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Impacts of ship noise on the nighttime foraging behaviors of the North Atlantic humpback whale (Megaptera novaeangliae)

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ABSTRACT

Hannah Blair

IMPACTS OF SHIP NOISE ON THE NIGHTTIME FORAGING BEHAVIORS OF THE NORTH ATLANTIC HUMPBACK WHALE (*MEGAPTERA NOVAEANGLIAE*)

The humpback whale (*Megaptera novaeangliae*) is an endangered baleen whale species with a cosmopolitan distribution. The coastal habitat of this species result in significant exposure to anthropogenic noise from human activities. Previous research in the well-studied Pacific populations has demonstrated changes in calling behavior in response to noise, but noise impacts on other critical behaviors such as foraging have not yet been investigated. This study examines the impacts of ship noise on the nighttime bottom foraging behavior of humpback whales in the North Atlantic – a region with substantial human activity including high levels of noise from commercial shipping traffic. Data were collected from 2006 to 2009 in the Stellwagen Bank National Marine Sanctuary in the southern Gulf of Maine during June and July. Data included underwater kinematic movement and acoustic recordings of surrounding environmental noise collected using an archival tag attached to nine individual whales. Here I use series of linear mixed models to assess the effects of ship noise on eight metrics of nighttime feeding behaviors. Fixed effects included the presence versus absence of ship noise, received level of ship noise, and the before, during or after ship noise exposure period. These variables had significant influence on three metrics: dive descent rate, ascent rate, and number of rolls indicative of feeding events. Descent rate decreased as noise level increased, while ascent rate was significantly faster in the during or after period when compared to the before period. The number of rolls significantly increased in the after exposure period, but at the greatest received levels, feeding rolls were completely absent during dives. These findings indicate that humpback whales on Stellwagen Bank show small, but significant, changes in foraging activity when exposed to ship noise. This study supports the hypothesis that environmental noise has an impact on the nighttime foraging activities of this species.

Impacts of ship noise on the nighttime foraging behaviors of the North Atlantic humpback whale (*Megaptera novaeangliae*)

by

Hannah Beth Blair

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INTRODUCTION

Anthropogenic Noise

A rapidly expanding human population has resulted in increasingly fewer places on earth that remain completely untouched by human impacts (Vitousek et al. 1997). Increasing quantities of resources are required to support this population, including more land for food production, more fish harvested, more raw materials for making products, and rapidly increasing habitat destruction and degradation (Naylor et al. 2000; Imhoff et al. 2004). A growing human population also means more waste is produced, more chemical runoff enters the environment, and more carbon dioxide is released by the burning of fossil fuels (Halpern et al. 2008). While many of these effects are readily observable, some more cryptic effects require further investigation. Human disturbance may be perceived as a source of predation risk by animals, with similar indirect implications for fitness and population dynamics (Frid & Dill 2002). Another such less obvious, but potentially serious, source of human disturbance is noise pollution, commonly referred to as anthropogenic noise.

Anthropogenic noise, sound generated by humans and human activity, has become increasingly widespread throughout the world in both terrestrial and marine environments (Slabbekoorn et al. 2010; Francis & Barber 2013). This noise may be chronic or acute, and each has different implications for the environment (Hildebrand 2004). Chronic anthropogenic noise is typically low in pitch (<1 kHz), and is generated from passing automobile and airplane traffic, from shipping vessel engines, and from multiple sources within urban centers (Barber et al. 2010). Acute sources are high-intensity, including pile driving or explosions resulting from operations such as seismic exploration (Hildebrand 2004).

Noise pollution has the potential to substantially impact animal species. Studies have been conducted on a variety of effects, investigating influences of noise on movement, stress levels, and behavior (Blickley & Patricelli 2010). Even species that do not rely on sound for communication can be impacted either directly or indirectly through noise pollution. For example, Kunc et al. (2014) found that common cuttlefish flashed colors more frequently during ship noise playbacks. Urban centers have been targeted by multiple studies, as the noise generated by vehicles, machinery, and other noise associated with urban development is an obvious point source (Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008). However, railways and highways extend from concentrated urban areas, bringing with them the noise of trains and vehicles (Bee & Swanson 2007). Even areas that at first appear pristine often have planes flying overhead or, in the case of marine systems, ship traffic generating noise (Frisk 2012).

Animal Responses to Anthropogenic Noise

Movement

Anthropogenic noise may lead to changes in movement and migration patterns, or in extreme cases, to complete abandonment of certain habitats. Kelly et al. (1988) found that ringed seals (*Phoca hispida*) abandoned breathing holes and lairs at higher than normal rates when exposed to anthropogenic noise. Abandonment of these resources may increase their risk of predation and likely decreases their foraging ability. Some studies of fish responses to anthropogenic noise have demonstrated changes in small-scale movements; for example, ship noise appears to disrupt schooling behavior in bluefin tuna (*Thunnus thynnus*) (Sarà et al. 2007).

Noise pollution may effect large-scale movements as well. A study by Francis et al. (2011) considered occupancy of two species of flycatchers in urban habitats. While one species increased the frequency and amplitude of its calls, the habitat occupancy of the other significantly declined in response to an increase in background noise amplitude, demonstrating a higher sensitivity to anthropogenic noise in the second species. In some instances, anthropogenic noise may cause species to avoid or abandon critical habitats such as breeding grounds, as observed in the migratory gray whale (*Eschrichtius robustus*) by Gard (1974). The habitat desertion demonstrated by these studies is troubling, as it indicates that noise pollution can degrade a habitat to the point that it becomes unsuitable for the animal.

Stress Responses

In addition to the variety of documented behavioral changes, physiological changes in noise exposure have been observed in a variety of species. Wright et al. (2007) compiled a review of how the subtle aspects and annoyances of anthropogenic noise that are difficult to study may act as secondary stressors. They concluded that exposure to noise pollution could cause noticeable physiological changes, suggesting that even short-term exposure could result in long-term consequences.

A study of North Atlantic right whales in the Bay of Fundy tested levels of stress-related fecal hormone metabolites in whale feces during a period of decreased vessel traffic after terrorist attacks on 9/11 in the United States compared to levels following the reinstatement of the heavy ship traffic noise that is normal for the Bay of Fundy area (Rolland et al. 2012). They found that the decrease in vessel noise corresponded to a decrease in fecal hormone metabolites, suggesting that noise pollution does increase stress in North Atlantic right whales. Similarly, increases in glucocorticoid stress hormones have been observed in anurans (wood frogs, *Lithobates sylvaticus*) and galliform birds (greater sage grouse, *Centrocercus urophasianus*) in the presence of noise (Tennessen et al. 2014; Blickley et al. 2012). Romano et al. (2004) found that blood levels of adrenaline hormones increased in odontocetes exposed to intense noise. Stress on these and other animals from anthropogenic noise could affect immune system function or the conservation of energy, among other physiological responses to stress, and thus could have significant impacts on survival.

Communication

A major focus of noise impact studies is to examine the effects of noise on animal communication systems – in particular, the effects on acoustic communication (Brumm & Slabbekoorn 2005). Low-frequency anthropogenic noise may mask all or part of acoustic signals, increasing the level of background noise and inhibiting the ability of conspecifics to receive them (Barber et al. 2010). This decrease in the signal-to-noise ratio, or the level of the signal strength compared to the level of background noise, prompted researchers to investigate modifications of acoustic signals in the presence of anthropogenic noise (Brumm & Slabbekoorn 2005). These studies consist of both observational studies of responses to anthropogenic noise in the wild and through controlled experimental exposure of animals through playbacks (Morley et al. 2014).

In response to noise exposure, some species adjust signal frequency components in order to emphasize the part of the vocalization that is outside of the masking noise frequency band. These responses have been seen in a wide range of organisms, ranging from invertebrates, to avian and mammalian species. In increased traffic noise, *Chorthippus biguttulus* grasshoppers increased the peak frequency of their calls (Lampe et al. 2012). Similarly, several species of oscine bird including great tits (*Parus major*), song sparrows (*Melospiza melodia*), and house finches (*Carpodacus mexicanus*) have been observed to increase the minimum frequency of their songs in response to low-frequency urban noise (Slabbekoorn & Peet 2003; Wood & Yezerinac 2006; Fernández-Juricic et al. 2005). These same frequency shifts are observed in mammals including bats (Brazilian free-tailed bat, *Tadarida brasiliensis*), whales (North Atlantic right whale, *Eubalaena glacialis*), and humans (Gillam & McCracken 2007; Parks et al. 2007; Lombard 1911).

Several species have been observed to maintain their signal-to-noise ratio in increased background noise by raising the amplitude or intensity of their calls (Zollinger & Brumm 2011). This response, first described as the Lombard effect in humans, has been observed in more than sixteen species of mammals and birds (Lombard 1911; Brumm & Zollinger 2011). For example, in response to broadcasts of increasing intensity levels of white noise, male nightingales (*Luscinia megarhynchos*) increased the sound level of their songs (Brumm & Todt 2002). Under similar playback conditions captive common marmosets (*Callithrix jacchus*) increased the intensity level of their calls in correlation with the increasing intensity of the broadcasted white noise (Brumm et al. 2004). This amplitude modulation has also been observed in high-frequency echolocation pulses. The Brazilian free-tailed bat (*Tadarida brasiliensis*) increased pulse amplitude with increased levels of broadband and band-limited noise playbacks, which respectively completely masked or partially masked the two loudest harmonics of the pulses (Tressler & Smotherman 2009). Though a few investigations have tested the responses of invertebrate groups, as of now the Lombard effect has only been observed in mammals and birds, with limited evidence in anurans (Love & Bee 2010; Brumm & Zollinger 2011; Cunnington & Fahrig 2010).

