NON-SONG SOUND PRODUCTION AND ITS BEHAVIORAL CONTEXT IN HUMPBACK WHALES (MEGAPTERA NOVAEANGLIAE)

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by

Alison K. Stimpert
“That which does not kill you makes you stronger.”

-My Mom (and Friedrich Nietzsche)

“No, no more whale! You can't speak whale!”

-Marlin in *Finding Nemo*
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ABSTRACT

Humpback whales (*Megaptera novaeangliae*) are famous for their sophisticated acoustic display called song, but the species also produces many sounds outside this context. Historically called “social sounds,” non-song sounds may also play an important role in communication between conspecifics. This dissertation explores the production of non-song sounds from humpback whales on both a breeding and feeding ground (Hawai‘i and the Northwest Atlantic, respectively). Sound emissions were measured using acoustic tags (DTAGs), and also using a towed hydrophone array. Sounds are described in detail acoustically, and behavioral context of focal individuals is investigated using body orientation and depth measurements from sensors that were integrated in the acoustic tags.

Humpback whales produced a variety of non-song sounds on both the breeding and feeding ground, most of which were higher in frequency and shorter in duration than the sounds of other baleen whale species. Sounds recorded from the feeding ground population were louder, had higher signal-to-noise ratio, and were more frequent than those from the breeding ground.

Higher sound production rates were recorded during periods when the tagged whales were approximately one body length beneath the surface. No significant variation in sound production rate was observed in relation to pitch or roll of the focal individual, or in relation to time of day, though a slight increase in sound production just after dawn and dusk on the feeding ground was evident. Further studies across wider habitat characteristics will help elucidate these trends.
Megapclicks are newly described sounds that show similarity to the click trains heard during odontocete echolocation. Megapclicks, recorded from tagged whales on a feeding ground, are paired with sharp body rolls along the sea floor that are probably feeding lunges. The description of megapclicks represents a new category of sound production for humpback whales, and for baleen whales in general.

These results enhance our understanding of this acoustically advanced species, and will also be useful in conservation and management efforts. Acoustic parameters can be used in detection algorithms, and behavioral contexts can assist in interpretation of passive acoustic monitoring research on humpback whales, and potentially other baleen whale species as well.
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CHAPTER 1

Introduction

1.1 Why study acoustic behavior?

An animal’s behavior is an important part of its life history and its identity. Currently, a common tool for managing endangered species is to count (or estimate) how many individuals of a given species are present, without considering behavior. But the behavior of the animal can be an important criterion in even defining which animals are of which species. For example, in the case of Lake Malawi cichlids, behavioral characteristics such as bower shapes and courtship patterns have been used to distinguish species, where diagnosis based on genetics and morphology were unclear (Stauffer et al. 1993; Stauffer et al. 2002). Also, without maintaining an environment in which the animal can behave normally, it may not be able to forage effectively or to find mates and reproduce, and the lack of ability to do either of these things could ultimately lead to the extinction of a species. Thus, protection of behavior should also be an important consideration when monitoring populations of endangered species.

Intraspecies communication is a critical aspect of behavior for many species. Communication is a broad term that can take many definitions (Herman and Tavolga 1980; Tyack 2000; Seyfarth and Cheney 2003), and can also take place via several modalities, including visual and acoustic. At its most basic, communication is the transfer of information, whether intentional or unintentional. Here I assume that energy
put into producing acoustic signals (that are capable of being detected by a recipient) implies a communicative purpose for those signals (Herman and Tavolga 1980).

The first step towards understanding animal communication is to study the animals’ behavior and capabilities in each sensory modality. Especially in marine species, the acoustic channel is one of the most salient, and therefore understanding and protecting acoustic behavior in marine species can be an important aspect of preserving communication and behavioral interactions amongst species, and thus marine biodiversity.

1.2.1 What we know about acoustic behavior

In large mammals, which are frequently influential, if not “keystone” species in an ecosystem (Mills et al. 1993; Sinclair 2003), visual and acoustic communication can be critical for information exchange during predator defense, cohesion within groups, mating displays, care of the young, and foraging activities. For example, vervet monkeys and lemurs are known to produce predator-specific alarm calls, directed towards conspecifics, which elicit appropriate evasive action depending on the type of threat posed by a predator (Seyfarth et al. 1980; Fichtel and Kappeler 2002). African elephants frequently maintain large separations between family groups, which are mediated by long distance, low frequency acoustic communication (Garstang 2004). Fallow bucks gather on leks and vocalize as a display to attract females, with qualities of their vocal displays giving information used by females in mate choice (McElligott et al. 1999). And some primates, including bonobos, marmosets, and white-faced capuchin monkeys, produce
food-associated calls, sometimes even specific to food type, upon discovering a food source during foraging (Gros-Louis 2004; Clay and Zuberbuhler 2009; Kitzmann and Caine 2009).

These examples are all representative of acoustic behaviors in terrestrial mammals. Imagine the importance of acoustics under water, where visibility is greatly decreased compared to that on land. Many marine species have developed a heavy reliance on sound to facilitate interaction with their environment, and marine bioacoustics is the study of these acoustic signals.

In some cases, marine animals produce sound that may indicate their current activities, which allows acoustic recording and analysis to be used as research tools for studying behavior. Snapping shrimp, for example, produce a loud snap through rapid closure of one of their claws. This movement creates an air bubble that cavitates, producing the snapping sound (Versluis et al. 2000). These snaps are produced as part of territorial interactions (Schmitz and Herberholz 1998) and are also an indicator of overall activity level – diel patterns in acoustic levels of snapping shrimp snaps have been recorded using passive acoustics, in this case with bottom-mounted autonomous recorders (Lammers et al. 2008). Many fish species also make stereotyped sounds which can be detected remotely, and therefore can be used as a tool to monitor populations for fisheries purposes (Gannon 2008; Luczkovich et al. 2008; Sirovic et al. 2009), or even to track behavioral activities when the functions of the sounds are already understood, for
example, if they occur during spawning, aggressive encounters, or sexual advertisement (Fine and Thorson 2008; Gannon 2008).

Marine mammals rely heavily on underwater sound and have evolved sophisticated mechanisms for sound perception and production. Behaviorists often organize cetacean sounds according to the taxonomic group that is producing them: either odontocetes (toothed whales) or mysticetes (baleen whales). One of the reasons for this delineation is the unique behavior observed from odontocetes called echolocation, which is essentially biosonar. Echolocation refers to the process of “object detection, localization, discrimination, recognition, and orientation or navigation by animals emitting acoustic energy and receiving echoes” (Au 1993, p. 2). Echolocation is used by odontocetes largely to find and capture prey (Au 1993; Au and Nachtigall 1997; Miller et al. 2004; Madsen et al. 2005). Though there has been debate in the literature (Beamish 1978; Frazer and Mercado 2000; Au et al. 2001; Mercado and Frazer 2001), mysticetes have not been confirmed to produce signals like the echolocation clicks of odontocetes, nor to demonstrate a use of sound that indicates biosonar (but see below).

Other types of sounds, such as whistles, are also produced by odontocetes in contexts such as coordination within a group in species like killer whales and spinner dolphins (Thomsen et al. 2002; Lammers and Au 2003). The sounds that have been attributed to mysticetes are generally much lower in frequency than those of odontocetes. Blue, fin, and sei whales produce sounds under 50 Hz (Cummings and Thompson 1971; Watkins et al. 1987; Stafford et al. 1999; Baumgartner et al. 2008), compared with odontocete
sounds that contain energy from several kHz at the lower end and up to 250 kHz in some
dolphins (Rasmussen and Miller 2002; Lammers et al. 2003). In some cases, sounds
recorded from baleen whales have been attributed to behavioral state of individuals.
“Gunshot” sounds produced by male right whales are thought to function as reproductive
advertisement (Parks et al. 2005; Parks and Tyack 2005), while the behavioral context of
some call types in blue whales (AB: reproductive, vs. D: foraging) has also been
identified (Oleson et al. 2007). Yet in many cases, scientists are still at the stage of
identifying which sounds from remote recorders were produced by which species (e.g.,
Watkins et al. 2004).

Some smaller odontocetes, such as bottlenose dolphins, can be easily studied in captivity,
allowing detailed investigation of the acoustic properties of their sounds (e.g., Au et al.
1986; Au 1993; e.g., Au et al. 1999). Scientists have developed a comprehensive
understanding of the mechanics of echolocation and how it is used by odontocetes during
foraging. The behavior of some species can therefore be studied in the wild through
passive acoustics. In other words, the presence of echolocation clicks is assumed to
represent feeding behavior, and trends in behavioral patterns can be monitored remotely
(Carlstrom 2005; Johnson et al. 2006).
1.2.2. What we don’t know about (marine mammal) acoustic behavior

Mysticetes as a whole are among the least understood marine mammals because of their large size (captive studies are not possible), wider ranges, and lower abundance. It follows that their sounds (and the behaviors that accompany those sounds) are also less described than those of other species. But based on what information does exist, many baleen whale species appear to have less conventional and more fluid social systems than many odontocetes (Clapham 1996), which suggests that they may use acoustic communication in potentially interesting and unconventional ways. Remote recordings can indicate presence or absence of species, but because the acoustic repertoire of baleen whales is still being described, remotely recorded sounds cannot give an indication of the behavior of individuals, and in some cases, even the species present. Many unusual and unknown sounds are recorded on a regular basis, and in some cases it can take years to determine what species is actually producing the sound, as was the case for the “boing” sound: over 40 years passed between the first description of the sound to the identification of its source as the minke whale (Rankin and Barlow 2005).

Humpback whales (*Megaptera novaeangliae*) have what has been termed a “fission-fusion” social system (Clapham 1996), with fluid group membership during both breeding and feeding activities. While some aspects of their sound production, such as song, have been heavily studied, a great deal remains to be understood about their additional prolific sound repertoire (see below). This, combined with their coastal distribution and easy accessibility, makes humpbacks an ideal study species for questions about baleen whale acoustic behavior.
1.3 Humpback whale life history

1.3.1. Migration: Breeding grounds non-acoustic behavior

Humpback whales spend the winter months of each year in low latitude waters, which they use as breeding grounds. For North Atlantic humpback whales, the breeding grounds are in the West Indies in the Caribbean (Larsen et al. 1996; Smith et al. 1999; Stevick et al. 2003). North Pacific humpback whales migrate south from Alaskan to Hawaiian waters, their principal wintering area (Calambokidis et al. 2008) to engage in breeding and mating activities.

The whales form a variety of types of transient social groups while on the breeding grounds, ranging from single whales to large groups of sometimes 20 or more individuals (Mobley and Herman 1985; Spitz et al. 2002). Single whales can be singers (see below), or may be traveling or resting stationary. Pairs of whales frequently spend a majority of time stationary at depth, without exhibiting many behaviors obvious to a human observer, either visual or acoustic ("breathholders", as in Darling 2009). Competitive groups (Tyack and Whitehead 1983; Baker and Herman 1984; Clapham et al. 1992) are composed of two or more males and a single female. The female frequently remains in the physical center of the group, while the males structure themselves around the periphery in an arrangement based on their individual endurance. Thus the presumed female is termed the “nuclear animal” (Tyack and Whitehead 1983). The male closest to the female is termed the primary escort (Tyack and Whitehead 1983), and defends the
position closest to her in the center of the group. Challengers (males showing consistent agonistic interactions with the primary escort) and secondary escorts (all other whales) are positioned on the periphery of the group (Tyack and Whitehead 1983). Displays between males include visual displays (inflating ventral pleats, blowing bubbles), chases, and even physical strikes (Tyack and Whitehead 1983; Baker and Herman 1984; Clapham 1996; Pack et al. 1998; Spitz et al. 2002; Herman et al. 2007).

1.3.2. Migration: Feeding grounds non-acoustic behavior

Humpback whales use high latitude waters as feeding grounds during the summer months. For the North Pacific population of whales, this includes Alaskan waters as well as some areas off Japan and British Columbia (Darling and Cerchio 1993). In the North Atlantic, the whales feed off the northeastern United States, in areas including Stellwagen Bank, the Great South Channel, Jeffreys Ledge, and Platt’s Bank (Weinrich et al. 1997).

