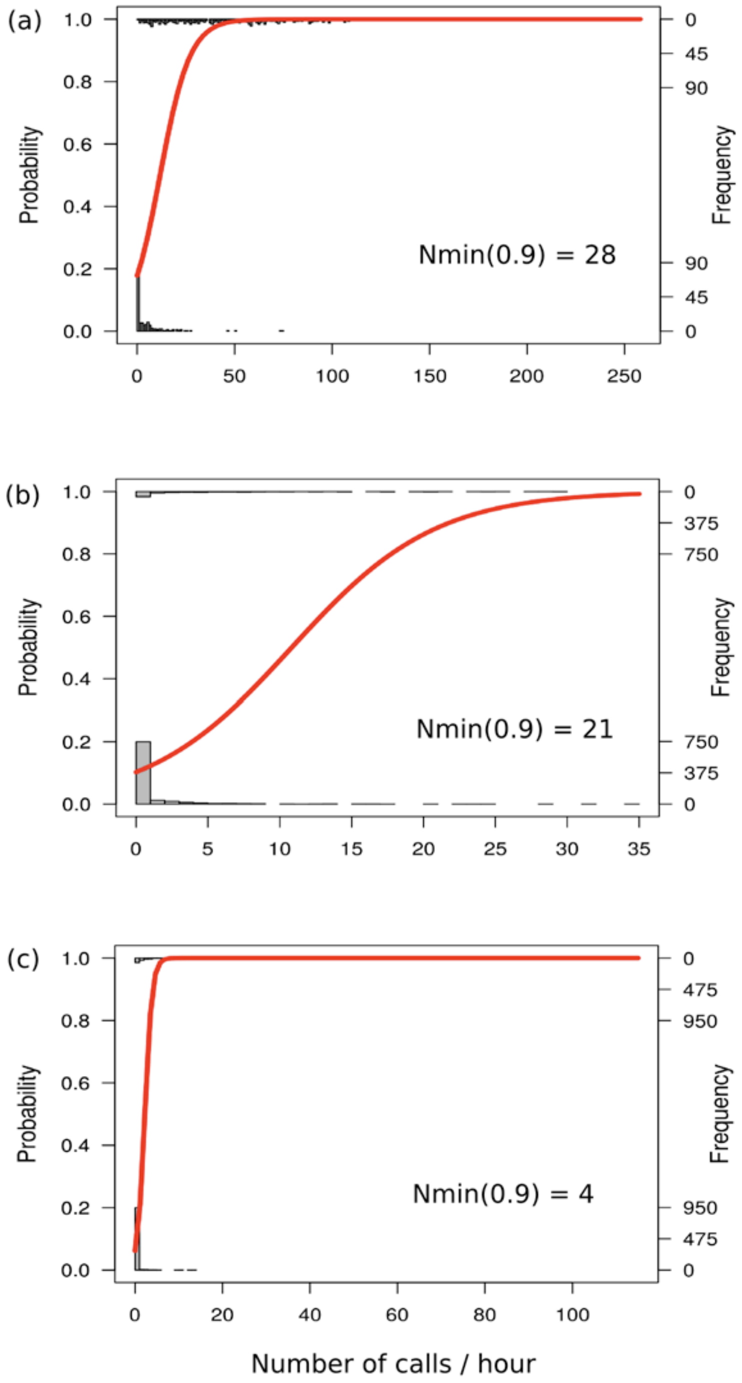

(a)
Probability
1.0
0.8
0.6
0.4
0.2
0.0
Frequency
0
45
90
90
45
0
Nmin(0.9) = 28
0
50
100
150
200
250
(b)
Probability
1.0
0.8
0.6
0.4
0.2
0.0
Frequency
0
375
750
750
375
0
Nmin(0.9) = 21
0
5
10
15
20
25
30
35
(c)
Probability
1.0
0.8
0.6
0.4
0.2
0.0
Frequency
0
475
950
950
475
0
Nmin(0.9) = 4
0
20
40
60
80
100
Number of calls / hour

Figure 4.

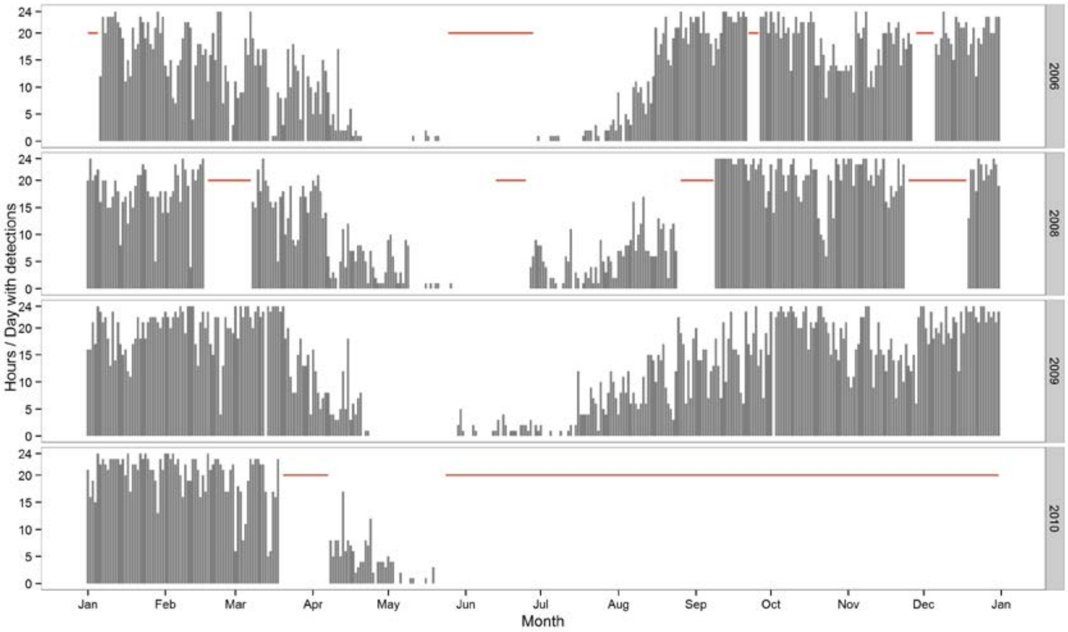

Hours / Day with detections
24
20
15
10
5
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Month
2006
2008
2009
2010

Figure 5.

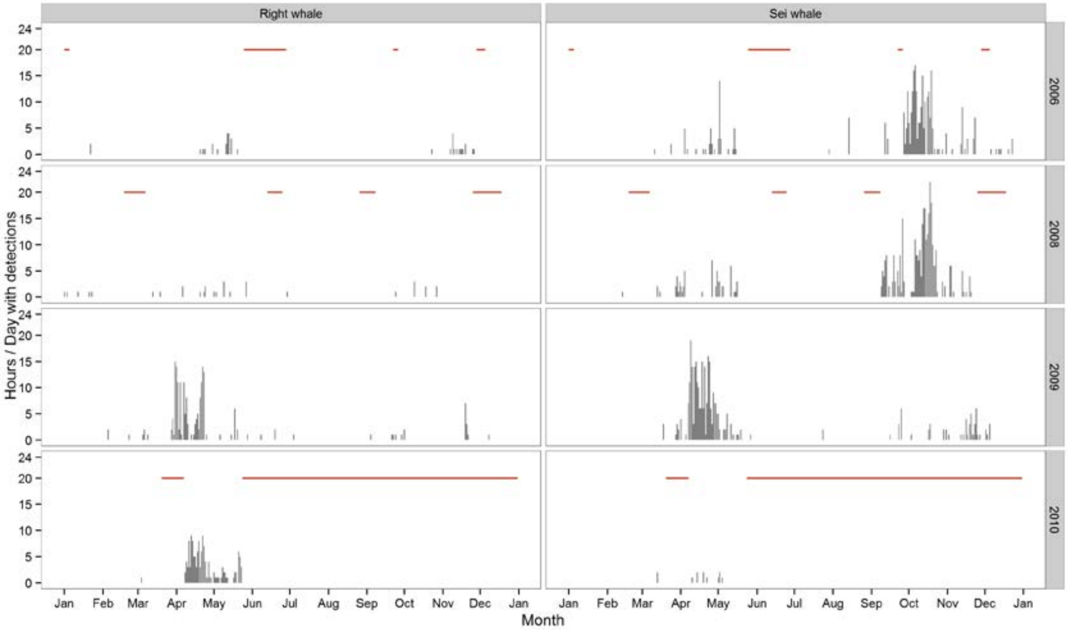
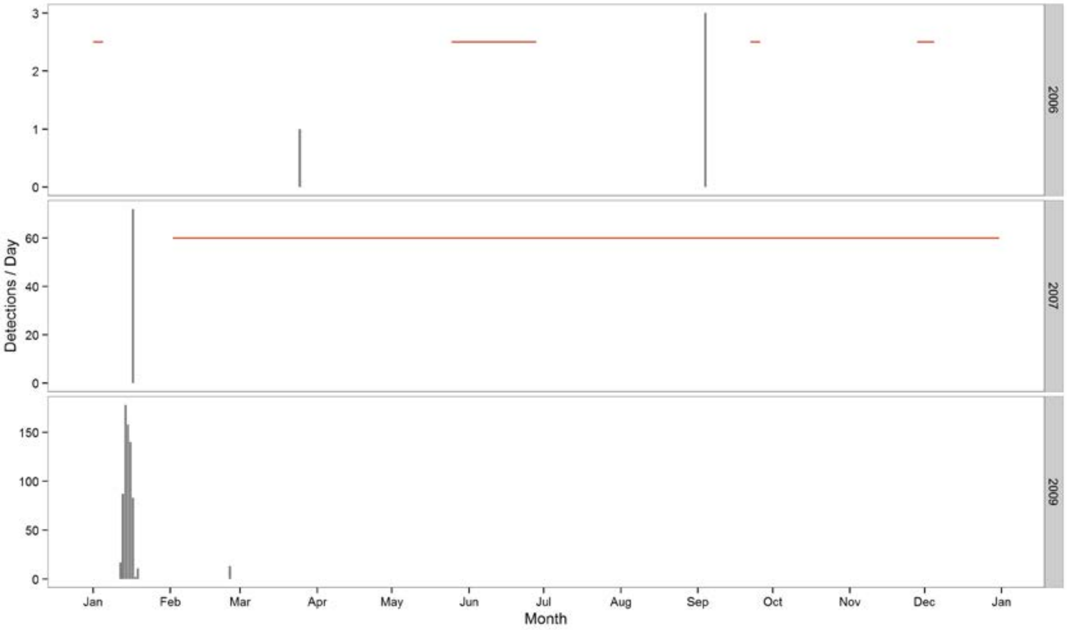

Right whale
Sei whale
2006
2008
2009
2010
Hours / Day with detections
24
20
15
10
5
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Month

Figure 6.


3
2
1
0
2006
60
40
20
0
2007
Detections / Day
150
100
50
0
2009
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Month

PART B

Passive acoustic monitoring & acoustic ecology of minke whales

Chapter III

Risch D, Clark CW, Dugan PJ, Popescu M, Siebert U, Van Parijs SM (2013) Minke whale acoustic behavior and multi-year seasonal and diel vocalization patterns in Massachusetts Bay, USA. *Marine Ecology Progress Series*. 489: 279-295. doi:10.3354/meps10426.

Photo: David Gaspard

North Atlantic minke whale (*Balaenoptera acutorostrata*).

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Minke whale acoustic behavior and multi-year seasonal and diel vocalization patterns in Massachusetts Bay, USA

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ABSTRACT: Passive acoustic monitoring (PAM) is a rapidly growing field, providing valuable insights in marine ecology. The approach allows for long-term, species-specific monitoring over a range of spatial scales. For many baleen whales fundamental information on seasonal occurrence and distribution is still missing. In this study, pulse trains produced by the North Atlantic minke whale, a highly mobile and cryptic species, are used to examine its seasonality, diel vocalization patterns and spatial distribution throughout the Stellwagen Bank National Marine Sanctuary (SBNMS), USA. Three and a half years (2006, 2007 to 2010) of near continuous passive acoustic data were analyzed using automated detection methods. Random forests and cluster analyses grouped pulse trains into 3 main categories (slow-down, constant and speed-up), with several subtypes. Slow-down pulse trains were the most commonly recorded call category. Minke whale pulse train occurrence was highly seasonal across all years. Detections were made from August to November, with 88% occurring in September and October. No detections were recorded in January and February, and only few from March to June. Minke whale pulse trains showed a distinct diel pattern, with a nighttime peak from approximately 20:00 to 01:00 h Eastern Standard Time (EST). The highest numbers of pulse trains were detected to the east of Stellwagen Bank, suggesting that minke whales travel preferably in deeper waters along the outer edge of the sanctuary. These data show that minke whales consistently use Stellwagen Bank as part of their migration route to and from the feeding grounds. Unlike other baleen whales in this area they do not appear to have a persistent year-round acoustic presence.

KEY WORDS: Minke whale · *Balaenoptera acutorostrata* · Vocalizations · Pulse train · Seasonality · Diel variation · Passive acoustic monitoring

INTRODUCTION

Many mammals live in fluid social networks, where individuals move over long distances and in relation to one another. In such social systems most aspects of behavior, such as maintaining social contact, mate attraction, territorial defense or anti-predator response, are often mediated by acoustic communication (see McComb & Reby 2005 for a review). Due to natural limitations of light propagation in the marine environment, cetaceans in particular have evolved to rely on sound for many aspects of their lives. For example, most baleen whales use low-frequency signals that can propagate over large distances for maintaining social contact during long migrations and in social contexts such as mating (e.g.

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Tyack & Clark 2000). Sound production may also be related to feeding and navigation (e.g. Clark & Ellison 2004, Stimpert et al. 2007).

In recent years, passive acoustic monitoring (PAM) has become an important tool for monitoring cetaceans. PAM is especially useful in remote areas, during nighttime or adverse weather conditions and in general for species that are difficult to study at sea (e.g. Moore et al. 2006, Mellinger et al. 2007a, Van Parijs et al. 2009). It can generate long-term records of seasonal occurrence and distribution patterns, providing valuable insights into the habitat utilization of vocally active species, their presence in certain areas and when they may be at risk of deleterious anthropogenic impacts (e.g. Gallus et al. 2012, Mussoline et al. 2012). Where detailed knowledge on the vocal behavior of species exists, these new methods can be used effectively in density estimations (e.g. Barlow & Taylor 2005, Lewis et al. 2007, Marques et al. 2013).

Given the high mobility and wide range of most baleen whale species, it is challenging to gather even elementary data on their ecology. New methods, such as PAM, may therefore provide a great opportunity to collect baseline ecological data, which cannot be acquired through other methods for some species. However, for many baleen whale species, including minke whales *Balaenoptera acutorostrata* in the North Atlantic, fundamental knowledge on their acoustic behavior is still missing, often rendering it difficult to interpret PAM data appropriately.

Minke whales occur widely throughout the North Atlantic. They range from Baffin Bay to the Caribbean in the western North Atlantic and from the Barents Sea to the west African continental shelf in the eastern North Atlantic (Van Waerebeek et al. 1999, Reilly et al. 2008). In the central North Atlantic pronounced sexual segregation exists on higher latitude feeding grounds, with females occurring farther north off western Greenland and males remaining further south and along the eastern coast of Greenland (Laidre et al. 2009). While there is evidence that minke whales undertake seasonal migrations between feeding and breeding grounds (e.g. Mitchell 1991, Van Waerebeek et al. 1999, Skaug et al. 2004), some individuals may also stay in temperate waters year-round (Macleod et al. 2004). Anderwald et al. (2011) suggest that there may be 2 separate breeding populations in the North Atlantic. However, to date no breeding grounds have been identified, and winter distribution and occurrence of this species is still barely understood.

North Atlantic minke whales are currently listed as a species of least concern under the IUCN Red List (Reilly et al. 2008). The current estimate for the North American east coast is 8987 (CV = 0.32) individuals (Waring et al. 2012). Nonetheless, the species is still commercially hunted across its summer range (Robards & Reeves 2011, see also www.iwcoffice.org). In addition, like most species of marine mammals, it is subject to indirect takes in fisheries (Benjamins et al. 2012) and is exposed to a variety of other threats, including ship-strike, chemical and noise pollution, and degradation and loss of habitat. Considering increasingly complex scenarios of human impacts on the marine environment (e.g. Halpern et al. 2008, Davidson et al. 2012) and the lack of distribution and abundance data for North Atlantic minke whales beyond their summer range, there is a clear need for improved monitoring to ensure that healthy populations are maintained across their entire habitat.

Current monitoring and abundance estimates for minke whales are based on visual data (e.g. Skaug et al. 2004, de Boer 2010, Bartha et al. 2011). However, visual detection of this species at sea can be difficult due to its small size and cryptic behavior (e.g. Rankin et al. 2007). Alternative methods, such as PAM, offer a great opportunity to significantly improve studies of the ecology, behavior, distribution and abundance of this species (Oswald et al. 2011).

Minke whales are known to produce a variety of sounds across their range of occurrence. Low-frequency downsweeps, higher frequency clicks and a variety of other sounds have been reported from the Antarctic (Schevill & Watkins 1972, Leatherwood et al. 1981). More recently, Rankin & Barlow (2005) attributed the North Pacific ‘boing’ sounds to this species, and Gedamke et al. (2001) described the distinct ‘star wars’ vocalization, produced by Australian dwarf minke whales *Balaenoptera acutorostrata*.

In the North Atlantic, Beamish & Mitchell (1973) attributed series of clicks in the 5 to 6 kHz range to minke whales, and Edds-Walton (2000) recorded frequency-modulated downsweeps (118 to 80 Hz) in the Gulf of St. Lawrence, Canada. Finally, in the Caribbean, Winn & Perkins (1976) and Mellinger et al. (2000) recorded low-frequency pulse trains with varying interpulse interval (IPI) structure.

Recent advances in statistical methodology enabled estimates of cell density for North Pacific minke ‘boing’ vocalizations (Marques et al. 2010, Martin et al. 2013). However, in order to convert these call densities to estimates of animal abundance, it is crucial to estimate cue rates reliably (Marques et al. 2010, 2013). The rate with which animals vocalize may vary with call type, sex of calling animal, behavioral state, season, location, group size and level of disturbance (e.g. Croll et al. 2002, Oleson et al. 2007a,b, Parks et al. 2011, Risch et al. 2012). Thus, a better understanding of basic minke whale vocal behavior is necessary to use PAM beyond species presence/absence detection.

In this study, minke whale pulse trains were recorded across 3.5 yr in the Stellwagen Bank National Marine Sanctuary (SBNMS), Massachusetts, USA. Pulse train characteristics were first examined in detail. Using multivariate statistical analyses, different types were then classified and their relative frequency of occurrence analyzed. In addition, an automated detection algorithm was developed to describe seasonal, spatial and diel patterns of pulse train occurrence.

MATERIALS AND METHODS

Data collection

Multi-year acoustic data were collected as part of 2 long-term monitoring projects carried out in 2006 and from December 2007 to May 2010 in the SBNMS (Fig. 1) and surrounding waters (see also Hatch et al. 2008, Hatch et al. 2012). Recordings were made using arrays of 9 to 10 marine autonomous recording units (MARUs) (Calupca et al. 2000). Each MARU was equipped with an HTI-94-SSQ hydrophone (High Tech Instruments; sensitivity: −168 dB re 1 V/µPa), connected to a pre-amplifier and A/D converter with 12 bit resolution, resulting in an effective system sensitivity of −151.7 dB re 1 V/µPa. All units sampled continuously at a rate of 2000 Hz, yielding an effective analysis bandwidth of 10 to 1000 Hz, with a flat frequency response (±1 dB) between 55 and 585 Hz. The units were moored 1 to 2 m above the sea floor in depths ranging from 30 to 100 m. Units were typically deployed for 3 mo at a time and were recovered and redeployed throughout the study period.

Pulse train measurements

Preliminary seasonal data analyses showed a peak of minke whale pulse train occurrence from late summer into autumn. Therefore, a subsample of the entire dataset, encompassing a total of 44 d in August, September and October in 2006 and 2008, were reviewed visually and aurally (fast Fourier transformation [FFT] size: 1024 points, 85% overlap, Hanning window), using the sound analysis software XBAT (Figueroa & Robbins 2008). Good quality (signal-to-noise ratio [SNR] > 10 dB), non-overlapping pulse trains were selected for detailed acoustic measurements. In an effort to reduce oversampling of single individuals, not more than 5 pulse trains per hour and a maximum of 40 pulse trains per day were selected for this analysis. Acoustic data were bandpass filtered from 30 to 800 Hz to remove environmental noise and sounds from other species.

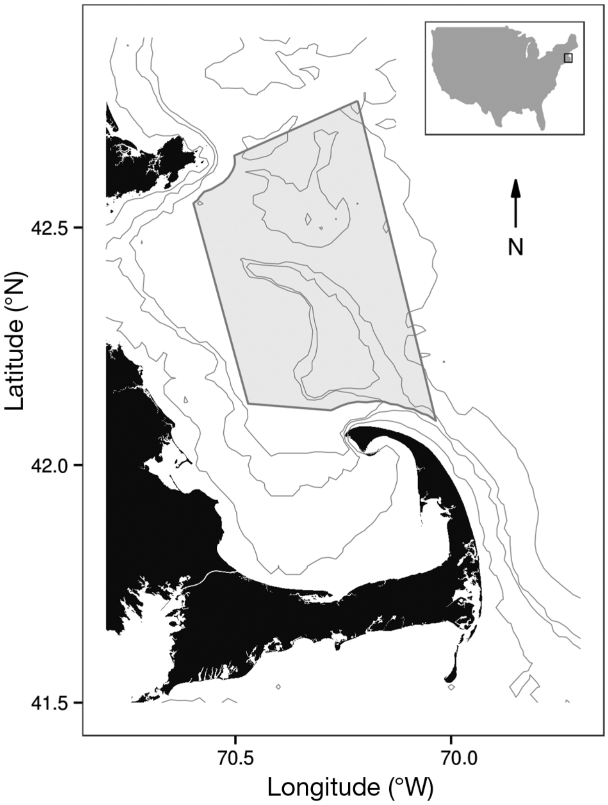

Fig. 1. Gulf of Maine with the Stellwagen Bank National Marine Sanctuary (SBNMS) outlined and shaded in gray. Inset map in upper right corner shows the position of the study area along the US eastern coast

Spectrograms (FFT size: 512 points, 96.9% overlap, Hanning window, time resolution: 8 ms, frequency resolution: 4 Hz) of this subset of data were generated and analyzed with Avisoft-SASLab Pro 5.1 (Avisoft Bioacoustics). The automatic parameter measurement tool was used to measure pulse trains. Individual pulses were detected using an amplitude threshold of −30 to −55 dB sound pressure level (SPL) relative to the maximum SPL in the sound file. The threshold was manually adjusted to ensure the detection of every pulse within a pulse train. For each detected pulse, the following parameters were measured: start and end time (s), peak, and 1st, 2nd and 3rd quartile frequencies (Hz). Frequency measurements were taken at the start, end and center of the pulse and over the mean spectrum of the pulse. From these measurements, pulse duration (s), interquartile range (IQR) and bandwidth (Hz) were derived. In addition, the following parameters were obtained to characterize the entire pulse train: duration (s; start of first pulse to end of last pulse), number of pulses, mean IPI (s; time between starts of 2 consecutive pulses), start and end IPI (s; averaged over the first and last 20 % of pulses, respectively), change in pulse rate (1/IPI (1/s); difference of averaged values for first and last 20 %) and change in frequencies over time (Hz; difference of averaged first and last 20 % mean spectrum measures).

Classification of pulse trains and relative rate of occurrence

From recordings obtained in the Caribbean, Mellinger et al. (2000) described 2 types of minke whale pulse trains, which differ in IPI structure: the slow-down and the speed-up type. Initial analysis of our data found both of these types, as well as a third, that showed no change in IPI over time. Based on these initial observations, pulse trains were grouped into 1 of 3 categories. Pulse trains were labeled as ‘speed-up’ if the change in pulse rate was <–0.5 and ‘slow-down’ if it was >0.5. If the change in pulse rate was in between these values, pulse trains were labeled as ‘constant’.

Subsequently, a supervised random forest model was fitted to the data and the resulting matrix of data dissimilarity was used as input for a fuzzy *c*-means cluster analysis. This multivariate statistical approach was taken to produce a less subjective and reproducible method of vocal repertoire classification, while taking the obvious importance of IPI structure and previous classification based on it into account. Random forests combine predictions of many classification trees, built on random subsets of the data (Breiman et al. 1984, Strobl et al. 2009). The strengths of random forests include high classification accuracy, the availability of methods to assess variable importance and measures of data similarity that allow classification of the original data set (e.g. Cutler et al. 2007). All statistical analyses were conducted using R v. 2.15 (available at www.R-project.org). The cforest function in the party package (Strobl et al. 2008) was used for random forest analysis and the number of trees was set to 1000. A total of 30 spectral and temporal predictor variables (see ‘Pulse train measurements’ above) were included in this analysis. Following suggestions in the literature (e.g. Cutler et al. 2007, Strobl et al. 2009), the number of randomly chosen predictor variables at each split was set to the square root of all available predictor variables (n = 6).

The fanny function of the cluster package (Maechler et al. 2012) was used for fuzzy *c*-means clustering and calculating silhouette plots. Fuzzy *c*-means clustering differs from other clustering algorithms in that each observation is assigned to various clusters and the degree of membership is quantified by a coefficient ranging from 0 to 1, with the sum over all clusters being equal to 1 (Kaufman & Rousseeuw 1990). This method was chosen since it allows for more ambiguity in the data than traditional ‘hard’ clustering methods and thus proves more realistic in most ecological contexts (e.g. Jackson et al. 2010). The average silhouette width index (Rousseeuw 1987) was used to determine the optimal number of clusters, *k*. The underlying technique determines the association between object *i* and other members of its cluster and the strength of this association as compared to *i*’s relation to members from other clusters. The silhouette value s_i ranges from −1 to 1, where 1 indicates that object *i* fits well within its cluster and −1 that it is not well classified. The average silhouette width of a cluster indicates how tightly grouped the data in the cluster are and the overall average silhouette width is a measure of how well the data is structured. The optimal number of *k* groups can be found by comparing the silhouette width indices for a range of clustering solutions using different *k*s and selecting the one yielding the highest average silhouette width, called the silhouette coefficient (SC). It has been suggested that a reasonable structure in the data is found when SC > 0.5 and that a strong structure is indicated by SC > 0.7 (Struyf et al. 1996).

In a next step, histograms of IPI for each cluster were calculated and the function mclust of the mclust package (Fraley & Raftery 2010) was applied to fit Gaussian mixture models in order to describe means and standard deviations of IPI distribution peaks for each cluster.

Finally, the relative frequency of occurrence of each cluster was examined by fully annotating 2 days with peak minke whale pulse train occurrence in 2006 (1 September and 7 October) and 2008 (18 September and 19 September). Each identifiable pulse train was placed in 1 of the clusters and results were plotted as histograms.

Automatic detection

Three and a half years (2006, 2007 to 2010) of data were examined with an automatic detection algorithm that was implemented in a high performance computing (HPC) platform, using custom-built Matlab R2012b scripts (Dugan et al. 2011). The automatic detection consisted of a multi-stage process based on spectrogram intensity binarization, energy projection, feature extraction and classification (Popescu et al. 2013). A set of 18 basic features was extracted from each detected event and passed to a ripple-down rule (RIDOR) learner (Gaines & Compton 1995) for final classification. While the detection stage was designed for general pulse train detection, the RIDOR was trained to identify minke whale pulse trains. However, the RIDOR did not distinguish between the different types of pulse trains as identified in this study.

Performance of the detector was evaluated by creating a truth data set, consisting of minke whale pulse trains mixed with segments of noise. Noise segments were selected to describe typical scenarios of variable seasonal background noise in this region. All pulse trains of the truth data set were scored on a scale of 1 to 4 by their signal quality, with Category 1 calls being of low quality and Category 4 calls appearing clear and well above background noise on the spectrogram. All detection data were post-processed and false positive detections were removed from the final dataset. Post-processing and assembly of the truth data set were performed by an experienced data analyst (D.R.).

Seasonality and diel patterns

To examine seasonal and diel patterns of pulse train occurrence, 1 channel of each multi-channel dataset was selected for analysis. Channels were selected with the aim to maximize recording time, while keeping a consistent recording location. Due to varying study designs over the years and MARU loss due to trawling, the latter was not always possible. Overall the mean ± SE distance between 19 different recording locations was 26 ± 16 km (n = 171). All data were binned by hour and results plotted by day.

Diel patterns were assessed during the peak season of pulse train occurrence (15 July to 15 November 2006, 2008 and 2009) and only days with detections were used for this analysis. To account for variation in calling rates from one day to the next, mean-adjusted hourly calling rates were calculated by subtracting the average number of detections per day from the number of calls in each hour of the same day (Stafford et al. 2005). Hourly calling rates were then averaged for 3 different light regimes: 'light', 'twilight' and 'dark'. The sun-methods function of the maptools package (Lewin-Koh & Bivand 2012) was used to determine sun altitude in each hour of analysis for Provincetown, Massachusetts (42.1° N, 70.2° W), the closest land point to the deployed acoustic recorders. 'Light' periods were defined as those hours with a sun altitude greater than 0° (approx. 05:30 to 17:00 h Eastern Standard Time, EST), 'twilight' was based on the definition of nautical twilight with sun altitude between 0° and −12° (approx. 04:30 to 05:30 and 17:00 to 18:00 h EST) and 'dark' were those hours, when the altitude of the sun was less than −12° (approx.18:00 to 04:30 h EST). Since the data were not normally distributed (Saphiro-Wilk test), a Kruskal-Wallis test was used to test for differences between light regimes. Wilcoxon rank-sum tests with Bonferroni corrections for multiple testing were used for post-hoc comparisons between pairs of light regimes.

Spatial patterns

In 2006 MARUs were spaced equally across the SBNMS and recording locations were kept constant throughout the whole year. This dataset was used to examine the spatial distribution of minke whale pulse trains during the peak of their occurrence (15 July to 15 November 2006). For each of the 9 available recording sites the total number of pulse train detections was determined and the data were normalized by the total number of recording days for each site.