Other observed vocal modifications include a change in the duration of signals or in the timing of delivery in the presence of anthropogenic noise. Kaiser and Hammers (2009) examined how male Amazonian treefrogs (*Dendropsophus triangulum*) reacted to broadcasted playbacks of motorcycle noise and music, and found that their call rates were almost doubled in response to both. However, other anuran species decrease the rate of their calls in anthropogenic noise playbacks (Sun & Narins 2005). In addition to an increase in call amplitude, Brumm et al. (2004) found that the common marmosets also increased the duration of each syllable of their calls in correlation with the increasing intensity of the broadcasted white noise. Different kinds of temporal changes may be observed in the same species, possibly depending on the type of vocalization or the type of noise. Male humpback whales (*Megaptera novaeangliae*) lengthen the duration of their songs when exposed to playbacks of low-frequency sonar (Miller et al. 2000). In contrast, humpback whales off of southeastern Alaska increased the length of time between individual feeding vocalizations in the presence of vessel noise (Hanser 2009).

Though these three methods of vocal modifications in noise have been presented independently of each other it is common for two or more of these responses to co-occur, as in Brumm et al. (2004). Beluga whales (*Delphinapterus leucas*) displayed both a reduced calling rate and increased vocalization mean frequency as vessels approach, with the more-persistent response seen to a large ferry than to smaller motorboats (Lesage et al. 1999). Scheifele et al. (2005) found that beluga whales also demonstrate the Lombard effect by varying the intensity of their calls in the presence of anthropogenic noise. North Atlantic right whales also exhibit both frequency and amplitude modification, vocalizing at a greater intensity and higher average fundamental frequency in periods of increased environmental noise as well as lowering the call rate (Parks et al. 2007; Parks et al. 2011).

All animal species have evolved in environments with background noise from natural sources, including wind, precipitation, and/or sounds from other species (Hildebrand 2004).

However, some of these environments are noisier than others. Animals living in these environments are adapted to the propagation conditions and natural background noise of their habitats, and are more likely to exhibit flexibility to some degree of increased environmental noise (Wiley & Richards 1982). For example, in their study comparing the frequencies of urban and nonurban congeneric songbird species, Hu & Cardoso (2009) suggested that species that naturally sing at higher minimum frequencies are pre-adapted to live in urban environments. In addition, low frequency sound may travel for large distances in the ocean, and many marine animals studied such as cetaceans demonstrate acoustic plasticity, likely as an adaptation for noisy marine habitats (Tyack & Clark 2000).

While these species may possess adaptive advantages for dealing with some noise exposure, these modifications may not be sufficient to avoid masking in all situations or in higher levels of noise. In some cases, the costs of modifications may begin to outweigh the benefits (Read et al. 2014). In addition, not all species are able to respond to the challenges of communicating in high-noise areas. Lengagne (2008) found that male European tree frogs (*Hyla arborea*) decreased their calling activity in traffic noise with no indication of other vocal plasticity, which has implications for mate choice in this species. This may also have an impact on individuals meant to receive signals - for example, females trying to locate or evaluate advertising males. Multiple studies have investigated this issue with insects: traffic noise playbacks limited female field crickets' (*Gryllus bimaculatus*) ability to locate calling males, possibly lowering the reproductive potential of the species (Schmidt et al. 2014). Similarly, responses of *Drosophila montana* females to male courtship songs decreased when exposed to high levels of environmental noise in the same frequency band as the songs (Samarra et al.

2009). These studies demonstrate a possible reason for decreased reproductive success for species that utilize communication to determine mate choice.

Foraging Behavior

Fewer studies have investigated changes in foraging behavior where foraging efforts were the focus. A number of species, particularly bats and odontocetes, utilize active acoustics to localize prey using echolocation (Barber et al. 2010). In a study investigating variation in call structure of Brazilian free-tailed bats (*Tadarida brasiliensis*), Gillam and McCracken (2007) found that they increased the frequency of their echolocation calls in response to other high-frequency environmental sounds. There is some evidence that sperm whales (*Physeter macrocephalus*) decrease the rate of foraging events when exposed to airgun noise, and they may delay foraging dives altogether in the presence of intense anthropogenic noise (Miller et al. 2009).

Other species use passive listening for prey cues, low-intensity adventitious noise produced by movement (Barber et al. 2010). An experiment studying the greater mouse-eared bat (*Myotis myotis*) demonstrated that bats avoid excessive environmental noise and that areas near highways are less suitable for bat foraging (Schaub et al. 2008). Similarly, Mcclure et al. (2013) found a significant decline in bird abundance near roadsides that was directly attributed to traffic noise. These analyses suggest that intense and high-frequency noise pollution, in addition to low-frequency noise, could be detrimental to the foraging efficiency of many species.

Further concerns related to foraging relate to impacts on predator-prey dynamics. Chan et al. (2010) tested whether noise pollution could increase a species' risk of predation. They allowed a simulated predator to approach Caribbean hermit crabs (*Coenobita clypeatus*) in silence and under the influence of boat motor noise, and found that the predator could get significantly closer to the crabs during the broadcast of boat noise. The authors suggested that the noise could be masking the sound of the predator's approach, or the noise distracted the crab.

Less research has been done on the impacts of noise on foraging behavior in marine environments. Playbacks of industrial noise caused temporary interruptions to feeding in both gray whales and orcas (*Orcinus orca*), suggesting an increased energy expenditure (Malme et al. 1988; Williams et al. 2006). Close ship passage or ship noise may also disrupt feeding events in beaked whales and result in decreased foraging time in blue whales (*Balaenoptera musculus*) (Soto et al. 2006; McKenna 2011). However, other investigations of foraging blue whales and fin whales (*Balaenoptera physalus*) found no obvious behavioral responses to loud low-frequency sound (Croll et al. 2001). These studies used surface behaviors to judge behavioral transitional states; however, the majority of marine mammal foraging occurs beneath the ocean's surface. One species of marine mammal, the humpback whale, has feeding grounds located in highly urbanized coastal water. However, no study has been published investigating how noise may impact the foraging behavior of this species, despite evidence of modifications to vocal behaviors. Therefore this thesis will investigate how noise affects the foraging behavior of humpback whales, both at and below the surface.

Humpback Whales

The humpback whale is a baleen whale species with a cosmopolitan distribution (Clapham & Mead 1999). This species travels great distances along coastlines, with many populations moving from temperate or polar summer feeding grounds to tropical breeding grounds in the winter (Clapham & Mead 1999). Humpback whales exhibit a variety of vocalizations, including long, complex songs and a repertoire of non-song vocalizations (Clark & Clapham 2004). Certain populations, including the whales inhabiting the North Atlantic, appear to be genetically distinct from other humpbacks whales (Jackson et al. 2014).

Despite near extermination from commercial whaling, humpback whale populations have shown a remarkable recovery in the last two to three decades (Clapham et al. 1999; Perry et al. 1999). However, this species still faces conservation challenges in the form of habitat degradation due to human activities. These include collisions with vessels and entanglement with fishing gear (Wiley et al. 1995; Robbins & Mattila 2001; Cassoff et al. 2011). The proximity to land also exposes humpback whales to anthropogenic noise from commercial shipping, seismic exploration, and naval exercises (Clapham et al. 1999; Hatch & Wright 2007; Todd et al. 1996).

Humpback whales have a relatively diverse diet compared to other mysticete whales, which includes invertebrates and various sizes of schooling bait fish (Laerm & Wenzel 1997; Witteveen et al. 2012). Humpback whales show equally diverse foraging techniques, with variation based on prey type, the environment, the population, or time of day (Jurasz & Jurasz 1979; Friedlaender et al. 2009). Within the Gulf of Maine, humpback whales show a variety of foraging techniques (Hain et al. 1995; Friedlaender et al. 2009; Allen et al. 2013). The first is lunge feeding, during which whales energetically lunge through prey aggregations and engulf large volumes of water and prey before pushing water out through baleen plates (Stimpert et al. 2007; Ware et al. 2011). Vocalizations termed “megapclicks” were observed to be associated with nighttime feeding lunges in the Gulf of Maine population, with a possible biosonar or prey manipulation function (Stimpert et al. 2007). Two additional foraging behaviors are frequently associated with lunge feeding. In bubble net or bubble cloud feeding, whales expel air underwater to produce bubbles that surround fish schools before lunging through them (Hain et al. 1982; Wiley et al. 2011). Lobtail feeding, in which whales slap the surface of the water with their flukes, may also produce a corralling effect (Allen et al. 2013).

Another foraging method observed in Gulf of Maine humpback whales is bottom side-roll feeding. Hain et al. (1995) presented the first evidence that humpback whales may be feeding on sand lance (*Ammodytes* sp.) on the sea floor, based on scuffing along the jaws of some individuals and co-occurring sand lance distributions in the Stellwagen Bank National Marine Sanctuary. This behavior is the primary feeding technique used during nighttime feeding in this population, though it has been observed during the day as well (Ware et al. 2006). When bottom feeding, the whale descends to the sea floor, where it swims along the bottom, occasionally performing lateral body rolls thought to be feeding events on sand lance in or just above the substrate (Ware et al. 2014). There is some evidence that this behavior might be cooperative, as pairs of whales often feed together (Parks et al. 2014; Ware et al. 2014).

The vocalizations associated with foraging vary among populations and depending upon foraging strategy. Some are specific to feeding techniques, discussed above. Other documented calls include moans, grunts, and the low-frequency pulse trains linked to bubble net feeding (Thompson et al. 1986). Non-vocalized sounds such as surface generated impacts and blowhole-associated sounds have also been observed on feeding grounds (Hanser 2009). While songs have been recorded on feeding grounds, it is the non-song calls produced in these areas that are typically associated with foraging (Clark & Clapham 2004).