Humpbacks feed on a variety of prey items, the majority of which are herring, sand lance, and krill (Hain et al. 1982; Hain et al. 1995; Weinrich et al. 1997). The whales feed by lunging at the surface (Hain et al. 1982), lunging along the ocean bottom (Hain et al. 1995), and using bubbles to corral prey (Jurasz and Jurasz 1979; Hain et al. 1982). In Alaska, some humpbacks are known to forage cooperatively (D’Vincent et al. 1985), but in general, social structure on the feeding grounds consists of small unstable groups of whales that are presumably feeding on the same transient food source (Clapham 1996). The mechanism through which humpbacks find a given food source is currently unknown.
1.3.3. **Sound production: Song**

Single males in the wintering grounds are often found singing. Song is a complex and highly organized acoustic behavior thought to serve as a male display (Payne and McVay 1971). Several hypotheses exist as to the function of song, among them advertisement to females, and also maintenance of dominance hierarchies and spacing among males (Herman and Tavolga 1980; Helweg et al. 1992; Frankel et al. 1995; Clapham 1996; Darling et al. 2006; Smith et al. 2008). Song was not considered in this study.

1.3.4. **Sound production: Non-song, or “social” sounds**

To date, the amount of research on humpback whale non-song acoustic behavior is relatively minor compared to song (Clapham 2000). Initial descriptions of these non-song “social sounds” and their contexts in the Hawaiian breeding grounds and Alaskan feeding grounds were published approximately twenty years ago (Silber 1986; Thompson et al. 1986, respectively). Only recently have acoustic studies again focused on non-song sounds (with the exception of the feeding cry in southeastern Alaska, described by D’Vincent et al. in 1985 and Cerchio and Dahlheim in 2001).

**Migration route:**

Dunlop and colleagues published a complete description of social sounds produced by humpback whales in Australia on their southward migration route from the breeding grounds on the Great Barrier Reef to the feeding grounds in the Antarctic (Dunlop et al. 2007; Dunlop et al. 2008). Because the whales had just departed the breeding grounds, it
is likely there was some overlap in behavior and sound production with the patterns that would be seen during interactions actually on the breeding grounds. Behavioral contexts of these sounds were described according to the activity of the group as a whole as opposed to being based on individual behavior.

**Feeding grounds:**

The southeast Alaska population of humpback whales in the North Pacific has been somewhat better studied than other feeding ground aggregations, but Thompson’s 1986 paper still remains the foremost description of social sounds on the feeding grounds. No studies of non-song sounds in the Atlantic have been published to date except for a description of a new type of sound that was recorded during night-time foraging in the Northwest Atlantic (Stimpert et al. 2007). That study comprises Chapter 4 of this dissertation.

**Breeding grounds:**

Silber (1986) reported on the rates of social sound production in different group types in Hawaiian waters, finding higher rates in larger groups of whales. Zoidis et al. (2008) reported the frequent production of social sounds by calves in lone mother calf pairs on the breeding grounds in Hawai‘i (also see the abstract by Pack et al. 2005), but did not make recordings from other types of groups of humpback whales, including adults actively competing for access to mates in competitive groups.
Social sounds may play a significant role in behavioral interactions between males within competitive groups (Silber 1986). Male-male acoustic competitive displays have been documented in other taxa, including mammals (e.g., Searcy and Andersson 1986; Kitchen et al. 2003, and as discussed above). But possibly due to logistical constraints, little study has taken place on sounds produced in this context in mysticetes. For example, in humpback whales, competitive groups are frequently very active and traveling at fast rates, which makes acoustic recordings quite challenging. It is necessary to use technology that can record sound while moving quickly through the water with the animals.

1.4 Importance of acoustic behavior in conservation

Returning to the idea that acoustic behavior can be central to the survival of a species, the importance of learning more about baleen whale acoustic behavior is clear. All baleen whales, including humpback whales, are endangered, and as highly migratory species (United Nations 1982), they could potentially be exposed to a wider range of anthropogenic threats in their different habitats, such as ship strikes or anthropogenic noise pollution. It may be appropriate to modify management regulations depending on the location and behavioral activities of the species in question (Gerber et al. 2005).

Relevant to acoustic behavior, anthropogenic noise pollution in the oceans is currently a high profile conservation concern. Increases in the ambient sound levels from sources such as offshore drilling, naval sonars, or commercial shipping traffic can affect marine species at a variety of levels, from masking the animals’ own communicative sounds to
actual physiological damage from high sound pressure levels (Nowacek et al. 2007; Tyack 2008). Several studies have been conducted that evaluate the behavioral and physiological effects of sound on odontocetes (e.g., McCormick et al. 1970; Mohl et al. 1999; Morton and Symonds 2002; Nachtigall et al. 2004; Romano et al. 2004; Holt et al. 2009). The most dramatic reactions were several mass strandings of beaked whales coincident with the use of naval sonars in the area (Cox et al. 2006; Rommel et al. 2006). Stranded whales have been found with gas bubble emboli in their tissues (Jepson et al. 2003; Dalton 2006), and hemorrhages in their ears (Balcomb and Claridge 2001). Though the exact mechanism that caused these stranding deaths is not known, unique behavioral characteristics of these species may put them at greater risk, and experimental research is currently underway to elucidate these causes (Allen et al. 2009; Southall et al. 2009).

Investigations into the potential effects of noise on several species of baleen whales have found what may seem to be slight behavioral effects, such as minimal changes in dive behavior, swim direction, or acoustic characteristics of the calls produced (Frankel and Clark 1998; Au and Green 2000; Frankel and Clark 2000; Miller et al. 2000; Frankel and Clark 2002; Fristrup et al. 2003; Nowacek et al. 2004; Parks et al. 2007). Though none of these effects were as obvious as the mass strandings exhibited by the beaked whales in the Bahamas (Balcomb and Claridge 2001), it is as yet unclear if these changes will translate to biologically significant effects on the species in the long term (Tyack 2008). In general, without understanding the role of sound production within a species, it is difficult to interpret a potential reaction to sound exposure or even shifts in sound
production characteristics. As recommended in the National Research Council’s report on Ocean Noise and Marine Mammals (2003), the first and most important step is to describe sounds produced during normal social and environmental conditions. We can then use the understanding gained to infer susceptibility of marine mammals to anthropogenic sounds.

**Summary and Research Questions**

In summary, terrestrial studies indicate that sound is used as communication in many contexts, including predator defense, foraging, and mating. Much of this knowledge was gained through experimental research and behavioral observations of focal individuals. Passive acoustic studies confirm that many species use sound under water, as expected, since visual communication is relatively limited, and when the sound functions are well understood, behavior can be inferred from recordings collected remotely. Marine mammals in particular rely heavily on sound, and captive studies of some smaller species have produced a baseline understanding of the types of sounds produced and how these sounds might be used. However, the study of the acoustic behavior of pelagic and highly mobile marine species is subject to many challenges, including the difficulty of obtaining continuous behavior measurements that can be associated with sound production in the field, especially in the case of larger, wide-ranging species like baleen whales. This is complicated by the relative lack of description of various sound types produced by baleen
whales. The humpback whale is an appropriate representative baleen whale species given its plentiful sound production and relatively easy accessibility. In addition, research to elucidate sound use in humpback whales is particularly appropriate given the conservation concerns relating to anthropogenic noise increases in the ocean.

In the research presented here, I conducted focal behavioral studies of humpback whales on both a breeding ground (Hawaiian Islands) and feeding ground (Gulf of Maine), with the goal of understanding non-song sound production in different behavioral contexts. Two methodologies were used. The primary method was non-invasive, animal-borne acoustic tags (Johnson and Tyack 2003). Recent developments in microelectronics technology have produced capabilities for miniaturized tags, which can be used to study cetacean acoustic behavior much more comprehensively than using some other methods, such as remote acoustic recordings (which lack the behavioral component) or boat-based focal follows (which lack the underwater component). Use of these tags, which contain hydrophones and body orientation sensors, results in longer continuous records of sound production by one focal animal, quantitative data on received levels of sounds nearby the focal individual, and synchronous body orientation and dive data above and under water that can be precisely paired with the tag’s acoustic record. The second method was a towed hydrophone array. Multiple hydrophones towed in a line behind the research vessel allowed localization on the whale producing each sound, from which a source level for the sound could be calculated. Both of these methods allowed recording from focal groups as they traveled.
My research questions were:

1. What are the acoustic properties of humpback whale non-song sounds?  
   (Chapter 2)

2. What behaviors are coincident with sound production and what can the sound 
   production patterns tell us about general humpback whale behavior?  (Chapter 3)

3. Do certain sounds indicate specific behaviors, such as certain types of feeding or 
   social interactions?  (Chapter 3, and Chapter 4, a case study)

I will also discuss how these sounds might be affected by the ambient acoustic 
environment, and what implications the results have for environmental management with 
respect to anthropogenic noise.
CHAPTER 2

Acoustic properties of humpback whale (*Megaptera novaeangliae*) non-song sounds on a breeding and feeding ground

Abstract

"Social sounds", or any non-song sounds produced by humpback whales, have been understudied relative to humpback whale song. In particular, source levels of these sounds have not been estimated, and acoustic descriptions are lacking in some areas. This study describes the acoustic repertoire of humpback whales on a breeding (Hawai‘i) and feeding (Northwest Atlantic) ground. Non-invasive acoustic tags (DTAGs) as well as a towed hydrophone array were used to obtain high quality recordings of sounds. Nine acoustic parameters were measured, and a cluster analysis was completed to group similar sound types. Source levels were calculated from localizations using the towed array data from the breeding ground. Feeding ground sounds had a mean peak frequency of 329 Hz (+/- 632 Hz), breeding ground sounds had a mean peak frequency of 223 (+/- 234) Hz, and most sounds were less than 1 s in duration. Mean source level of internally produced sounds on the breeding ground was 149 +/- 22 dB re rms. Sounds were more frequently produced on the feeding ground, and signal-to-noise ratio of these sounds was higher. These results imply that non-song sound production may be more useful during foraging, or perhaps simply more efficient on the feeding ground. This may be due to the high levels of background song chorusing on the breeding ground.
**Introduction**

Humpback whales are one of the best-studied large baleen whales, especially in terms of acoustics. Since humpback whale song was first described (Payne and McVay 1971), a large body of work has been developed to investigate its behavioral context (e.g., Winn et al. 1981; Tyack 1983; Chu and Harcourt 1986; Chu 1988; Frankel et al. 1995; Au et al. 2000; Frazer and Mercado 2000; Miller et al. 2000; Noad et al. 2000; Au et al. 2001; Au et al. 2006). Recent suggestions for the function of song range from the hypothesis that song organizes males on the breeding ground by providing a metric of past associations (Darling et al. 2006) to the idea that song serves an intersexual advertisement function (Smith et al. 2008). But a clear understanding of the acoustic display remains elusive.

Even less understood are “social sounds”, or any non-song phonations, though some headway has been made in recent years. A social sound, as defined by Silber, is “any phonation that does not possess the rhythmic and continuous patterning of song” (Silber 1986, p. 2076). These social sounds are produced on both the feeding and breeding grounds of humpback whales.

Until recently, we drew the bulk of knowledge about social sounds from work done on the feeding grounds (D’Vincent et al. 1985; Thompson et al. 1986; Cerchio and Dahlheim 2001) and breeding grounds (Silber 1986), where sounds were recorded using a single hydrophone from a small research vessel. Thompson et al. described five types of aurally classified sounds (moans, grunts, pulse trains, blowhole-associated sounds, and
surface impacts). Moans and grunts were distinguished by duration and presence of harmonic content. Back-calculated source levels were based on visually estimated distances to the group, and ranged from 162 to 192 dB re 1uPa. D’Vincent described a distinctive feeding call used in coordinated foraging in Southeast Alaska.

Silber (1986) recorded social sounds from humpback whales in Hawai’i using a single hydrophone from a stationary vessel. He found that sounds were most often produced from larger, interactive groups, especially when more activity was seen from the surface. However, no detailed description of sounds and sound types was given. Sounds were generally described as being generally low in frequency (under 2 kHz) and simple in structure (frequency-modulated upsweeps).