RESULTS

Characterization, classification and relative occurrence

From the initial 44 d subsample of the dataset, 396 minke whale pulse trains were selected for detailed analyses. Using the combined approach of supervised random forest and cluster analyses, the best supported grouping of these data resulted in 6 main clusters of pulse trains (Fig. 2). However, the average silhouette width was relatively weak (0.42), suggesting that not all clusters are strongly supported (Kaufman & Rousseeuw 1990). Thus, distinction between

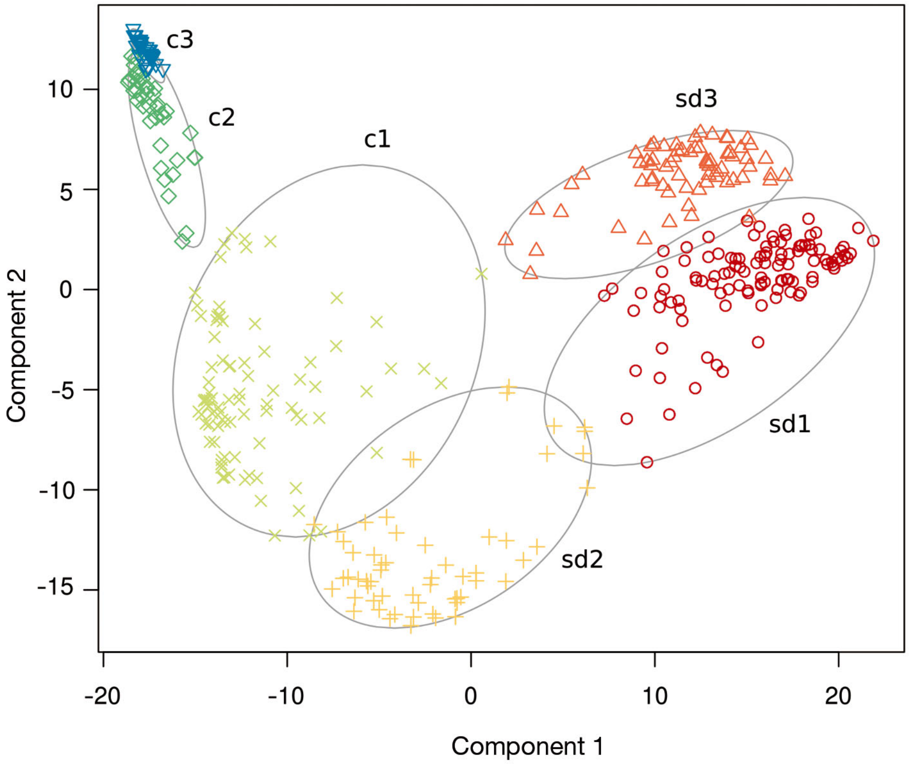

Fig. 2. Bivariate plot of fuzzy cluster analysis results. The 2 components explain 62.76% of the point variability. Data points represent individual pulse trains and are colored and labeled by pulse train type (c: constant; sd: slow-down), as identified by random forest and cluster analyses

some groups may lie along a gradient of similarity. Temporal features such as IPI at the beginning and end of pulse trains, as well as total pulse train duration, number of pulses and mean IPI, were the most important variables for splitting data into groups.

Based on changes in IPI structure, pulse trains recorded in SBNMS can be split into 3 main categories. While the IPI of slow-down pulse trains (Fig. 3a) increases towards the end of the call, constant pulse trains show a constant IPI throughout the entire duration of the call (Fig. 3b). Speed-up pulse trains, as described by Mellinger et al. (2000), were found in our dataset but in much smaller numbers than the other 2 types. In our sample, they accounted for only 14 out of 396 measured pulse trains and thus did not fall out as a separate cluster. Cluster analysis divided the slow-down and constant pulse trains into 3 subgroups for each type. Table 1 summarizes the basic spectral and temporal measurements for all types of pulse trains that were classified in this study.

In general, slow-down pulse trains were characterized by differences in IPI structure and duration. All calls in this category had a bimodal distribution in IPI. While slow-down types 1 and 2 (sd1 and sd2) showed mean peaks in IPI at about 0.30 and 0.47 s, type 3 (sd3) differed, with mean peaks at 0.42 and 0.70 s. Median total call durations were 35.6 and 39.8 s for sd1 and sd3, respectively, while sd2 calls were much shorter in duration, with a median of 17.5 s (Fig. 3a).

Constant pulse trains were subdivided, based primarily on differences in IPI. While constant pulse trains of type 1 (c1) had a mean IPI of 0.39 s, mean IPI for type 2 (c2) and type 3 (c3) were 0.64 and 0.83 s, respectively (Fig. 3b). Median peak frequencies (PF) for all types of slow-down and constant pulse trains were similar and ranged from 106 to 136 Hz, except for c3, which exhibited a lower median PF of 58 Hz. In addition, most types showed an increase in PF throughout the duration of the call. Although highly variable, the median change in PF ranged from 6 to 23 Hz. Type c3 was the only type with a slight decrease (–5 Hz) in median PF from start to end. With the longest mean IPI and a silhouette width of 0.76, type c3 was also the most distinct group.

Speed-up pulse trains had a median PF of 106 Hz and showed a bimodal IPI distribution, decreasing from 0.54 to 0.37 s throughout the call (Table 1).

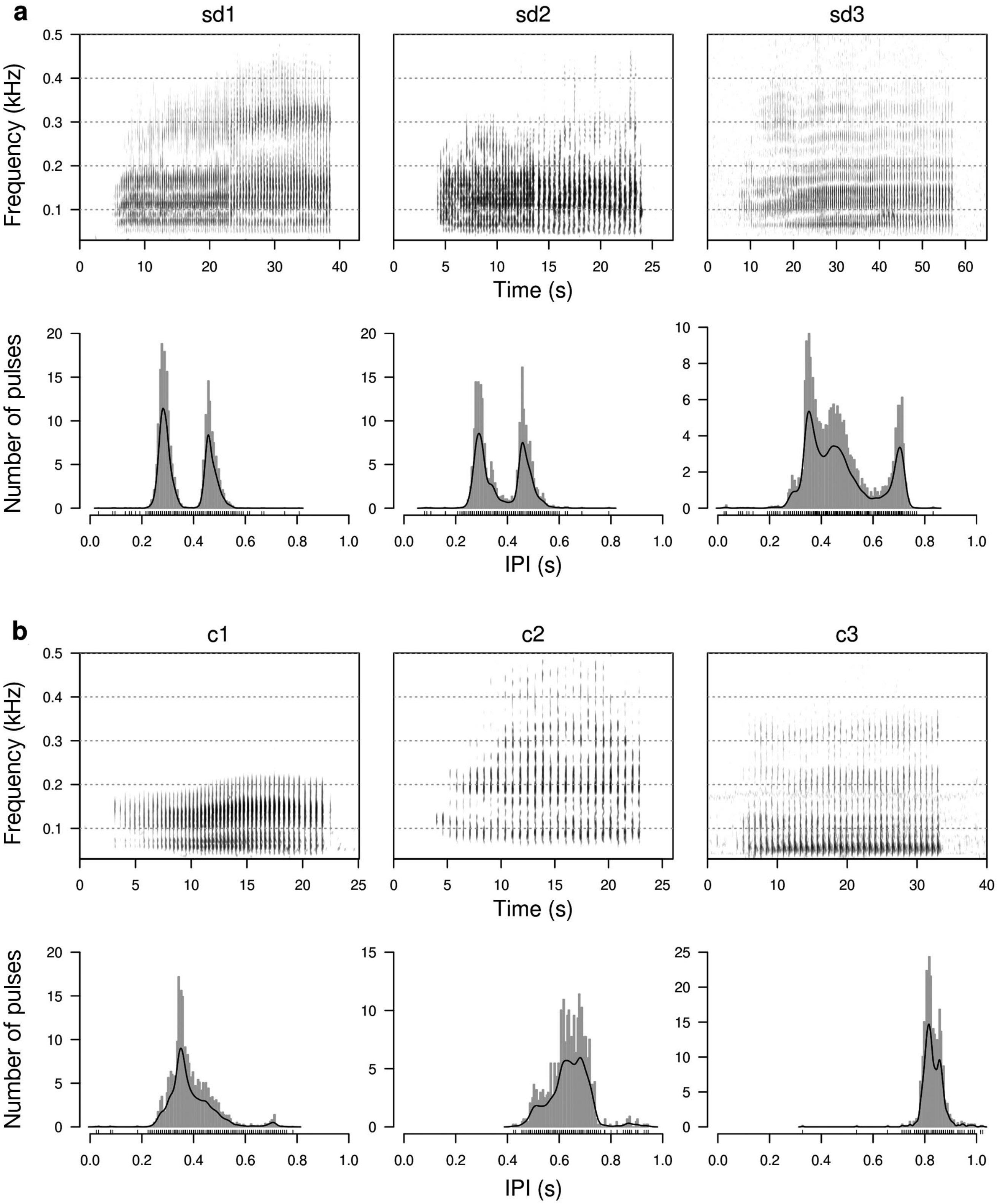

Fig. 3. Spectrograms for (a) slow-down (sd) and (b) constant (c) pulse trains types 1 to 3 and histograms of interpulse interval (IPI). Note the different *x*- and *y*-axis scales for spectrograms and histograms, respectively. Spectrogram parameters: fast Fourier transform (FFT) size = 512 points, overlap = 75%, sample rate = 2000, resolution = 3.9 Hz and 64 ms. Black lines on histograms indicate fit of Gaussian kernel density functions with bin widths 0.005 for sd1 and c3 and 0.01 for all other plots

Table 1. Descriptive statistics of minke whale pulse trains recorded in the Stellwagen Bank National Marine Sanctuary (SBNMS). Measurements are median values with 25th and 75th percentiles (in parentheses); interpulse interval (IPI) peaks are mean values ± SD

Pulse train type	n	No. of pulses (s)	Pulse train duration (s)	Pulse duration (s)	Peak frequency (Hz)	Change in peak frequency (Hz)	1st IPI peak (s)	2nd IPI peak (s)
Slow-down								
Type 1	109	102 (87, 122)	35.6 (30.6, 43.9)	0.1 (0.09, 0.11)	131 (126, 138)	6 (−1, 13)	0.29 ± 0.02	0.47 ± 0.03
Type 2	58	48 (30, 57)	17.5 (11.5, 20.9)	0.1 (0.08, 0.11)	129 (121, 138)	11 (−1, 22)	0.30 ± 0.03	0.47 ± 0.04
Type 3	68	86 (74, 93)	39.8 (35.0, 44.1)	0.08 (0.07, 0.09)	120 (116, 126)	23 (6, 33)	0.42 ± 0.08	0.70 ± 0.02
Constant								
Type 1	73	46 (36, 58)	17.7 (12.5, 23.2)	0.07 (0.06, 0.08)	129 (114, 133)	15 (0, 22)	0.39 ± 0.08	–
Type 2	40	20 (15, 28)	12.6 (9.5, 17.0)	0.08 (0.07, 0.09)	136 (117, 162)	13 (−2, 47)	0.64 ± 0.08	–
Type 3	34	29 (24, 38)	23.3 (19.4, 30.8)	0.12 (0.10, 0.13)	58 (55, 61)	−5 (−10, −1)	0.83 ± 0.04	–
Speed-up	14	29 (26, 38)	12.4 (9.9, 18.0)	0.08 (0.07, 0.09)	106 (95, 137)	19 (−14, 31)	0.54 ± 0.12	0.37 ± 0.02

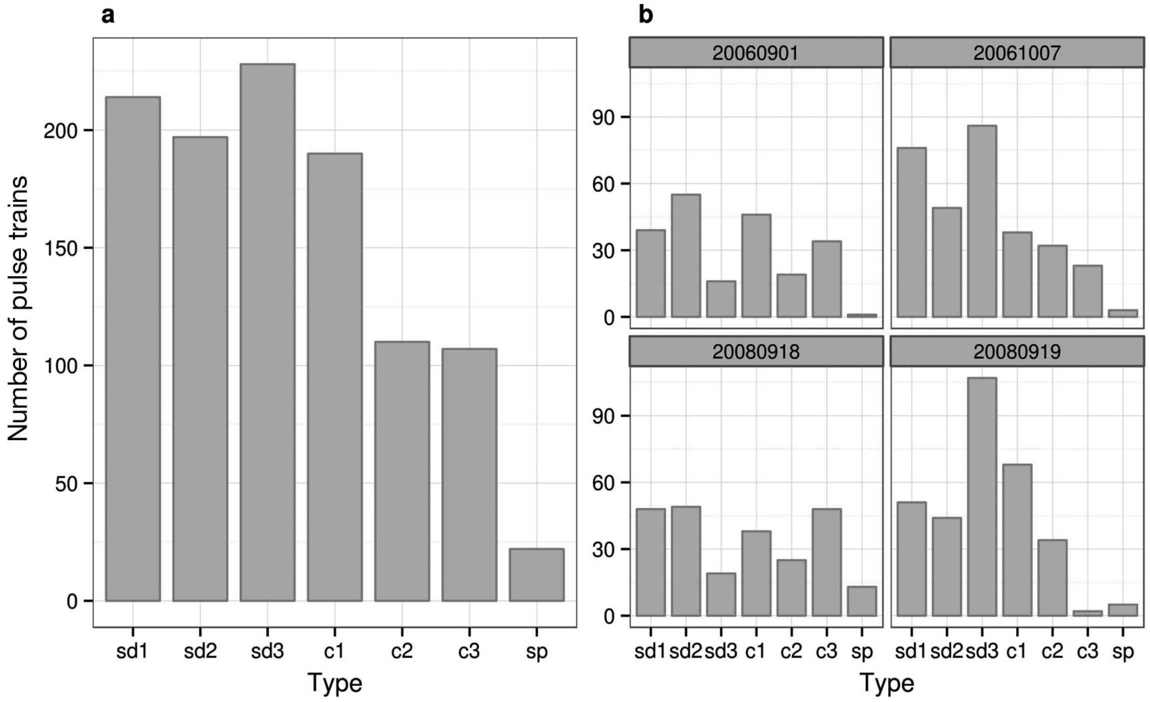

Fig. 4. Frequency distribution of different pulse train types (sd: slow-down; c: constant; sp: speed-up) for 4 randomly sampled days (a) frequency of occurrence over all and (b) split by days. Dates in (b) are given as yyyymmdd

Overall, for all types of pulse trains, most energy was distributed between 50 and 300 Hz.

The pulse train occurrence analysis found all types of identified pulse trains present on each of the 4 selected days (Fig. 4b). The most commonly recorded types were slow-down pulse trains, accounting for 60% of all pulse trains in this sample (n = 1068). While constant pulse trains represented 38% of the sample, only 2% were speed-up pulse trains (Fig. 4a). It should be noted that c1 pulse trains, occurred more frequently than the other 2 constant pulse train types. Structurally, this pulse train category lies between slow-down and constant pulse trains, with an overall mean IPI of 0.39 s (see above) but a few IPIs measured at 0.80 s. Additionally, this group showed some overlap with sd3 (Fig. 2) and had the lowest silhouette width of only 0.3.

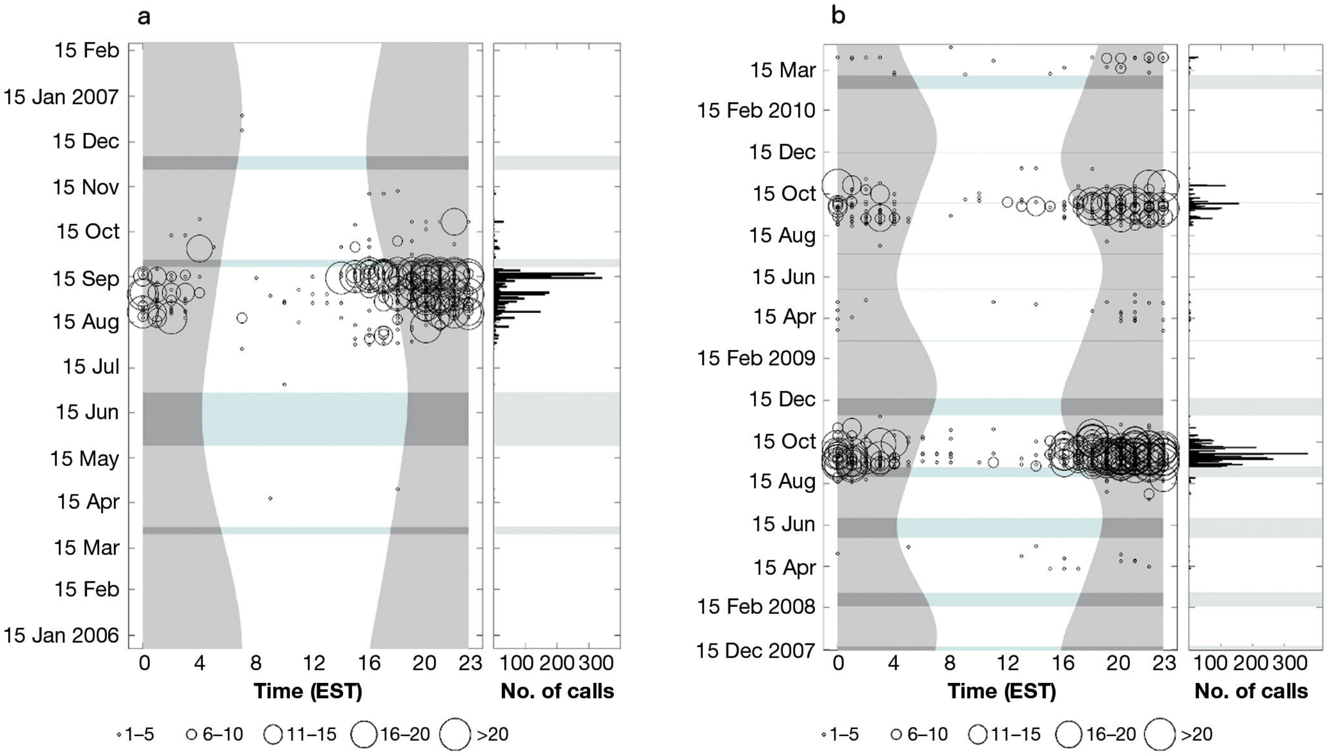

Fig. 5. Seasonal and diel distribution of minke whale pulse trains in (a) 2006 and (b) from December 2007 to March 2010 in the Stellwagen Bank National Marine Sanctuary (SBNMS). Distributions are based on analyses of automatic detection results of 1 channel of data. *Y*-axis shows date; left *x*-axis time of day (h) in US Eastern Standard Time (EST); right *x*-axis number of calls d^{-1}. Grey shading illustrates times between sunset and sunrise. Light blue shading indicates periods of missing data. Circles indicate the number of calls per hour

Detector performance

The truth data set consisted of 2428 manually selected minke whale pulse trains, which had been labeled from low signal quality (1) to high quality calls (4). The automated detector used in this analysis missed 0% (i.e. none) of the pulse trains labeled as Category 4 (n = 54), 8% of Category 3 (n = 415), 21% of Category 2 (n = 1275) and 51% of Category 1 (n = 684). The overall false negative rate for this version of the detector was 27%. The approximately 120 h of truthed data yielded 181 false positive detections.

Seasonality and diel patterns

A total of 8790 minke whale pulse trains were detected across the 3.5 yr of 1-channel recordings from the SBNMS. The detection of minke whale pulse trains was highly seasonal. Detections peaked during August and September, with 8639 (98%) of events detected over the entire analysis period occurring from mid-July to mid-November. Fig. 5 illustrates the seasonal and diel patterns of pulse train occurrence. Detections generally increased over the month of August and peaked in September and October, with 7769 (88%) of all detections from all years taking place during these 2 mo. No pulse trains were recorded during January or February of any year, and only a few detections were made from March to June. This strong seasonal pattern was repeated in all 3 full recording years (2006, 2008 and 2009; Fig. 5).

Pulse train occurrence during the peak season (July to November) followed a very distinct diel pattern, with most detections recorded during the 'dark' period, from about 18:00 to 00:00 h EST (Figs. 5 & 6). The mean number of calls per hour increased around twilight, and was highest around 19:00 EST and lowest during daylight hours (Fig. 6a). Hourly mean ± SE adjusted values were −1.47 ± 0.08, −0.42 ± 0.28, 1.95 ± 0.24 for 'light', 'twilight' and 'dark' periods, respectively (Fig. 6b). Differences between means were statistically significant (Kruskal-Wallis test, χ^2 =

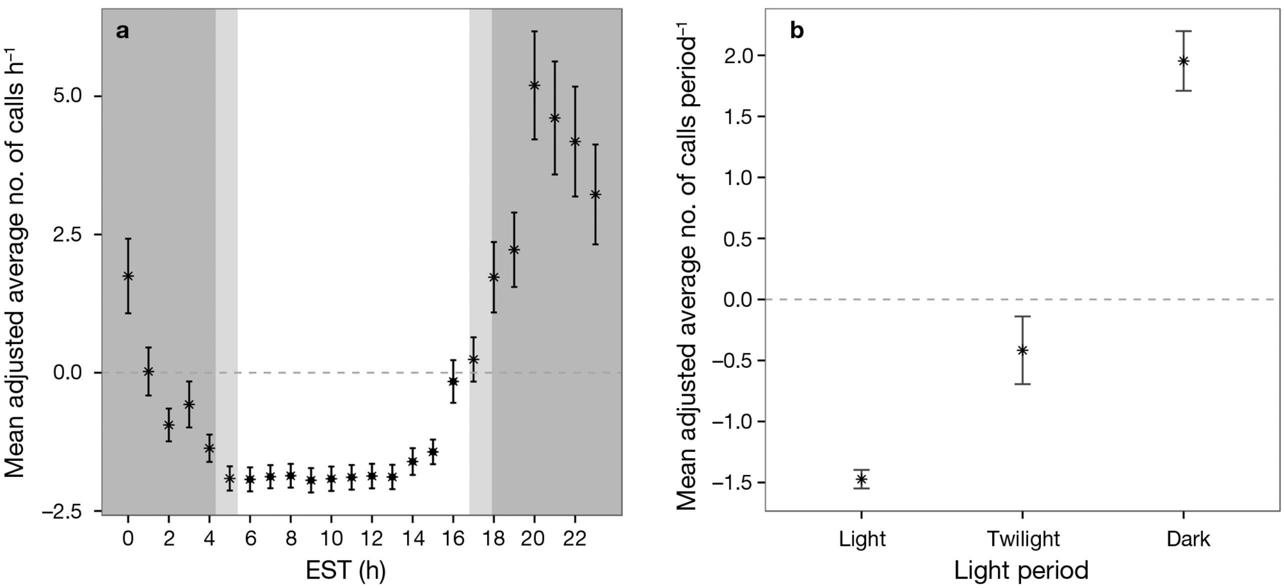

Fig. 6. (a) Mean ± SE of minke whale pulse trains per hour over the course of a day. Dark gray shading indicates average dark hours and light gray shading represents twilight hours. (b) Mean ± SE of minke whale pulse trains per light period, as determined by sun altitude. Light: >0° (~05:30 to 17:00 h EST); twilight (nautical twilight): ≤0° and ≥−12° (~04:30 to 05:30 and 17:00 to 18:00 h EST); dark: <−12° (~18:00 to 04:30 h EST). Diel analyses were based on data recorded from 15 July to 15 November 2006, 2008 and 2009

240.67, df = 2, p < 0.0001), and post-hoc comparisons between all pairs of means were significant at an alpha level of 0.001.

Spatial patterns

From 15 July to 15 November 2006, 32 029 minke whale pulse trains were recorded on 9 MARUs, deployed throughout SBNMS. Fig. 7 illustrates the spatial distribution of these detections by plots of circles with radii of approximately 15 km around the MARU's location. This representation incorporates a conservative detection range estimate for these calls based on preliminary source level data (D. Risch unpubl. data) and illustrates almost full range coverage of SBNMS, with some overlap between units. Since our main interest was in the relative spatial occurrence patterns, no adjustment for detection range overlap between units was performed in this analysis. Therefore, some pulse trains may have been detected on multiple units.

Although, pulse trains were detected across SBNMS, the majority of detections occurred in the eastern and southeastern parts of the sanctuary (Fig. 7). Overall, there were 120 detections/recording days on the most southeastern MARU, compared to a low of 5 detections/recording days at the most northern location.

DISCUSSION

Prior to this study, minke whale pulse trains in the North Atlantic were described most comprehensively from an area northeast of Puerto Rico by Mellinger et al. (2000), while Clark & Gagnon (2004) described the seasonal occurrence of minke whale pulse trains in parts of the western North Atlantic. Although these authors could not visually confirm species identity, they concluded that the sounds they described were produced by minke whales, based on structural sound similarity to and geographic overlap of sample regions with Winn & Perkins (1976). In their earlier study, Winn & Perkins (1976) had been able to match acoustic recordings with visual observations of minke whales during several single species encounters in deeper waters of the Caribbean region. The present study is the first to describe long-term occurrence and distribution patterns of minke whale pulse trains in the western Gulf of Maine.

Detector performance

Minke whale pulse trains are structurally variable and their long signal durations frequently result in overlap in frequency and timing of vocal activity. In addition, they overlap with other baleen whale species, particularly humpback whales, communicat-

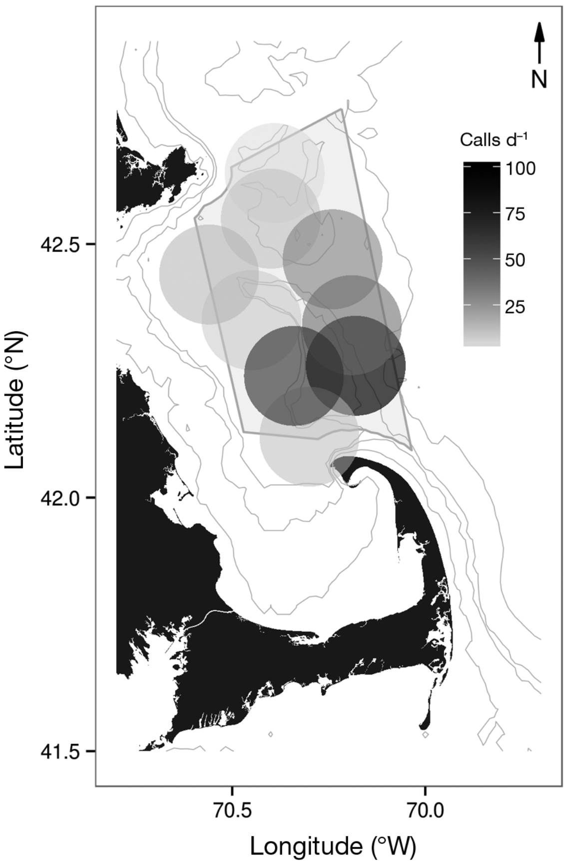

Fig. 7. Spatial distribution of minke whale pulse trains recorded throughout the Stellwagen Bank National Marine Sanctuary (SBNMS) from 15 July to 15 November 2006. Circles extend approximately 15 km in radius from marine autonomous recording unit (MARU) locations, and shadings reflect total number of recorded pulse trains per day, normalized by the number of recording days for each site

ing in a similar frequency range. These conditions, along with year-round high underwater noise levels, created a challenging acoustic scene for developing species-specific detectors for our study area. However, with an overall false negative rate of 27% (below 10% for strong signals), and a relatively low false positive rate, the pulse train detector used in this study served well for our broad-scale questions of seasonal, diel and spatial occurrence patterns.

Classification and characterization

In order to compare our data to Mellinger et al. (2000), we initially classified pulse trains according to their IPI structure. We then described further variability in the dataset using a combination of supervised random forests and cluster analysis in an effort to increase repeatability of our classification scheme.

The classification of the current dataset yielded 2 main categories: slow-down and constant pulse trains, with 3 sub-types each (Fig. 3). While Mellinger et al. (2000) described the first category, they did not describe the latter. Both types of signals have also been found and associated with minke whales in Onslow Bay, North Carolina, USA (Williams Hodge 2011). Additionally, in the Caribbean data analyzed by Mellinger et al. (2000), 100 out of 110 pulse trains were speed-up, while only 10 were slow-down pulse trains. In contrast, in the SBNMS dataset, only 2% of a 4 d sample (n = 1068) were of this category. Instead, 60% of all calls in SBNMS were slow-down pulse trains.

These observed differences in minke whale vocal repertoire may be due to several reasons. First, the 2 datasets differed markedly in size and temporal scale. While Mellinger et al. analyzed 49 h of recordings, we explored 4 d of continuous acoustic data, collected over 2 different seasons. Since most of our detections occurred at night, while Mellinger et al. recorded mainly during the day, it is conceivable that the observed difference in vocal repertoire is due to a change in vocal repertoire from day- to nighttime. However, our data did not show any indication that this may be the case in our study area.

Second, since the majority of pulse trains recorded by Mellinger et al. were of low SNR, it is possible that the shorter constant pulse trains might have been missed. In addition, Mellinger et al. high-pass filtered their data at 100 to 200 Hz. However, some constant pulse trains described in the current study have PFs between 55 and 61 Hz (e.g. c3; Table 1), and thus, differences in analysis bandwidth might also explain some disparities in vocal repertoire between studies. In this context it is noteworthy that Williams Hodge (2011) described the occasional association of constant pulse trains that match type c3, as described here, with high frequency clicks (PF ~20 kHz). However, our recording bandwidth was too narrow to detect such high frequencies in our data.

Lastly, geographic variation in repertoire size or usage may be responsible for the observed differences. As a specific form of geographic variation, dialects are commonly defined as vocal variation between potentially interbreeding populations (Conner 1982) and have been shown to exist in several species of cetaceans (e.g. Ford 1991, Noad et al. 2000, Rendell & Whitehead 2003). Dialects can arise due to genetic, environmental or social factors, including vocal learning. More simply, if vocal signals are associated with particular behaviors, vocal production may change with behavioral state, which in turn can vary by season and habitat (e.g. Oleson et al. 2007a, Van Parijs et al. 2009).