Hypothesis

In the oceans, ship noise is a chief contributor to low-frequency anthropogenic noise (Hildebrand 2004). Little research on humpback whale responses to anthropogenic noise has been conducted in the North Atlantic Ocean. The region around the North American eastern seaboard is predicted to be increasingly impacted by human activity, and this region has some of the densest concentrations of shipping lanes in the world (Halpern et al. 2008). This immense level of vessel traffic in turn generates a large amount of noise. I hypothesize that humpback whales alter their foraging behavior in the presence of ship noise. I predict that whales will engage in fewer feeding events and shorten dive times in the presence of noise. The goal of this research is to compare feeding behaviors during periods of no noise against those in periods of ship noise. The conclusions from this study will provide information on the potential for plasticity in humpback whale foraging behavior in response to noise and implications of ship noise on the foraging efficiency of this species.

MATERIALS AND METHODS

Field Data Collection

Field data were collected in the southern Gulf of Maine in the vicinity of the Gerry E. Studds Stellwagen Bank National Marine Sanctuary off the coast of Massachusetts during June and July from 2006 to 2010 and 2012 and April 2009 and 2010. The data were collected using archival digital acoustic recording tags, DTAGS (Johnson & Tyack 2003), to simultaneously record kinematic behavior of the whale and the acoustic environment. These archival tags contained accelerometers, a three-axis magnetometer to record pitch, roll, and heading, and a pressure sensor sampled at 50 Hz. The tags also contained a hydrophone to continuously record acoustic data (sampling rate 96 kHz, system sensitivity -171 dB re 1 μPa (Stimpert et al. 2011)). The tags included a high pass filter at 400 Hz to minimize the contribution of flow noise to the recording. The tags also contained a VHF radio beacon to allow for tracking of the tagged whale and for tag recovery.

Tags were placed high on the back of animals, anterior to the dorsal fin, using either a 15 m bow-mounted cantilevered pole from a 7 m rigid-hulled inflatable boat (RHIB) (2006-2010) or a 7 m handheld pole from a 4m RHIB (2010) (Figure 1). Tags were attached via suction cups and deployed for up to 24 hours. Following placement of the tag during the daytime hours, behavioral focal follows of the tagged animal were conducted from RHIBs at a distance of 100-400 m. At night, support vessels (the 70 m R/V Nancy Foster (2006-2009) or 21 m R/V Stellwagen (2009-2010) followed from a greater distance, maintaining proximity by the tag's VHF signal. Following the recovery of the tag, the data were downloaded for calibration and analysis (Johnson & Tyack 2003).

Figure 1: A handheld 7 m carbon fiber pole is used to place the DTAG onto a humpback whale's back. (Photo credit: A. Stimpert, NOAA Fisheries Permit #14245)

Data Analysis

Before-During-After Impact Analysis

The statistical design for this experiment was a before-during-after (BDA) analysis of the impact of ship noise on the foraging behaviors of humpback whales. This design uses a pre-exposure or "before" period as a control, where the natural behavioral state is assumed to be undisturbed. Any significant effect of the disturbance evident during the exposure period or post-exposure may then be tested for (Underwood 1992; Smith 2002). This method is commonly used in environmental studies examining possibly altered behavioral states caused by human disturbances (Miller et al. 2000; Lemon et al. 2006; Lengagne 2008).

Tag Record Selection

During daytime hours ship noise was almost continuously detected on the tags, resulting in few periods with no ship noise to act as a control. If two or more ship passages occurred very close to each other in time or overlapped, the behaviors occurring during a ship noise event could not be accurately compared to behaviors occurring in a non-ship noise period. This made a BDA analysis of impact impossible during the daytime hours, therefore, data were restricted to nighttime hours. Tag recordings selected for analysis contained data occurring between sunset and sunrise (approximately 2015-0515 hr in June and July and 1730-0600 hr in April, www.almanac.com). Selected records also included five or more feeding dives by the tagged whale and the passage of at least one large ship. For the purposes of this study, dives were defined as dives deeper than 10 m showing clear behaviors associated with bottom feeding (Ware et al. 2014).

Dive Measurements

Whale behaviors recorded by DTAG sensors were visualized and quantified using the software application TrackPlot (Ware et al. 2006). TrackPlot utilizes the heading, pitch, roll, depth, and time data from the DTAG to create a dead reckoned pseudotrack of the whale’s three-dimensional path (Ware et al. 2006). This pseudotrack is represented by a ribbon marked by a chevron pattern on the dorsal surface to indicate travel direction and orientation (Figure 2A). A side roll exceeding 40 degrees from a vertical orientation of the dorsal ridge is signified by the yellow coloration of the ribbon (Figure 2B).

Analysis of nighttime periods restricted analysis to bottom feeding, as humpback whales forage exclusively on the bottom at night in this habitat (Friedlaender et al. 2009). Bottom feeding consists of highly stereotyped bottom side roll dives, which allow for intra and inter-individual comparison of dive parameters (Ware et al. 2014). Using TrackPlot, I extracted eight dive behavior measurements: the total duration of each dive from surface to surface (s), the bottom time of each dive defined as the time between the end of the descent and the beginning of the ascent (s), the rate of descent and ascent (m/s), the maximum depth of each dive (m), the number of bottom side roll events, the time between dives (s), and the surface time immediately following each dive (s) (Figure 2B). Each of these metrics was tested to determine any change in behavior correlated with the presence and intensity of vessel noise. Depth profiles alone were also examined in MATLAB R2013a (MathWorks 2013).

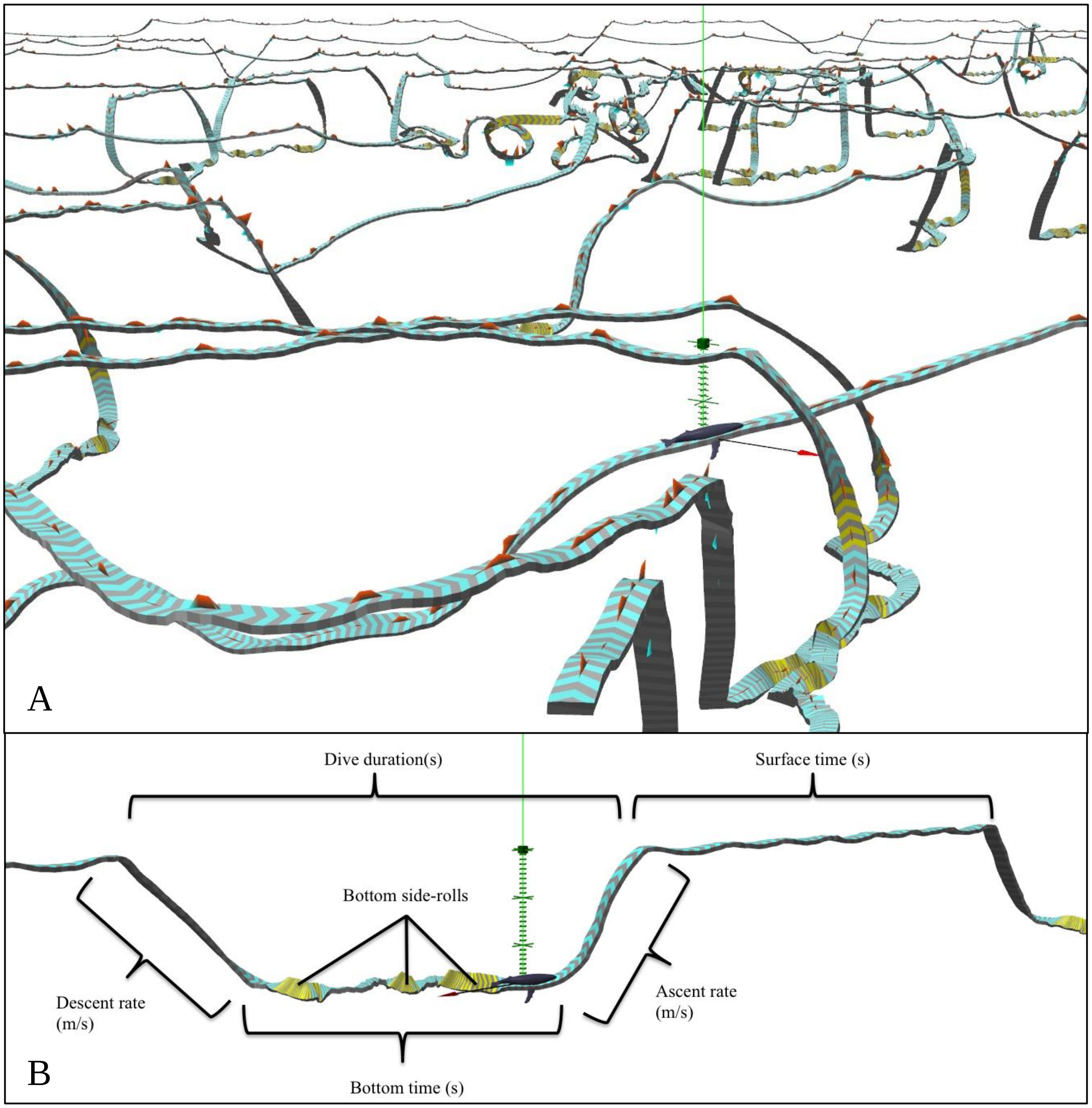

Figure 2: A) Still image from TrackPlot displaying part of the ribbon track for animal mn06_192a. B) A TrackPlot still demonstrating the dive measurements for one bottom-feeding dive for animal mn08_182a.

Vessel Noise

Ship presence was determined by the detection of vessel noise in DTAG hydrophone recordings (Figure 3). All recordings were decimated to 16 kHz in MATLAB R2013a to standardize sampling rates and for ease of analysis. Files were viewed in and received level (RL) was measured using RavenPro 1.5 (Bioacoustics Research Program 2014). Time periods with noise of a ship detected were defined as the "during" exposure period. Time periods of the same duration as the "during" period immediately preceding and following the "during" period were defined as the "before" and "after" exposure periods respectively. Sound pressure level (SPL) measurements to quantify the absolute RL of ship noise on each tag record were taken for a one-minute period. RL was measured in the 2-3 kHz frequency band during the bottom time periods of each dive to minimize flow noise. The one-minute period occurred directly following the end of the whale's descent or as soon afterward as feasible, to minimize the interference of acoustic energy from whale vocalizations and sand grating caused by the rolling behaviors.