In 2007, Dunlop et al. published the first description of social sounds produced by migrating humpback whales off the eastern coast of Australia. Using 13 acoustic parameters and aural classification as well as several statistical techniques, Dunlop et al. reported 34 discrete call types as produced by the whales, including several that were also heard as part of the song in that area. This study used an array of sonobuoys, which produced continuous recordings as well as good spatial information on the location of the group producing the sounds. However, this passive method precluded detailed behavioral observations on the individuals in the group producing the sounds, and source levels of these sounds were not reported.
Zoidis et al. (2008) documented production of non-song vocalizations from a calf in the Hawaiian breeding grounds waters, but the sample size was small and also source levels could not be measured because a precise location of the sound source could not be calculated.

Two methodologies can address these gaps in knowledge of non-song phonations in humpback whales: tags and towed hydrophone arrays. Digital acoustic recording tags contain hydrophones and are a means of obtaining continuous acoustic recordings from within the group of whales for a significant length of time (Burgess et al. 1998; Johnson and Tyack 2003). The tags attach non-invasively and are placed on the whale’s back for high quality recordings of whatever sounds are produced by the tagged animal and other surrounding whales. The tags also record synchronous body movements of the focal individual, which can indicate specific behavior.

Though acoustic tags can produce high-fidelity recordings, there are inherent limitations such as large amounts of low frequency flow noise that obscures accurate representation of the lower end of the spectrum (generally 500 Hz and below). Also, especially without an understanding of the physiological mechanism of sound production of humpbacks, we cannot determine with certainty whether or not the tagged animal was the producer of the sounds, and how tag placement might affect the recordings. A towed hydrophone array allows localization of sounds, giving a precise distance from the recording source, which can then be used to calculate source levels.
At this point, social sounds on the feeding grounds have been measured only from afar, and social sounds on the breeding grounds remain poorly described acoustically. Source level estimates using known distances to the sound source are lacking in both locations. We used the two techniques discussed above to a) obtain synchronous and continuous acoustic and behavioral data from socially interacting and feeding humpback whales, and b) calculate source levels of social sound types in the breeding ground context.

Materials and Methods

Tagging

To obtain high quality recordings of humpback whale social sounds, tags containing hydrophones were deployed on humpback whales exhibiting target behaviors, such as foraging behavior on the feeding grounds, or active competition on the breeding grounds. The tags were DTAGs: non-invasive, suction-cup-attached acoustic recording tags (Johnson and Tyack 2003), that recorded body orientation (pitch, roll, and heading) and depth (both at a 50 Hz sampling rate) as well as continuous acoustics at a sampling rate of either 48, 64, or 96 kHz. Acoustic system sensitivity on the tags was -171 dB re 1 V/µPa (hydrophone sensitivity -205 dB re 1 V/µPa, 20 dB pre-amp, 2 dB ADC converter, and 12 dB of user-controlled gain). The tags also contained a high pass filter at 400 Hz to minimize flow noise.
Tags were deployed from one of several small vessels (between 7 m and 11 m) using either an 8 m handheld or 15 m cantilevered pole. Social sounds from the feeding grounds were recorded in the Northwest Atlantic Ocean, in the Stellwagen Bank National Marine Sanctuary (SBNMS) during 2006. Sounds from the breeding grounds were recorded within the Hawaiian Islands Humpback Whale National Marine Sanctuary (HIHWNMS), in the waters off the leeward coast of Maui in 2007 and 2008.

**Towed array**

In the winter season of 2009, social sounds were also captured by towing a 3-element hydrophone array next to groups of humpback whales. The array was 43 m in length, with hydrophones spaced as follows: 7 m between hydrophones 3 and 2, and 22 m between hydrophones 2 and 1. The array had previously been used as a 5-element vertical array, and was modified with the addition of epoxy hydrodynamic shells for smoother and quieter towing through the water. Two of the original hydrophones were not functional, hence the non-uniform spacing of the elements. The hydrophones were constructed of lead zirconate titanate piezoelectric ceramic tubes. The inner diameter of the tube was filled with corprene and the element was encapsulated in degassed epoxy. The sensor was attached to an amplifier-line driver having a gain of 30 dB. The hydrophones were calibrated in an open bay and had similar responses and a sensitivity of approximately $-175 \pm 3$ dB re 1 V/µPa between 100 Hz and 10 kHz (Au et al. 2006).

Array recordings were made on an Edirol R-4 4-channel Portable Recorder with a sampling rate of either 44.1 kHz or 96 kHz and zero gain. On each surfacing, the
distance to the closest whale in the group was measured using a monocular laser range finder. This distance was from the stern of the research vessel to the closest surfacing whale instead of from the center hydrophone to the whale producing a given sound, but it served as a rough estimate to which calculated distances to the sound source could be compared.

Analysis: Sound descriptions from tag data

Detection
All occurrences of social sounds were identified manually. Automatic detection algorithms were unsuccessful due to the inconsistent nature of the background noise, especially noise from water flow (which varies by swim speed) and surfacings. Sounds were therefore logged in Matlab using XBAT (Mills and Figueroa 2005), by listening to tag records and also by visually examining the spectrograms of the recordings in short enough segments that acoustic events less than one second in duration would be visible. Social sounds were identified based on the qualities described in the introduction; on the breeding grounds, this was largely based on whether the sounds fit into a surrounding pattern of vocalizations that were background song chorusing. On the feeding grounds, most sounds below 10 kHz with some biological quality were judged to be humpback-produced, as few other large whale species were known to be in the immediate vicinity. Sounds were identified by experienced listeners, and in all cases on feeding and breeding grounds were verified visually (on the spectrogram) and aurally by the author. Sections
of background noise of the same length of each sound were also logged either directly before or after each sound.

**Pre-processing**

The DTAG hardware contains a single pole high pass filter at 400 Hz in order to minimize flow noise. Therefore, a single-pole low frequency emphasis filter with a gain of 20 dB between 40 Hz and 400 Hz was applied to signals to compensate for the high pass filter, re-amplifying both signal and noise clips in the lower portion of the spectrum. An rms (root mean square) signal-to-noise ratio (SNR) was then calculated using the corresponding noise clip for each signal. The subset of sound clips that contained SNRs greater than 10 dB was selected for analysis.

**Parameter calculation**

For determining the acoustic parameters, the linear spectrum of the corresponding noise clip was subtracted from the spectrum of the corresponding signal clip to remove energy that was due to the ambient environment. In the case of start and end frequencies of the signal, the first and last 10% of this signal were used to find the starting and ending frequencies of the signal overall, defined below.

Calculated sound parameters related to both frequency and time, and are listed in Table 2.1 and depicted in Figure 2.1. Several of these parameters were also used by Dunlop et al. (2007) to classify social sounds on the migration route. Duration was determined
manually through visual examination of the sound’s waveform. Other parameters were calculated using custom-written algorithms in Matlab.

Table 2.1. Acoustic parameters calculated from sounds recorded on DTAGs, and description of these parameters.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duration of sound (s)</td>
<td>Dur</td>
<td>Length of sound</td>
</tr>
<tr>
<td>Peak frequency (Hz)</td>
<td>pkF</td>
<td>Frequency of the spectral peak</td>
</tr>
<tr>
<td>3 dB bandwidth (Hz)</td>
<td>BW</td>
<td>Frequency band between the lower and upper half power points (3 dB down from pkF) in the frequency spectrum</td>
</tr>
<tr>
<td>Center frequency (Hz)</td>
<td>F0</td>
<td>Energy midpoint of the spectrum (energy above and below this frequency are equal). Generally a more representative measure for bimodal or complex signals than is peak frequency</td>
</tr>
<tr>
<td>rms bandwidth (Hz)</td>
<td>BWrms</td>
<td>Frequency band encompassing the standard deviation of the spectrum about the center frequency</td>
</tr>
<tr>
<td>Start frequency (Hz)</td>
<td>startF</td>
<td>Peak frequency of the signal during the first 10% of sound duration</td>
</tr>
<tr>
<td>End frequency (Hz)</td>
<td>endF</td>
<td>Peak frequency of the signal during the last 10% of sound duration</td>
</tr>
<tr>
<td>Maximum frequency (Hz)</td>
<td>maxF</td>
<td>The largest frequency in the spectrum at which the signal is 10 dB below its level at peak frequency (high frequency)</td>
</tr>
<tr>
<td>Frequency trend (ratio)</td>
<td>trendF</td>
<td>Start freq/end freq</td>
</tr>
</tbody>
</table>
We chose to group the sound types using a cluster analysis based on the calculated acoustic parameters in order to objectify the process. Though many studies use human aural classification (e.g., Parks and Tyack 2005; Au et al. 2006; e.g., Deecke and Janik 2006; Riesch et al. 2006; Dunlop et al. 2007), it is unlikely that any currently-used method will identify the features actually salient to and used by the whales themselves. Thus we attempted to make our classification as repeatable as possible. Hierarchical agglomerative cluster analysis in Minitab 13.3 and Matlab 7.1 was used to describe natural groupings in the sound data based on selected acoustic parameters (duration, peak frequency, center frequency, RMS bandwidth, and maximum frequency). Variables were normalized and log-transformed to minimize skewness and also the effects of scale differences since variables were in different units. The log transformation was also used to better represent mammalian perception of pitch, which is normally logarithmic with respect to frequency in Hz (though there are no direct measures of mysticete hearing). A
dendrogram was generated using Mahalanobis distances and Ward’s distance linkage
method. A cutoff point in similarity between groups on this tree was chosen, resulting in
eight clusters of sounds from the feeding ground data and six clusters from the breeding
ground data. Sounds in each group were examined visually and aurally to determine a
subjective description for the cluster.

*Analysis: Source levels from towed array data*

*Detection*

Audio files from the 3-element hydrophone array were opened in XBAT in Matlab 7.4.0.
Sounds that had been noted aurally in the field during recording were identified visually
within the spectrograms and confirmed aurally.

*Localization and source level estimation*

Custom algorithms in Matlab were used to identify time of arrival differences (TOADs)
between sounds on each of the three hydrophones. Short clips surrounding the sound of
interest were bandpass filtered in a third-octave band around a frequency identified from
the spectrogram as being the most unencumbered by noise on all three channels. The
waveforms of these filtered clips were cross-correlated, and the maximum of the absolute
value of the envelope of the cross-correlation output (Kristian Beedholm, personal
communication) was identified. The corresponding time lag of this maximum was used
as the TOAD from the center hydrophone, and was used to calculate the distance to the
sound source, R, using the Pythagorean Theorem.
Noise clips of the same length as the signal were extracted from surrounding portions of the acoustic record. A third-octave band analysis was performed on both signal and noise clips. For each clip, the rms noise level in each third octave was subtracted from that of the signal. Adjusted signal values from each third-octave band were then summed to give a total sound pressure level at the hydrophone, which was then adjusted for transmission loss to obtain a source level. Because the whales were close to the array (within 100 m), absorption was ignored, leaving the most basic form of the sonar equation for calculating source level:

\[
\text{SL} = M_h - G + 20 \log(v_{signal}) + TL
\]

where \( M_h \) is the sensitivity of the hydrophone system, \( G \) is the gain in the system, and \( TL \) is transmission loss, which is calculated as \( 20 \log(R) \), where \( R \) is the distance to the sound source. All terms are expressed in dB re 1µPa except for the voltage, \( v_{signal} \).

**Quality control**

Only sounds that were localized to an area inside the aperture of the array and within 100 m were used for analysis to ensure the best possible sound quality. The aperture of the array is the length between the imaginary line drawn from the first and last hydrophones, perpendicular to the array. In other words, if a sound was plotted to be further away than the end of the array, or ahead of the first hydrophone (including abeam or ahead of the boat), these sounds were not used. Localizations of sounds outside the array become
progressively more inaccurate as the source moves away from the area inside the array aperture. The sounds are difficult to locate because small errors in the TOAD calculation can lead to large errors in distance estimation (Clark and Ellison 2000). Also, in most cases the array was within 100 m of the target group, so sounds calculated to be further away may have been from non-target animals. Sound clips with cross-correlation values below 0.25 were eliminated from analysis in an attempt to avoid cross-correlation of noise. Distances were also compared with the visual observations and ranges taken during the recordings. For determining source levels, channel two was used, as it was the hydrophone of best consistent quality and least noise from the boat engine.