The behavioral function of minke whale pulse trains is currently unknown. However, it is conceivable that the observed differences in call type distribution might indicate a switch in activity from higher latitude summer feeding to presumed breeding at lower latitude winter grounds (Mitchell 1991, Van Waerebeek et al. 1999). This idea is further supported by structural differences between pulse trains recorded in SBNMS and those from the Caribbean, with the latter lasting about 20 s longer and exhibiting more than twice as many pulses per pulse train (Table 1; Mellinger et al. 2000). A correlation between call duration and arousal state has been demonstrated in some mammal species (Rendall 2003, Charlton et al. 2011). In several baleen whales only the males produce songs, which intensify during the breeding season and seem to play an important role in reproduction (e.g. Tyack 1981, Croll et al. 2002, Oleson et al. 2007b).

Dwarf minke whales wintering on the Great Barrier Reef have been shown to produce repetitive sequences of stereotypic 'star wars' vocalizations, which exhibit characteristics similar to reproductive displays found in other baleen whale species (Gedamke et al. 2001). However, it is currently unknown whether the 'star wars' calls, minke whale 'boings' from the North Pacific, or North Atlantic pulse trains are produced by only one sex or age class and which function they serve in the species' ecology (Gedamke et al. 2001, Oswald et al. 2011).

Thus, it is important to explore the behavioral significance of minke whale vocalizations and whether they may be gender or age specific. Such knowledge is particularly important when analyzing PAM data in the light of species distribution and density. Only part of a population may be successfully captured by monitoring sounds that are exclusively produced by a certain demographic. Minke whale migration in the North Atlantic appears to be segregated by sex, and females prefer higher latitudes during summer (e.g. Øien 1988, Laidre et al. 2009). If minke whale pulse trains are only produced by males, as shown for songs of other species, these sounds should be almost absent from these higher latitudes of the North Atlantic, where mainly females are present. Thus, depending on recording location, PAM data might produce very different results as a function of vocal behavior and/or demographic differences in distribution.

Seasonality and diel patterns

Our data show a strongly seasonal distribution of minke whale pulse trains in SBNMS, and the same general pattern was repeated in 3 separate years (Fig. 5). Pulse trains increased in abundance in July, peaked in September and October and decreased again in December. No detections were made during January and February, and only a few detections were recorded from March to June. This seasonality may either indicate the absence of minke whales from the area at times of the year when they are not recorded, a switch in sex ratio, if vocalizations are gender specific, or a change in behavior. While the first 2 explanations would indicate seasonal movement, the latter would allow for year-round site fidelity, both of which have been reported to exist in minke whales from different areas of the North Atlantic and are not mutually exclusive (Macleod et al. 2004, Bartha et al. 2011).

Visual sightings data from this area support the seasonal movement hypothesis. Year-round data (Murphy 1995), collected over a period of 13 consecutive years in Massachusetts Bay, including SBNMS, show a striking similarity to the pulse train occurrence patterns reported here. In over a decade of observations in this area, no minke whales were sighted in the months of January and February, and a distinct peak in occurrence was observed to start in July, increasing through September and decreasing in November. The combined visual and acoustic data therefore suggest the absence of minke whales from Massachusetts waters during winter, a limited occurrence during spring and summer and a directed movement into this area in autumn.

Minke whales in the North Atlantic are widely distributed across summer feeding grounds north of 50° N, which range from Newfoundland-Labrador to Greenland, Iceland and northern Norway, and extend into the Barents and North Seas (e.g. Horwood 1990, Andersen et al. 2003). SBNMS might therefore be a transitory location for minke whales migrating along the US and Canadian east coasts. The relative strong peak in vocal abundance in autumn compared to the spring would suggest a more offshore occurrence of this species on their northbound migration and a more coastal distribution later in the year, when the whales are headed south.

A greater abundance of minke whales in coastal waters in September and October might also be related to the distribution of their prey. Humpback and fin whales visit Massachusetts waters around

Stellwagen Bank during summer to feed on sandlance *Ammodytes* spp. (e.g. Overholtz & Nicolas 1979, Friedlaender et al. 2009). Sandlance, as well as herring and other small shoaling fish, are an important prey for minke whales in the North Atlantic (e.g. Haug et al. 1995, Lindstrøm et al. 2002, Anderwald et al. 2012). Although she observed only little surface feeding activity, Murphy (1995) suggested Massachusetts Bay as a possible feeding ground also for minke whales, citing the notable absence of minke whales during a crash of the local sandlance population in the mid-1980s (Payne et al. 1990, Murphy 1995).

Recent work on humpback whale song provides evidence for widespread occurrence of song on feeding grounds and outside the traditional breeding season (e.g. Stimpert et al. 2012, Vu et al. 2012), as well as on migration routes (e.g. Charif et al. 2001). Similarly, fin whale song has been shown to persist on feeding grounds much later in the year than previously thought (e.g. Simon et al. 2010, Morano et al. 2012). In both species it has been shown that only males sing and that songs serve in a mating context (Tyack 1981, Glockner 1983, Croll et al. 2002). Studies on changes in sex hormones in North Atlantic minke whales have shown a rise in blood testosterone levels in adult males and progesterone levels in females during the feeding season (Kjeld et al. 2004). Thus, if minke whale pulse trains were to serve in a mating context, their occurrence on migration and on a potential feeding ground is consistent with the behavioral flexibility observed in other baleen whales, as well as observed hormonal changes at the end of their summer feeding period. In addition, if minke whale pulse trains were to serve in a mating context, their occurrence on a potential feeding ground is consistent with observed hormonal changes at the end of their summer feeding period.

Minke whale pulse trains exhibited diel periodicity, with calling rates being lowest during light and peaking during dark periods. Without more knowledge on individual calling rates, the reason for the observed diel pattern cannot be conclusively resolved. It may be the result of higher individual calling rates, an increase of the overall number of vocalizing individuals at night or a change of animal abundance from day- to nighttime.

Diel variation in calling rates has been observed in several other baleen whale species and may vary by species and/or habitat. Sei whales in the Gulf of Maine and right whales on Emerald Bank, Nova Scotia, Canada, exhibited higher calling rates during the day (Mellinger et al. 2007b, Baumgartner & Fratantoni 2008). In contrast, right whales in the Pacific and the Gulf of Maine (Matthews et al. 2001,Wiggins et al. 2005, Munger et al. 2008, Mussoline et al. 2012) showed increased calling activity at nighttime and both blue and humpback whales have been shown to increase singing activity at night (Au et al. 2000, Stafford et al. 2005). For signals that serve in a reproductive context, such as humpback whale song, an increase in nighttime vocal activity might be related to the lack of visual cues for advertising and competitive display behavior (Au et al. 2000). In addition, calling could be directly or inversely related to feeding activity. Vocalizations might be used to advertise resources and thus be a proxy for feeding behavior (Croll et al. 2002, Stafford et al. 2005). On the other hand, if calls are generally serving in a social context, higher vocalization rates would be expected when whales are not actively feeding. Such a relationship has been suggested for right and sei whales, which, in some areas, show higher calling rates during the day, when their primary prey, *Calanus finmarchicus*, is aggregated at depth and thus less accessible (Mellinger et al. 2007b, Baumgartner & Fratantoni 2008). The behavioral context of minke whale vocalizations in SBNMS is currently unknown, but if the diel pattern observed here is related to feeding activity, an inverse relationship would suggest that minke whales feed primarily during the day and either advertise resources or spend more time socializing at night.

In the North Pacific, minke whale 'boing' rates recorded in Hawaii, USA, did not show a significant diel pattern (Oswald et al. 2011). In contrast to SBNMS, Hawaii is likely not a feeding area for minke whales but serves more likely as a breeding ground for the species (Oswald et al. 2011). Therefore, although the behavioral contexts are not completely understood for either area, the strong diel pattern recorded here might indicate that the direct or indirect relationship between vocalizations and presumed feeding behavior is stronger than the influence of light on visual-acoustic displays in a primarily reproductive context.

Spatial patterns

The spatial distribution of minke whale pulse trains in 2006 suggests that minke whales prefer the deeper waters to the east of Stellwagen Bank. On their summer feeding grounds, minke whales in the North Atlantic are commonly found close to shore (e.g. Macleod et al. 2004, Bartha et al. 2011, Anderwald et al. 2012). However, despite fairly consistent visual monitoring efforts for other species in the southeastern United States (e.g. Keller et al. 2012), there are large data gaps concerning the winter distribution and migratory routes of this species in the North Atlantic. This lack of data, even including opportunistic observations, suggests a more offshore distribution during winter and spring. In support of this hypothesis, recent satellite tracking data show the southbound migration of individuals summering around Iceland to take place in the middle of the North Atlantic (Víkingsson & Heide-Jørgensen 2012). In addition, in the western North Atlantic, visual sightings data from North Carolina and Florida, USA, found minke whales offshore of the continental shelf in the winter time (Nilsson et al. 2011). The spatio-temporal pattern of sporadic vocalizations in spring and a peak in vocal abundance to the east of SBNMS in autumn, is consistent with the idea of Massachusetts Bay serving as part of the migration corridor for minke whales. A potentially more inshore distribution, and therefore higher acoustic detection rate on the southbound migration, may be related to the distribution of their prey at this time of year. However, more data on prey distribution, the feeding behavior and individual movement patterns of minke whales in the Gulf of Maine are needed to draw final conclusions.

CONCLUSION

Little is known about the abundance and distribution of North Atlantic minke whales outside their known summer feeding habitats, where they are still hunted commercially in soma areas. This study documents their seasonal occurrence in Massachusetts waters and shows that PAM can be used successfully to monitor and describe this species' vocalizations. The lack of data on minke whale migration patterns and winter habitats is likely due to an offshore distribution of the species during winter and spring. Thus, because of its potential for monitoring remote areas, independent of weather conditions, PAM data will be crucial in our future understanding of important minke whale habitat. However, more concurrent visual and acoustic data sampling is needed to interpret such data better, particularly when trying to determine whether an absence of acoustic detections can be interpreted as species absence or not. In addition, future work is needed on the behavioral context of known minke whale vocalizations, including caller identity, source levels and calling rates, as well as the description of the full vocal repertoire for the species. Understanding the basic acoustic ecology will provide a better understanding of the year-round spatio-temporal distribution of North Atlantic minke whales. In turn, these data will help to predict important species-specific habitat and ultimately identify and mitigate potential threats to the species, particularly in areas where they have not been monitored traditionally.

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Chapter IV

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Individual calling behaviour and movements of North Atlantic minke whales (*Balaenoptera acutorostrata*)

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Abstract

Information on individual calling behaviour and source levels are important for understanding acoustically mediated social interactions of marine mammals, for which visual observations are difficult to obtain. Our study, conducted in the Stellwagen Bank National Marine Sanctuary (SBNMS), located in the Gulf of Maine, USA, used passive acoustic arrays to track North Atlantic minke whales and assess the sound production behaviour of individuals. A total of 18 minke whales were acoustically tracked in this study. Individual calling rates were variable, with a median inter-call interval (ICI) of 60.3 s. Average source levels (SL_{rms}) for minke whales pulse trains ranged between 164 and 168 dB re 1 μPa, resulting in a minimum detection range of 0.4–10.2 km for these calls in this urban, coastal environment. All tracked animals were actively swimming at a speed of 5.0 ± 1.2 km/h, which matches swimming speeds of migrating minke whales from other areas and confirms SBNMS as part of the migration route of this species in the Western North Atlantic. Tracked minke whales produced 7 discrete call types belonging to 3 main categories, yet no individual produced all call types. Instead, minke whales produced 2 multisyllabic call sequences (A and B) by combining 3–4 different call types in a non-random order. While 7 of the tracked individuals produced calling pattern A, 10 whales used calling pattern B, and only 1 animal combined call types differently. Animals producing different call sequences were in acoustic range of one another on several occasions, suggesting they may use these sequences for mediating social interactions. The fact that the same calling patterns were shared by several individuals suggests that these patterns may contain information related to sex, age or behavioural context.

DOI:10.1163/1568539X-00003187

Keywords
minke whales, *Balaenoptera acutorostrata*, passive acoustic tracking, vocalization, behaviour, calling patterns, source level, movement, pulse trains.

1. Introduction

Understanding the behavioural context of individual calling behaviour and the temporal patterns of call production is an important aspect of studying animal communication systems. Several taxa arrange different calls or syllables into larger units of sound. Such combinations allow for syntactical rule building, and increase information transfer over monosyllable communication. Songbirds, in particular, recombine simple calls to form a variety of higher-order songs that function primarily in a reproductive context (Nowicki & Searcy, 2004; Catchpole & Slater, 2008). In addition, multi-syllable phrases may convey information about group membership, as well as the size and threat of predators (Templeton et al., 2005; Briefer et al., 2013). In mammals, males of the Brazilian free-tailed bat produce songs that share several structural and functional traits with bird song and vary based on social context (Bohn et al., 2013). Several non-human primate species also produce higher-order call combinations, which may carry meaning related to predator presence and type or food source (Clarke et al., 2006; Ouattara et al., 2009; Clay & Zuberbühler, 2011).

In a marine context, many cetacean species exhibit highly advanced vocal systems, some of which have been studied extensively. In an environment, where light is attenuated quickly, behaviours such as the advertisement of breeding condition, coordination of group movements or the maintenance of social bonds are often mediated through sound (e.g., Tyack & Clark, 2000). However, due to the fact that most marine mammals spend only little time at the surface, and underwater observations are often infeasible, the visual quantification of behaviour and identification of individuals at sea is severely limited. Thus, there is a lack of knowledge on individual calling behaviour and the behavioural context of vocalizations.

Call sequences and their behavioural correlates have mainly been studied in odontocetes. For example, bottlenose dolphin signature whistles, which encode individual identity, are often produced in sequence both by individual animals, as well as groups (e.g., Quick & Janik, 2012; Janik & King, 2013). Similarly, short-finned pilot whales and killer whales produce non-random sequences of stereotyped call types, which most likely function in individual recognition and to maintain group cohesion (e.g., Ford et al., 1989; Sayigh et al., 2013).

Several species of baleen whales combine individual sound units to form songs that, similar to bird song, represent a series of notes arranged in a recognizable temporal pattern (Payne & McVay, 1971). These patterned sequences have been termed songs, based on the definition by Broughton (1963) that song is: '. . . a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time'. In particular, humpback whales (*Megaptera novaeangliae*) produce complex, hierarchically structured songs (Payne & McVay, 1971; Cholewiak et al., 2013). Similarly, bowhead whales (*Balaena mysticetus*) sing elaborate songs (Stafford et al., 2008; Tervo et al., 2011), while blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales produce high intensity song units at very low frequencies (approx. 15–30 Hz) (McDonald et al., 2001; Croll et al., 2002). In humpback, fin, and blue whales it has been shown that only males produce songs (Glockner, 1983; Croll et al., 2002; Oleson et al., 2007a). In these species, songs function as male advertisement or to mediate interactions between competing males (Tyack, 1981; Tyack & Whitehead, 1983; Oleson et al., 2007a). Recent acoustic recording efforts of marine mammals are beginning to show that song occurs not only during the traditional breeding season but also on feeding grounds and during migration (Stafford et al., 2007; Simon et al., 2010; Vu et al., 2012). And alternative functions of songs, such as navigation and prey detection, have also been suggested (Clark & Ellison, 2004). In addition to song production, in most species of baleen whales, both sexes produce a range of different call types in various contexts. Several species produce feeding-associated vocalizations that may be repeated in monosyllabic sequences (Cerchio & Dahlheim, 2001; Oleson et al., 2007b; Širović et al., 2013). In addition, sequences of frequency modulated call-counter calls occur in fin, blue and right whales (*Eubalaena* spp.) and serve as contact calls to maintain group cohesion (Clark, 1982; Oleson et al., 2007b; Širović et al., 2013). A variety of variable social calls have been described for most species (Oleson et al., 2007a; Dunlop et al., 2008; Stafford et al., 2008; Parks et al., 2011; Stimpert et al., 2011); the function of these calls is largely unknown but many of the calls are stable over several years suggesting an important role in mediating social interactions (Rekdahl et al., 2013).

Sounds produced by North Atlantic minke whales have only recently been described in more detail. Mellinger et al. (2000) described low-frequency pulse trains with a varying interpulse interval (IPI) structure; and a recent study in the Gulf of Maine described 7 distinct pulse train types, which fall into 3 main categories and occur with varying frequency (Risch et al., 2013). However, the behavioural significance of these vocalizations and whether they are specific to sex, age, recording site or season is unknown.

Given the identification of several stereotypic call types in the minke whale vocal repertoire, the main objective of the current study was to investigate whether individual minke whales use the full vocal repertoire, whether they combine pulse trains in predictable vocal sequences and how individuals use these sounds when engaging in vocal exchanges with conspecifics. Despite the reliance on primarily passive acoustic data and the lack of visually observed context, answers to these questions will allow the development of testable theories with respect to the behavioural function of minke whale pulse trains.

In addition, passive acoustic localization can also elucidate other, non-vocal aspects of behaviour, such as swimming speeds and movement behaviour (e.g., Stanistreet et al., 2013). Thus, a secondary goal of this study was to use acoustic data to quantify fine-scale movements of minke whales in the Gulf of Maine study area, where little is known about the general behaviour of this species.

Lastly, basic data on individual vocal behaviour, source level and detection range, as obtained by acoustic localization, is necessary for passive acoustic monitoring (PAM) applications. North Atlantic minke whales are still exploited commercially. Thus, although the species is currently listed as 'a species of least concern' in the IUCN Red List (Reilly et al., 2008), accurate monitoring of population size and structure is essential for its conservation. Most current monitoring and abundance estimates for minke whales are based on visual sightings data (Skaug et al., 2004; de Boer, 2010; Bartha et al., 2011). However, new methods such as PAM, coupled with new analytical approaches (Marques et al., 2013), offer an opportunity to significantly improve abundance estimates for this cryptic species (Oswald et al., 2011; Martin et al., 2013). Since PAM depends on the detection of vocalizing animals, it is critical to understand how individual calling behaviours influence calling rates, as well as any sex, season or site specificity of different call types. Only a few studies have collected such vocalization data for baleen whales using either acoustic recording tags or passive acoustic array configurations (Matthews et al., 2001; Parks et al., 2011, 2012; Stanistreet et al., 2013). For North Atlantic right whales, considerable variability in individual calling rate patterns, related to behaviour, age, sex and season has been documented (Parks & Tyack, 2005; Parks et al., 2005, 2011; Van Parijs et al., 2009). These results reinforce the importance of describing and considering such variability when interpreting passive acoustic data.

2. Material and methods

2.1. Acoustic data collection

During 2 October–30 November 2009 and 17 August–11 October 2011, acoustic data were continuously recorded in the Stellwagen Bank National Marine Sanctuary (SBNMS) located in the Southern Gulf of Maine, Northwest Atlantic Ocean (Figure 1). Arrays of 10 and 11 (2009 and 2011, respec-

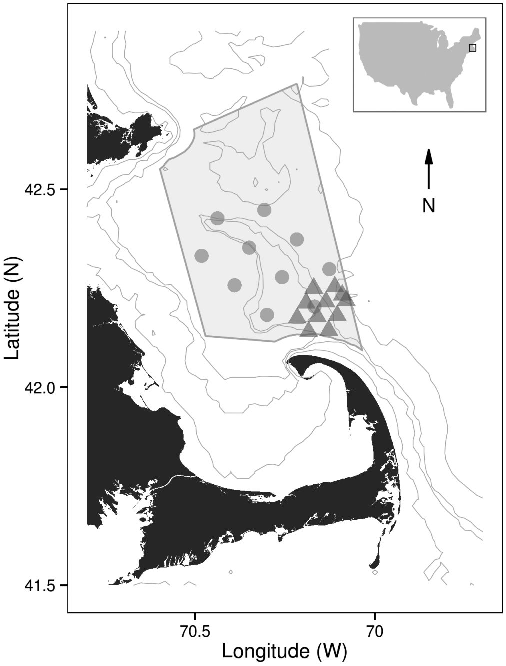

Figure 1. Map of Massachusetts Bay with the Stellwagen Bank National Marine Sanctuary (SBNMS) outlined and shaded in gray. Inset map in upper right corner shows the position of the study area along the US East coast. Filled dots represent acoustic recording units deployed from 2 October–30 November 2009; triangles represent recorders deployed from 17 August to 11 October 2011.

tively) marine acoustic recording units (MARUs) (Calupca et al., 2000) were deployed at depths ranging from 25 to 114 m, and anchored 1–2 m above the sea floor. Units were spaced approx. 11 and 5 km apart in 2009 and 2011, respectively (Figure 1). Each MARU was equipped with a HTI-94-SSQ hydrophone (sensitivity -168 dB re 1 V/μPa), connected to a pre-amplifier and A/D converter, resulting in an effective system sensitivity of -151.7 dB re 1 V/μPa. All units sampled at 2000 Hz and 12 bit resolution, yielding an effective analysis bandwidth of 10–1000 Hz, with a flat frequency response (± 1 dB) between 55 and 585 Hz. Recordings from individual units were time-aligned using calibration signals recorded at the beginning and end of the deployments and compiled into multi-channel data files.

2.2. *Individual calling behaviour*

All acoustic data were examined manually for the presence of minke whale pulse trains by generating multi-channel spectrograms using the sound analysis software XBAT (Figueroa & Robbins, 2008; FFT size 1024, 85% overlap, Hanning window). Pulse train types were assigned to one of seven categories within three main groups, based on interpulse interval (IPI) structure, as described in (Risch et al., 2013). These main groups were slow-down (sd), constant (c) and speed-up (sp) pulse trains (Figure 2). All pulse trains that were not stereotypic, or of too low quality for categorization, were placed in a variable (v) group. Calling rates for each animal were calculated as the total number of calls/min, and intercall interval (ICI) was calculated as the difference between the start times of two consecutive pulse trains produced by the same individual. All temporal measurements were carried out in XBAT based on manually delineated event boxes.

To determine whether transitions between call types were random, transition frequencies were analysed as a first-order Markov chain, where a succeeding event is only dependent on the immediately preceding event. R package *msm* (Jackson, 2011) was used to arrange the continuous call data into a 2-way contingency table of preceding and following pulse train types and a transition probability matrix was estimated based on maximum likelihood. Observed and expected transition matrices were compared using a goodness-of-fit test and a 2-tailed Z-test for proportions (Fleiss, 1981) was used to compare each observed transition to its corresponding expected transition.

The transition frequencies for each call type combination were used to calculate an index of association (Ford, 1989). This index, based on Dice's

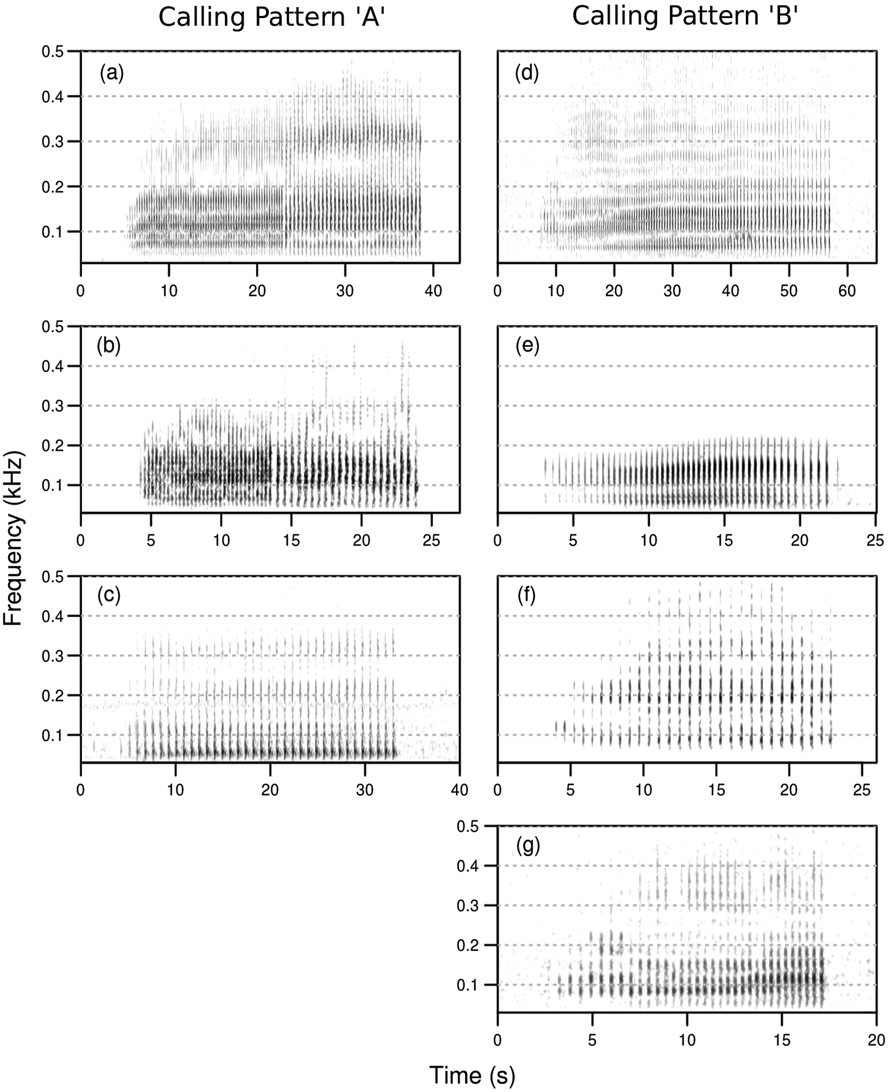

Figure 2. Spectrograms of North Atlantic minke whale pulse trains, as described in Risch et al. (2013). Identified calling patterns are based on transition frequencies and association patterns of individual pulse trains. (a–c) Calling pattern A, consisting of pulse train types: sd1, sd2 and c3. (d–g) Calling pattern B, consisting of pulse train types: sd3, c1, c2 and sp. Note the different time scales for spectrograms. Spectrogram parameters: FFT = 512, overlap = 75%, sample rate = 2000, resulting in a spectrogram resolution of 3.9 Hz and 64 ms.

coefficient of association, normalizes the data to account for call type abundance:

$$2(N_{\mathrm{ij}} + N_{\mathrm{ji}})/(S_{\mathrm{i}} + S_{\mathrm{j}}),$$

where i and j are consecutive pulse trains, N is the number of transitions from one pulse train to the next, and S is the total number of transitions of a particular type. Hierarchical clustering of this association matrix was performed by applying the UPGMA method, using function hclust in the R *stats* package (R Core Team, 2013). The cluster results were then plotted as a dendrogram.

2.3. Localization and movement

Series of pulse trains recorded on three or more channels and occurring for a period of at least 20 min, with gaps not exceeding 10 min, were chosen for localization. Individual pulse trains were localized using a correlation sum estimation algorithm (CSE), applied in XBAT (Cortopassi & Fristrup, 2005). This localization method differs from techniques based on time differences of arrival (TDOA) and hyperbolic fixing as it does not rely on the selection of waveform cross-correlation peaks to estimate locations. Instead, it calculates accumulated cross-correlation sums for all channel pairs across a grid of spatial points and chooses the point that maximizes the correlation sum as the most likely location. Due to this process, the method is considered to be more robust to background noise (Cortopassi & Fristrup, 2005). Each localized signal was verified visually in multi-channel spectrograms to ensure that the same pulse train was picked on all channels and the candidate location, as determined by the CSE algorithm, agreed with the observed TDOAs. Pulse trains for which reliable and repeatable location estimates could not be obtained using CSE, were removed from all further movement analyses. However, if the visually observed TDOA estimates of these calls agreed with the general pattern of the tracked animal, they were still included in temporal calling pattern analyses (see next paragraph). After manual review of each localization, animal tracks were defined as the time-ordered collection of locations from a single source connected by a straight line (Turchin, 1998). Tracks were smoothed with a 5-point moving average (MA) to reduce the influence of localization error. Statistical simulation tests using the CSE algorithm and comparable array geometry show, that localization accuracy depends on the position of the source relative to the array and increases with distance from the centre of the array (Urazghildiiev & Clark, 2013). Thus, movement characteristics were calculated only for tracks within 5 km of the array boundaries to reduce the impact of increasing error outside of the array. R package *adehabitat* (Calenge, 2006) was used to calculate track statistics, including track duration (h), net displacement (km), total distance (km) and average speed (km/h). A straightness index (SI), defined as the quotient of net displacement and total distance ($1 =$ straight line path, $0 =$ meandering path), was calculated to assess directness of movement. All analyses using R were performed using version 2.15.3 (R Core Team, 2013). Location error for the arrays was determined by conducting calibration experiments on 22 October 2009 and on 9 October 2011 at two and five sites within the array, respectively. A series of 5 to 10 frequency modulated sweep tones were played at each site. The source location of each playback sweep was estimated using the CSE algorithm. Location error in meters was then quantified by subtracting the estimated position for each locatable sweep from the known speaker location. Differences between known and estimated source locations were averaged over all sweeps and transmission sites.