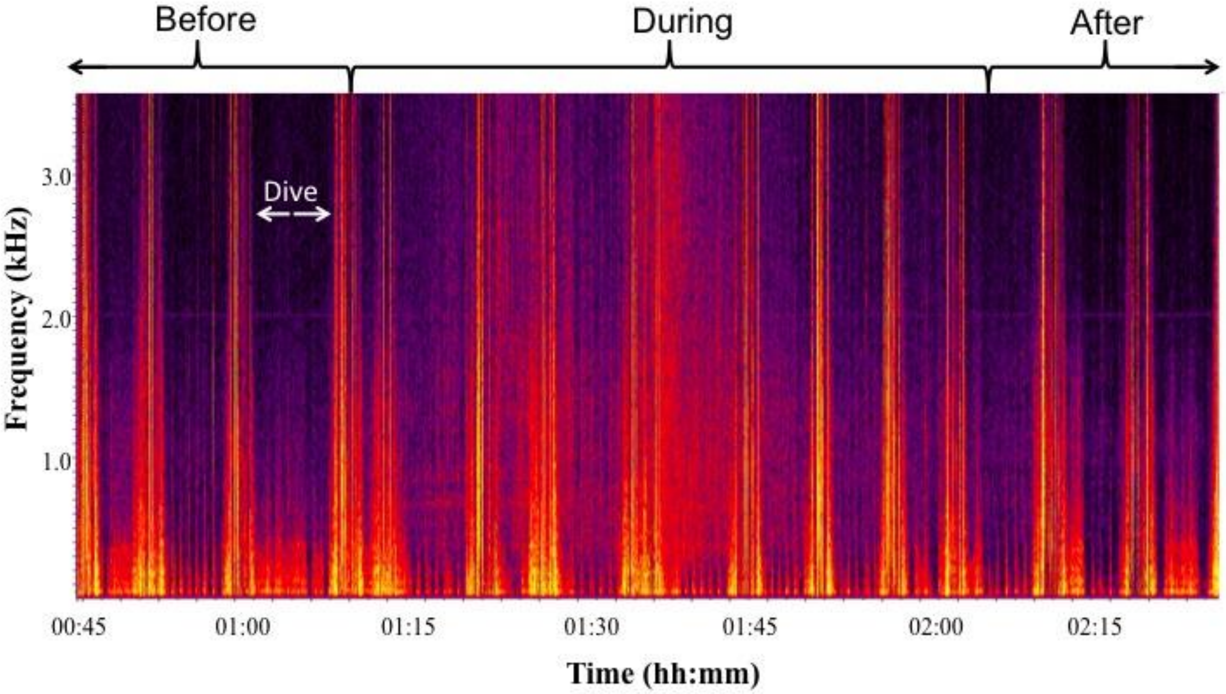

Figure 3: Spectrogram from RavenPro 1.5 displaying a ship noise period. Yellow and orange indicates more acoustic energy; purple indicates less acoustic energy. The yellow-orange vertical lines are indicative of surfacings, while areas between surfacings are dives. The large orange area indicates a ship passage, marked as the "During" exposure period.

Statistical Analysis

All statistical analyses were performed in R version 2.15.3 (R Core Team 2013). The dependent variable data were square root transformed to achieve a normal or near-normal distribution of model residuals. A series of linear mixed-effects models were applied to the data using the *lmer* function in the *lme4* package. The full model included three fixed effects with two interactions:

$$Y = \beta_0 + \beta_1 SN*RL + \beta_2 BDA*RL + RE_{subject} + RE_{year}$$

where the dependent variable (Y) was the dive measurement, SN was a binomial factor representing in ship noise exposure period (1) or in a period of no ship noise (0), RL was received level measured in dB re 1 μPa, and BDA is a factor representing the before (1), during (0), and after (2) noise exposure categories. Two random effects applied to all models were the individual ($RE_{subject}$) and the year the tag record was from (RE_{year}) to account for any by-individual or by-year sources of variation.

Models were first evaluated by likelihood ratio tests, where each candidate model was tested against a null model without fixed effects (Winter 2013). For each dive measurement the significance of each of the fixed effects combinations, of additive candidate models, and of interactions was also examined. Best model fit was evaluated using the differences in Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson 2002). Akaike weights (w_i) for each model were calculated based on AICc values (Wagenmakers & Farrell 2004). Variable importance values were then calculated by summing weights of all models including a particular variable (Burnham & Anderson 2002). A follow-up analysis was conducted to determine direction of affected behaviors in BDA periods using post-hoc pairwise comparisons of least-square means.

RESULTS

Tag Record Selection

A total of nine tag records from years 2006 (three records), 2008 (three records), and 2009 (three records) met the selection requirements and were used in the analysis (Table 1). A total of 171 dives across the nine records were included in the analysis. Of these, 61 occurred in ship noise exposure periods while 110 occurred in no ship noise. Of the individuals, one whale ('Division') had two tag records from two different years (Table 1).

Table 1. Tag records used in analysis

Year	**Tag ID**	**Animal**	**Tag Duration (hh:mm)**	**Dates (mm/dd)**	**Tag On Time (hh:mm)**	**Tag Off Time (hh:mm)**
2006	mn06_192a	Division	22:06	07/11 - 07/12	08:13	06:19
2006	mn06_195a	Fulcrum	10:43	07/14 - 07/15	14:17	01:00
2006	mn06_196a	Dyad	21:47	07/15 - 07/16	08:51	06:38
2008	mn08_182a	Lavalier	18:31	06/30 - 07/01	10:28	05:00
2008	mn08_184b	Nile	12:32	07/02 - 07/03	13:37	02:10
2008	mn08_189a	Falcon	17:00	07/07 - 07/08	14:29	07:30
2009	mn09_108a	Division	17:31	04/18 - 04/19	17:43	11:15
2009	mn09_201a	Entropy	15:07	07/20 - 07/21	09:47	00:55
2009	mn09_206b	Samovar	18:44	07/25 - 07/26	16:18	11:03

Linear Mixed Effect Models

Of the eight dive measurements evaluated, descent rate, ascent rate, and number of bottom side rolls were significantly affected by one or more of the independent variables tested. In a linear mixed effect model with descent rate as the dependent variable, four candidate models have the best fit (ΔAICc < 2) (Table 2). Likelihood ratio tests support the non-significance of all interactions tested (p-value > 0.05). Coefficients for all variables are displayed in Table 5. Variable importance values indicate that the received level of ship nose is the most important of the examined variables influencing descent rate (Table 6). Descent rate tended to decrease as received level increased (Table 5).

Table 2. Mixed-effect models used to assess change in descent rate. Bolded models indicate ΔAICc < 2. SN = Ship noise present or absent, RL = received level of ship noise, and BDA = before, during, or after exposure period. k indicates number of free parameters in each model.

Models for Descent Rate	**k**	**AICc**	**ΔAICc**	w_i
SN, RL	**6**	**-304.97**	**0**	**0.28**
RL	**5**	**-304.50**	**0.47**	**0.22**
SN, RL, BDA	**7**	**-303.76**	**1.21**	**0.15**
BDA, RL	**7**	**-303.76**	**1.21**	**0.15**
SNxRL	7	-302.79	2.17	0.09
SNxRL, BDA	8	-301.58	3.39	0.05
SNxRL, BDAxRL	9	-299.42	5.55	0.02
SN, BDAxRL	9	-299.42	5.55	0.02
BDAxRL	9	-299.42	5.55	0.02
Null (random effects only)	4	-289.32	15.65	<0.01
SN	5	-288.60	16.37	<0.01
BDA	6	-288.06	16.90	<0.01

In a linear mixed effect model with ascent rate as the dependent variable, two candidate models have the best fit (ΔAICc < 2) (Table 3). Likelihood ratio tests support the non-significance of all interactions tested (p-value > 0.05). Coefficients for all variables are displayed in Table 5. The variable importance values indicate that the BDA exposure period and the received level are the most important of the examined variables influencing ascent rate (Table 6). Comparisons of least squares means in the before, during, and after exposure periods demonstrate a significantly slower ascent rate before ship noise exposure than in the during period (estimate = -0.06, p-value < 0.05) and marginally significantly slower than in the after periods (estimate = -0.05, p-value = 0.05). Ascent rate is not significantly lower in the after period than it is in the during period (estimate = -0.005).

Table 3. Mixed-effect models used to assess change in ascent rate. Bolded models indicate ΔAICc < 2. SN = Ship noise present or absent, RL = received level of ship noise, and BDA = before, during, or after exposure period. k indicates number of free parameters in each model.

Models for Ascent Rate	**k**	**AICc**	**ΔAICc**	w_i
SN, RL, BDA	**7**	**-200.92**	**0**	**0.30**
BDA, RL	**7**	**-200.92**	**0**	**0.30**
SNxRL, BDA	8	-198.75	2.17	0.10
SN, RL	6	-197.48	3.43	0.05
BDA	6	-197.46	3.46	0.05
SNxRL, BDAxRL	9	-196.67	4.24	0.04
SN, BDAxRL	9	-196.67	4.24	0.04
BDAxRL	9	-196.67	4.24	0.04
RL	5	-196.19	4.72	0.03
SNxRL	7	-195.65	5.27	0.02
Null (random effects only)	4	-195.22	5.70	0.02
SN	5	-193.27	7.65	0.01

In a linear mixed effect model with number of bottom side rolls per dive as the dependent variable, three candidate models have the best fit (ΔAICc < 2) (Table 4). Likelihood ratio tests support the non-significance of all interactions tested (p-value > 0.05). Coefficients for all variables are displayed in Table 5. Variable importance suggests that the BDA exposure period and the received level are the most important of the examined variables influencing number of bottom side rolls (Table 6). A comparison of least squares means in the before, during, and after exposure periods demonstrates a significantly higher number of rolls after ship noise exposure than in the before exposure period (estimate = 0.31, p-value < 0.05). Mean number of rolls in the during exposure period is not significantly different from either the before or after periods. Overall, the number of rolls tends to decrease as received level increases (Table 5).