SNR levels for the Hawaiian breeding ground datasets in general were extremely low because of levels of chorusing, or background song. Therefore the assumption was made that some auditory filtering may be taking place by the whale’s hearing system that allows some parts of the social sound signals to be heard over general ambient chorusing, as was the case for human ears as well. The signal and noise clips were thus filtered in a third octave band around the frequency identified to be outside the noise (described above), and a modified SNR was calculated based on this frequency band. Clips with modified SNRs above 10 dB were identified for source level analysis, which was completed with a third-octave band analysis of the original, unfiltered clips (also described above).
Results

General sound characteristics

Fifteen tags were deployed on Stellwagen Bank during the 2006 feeding season (resulting in 95.3 hours of recorded data). From this dataset, 1542 sounds were of sufficient quality for analysis (approximately 16 sounds per hour). Sound parameters were variable, with a mean peak frequency of all sounds of 329 Hz, but with a standard deviation +/- 632 Hz, and peak frequencies ranging as high as 12 kHz. Sounds averaged 0.7 (+/- 0.5) seconds in duration, ranging from 0.02 s to 6.3 s.

During the 2007 and 2008 breeding seasons in Hawai‘i, 19 tags were deployed (resulting in 55.4 hours of recorded data). Only 46 sounds from the 2007 season, and 6 sounds from the 2008 season were of a high enough signal-to-noise ratio to be included in analysis (less than one sound per hour). Mean peak frequency of all sounds was 223 (+/- 234) Hz, ranging to a high of 1304 Hz. The highest maximum frequency was only 3000 Hz. Durations were 0.65 (+/- 0.6) seconds, ranging from 0.03 s to 3.02 s.

Sound types

Five parameters of the sounds (log-transformed and normalized duration, peak frequency, center frequency, RMS bandwidth, and maximum frequency) were selected for use in cluster analysis to attempt a grouping of different sounds based on objective measurements. Figure 2.2 depicts how the sounds grouped based on those variables. The distance value by which different clusters were partitioned was chosen based on these
dendrograms. Table 2.2 summarizes all the calculated acoustic parameters by sound type from this cluster analysis, and includes samples sizes in each cluster and subjective descriptions of a sample of sounds in each cluster. Figure 2.3 shows examples of some of the most common sound types.

Figure 2.2a. Results of cluster analysis, SBNMS Feeding ground, 2006. Each cluster is represented by a different color. Descriptions and acoustic summaries of each cluster are in Table 2.2a.
Figure 2.2b. Results of cluster analysis, HIHWMS Breeding ground, 2007-2008. Each cluster is represented by a different color. Descriptions and acoustic summaries of each cluster are in Table 2.2a.
Table 2.2a. Summary of acoustic parameters by sound “type” or cluster, SBNMS Feeding grounds, 2006. Mean parameters are in bold. Standard deviations are listed below each variable, and number of observations in each cluster is in parentheses after the cluster number. Description was subjectively determined after listening to a sample of the cluster and viewing plots of the sound waveforms.

<table>
<thead>
<tr>
<th>Cluster number</th>
<th>Description</th>
<th>Duration (s)</th>
<th>pkF (Hz)</th>
<th>F0 (Hz)</th>
<th>BWrms (Hz)</th>
<th>BW (Hz)</th>
<th>startF (Hz)</th>
<th>endF (Hz)</th>
<th>maxF (Hz)</th>
<th>trendF (startF/endF)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (N=152)</td>
<td>Grunts/upsweeps</td>
<td>0.24</td>
<td>211</td>
<td>450</td>
<td>404</td>
<td>180</td>
<td>344</td>
<td>265</td>
<td>937</td>
<td>39.60</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.15</td>
<td>138</td>
<td>244</td>
<td>154</td>
<td>291</td>
<td>413</td>
<td>391</td>
<td>567</td>
<td>164.46</td>
</tr>
<tr>
<td>2 (N=276)</td>
<td>Short grunts/upsweeps</td>
<td>0.27</td>
<td>376</td>
<td>421</td>
<td>300</td>
<td>177</td>
<td>277</td>
<td>249</td>
<td>584</td>
<td>25.15</td>
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<td></td>
<td></td>
<td>0.14</td>
<td>280</td>
<td>241</td>
<td>187</td>
<td>280</td>
<td>392</td>
<td>335</td>
<td>450</td>
<td>130.10</td>
</tr>
<tr>
<td>3 (N=101)</td>
<td>Moans and squeaks</td>
<td>0.94</td>
<td>1039</td>
<td>1048</td>
<td>372</td>
<td>232</td>
<td>545</td>
<td>708</td>
<td>1315</td>
<td>15.75</td>
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<tr>
<td></td>
<td></td>
<td>1.03</td>
<td>950</td>
<td>918</td>
<td>241</td>
<td>275</td>
<td>791</td>
<td>954</td>
<td>1017</td>
<td>119.43</td>
</tr>
<tr>
<td>4 (N=214)</td>
<td>Upsweep gurgle</td>
<td>0.77</td>
<td>803</td>
<td>1149</td>
<td>973</td>
<td>483</td>
<td>370</td>
<td>380</td>
<td>1892</td>
<td>20.18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.58</td>
<td>1303</td>
<td>1204</td>
<td>627</td>
<td>1028</td>
<td>777</td>
<td>596</td>
<td>1701</td>
<td>148.97</td>
</tr>
<tr>
<td>5 (N=146)</td>
<td>Grunts and wops</td>
<td>0.64</td>
<td>137</td>
<td>738</td>
<td>670</td>
<td>419</td>
<td>411</td>
<td>342</td>
<td>1335</td>
<td>23.35</td>
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<td></td>
<td></td>
<td>0.51</td>
<td>73</td>
<td>574</td>
<td>478</td>
<td>776</td>
<td>873</td>
<td>541</td>
<td>979</td>
<td>210.34</td>
</tr>
<tr>
<td>6 (N=371)</td>
<td>Wops</td>
<td>1.08</td>
<td>110</td>
<td>176</td>
<td>208</td>
<td>38</td>
<td>144</td>
<td>123</td>
<td>229</td>
<td>1.98</td>
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<td></td>
<td></td>
<td>0.30</td>
<td>39</td>
<td>55</td>
<td>75</td>
<td>48</td>
<td>173</td>
<td>121</td>
<td>103</td>
<td>6.44</td>
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<tr>
<td>7 (N=111)</td>
<td>Paired bursts and low grumbles</td>
<td>0.42</td>
<td>108</td>
<td>207</td>
<td>645</td>
<td>61</td>
<td>137</td>
<td>112</td>
<td>312</td>
<td>40.66</td>
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<tr>
<td></td>
<td></td>
<td>0.19</td>
<td>55</td>
<td>203</td>
<td>399</td>
<td>73</td>
<td>190</td>
<td>237</td>
<td>511</td>
<td>151.91</td>
</tr>
<tr>
<td>8 (N=171)</td>
<td>Wops and upsweep grunts</td>
<td>0.74</td>
<td>125</td>
<td>369</td>
<td>533</td>
<td>23</td>
<td>311</td>
<td>246</td>
<td>193</td>
<td>4.31</td>
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<td></td>
<td></td>
<td>0.43</td>
<td>77</td>
<td>219</td>
<td>428</td>
<td>32</td>
<td>428</td>
<td>489</td>
<td>102</td>
<td>14.40</td>
</tr>
</tbody>
</table>
Table 2.2b. Summary of acoustic parameters by sound “type” or cluster, HIHWNMS Breeding ground, 2007-2008. Mean parameters are in bold. Standard deviations are listed below each variable, and number of observations in each cluster is in parentheses after the cluster number. Description was subjectively determined after listening to a sample of the cluster and viewing plots of the sound waveforms.

<table>
<thead>
<tr>
<th>Cluster number</th>
<th>Description</th>
<th>Duration</th>
<th>pkF (Hz)</th>
<th>F0 (Hz)</th>
<th>BWrms (Hz)</th>
<th>BW (Hz)</th>
<th>startF (Hz)</th>
<th>endF (Hz)</th>
<th>maxF (Hz)</th>
<th>trendF (startF/endF)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (N=15)</td>
<td>Wops and grumbles</td>
<td>1.19</td>
<td>103</td>
<td>225</td>
<td>297</td>
<td>51</td>
<td>229</td>
<td>136</td>
<td>291</td>
<td>4.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.83</td>
<td>62</td>
<td>118</td>
<td>215</td>
<td>61</td>
<td>229</td>
<td>128</td>
<td>263</td>
<td>10.50</td>
</tr>
<tr>
<td>2 (N=5)</td>
<td>Grunts and snorts</td>
<td>0.36</td>
<td>70</td>
<td>143</td>
<td>252</td>
<td>2</td>
<td>186</td>
<td>78</td>
<td>130</td>
<td>2.17</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.14</td>
<td>31</td>
<td>35</td>
<td>88</td>
<td>2</td>
<td>303</td>
<td>38</td>
<td>89</td>
<td>3.13</td>
</tr>
<tr>
<td>3 (N=10)</td>
<td>Grunts and grumbles</td>
<td>0.23</td>
<td>235</td>
<td>376</td>
<td>369</td>
<td>105</td>
<td>349</td>
<td>440</td>
<td>596</td>
<td>1.23</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.10</td>
<td>150</td>
<td>166</td>
<td>256</td>
<td>135</td>
<td>306</td>
<td>380</td>
<td>289</td>
<td>1.36</td>
</tr>
<tr>
<td>4 (N=15)</td>
<td>Double grunts</td>
<td>0.65</td>
<td>414</td>
<td>816</td>
<td>679</td>
<td>404</td>
<td>167</td>
<td>336</td>
<td>1394</td>
<td>1.77</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.27</td>
<td>308</td>
<td>351</td>
<td>247</td>
<td>343</td>
<td>177</td>
<td>322</td>
<td>757</td>
<td>3.49</td>
</tr>
<tr>
<td>5 (N=4)</td>
<td>Grunts</td>
<td>0.39</td>
<td>37</td>
<td>724</td>
<td>726</td>
<td>263</td>
<td>66</td>
<td>1029</td>
<td>0.63</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.20</td>
<td>6</td>
<td>378</td>
<td>223</td>
<td>443</td>
<td>29</td>
<td>41</td>
<td>831</td>
<td>0.48</td>
</tr>
<tr>
<td>6 (N=3)</td>
<td>Low short bursts</td>
<td>0.20</td>
<td>338</td>
<td>502</td>
<td>605</td>
<td>395</td>
<td>485</td>
<td>1</td>
<td>1096</td>
<td>485.09</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.03</td>
<td>279</td>
<td>411</td>
<td>354</td>
<td>206</td>
<td>421</td>
<td>0</td>
<td>905</td>
<td>420.78</td>
</tr>
</tbody>
</table>
Figure 2.3. Example waveforms and spectrograms for four of the most common sound types identified via cluster analysis and confirmed aurally (SBNMS Feeding ground 2006). Note the difference in time scales.

*Sound amplitudes*

Source levels varied over a wide range, as can be seen in Table 2.3a. Externally produced sounds included some sounds from surface active behaviors visible from the boat, such as breaches and pectoral flipper slaps. This category also included several sounds that were interpreted as body strikes between two animals, and were heard during periods of intense competition while the whales were under water. These sounds were generally preceded by frequent visual displays at the surface by the primary escorts (males) in the group, and often by a chase between two animals. All externally produced sounds were transients of a broadband nature and of short duration (0.08 +/- .03 s).

Signal-to-noise ratios were less than 3 dB in most cases for the sounds recorded on the hydrophone array, which makes quantitative comparisons with the tag data difficult.
Internally produced sounds generally had more tonal and harmonic components than externally produced sounds, and included mostly sounds that were similar to the grunts and squeaks recorded on the tags, described above. These sounds were much quieter than those that were externally produced, and exhibited greater variation in overall levels (Table 2.3a).

Table 2.3a. Calculated source levels of externally and internally produced whale sounds (see text for description) recorded from towed hydrophone array. Bold measurements indicate the more appropriate measure for each type of sound (Madsen 2005).

<table>
<thead>
<tr>
<th>Sound category</th>
<th>Mean Source level (peak-to-peak)</th>
<th>Mean Source level (rms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Externally produced (surface activity or underwater body strike) (N = 14)</td>
<td>181 +/- 19 dB re 1µPa</td>
<td>167 +/- 19 dB re 1µPa</td>
</tr>
<tr>
<td>Internally produced whale sound (N = 89)</td>
<td>166 +/- 12 dB re 1µPa</td>
<td><strong>149 +/- 22 dB re 1µPa</strong></td>
</tr>
</tbody>
</table>

Sound levels as received on the tags were slightly lower than source levels as calculated from the towed array, though the large amount of variability in the towed array data obscures this difference (Table 2.3b).