2.4. Source level estimation

To estimate pulse train source levels (SL), received levels (RL) were measured for a subset of the 2011 data, based on several detection criteria that included (a) a high signal-to-noise ratio ($\mathrm{SNR} > 10$ dB); (b) could be reliably located; and (c) did not overlap with other sounds. The signals were bandpass filtered between 50 and 250 Hz. RL measurements were carried out in Raven Pro version 1.5 (Bioacoustics Research Program, 2013) for every fifth individual pulse and for the entire pulse train. Minimum and maximum frequencies of the measured signals were defined as the -10 dB end points relative to the signal peak in the power spectrum. Measurements included peak-to-peak ($\mathrm{RL}_{\mathrm{pp}}$) and root-mean-square ($\mathrm{RL}_{\mathrm{rms}}$) sound pressure levels (dB re 1 μPa) for every pulse, and $\mathrm{RL}_{\mathrm{rms}}$ for the whole pulse train. $\mathrm{RL}_{\mathrm{rms}}$ was measured over a time window encompassing 90% of the total signal energy in the selection window (Madsen & Wahlberg, 2007). Following these measurements, SL was calculated from RL by compensating for transmission loss (TL). Under the assumption of mainly spherical spreading, TL equals $20\log(R)$, where R is the range of the whale from the receiver (Urick, 1983). In shallow water environments refraction and reflections from the sea bottom or surface will considerably affect TL, making the cylindrical spreading law ($\mathrm{TL} = 10\log(R)$) more appropriate, while in many environments an intermediate term is most appropriate. Due to empirical measurements

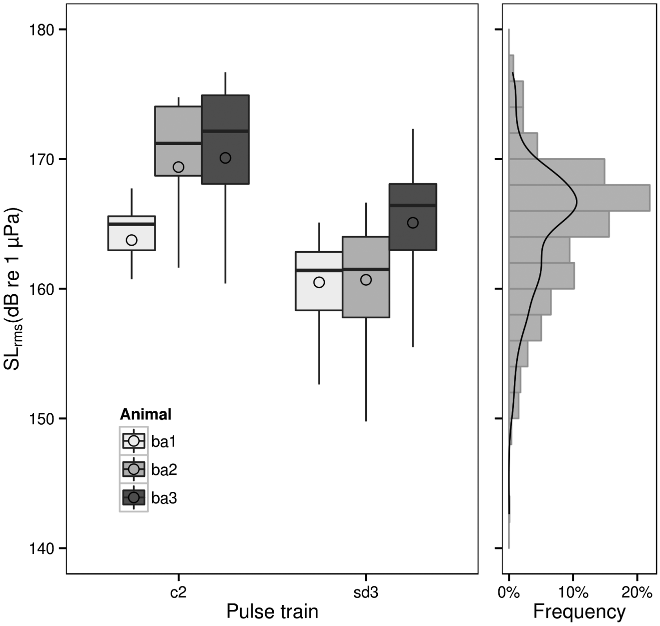

Figure 3. Boxplot of source levels (SL_{rms}) showing results for individual pulses measured from pulse train types: c2 and sd3 for three individuals (animal ba1–ba3). Lower and upper bounds of boxes represent lower and upper quartiles, respectively. Solid lines represent medians and non-filled circles represent means. Whiskers represent farthest data points within $1.5\times$ interquartile range (IQR) of the lower and higher quartile, respectively. Histogram shows frequency of occurrence of different source levels (binwidth $= 2$ dB) and a smoothed Gaussian kernel density plot for all measured pulses/pulse trains ($N = 993$ ($N = 57$)).

showing that $17\log(R)$ is a reasonable approximation for TL in the study area (unpublished data), we chose this term for all SL estimations. SL results were averaged by pulse train and reported in terms of peak-to-peak (SL_{pp}, dB re 1 μPa), root-mean-square (SL_{rms}, dB re 1 μPa) and energy flux density (SL_{efd}, dB re 1 μPa^2s).

Assuming source and receiver depths of 20 m and using averaged minke whale SLs from our study, signal propagation in the SBNMS was then modelled using the Acoustic Integration Model (Hatch et al., 2012). Hourly ambient noise level (NL) values were calculated for the week of 4–10 October 2009. NLs were averaged over the frequency band containing the most pulse train energy (56.2–355 Hz) and summarized as 5th, 25th, 50th 75th and 95th percentiles. In the absence of hearing and detection threshold data for minke whales, these NL values were compared with the signal propagation curve, and the range at which SNR = 0 was determined.

3. Results

3.1. Individual calling behaviour

Since whales could only be successfully tracked to a certain range (< 8 km) outside the array boundaries, the data analysed were effectively censored; that is, start and end times of tracks did not necessarily mark the beginning or end of a calling bout. In addition, in order to reliably track individual animals and minimize the possibility of switching individuals, we only analysed tracks for which gaps in calling did not exceed 10 min (see Methods). Thus, all calling rate parameters are based on the time period during which an animal could be reliably tracked, given the acoustic range of the hydrophone arrays and limitations set by the analysis approach. Calling rates for individual whales ranged from a minimum of 8.7 to a high of 133.3 pulse trains/h. Figure 4 illustrates the distribution of observed intercall intervals (ICI). Tracked minke whales tended to call at a regular rate, with a median ICI of about 60.3 s (Figure 4, Table 1). The average call rate was 48.6 ± 27.5 calls/h, and the maximum silence between tracked calls extended to an average of 392.6 ± 292.1 s, with a maximum of about 6.5 min (Figure 4).

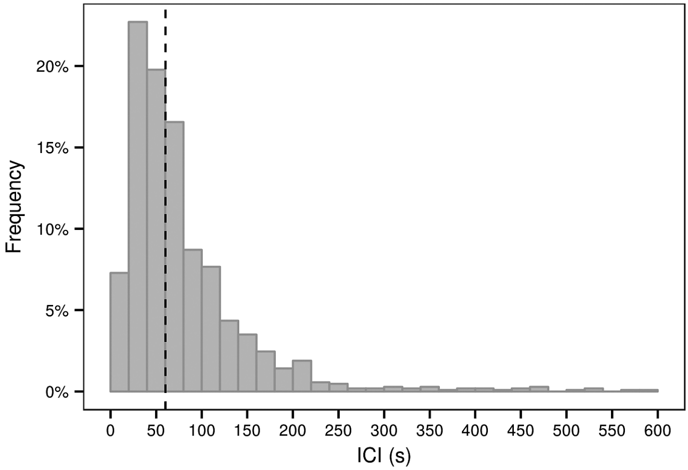

Figure 4. Histogram showing the frequency of occurrence of different Intercall Intervals (ICI) (binwidth = 20 s). The dotted line represents the median ($N = 1060$).

Table 1.
Summary statistics of movements and calling rate parameters for individual minke whales recorded in the Stellwagen Bank National Marine Sanctuary (SBNMS) during autumn 2009 and 2011.

	Parameter	Unit	Mean ± SD	Median (25–75%)
Movement ($N = 13$)	N pulse trains	–	67 ± 34	
	Track duration	h	1.2 ± 0.8	0.9 (0.7–2.0)
	Total distance	km	5.3 ± 4.2	3.5 (2.9–6.9)
	Net displacement	km	3.1 ± 2.4	2.0 (1.8–3.2)
	Mean speed	km/h	5.0 ± 1.2	4.8 (4.2–5.6)
	± SD speed	km/h	3.9 ± 0.6	3.9 (3.6–4.4)
	Straightness index	–	0.7 ± 0.2	0.6 (0.5–0.8)
Calling rate ($N = 18$)	N pulse trains	–	60 ± 37	
	Track duration	h	1.4 ± 0.8	1.0 (0.8–1.5)
	Call rate	calls/h	48.6 ± 27.5	44.3 (35.2–52.2)
	Min ICI	s	19.1 ± 15.2	11.4 (9.5–20.7)
	Max ICI	s	392.6 ± 292.1	321.2 (221.8–459.6)
	Mean ICI	s	82.4 ± 87.9	60.3 (34.7–100.6)

N, number of tracked animals; ICI, intercall interval.

The 18 individual minke whales tracked in this study produced all major pulse train categories defined in a larger scale study from the same area (Risch et al., 2013): slow-down pulse trains (sd1–sd3), constant pulse trains (c1–c3), and speed-up pulse trains (sp) (Figure 2). However, pulse train type transitions were not random. The results of the Markov chain analysis showed that some types were highly likely to occur before or after other pulse train types (Goodness-of-fit test, $\chi^2 = 733.25$, df $= 56$, $p < 0.001$, Figure 5). This pattern was not evenly distributed between pulse train type transitions. While 15 out of 64 transitions were positively correlated, 17 were negatively correlated (Figure 5). The calculated index of association between pulse train types showed strong positive associations between types sd1–c3 (0.39), sd3–c1 (0.29) and sd3–c2 (0.30) (Figures 5 and 6). Hierarchical cluster analysis of the association matrix grouped pulse train types sd1, sd2 and c3 as calling pattern A, while pulse train types sd3, c1, c2 and sp were grouped as calling pattern B (Figures 2 and 6). When Markov chain analyses were run by individual, the resulting probability matrices showed that pulse train type association patterns reflected differential call type usage by individual minke whales. While 39% ($N = 7$) of the tracked animals preferably used pattern A, 56% ($N = 10$) used pattern B, and only one animal combined call types

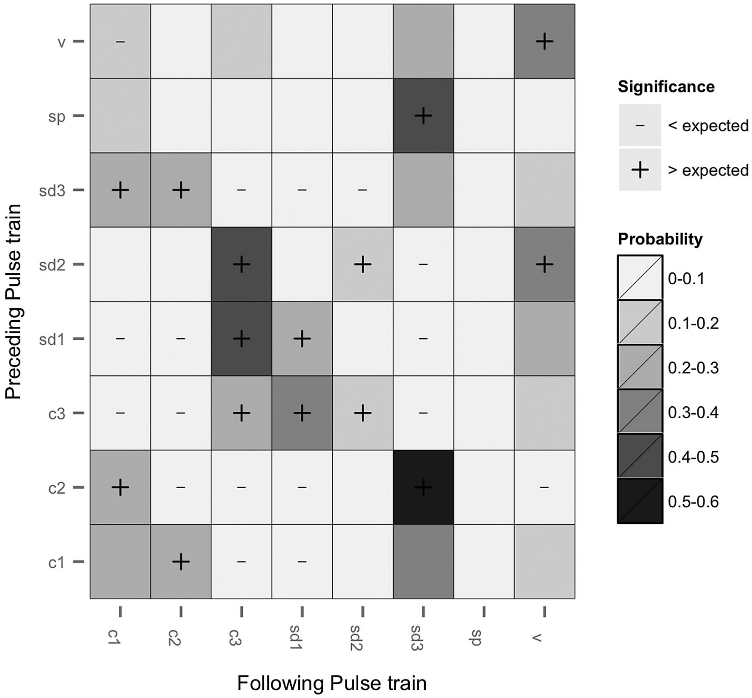

Figure 5. Matrix of transition probabilities between different pulse trains. Preceding pulse trains are shown vertically and following pulse trains are plotted horizontally. (+/−) indicate transitions that are significantly greater or smaller than expected ($p < 0.05$).

in a different pattern (pattern C, Figure 7). In our sample, tracked minke whales used calling patterns A and B simultaneously during five occasions, when vocalizing individuals were at an average distance of 4.6 ± 2.5 km, and thus likely within acoustic range of one another.

3.2. *Localization and movement*

Average localization error as quantified during the calibration experiments (mean ± SD) was 422.7 ± 5.0 m for the 2009 array ($N = 9$) and 105.1 ± 64.4 m for the smaller aperture array in 2011 ($N = 20$). A total of 18 individual minke whales were tracked during the study: 3 in 2009 (4.3 h) and 15 (20.1 h) in 2011. Track duration ranged from 0.4 to 3.1 h and lasted on average 1.4 ± 0.8 h (mean ± SD). While all analysed tracks were within 8 km of the array perimeter, only 13 of these, which were less than 5 km outside the array, were further analysed to obtain movement parameters (see summary data in Table 1). Vocalizing animals were generally moving and covered dis-

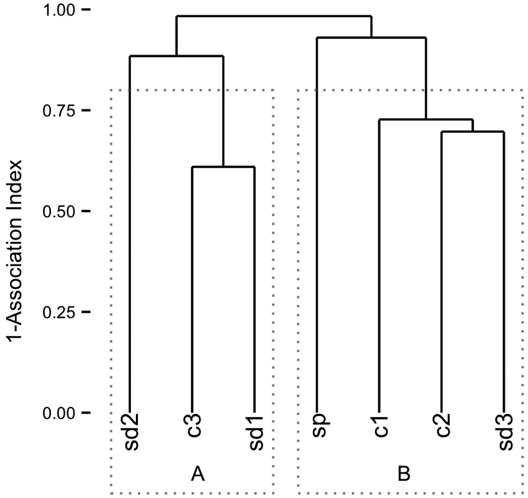

Figure 6. Dendrogram of association index, based on transition frequencies of pulse trains produced by individual North Atlantic minke whales, showing two distinct groups of associated pulse train types, resulting in calling patterns A and B.

tances between 0.9 and 9.2 km with a mean ± SD distance of 5.3 ± 4.2 km, a net displacement of 3.1 ± 2.4 km, and an average speed of 5.0 ± 1.2 km/h. Movement directionality, as expressed by the straightness index (SI), varied between individuals but was closer to direct path travel (mean ± SD = 0.7 ± 0.2).

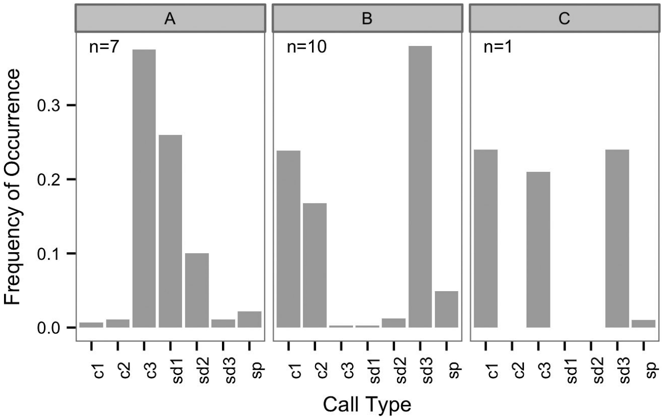

Figure 7. Bar graph showing frequency of occurrence of different pulse train types, grouped by calling patterns A, B and C, which were identified based on transition frequencies and association of stereotypic pulse train types produced by individual North Atlantic minke whales.

3.3. Source level estimation

A large enough sample of non-overlapping high quality calls could only be obtained for pulse trains c2 and sd3 (Figure 2). These pulse trains were measured from three individuals at an average radial distance of 2145.8 ± 845.1 m from the nearest MARU. A total of 57 pulse trains and 993 individual pulses were measured. The results are summarized in Table 2. Peak-to-peak source levels (mean ± SD) were 181.6 ± 6.6 dB re 1 μPa and 176.7 dB re 1 μPa for types c2 and sd3, respectively. Root-mean-square source levels (SL_{rms}) averaged over individual pulses were 168.9 ± 6.6 dB re 1 μPa and 164.0 ± 4.6 dB re 1 μPa for type c2 and sd3, and averaged over the whole pulse train, SL_{rms} were 166.3 ± 3.3 and 161.8 ± 2.5 dB re 1 μPa, respectively (Table 2). Source levels varied by individual (Figure 3) and increased throughout the duration of the pulse train. While the first measured pulses had a mean calculated SL_{rms} of 154.7 ± 4.1 dB re 1 μPa, pulses measured towards the end of the pulse train (e.g., pulse No. 25) were about 12 dB louder, with a mean SL_{rms} of 166.5 ± 1.5 dB re 1 μPa.

During the week of 4–10 October 2009, the average hourly ambient noise levels (NL) for the frequency band between 56.2–355 Hz was 101.7 ± 7.0 dB re 1 μPa and ranged from 92.2–115.7 dB re 1 μPa (5th–95th percentile). Given average SL_{rms} values of 168.9 and 164.0 dB re 1 μPa for pulses in pulse train types c2 and sd3, respectively and an assumed source and receiver depth of 20 m, the range over which these signals propagate in the SBNMS

Table 2.
Summary statistics of measured source levels.

	Parameter	Unit	Mean ± SD	Median (25–75%)
c2 (N pulse trains = 16, N pulses = 115)	SL_{pp}	dB re 1 μPa	181.6 ± 6.6	183.7 (178.2–186.5)
	SL_{rms}	dB re 1 μPa	168.9 ± 6.6	171.1 (165.1–174.0)
	SL_{efd}	dB re 1 μPa2s	162.4 ± 6.5	164.3 (158.5–167.9)
	SL_{rms} (pulse train)	dB re 1 μPa	166.3 ± 3.3	167.2 (165.1–168.9)
sd3 (N pulse trains = 41, N pulses = 878)	SL_{pp}	dB re 1 μPa	176.7 ± 4.2	177.4 (174.0–180.1)
	SL_{rms}	dB re 1 μPa	164.0 ± 4.6	165.4 (161.1–167.3)
	SL_{efd}	dB re 1 μPa2s	157.5 ± 4.5	158.9 (154.7–160.9)
	SL_{rms} (pulse train)	dB re 1 μPa	161.8 ± 2.5	162.0 (160.9–163.4)

SL_{pp}, peak-to-peak source level; SL_{rms}, RMS source level; SL_{efd}, energy flux density.

environment before SNR equals 0 is 0.7–10.2 km for c2 and 0.4–7.3 km for sd3.

4. Discussion

Little is known about vocalizations produced by North Atlantic minke whales and how they use these sounds to mediate behaviour. Our study is the first to use stationary passive acoustic array recordings to acoustically track this species in order to investigate individual calling and movement behaviour. Although passive acoustic tracking is spatially restricted and lacks the behavioural context and demographic information that can be obtained in conjunction with visual observations and acoustic recording tags, it is more feasible and less logistically costly than these other approaches. The successful tracking of 18 individual minke whales in our study demonstrated the feasibility of using long-term passive acoustic arrays for this purpose.

Tracked minke whales produced all major pulse train categories defined by Risch et al. (2013). However, certain call types were more closely associated than others (Figure 6). In particular, most individuals combined pulse trains in either of two call sequences (A and B, Figure 6), and only 1 animal combined call types in a different pattern (C, Figure 7). The structural organization of pulse trains in distinct sequences is an unexpected and interesting finding. Males of several baleen whale species produce hierarchically organized songs associated with reproductive behaviour (Payne & McVay, 1971; Croll et al., 2002; Oleson et al., 2007a). And it has been noted that the ‘star wars’ vocalizations produced by dwarf minke whales wintering on the Great Barrier Reef share characteristics, such as stereotypy and repetitiveness, with these reproductive displays of other species (Gedamke et al., 2001). Since the sex, as well as the context of vocalizing North Atlantic minke whales remain unknown, it is impossible to attribute pulse trains to any particular behaviour. However, based on structural differences between pulse trains recorded in the Gulf of Maine, and those recorded in the Caribbean winter grounds (the latter lasting considerably longer and exhibiting more than twice as many pulses), a reproductive function of these calls has been suggested (Risch et al., 2013). A common feature of baleen whale song is that males vocalizing in the same region and time period typically share the same song (Cerchio et al., 2001; Stafford et al., 2007; Simon et al., 2010). A notable exception to this pattern occurs in bowhead whales where multiple distinct songs occur within a continuous space and time. However, whether these distinct songs are shared between individuals is unknown (Stafford et al., 2008, 2012; Delarue et al., 2009).

Our results show that individual minke whales share the same calling patterns, which thus may reflect different behavioural functions, sex or age of the caller, rather than individual identity. This interpretation is further supported by the fact that both main calling patterns were present in 2009 and 2011, indicating that calling patterns are stable across years. During our study, there were five occasions where minke whales producing different calling patterns were in acoustic range of one another. Independent of the question whether minke whale call sequences serve in a reproductive context, it is likely that the simultaneous production of two different types of calling patterns by two individuals serves a specific function such as maintaining spacing between individuals within a shared acoustic environment (Gedamke, 2004).

Individual calling rates were variable, ranging from 8.7 to 133.3 calls/h (mean ± SD: 48.6 ± 27.5). The median intercall interval (ICI) was about 1 min (mean ± SD: 82.4 ± 87.9 s) and the longest period of silence between two calls was about 6.5 min (Table 1). One of the constraints of tracking individuals using passive acoustic techniques is that the tracked animal needs to vocalize consistently in order to be reliably tracked. The concentration on high quality, relatively long acoustic tracks may have biased our sample to only vocally active animals (and possibly particular types of behaviour), rather than being representative of the overall calling behaviour of North Atlantic minke whales in our study area. Thus, while it is possible to estimate calling rates for vocally active individuals using passive acoustics, it is not possible to accurately assess the time animals spend vocalizing throughout the day using this approach alone. For example, most of the tracks that we analysed were recorded at night. A strong diel pattern has been described for minke whale pulse trains in the SBNMS (Risch et al., 2013). Such diel variation in the occurrence of vocalizations occurs in several other baleen whale species and has often been attributed to a switch from less vocal behaviours such as feeding to more vocal behaviours such as social interactions (Mellinger et al., 2007; Baumgartner & Fratantoni, 2008; Parks et al., 2011). Thus, calling rates as measured in this study have to be evaluated based on the context in which they have been recorded.

Although track parameters varied by individual, all tracked animals were actively moving while vocalizing. Minke whales in Monterey Bay, CA, USA were estimated to have mean swimming speeds between 6.5 and 8.3 km/h (Stern, 1992). Rankin & Barlow (2005) reported a swimming speed of 5.6 km/h during an encounter with a North Pacific minke whale. While the behavioural context of these observations was unclear, feeding minke whales tracked with satellite tags in northern Norway travelled at much lower average daily speeds of 2.2–2.7 km/h (Heide-Jørgensen et al., 2001). A recent study employing satellite tags on minke whales in Icelandic waters found average swimming speeds to be considerably lower in inshore waters where whales are presumably feeding, as compared to offshore waters, where migratory behaviour was evident and where average swimming speeds ranged from 4.6 to 7.3 km/h (Víkingsson & Heide-Jørgensen, 2013). The average swimming speed of minke whales in the SBNMS was 5.0 ± 1.2 km/h (Table 1), similar to that reported for North Pacific minke whales (Stern, 1992; Rankin & Barlow, 2005), and well within the range reported for migrating minke whales around Iceland (Víkingsson & Heide-Jørgensen, 2013). All tracks analysed in our study were recorded during the peak season (September–October) of minke whale pulse train occurrence in the Stellwagen Bank National Marine Sanctuary (SBNMS) (Figure 1) (Risch et al., 2013). Peak minke whale abundance during these months is corroborated in visual sighting records from this area (Murphy, 1995). The summer feeding grounds of minke whales in the North Atlantic generally extend north of SBNMS, starting at around 50°N, and range from Labrador in the Northwest Atlantic to the Barents Sea in the Northeast Atlantic (Horwood, 1990; Andersen et al., 2003). Noting that minke whale pulse trains and visual sightings are mostly absent during the summer feeding season, it has been suggested that SBNMS is part of the migration route of North Atlantic minke whales (Risch et al., 2013), rather than a feeding ground destination. The swimming speed estimates derived for minke whales in our study lend further support to this theory. In addition, although individual tracks were generally too short to explore movement direction in more detail, our observations of generally straight-line, rather than meandering path movements and a net displacement of 3.1 ± 2.4 km/h (Table 1) are also indicative of migratory behaviour.

Source levels for pulse trains produced by minke whales in our study varied by individual, but averaged 161.8 ± 2.5 and 166.3 ± 3.3 $\mathrm{dB_{rms}}$ re 1 μPa, for pulse trains sd3 and c2, respectively (Table 2, Figure 3). Source levels for both measured call categories ranged between 160.9 and 168.9 $\mathrm{dB_{rms}}$ re 1 μPa (25th–75th percentiles; Table 2). We found an average increase in pulse source level of about 12 dB from the start to the end of the measured pulse trains. Lacking information about the depth of a calling animal, it is not possible to discern whether this apparent increase in source power is produced by the calling animal or is a function of the animal's position in the water column. Signal propagation is dependent on depth of both sound production and reception. Shallow sources, in particular, may be influenced by the Lloyd mirror effect, in which sound reflected by the surface may cause positive or negative interference on the propagating signal (Jensen et al., 1994). Although transmission loss is generally less dependent on depth in the deeper parts of the water column, it increases substantially closer to the surface, ranging between 10–20 dB in the upper 10 m of the water column (Jensen, 1981). The acoustic recorders in the present study were moored just above the sea floor. Thus, an alternative explanation for the apparent increase in source level over the duration of the pulse trains could be that the animals were actively diving while vocalizing. Assuming a signal directivity of close to 0 dB, if the calling animal was at or close to the surface at the start of the pulse train and continued to dive throughout the production of the call, it is conceivable that a reduction in received level (and thus estimated source level, when depth is not considered) of about 10–15 dB would be observed.

Source level measurements obtained in this study are slightly higher than reported source levels for 'boing' sounds recorded from North Pacific minke whales (150 dB re 1 μPa; Thompson & Friedl, 1982) and the 'star-wars' vocalization produced by Australian dwarf minke whales (150–165 dB re 1 μPa; Gedamke et al., 2001). Peak-to-peak source levels were 13 dB greater than rms source levels, similar to values reported by Munger et al. (2011) for right whale upcalls. Compared to other baleen whale species, our measured minke whale source levels are most similar to North Atlantic right whale tonal calls (137–162 $\mathrm{dB_{rms}}$ re 1 μPa; Parks & Tyack, 2005) and also to individual humpback whale song units (144–169 $\mathrm{dB_{rms}}$ re 1 μPa; Au et al., 2006), but about 25–30 dB lower than the high-intensity low-frequency calls produced by blue and fin whales (Thode et al., 2000; Charif et al., 2002; Širović et al., 2007). Given these data, the potential detection radius of minke whale pulse trains in SBNMS is between 0.4 km and 10.2 km. This theoretical detection range will vary based on spatial and seasonal variability in sound propagation and noise levels and is also dependent on the animal's ability to recognize the signal in background noise (Clark et al., 2009). Yet, our results suggest that the detection radius of these calls in an urbanized coastal area, which is highly impacted by anthropogenic noise (Hatch et al., 2012), is relatively small compared to calls recorded from other baleen whale species and in different environments (e.g., Stafford et al., 2007; Samaran et al., 2010; Širović et al., 2011).

In conclusion, this study showed that North Atlantic minke whales produce at least two distinct call sequences, consisting of 3–4 stereotyped call types. These sequences were stable across years and are shared between individuals. Although their specific behavioural function is currently unknown, these patterns may be important in mediating social interactions between individuals or may reflect age or sex differences. In addition, this study provided data on calling rates and call source levels for North Atlantic minke whale pulse trains, which are useful for developing models of detectability as a basis for acoustic density estimation (Marques et al., 2013; Martin et al., 2013). The documented variability in individual calling behaviour should be considered when monitoring this species using passive acoustics.

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Chapter V

Risch D, Castellote M, Clark CW, Davis GE, Dugan PJ, Hodge LEW, Kumar A, Lucke K, Mellinger DK, Nieukirk SL, Popescu CM, Ramp C, Read AJ, Rice AN, Silva MA, Siebert U, Stafford KM, Verdaat H & Van Parijs SM (2014) Seasonal migrations of North Atlantic minke whales: Novel insights from large-scale passive acoustic monitoring networks. (Accepted in *Movement Ecology*).

North Atlantic minke whale (*Balaenoptera acutorostrata*).

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Seasonal migrations of North Atlantic minke whales: Novel insights from large-scale passive acoustic monitoring networks

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Abstract

Background

Little is known about migration patterns and seasonal distribution away from coastal summer feeding habitats of many pelagic baleen whales. Recently, large-scale passive acoustic monitoring networks have become available to explore migration patterns and identify critical habitats of these species. North Atlantic minke whales (*Balaenoptera acutorostrata*) perform seasonal migrations between high latitude summer feeding and low latitude winter breeding grounds. While the distribution and abundance of the species has been studied across their summer range, data on migration and winter habitat are virtually missing. Acoustic recordings, from 16 different sites from across the North Atlantic, were analyzed to examine the seasonal and geographic variation in minke whale pulse train occurrence, infer information about migration routes and timing, and to identify possible winter habitats.

Results

Acoustic detections show that minke whales leave their winter grounds south of 30° N from March through early April. On their southward migration in autumn, minke whales leave waters north of 40° N from mid-October through early November. In the western North Atlantic spring migrants appear to track the warmer waters of the Gulf Stream along the continental shelf, while whales travel farther offshore in autumn. Abundant detections were found off the southeastern US and the Caribbean during winter. Minke whale pulse trains showed evidence of geographic variation, with longer pulse trains recorded south of 40° N. Very few pulse trains were recorded during summer in any of the datasets.

Conclusion

This study highlights the feasibility of using acoustic monitoring networks to explore migration patterns of pelagic marine mammals. Results confirm the presence of minke whales off the southeastern US and the Caribbean during winter months. The absence of pulse train detections during summer suggests either that minke whales switch their vocal behaviour at this time of year, are absent from available recording sites or that variation in signal structure influenced automated detection. Alternatively, if pulse trains are produced in a reproductive context by males, these data may indicate their absence from the selected recording sites. Evidence of geographic variation in pulse train duration suggests different behavioural functions or use of these calls at different latitudes.

Keywords

Passive acoustic monitoring (PAM), Minke whales, *Balaenoptera acutorostrata*, Migration, Pulse trains, Seasonality, Geographic variation

Background

Animal migration is a common phenomenon and has evolved at multiple times and in a variety of species [1]. Typically, migration develops as an adaptation to take advantage of seasonal peaks in resource abundance, escape inter- and intra-specific competition, or avoid predators and parasites [2]. Most baleen whale species perform to-and-fro migrations [3] between productive high latitude summer feeding and low latitude winter breeding grounds [4,5] and have been shown to cover very large distances, including the longest documented migration distance by any mammal [6]. The driving forces for these long-range migrations to often unproductive breeding grounds are still debated and a number of explanations have been suggested, including increased calf survival and avoidance of killer whale (*Orcinus orca*) predation [7]. However, there is also increasing evidence that partial (a fraction of the population stays on the feeding grounds) or differential (differences in migratory behaviour between different age classes or sexes) migration [3,8] might be more the norm than the exception in baleen whales. For example, several long-term passive acoustic monitoring (PAM) studies show the extended year-round presence of baleen whales on higher-latitude feeding grounds [9-12]. Nonetheless, at least parts of most populations of baleen whales seasonally migrate between summer feeding and winter breeding grounds [13-17].

Due to the high mobility of individuals, short surface times and the dependence on daylight and favorable weather conditions, it is generally difficult to visually survey for marine mammals. These limitations are intensified during migration, when their locations and movements are generally less predictable. Thus, baleen whale migration routes in the North Atlantic Ocean are still poorly understood for most species. In addition, while summer and winter destinations are fairly well described for the more coastally distributed species such as humpback (*Megaptera novaeangliae*) and right whales (*Eubalaena glacialis*) [18,19], little is known about the winter distribution of most other baleen whale species in the North Atlantic. For blue (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) there are some passive acoustic data indicating low latitude winter distributions [20,21], while more recent recordings also suggest year-round presence in higher latitudes [9,11]. Apart from these observations most knowledge on migration routes still originates from historical whaling records [22,23].

Such lack of data is not limited to baleen whales, but extends to other long-distance migrants that spend much of their lives in open ocean regions, such as sea turtles and pelagic seabirds [24,25]. Given current ocean-scale impacts of climate change and an increase in offshore, anthropogenic activities [26-28], a better understanding of migration timing and the location and extent of migration corridors of highly mobile marine mammals and other top predators is crucial for effective marine conservation efforts, which are currently concentrated in coastal habitats [24,29,30]. New methods such as statistical modeling, electronic tracking, as well as PAM are emerging as promising tools to gather such fundamental information on marine mammal movement and seasonal habitats [30-33].