Likelihood ratio comparisons of models support no significant effect of either the presence or intensity of ship noise on dive duration, bottom time, maximum depth, time between dives, or surface time following dives. Likewise, AICc differences for models of these variables suggest poor model fit (Tables I-V, Appendix I).

Table 4. Mixed-effect models used to assess change in number of rolls. Bolded models indicate ΔAICc < 2. SN = Ship noise present or absent, RL = received level of ship noise, and BDA = before, during, or after exposure period. k indicates number of free parameters in each model.

Models for Number of Rolls	**k**	**AICc**	**ΔAICc**	w_i
SN, RL, BDA	**7**	**323.84**	**0**	**0.27**
BDA, RL	**7**	**323.84**	**0**	**0.27**
BDA	**6**	**324.97**	**1.13**	**0.15**
SNxRL, BDA	8	326.03	2.19	0.09
RL	5	326.89	3.05	0.06
SNxRL, BDAxRL	9	328.18	4.34	0.03
SN, BDAxRL	9	328.18	4.34	0.03
BDAxRL	9	328.18	4.34	0.03
Null (random effects only)	4	328.46	4.62	0.03
SN, RL	6	328.55	4.71	0.03
SN	5	330.24	6.40	0.01
SNxRL	7	330.62	6.78	0.01

Table 5. Model coefficients, standard errors and t-values for best model fits for descent rate, ascent rate and number of rolls. BDA1 and BDA2 represent the slope for the categorical effect between the during period and the before period (BDA1) and between the during period and the after period (BDA2). Additive models with all three fixed effects tested (SN, RL, and BDA) are excluded as they are redundant to another model (Table 2, 3, and 4).

Response	Model	Variable	Estimate	Std. Error	t-value
Descent Rate	**SN, RL**	(Intercept)	1.750	0.161	10.895
		SN	0.030	0.017	1.630
		RL	-0.008	0.002	-4.475
	RL	(Intercept)	1.607	0.136	11.826
		RL	-0.006	0.001	-4.306
	BDA, RL	(Intercept)	1.764	0.171	10.339
		BDA1	-0.034	0.018	-4.391
		BDA2	-0.016	0.021	-1.861
		RL	-0.008	0.002	-0.763
Ascent Rate	**BDA, RL**	(Intercept)	1.588	0.230	6.910
		BDA1	-0.063	0.024	2.561
		BDA2	-0.005	0.029	-0.174
		RL	-0.006	0.002	-2.425
Number of Rolls	**BDA, RL**	(Intercept)	3.794	1.058	3.588
		BDA1	-0.180	0.117	-1.539
		BDA2	0.128	0.137	0.937
		RL	-0.022	0.012	-1.889
	BDA	(Intercept)	1.819	0.141	12.898
		BDA1	-0.064	0.101	-0.627
		BDA2	0.261	0.118	2.208

Table 6. Variable importance for descent rate, ascent rate and number of rolls

Response	Variable	Variable Importance
Descent Rate	RL	0.80
	SN	0.44
	BDA	0.37
	SNxRL	0.16
	BDAxRL	0.05
Ascent Rate	BDA	0.76
	RL	0.69
	SN	0.40
	SNxRL	0.16
	BDAxRL	0.11
Number of Rolls	BDA	0.78
	RL	0.62
	SN	0.33
	SNxRL	0.13
	BDAxRL	0.09

Dive Responses to Intense Ship Noise

In some individuals, one or more abnormal dives were observed in the presence of ship noise, usually during the peak intensity of a ship noise period. These dives were characterized by an absence of bottom side rolls despite a maximum depth close to that of the feeding dives occurring directly before or after, though some of the no-roll dives were shallower than the surrounding dives (Figure 5).

Whales did not demonstrate bottom side rolls in 10 out of 171 dives. Of the 10 dives with no rolling behavior exhibited, six occurred in ship noise exposure periods while four occurred in no ship noise. A McNemar’s test with continuity correction indicates that the percentage of dives with no rolls significantly differed in periods of ship noise exposure versus in periods of no ship noise (McNemar’s X^2 (1, N = 171) = 87.51, p-value < 0.01) (Figure 6). Of the whales that demonstrated atypical dives in a noise period, it was either the dive at which RL was most intense for the night overall or it was a dive during the ship noise period of greatest intensity for the night.

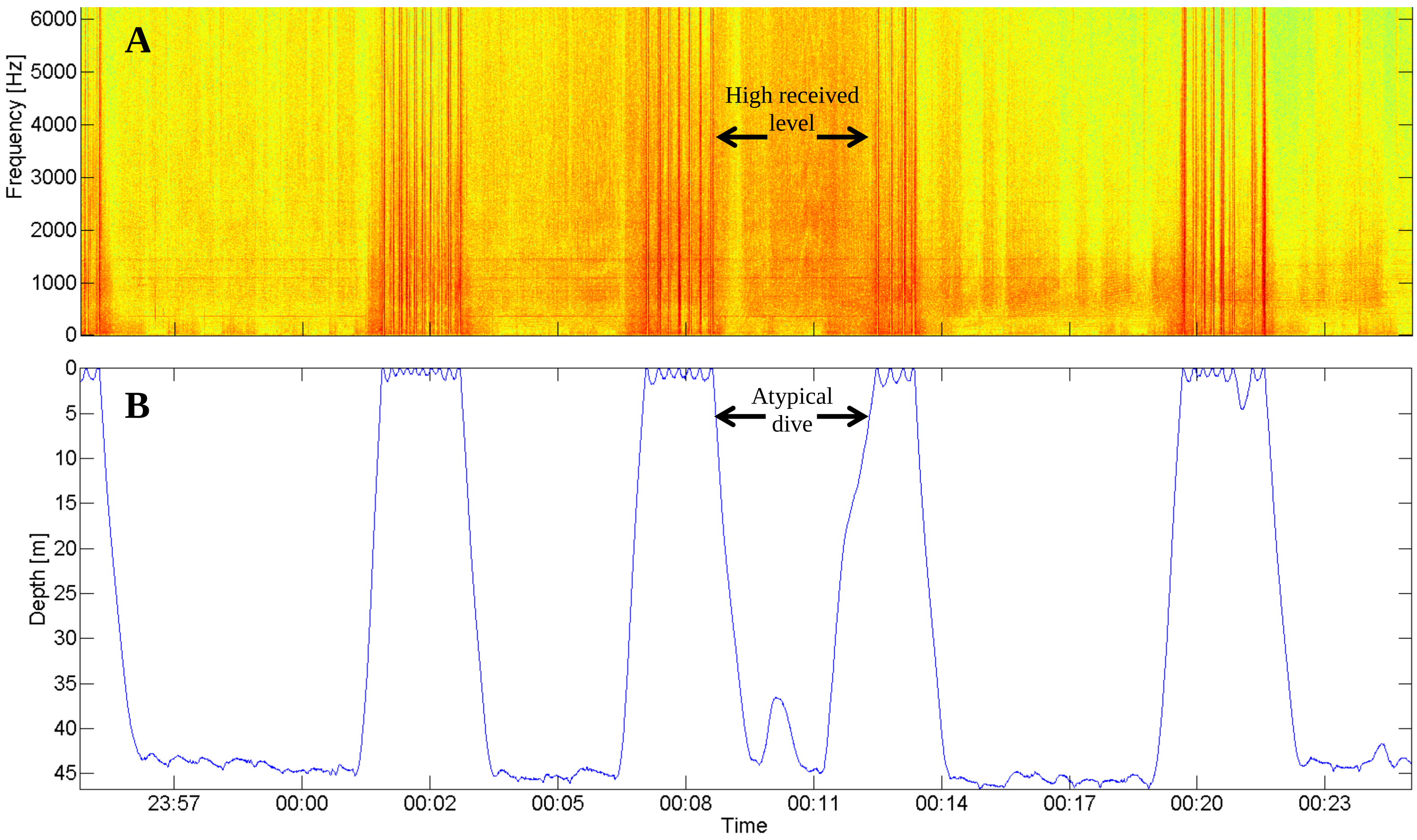

Figure 4. A) Spectrogram and B) depth profile of whale mn08_182a demonstrating atypical dive in presence of ship noise

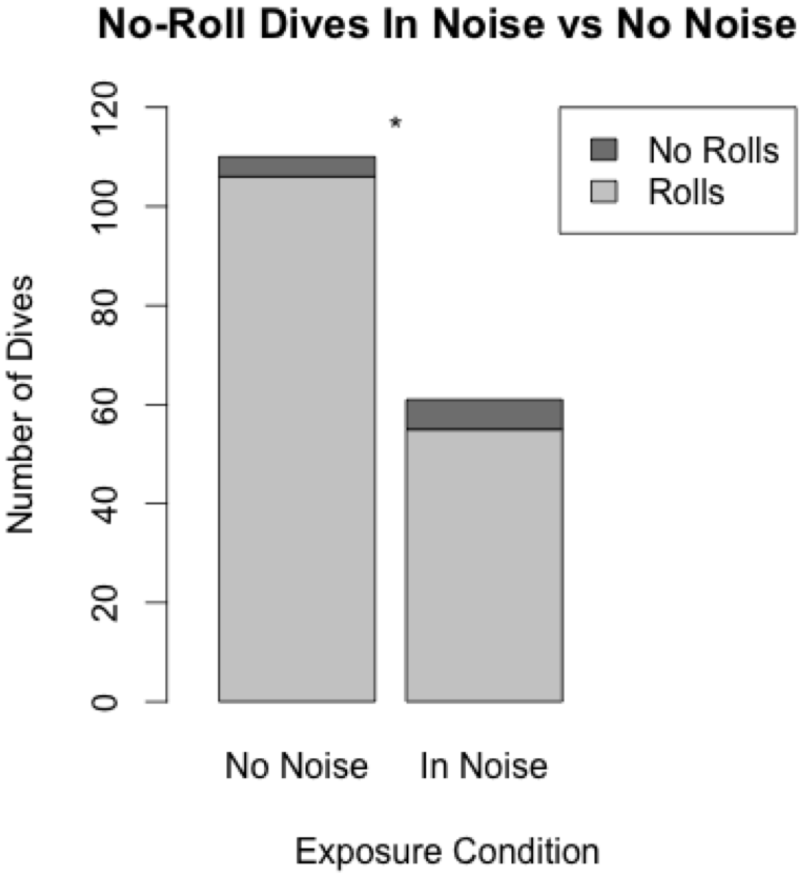

Figure 5. A McNemar’s test demonstrating significantly different proportions of non-roll dives in noise exposure conditions versus non-noise conditions.