Table 2.3b. Calculated received levels of all internally-produced whale sounds recorded from tag acoustic records. Records used were signal including background noise, but with SNR > 10 dB.

<table>
<thead>
<tr>
<th>Location of tag record</th>
<th>Mean Source level (rms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding ground (Stellwagen Bank National Marine Sanctuary) (N = 1543)</td>
<td><strong>140 +/- 10 dB re 1µPa</strong></td>
</tr>
<tr>
<td>Breeding ground (Hawaiian Islands Humpback Whale National Marine Sanctuary (N = 52)</td>
<td><strong>135 +/- 7 dB re 1µPa</strong></td>
</tr>
</tbody>
</table>
Sound production by individual and location

Sound production by tagged animal record was variable as well. All acoustic records from animals tagged on the feeding grounds contained at least some sounds of high enough quality for inclusion in this analysis. However, the record from one whale, mn06_196a, contained more than half of all sounds used in the analysis, indicating that either this individual produced a great number of sounds, or it was near other animals that were doing so.

On the Hawaiian breeding grounds on the other hand, eleven of the nineteen acoustic records from tagged animals did not contain sounds of sufficient amplitude for analysis. Sounds that were recorded tended to be less tonal and frequently sounded more like body or water movements than something that was internally produced. It was also sometimes difficult to distinguish between song units from nearby singers and social sounds from the focal group. This was generally done by looking for a continual pattern in the sounds, which is characteristic of song. However, if a nearby singer started and stopped briefly, those units may have been included as social sounds.

Discussion

Sound types and descriptions

The humpback whale social sounds described here were low in frequency (under 500 Hz peak frequency, but ranging as high as 12 kHz for the maximum frequency in a sound)
and short in duration (generally less than 1 second). Song units, by comparison, are frequently 1 second or more (Au et al. 2006). The cluster analysis was successful in distilling the dataset into a small number of groups of similar sound types. Though membership in these groups has some overlap according to the human ear, related groups as seen in the dendrograms (Figure 2.2) do seem to have similar sound types, giving weight to the classification.

The analysis did break out several sounds that were considered distinctive from an aural perspective and from visual inspection of the waveform (Figure 2.3). Among these is the “wop”. Dunlop et al. (2007) termed two of their most commonly recorded sounds the “wop” and the “thwop”. These two sounds were both brief harmonic upsweeps, and together comprised approximately 20% of the 660 sounds they recorded. The dataset in this study also contained a large number of sounds aurally similar to “wops” (clusters 6, and partially clusters 5 and 8). We also recorded several wops on the breeding grounds, even given the small sample size (cluster 1). That this sound type occurs in all three of the major behavioral contexts of humpbacks (feeding, breeding, and migration) and in three different populations (North Pacific, North Atlantic, and East Australian) indicates that it may be an important communicative sound, and one with a flexible context, or with multiple uses during different activities.

**Sound amplitudes**

The sound amplitudes, while extremely variable, were still much lower than expected based on previous work on other species. Though source level measurements of baleen
whale sounds are few, those reported are higher than the results of this study. Au et al. (2006) reported humpback whale song source levels to vary between 144 and 169 dB re 1µPa rms. Gunshot sounds from right whales (Parks and Tyack 2005, mean 183 dB re 1µPa rms), blue and fin whale calls (Sirovic et al. 2007, mean 189 dB re 1µPa rms), and dwarf minke whale “star wars” vocalizations (Gedamke et al. 2001, 150-165 dB re 1µPa rms) are also higher than values reported here. However, those types of sounds are generally hypothesized to be for longer distance (inter-group) communication, generally for reproductive advertisement (but see Smith et al. 2008).

Given that social sounds in Hawai'i are heard most frequently in competitive groups (Silber 1986), it follows that they may also function in a reproductive context since whales in these groups are thought to be competing for access to mates, though mating has never been observed (Clapham 2000; Pack et al. 2002). In particular, non-song sounds could be used for communication between competing males or perhaps produced by the central female. The sounds may then only be directed towards the other whales in that particular group. In other words, it may make sense that the social sounds we have recorded here have lower source levels than song. If the sounds are directed towards animals that are only several whale lengths away, it would not be efficient to put the energy into the sounds that is required to produce levels as loud as song. Though social sounds may be audible at greater distances by eavesdropping listeners (Tyack and colleagues 1983) documented approach responses of humpbacks to social sound playbacks, although these researchers were playing unusual sounds at higher amplitudes than recorded here), if the sounds were meant as long-distance advertisement they would
be of greater amplitude and longer duration, as is song. In fact, Parks and Tyack (2005) also found other sounds produced by right whales in surface active groups (thought to have a similar function to humpback whale competitive groups) to range down to 137 dB re 1µPa rms. Though those were the minimum values of those sounds, they are at least in the same range as the values calculated here for humpback social sounds.

Thompson (1986) reported levels of social sounds between 162 and 192 dB re 1µPa rms. The differences here may be due to error in distance estimation (either in our localization technique, or Thompson’s visual estimation technique), or the feeding ground sounds may just be louder than those on the breeding grounds. This is likely, given the trend from our tag recordings that the feeding grounds sounds recorded were louder and of better signal-to-noise ratio. Unfortunately, we do not have towed array data from the feeding grounds to compare source levels.

*Received levels on tags.* The amplitude levels of sounds received at the tag location, while within the range of the source levels calculated using the towed array, were slightly lower overall. This may be because not all sounds recorded on the tags were actually produced by the tagged animal, and thus the animal producing the sound could be as far away as were animals that were recorded on the towed array. However, the loudest received levels on the tags were still lower than the loudest calculated source levels. If we assume that the loudest received levels were in fact produced by the tagged individual, this may indicate some sort of shielding taking place by the animal’s body because of the tag placement behind the head. Though the sound production mechanism
for humpback whales is still unknown, some hypothesize that sound in baleen whales is
generated through the larynx, which would cause sound to propagate out below the
whale, in the region of the ventral pleats (Reidenberg and Laitman 2007). This would
mean that tag placement on the animal’s back would make acoustic records subject to
severe attenuation (and possibly distortion) through the animal’s body, causing a decrease
in received level on the tag. Even slight directionality in the sounds, which may be
possible even at these low frequencies (Au et al. 2006), could result in attenuation of
sounds recorded from behind or above the sound source.

*Sound production on the breeding grounds vs. the feeding grounds*

On the feeding grounds, many more sounds were recorded, and the sounds were at a
higher signal-to-noise ratio than those on the breeding grounds. This indicates either that
the tagged animal was producing a higher percentage of the sounds, or that sounds in
general were louder on the feeding grounds. It is actually likely that both of these
scenarios are true, given the sheer magnitude of the difference between the two locations,
and given the subjective qualities of some of the feeding ground recordings that indicate
possible production by the tagged animal, such as extremely clear recordings and an
echo-like quality of some of the sounds, as if they are resonating inside the body.

This difference between the two locations is surprising, given the importance of mating
activities on the Hawaiian breeding grounds, and the prevalence of the use of sound for
sexual advertisement and other mating-related communication in other animal taxa.

Female birds use the qualities of male song to judge the potential mate quality of a
displaying male (Searcy and Andersson 1986; Catchpole 1987; Galeotti et al. 1997; Duffy and Ball 2002), and evidence of female choice mediated by acoustic displays also exists for frogs and insects (e.g., Gerhardt 1994; Ryder and Siva-Jothy 2000). Male fallow bucks gather on leks to produce their vocal displays, which facilitates female choice amongst them (McElligott et al. 1999). It has also been proposed that humpback whales on the breeding grounds are also organized in “floating leks” (Clapham 1996), where female choice, possibly based on song displays, takes place amid a looser spatial structure than a traditional resource-based lek.

It thus seems likely that humpback whales, which are relatively soniferous amongst the marine mammals and exhibit a varied acoustic repertoire, would heavily utilize sound when directly competing for mates, in addition to when individual males are alone and singing. So why the depressed sound production in competitive groups on the breeding grounds? It is true that the sounds recorded in this study were from two different whale populations. Perhaps the North Atlantic population is simply more verbose than that of the North Pacific? There are records of large amounts of sound production in Alaskan waters (Thompson et al. 1986), indicating that non-song sound production is indeed commonplace in some contexts with the North Pacific population. Also, the similarity of some sounds to those produced by the Southern Hemisphere migrating population suggests that humpback whales around the world have similarities in their acoustic repertoire.
Ultimately, it is a misnomer to say that the breeding ground population was relatively mute compared to whales on the feeding ground. In fact the opposite is true – chorusing, or song production, was continuous in every tag record. This may actually be the reason for the depressed amount of social sound production. The ambient sound levels on the breeding grounds may be so overwhelmed with sound from chorusing that it is not as efficient to rely on sound for other types of communication. In the clear waters of Hawai‘i, visual displays may be more effective within groups. Future work should look in greater detail at social sound production during the nighttime hours, when visual displays may be less effective. However, chorusing has also been found to increase at night (Au et al. 2000), which may further obscure the use of social sounds.

Implications

The large amounts of background chorusing likely obscured many social sounds in Hawai‘i, both aurally and visually on the spectrograms. It is likely that these sources of external noise are also masking the sounds for the whales themselves, meaning that those signals that were identified here are likely some of the most salient signals to the whales as well in terms of their ambient acoustic environment. This may be due to their frequency content, or perhaps the timing of the signals amongst the far more regular song patterns. In either case, detecting signals above noise amongst the cacophony of song chorusing in Hawai‘i is clearly a more difficult task than in areas where the background noise is either lower, or less similar to the sounds being produced by the whales.
This may also mean that social sounds in Hawai‘i are more vulnerable to masking by increased anthropogenic noise, given the already noisy ambient environment. Future work on the concurrent behavior of the whales during different types of sound production may help elucidate the function of different sound types, which would help understand what activities might be hindered by this potential masking.
CHAPTER 3

Individual behavioral context during non-song sound production by humpback whales (*Megaptera novaeangliae*)

Abstract

Most passive acoustic studies are unable to record the behavior of individual animals during periods of sound production, and this lack of knowledge hampers interpretation of sound function. We deployed non-invasive acoustic tags (DTAGs) on humpback whales on both a breeding and feeding ground in order to describe the underwater behavior of focal individuals during sound production. Sound production rates were evaluated over variation in depth, pitch, roll, and time of day. We observed significant variation in depth only: sounds were more frequently recorded when the focal individual was just below the surface, between 14 and 28 m in depth. A crepuscular trend was also seen in the feeding ground data, with more sound production around dawn and dusk. These results suggest that the sounds described here may be used in social interactions instead of active feeding, but this conclusion would benefit from further data collected over a wider range of foraging strategies and habitat depths.
Introduction

In the past, one of the major methods for studying baleen whale sounds was through remote recordings (e.g., Cummings and Thompson 1971; Payne and McVay 1971). Association of various sounds with behavior of individuals was difficult since calls take place under water and out of sight of any possible visual observations. However, recent studies of mysticete acoustic behavior have made great strides towards determining the function of many of the calls and songs produced by these wide-ranging cetaceans.

Parks and Tyack (2005) made detailed recordings of sounds produced in North Atlantic right whale surface active groups (SAGs), and attempted to assign specific behavior of individuals to production of particular call types. Using both a single hydrophone and a 3-element hydrophone array, the researchers paired sound production with surface visual and video observations. Six major call types were identified, and in most cases production could be assigned to a particular individual, such as the focal female of the group, allowing inferences as to the potential function of the sounds. Unfortunately, behavioral data could only be recorded while the whales were stationary and at the surface, limiting the range of acoustic behavior that could be investigated.

Humpback whales are well known for their prolific production of song on their wintering grounds (Payne and McVay 1971; Winn et al. 1981; Frankel et al. 1995; Noad et al. 2000; Darling et al. 2006; Smith et al. 2008). But humpbacks also produce non-song sounds in many contexts, including during competitive interactions on the breeding
grounds, foraging activities on the feeding grounds, and migration (Silber 1986; Thompson et al. 1986; Dunlop et al. 2007, respectively). Dunlop et al. (2008) reported on the behavioral contexts of these non-song sounds on the migration route of the East Australian population of Southern Hemisphere humpback whales. Sounds were recorded as the migrating whales passed through a large stationary array, and visual observations on the group as a whole were taken from a shore-based field station. Several sound types were identified to be coincident with certain whole-group behaviors, such as joining individuals, disaffiliation, or active competition. But detailed behavior of individuals, including underwater activities such as dive behavior, was not able to be measured.