Although North Atlantic minke whales (*Balaenoptera acutorostrata*) are well studied on their summer foraging grounds [34-38], large knowledge gaps exist concerning their distribution and abundance for much of the rest of the year. As far as it is known, their range extends from Baffin Bay to the Caribbean in the western North Atlantic and from the Barents Sea to the African continental shelf in the eastern North Atlantic [39,40]. Similar to the life cycle of other baleen whales, there is evidence of large-scale seasonal migrations between summer feeding in higher latitudes and winter breeding grounds in lower latitudes [39,41], but winter habitats have not been identified for this species. North Atlantic minke whales are currently listed as a species of least concern under the IUCN Red List [40], but are still commercially hunted in significant numbers in the North Atlantic. Based on limited data from feeding grounds, the International Whaling Commission (IWC) partitions North Atlantic minke whales into four discrete management areas: the Canadian East coast stock, the West Greenland stock, the Central stock (Iceland) and the Northeastern stock (Norway) [42]. However, there is increasing evidence for the possible existence of two breeding populations in the North Atlantic, but lack of genetic structure suggests extensive movements across and mixed assemblages at summer feeding grounds [43-45]. To confirm these data, it is important to establish the location of and obtain genetic samples from minke whale winter breeding grounds. This could have important impacts for the conservation of the species, because potential differences in genetic variability between breeding populations, for which the proportional representation in summer feeding and hunting grounds is unknown, may lead to overexploitation of small populations [43].

A general lack of winter sightings in coastal waters of the North Atlantic, reports of a few scattered sightings [39,46] and recent aerial surveys [47] observing minke whales east of the North American continental shelf-break, suggest an offshore distribution at that time of year. Recent satellite tracking data from Iceland show that individuals that feed in Icelandic waters during summer migrate south in the middle of the North Atlantic [48], corroborating passive acoustic detections at the Mid-Atlantic ridge [49] and offshore array data from the Integrated Undersea Sound Surveillance System (IUSS-SOSUS) that showed higher counts of individual singers in lower latitudes during winter [50]. Compared to the acoustic signals of other baleen whale species, until recently, minke whale sounds in the North Atlantic have not been studied extensively. While [51] described series of clicks in the 5–6 kHz range and [52] attributed low-frequency downsweeps (118–80 Hz) to the species, the best described sounds associated with North Atlantic minke whales are low-frequency pulse trains with variable interpulse interval (IPI) structure and peak frequencies from 55–150 Hz (Figure 1) [50,53-55]. A recent long-term study of these pulse trains at Stellwagen Bank, USA demonstrated the feasibility of PAM to explore seasonal, diel and spatial occurrence patterns of this species [55]. With its obvious advantages in sampling remote areas over extended time periods regardless of weather conditions [31,56,57], PAM provides an effective tool for identifying the location and expanse of migratory corridors, especially when acoustic recorders are deployed in large spatial networks. In addition, PAM data can provide valuable information about the timing of migration periods and thus complement visual observations or satellite tracking data. Furthermore, in remote offshore areas PAM may be useful in delineating seasonally important habitats that are difficult to survey using other methods [58]. The main aims of this study were to explore the geographic and seasonal variation in minke whale pulse train occurrence across multiple sites in the North Atlantic Ocean in order to better understand minke whale seasonal and spatial movement patterns. Data from locations ranging from Nova Scotia to the Caribbean in the western North Atlantic were analyzed in detail, in order to describe migration timing and a possible migration corridor along the North American continental shelf. Data from Florida and the Caribbean were used to explore the suggested winter distribution of this species in waters off the southeastern US. Finally, geographic variation in minke whale pulse train structure was examined in order to investigate possible variation in minke whale acoustic behavior across regions.

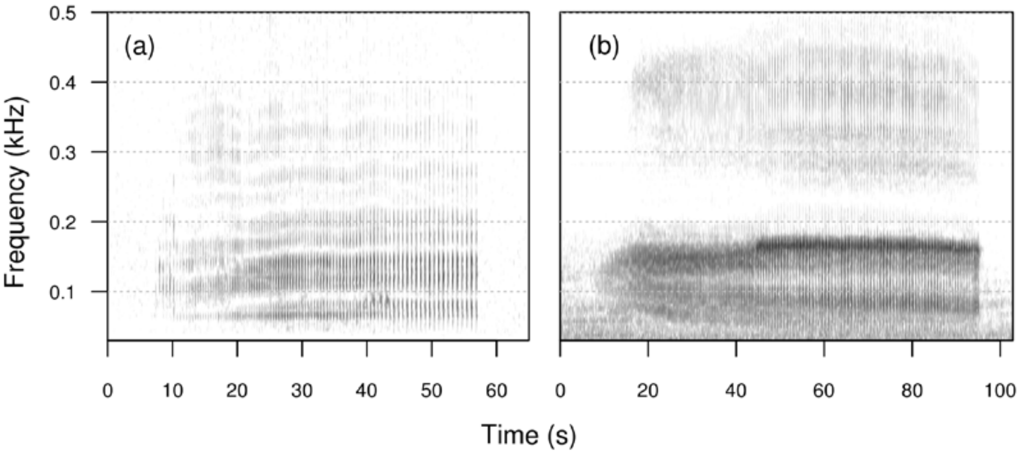

Figure 1 Spectrograms for slow-down pulse train (sd3) (a) from Stellwagen (site 4) and (b) from Jacksonville 2 (site 8) (Figure 2 for overview map). Spectrogram parameters: fast Fourier transform (FFT): size =512 points, overlap =75%, sample rate =2000 Hz, resolution =3.9 Hz and 64 ms. Y-axis starts at 0.03 kHz to remove low-frequency noise. Spectrograms made with Seewave [59].

Results

a) *Ambient noise analysis and estimated maximum detection ranges*

Ambient noise levels within the 89.1-355 Hz frequency bands varied spatially and temporally (Table 1). Overall, lowest median noise levels (93.09 dB re 1 µPa) were measured for Jacksonville (site 8, Figure 2) and differed from the highest median levels (105.08 dB re 1 µPa) measured at Stellwagen Bank (site 4, Figure 2) by 12 dB. Ambient noise levels for recording sites at Stellwagen Bank and New York (site 5, Figure 2) were similar in all seasons. For both sites noise levels were higher during winter and spring, as compared to data from summer and autumn months. Based on these ambient noise level measurements, estimated detection ranges for minke whale pulse trains were compared between sites and seasons. While median detection ranges for sources at Stellwagen Bank and New York are between 7.6 and 17.2 km, median detection ranges for the Jacksonville site are about 10 km greater, ranging between 20.4 and 29.4 km (Table 1, Figure 3).

Table 1 Median, 25th and 75th percentile ambient noise levels (NL) measured as RMS pressure over $\Delta T = 600$ s and over one-third octave bands 20–25 (89.1-355 Hz) for locations at Stellwagen Bank (site 4; SBNMS), New York (site 5; NY) and Jacksonville 2 (site 8, JAX) (see Figure 2 for overview map), across four seasons; and estimated maximum communication ranges based on a BELLHOP propagation model and the ambient noise levels above

	Location (site)	Winter	Spring	Summer	Autumn
NL (RMS)	SBNMS (4)	105.08 (103.08, 107.31)	102.96 (100.50, 104.81)	99.74 (97.80, 103.42)	99.38 (97.01, 101.53)
(dB re 1 µPa [89.1-355 Hz])	NY (5)	104.10 (102.99, 106.08)	103.19 (100.55, 105.52)	96.07 (94.13, 98.83)	100.10 (98.30, 102.04)
	JAX (8)	93.12 (90.00, 95.28)	–	–	93.09 (90.58, 99.89)
Range (km)	SBNMS (4)	7.62 (5.26, 11.25)	9.74 (7.01, 12.56)	10.81 (7.68, 14.58)	11.40 (9.02, 14.12)
	NY (5)	9.45 (6.69, 13.61)	12.49 (7.30, 20.55)	17.18 (12.86, 20.95)	12.95 (10.43, 16.42)
	JAX (8)	20.40 (15.55, 25.55)	--	--	29.47 (11.18, 40.16)

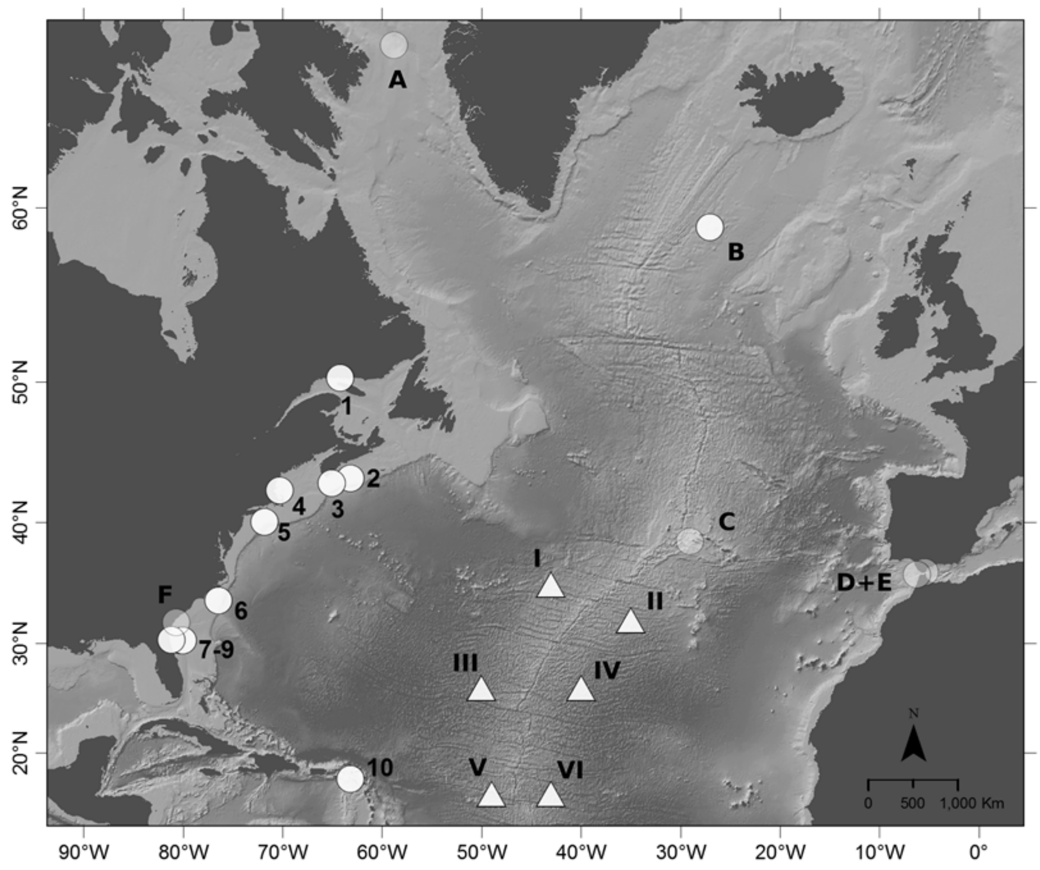

Figure 2 Overview map of all North Atlantic recording sites available for this project. Circles indicate recording sites analyzed in this study. Triangles show recording sites at the Mid-Atlantic ridge analyzed by [49] for reference. Transparent symbols show sites without detections, while white filled symbols indicate the detection of minke whale pulse trains at this site. With the exception of site 9, numbered sites 1–10 had more than 5 detections and results are shown in Figure 4. Sites A and C-F, had no detections. Site A = Davis Strait, B = SW Iceland, C = Azores, D = Cape Espartel East, E = Strait of Gibraltar West, F = Savannah. Site 1 = Gulf of St. Lawrence, 2 = Roseway Basin, 3 = Emerald Basin, 4 = Stellwagen Bank, 5 = New York, 6 = Onslow Bay, 7–9 = Jacksonville 1–3, 10 = Saba Bank. Site I-VI = NW, NE, CW, CE, SW, SE hydrophones deployed at the Mid-Atlantic ridge. Map made with data downloaded from Natural Earth. Free vector and raster map data @ naturalearthdata.com. Map projection: Mercator.

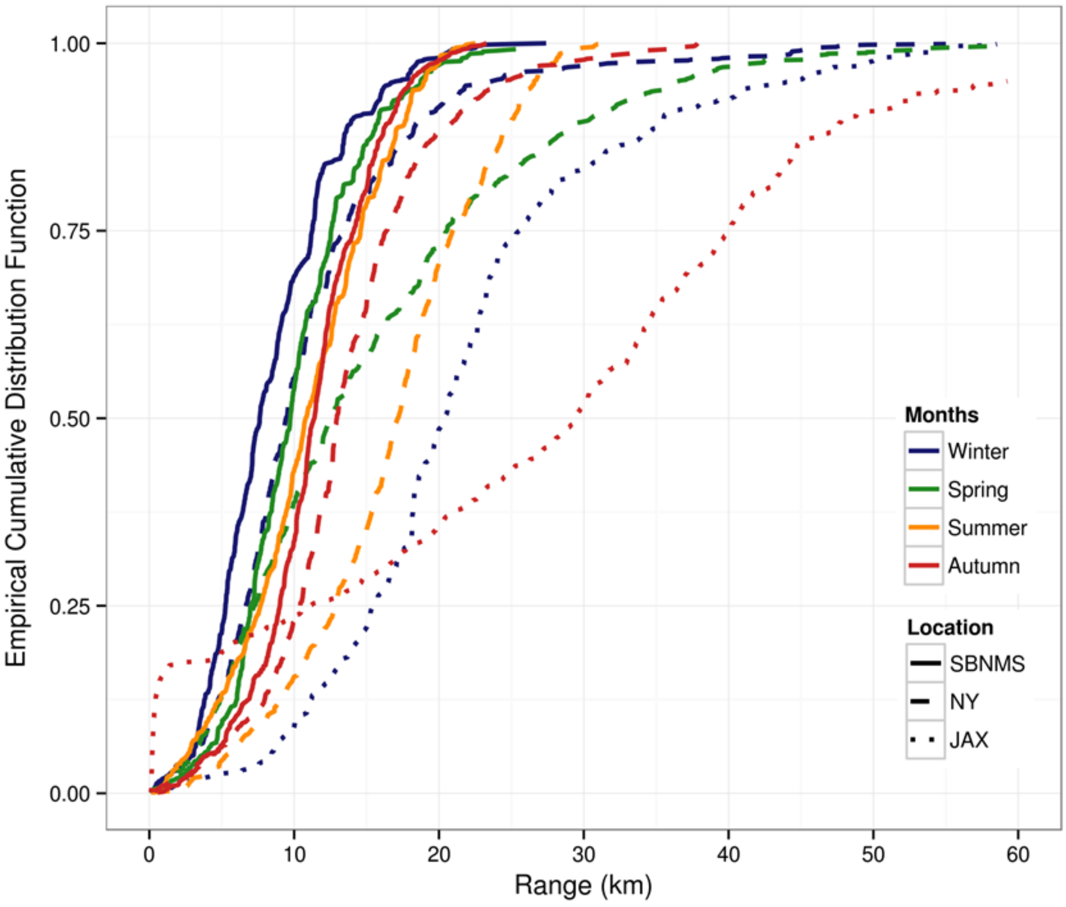

Figure 3 Cumulative distribution of estimated detection ranges at sites 4, 5 and 8 (Stellwagen Bank (SBNMS), New York (NY), Jacksonville 2 (JAX); see Figure 2 for overview map). Estimates are derived from ambient noise analyses of a subset of data (see Additional file 2: Table S1) and propagation modeling using the

BELLHOP model, as implemented in ESME at the different locations and for all four seasons [60].

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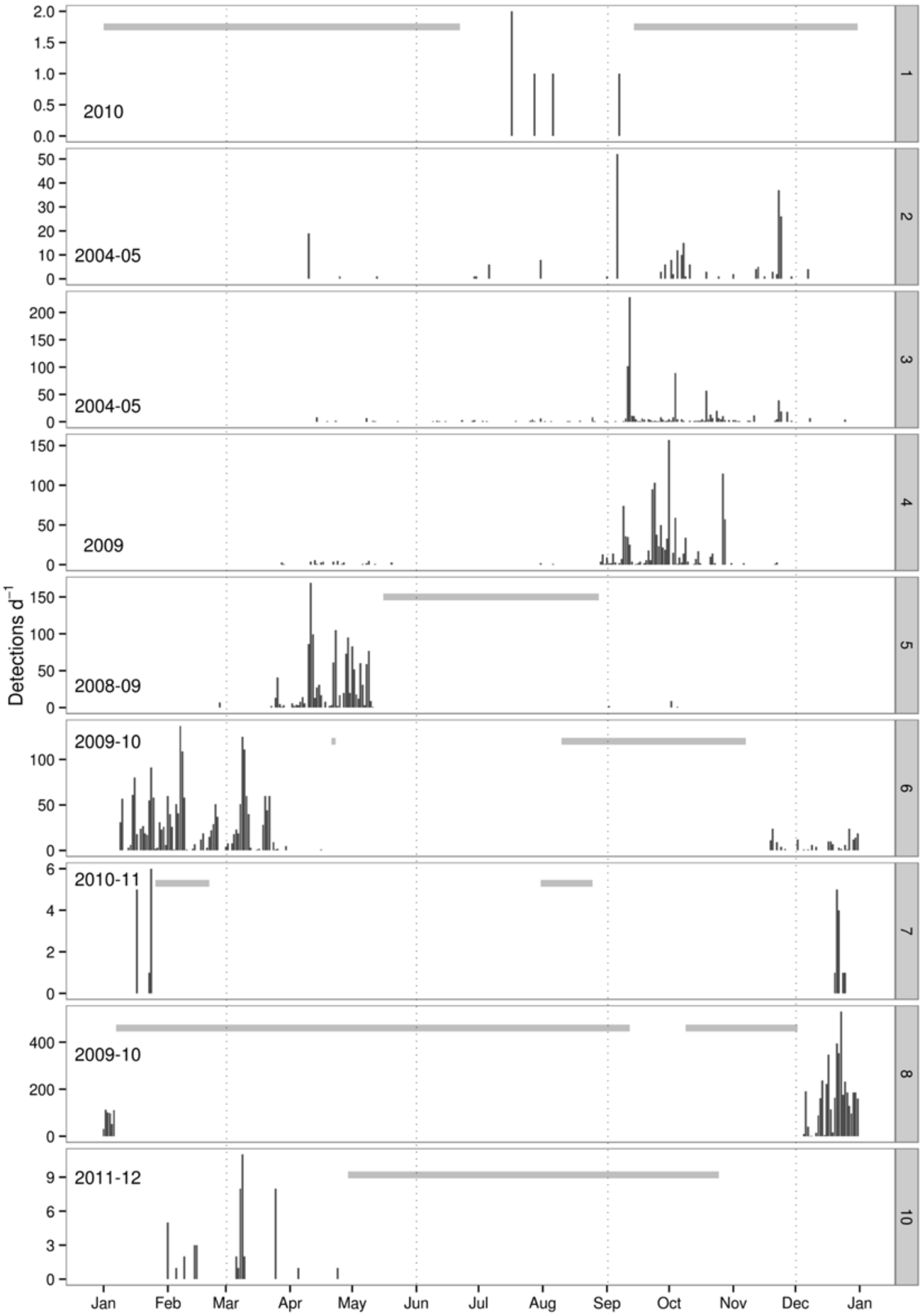
b) *Seasonal and spatial variation of pulse train occurrence*

A total of 3858 days of recordings were analyzed and 9411 minke whale pulse trains were detected during this analysis. The number of detections varied by geographic location and season. No pulse trains were detected in datasets from Davis Strait, the Azores, the Strait of Gibraltar or Savannah (sites A, C-F; Figure 2).

While most detections were made along the US east coast, where most the recording effort was located, one pulse train was detected on the recorder deployed off Southwest Iceland (site B; Figure 2) on October 21st 2007, and 48 detections were made at the Saba Island site in the Caribbean during winter and spring (February to April; site 10; Figure 2). The seasonal distributions of minke whale pulse trains for sites with at least five detections (sites 1–8 & 10; Figure 2) are summarized in Figure 4. During the 2.5 months of summer (June to August) recordings in the Gulf of St. Lawrence (site 1; Figure 2) only five pulse trains were detected. Recording sites in Nova Scotia (sites 2 & 3; Figure 2) and Stellwagen Bank (site 4; Figure 2) all showed a peak in detections in autumn and early winter (early September to December). These sites had no detections in winter (late December to March), and only a few detections in spring and summer (April to August). In contrast, at the New York recording site (site 5; Figure 2) a peak of detections occurred in spring (mid-March to mid-May). While there was no summer data available for this site, only a few detections occurred here in autumn and none in winter. In Onslow Bay (site 6; Figure 2) most of the detections occurred during winter and spring (December to early April). No pulse trains were recorded from late April to early August and there was a gap in recording effort from late August to November. All recording sites in Jacksonville (sites 7–9; Figure 2) had detections during winter. While recordings for site 8 were only available from September to October and December to January, site 7 had gaps in recording in February and August (Figure 4).


Detections d^{-1}
2010
2004-05
2004-05
2009
2008-09
2009-10
2010-11
2009-10
2011-12
1
2
3
4
5
6
7
8
10
Jan
Feb
Mar
Apr
May
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Sep
Oct
Nov
Dec
Jan
0.0
0.5
1.0
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50
100
150
0
50
100
0
2
4
6
0
200
400
0
3
6
9

Figure 4 Minke whale pulse train detections per day for all sites with more than 5 detections. Data are presented for one fictional, continuous year to show seasonality by site. True recording years are indicated in lower left corner on each panel. Missing data indicated by grey horizontal bars. Panel numbers correspond to numbered sites in overview map (see Figure 2). Note the different y-axes scales for each panel.

Exploring the spatial distribution of pulse train occurrence at the New York and Jacksonville recording sites (sites 5, 7–9; Figure 2) revealed that at both recording locations the overwhelming majority of pulse trains were detected on the easternmost recording sites, which were located farthest from the coast and closest to the edge of the shelf break (Figure 5).

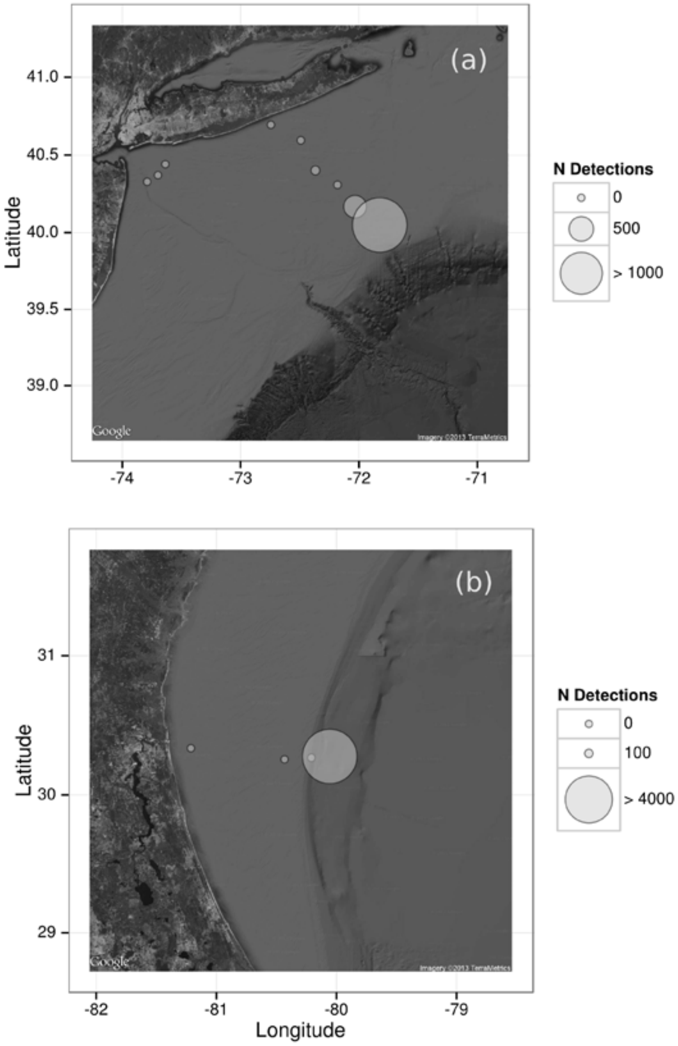

Figure 5 Maps illustrating the spatial distribution of all minke whale pulse trains detected at recorders located at sites (a) New York (site 5) and (b) Jacksonville (sites 7–9) (see Figure 2 for overview map).

c) *Geographic variation*

Duration measurements were positively correlated with SNR for data from Jacksonville (R^2 = 0.2094, p =0.006) but not for Onslow Bay (R^2 = 0.1274, p =0.073) or Stellwagen Bank (R^2 = 0.0164, p =0.298) (Additional file 1: Figure S1). The comparison of duration and number of pulses for pulse train type sd3 (Figure 1) revealed significant differences between pulse trains recorded at Stellwagen Bank as compared to both Onslow Bay and Jacksonville (sites 4, 6, 8; Figure 6). The null hypothesis that the duration and number of pulses is equal across the three different sites was rejected (Kruskal-Wallis test: (a) pulse duration: X^2 = 93.3, df =2, p <0.001; (b) pulse number: X^2 = 90.1, df =2, p <0.001). Comparisons between Stellwagen Bank and Onslow Bay, and Stellwagen Bank and Jacksonville, showed significant differences in both pulse duration, as well as the number of pulses per pulse train (p <0.001). No significant differences were found between pulse trains recorded in Onslow Bay compared to Jacksonville (p =1). In general, pulse trains recorded at Onslow Bay (mean ± sd: 75.9 ± 13.5 s; 186.9 ± 37.3) and Jacksonville (76.5 ± 10.1 s; 191.3 ± 34.5) were longer and had more pulses per pulse train as compared to pulse trains recorded at Stellwagen Bank (39.9 ± 6.5 s; 85.4 ± 13.6).

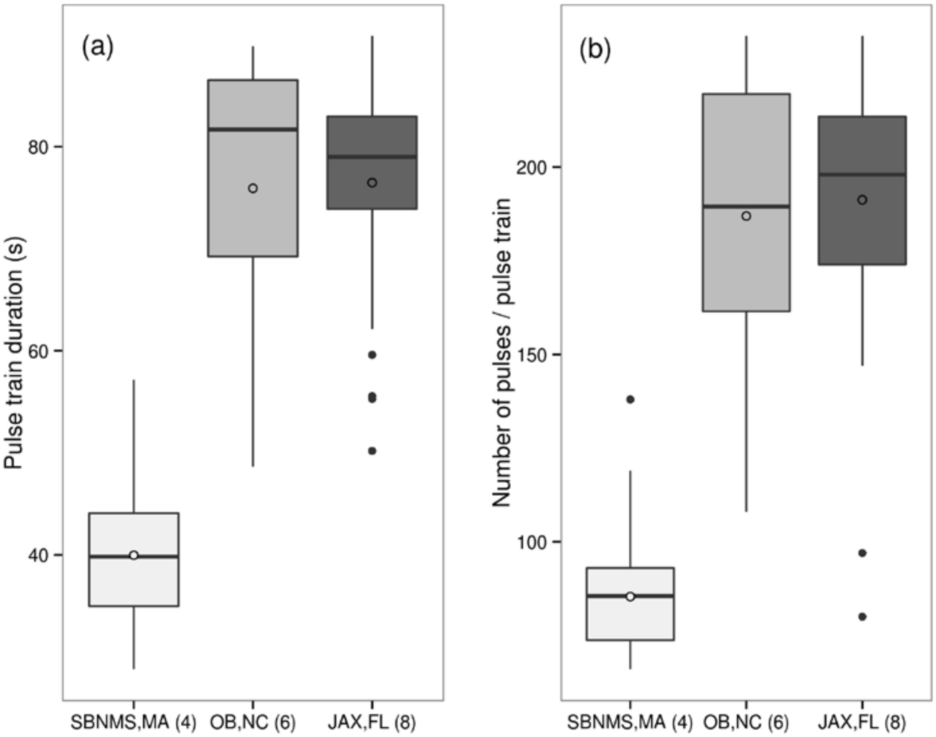

Figure 6 Box-and-Whisker plot of (a) pulse train duration (s) and (b) number of pulses per pulse train at three different geographic locations: Stellwagen Bank (site 4), Onslow Bay (site 6), Jacksonville 2 (site 8) (see Figure 2. for overview map). Lower and upper bounds of boxes represent lower and upper quartiles, respectively. Solid lines represent medians and non-filled circles are means. Whiskers represent furthest data points within 1.5 x interquartile range (IQR). Filled dots are outliers.

Discussion

a) *Comparison of ambient noise levels and detection range estimation*

Ambient noise levels varied between sites and seasons, with the southernmost recording site experiencing lowest median noise levels during the selected analysis periods (Table 1) and with lower median noise levels in winter as compared to summer and autumn measurements. This spatial gradient of decreasing ambient noise levels from north to south along the US East coast matches a recent in-depth analysis of noise levels from ten different sites along the western North Atlantic coast [61]. Estimated detection ranges based on these measured background noise levels differed accordingly. For example, detection ranges of about 20–30 km, estimated for Jacksonville (site 8, Figure 2), are about 10–20 km greater than estimates for Stellwagen Bank, and detection ranges between seasons differed by 5–10 km (Figure 3). These spatio-temporal differences in ambient noise levels have important implications for behavioural and physiological responses to noise, as well as potential communication ranges for minke whales in their different seasonal habitats [62-65]. In addition, this preliminary analysis highlights that increased ambient noise levels will affect signal-to-noise ratio (SNR) and thus influence detection probability and range in different habitats. Such differences will likely not dramatically change large-scale patterns of seasonal occurrence, which were the focus of this study. However, together with site-specific propagation characteristics, they need to be taken into account when absolute number of detections are compared on smaller spatial and temporal scales or used to infer absolute or relative abundance of animals [66,67].

b) *North Atlantic minke whale migration and winter habitats along the US continental shelf*

Minke whale pulse trains were recorded at 11 sites throughout the North Atlantic. It is currently unknown what proportion of the population produces pulse trains and whether there are differences between sexes and/or age-classes in pulse train production. Although it is unclear what proportion of the population is represented by this analysis, a recent study at Stellwagen Bank showed general agreement of visual sighting rates and frequency of acoustic detections [55]. Thus, the minimum assumption is that an increase in acoustic detections represents an increase in vocally active individuals rather than a change in behaviour of the population. However, as mentioned above, propagation characteristics and ambient noise levels need to be considered as well, especially in the absence of visual sightings.