DISCUSSION

The impact of anthropogenic noise on the behavioral ecology of marine animals is an area of increasing conservation concern. While numerous studies have demonstrated behavioral modifications of acoustic communication in noise, relatively few have assessed behavioral changes in foraging behavior. This study investigated eight metrics of stereotyped humpback whale bottom feeding dives to assess whether humpback whales modify their foraging efforts in the presence of ship noise. These metrics were the total duration of each dive from surface to surface, the bottom time of each dive between the end of the descent and the beginning of the ascent, the rate of descent and ascent, the maximum depth of each dive, the number of bottom side roll events, the time between dives, and the surface time immediately following each dive. Of these, three were found to be significantly modified in the presence of noise: descent rate, ascent rate, and the number of feeding rolls at the bottom of the dive.

When exposed to ship noise, the descent rate of dives decreased as received level of ship noise increased. Of the variables examined, the intensity of received ship noise is most likely to be important in whether this response will be observed. For the rate of ascent at the end of feeding dives, it was the BDA exposure period that was most influential. Ascent rate was significantly increased in periods during and post-exposure than in the dives immediately preceding exposure periods.

In addition to changes in descent and ascent rate, the number of bottom side rolls indicative of feeding events on sand lance was altered in the presence of ship noise. Of the variables tested, the BDA exposure period was again the most important to model fit, though received level was also a strong indicator. Number of rolls were significantly higher in the after period than the before period, and overall number of rolls decreased as received level increased. In addition, there is evidence that intensity of ship noise was correlated with abnormal dives with a complete cessation of feeding as evidenced by no bottom side rolls, with these occurring during particularly loud or close passes of vessels. These results are some of the first evidence to demonstrate statistically significant alterations in baleen whale foraging behavior from ship noise exposure.

There are a few issues to be considered for this study. First, these models were applied to a relatively small sample size of nine individuals. Though all efforts were made to correct for small sample sizes in statistical tests, data from more individuals would give better support for the hypothesis that ship noise affects foraging behavior. In addition, behavioral effects were only tested at night due to near continuous ship noise during the day. This restriction made measuring behavioral changes more feasible and made metrics easier to compare. However, given the differing feeding techniques utilized by this humpback population during the day as well as the greater occurrence of shipping vessels, it is possible that different responses could be observed in the daytime (Friedlaender et al. 2009). Another matter is that the responses of the group of individuals tested were not compared to a control group. However, this would be difficult to do in this particular study; it is not known whether other humpback populations utilize this foraging technique, and a control population would likely have to be in a different region with fewer shipping lanes as in Parks et al. (2007). Finally, because this study concerned only nighttime foraging behavior, range of vessels to whales was unknown due to lack of GPS positions for the whales at night. This could certainly have implications, as some of the effects observed could have been compounded by proximity to the vessels themselves, rather than the higher intensity noise closer ships produce. An effect of vessel proximity has been observed in both odontocetes and mysticetes (Pirotta et al. 2015; Mckenna 2009).

Since we have observed significant alterations in feeding behaviors at night, we must consider whether they are also occurring during the day. As previously stated, during the daytime hours ship passages were frequent enough that a before-during-after analysis would have been difficult. If similar behavioral responses are extrapolated to daytime foraging, when frequency of ship passages increases, there is a possibility of an overall increase in energetic expenditure in whales caused by faster rates along with missed feeding opportunities.

In this study, humpback whales dove more slowly as the intensity of ship noise increased. Ascents through the water column significantly increased in the presence of ship noise, and remained increased for a time even after the ship noise had ceased. Feeding events ceased altogether at some threshold of received level, but were overall increased in the after period. Although these results demonstrate statistical significance, it is unknown what the biological significance of these changes might be. The effect sizes estimated by the strongest models tended to be small, and more research must be done in order to see if whales suffer a real survival impact. However, it is notable that statistically significant reactions were observed despite this population’s near constant exposure to chronic shipping noise, especially since heavy shipping traffic in the North Atlantic has existed for many years and is only increasing (Hildebrand 2004).

There are a number of possible explanations for the behavioral responses observed. A decreased descent rate in noise may indicate caution on the part of the whale, which requires access to the surface to breathe. The increased ascent rates could be part of a startle response to louder noise, ship proximity, or both. The continued effect into the after exposure period, however, suggests that caution or need to reach the surface to breathe may also play a roll. There seems to be a threshold-received level where a disturbance is meaningful to the whale, though that threshold may vary by individual. This threshold represents where a whale might consider a ship a potential threat, or where the acoustic disturbance reaches an intensity level that incites a quickened pace or distracts from feeding. An increase in bottom side rolls in the after exposure period was not predicted. This behavior could be explained, however, by a perceived increased need to make up for missed foraging opportunities during ship noise exposure.

A unique vocalization termed a “paired burst” is frequently given by humpback whales bottom feeding under low light conditions in this population (Parks et al. 2014). This sound is hypothesized to function in either communicating with conspecifics, to actively affect sand lance prey, or a combination of the two. It is conceivable that this signal is necessary or at least highly advantageous for efficient bottom feeding in low light conditions. The masking of all or part of this acoustic signal by intense ship noise is a possible explanation for the cessation of bottom side rolls in periods of ship noise exposure.

An additional explanation for these non-roll dives in periods of intense noise could be the response of the prey species, sand lance. In the Gulf of Maine region sand lance density is positively correlated with a sand seafloor substrate, into which this species seeks refuge in response to a perceived threat (Hazen et al. 2009). If sand lance are retreating into the substrate in response to high noise levels, this could put them out of easy reach of the bottom-side-roll feeding maneuver. This would explain why, despite diving to the sea floor, the whales did not engage in rolling behavior.

Humpback whales are a highly adaptable species, able to exploit multiple food sources and utilize different foraging techniques to feed on them. They frequently occupy habitat near urbanized coastlines worldwide, which exposes them to regular risk from human impacts like anthropogenic noise. This species has already been observed to alter certain vocalizations in response to noise, demonstrating vocal plasticity (Miller et al. 2000). This thesis provides evidence that North Atlantic humpback whales also alter foraging behaviors in anthropogenic noise. Given their adaptability, it would make sense that this population could be habituated to non-fatal sources of human disturbance. It is especially interesting, therefore, that small alterations to foraging behaviors are still detectable despite chronic ship noise exposure in this habitat. When considering that these behavioral changes were observed at night when there are fewer ship passages as compared to the daytime hours and there is the addition of visual stimuli, this becomes a potential cause for concern for this species, and should be investigated further.

Frid & Dill (2002) argue that the way animals respond to the human disturbance stimuli is analogous to an antipredator response, which is costly in terms of energy and missed opportunities for foraging and reproducing and indirectly affects fitness. Cetaceans function as apex predators in a variety of marine ecosystems; thus, any significant alterations to their foraging or overall survival may reverberate through the trophic levels of the community. Changes in fine-scale foraging behavior caused by anthropogenic noise should also be investigated in other marine predators, as any major impacts to foraging efficiency in these species could have detrimental effects for marine ecosystems.

APPENDIX I

SUPPLEMENTARY MATERIAL

Table I. Mixed-effect models used to assess change in duration of dive. Bolded models indicate ΔAICc < 2. SN = Ship noise present or absent, RL = received level of ship noise, and BDA = before, during, or after exposure period. k indicates number of free parameters in each model.

Models for Dive Time	**k**	**AICc**	**ΔAICc**	w_i
Null (random effects only)	**4**	**749.78**	**0**	**0.35**
BDA	**6**	**751.40**	**1.61**	**0.16**
RL	**5**	**751.60**	**1.82**	**0.14**
SN	**5**	**751.69**	**1.90**	**0.14**
BDA, RL	7	753.53	3.74	0.05
SN, RL, BDA	7	753.53	3.74	0.05
SN, RL	6	753.72	3.93	0.05
SNxRL, BDA	8	755.70	5.91	0.02
SNxRL	7	755.88	6.10	0.02
BDAxRL	9	757.48	7.69	<0.01
SN, BDAxRL	9	757.48	7.69	<0.01
SNxRL, BDAxRL	9	757.48	7.69	<0.01

Table II. Mixed-effect models used to assess change in bottom time. Bolded models indicate ΔAICc < 2. SN = Ship noise present or absent, RL = received level of ship noise, and BDA = before, during, or after exposure period. k indicates number of free parameters in each model.