In 2007, Oleson et al. published a study on the context of blue whale calling behavior using suction-cup attached acoustic tags. This technology allows detailed individual behavioral data on individuals, including pitch, roll, and depth to be collected concurrently with the acoustic record containing the calls. Sounds were only recorded while the whales were near the surface, and as such were determined to be used for communication and not active feeding, which occurs at depth. The blue whales in this study, however, did not associate as tightly (close in distance) in their groups as do humpback whales, and also many of the tagged whales did not produce sound at all. This observation along with the smaller call repertoire of the species compared with humpback whales indicates that acoustic behavior may be less complex.

Here we attempted to describe the individual behavioral context of humpback whale non-song sound production in terms of pitch, roll, and depth of the tagged individual. These
results along with the time of day of sound production and differences between breeding and feeding ground behavior are used in discussion of the role of non-song sounds and acoustic behavior during breeding and feeding activities.

**Materials and Methods**

*Field work*

Focal follows of individual humpback whales were accomplished through the use of suction-cup attached acoustic tags (DTAGs, Johnson and Tyack 2003). Tags were deployed on animals involved in active competition on the breeding grounds or active foraging behavior on the feeding grounds, and remained attached for time periods from approximately 0.5 – 24 hours. The tags recorded body orientation (pitch, roll, and heading) and depth (both at a 50 Hz sampling rate) as well as continuous acoustics at a user-defined sampling rate of either 48, 64, or 96 kHz. Acoustic system sensitivity on the tags was -171 dB re 1 V/µPa (hydrophone sensitivity -205 dB re 1 V/µPa, 20 dB pre-amp, 2 dB ADC converter, and 12 dB of user-controlled gain). The tags also contained a high pass filter at 400 Hz to minimize flow noise.

The feeding ground used in this study was Stellwagen Bank National Marine Sanctuary (SBNMS), in the Northwest Atlantic Ocean. The breeding ground was the Hawaiian Islands Humpback Whale National Marine Sanctuary (HIHWNMS), in the waters off the leeward coast of Maui, Hawai‘i. During daylight hours of tag attachments, whales were
tracked from small vessels at a distance of approximately 100 m or more (to minimize the effect of the research vessel on the whale’s behavior), depending on conditions. Over the course of 2006, 2007, and 2008, 34 tags were deployed, for a total of 150.7 hours of recorded data.

Data analysis

Sound identification and selection: All occurrences of social sounds in the acoustic recordings were identified manually, using visual identification on spectrograms as well as aural listening (XBAT running in Matlab 7.0.4, Mills and Figueroa 2005). The start times and durations of each sound clip were subsequently paired with the corresponding regions of the orientation sensor records to describe pitch, roll, heading, and depth of the tagged animal during periods of social sound production in the focal group. It is important to keep in mind that it is not certain that all the sounds recorded on the tags were produced by the tagged animal itself. In fact, because of the close proximity the whales keep to one another, especially when they are interacting in a tight competitive group as in Hawai‘i, it is likely that sounds produced by neighboring whales would also be recorded on the tag. Therefore only sounds with signal-to-noise ratios greater than 10 dB rms were considered, under the assumption that the closest and most salient sounds would be the ones most likely to influence the behavior of the tagged individual, even if the tagged individual did not produce them directly. We also analyzed a subset of data containing only the loudest sounds (30 dB rms) for one whale on the feeding grounds. In this case we assumed that these sounds were produced by the tagged animal, to compare the behavior pattern during sound production with that of the larger dataset. On the
SBNMS feeding ground, acoustic records of all 14 tagged whales contained sounds of high enough quality for inclusion in the main analysis. On the HIHWMS breeding ground 8 tagged whales’ acoustic records contained high enough quality sounds.

Behavior during sound production: For each sound included, a corresponding depth, pitch, and roll orientation of the tagged whale was calculated from the associated body orientation sensors. Because each whale spent different amounts of time at different depths and body orientations, we compared sound production rates instead of analyzing the raw number of sounds produced. To calculate the rates, data were binned into depth and orientation categories, and activity budgets for each whale were determined as follows: the number of sounds recorded while the tagged whale was at a given depth (or body orientation) was divided by the amount of time in minutes spent in that depth or body orientation. For example, if a tagged whale’s record contained 10 sounds while that whale’s depth was between 0 and 14 m, and the whale spent 100 minutes in that depth range during the tag attachment, the sound production rate for that whale in depth bin 1 would be 0.1 calls/min.

Depth bins were created using the assumption that changes in depth less than one whale length may be meaningless to the whale. The 14 m increment is approximately the length of the largest whale measured by Spitz and colleagues, and is one meter greater than the average whale length of male whales in competitive groups (Spitz et al. 2002). This distance was chosen to ensure that the differences between depth bins were greater than the length of any whale in the group. Pitch and roll were divided into bins of
approximately 30 degree increments. Negative pitch indicates an orientation where the tagged whale’s head is tilted down. Negative roll indicates an orientation where the tagged whale is rolled to the left. Pitch was only considered between +90 and -90 degrees since the whales were not observed in more extreme pitch orientations.

Statistical comparisons: We performed a 2-factor mixed model ANOVA (Analysis of Variance) to compare sound production rates in different depth and orientation categories. Each whale was treated as a random block, and depth/orientation categories as fixed effects. Because the dataset only included one replication in each block, an interaction effect could not be calculated, but we tested the depth/orientation effects over the error, viewing the error term as the interaction.

Results

Feeding ground

Tagged whales on the feeding grounds spent 54% of their time between the surface and 14 m depth. The whales generally remained at horizontal, ventral-side down orientations: less than 10 degrees from center in either direction for pitch (approximately 65% of time spent at these orientations) and roll (approximately 70% of time spent at these orientations).
Figure 3.1 shows an example dive profile of a tagged whale, with locations of recorded sounds notated as red dots. The whale represented here spent the majority of its time (61%) at depths shallower than 14 m, but most of the sounds occur at depths greater than 14 m.

This pattern held when examining the acoustic records from all tagged whales, as seen in Figure 3.2. Sound production rates varied significantly across depth ($F=3.17$; $P=0.008$), and this difference was strong enough to hold despite a significant variation amongst whales ($F=2.25$; $P=0.015$), which can be seen via the outliers in the boxplot. Sound production rates overall were higher in the top half of the water column, where the whales spent most of their time. The highest rates, however, were in the second depth category (14 - 28 m), despite a majority of time spent in the first depth category (0 - 14 m).
m). In other words, most sounds were produced just under the surface, as opposed to when the whales were actually at the surface.

![Box plot of sound production rates by depth (SBNMS Feeding ground). For each whale, a sound production rate was determined at each of these seven depth bins (incremented by the equivalent of one whale’s length at each bin).](image)

The acoustic records from the tagged whales on the feeding ground contained the highest rates of sound production when the tagged whale was swimming pitched moderately upward or downward, possibly indicating the whale was on the ascent or descent of a dive (Figure 3.3). However, the two-way ANOVA resulted in no significant difference amongst pitch categories (F=1.23; P=0.300), but a large variation amongst whales (F=3.06; P=0.001). It appeared the whales rolled more frequently to the left than the right during periods of sound production (Figure 3.3), but again, no significant variation across roll categories was found (F=1.57; P=0.105; inter-whale variation F=4.82; P<0.001).
Sound production rates appeared to be highest during the early morning, around 9 am.

There was a secondary peak just after sunset, at approximately 9 pm, indicating that much of the sound production recorded from tagged whales was crepuscular (Figure 3.4), but this was not significant ($F=1.10; P=0.345$; inter-whale variation $F=5.63; P<0.001$).

The tags recorded much less sound production during late afternoon, and none during the early hours of the morning, though only two of the tags were attached during that early morning time period. A large peak in sound production is seen around midnight in Figure 3.4, which is largely due to one whale whose record contained a much higher number of sounds than those of the other whales. This whale is discussed in more detail below.

Figure 3.3. Box plots of sound production rates by pitch (left panel) and roll (right panel) (SBNMS Feeding ground). For each whale, a sound production rate was determined at each of 13 bins (incremented by approximately 30 degrees at each bin; x-axis labels are the lower edge of each bin).
Breeding ground

The sample size of sounds produced was much smaller for the breeding ground, but some patterns still emerged. Once standardized for the activity budgets of the whales, the sound production rates were still highest close to the surface. In addition, three whales did perform deep dives to over 100 m, but no sounds were recorded at these depths (Figure 3.5). A two-way ANOVA revealed no significant difference between sound production at different depths (F=0.95; P=0.504; inter-whale variation F=0.88; P=0.528).
Likewise, no difference was found between sound production at different pitch angles 
\( (F=1.27; \ P=0.292; \ \text{inter-whale variation} \ F=2.92; \ P=0.014) \) or roll angles \( (F=1.02; \ P=0.440; \ \text{inter-whale variation} \ F=1.66; \ P=0.131) \). The highest rates of sound production on the breeding ground were in the early afternoon, around 13:00 (Figure 3.7). Unfortunately, we did not have an adequate sample size outside this window of several hours during midday for a comparison across the complete diel cycle. Only one tag was attached during nighttime hours on the breeding ground (‘mn08_064b’), and no sounds were recorded from that whale at night.
Figure 3.6. Box plot of sound production rates by pitch (left panel) and roll (right panel) (HIHWNMS breeding ground). For each whale, a sound production rate was determined at each of 13 bins (incremented by approximately 30 degrees at each bin; x-axis labels are the lower edge of each bin).

Figure 3.7 Box plot of sound production rates by time of day (HIHWNMS Breeding ground). The number of calls produced by each whale during each hour of the day was standardized by the amount of time the tag was attached during that hour.
Identity of sound producer

Again, it is important to remember that we cannot confirm that the tagged whale produced all of the sounds included in this analysis. However, we can restrict the dataset to increase the chances that that is the case, and compare the resulting pattern. Returning to one of the whales with the highest rates of sound production on its acoustic record, ‘mn06_196a’ (SBNMS feeding ground), we subsampled the sounds from its tag to look at the context of only the loudest sounds, assuming that these would be the most likely to have been produced by the tagged whale itself. Fifty-three sounds had an rms signal-to-noise ratio of 30 dB or greater, and many of them occurred around the same time, midway through the focal follow, at around midnight. These sounds are overlaid on that section of the dive profile in Figure 3.8. The line plot is color-coded by the degree of roll of the tagged whale, and what are likely foraging dives (steep, repetitive dives targeted to a certain depth, and with repetitive rolling lunges along the bottom of the dive) occur on either end of the section where many of the loudest sounds were recorded. Of note is that these sounds occurred during a time of shallower dives, not during the repetitive feeding behavior.
Figure 3.8 Section of the dive profile of ‘mn06_196a’ on the SBNMS Feeding ground. The dive track is color coded by degree of roll of the tagged animal, with warmer colors representing greater degrees of roll. White dots mark the location of recorded sounds with over a 30 dB SNR.

Discussion

Despite variation amongst whales, there were general trends in behavior and sound production that emerged to describe the behavioral context of the tagged whales during periods of recorded sound production.

Depth and body orientation

Stellwagen Bank and its surrounding basin are shallow areas (20 – 100 m depth) where the humpbacks are believed to feed on sand lance (Hain et al. 1995). Northern sand lance is a bottom-schooling fish that congregates in areas where bottom substrate is sandy and with a high density of shells and shell fragments (Winters 1983). Humpbacks have been
observed to travel along the ocean bottom, scuffing their jaw through the sand to flush the sand lance up into the water column (Hain et al. 1995). That most of the sounds in this study were recorded when the tagged whales were away from the bottom indicates that they may not use internally-produced sound while actively foraging on sand lance. This is supported by the example from ‘mn06_196a’ (Figure 3.8), where foraging dives were interrupted for what may have been a social interaction, and is also similar to the conclusions by Oleson et al. (2007) that blue whales limit calling activities to when they are in shallower depths. However, because of the time of night, we have no visual confirmation that other whales were in the area during the break in foraging by ‘mn06_196a’, thus, the idea that this period of sound production was socially driven remains speculative. Also, the higher sound production rates (though not significant) during pitch angles indicating ascent and descent suggests that the sounds may be produced in preparation for some type of foraging, perhaps cooperative, that is taking place at the foot of the dives, and in preparation for some type of behavioral activity at the surface, perhaps social interaction.