The results from this study show seasonal variability in minke whale pulse train occurrence along the North American continental shelf consistent with seasonal migratory movement between northern and southern latitudes in summer and winter, respectively. A gradual decrease of detections at sites north of 40° N in late autumn, and an increase in recorded pulse trains in waters between 20° and 30° N during winter and north of 35° N during spring, clearly indicate movement between high-latitude summer feeding grounds and low-latitude winter habitats (Figures 2 & 4). The timing of these movements agree with recent satellite tagging data from Iceland demonstrating the departure of individual minke whales from Icelandic waters from late September to late October [48]. In addition, winter presence in tropical waters and arrival in and departure from these regions closely matched pulse train distribution recorded at the Mid-Atlantic ridge in an earlier study [49] (Figure 7), indicating that minke whales are spread out at low latitudes ranging from the US continental shelf to the Mid-Atlantic ridge during winter. Results from the current study also add further support for the suggested location of a minke whale winter breeding ground offshore the Southeastern US and the Caribbean [41,54]. Recent winter sightings from aerial surveys in the South Atlantic Bight included sightings of mother-calf pairs off North Carolina and Florida. These sightings were corroborated by long-term sighting and stranding records of calves, which occurred primarily during winter and spring in this region [47]. Together, these data confirm the presence of minke whales offshore the Southeastern US shelf break and emphasize the importance of this region as a potential breeding and calving ground for this species. The general seasonal pattern of migration that was observed along the US North Atlantic shelf break can be observed at the Mid-Atlantic ridge as well, with highest detection rates on the southernmost locations (Figures 2 & 7) during winter. Interestingly, no pulse trains were recorded on the northeastern most hydrophone, located at Latitude 32° N. This suggests that minke whales in the western North Atlantic may pass this location further to the west and begin to spread out towards the Caribbean in the west and the Mid-Atlantic ridge to the east, once they have reached lower latitudes.

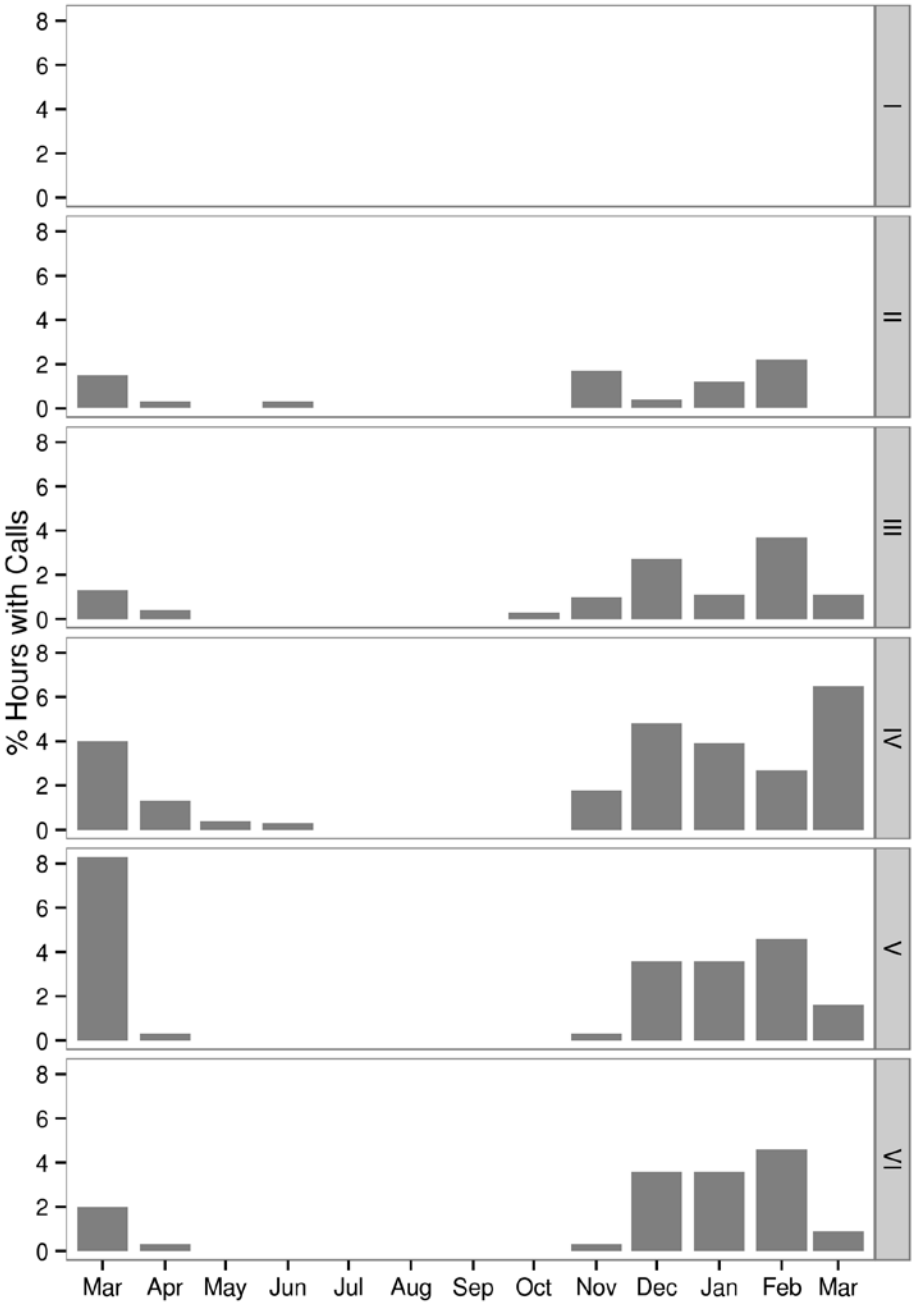

Figure 7 Minke whale pulse train detections expressed as proportion of hours with detections/month at the Mid-Atlantic ridge. Panels show different recording sites as labeled in Figure 2. Figure adapted from [49]. Reprinted and adapted with permission of the author.

Acoustic array data from New York (site 5; Figure 2) and Jacksonville (sites 7 & 8; Figure 2) demonstrate that minke whales preferentially migrate in the deeper waters to the east of the continental shelf break (Figure 5). A similar spatial distribution has been found at Stellwagen Bank [55]. Although better sound propagation characteristics in deeper waters could be partly responsible for these observed patterns in detections [68], the general scarcity of winter sightings and results from recent aerial surveys sighting minke whales exclusively offshore of the continental shelf break [47] indicate that differences in seasonal acoustic detections reflect actual animal distribution.

One of the most surprising results of this study was the relative scarcity of detections in the New York (site 5; Figure 2) autumn data compared to a peak in detections during spring in this region. This seasonality is contrary to the one found at Stellwagen Bank (site 4; Figure 2), located about 200 miles further to the north (Figure 4). Yet, similar to seasonal patterns off New York, a peak in late winter and springtime detections compared to less detections during early winter months was observed in Onslow Bay, North Carolina (site 6; Figure 2) (Figure 4). Combined, these data suggest that minke whales are distributed closer to the shelf break edge during their northbound migration in spring than during their southbound migration in autumn. However, high numbers of detections in data from Jacksonville (sites 7 & 8; Figure 2) and several detections at the inshore Saba Island site (site 10; Figure 2) indicate that whales are moving closer inshore again during winter months (Figure 4). Similar observations of a clockwise movement, with minke whales entering southern winter grounds from the northeast and moving in a westerly direction towards the US shelf break, have also been described from IUSS-SOSUS acoustic array data [50]. A possible explanation for these clockwise movements in western North Atlantic wintering grounds is that during spring minke whales are following the northward currents of the Gulf stream, while during autumn, after leaving seasonal feeding habitats north of 40° N, they follow a more directed southerly route, thereby reaching warmer waters more quickly and avoiding swimming against the Gulf Stream that may have surface currents velocities of up to 2.6 m/s [69] (Figure 8). A northward migration following the Gulf Stream and the shelf break could also explain the absence of minke whale pulse train detections and visual observations at Stellwagen Bank (site 4; Figure 2) [70] and at recording sites in Nova Scotia (sites 2 & 3; Figure 2) (Figure 4) during spring, since minke whales may be moving along the shelf break and not spread out into coastal feeding habitats, such as the Gulf of St. Lawrence [71], until they reach higher latitudes.

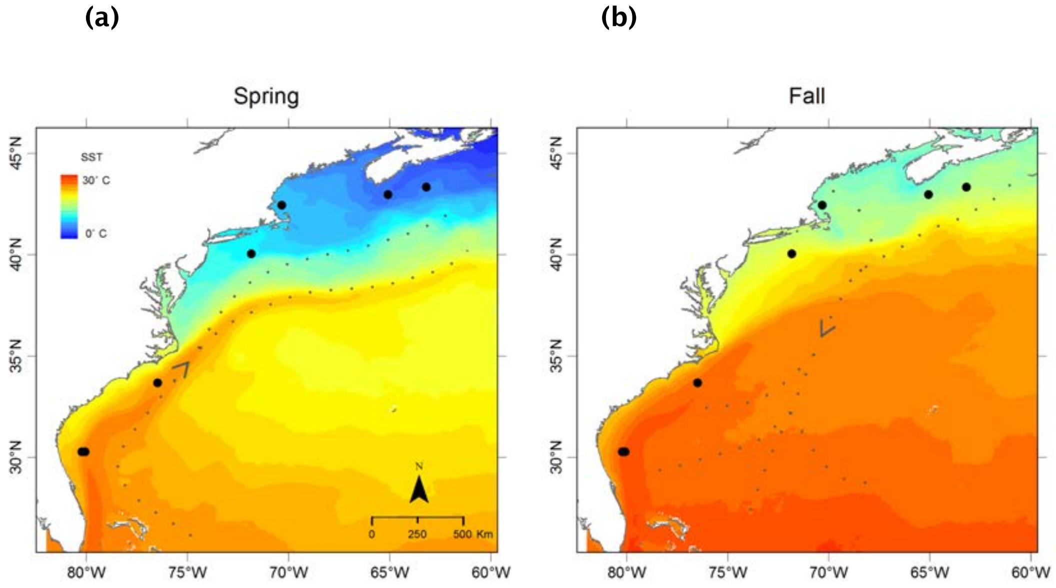

Figure 8 Maps of Sea Surface Temperature (SST) data for 2012, averaged by season (a) spring (March-May) and (b) autumn (September-November). Black dots represent recording sites 2–9 as analyzed in this study (see overview map in Figure 2) and dotted lines show hypothetical migration pathways based on frequencies of acoustic detections at different recording sites. For sea surface temperature (SST) raster generation, daily, 1 km resolution, level 4 GHRSST data were downloaded and aggregated into monthly climatological SST rasters using the Marine Geospatial Ecology Tools (MGET) [72]. Monthly SST rasters were then averaged to create seasonal climatological SST rasters. Data available at: http://podaac.jpl.nasa.gov/dataset/JPL_OUROCEAN-L4UHfnd-GLOB-G1SST

It has been well documented that minke whale presence is related to prey distribution in their summer foraging ground, where they feed primarily on pelagic shoaling fish such as sand lance (*Ammodytes sp.*) and herring (*Clupea harengus*) [34,38,71,73]. However, it has also been shown that baleen whales may pause migration and feed on the way to or from their summer habitats [16,74]. Following the Gulf Stream (Figure 8) might also be related to prey availability on their migratory pathway and could have energetic advantages for western North Atlantic minke whales that exploit the main current direction. Similarly, acoustic presence of minke whales off Nova Scotia (sites 2 & 3; Figure 2) and at Stellwagen Bank (site 4; Figure 2) during autumn migration (Figure 4; Figure 2) may be related to prey availability. Although low site fidelity [36] and swimming speeds [75] indicate that both of these areas are part of the migration route, whales might take advantage of herring spawning activity peaking from late August to mid-October in this region [76], while en route to lower latitudes.

The potential relationship between minke whale migration and the Gulf Stream may have important implications in a changing climate. In 2011 warm waters originating in the Gulf Stream were observed much closer to the shelf break south of New England than in previous years [77]. Such shifts in temperature may affect primary productivity, can result in major shifts of fish populations [78,79], and ultimately impact the distribution and abundance of top predators. For example, changes in sea surface temperature (SST) during an El Niño event in the Southern Ocean have been related to reduced calving rates in Southern right whales (*Eubalaena australis*), likely due to reduced prey availability [80]. If minke whales are indeed following the warmer surface waters of the Gulf Stream, a change of its location may potentially shift their migration path and change their overlap with other species, including important prey, as well as anthropogenic activities.

c) *Absence of pulse trains from summer feeding grounds and the eastern North Atlantic*

Very few to no minke whale pulse train detections were recorded during summer in any of the datasets (Figure 4). In traditional summer feeding habitats, such as the Mingan Islands in the Gulf of St. Lawrence [71], only five acoustic detections were made during two months of recording (Figure 4) despite a regular presence of minke whales in the area (Risch D, pers. obs.). In Davis Strait, no detections were made and in Southwest Iceland only one pulse train was detected in the month of October (Figure 2). The absence of acoustic detections from these areas could be related to a switch in behaviour at this time of year and reduced or changed vocalization activity during summer when whales are primarily feeding. For example, in humpback whales, only males produce songs in a reproductive context [81], which, although more prolific on summer feeding grounds than previously thought, shows a strong seasonality, with reduced occurrence during summer when whales are actively feeding [82]. During summer, humpback whale vocal presence on higher latitude feeding grounds is better represented by ‘social sounds’, which are produced by males and females [83,84]. Similar seasonal patterns have been found for fin whale song on high latitude feeding grounds [9]. Therefore, more data on the behavioural function of the full vocal repertoire of minke whales, which in the North Atlantic may include low-frequency downsweeps and other sounds [51,52], is needed to evaluate whether a switch in behaviour may be responsible for the absence of pulse train detections in these areas.

An alternative explanation for the absence of pulse trains in higher latitudes is that the proportion of the population producing pulse trains is not adequately captured in those areas. In the Mingan Islands, Gulf of St. Lawrence (site 1; Figure 2) the sex ratio appears to be heavily skewed towards females [85]. In Davis Strait, to the west of Greenland (site A; Figure 2), sexual segregation results in a higher proportion of females as compared to regions east of Greenland and females are also found in higher latitudes than males [86]. In humpback whales and, both blue and fin whales, only males produce songs that are thought to serve in a reproductive context [87,88]. Although it is currently unknown whether minke whale pulse trains are sex-specific also, the absence of pulse train detections in two different areas with a high proportion of females suggests that they may be.

An absence of minke whale pulse trains from recording sites in the Strait of Gibraltar in the Eastern North Atlantic (sites D + E; Figure 2) may represent an actual absence of minke whales at these sites. Although minke whales have been observed to enter the Mediterranean Sea [89], sightings are generally few, and it is unclear whether minke whales have a year-round presence or enter the Mediterranean Sea seasonally [39]. However, only three months of winter recordings were available for these sites (Table 2) and for final conclusions, recordings at other times of year need to be explored, since migrating whales might have been missed by the restricted sampling duration.

Table 2 Summary of recording sites, geographic locations, depth, available recording days, duty cycle (recording period/time period), sample rate and recorder type

Site	Location	Depth (m)	Recording period (n days)	Duty cycle (min)	Sample rate (kHz)	Recorder type
Davis Strait (A)	*67.24/-58.8*	*350*	*10/23/06-10/05/07 (348)*	*Cont.*	*2*	*HARU*[1]
SW Iceland (B)	58.0/-26.0	800	05/16/07-07/25/08 (437)	Cont.	2	HARU[1]
Gulf of St. Lawrence (1)	50.25/-64.22	25	06/23/10-09/13/10 (83)	Cont.	2	MARU[2]
Roseway Basin (2)	42.97/-65.06	145	07/02/04-08/17/05 (412)	Cont.	2	HARU[1]
Emerald Basin (3)	43.34/-63.16	153	07/02/04-10/13/05 (469)	Cont.	2	HARU[1]
Stellwagen Bank (4)	42.45/-70.31	71	12/18/08-03/19/10 (457)	Cont.	2	MARU[2]
New York (5)	40.05/-71.82	90	02/29-05/15/08; 08/29-03/05/09 (266)	Cont.	2	MARU[2]
Azores (C)	*38.54/-29.04*	*190*	*04/10-09/17/10; 09/29/10-5/19/11(424)*	*1.5/30*	*50*	*EAR*[3]
Cape Espartel East (D)	*35.87/-6.20*	*340*	*10/28/08-01/30/09 (95)*	*5/10*	*2*	*EAR*[3]
Strait of Gibraltar West (E)	*36.03/-5.42*	*100*	*10/28/08-01/30/09 (95)*	*5/10*	*2*	*EAR*[3]
Onslow Bay (6)	33.68/-76.48	335	04/24-08/09/09; 11/08/09-04/20/10 (271)	5/10	200	HARP[4]
Savannah (F)	*31.83/-80.70*	*17*	*11/18/09-03/16/10 (119)*	*Cont.*	*2*	*MARU*[2]
Jacksonville 1 (7)	30.27/-80.06	91	02/22-07/30/10; 08/26/10-01/25/11 (312)	5/10	200	HARP[4]
Jacksonville 2 (8)	30.28/-80.06	305	09/13-10/08/09; 12/03/09-01/07/10 (62)	Cont.	2	MARU[2]
Jacksonville 3 (9)	30.34/-81.21	17	11/19/09-06/04/10 (197)	Cont.	2	MARU[2]
Saba Bank (10)	17.51/-63.19	30	10/27/11-04/28/12 (185)	30/120	16	MARU[2]

Sites at which no minke whale pulse train detections were made are in italics. See the following references for details about recorder electronics and sensitivities: (1) HARU phones: [90]; (2) Marine Autonomous Recording Unit (MARU): [91]; (3) Ecological Acoustic Recorder (EAR): [92]; (4) High-frequency Acoustic Recording Package (HARP) [93].

Very little is known about minke whale migration in the middle and eastern North Atlantic, but it has been suggested here too, that migration takes place in open, offshore waters [39,46] and recent satellite tracking data are in support of this idea [48]. The absence of minke whale pulse trains from recording sites located in the Azores, where minke whales are occasionally sighted during spring and early summer [16], is thus surprising. However, most minke whales may be passing the archipelago too far offshore to be acoustically detected. In contrast, from November to June, minke whale pulse trains were frequently recorded at recorders deployed to the east and west of the Mid-Atlantic ridge [49] (Figure 7), indicating that minke whale breeding grounds extend eastwards from the Caribbean to at least the Mid-Atlantic ridge.

Finally, the absence of minke whale pulse trains from recording sites in the eastern North Atlantic may be in part related to geographic differences in vocalizations that could not be resolved by the automated detector used in this study. For example, while [53] found mainly speed-up pulse trains in data from the Caribbean, data from Stellwagen Bank showed a predominance of slow-down pulse trains [55]. Although the automated pulse train detector used here was built on data originating from Stellwagen Bank, North Carolina and Jacksonville, most pulse trains used for training were of the slow-down type. There are differences in the frequency distribution between these two types [53], thus a concentration on slow-down pulse trains from the western North Atlantic for detector development might have influenced detector performance at other sites, especially those that are geographically more distant.

d) *Geographic variation in signal structure*

Although a thorough comparison of the full vocal repertoire was beyond the scope of this study, preliminary data from Onslow Bay, North Carolina suggest that the main minke whale call categories found at Stellwagen Bank [55] are present in southern recording sites also [94]. A comparison of pulse train type sd3 recorded at Stellwagen Bank, North Carolina and Jacksonville (Figure 1) shows evidence for geographic variability in signal structure with pulse trains being about 30 seconds longer and containing about 100 more pulses on southern recording sites as compared to recording sites in higher latitudes (Figure 6). Although pulse train duration measurements for the Jacksonville site were correlated with SNR (Additional file 1: Figure S1), and are thus a minimum estimate, these results corroborate pulse train measurements from the Caribbean which were similar in length and number of pulses to pulse trains from North Carolina and Jacksonville [53]. As mentioned above, the majority of pulse trains found in the Caribbean were of the speed-up type as opposed to a majority of slow-down types in northern sites. The reasons for this difference are unclear but individual differences in call type production could be partly responsible [75]. A more in depth comparison of minke whale vocal repertoire and call type occurrence may help to elucidate more differences and similarities between sites and shed light on the behavioural function of these sounds. Although it is unclear whether the significant increase in signal duration is true for all types of pulse trains, none of the pulse trains from Stellwagen Bank measured during an earlier study [55] lasted as long as some of the pulse trains recorded on southern recording sites in this study.

Testosterone mediated male singing behaviour, increased signal duration and complexity are well documented in a range of vertebrates [95-97]. The increased duration of minke whale pulse trains on potential winter breeding grounds, the general scarcity of these signals on feeding grounds and their increased occurrence during autumn migration, when testosterone levels in adult males are rising [98], are all strong indicators for a reproductive function of these sounds. As argued above, there is also some evidence indicating that females are not producing these sounds. However, more data from breeding grounds, higher latitude feeding grounds with an even distribution of sexes or acoustic tag recordings from individuals of known sex are necessary to conclusively answer the question of sex-specificity and behavioural context of minke whale pulse trains.

Conclusion

This study confirms the seasonal migration of North Atlantic minke whales offshore the eastern US continental shelf in spring and autumn and their winter presence in southeastern US and Caribbean waters. The identification of a potential breeding ground offshore of the southeastern US may enable more directed genetic sampling of this species in order to help elucidate population structure [43], with potentially important implications for current management of this species in the North Atlantic Ocean. Another important result of this study is the scarcity of pulse train detections north of 50° N during summer, when minke whales are abundant in coastal feeding habitats. These results either indicate a switch of vocal behaviour at this time of year, or, if signals are sex-specific, illustrates the sexual segregation of North Atlanic minke whales on their feeding grounds as described in earlier studies [86].

These results emphasize the feasibility of using passive acoustic monitoring (PAM) networks for investigating the spatial and seasonal distribution of pelagic baleen whale species that are difficult to survey by visual methods alone. However, in order to interpret these detection results beyond presence/absence of species and in the context of animal population density, there is a clear need for extended baseline data collection. Currently missing data include vocalization rates based on group size, in different behavioural contexts, by sex and age class, as well as data collected at different seasonal and spatial scales [99]. These data are extremely scarce for most marine mammal species. Yet, recent developments in technologies such as digital recording tags [88,100-102], as well as analysis techniques for localization and tracking of individual animals using passive acoustic data [103-105] may help to close some of these current data gaps in the future.

Methods

Acoustic data collection

Long-term acoustic data for this project were collected across multiple years and at 16 different sites throughout the North Atlantic Ocean using a variety of different recording packages (Figure 2, Table 2). Data availability and temporal consistency was limited by the goals of the various long-term monitoring projects, with differing analysis targets, which contributed data to this large-scale meta-analysis [11,55,58,106-109]. However, the main objective of this project was to explore large-scale migration and characterize the seasonal occurrence of minke whale pulse trains at different sites throughout the North Atlantic. Thus, recording periods were selected to maximize the overall spatial coverage and the seasonal coverage within each site, rather than to keep annual consistency. Table 2 summarizes recording locations, available recording days, recording schedules, sample rates and equipment types used. Most recording effort was concentrated along the United States (US) east coast and used four types of bottom-mounted recorders deployed in depths ranging from 17 to 800 meters (Figure 2). While most recorders sampled continuously at 2 kHz, some recordings were scheduled to record every 1.5 to 30 minutes and sampling rates ranged up to 200 kHz for some recorders (Table 2). All data were downsampled to 2 kHz before automatic detection and further data processing.

Data analysis

a) *Automatic detection*

North Atlantic minke whales are known to produce up to seven types of low-frequency pulse trains, which can be assigned to three major categories (slow-down, constant and speed-up pulse train), based on varying interpulse interval structure (IPI) [53,55]. An automated detector was developed to examine selected recordings for the presence of these pulse trains. The automatic detection consisted of a multi-stage process based on spectrogram intensity binarization, energy projection, feature extraction and classification [110]. While the detection stage was designed for general pulse train detection, a Rippledown Rule (RIDOR) learner [111] was trained to identify minke whale pulse trains, taking into account, but not distinguishing among, the different types of pulse trains. A total of 18 basic features were extracted from each detected event and passed to the RIDOR for classification (see details in [110]). The overall false negative rate (FNR) of the detector was assessed in an earlier study and was found to be 27% (647 out of 2428 true positive (TP) detections), with 181 false positive (FP) detections in 120 hours (or 29,847 signal slices) of evaluated data [55]. Experienced data analysts (GD & DR) manually verified all detected pulse trains using the MATLAB (Mathworks, Natick, MA) based custom software program SEDNA [112]. All false positive detections were removed from each analyzed dataset.

b) *Ambient noise levels and estimated maximum detection ranges*

Since variations in ambient noise levels (NL) by site and season can have a profound impact on the detection probability of acoustic signals [67], an exploratory ambient noise analysis was conducted for three recording sites (sites 4, 5, 8: Stellwagen Bank, New York, Jacksonville 2; Figure 2), for which equipment calibration information was available. LTSpec, a custom-written MATLAB script [113], was used to aggregate and compute long-term spectrograms and extract absolute root-mean-square (RMS) received levels over a frequency band encompassing six third-octave bands (center frequencies at 100, 125, 160, 200, 250, and 315 Hz). This frequency band was chosen to include most energy content of minke whale pulse trains, which is concentrated between 50 and 300 Hz (Figure 1) [53,55]. Site-specific and seasonal week-long data (Additional file 2: Table S1) were aggregated over a time period of ΔT =600 s. Spectrograms were created using a sampling rate of 2000 Hz, a FFT size of 2048, and a Hanning window function, resulting in a frequency resolution of 0.98 Hz. Ambient noise levels (NL) were used to estimate maximum detection ranges of minke whale pulse trains. Assuming source and receiver depths of 20 m, an average source level of 165.4 dB [75] and pulse length of 0.1 s, signal propagation was modeled for an omni-directional source of 120 Hz over 8 horizontal radii and for all four seasons, using a BELLHOP acoustic simulation model implemented in ESME [60], and environmental databases provided by the Oceanographic and Atmospheric Master Library (OAML) (available at http://esme.bu.edu/). The maximum propagation radius was selected and compared to all measured ambient noise levels. The maximum detection range was then estimated as the point at which SNR (RL-NL) equals zero and ranges for different sites and seasons were compared using empirical cumulative distribution functions, calculated with function ecdf of the R v. 3.1 stats package (available at www.R-project.org).

c) *Geographic variation in acoustic features*

A subset of non-overlapping detections of high signal-to-noise ratio [SNR >10 dB] from three sites (n =68, 26, 35 for sites 4, 6, 8: Stellwagen Bank, Onslow Bay, Jacksonville 2; Figure 2) were selected to measure and compare slow-down pulse train type sd3 as defined by [55]. This type of pulse train is characterized by a bimodal distribution in IPI, peaking at 0.4 and 0.7 s (Figure 1) [55]. It was selected for this geographic comparison, since it was one of the most frequently occurring and easily distinguishable pulse train types in all datasets [55]. Acoustic data for this analysis were bandpass filtered from 30 to 800 Hz to remove environmental noise and signals from other species. Spectrograms (FFT size: 512 points, 96.9% overlap, Hanning window, time resolution: 8 ms, frequency resolution: 4 Hz) were created and analyzed using Avisoft-SASLab Pro 5.1 (Avisoft Bioacoustics). The automatic parameter measurement tool was used to measure pulse train duration and identify the total number of pulses per pulse train using an amplitude threshold of −30 to −55 dB sound pressure level (SPL) relative to the maximum SPL in the sound file. The threshold was manually adjusted to ensure the detection of most pulses within a pulse train. Given that the data were not normally distributed (Saphiro-Wilk test), the hypothesis that mean pulse duration and number of pulses differed between sites was tested using a Kruskal-Wallis test. Wilcoxon rank-sum tests with Bonferroni corrections for multiple testing were used for post-hoc comparisons between pairs of sites. All statistical analyses were conducted using R v. 3.1. In order to select high quality signals for this analysis and test whether SNR affected the duration measurements, SNR of the whole signal was measured within a selection box including the signal and time periods just before and after a pulse train, using the MATLAB based sound analysis tool Osprey [114].

d) *Seasonal and spatial variation*

One recorder per site and deployment period was selected in order to examine seasonal patterns of minke whale pulse train occurrence. Since preliminary data from migration and winter habitats suggest an offshore distribution of minke whales [47,55], at sites where multiple recorders were available, preference was given to the recorders deployed farthest from shore. All data from sites with at least five detections were binned and plotted by day. In addition, the seasonal and geographic patterns of pulse train occurrence along the US east coast continental shelf, where most recording effort was concentrated, were compared to seasonal minke whale pulse train occurrence from the Mid-Atlantic ridge [49]. In order to simplify the description of seasonal patterns of pulse train occurrence the four seasons will be defined as follows for the remainder of the paper: winter = December to February, spring = March to May, summer = June to August and autumn = September to November.

For the New York recording site (site 5; Figure 2), data from nine recorders, stretching from west to east across the continental shelf, were available for analysis. For Jacksonville, data from four recording units, deployed from west to east, were available (sites 7–9; Figure 2). For these two geographic sites, the total number of detections was evaluated for all available recording units in order to characterize the spatial distribution of minke whale pulse train detections as a function of distance from shore and shelf break.