Models for Bottom Time	**k**	**AICc**	**ΔAICc**	w_i
BDA	**6**	**835.16**	**0**	**0.26**
Null (random effects only)	**4**	**835.76**	**0.61**	**0.19**
RL	**5**	**836.59**	**1.43**	**0.13**
BDA, RL	**7**	**836.90**	**1.74**	**0.11**
SN, RL, BDA	**7**	**836.90**	**1.74**	**0.11**
SN	5	837.37	2.22	0.08
SN, RL	6	838.72	3.57	0.04
SNxRL, BDA	8	839.06	3.90	0.04
SNxRL	7	840.88	5.72	0.01
BDAxRL	9	841.26	6.11	0.01
SN, BDAxRL	9	841.26	6.11	0.01
SNxRL, BDAxRL	9	841.26	6.11	0.01

Table III. Mixed-effect models used to assess change in maximum depth. Bolded models indicate ΔAICc < 2. SN = Ship noise present or absent, RL = received level of ship noise, and BDA = before, during, or after exposure period. k indicates number of free parameters in each model.

Models for Maximum Depth	k	AICc	ΔAICc	w_i
SN	**5**	**81.57**	**0**	**0.16**
Null (random effects only)	**4**	**81.57**	**<0.01**	**0.16**
BDA	**6**	**82.24**	**0.67**	**0.11**
SNxRL, BDAxRL	**9**	**82.34**	**0.77**	**0.11**
SN, BDAxRL	**9**	**82.34**	**0.77**	**0.11**
BDAxRL	**9**	**82.34**	**0.77**	**0.11**
RL	**5**	**83.08**	**1.51**	**0.08**
SN, RL	6	83.71	2.14	0.05
SN, RL, BDA	7	84.38	2.80	0.04
BDA, RL	7	84.38	2.80	0.04
SNxRL	7	85.88	4.31	0.02
SNxRL, BDA	8	86.55	4.98	0.01

Table IV. Mixed-effect models used to assess change in time between dives. Bolded models indicate ΔAICc < 2. SN = Ship noise present or absent, RL = received level of ship noise, and BDA = before, during, or after exposure period. k indicates number of free parameters in each model.

Models for Time Between	k	AICc	ΔAICc	w_i
Null (random effects only)	**4**	**739.03**	**0**	**0.41**
SN	**5**	**740.68**	**1.65**	**0.18**
RL	5	741.07	2.04	0.15
SN, RL	6	742.08	3.04	0.09
BDA	6	742.73	3.70	0.06
SN, RL, BDA	7	744.10	5.07	0.03
BDA, RL	7	744.10	5.07	0.03
SNxRL	7	744.24	5.21	0.03
SNxRL, BDA	8	746.28	7.25	0.01
SNxRL, BDAxRL	9	748.34	9.31	<0.01
SN, BDAxRL	9	748.34	9.31	<0.01
BDAxRL	9	748.34	9.31	<0.01

Table V. Mixed-effect models used to assess change in surface time. Bolded models indicate ΔAICc < 2. SN = Ship noise present or absent, RL = received level of ship noise, and BDA = before, during, or after exposure period. k indicates number of free parameters in each model.

Models for Surface Time	**k**	**AICc**	**ΔAICc**	w_i
Null (random effects only)	**4**	**696.81**	**0**	**0.34**
RL	**5**	**697.45**	**0.64**	**0.25**
SN	5	698.89	2.08	0.12
SN, RL	6	699.21	2.40	0.10
BDA	6	700.81	4.00	0.05
SN, RL, BDA	7	701.26	4.45	0.04
BDA, RL	7	701.26	4.45	0.04
SNxRL	7	701.26	4.45	0.04
SNxRL, BDA	8	703.37	6.56	0.01
SNxRL, BDAxRL	9	704.25	7.44	0.01
SN, BDAxRL	9	704.25	7.44	0.01
BDAxRL	9	704.25	7.44	0.01

LITERATURE CITED

Allen, J. et al., 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, 340, pp.485–8.

Barber, J.R., Crooks, K.R. & Fristrup, K.M., 2010. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology and Evolution*, 25, pp.180–189.

Bee, M. a. & Swanson, E.M., 2007. Auditory masking of anuran advertisement calls by road traffic noise. *Animal Behaviour*, 74, pp.1765–1776.

Bioacoustics Research Program, 2014. RavenPro.

Blickley, J. & Patricelli, G., 2010. Impacts of Anthropogenic Noise on Wildlife: Research Priorities for the Development of Standards and Mitigation. *Journal of International Wildlife Law & Policy*, 13, pp.274–292.

Blickley, J.L. et al., 2012. Experimental Chronic Noise Is Related to Elevated Fecal Corticosteroid Metabolites in Lekking Male Greater Sage-Grouse (*Centrocercus urophasianus*). *PLoS ONE*, 7.

Brumm, H. et al., 2004. Acoustic communication in noise: regulation of call characteristics in a New World monkey. *The Journal of Experimental Biology*, 207, pp.443–448.

Brumm, H. & Slabbekoorn, H., 2005. Acoustic Communication in Noise. *Advances in the Study of Behavior*, 35, pp.151–209.

Brumm, H. & Todt, D., 2002. Noise-dependent song amplitude regulation in a territorial songbird. *Animal Behaviour*, 63, pp.891–897.

Brumm, H. & Zollinger, S.A., 2011. The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour*, 148, pp.1173–1198.

Burnham, K.P. & Anderson, D.R., 2002. *Model selection and multimodel inference: a practical information-theoretic approach.*, New York: Springer-Verlag.

Cassoff, R.M. et al., 2011. Lethal entanglement in baleen whales. *Diseases of Aquatic Organisms*, 96, pp.175–185.

Chan, A.A.Y.-H. et al., 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biology Letters*, 6, pp.458–461.

Clapham, P.J. & Mead, J.G., 1999. *Megaptera novaeanglia*. *Mammalian Species*, 604, pp.1–9.

Clapham, P.J., Young, S.B. & Brownell, R.L., 1999. Baleen whales: conservation issues and the status of the most endangered populations. *Mammal Review*, 29, pp.35–60.

Clark, C.W. & Clapham, P.J., 2004. Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late Spring. *Proceedings. Biological Sciences / The Royal Society*, 271, pp.1051–7.

Croll, D.A. et al., 2001. Effect of anthropogenic low-frequency noise on the foraging ecology of Balaenoptera whales. *Animal Conservation*, 4, pp.13–27.

Cunnington, G.M. & Fahrig, L., 2010. Plasticity in the vocalizations of anurans in response to traffic noise. *Acta Oecologica*, 36, pp.463–470.

Fernández-Juricic, E. et al., 2005. Microhabitat Selection and Singing Behavior Patterns of Male House Finches (*Carpodacus mexicanus*) in Urban Parks in a Heavily Urbanized Landscape in the Western U.S. *Urban Habitats*, 3, pp.49–69.

Francis, C.D. & Barber, J.R., 2013. A framework for understanding noise impacts on wildlife: An urgent conservation priority. *Frontiers in Ecology and the Environment*, 11, pp.305–313.

Francis, C.D., Ortega, C.P. & Cruz, A., 2011. Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. *Proceedings. Biological sciences / The Royal Society*, 278, pp.2025–2031.

Frid, A. & Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6, p.11 [online].

Friedlaender, A.S. et al., 2009. Diel changes in humpback whale *Megaptera novaeangliae* feeding behavior in response to sand lance Ammodytes spp. behavior and distribution. *Marine Ecology Progress Series*, 395, pp.91–100.

Frisk, G. V., 2012. Noiseonomics: The relationship between ambient noise levels in the sea and global economic trends. *Scientific Reports*, 2, pp.2–5.

Gard, R., 1974. Aerial census of gray whales in Baja California lagoons, 1970 and 1973, with notes on behavior, mortality and conservation. *California Fish and Game*, 60, pp.132–143.

Gillam, E.H. & McCracken, G.F., 2007. Variability in the echolocation of *Tadarida brasiliensis*: effects of geography and local acoustic environment. *Animal Behaviour*, 74, pp.277–286.

Hain, J.H.W. et al., 1995. Apparent bottom feeding by humpback whales on Stellwagen Bank. *Marine Mammal Science*, 11, pp.464–479.

Hain, J.H.W. et al., 1982. Feeding-behavior of the humpback whale, *Megaptera novaeangliae*, in the western North-Atlantic. *Fishery Bulletin*, 80, pp.259–268.

Halpern, B.S. et al., 2008. A Global Map of Human Impact on Marine Ecosystems. *Science*, 319, pp.948–952.

Hanser, S.F.T., 2009. *Toward the Social and Acoustic Ecology of Social Foraging Humpback Whales in Southeast Alaska*.

Hatch, L.T. & Wright, A.J., 2007. A brief review of anthropogenic sound in the ocean. *International Journal of Comparative Psychology*, 20, pp.121–133.

Hazen, E. et al., 2009. Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae*. *Marine Ecology Progress Series*, 395, pp.75–89.

Hildebrand, J., 2004. Sources of Anthropogenic Sound in the Marine Environment. *Report to the Policy on Sound and Marine Mammals An International Workshop US Marine Mammal Commission and Joint Nature Conservation Committee UK London England*, 50, pp.1–16.

Hu, Y. & Cardoso, G.C., 2009. Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? *Behavioral Ecology*, 20, pp.1268–1273.

Imhoff, M.L. et al., 2004. Global patterns in human consumption of net primary production. *Nature*, 429, pp.870–873.

Jackson, J.A. et al., 2014. Global diversity and oceanic divergence of humpback whales (*Megaptera novaeangliae*). *Proceedings of the Royal Society B*, 281.

Johnson, M.P. & Tyack, P.L., 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering*, 28, pp.3–12.

Jurasz, C.M. & Jurasz, V.P., 1979. Feeding modes of the humpback whale, *Megaptera novaeangliae*, in southeast Alaska. *Scientific Reports of the Whales Research Institute*.

Kaiser, K. & Hammers, J., 2009. The effect of anthropogenic noise on male advertisement call rate in the neotropical treefrog, Dendropsophus triangulum. *Behaviour*, 146, pp.1053–1069.

Kelly, B.P., Burns, J.J. & Quakenbush, L.T., 1988. Responses of ringed seals (*Phoca hispida*) to noise disturbance. *PORT AND OCEAN ENGINEERING UNDER ARCTIC CONDITIONS SYMPOSIUM ON NOISE AND MARINE MAMMALS*, 2.