No significant trends were seen in the pitch or roll data from the breeding ground either, though whales tended to exhibit higher sound production rates while in standard horizontal, ventral-down orientations, probably while actively swimming or resting at the surface. In the case of the depth results from the breeding ground, the data again showed a bias toward sound production in shallower depths. In Hawai‘i, much of the display behavior in competitive groups is visual and takes place near the surface, which corresponds to the depths at which most sounds were recorded. But recent evidence does
suggest continuation of competitive behavior all the way to the seafloor, which in some cases was nearly 300 m in depth (Herman et al. 2007). It may be that from the perspective of a humpback whale, the depth bins as defined here are insignificant, and a dataset with greater excursions in dive depth is needed to fully investigate dependence of sound production on depth. It may also be that the energetic demands of physical competition make sound production more efficient near the surface.

**Time of Day**

On the feeding ground, a crepuscular pattern was evident in the time of day data, with higher rates of sound production just following sunrise and sunset. Though the pattern was not significant, the diel tendency likely relates to the foraging behavior of the whales on sand lance. Sand lance have been shown to be vulnerable to predation during the transition between day and night, because of their movements from an active mode in the water column to a refuge resting in the sediments (Hobson 1986). If sound production is increasing due to feeding on sand lance, this would support the hypothesis that some kind of social foraging may be taking place. Some other taxa, such as primates and birds, show evidence of using food-associated calls to either indicate specific food types (Evans and Evans 1999; Kitzmann and Caine 2009), which may draw in conspecifics, or as food ownership, to decrease aggression from conspecifics (Gros-Louis 2004). The increase in sound production on the feeding ground records could therefore indicate either cooperative or aggressive acoustic interactions during foraging.
Although it has been proposed that some internally-produced sounds are used by humpback whales for foraging (Stimpert et al. 2007, Ch.4 this volume), those sounds were made during foraging on herring. Herring have air bladders, which make them more acoustically reflective targets than other fish species without air bladders, and herring also have good hearing capacity compared to other fish species (Popper et al. 2004; Mann et al. 2005; Doksaeter et al. 2009). The hearing of sand lance is less sensitive (Suga et al. 2005), and as such it is likely that any sounds produced by the whales during feeding would be directed towards conspecifics rather than the fish themselves. This conspecific communication would likely be for social mediation during foraging, but whether it is cooperative or competitive remains unclear.

It is interesting to note that on the breeding ground, where no feeding is taking place, an opposite trend was seen, with higher rates of sound production during mid-late afternoon. This is consistent with an increase in large whale groups and also a peak in male-male aggression in the Hawaiian waters in the late afternoon (Helweg and Herman 1994). Unfortunately, the sample size at other times of day was too small to make a comparison with the acoustic behavior on the feeding ground.

Conclusions

Overall, it appears most likely that sounds are produced during social periods, near the surface, as opposed to during foraging behavior (e.g. bottom feeding) or stationary rest periods (at depth on the breeding ground). This suggests that sound production in large groups may be agonistic on the breeding grounds and non-agonistic on the feeding
grounds. However, this conclusion requires more detailed investigation of the context of sound production on the feeding ground, including supporting data on prey distribution to confirm feeding behavior, and double tag attachments to investigate vocal exchanges between groups of animals in an interacting, and potentially cooperative, group.
CHAPTER 4

“Megapclicks”: a case study of detailed behavior paired with non-song sound production in humpback whales (*Megaptera novaeangliae*)

**Note:** This chapter has been published as below in *Biology Letters*.


Abstract: Humpback whales (*Megaptera novaeangliae*) exhibit a variety of foraging behaviors, but neither they nor any baleen whale are known to produce broadband clicks in association with feeding, as do many odontocetes. We recorded underwater behavior of humpback whales in a northwest Atlantic feeding area using suction-cup attached, multi-sensor, acoustic tags (DTAGs). Here we describe the first recordings of click production associated with underwater lunges from baleen whales. Recordings of over 34,000 “megapclicks” from two whales indicated relatively low received levels at the tag (between 143 and 154 dB re 1 µPa pp), most energy below 2 kHz, and interclick intervals often decreasing toward the end of click trains to form a buzz. All clicks were recorded during nighttime hours. Sharp body rolls also occurred at the end of click bouts containing buzzes, suggesting feeding events. This acoustic behavior seems to form part of a nighttime feeding tactic for humpbacks, and also expands the known acoustic repertoire of baleen whales in general.
Introduction

Broadband, pulsed click sounds are produced by many marine mammals. By far the best known users of clicks are odontocetes that emit echolocation signals during foraging (Au 1993). Outside odontocete taxa, Parks et al. (2005) described broadband, short duration “gunshot” sounds from North Atlantic right whales. These sounds (20 Hz – 20 kHz, 1-4 pulses in a group, average interpulse interval 53 ms) were associated with surface active (mating) groups or produced by lone males, and appear to be used in social communication. Some transient click sounds have also been recorded in the presence of minke whales (4-7 kHz, 7 clicks/second; Beamish 1973), but without any documentation of concurrent behavior. One broadband pulse train has been reported from humpbacks (Thompson et al. 1985; 1 ms pulses and irregular interpulse interval), which was attributed to baleen rattle. However, the use of broadband clicks in association with foraging has not been documented for any baleen whale or pinniped, and arguments have been made against echolocation in both of these taxonomic groups (Au et al. 2001, Schusterman et al. 2000).

Humpback whales (*Megaptera novaeangliae*) are an acoustically active species, known to produce and use various types of sound, including complex songs on their breeding grounds (Payne and McVay 1971, Darling et al. 2006) and cooperative feeding calls in Alaska (D’Vincent et al. 1985). Foraging is confined primarily to higher latitudes, such as our study area, during the summer months. Animals feed by lunging through schools of small fish and euphausiids, often using bubbles or other tactics to corral prey (Hain et
al. 1982). However, knowledge about humpback sound production on the feeding grounds is limited, and most comes from the North Pacific (Thompson et al. 1985).

To investigate acoustic and underwater foraging behavior of North Atlantic humpback whales, we used DTAGs, which are suction-cup tags that record sound and body orientation of tagged individuals (Johnson and Tyack 2003). Since their inception, these tags have been used with a variety of cetaceans and are opening a window into marine mammal behavior under water that has historically been almost inaccessible. We deployed DTAGs on nine humpback whales in the Gulf of Maine. Of these nine, two individuals displayed a previously unreported acoustic behavior: multiple bouts of broadband clicks that we termed “megapclicks” (after the scientific name for humpback whales and to distinguish them from the acoustically different odontocete clicks). Here we describe the temporal and spectral patterns of these megapclicks and place them in the context of concurrent behaviors contained in the DTAG record.

Materials and Methods

Data collection

DTAGs (non-invasive, digital, acoustic recording tags with orientation and depth sensors; acoustic sampling rate 64 kHz; sensor sampling rate 50 Hz; Johnson and Tyack 2003) were deployed on feeding humpback whales. Five whales in 2004 and four whales in
2005 were tagged from a 7 m rigid-hulled inflatable boat (RHIB) deployed from a NOAA Research Vessel, the Nancy Foster. Tags attached via suction cups, and were placed midway between the dorsal fin and the blowhole using a 15 m cantilevered pole mounted in the bow of the RHIB (from photographic estimates, the tag on mn178a was approximately 1.5 m further forward than the tag on mn177a). Tagged whales were tracked visually and by VHF radio, with the observation vessel remaining 100 m or further from the tagged animal at all times. Tags remained attached for 21.3 (mn177a) and 23 (mn178a) hours. Both whales were visually observed lunge feeding near the surface after tagging, and both continued this behavior at least until dark.

Clicks were noticed when listening to the tag recordings and were later located automatically using custom programs in Matlab. A representative click was Hilbert-transformed, bandpass filtered (400 to 3500 Hz) and cross-correlated with similarly transformed audio files to identify bouts of click sounds. Complete bouts were then extracted manually, and aurally categorized according to the presence or absence of one or more fast-clicking “buzzes” (described below). Presence of buzzes was noted without knowledge of the whale’s depth or body orientation. Received levels were calculated after highpass filtering acoustic files at 400 Hz to reduce flow noise and downsampling to an 8 kHz sampling rate to minimize file size. Data were also visualized in GeoZui4D, which integrates time, 3D body orientation, and sound (Arsenault et al. 2004). GeoZui4D allowed detailed visualizations of whale behavior concurrent with megapclick production. (Supplementary Video 1).
All clicks described here were recorded from a position that is likely off-axis and so may give a poor estimate of the click spectrum and amplitude in the forward direction. No megapclick echoes (from which on-axis properties could have been obtained) were observed using techniques from Johnson et al. (2004). We assumed that the clicks recorded were produced by the tagged whale based on the tight relationship of clicks with body movements (see below), and also the consistency in acoustic characteristics of the clicks. If the recorded clicks were produced by other animals, they would probably have arrived from different directions, and the received levels and spectral information would be more variable across the dataset.

Results

“Megapclicks” were short pulses of broadband sound (Figure 4.1), grouped together into bouts. A total of 101 bouts (17 from mn177a and 84 from mn178a), containing 34,026 clicks, were identified from two whales on different days. The sounds had peak frequencies of approximately 800 and 1700 Hz (Figure 4.1), and received levels at the DTAG of 143 +/- 5 dB re 1 μPa pp for mn177a, and 154 +/- 5 dB re 1 μPa pp for mn178a.
Figure 4.1. (a) Waveform of a representative megapclick and (b) its normalized spectrum, as recorded by the tag attached midway between the dorsal fin and blowhole. The signal was highpass filtered at 400 Hz to remove flow noise.

**Timing**

98% of interclick intervals (ICIs) during click bouts were between 19 ms and 200 ms.

The shortest ICIs generally occurred at the end of bouts as part of an acceleration in click rate. This pattern was aurally similar to an odontocete or bat “terminal buzz” (e.g., Griffin et al. 1960, Johnson et al. 2004). We therefore used the term “buzz” to describe these sequences, recognizing that they may not serve the same purpose as those recorded from odontocetes or bats. Buzzes contained megapclicks with ICIs of 25 ms or less and had durations of at least 0.5 s. Four click bouts with one or more buzzes were noted from mn177a, and 35 from mn178a.

All megapclick bouts occurred during nighttime hours (between sunset at 20:26 and sunrise at 05:05). Megapclick bouts generally occurred near the bottom of dives, and
average whale depth at time of bout production was 38 m +/- 12 m, which was near the sea floor in this area.

*Body Orientation*

All bouts that ended in buzzes also ended with a sharp body roll by the tagged animal (in both whales, n = 39). Almost none (1 of 62) of the bouts lacking buzzes ended with such a roll (Figure 4.2). These rolls were qualitatively similar to body movements during surface feeding lunges. Mean body roll orientations at the end of megapclick bouts with buzzes were -119° +/- 2° (mn177a) and -108° +/- 22° (mn178a), and when buzzes were not present were -8° +/- 7° (mn177a) and -6° +/- 16° (mn178a) (Figure 4.2). Rolls with magnitudes and angular rates similar to those co-occurring with buzzes occurred frequently during tag attachments overall (180 performed by mn177a and 515 by mn178a), including some during nighttime hours, which is not unusual if these rolls do represent feeding events.
Discussion

Few studies of baleen whales have paired the production of specific sounds with specific behavior, especially under water. Here we have reported production of click sequences by two tagged humpback whales on a feeding ground. These "megapclicks" were produced during nighttime hours and with a pattern of decreased ICIs towards the end of the bouts. These intervals of faster clicking, or buzzes, co-occurred with rolls resembling body movements during feeding lunges. We therefore suggest a foraging function for megapclicks, and discuss several hypotheses below.