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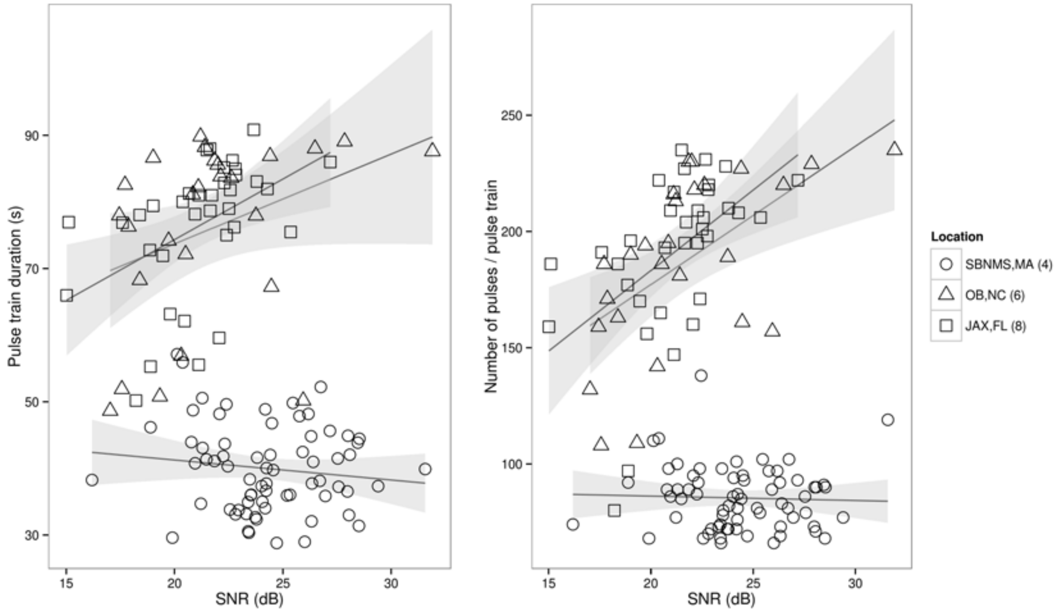
Additional files

Additional file 1

Figure S1:
Scatterplots and regression lines (CI=95%) of Signal-to-Noise Ratio (SNR) in dB against pulse train duration and number of pulses/pulse train, comparing data from Stellwagen Bank (SBNMS), Massachusetts (site 4); Onslow Bay, North Carolina (site 6); and Jacksonville, Florida (site 8).



Additional file 2:

Table S1 Overview of weeks analyzed for ambient noise analysis.

Location (Site)	Winter	Spring	Summer	Autumn
SBNMS (4)	01/01/09-01/07/09	04/01/09-04/07/09	08/01/09-08/07/09	11/01/09-11/07/09
NY (5)	01/01/09-01/07/09	04/01/08-04/07/08	08/30/08-09/05/08	11/01/08-11/07/08
JAX (8)	12/18/09-12/24/09	--	--	10/01/09-10/07/09

Chapter VI

Risch D, Gales NJ, Gedamke J, Kindermann L, Nowacek DP, Read AJ, Siebert U, Van Opzeeland IC, Van Parijs SM & Friedlaender AM (2014) Mysterious bioduck signal attributed to the Antarctic minke whale (*Balaenoptera bonaerensis*). *Biology Letters*. 10(4): 20140175. doi: 10.1098/rsbl.2014.0175.

Photo: Ari Friedlaender

Antarctic minke whale (*Balaenoptera bonaerensis*) tagged with Acousonde™ tag.

biology
letters

Mysterious bio-duck sound attributed to the Antarctic minke whale (*Balaenoptera bonaerensis*)

Denise Risch, Nicholas J. Gales, Jason Gedamke, Lars Kindermann, Douglas P. Nowacek, Andrew J. Read, Ursula Siebert, Ilse C. Van Opzeeland, Sofie M. Van Parijs and Ari S. Friedlaender

Biol. Lett. 2014 **10**, 20140175, published 23 April 2014 biology letters

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Research

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Animal behaviour

Mysterious bio-duck sound attributed to the Antarctic minke whale (*Balaenoptera bonaerensis*)

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For decades, the bio-duck sound has been recorded in the Southern Ocean, but the animal producing it has remained a mystery. Heard mainly during austral winter in the Southern Ocean, this ubiquitous sound has been recorded in Antarctic waters and contemporaneously off the Australian west coast. Here, we present conclusive evidence that the bio-duck sound is produced by Antarctic minke whales (*Balaenoptera bonaerensis*). We analysed data from multi-sensor acoustic recording tags that included intense bio-duck sounds as well as singular downsweeps that have previously been attributed to this species. This finding allows the interpretation of a wealth of long-term acoustic recordings for this previously acoustically concealed species, which will improve our understanding of the distribution, abundance and behaviour of Antarctic minke whales. This is critical information for a species that inhabits a difficult to access sea-ice environment that is changing rapidly in some regions and has been the subject of contentious lethal sampling efforts and ongoing international legal action.

1. Introduction

The bio-duck sound has been recorded ubiquitously in the Southern Ocean by researchers for over five decades. First described and named by submarine personnel in the 1960s, the bio-duck has since been recorded at various locations in the Southern Ocean, but its source remained a mystery [1–6]. The sound consists of a regular series of downswept pulses, ranging from 50 to 300 Hz, with harmonics of up to 1 kHz. The number of pulses within a series can differ within and between recording locations, but the sound is highly repetitive with a typical interval of 3.1 s between the start of two series [1]. The enigma surrounding the sound has been further deepened by its discordant seasonal occurrence patterns. During winter and spring, the bio-duck occurs simultaneously in the eastern Weddell Sea and off Western Australia, indicating a very widespread distribution of the species, or potentially a seasonal migration by one segment of the population and year-round presence in Antarctic waters by another [3,6].

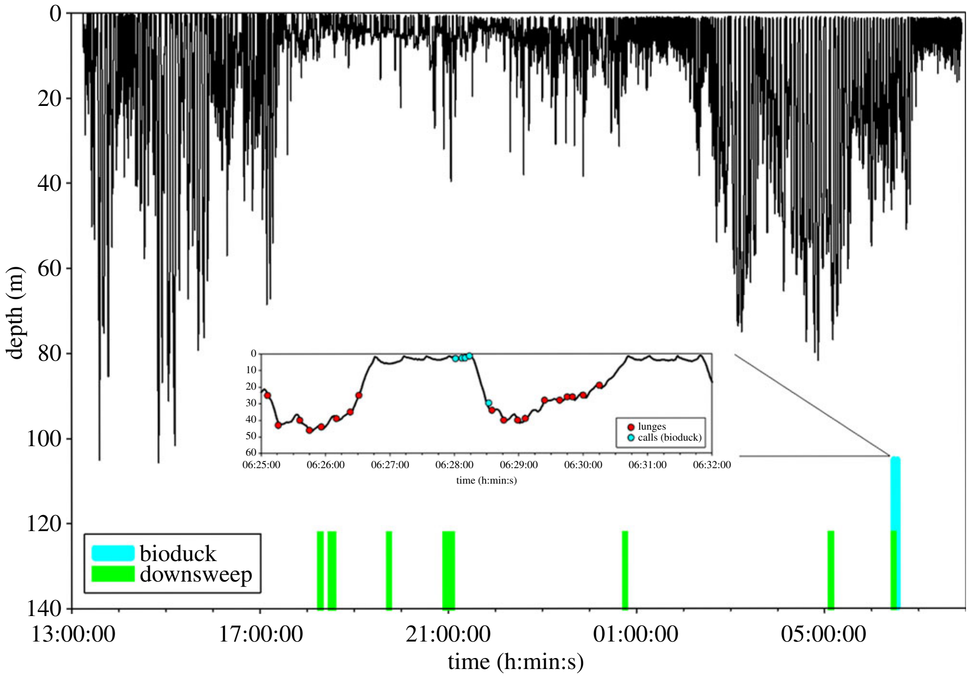

Figure 1. Complete dive profile of the Antarctic minke whale tagged in Wilhelmina Bay (64°41′ S, 62°13′ W) on 13/14 February 2013. Times at which vocalizations occurred are marked with vertical bars (green, downsweep; turquoise, bio-duck sound). Inset shows detail of two lunge-feeding dives (lunges marked by red circles) during which bio-duck sounds were recorded on the tag.

Here, we present conclusive evidence attributing the bio-duck sound to Antarctic minke whales. We describe acoustic recordings from multi-sensor acoustic recording tag (Acousonde) deployments on two Antarctic minke whales in Wilhelmina Bay, Antarctic Peninsula. These were the first acoustic tags deployed on Antarctic minke whales, providing a unique opportunity for detailed study of their vocalizations.

2. Material and methods

In the austral summer (13 and 15 February) 2013, two Antarctic minke whales were tagged with multi-sensor suction-cup tags, equipped with an HTI-96-MIN hydrophone (High Tech, Inc., Long Beach, MS, USA; sensitivity: -187.2 dB re 1 V μPa^{-1}), recording continuously at a sample rate (SR) of 25811 Hz. The recording system had a flat frequency response (± 3 dB) in the 22–9292 Hz frequency band. In addition to acoustic data, auxiliary sensors sampled temperature, pressure, 3-axis accelerometry and magnetometry at 10 Hz. Tags were deployed in Wilhelmina Bay, off the western Antarctic Peninsula (64°41′ S, 62°13′ W and 64°38′ S, 62°16′ W) using a hand-held carbon fibre pole from a rigid-hulled inflatable boat (RHIB).

Spectrograms (fast Fourier transform (FFT) size: 4096 points, 95% overlap, Hanning window, time and frequency resolution: 8 ms and 6 Hz) were generated and analysed using RAVEN PRO v. 1.5 [7]. Presence of vocalizations was evaluated manually based on these spectrograms, and start and end time (s), 90%-energy duration (s), peak, centre and first and third quartile frequencies (Hz) were measured for each identified sound. Vocalizations were filtered between 22 and 200 Hz using a 4-pole Butterworth bandpass filter, and RMS received levels (RLs) were calculated within the 90% duration time window using MATLAB (2007a, The MathWorks Inc., Natick, MA, USA).

In addition, vocalizations were compared to example data from PALAOA (22 July 2006; 70°31′ S, 8°13′ W) [8]; Dumont D'Urville (3 June 2006; 65°33′ S, 140°32′ E) [9] and Ross Island (22 November 1964; 77°30′ S, 168°00′ E) [10].

3. Results

The two tags recorded for 18 and 8 h, respectively. During both deployments the tagged whales were in large single-species groups of five to about 40 animals and fed almost continuously [11]. Vocalization rates were low; only 32 clear calls, with a signal-to-noise ratio of more than 10 dB, were recorded in this entire dataset. Most calls ($n = 26$) were recorded when the tagged animal was close to the surface (mean $\pm$ s.d.: 2.6 ± 0.7 m). The bio-duck sound ($n = 6$) was recorded on one of the tags, just before a feeding dive (figure 1). The vocalization consisted of series of 5–12 pulses, produced in regular sequences at an interval of 3.1 s (measured from the start of one series to the start of the next). Most energy was contained between 146 ± 12 and 165 ± 16 Hz (mean $\pm$ s.d., first and third quartiles), and pulses exhibited peak frequencies of 154 ± 13 Hz. The 90% energy duration of individual pulses was 0.1 s. The identification of these sounds as the bio-duck was based on comparisons with the published literature [1,3–6]. In addition, based on spectral and temporal content, tag recordings were matched to bio-duck sounds recorded on long-term, bottom-mounted recorders at PALAOA [8] (70°31′ S; 8°13′ W) and at Dumont D'Urville [9] (65°33′ S; 140°32′ E) (figure 2*a–c*). Comparisons with the PALAOA recordings in particular revealed similarity in frequency range, number of pulses, and in the stereotypic interval of 3.1 s between bio-duck series (figure 2*a*,*b*).

Apart from the bio-duck sound, low-frequency downsweeps ($n = 26$) were the most frequently recorded sound on both tags, with a mean peak frequency of 83.1 ± 16.7 Hz, and a duration of 0.2 s (figure 2*d–f*). Low-frequency downsweeps (60–130 Hz) have previously been recorded in the Ross Sea (77°30′ S 168°00′ E) during a close encounter with two Antarctic minke whales [10]. These sounds have very similar characteristics to our data (figure 2*d*,*e*). In addition, similar downsweeps were recorded in conjunction with the

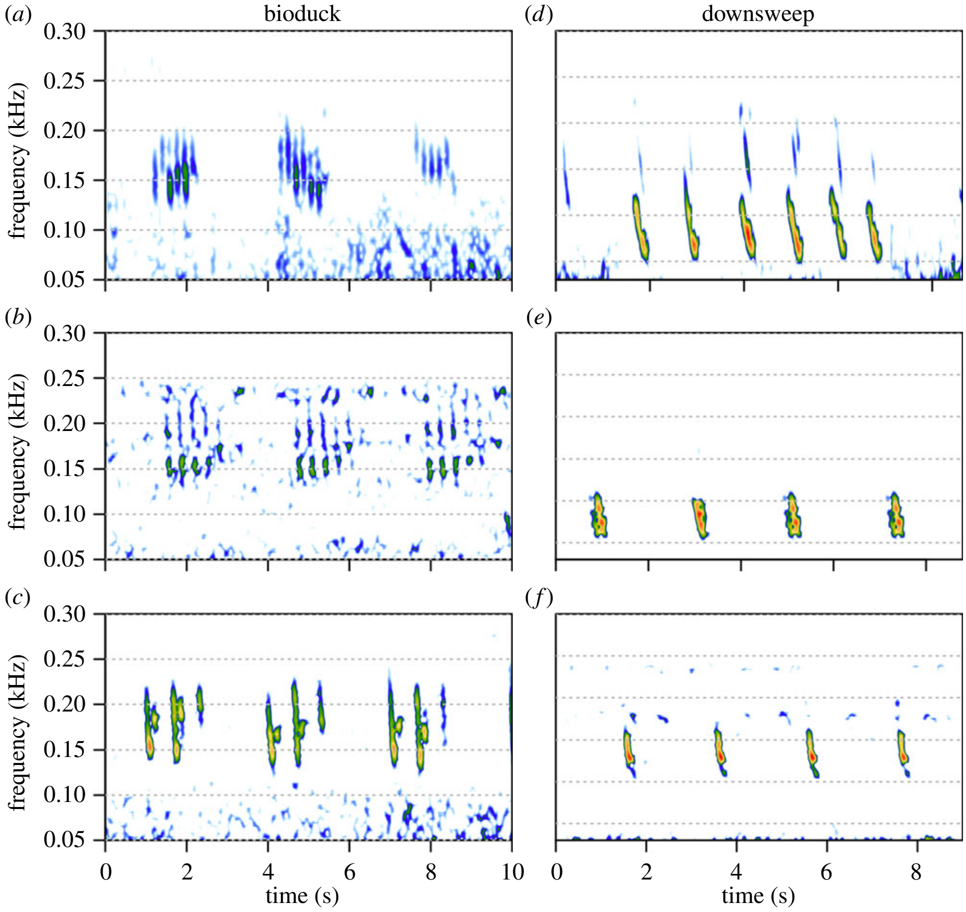

Figure 2. Bio-duck and downsweep sounds compared between different recording locations. *Bio-duck*: (*a*) Wilhelmina Bay (14 February 2013; 64°41′ S, 62°13′ W; acoustic recording tag; SR: 25 811 Hz; filtered and downsampled to 2000 Hz; FFT: 512; 95% overlap; Hanning window); (*b*) PALAOA station (22 July 2006; 70°31′ S, 8°13′ W; long-term recorder; SR: 48 000 Hz; filtered and downsampled to 2000 Hz; FFT: 512; 95% overlap; Hanning window); (*c*) Dumont D'Urville (3 June 2006; 65°33′ S, 140°32′ E; long-term recorder; SR: 4000 Hz; filtered and downsampled to 2000 Hz; FFT: 512; 95% overlap; Hanning window). *Downsweeps*: (*d*) Wilhelmina Bay (13 February 2013; 64°41′ S, 62°13′ W; acoustic recording tag; SR: 25811 Hz; FFT: 4096; 95% overlap; Hanning window); (*e*) Ross Island (22 November 1964; 77°30′ S, 168°00′ E; opportunistic recording; SR: 2000 Hz; FFT: 512; 95% overlap; Hanning window); (*f*) PALAOA station (22 July 2006; 70°31′ S, 8°13′ W; long-term recorder; SR: 48 000 Hz; filtered and downsampled to 2000 Hz; FFT: 512; 95% overlap; Hanning window) (see the electronic supplemental material for all sound files). (Online version in colour.)

Table 1. Acoustic parameters (mean ± s.d.) of bio-duck ($N = 6/n = 41$ pulses) and downsweep ($N = 26$) sounds recorded on two acoustic recording tags. *n*(P), number of individual pulses; PF, peak frequency; CF, centre frequency; Q25, first quartile frequency (25%); Q75, third quartile frequency (75%); DUR90(P), 90% energy duration of individual pulses/downsweeps; RMS RL, RMS received level.

	n(P)	PF (Hz)	CF (Hz)	Q25 (Hz)	Q75 (Hz)	DUR90 (P) (s)	RMS RL (dB re 1 µPa)
bio-duck	7 ± 3	154 ± 13	155 ± 13	146 ± 12	165 ± 16	0.1 ± 0.0	140.2 ± 3.6
downsweep	—	83 ± 17	84 ± 17	75 ± 15	94 ± 15	0.2 ± 0.1	147.3 ± 5.3

bio-duck sound at PALAOA (figure 2*f*) and in Western Australia [1].

Bio-duck RLs at the tag averaged 140.2 ± 3.6 dB re 1 µPa, and downsweeps were received at a mean RL of 147.3 ± 5.3 dB re 1 µPa (table 1). One complication of acoustic tag recordings is the difficulty in ascribing calls to the focal animal [12]. However, during daylight, tagged whales were visually tracked from a RHIB. During these focal follows, no other marine mammal species were observed within 1 km of the focal minke whale groups. Previous calculations of source levels for minke whale vocalizations were in the range of 160–165 dB re 1 µPa [13,14]. Given the reported RLs, assuming spherical spreading ($20 \times \log(R)$) [15] and source levels for the bio-duck sound to be similar to those reported for other minke whale sounds, the sound source was within one to two body lengths of the recording tag. Given the observation of large groups in which animals were frequently associated, the absence of other species during the time when calls were recorded and RLs that indicate a source close to the tagged animals, we conclude that recorded sounds were produced by either the focal animal or other Antarctic minke whales in the immediate vicinity.

4. Discussion

This study is the first to analyse acoustic tag recordings from Antarctic minke whales. Our results solve the mystery around the source of the bio-duck sound, which is one of the most prevalent sounds in the Southern Ocean during austral winter and can now be attributed unequivocally to the Antarctic minke whale. These results have important implications for our understanding of this species, which is of particular priority to the International Whaling Commission [16,17].

Antarctic minke whales live in remote open-water environments and within sea ice habitats [18]. Traditional ship-based study methods are extremely expensive, and data from such studies are complex and difficult to interpret [19–21]. The acoustic identification of Antarctic minke whales offers the opportunity to retrospectively analyse several years' worth of existing long-term recordings to explore seasonal occurrence and migration patterns of this species, including the possibility of using acoustics to estimate abundance [22]. Of particular interest in this respect is the prevalence of the bio-duck in Antarctic waters during austral winter [6], indicating that a large part of the population may stay in ice-covered waters year-round. Similar results have been suggested from visual sighting records [23,24]. However, recordings of the sound off Western Australia also during winter indicate that while one population segment remains in the ice, part of the population may undertake seasonal migrations to lower latitudes [3]. A reduced occurrence of the bio-duck sound in Antarctic summer recordings [6] probably relates to a change in behaviour and reduced vocal activity during times of intense foraging [11] as suggested by the low call rates in our recordings, rather than a change in the relative abundance of whales during this time.

Acoustic recordings can provide insight into potential population differentiation based on geographical differences in vocal behaviour. For example, bio-duck sounds from Dumont D'Urville, East Antarctica [9], as well as sounds reported in archived recordings made in the Ross Sea [2], exhibited three pulses per burst. In contrast, recordings of bio-duck sounds from West Antarctica [8], including the sounds described here, typically have five to six pulses.

In conclusion, the identification of the Antarctic minke whale as the source of the bio-duck sound will allow a more detailed understanding of the behavioural ecology of this abundant, but poorly understood species. Furthermore, the value of passive acoustic monitoring will be significantly increased in remote areas of the Antarctic, especially during austral winter, when visual surveys are essentially infeasible.

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PART C

Impact of noise on marine mammal behaviour

Chapter VII

Risch D, Corkeron PJ, Ellison WT & Van Parijs SM
(2012) Changes in Humpback Whale Song Occurrence
in Response to an Acoustic Source 200 km Away.
PloS ONE. 7(1): e29741.
doi: 10.1371/journal.pone.0029741.

Humpback whale (*Megaptera novaeangliae*).

Changes in Humpback Whale Song Occurrence in Response to an Acoustic Source 200 km Away

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Abstract

The effect of underwater anthropogenic sound on marine mammals is of increasing concern. Here we show that humpback whale (*Megaptera novaeangliae*) song in the Stellwagen Bank National Marine Sanctuary (SBNMS) was reduced, concurrent with transmissions of an Ocean Acoustic Waveguide Remote Sensing (OAWRS) experiment approximately 200 km away. We detected the OAWRS experiment in SBNMS during an 11 day period in autumn 2006. We compared the occurrence of song for 11 days before, during and after the experiment with song over the same 33 calendar days in two later years. Using a quasi-Poisson generalized linear model (GLM), we demonstrate a significant difference in the number of minutes with detected song between periods and years. The lack of humpback whale song during the OAWRS experiment was the most substantial signal in the data. Our findings demonstrate the greatest published distance over which anthropogenic sound has been shown to affect vocalizing baleen whales, and the first time that active acoustic fisheries technology has been shown to have this effect. The suitability of Ocean Acoustic Waveguide Remote Sensing technology for *in-situ*, long term monitoring of marine ecosystems should be considered, bearing in mind its possible effects on non-target species, in particular protected species.

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Competing Interests: DR and PJC are employed by Integrated Statistics Inc. The company employs contract biologists and other personnel working for the Northeast Fisheries Science Center in Woods Hole. Additionally, PJC is professionally related to the marine mammal research group at the New England Aquarium. WTE is the founder of Marine Acoustics Inc., an environmental consulting company. These professional affiliations do not alter the authors' adherence to all the PLoS ONE policies on sharing data and materials.

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Introduction

The last decade has seen an increased awareness of the impacts of anthropogenic underwater noise on marine mammals. Impacts have been described for several different sources, including seismic airguns [1,2], underwater explosions [3], construction and pile driving [4], acoustic deterrent devices [5], and scientific and military sonar systems [6–9]. Possible effects include lethal injuries, short- or long-term hearing damage, and the disruption of normal behavior, including feeding, mating and communication [10–11]. Disruption of communication behavior may include signal modifications, for example changes to signal duration, frequency or amplitude [12–14], as well as changes in signal usage, repetition, or the cessation of signaling [15,16,13,9]. Changes in communication behavior have been demonstrated across several baleen whale species and in response to various noise sources [17,2,14].

This study investigates the effect of low-frequency pulses on the occurrence of humpback whale song. The pulses were produced by an Ocean Acoustic Waveguide Remote Sensing (OAWRS) experiment, roughly 200 km from the whales. The mobile OAWRS system was used to image fish shoals over a 100 km diameter area [18–20].

Male humpback whales (*Megaptera novaeangliae*) sing long, complex songs on their breeding grounds [21]. In addition, humpback whales have been shown to sing on migration [22] and feeding grounds [23]. On breeding grounds, humpback whales may alter song production in response to boat noise, seismic surveys and military sonar [24,8,25,26].

Most published examples of the effects of non-chronic anthropogenic noise on marine mammals have dealt with sources within kilometers or perhaps tens of kilometers of the study animals [9]. Effects over hundreds of kilometers have seldom been investigated or demonstrated [27].

Arrays of Marine Autonomous Recording Units (MARUs) [28] gathered low-frequency acoustic data within the Stellwagen Bank National Marine Sanctuary (SBNMS) in 2006 and from December 2007–May 2010 [29,30]. In autumn 2006, these recordings happened to coincide with an OAWRS experiment in the Gulf of Maine, approximately 200 km distant. Initial perusal of the 2006 data indicated that (a) a novel anthropogenic sound was detected in SBNMS and (b) that humpback whale song in SBNMS occurred less often, coincident with the sound. Despite having before-during-after data for 2006, we could not make inference on the effect of the OAWRS experiment without appropriate control data. Therefore, we collected recordings from approximately the same place, and at the same time, in 2008 and 2009, two years when an OAWRS experiment was not conducted. Thus, despite having what was initially observational data, we configured a design that allowed us to make planned comparisons from our data.

Materials and Methods

Data were collected on arrays of 5–10 MARUs, deployed in SBNMS during September and October of 2006, 2008 and 2009 (Figure 1). Deployments were carried out in cooperation with SBNMS staff and deployment sites were surveyed for archaeological artifacts. Deployment depths ranged from 30–40 m and recorders sampled continuously at a rate of 2000 Hz. Hydrophones were connected to a 23.5 dB preamplifier and had a sensitivity of -168.4 dB re 1 V/μPa. The frequency response was flat (±1 dB) over 55–585 Hz and approximately ±3 dB for 585–1000 Hz.

From September 22 to October 6, 2006 we recorded 3 types of frequency modulated (FM) pulses, centered at 415, 734 and 949 Hz, respectively (Figure 2). Based on frequency range and duty cycle, these could be positively identified as FM pulses transmitted as part of an Ocean Acoustic Waveguide Remote Sensing (OAWRS) experiment, conducted in the Gulf of Maine during the same time frame [18–20].

For 11 days (September 26 to October 6, 2006) of the 15 day time series, the frequency of occurrence of these pulses exceeded 1 hour/day (Figure S1). We regarded these 11 days as the "OAWRS treatment" period. We determined the number of minutes with humpback whale song/day for a period of 33 days in 2006, encompassing 11 days prior, during and after "OAWRS treatment" (Figure S2). Additionally, presence of song was determined for the same 33 calendar days in 2008 and 2009 (Figures S3, S4).

Spectrograms of sound files were viewed with the software program XBAT [31]. Data from 1 representative MARU were carefully examined (aurally and visually) by an experienced analyst (D Risch). We used 1 MARU, since all simultaneously deployed MARUs spatially overlapped in their detection range for humpback whale song, which in our study area can be detected up to about 30 km [23]. For the purpose of this study, we defined song as consisting of at least 2 full themes, with gaps not exceeding 10 minutes. All instances of song were logged manually. An automated template detector in XBAT was used to find instances with OAWRS FM pulses in the 2006 data and characterize their temporal occurrence. The detector assessed acoustic similarity between a data template and possible events by spectrogram cross-correlation and logged all events exceeding a correlation threshold of 0.4. Automatically detected events were manually checked to verify signal presence and signals that were missed by the detector were logged manually.