Kunc, H.P. et al., 2014. Anthropogenic Noise Affects Behavior across Sensory Modalities. *The American Naturalist*, 184.

Laerm, J. & Wenzel, F., 1997. New prey species for northwestern Atlantic humpback whales. *Marine Mammal Science*, 13, pp.705–711.

Lampe, U. et al., 2012. Staying tuned: Grasshoppers from noisy roadside habitats produce courtship signals with elevated frequency components. *Functional Ecology*, 26, pp.1348–1354.

Lemon, M. et al., 2006. Response of travelling bottlenose dolphins (*Tursiops aduncus*) to experimental approaches by a powerboat in Jervis Bay, New South Wales, Australia. *Biological Conservation*, 127, pp.363–372.

Lengagne, T., 2008. Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. *Biological Conservation*, 141, pp.2023–2031.

Lesage, V. et al., 1999. The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River estuary, Canada. *Marine Mammal Science*, 15, pp.65–84.

Lombard, E., 1911. Le signe de le elevation de la voix. *Ann. Malad. l'Orielle. Larynx. Nez. Pharynx*, 37, pp.101–119.

Love, E.K. & Bee, M. a., 2010. An experimental test of noise-dependent voice amplitude regulation in Cope's grey treefrog, *Hyla chrysoscelis*. *Animal Behaviour*, 80, pp.509–515.

Malme, C.I. et al., 1988. Observations of feeding gray whale responses to controlled industrial noise exposure. *Port and ocean engineering under arctic conditions vol II Symposium on noise and marine mammals*, pp.55–73.

MathWorks, 2013. MATLAB.

Mcclure, C.J.W. et al., 2013. An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. *Proceedings of the Royal Society B*, 280, p.20132290.

McKenna, M.F., 2011. *Blue whale response to underwater noise from commercial ships*. UC San Diego.

Miller, P.J. et al., 2000. Whale songs lengthen in response to sonar. *Nature*, 405, p.903.

Miller, P.J.O. et al., 2009. Using at-sea experiments to study the effects of airguns on the foraging behavior of sperm whales in the Gulf of Mexico. *Deep-Sea Research Part I: Oceanographic Research Papers*, 56, pp.1168–1181.

Morley, E.L., Jones, G. & Radford, A.N., 2014. The importance of invertebrates when considering the impacts of anthropogenic noise. *Proceedings of the Royal Society B: Biological Sciences*, 281, p.20132683.

Naylor, R.L. et al., 2000. Effect of aquaculture on world fish supplies. *Nature*, 405, pp.1017–1024.

Parks, S.E. et al., 2014. Evidence for acoustic communication among bottom foraging humpback whales. *Scientific Reports*, 4.

Parks, S.E. et al., 2011. Individual right whales call louder in increased environmental noise. *Biology letters*, 7, pp.33–5.

Parks, S.E., Clark, C.W. & Tyack, P.L., 2007. Short- and long-term changes in right whale calling behavior: the potential effects of noise on acoustic communication. *The Journal of the Acoustical Society of America*, 122, pp.3725–31.

Patricelli, G. & Blickley, J.J.L., 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. *The Auk*, 123, pp.639–649.

Perry, S.L., DeMaster, D.P. & Silber, G.K., 1999. The great whales: History and status of six species listed as endangered under the US Endangered Species Act of 1973. *Marine Fisheries Review*, 61, pp.1–74.

R Core Team, 2013. R: A language and environment for statistical computing. Available at: http://www.r-project.org/.

Read, J., Jones, G. & Radford, A.N., 2014. Fitness costs as well as benefits are important when considering responses to anthropogenic noise. *Behavioral Ecology*, 25, pp.4–7.

Robbins, J. & Mattila, D.K., 2001. Monitoring entanglements of humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine on the basis of caudal peduncle scarring. *Unpublished report to the Scientific Committee of the International Whaling Commission*.

Rolland, R.M. et al., 2012. Evidence that ship noise increases stress in right whales. *Proceedings. Biological Sciences / The Royal Society*, 279, pp.2363–8.

Romano, T. a et al., 2004. Anthropogenic sound and marine mammal health: measures of the nervous and immune systems before and after intense sound exposure. *Canadian Journal of Fisheries and Aquatic Sciences*, 61, pp.1124–1134.

Samarra, F. et al., 2009. Background noise constrains communication: acoustic masking of courtship song in the fruit fly *Drosophila montana*. *Behaviour*, 146, pp.1635–1648.

Sarà, G. et al., 2007. Effect of boat noise on the behaviour of bluefin tuna Thunnus thynnus in the Mediterranean Sea. *Marine Ecology Progress Series*, 331(February), pp.243–253.

Schaub, A., Ostwald, J. & Siemers, B.M., 2008. Foraging bats avoid noise. *The Journal of Experimental Biology*, 211, pp.3174–3180.

Scheifele, P.M. et al., 2005. Indication of a Lombard vocal response in the St. Lawrence River Beluga. *The Journal of the Acoustical Society of America*, 117, pp.1486–1492.

Schmidt, R., Morrison, A. & Kunc, H.P., 2014. Sexy voices - no choices: Male song in noise fails to attract females. *Animal Behaviour*, 94, pp.55–59.

Slabbekoorn, H. et al., 2010. A noisy spring: The impact of globally rising underwater sound levels on fish. *Trends in Ecology and Evolution*, 25, pp.419–427.

Slabbekoorn, H. & Peet, M., 2003. Ecology: Birds sing at a higher pitch in urban noise. *Nature*, 424, p.267.

Slabbekoorn, H. & Ripmeester, E.A.P., 2008. Birdsong and anthropogenic noise: Implications and applications for conservation. *Molecular Ecology*, 17, pp.72–83.

Smith, E.P., 2002. BACI Design. *Encyclopedia of Environmetrics*, Volume 1, p.141-148.

Soto, N.A. et al., 2006. Does intense ship noise disrupt foraging in deep-diving cuvier's beaked whales (*Ziphius cavirostris*)? *Marine Mammal Science*, 22(3), pp.690–699.

Stimpert, A.K. et al., 2011. Common humpback whale (*Megaptera novaeangliae*) sound types for passive acoustic monitoring. *The Journal of the Acoustical Society of America*, 129(1), pp.476–82.

Stimpert, A.K. et al., 2007. "Megapclicks": acoustic click trains and buzzes produced during night-time foraging of humpback whales (*Megaptera novaeangliae*). *Biology letters*, 3, pp.467–70.

Sun, J.W.C. & Narins, P.M., 2005. Anthropogenic sounds differentially affect amphibian call rate. *Biological Conservation*, 121, pp.419–427.

Tennessen, J.B., Parks, S.E. & Langkilde, T., 2014. Traffic noise causes physiological stress and impairs breeding migration behaviour in frogs. *Conservation Physiology*, 2, pp.1–8.

Thompson, P.O., Cummings, W.C. & Ha, S.J., 1986. Sounds, source levels, and associated behavior of humpback whales, southeast Alaska. *The Journal of the Acoustical Society of America*, 80, pp.735–740.

Todd, S. et al., 1996. Behavioural effects of exposure to underwater explosions in humpback whales (*Megaptera novaeangliae*). *Canadian Journal of Zoology*, 74, pp.1661–1672.

Tressler, J. & Smotherman, M.S., 2009. Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 195, pp.923–934.

Tyack, P.L. & Clark, C.W., 2000. Communication and acoustic behavior of dolphins and whales. In W. W. Au, A. N. Popper, & R. R. Fay, eds. *Hearing by whales and dolphins*. New York: Springer-Verlag, pp. 156–224.

Underwood, A.J., 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *Journal of Experimental Marine Biology and Ecology*, 161, pp.145–178.

Vitousek, P.M. et al., 1997. Human Domination of Earth’s Ecosystems. *Science*, 277, pp.494–499.

Wagenmakers, E.-J. & Farrell, S., 2004. AIC model selection using Akaike weights. *Psychonomic bulletin & review*, 11, pp.192–196.

Ware, C. et al., 2014. Bottom side-roll feeding by humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine, U.S.A. *Marine Mammal Science*, 30, pp.494–511.

Ware, C. et al., 2006. Visualizing the underwater behavior of humpback whales. *IEEE Computer Graphics and Applications*, 26, pp.14–18.

Ware, C., Friedlaender, A.S. & Nowacek, D.P., 2011. Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. *Marine Mammal Science*, 27, pp.587–605.

Wiley, D. et al., 1995. Stranding and mortality of humpback whales, *Megaptera novaeangliae*, in the mid-Atlantic and southeast United States, 1985-1992. *Fishery Bulletin*, 93, pp.196–205.

Wiley, D. et al., 2011. Underwater components of humpback whale bubble-net feeding behaviour. *Behaviour*, 148, pp.575–602.

Wiley, R.H. & Richards, D.G., 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In *Acoustic communication in birds*. pp. 131–181.

Williams, R., Lusseau, D. & Hammond, P.S., 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biological Conservation*, 133, pp.301–311.

Winter, B., 2013. Linear models and linear mixed effects models in R with linguistic applications.

Witteveen, B.H. et al., 2012. Modeling the diet of humpback whales: An approach using stable carbon and nitrogen isotopes in a Bayesian mixing model. *Marine Mammal Science*, 28, pp.1–18.

Wood, W.E. & Yezerinac, S.M., 2006. Song sparrow (*Melospiza melodia*) song varies with urban noise. *Auk*, 123, pp.650–659.

Wright, A.J. et al., 2007. Anthropogenic Noise as a Stressor in Animals: A Multidisciplinary Perspective. *International Journal of Comparative Psychology*, 20, pp.250–273.

Zollinger, S.A. & Brumm, H., 2011. The Lombard effect. *Current Biology*, 21, pp.R614–R615.

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