Given the superficial similarity of the production pattern of megapclicks to odontocete echolocation sounds, biosonar arises as a possible explanation. That humpback whales may echolocate has been proposed in the past, but based on song rather than clicks
(Frazer and Mercado 2000). Acoustically, megapclicks recorded here were substantially lower amplitude and frequency and longer duration than odontocete echolocation signals, even given humpbacks’ larger body size and tag placement behind the head. These are unlikely properties for signals with an echolocation function. However, the temporal pattern of many of the bouts was reminiscent of odontocete clicks in echolocation-mediated foraging, where terminal buzzes after click bouts appear to be associated with prey capture attempts (e.g., sperm whale “creaks” in Miller et al. 2004). Depending on hearing sensitivities and directionality of the humpback sound production system, sounds with these characteristics could be useful for some form of rough acoustic detection such as identifying the sea-floor or other large target.

Alternatively, megapclicks could be used to manipulate prey. Humpbacks have been shown to manipulate prey in non-acoustic ways (Hain et al. 1982), and some have hypothesized that sound itself may be a means of stunning prey (Norris and Mohl 1983, but see Benoit-Bird et al. 2006). In the case of humpbacks feeding on bottom-dwelling species (Hain et al. 1995), the whales might use the sounds to flush prey into the water column, as has been speculated for bottlenose dolphins (Nowacek 2005). However, of note is that of nine animals tagged, only these two have produced clicks, and these are also the only two whales tagged on Jeffreys Ledge, which is an area thought to be dominated by Atlantic herring (*Clupea harengus*); other tagged whales were located in the Great South Channel and on Platt’s Bank and Georges Bank, which may differ in prey composition (Chase 2002).
Many unknowns remain surrounding baleen whale hearing and sound production mechanisms, and this lack of knowledge hinders our interpretation of the function of these megapclicks. Additional recordings of baleen whale clicks and information on how the sounds appear in the far-field are needed to distinguish amongst various hypotheses for how megapclicks might be used. But despite uncertainties in function, this is the first documentation of click production by a baleen whale that is likely related to feeding. This discovery furthers our understanding of humpback whale behavior on the feeding grounds, and also greatly expands the known repertoire of sound production by baleen whales in general.
All of the work described in this dissertation was directed toward the goal of developing a better understanding of the use of non-song sound production in humpback whales. Through acoustic description and investigation of behavioral context, we can begin to make inferences on the function of these sounds. This research also lays the groundwork for more detailed study of particular sounds, which may ultimately further conservation and management efforts for this endangered species.

Summary of conclusions

1. Humpback whales produced a wide variety of non-song sounds during group activities on both the mating and feeding grounds. Center frequencies were less than 1 kHz and durations generally less than 1 s, making humpback social sounds higher and shorter than the sounds of most other baleen whales.

2. Some sounds produced were similar between the two study locations/populations, and also similar to published sounds from the Southern Hemisphere humpbacks on their migration route, indicating a cosmopolitan and flexible usage of sound across the species.

3. Sounds recorded from the feeding ground population were louder and more frequent than on the breeding ground, suggesting a heavier reliance on non-song sound during foraging activities than during competition on the breeding grounds. This could also
mean that social sounds on the breeding ground are directed at conspecifics at much
closer range than are song or feeding group sounds.

4. The loud and omnipresent song chorusing on the breeding ground may be a reason for
depressed social sound production in competitive groups, and may be an example of
natural masking.

5. More sounds were recorded during periods when the tagged whales were close to the
surface, and more likely to be socializing than feeding. On the feeding ground, sounds
were also frequent during crepuscular periods and the ascent/descent of dives, and thus
may be related to some type of conspecific interaction related to foraging.

6. Megapclicks are a new type of sound not previously recorded from baleen whales, and
are reminiscent of the click trains heard during odontocete echolocation.

7. Megapclicks are used during foraging (likely on herring), and are paired with sharp
rolls along the bottom that are likely feeding lunges.

New terminology?

Though many of the sounds recorded here seem to have a social context, in some cases
sounds seem more closely related to feeding than socializing (such as megapclicks on the
feeding ground). Some sounds may also be produced when no conspecifics are nearby.
Therefore, it no longer seems appropriate to group all non-song sounds under the singular
label “social sounds”. I propose to drop the use of the descriptive phrase “social sounds”
and to refer to all of these sounds as “non-song sounds”. An even more descriptive, and
yet still accurate naming scheme might create categories such as “internally produced
non-song sounds” and “externally produced non-song sounds”, while retaining sound-
specific names such as “wop” and “megapclick”, to more specifically describe the species’ acoustic repertoire.

**Future work**

The behavioral context of externally-produced sounds (from surface activity, or repetitive body movements under water such as feeding actions) was not considered in this study, but may also give great insight into the current activities of humpback whales. More comprehensive description of the context of individual sound types (similar to the work done with megapclicks) such as wops and moans, is also needed. Further analysis is possible with more detailed investigation of body movements, including changes in acceleration and geographic orientation, the data for which are included in the suite of data from the DTAG.

On the feeding grounds, it is also important to confirm and understand how the whales’ behavior relates to the actual prey field. Combination of tagging studies with fine-scale prey mapping using scientific echosounders would produce a more complete picture of the underwater environment through which the whales must navigate to find prey. Using visualization techniques such as crittercam tags (Marshall 1998), which contain video recorders, may also elucidate how the whales interact with the prey during foraging. Tagging multiple whales in a group and/or towing a hydrophone array next to a group containing tagged whales would also help us understand how the whales interact, which animals are actively producing sound, and how the recording of the sound produced by an animal is affected by the tag placement and animal’s body.
Lastly, it would be helpful to expand this research to include other whale populations. How do the sounds produced by the whales in Hawaiian waters compare to those of these same whales when they are feeding in Alaska? Are similar sounds produced in Southern Hemisphere breeding and feeding grounds? How does humpback acoustic behavior compare to other baleen whale species, and can we extrapolate to species that are more difficult to study?

But most importantly, why does this matter? Can we use what we have learned to help protect whale populations? In addition to determining simple presence of humpback whales using remote autonomous recorders, an aim should be to identify the activities of the whales by the types of sounds they are producing. High rates of production of sounds known to occur concurrently with feeding or competitive activities could indicate a geographic location used for mating, or one with large concentrations of prey, and thus an area around which more stringent protection measures (such as approach limits or vessel speed restrictions) should be implemented.
APPENDIX

Methodology: Equipment descriptions and Field protocols

A.1 Why tags?

Because social sounds have been largely recorded from humpback whales that are engaged in highly mobile activities, such as associating in competitive groups (Silber 1986) and actively foraging on mobile prey like schooling fish (Thompson et al. 1986), the technique of recording from a single hydrophone from a stationary vessel would not have been productive. Bottom-mounted or free-floating autonomous recorders have the same limitations: as soniferous whales pass by, these types of equipment record only a snapshot of the sounds produced, and that without any concurrent behavioral information.

A towed hydrophone array, though useful for localization for acoustic measurements (and used for a portion of the research described here in Chapter 2), does not record body orientation or dive behavior as the sounds are being recorded. For these reasons, we chose non-invasive acoustic tags as the methodology most appropriate for our research goals.

A.2 Tag descriptions:

Research in waters off the northeastern United States utilized a digital bioacoustic tag called the DTAG (Figure A.1), developed by Mark Johnson and Peter Tyack at Woods Hole Oceanographic Institution (Johnson and Tyack 2003). With a user-defined
sampling rate ranging between 24 and 96 kHz, the DTAGs recorded whale sounds over a large bandwidth (up to 48 kHz), allowing a more complete description of social sounds than had been accomplished to this point. In addition, behavioral sensors on the tags including accelerometers and magnetometers recorded body orientation (pitch, roll, and heading) of the whale as it swam, and a pressure sensor recorded depth.

Research in Hawai’i utilized both DTAGs and a digital bioacoustic tag called the Bioacoustic probe (Bprobe, Figure A.2), developed by Bill Burgess et al. (1998). The tag combined a hydrophone with a depth sensor and other behavioral sensors in order to measure changes in sound production and dive behavior of a free-ranging subject. The electronic tag was a cylinder measuring 3.2 cm x 19.3 cm, and weighing 200 g in air, without flotation, attachment, or recovery gear.

Attachment of the tags to the whales was by suction cup, and the attachment, flotation, and recovery package for the Bprobes were custom-designed. Location of tag attachment was generally as close to the dorsal midline as possible, between the blowhole and the
dorsal fin (Figure A.3). This maximized durability of the attachment by choosing as large and as flat a surface as possible. Also, the tags contain a VHF transmitter that emits a continuous radio signal throughout the deployment. VHF transmissions are line of sight, and small increases in height of transmitter or receiver can result in much longer transmission distances. As such, the best location for radio tracking of the animal is also to have the tag close to the dorsal fin on the center back. This portion of the animal is most likely to be out of the water and at the greatest height whenever the whale takes a breath, and thus delivered the best VHF signal for assistance tracking the tag while it is still on the animal.

A.3. Field Protocols

All research was conducted under required Federal and State permits, which contained approach limits and imposed strict requirements on the amount and type of research conducted. Reports were submitted each year detailing the activities that took place and the number of animals approached. Tagging was conducted from small boats, and tags were attached using a long aluminum or carbon-fiber poles from the bow of the tagging vessel (Figure A.3). Drivers of tag boats each
had over fifteen years of experience driving small boats around and in close proximity to humpback whales, either for tagging or disentanglement efforts, and were well-versed in the safety considerations of close work with these large animals in various behavioral states.

In Hawai‘i (Figure A.4), we launched from Maalaea harbor each day and returned each evening, because NOAA regulations did not allow the small boats to stay out overnight. We used one of two boats: a 22’ SeaCat (Figure A.5) that belonged to the Hawaiian Islands Humpback Whale National Marine Sanctuary (HIHWNMS); or a 36’ AMBAR named the Hihimanu (Figure A.6) that also belonged to HIHWNMS. Tags were attached via a 27 or 30 foot handheld pole, with the tagger standing on the bow of the vessel (Figures A.3 and A.5). The humpback whale tagging and research permit was issued to Dr. Whitlow W.L. Au, federal permit #1000-1617 and state permits #SH2007-04, SH2008-09, and SH2009-09, IACUC protocol #04-038-2.
Figure A.4. Study area in the Hawaiian Islands: Research took place in the shallow, protected waters south of Maui in the Hawaiian Islands Humpback Whale National Marine Sanctuary (HIHWNMS).

Figure A.5. HIHWNMS R/V Seacat. The 30’ aluminum tagging pole can be seen in this figure.

Figure A.6. HIHWNMS R/V Hihimanu
For the work in the northwest Atlantic, research was based off a NOAA Research Vessel, the *R/V Nancy Foster*, in collaboration with the Stellwagen Bank National Marine Sanctuary (SBNMS, Figure A.7) and several other cooperating institutions (see acknowledgements). Small boats (24’) were launched from the mother ship each day, and tags were attached via a 46 foot cantilevered pole, with the tagger standing midship in the vessel. The federal permit for this work was #981-1707 (SBNMS and Woods Hole Oceanographic Institution).

The tags were non-invasive in that they attached to the whale by suction cup, and remained attached only for a period of several hours. The tags had to be retrieved to download the data. Behavioral responses of individuals to tagging were observed and recorded, and disturbance to animals was minimized by approaching at slow speeds from behind or beside the group. In most cases, reactions were classified as “mild” (fast dive or mild tail flick) or “none”. Less than 5% of all tagging attempts were categorized as “moderate” (stronger tail flick) and none were categorized

Figure A.7. Study area off the Northeastern United States: Stellwagen Bank National Marine Sanctuary (SBNMS). Map courtesy Office of National Marine Sanctuaries.
as “severe” (immediate surface activity or other strong physical reaction). Tagged animals were followed by boat at distances averaging 100 m to record surface behavior and to facilitate tag retrieval upon release.

In 2009, a 3-element hydrophone array (Figure A.8) was towed beside traveling competitive groups of humpback whales in Hawai‘i. The array was kept between 30 and 50 m from the group of whales, and we attempted to match the speed and direction of the group. These recordings were made to ground truth tag recordings with an alternate methodology, and to compensate for the high-pass filter on the acoustic recording system on the DTAGs. The array recordings also allowed localization of the individuals producing specific sounds, which made possible the calculation of source levels of those sounds.

Figure A.8. Three-element towed hydrophone array used in 2009 fieldwork. The large cylindrical apparatus hanging at the right end of the array is a weighted towfish that sank the array approximately 20 feet below the surface and facilitated its relatively flat orientation during towing.
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