Spectral, temporal and received level (RL) measurements of OAWRS pulses were made in Seewave [32] and Raven Pro 1.4

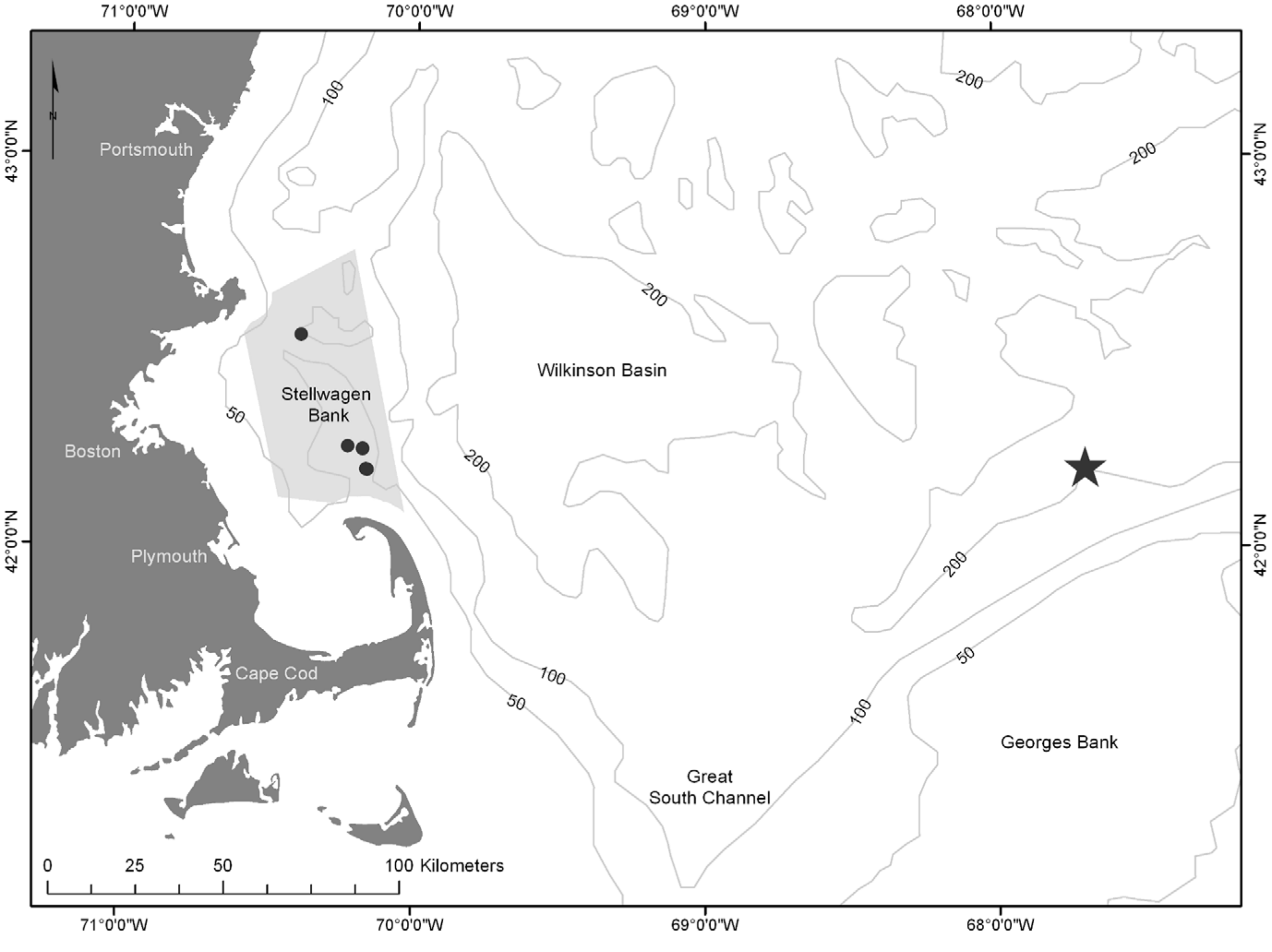

Figure 1. Map of study area (Stellwagen Bank National Marine Sanctuary, shaded in grey) in relation to the location of the moored OAWRS source, as deployed on October 1–3, 2006 (Gong *et al.* 2010). Star indicates approximate OAWRS source location (42.2089 N, 67.6892 W). Dots indicate locations of all MARUs that were used for analysis in 2006, 2008 and 2009. Map projection: Mercator.
doi:10.1371/journal.pone.0029741.g001

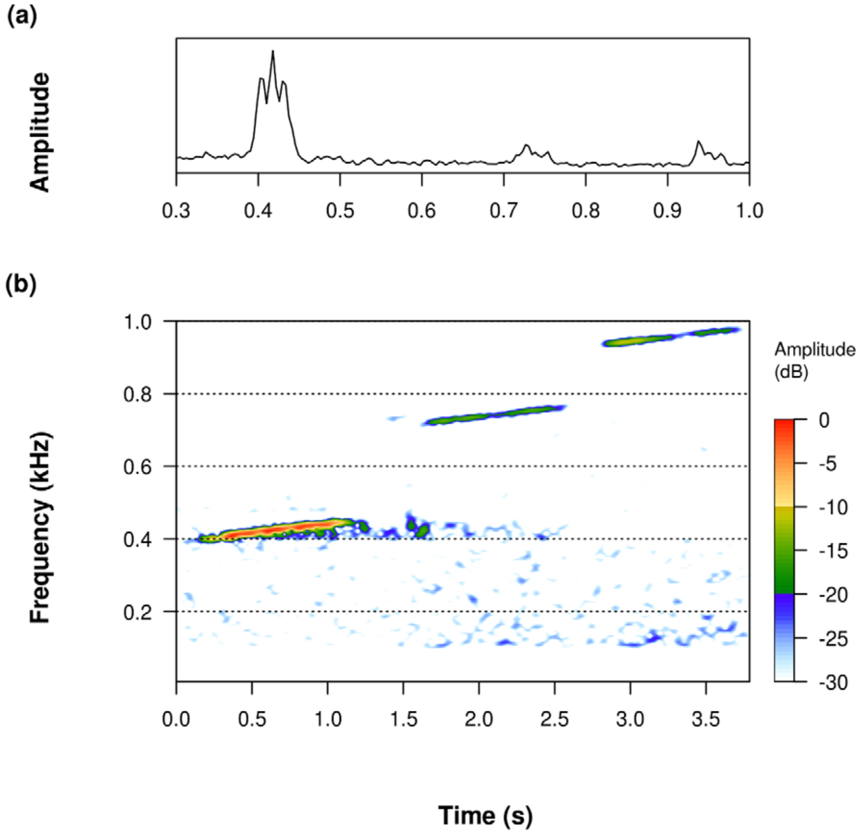

Figure 2. Characteristics of OAWRS signals recorded on MARUs deployed in the Stellwagen Bank National Marine Sanctuary. (a) Mean frequency spectrum, showing local peaks at center frequencies (approx. 415, 735, 950 Hz) of recorded OAWRS FM pulses. (b) Spectrogram (FFT: 512, Hanning window, 75% overlap) of the same pulses as shown in (a). Time interval between successive signals was changed for display purposes; dB scale is relative.
doi:10.1371/journal.pone.0029741.g002

(http://www.birds.cornell.edu/raven, accessed 7 June 2011) using a Fast Fourier Transform (FFT) length of 512 samples, 75% overlap and Hanning window, giving a time and frequency resolution of 64 ms and 4 Hz, respectively. OAWRS signal RLs (dB re 1 µPa) were calculated by measuring dB RMS over an event box (approx. 380–440, 710–760, 930–980 Hz; 1 s). Using the same time and frequency bounds, background noise levels (NL) were measured 50 ms before or after each event for windows without the signal. Subsequently, signal-to-noise ratio (SNR) was calculated by subtracting NLs from signal RLs.

To assess changes in background noise other than the occurrence of OAWRS pulses in 2006, and as compared to the two control years, ambient sound levels in frequency bands covering the frequency range of our recording system (10–1000 Hz) as well as in the frequency band with most humpback whale song energy (70–300 Hz, pers. obs.) were measured over the entire analysis period using a customized Matlab script (LTSpec, K. Cortopassi, unpublished).

Statistical analysis was conducted using R 2.13.2 [33]. We used a quasi-Poisson generalized linear model (GLM) with log link to test the effects of period (11 days: 'before', 'during', 'after') and year ('2006', '2008', '2009') on the number of minutes with humpback whale song. The OAWRS pulses were recorded only during 2006. The other years serve as controls in the temporal equivalent of a BACI design [34]. This was a planned comparison, as we noted a possible effect in 2006, and collected control data in 2008 and 2009 in response to this possibility.

GLMs assume the independence of response variables. Since we analyzed a time series of singing behavior of possibly the same individuals, we checked for residual correlation and plotted temporal autocorrelation of our data. No temporal correlation of residuals was found (Figure S5). Tukey contrasts were calculated from the fitted model to test for differences between periods across and within years, using the function 'glht' in R package 'multcomp' [35].

Results

The FM pulses recorded in SBNMS from September 26 to October 6, 2006 had a bandwidth of roughly 50 Hz, duration of 1 s, and mean center frequencies of 415, 734 and 949 Hz (Figure 2, Table 1). FM pulses of each center frequency were recorded every 150 s. FM pulses centered at 415 and 734 Hz were recorded seconds apart, followed by the pulse centered at 949 Hz after 75 s. The frequency range and duty cycle of these pulses allowed their positive identification as pulses produced during the OAWRS 2006 experiment in the Gulf of Maine [18–20]. A fourth pulse centered at 1125 Hz was transmitted during this experiment but was not recorded by our system, which was limited to an effective recording bandwidth of 1000 Hz.

A total of 83 hours of recordings contained OAWRS pulses (mean ± SD: 8±3 hours/day, n = 11 days), with more than 7 hours of signal occurrence/day from September 27 to October 4, 2006 (see Figure S1). The OAWRS source array was deployed at the northern flank of Georges Bank (42.2089 N, 67.6892 W),

Table 1. Summary of OAWRS FM pulse characteristics (mean±SD), as measured from spectrograms (FFT: 512 samples, Hanning window, 75% overlap) and waveforms of MARU recordings on October 1–3, 2006 (sample rate: 2000 Hz, recording depth: 30–40 m).

	FM 1	FM 2	FM 3
Signal duration (s)	1.0±0.1	1.0±0.1	1.0±0.1
Low Frequency (Hz)	388.3±2.0	709.1±2.7	923.5±2.8
High Frequency (Hz)	441.2±2.2	759.3±3.7	972.4±3.6
Bandwidth (Hz)	52.8±2.7	50.2±3.7	50.5±3.5
Center Frequency (Hz)	414.8±7.0	733.6±7.0	948.7±6.3

N = 60.

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about 200 km from our bottom-mounted acoustic recorders at the western edge of Stellwagen Bank (Figure 1) [19]. Signal RLs on these days ranged from 88–110 dB re 1 μPa (Table 2). Over the 99 days for which data were collected, there were 219.9 hours of humpback whale song recorded.

The amount of recorded humpback whale song differed between periods and years. The occurrence of song in the control years increased steadily across the three test periods; conversely there was a marked decrease in the occurrence of song in 2006 in the 'during' period, when the OAWRS transmission was recorded, that was not evident in the control years (Figure 3). While the 'before' and 'after' periods differed significantly within the years 2008 and 2009 (Figure 3, Tukey contrasts, $P<0.001$), with more song recorded in the later period in both years, this increase was not significant in 2006 ($P = 0.2147$). In 2006, the 'during' period, (i.e. during the OARWS experiment), was significantly different from the period 'after' ($P = 0.0093$), with more song recorded later. The 2006 'during period' was not detectably different from the period 'before' ($P = 0.5226$). When comparing the 'during' period across years, 2006 differed significantly from 2009 ($P = 0.0057$). The same time period did not differ significantly between 2006 and 2008 ($P = 0.1842$), or between 2008 and 2009 ($P = 0.4819$). Yet, overall there was considerably less song recorded in the 11 'during' days in 2006 compared to both 2008 and 2009 (Figure 3). Throughout the whole analysis period, ambient noise levels in the 70–300 Hz and 10–1000 Hz frequency band were within 4 dB of each other [mean(70–300 Hz) ± SD: 107.7±3.8 dB re 1 μPa; mean(10–1000 Hz) ± SD: 114.6±3.5 dB re 1 μPa; n = 99 days].

Table 2. Received level (RL) measurements over full bandwidth of OAWRS FM pulses, ambient noise (NL) measurements over the same bandwidths, signal-to-noise ratios (SNR) and signal excess (SE) (mean±SD).

	FM 1	FM 2	FM 3
Center Frequency (Hz)	415	734	949
RL Signal (dB re 1 μPa)	110.3±3.3	88.0±3.2	89.8±3.3
NL Ambient (dB re 1 μPa)	88.0±3.3	82.9±2.6	81.6±2.5
SNR = RL-NL (dB)	22.3±4.8	5.1±4.0	8.2±3.9
SE = SNR-10 dB	12.3±4.8	−4.9±4.0	−1.8±3.9

N = 677.

doi:10.1371/journal.pone.0029741.t002

Discussion

In general, we detected humpback whale song less in our study area concurrent with OAWRS signal transmissions than at other times. The RLs of OAWRS pulses approximately 200 km from the source array were 5–22 dB above ambient noise levels. Pulses centered at 415 Hz had a mean SNR of 22.3 dB. For pulses at 734 Hz and 949 Hz mean SNR was 5.1 and 8.2 dB, respectively (Table 2). Signal detection in background noise is usually not at SNR = 0 dB, but is dependent on a receiver characteristic, the detection threshold (DT). The difference between SNR and DT is signal excess (SE). A nominal DT value of 10 dB is well supported in the current literature [30]. In common practice, the value of SE = 0 is established at the point of 50% detection probability. In application to our data, SE for pulses at 415, 734 and 949 Hz was 12.3, −4.9 and −1.8 dB, respectively (Table 2). With SE values slightly lower than 0 dB the detection of the two FM pulses with higher center frequencies was probably right on the edge of perception for humpback whales in our study area. For the pulse at 415 Hz SE was still relatively low at 12 dB.

Thus, in response to OAWRS FM pulses, with relatively low SE, male humpback whales either moved out of the study area or sang less. Our data were collected using passive acoustic monitoring, so we cannot differentiate between these two options. However, although very limited, visual data collected in SBNMS before, during and after the 2006 experiment give more weight to the second alternative. Several known, sexually mature males (ages 6–28 years) were photographically identified in SBNMS during the OAWRS experiment. While only two known males were identified prior to the experiment, four individuals were present in the area in the "during" period (J. Robbins, pers. comm.). This suggests that individuals did not leave the area but instead ceased singing. Multi-year data from SBNMS [36] show that humpback whale song generally increases at the end of summer and into early winter, when the whales start to migrate south.

Ambient noise levels over the whole analysis bandwidth (10–1000 Hz) and in the frequency band with most humpback whale song energy (70–300 Hz) did not vary dramatically within or between years. However, the drop in humpback whale song, recorded during the OAWRS experiment in October 2006, was not repeated in the two control years (Figure 3). Therefore, our data provide clear evidence for the reduction of humpback whale song in response to the reception of OAWRS pulses. We interpret this decrease as a change in singing behavior by individual whales.

Several large whale species have been shown to stop vocalizing in response to anthropogenic noise. For example, sperm (*Physeter macrocephalus*) and blue whales (*Balaenoptera musculus*) reacted to seismic survey activities with silence [15,37]. Blainville's beaked whales have recently been shown to avoid ships using active mid-frequency sonar and decrease the duration of vocal periods during sonar exercises [9].

Current approaches to management of anthropogenic noise in marine mammal habitats are predicated on a dose-response model, based on maximum RLs proximate to the source [11]. However, the alteration of male humpback whale song in SBNMS in response to sounds with low SE values, received roughly 200 km from the source, suggests that factors other than absolute RLs must also be considered when assessing the effects of anthropogenic sound on marine mammals. Behavioral change in response to low levels of noise is likely strongly dependent on the behavioral state of the individual as well as the exposure context (i.e. proximity, encroachment, novelty, including similarity to other biologically relevant signals) [38]. Given the short duration of the OAWRS experiment, the novelty of the FM pulses to humpback whales in

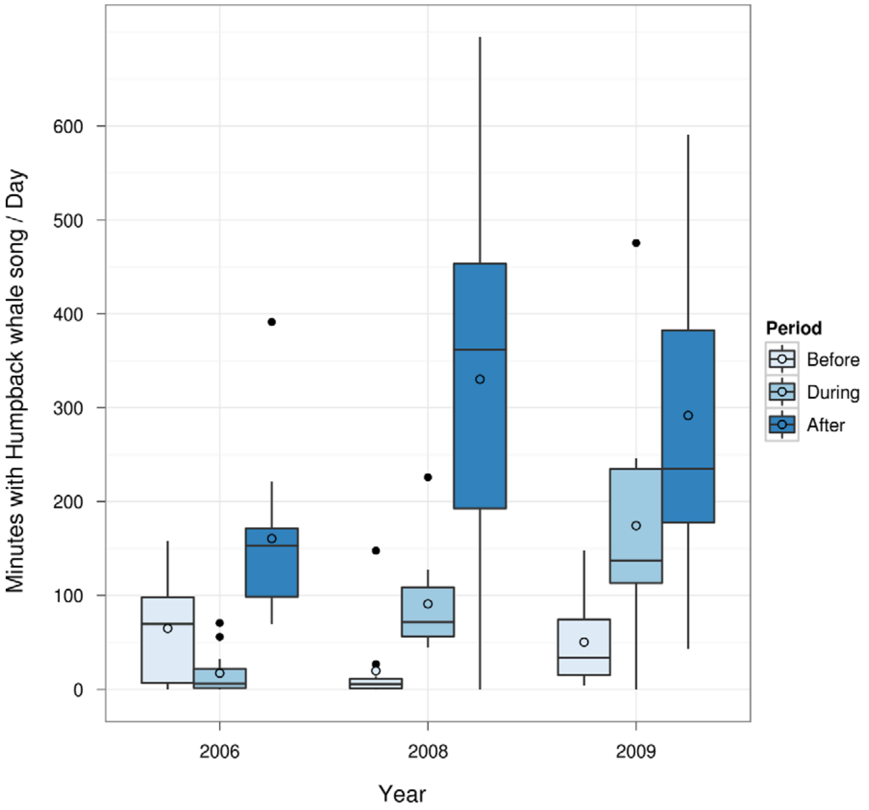

Figure 3. Box-and-Whisker plot of minutes/day containing humpback whale song for 33 days 'before-during-after' OAWRS FM pulse transmissions in 2006, and for the same 33 calendar days in 2008 and 2009. Lower and upper bounds of boxes represent lower and upper quartiles, respectively. Solid lines represent medians and non-filled circles are means. Whiskers represent furthest data points within 1.5× interquartile range (IQR) of the lower and higher quartile, respectively. Filled dots are outliers.
doi:10.1371/journal.pone.0029741.g003

SBNMS in particular provides a compelling contextual probability for the observed effects. In addition, OAWRS pulses overlap with humpback whale sounds in frequency band (400–900 Hz), duration (1 second) and signal type (FM). This acoustic similarity paired with a relatively low signal excess (SE) might have been another factor driving the observed behavioral or distributional changes. These findings stress the importance of adding contextual information to behavioral assessments of noise impacts. They also illustrate the requirement to both measure and assess background noise [38].

We initially detected this behavioral effect serendipitously. However, our ability to make inference on its existence is thanks to our (within year) before-during-after and (between year) control-impact design. To our knowledge, no-one has tested for behavioral effects of sound on whales at distances of greater than tens of kilometers. Our results suggest that this is an oversight.

In the absence of effective far field source level (SL) data, we cannot make inference on the effects of the OAWRS signal on those humpback whales that may have been closer to the sound source than our study site. Yet, Gong *et al.* [39] recorded marine mammal vocalizations, presumably humpback whales, on George's Bank much closer to the source (Figure 1), concurrent with the 2006 OAWRS experiment. However, as these authors present no data on humpback whales' use of George's Bank at any time other than during this experiment it is difficult to make inference on its effect on humpback whale behavior at these closer spatial ranges. The response of individuals can also be variable. In a playback experiment using low-frequency active (LFA) sonar, Miller *et al.* [8] showed that, on average, humpback whale songs were longer during playback as compared to before or after control periods. Yet, these authors also noted the cessation of singing by 5 of their 18 focal animals in response to the playback. Due to differences in behavioral context, location and proximity to the sound source it is difficult to directly compare our findings to either of the mentioned studies. However, it is worth noting that plasticity in behavioral responses is likely to exist on several different levels, including the individual level.

The current paradigm for assessing effects of anthropogenic noise is for short-term, short distance experiments, with a focus on acute events and the absolute level of received sound. Our results indicate that longer-term, larger scale monitoring of anthropogenic sound is also necessary.

Supporting Information

Figure S1 Time series of hourly detections of OAWRS signals recorded on MARUs deployed in the Stellwagen Bank National Marine Sanctuary in September/October 2006.
(TIF)

Figure S2 Time series of minutes with humpback whale song detections in September/October 2006. Plot is split in three panels representing (a) 'Before', (b) 'During' and (c) 'After' periods. Right y-axis displays date.
(TIF)

Figure S3 Time series of minutes with humpback whale song detections in September/October 2008. Plot is split in three panels

representing time periods equal to (a) 'Before', (b) 'During' and (c) 'After' periods in 2006. Right y-axis displays date.
(TIF)

Figure S4 Time series of minutes with humpback whale song detections in September/October 2009. Plot is split in three panels representing time periods equal to (a) 'Before', (b) 'During' and (c) 'After' periods in 2006. Right y-axis displays date.
(TIF)

Figure S5 (a) Plot of residuals of quasi-poisson GLM model for OAWRS data. (b) Temporal autocorrelation plot based on residuals of quasi-poisson GLM model used in OAWRS analysis. Blue dashed line indicates approximate 95% confidence interval.
(TIF)

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Author Contributions

Conceived and designed the experiments: DR PJC SMVP. Performed the experiments: DR. Analyzed the data: DR PJC. Contributed reagents/materials/analysis tools: DR PJC WTE. Wrote the paper: DR PJC WTE SMVP.

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DESCRIPTION OF INDIVIDUAL SCIENTIFIC CONTRIBUTIONS TO MULTIPLE-AUTHOR PAPERS

The chapters of this thesis are published (Chapters I, III, IV, VI and VII), accepted (Chapter V), or prepared for submission to peer reviewed journals (Chapter II). The following list provides an overview of my personal contributions to each of the publications:

Chapter I: Passive acoustic monitoring of marine mammals.

published as:

Cholewiak D, Risch D, Valtierra R & Van Parijs SM (2013) Methods for passive acoustic tracking of marine mammals: estimating calling rates, depths and detection probability for density estimation. Chapter 6 – In: Detection, Classification and Localization of Marine Mammals using passive acoustics. (Adam, O. & Samaran, F. ed.), p. 107–145.

Contributions: DC, DR, RV and SVP developed the idea for this study. DC, DR and RV conducted the data analysis. DC, DR, RV and SVP discussed the results. DC, DR and RV wrote the manuscript. All authors read and approved the final manuscript.

Chapter II: Occurrence patterns of baleen whales in Massachusetts Bay.

prepared for submission to Marine Ecology Progress Series:

Risch D, Baumgartner M, Brady SP, Cholewiak DM, Clark CW, Davis G, Hatch, LT, Thompson MA, Wiley D & Van Parijs SM (manuscript) Multi-year seasonal occurrence patterns of four species of baleen whales in Massachusetts Bay.

Contributions: DR, SM and SVP developed the idea for this study. CWC, LTH, DW and SVP developed the idea, secured funding for and managed the larger ocean noise project this study was part of (NOPP grant: N00014-07-1-1029). DR, SVP, DC, DW and MAT conducted field work. DR, MB, DC, GD and SB analyzed the data. DR wrote the draft manuscript.

Chapter III: Minke whale vocal behaviour in Massachusetts Bay.

published as:

Risch D, Clark CW, Dugan PJ, Popescu M, Siebert U & Van Parijs SM (2013) Minke whale acoustic behavior and multi-year seasonal and diel vocalization patterns in Massachusetts Bay, USA. Marine Ecology Progress Series. 489: 279-295. doi: 10.3354/meps10426.

Contributions: DR and SVP developed the idea for this study. DR and SVP conducted part of the fieldwork. CWC provided access to data and resources as well as ideas for this study. PJD, MP and DR conducted data analysis. SVP, DR, US and CWC discussed the results. DR wrote the manuscript. All authors read and approved the final manuscript.

Chapter IV: Minke whale vocal behaviour on a fine scale.

published as:

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Contributions: DR and SVP developed the idea for this study. DR conducted fieldwork. DR analyzed the data and wrote the manuscript. DR, US and SVP discussed the results. All authors read and approved the final manuscript.

Chapter V: Geographic variation in minke whale vocal behaviour.

accepted as:

Risch D, Castellote M, Clark CW, Davis G, Dugan PJ, Hodge LEW, Kumar A, Lucke K, Mellinger DK, Nieukirk SL, Popescu CM, Ramp C, Read AJ, Rice AN, Silva MA, Siebert U, Stafford KM, Verdaat H & Van Parijs SM (2014) Seasonal migrations of North Atlantic minke whales: Novel insights from large-scale passive acoustic monitoring networks. Movement Ecology.

Contributions: DR and SVP developed the idea for this study. MC, CWC, LEWH, AK, KL, DKM, SLN, CR, AJR, AR, MAS and HV provided data and conducted field work. DR, GD, PJD and CMP analyzed the data. DR, SVP and US discussed the results. DR wrote the manuscript. All authors read and approved the final manuscript.

Chapter VI: Acoustic behaviour of Antarctic minke whales.

published as:

Risch D, Gales NJ, Gedamke J, Kindermann L, Nowacek DP, Read AJ, Siebert U, Van Opzeeland IC, Van Parijs SM & Friedlaender AM (2014) Mysterious bioduck signal attributed to the Antarctic minke whale (Balaenoptera bonaerensis).
Biology Letters: 10(4): 20140175; doi: 10.1098/rsbl.2014.0175.

Contributions: DPN, AMF and AJR developed idea for the study and conducted all field work. DR and AMF analyzed the data. LK, JG, NJG and ICVO provided additional data and ideas. DR, SVP, US, DPN, AJR and AMF discussed the results. DR wrote the manuscript. All authors read and approved the final manuscript.

Chapter VII: Anthropogenic impacts on vocally active baleen whales

published as:

Risch D, Corkeron PJ, Ellison WT & Van Parijs SM (2012) Changes in Humpback Whale Song Occurrence in Response to an Acoustic Source 200 km Away. PloS ONE. 7(1): e29741. doi: 10.1371/journal.pone.0029741.

Contributions: DR, PJC and SVP conceived and designed the study. DR and PJC conducted data analysis. DR, PJC, WTE and SVP discussed the results and wrote the manuscript. All authors read and approved the final manuscript.

DENISE RISCH

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PERSONAL DETAILS

Date / place of birth:	11 October 1978, Berlin, Germany
Nationality / Citizenship:	German
Languages:	German (fluent), English (fluent), French (moderate)

EDUCATION

1998-2000	BSc, Biological Sciences, Christian-Albrechts-University Kiel
2001-2004	MSc, Zoology, Ethology & Ecology, Alexander von Humboldt University Berlin - MSc thesis: *„Geographical and temporal variation in the vocal behaviour of bearded seals (Erignathus barbatus)"*
2008-2013	PhD, Marine Biology & Zoology, Christian-Albrechts-University Kiel - PhD dissertation: *„A multi-species approach for studying baleen whale acoustic ecology with focus on minke whales and reference to anthropogenic noise"*

CURRENT POSITION

2014-present	PostDoc/Acoustician in EU MERIKA project, Scottish Association for Marine Science (SAMS), Oban, Scotland, UK

PREVIOUS EMPLOYMENT

2007-2014	Senior Passive Acoustic Analyst, Northeast Fisheries Science Center (NEFSC), Protected Species Branch, Woods Hole, MA, USA: *Passive Acoustic Monitoring & Ocean Noise Project*
Winter/Spring 2006 & 2007	Biologist, Provincetown Center for Coastal Studies, MA, USA: *Aerial surveys & photo-ID of North Atlantic right whales*

2004-2005, 2006	Biologist, Research & Technology Center (FTZ), Büsum, Germany: *Aerial & ship-based passive acoustic porpoise surveys & data analysis – MINOS+ (Marine Mammals in the North and Baltic Seas) project*

TRAINEESHIPS / SPECIALIZED COURSES

Summer 2006	GIS training (ArcView 3.3, ArcGis 9, MS Access) Berlin
2002-2003	Internship, Research & Technology Center (FTZ), Büsum: *Passive acoustic work (T-PODs) – MINOS project*
2000-2001	Trainee, Whale and Dolphin Conservation Society (WDCS), Munich, Germany

FIELDWORK EXPERIENCE

2007 – 2010 – Stellwagen Bank National Marine Sanctuary, MA, USA:
Deployment & Retrieval of Passive acoustic arrays, Equipment Refurbishment

Summer 2010 (4 weeks) - Mingan Islands, Quebec, Canada:
Minke whale passive acoustic research project (PI)

Summer 2002/2003 (3 weeks) - Bardsey Island, North Wales, UK:
Land-based visual survey for harbour porpoises & Risso´s dolphins

Spring/Summer 2001 (16 weeks) - Húsavík Whale Center, North Iceland:
Guide in museum & on whale watching boats, photo-ID of minke & humpback whales

Summer 1998/1999/2001 (24 weeks) - Orcalab, Hanson Island, Canada:
Land-based acoustic research on Northern Resident Orcas

Summer 1995-1999 (16 weeks) - Sylt, Germany:
Land-based behavioural observations of harbour porpoises

Summer 1997 (3 weeks) - Crete, Greece:
Loggerhead sea turtle project

RESEARCH CRUISES (13 CRUISES)

Summer 2012 (2 weeks) – RV Henry B. Bigelow, Georges Bank:
Retrieval of passive acoustic array & photo-ID of North Atlantic right whales (NOAA NEFSC, PI: Dr. Sofie Van Parijs/Allison Henry)

Winter 2010/2011 (12 weeks) - RV Polarstern, Antarctica:
Visual helicopter survey for marine mammals (FTZ Westcoast, PI: Dr. Ursula Siebert/Linn Lehnert)

Summer 2009 (3 weeks) - RV Henry B. Bigelow, Western North Atlantic:
Visual & acoustic marine mammal survey (NOAA NEFSC, PI: Dr. Debi Palka)

Fall 2008 (6 weeks) - Vaquita Express, Gulf of California, Mexico:
Passive acoustic Vaquita survey (NOAA SWFSC, PI: Dr. Jay Barlow/Shannon Rankin)

Summer 2008 (2 weeks) - RV Nancy Foster, Stellwagen Bank:
Visual marine mammal survey (NOAA SBNMS, Dr. Dave Wiley)

Summer 2007 (4 weeks) - RV Henry B. Bigelow, Gulf of Maine:
Visual & acoustic harbour porpoise survey (NOAA NEFSC, Dr. Debi Palka)

Summer 2006 (4 weeks) - RV Solea, North Sea:
Visual & acoustic harbour porpoise survey (FTZ Westcoast, PI: Dr. Meike Scheidat)

Summer 2005 (4 weeks) - RV Skagerak, Baltic Sea:
SCANS II survey (acoustic observer) (PI: Dr. Jonas Teilmann)

Spring 2005 (4 weeks) - RV Walther Herwig III, Baltic Sea:
Visual & acoustic harbour porpoise survey (FTZ Westcoast, PI: Dr. Meike Scheidat)

Summer 2004 (4 weeks) - RV Walther Herwig III, Southern North Sea:
Visual & acoustic harbour porpoise survey (FTZ Westcoast, PI: Dr. Meike Scheidat)

Spring 2004 (3 weeks) - CCGS Ann Harvey, Newfoundland, Canada:
Harp seal survey: acoustic recordings & behavioural observations of mother/pup pairs (DFO Canada, PI: Dr. Gary Stenson)

Spring/Summer 2003 (2 weeks) – Sylt, Germany:
Ship-based line transect surveys for harbour porpoises (FTZ Westcoast, PI: Dr. Meike Scheidat)

Summer 2002 (2 weeks) - RV Song of the Whale, Eastern Baltic Sea:
Visual & acoustic harbour porpoise survey (IFAW)

COMPUTER SKILLS

Operating Systems: Linux (Ubuntu Debian), Mac, Windows
Specialized Software: R, Matlab, ArcGIS, QGIS, XBAT, Avisoft, Raven, PAMGuard, Ishmael, Logger

TEACHING / MENTORSHIP

NOAA Hollings Program (2008-2012): 8 students
Woods Hole Partnership Education Program (PEP) (2008-2012): 5 students
Other Internships (2008-2012): 5 students

SCHOLARSHIPS / FUNDING

2011-2014	Partially funded by NOAA Acoustic Program and N45 CNO Navy
2007-2011	Funded through Office of Naval Research Grant (Number: N00014–07-1–1029) awarded by National Oceanographic Partnership Program
2004:	Kölner Gymnasial-und Stiftungsfund, PADI Project AWARE, EU Erasmus Program

REVIEWER

Aquatic Mammals, Aquatic Biology, Ethology, Polar Biology, Journal of Wildlife Management, Marine Mammal Science, Biological Conservation, Journal of Marine Science: Research & Development, Open Journal of Marine Science, PLOS ONE, PeerJ, Polarforschung, Progress in Oceanography

SOCIETY MEMBERSHIPS

Society of Marine Mammology

Acoustical Society of America

International Society of Ecoacoustics (Treasurer 2014-present)

REFERENCES

Dr. Sofie Van Parijs, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1026, USA, ph: +1 (508) 495-2119, sofie.vanparijs@noaa.gov
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