

Behavioral Ecology of the Western Atlantic Short-finned Pilot Whale (*Globicephala*
macrorhynchus)

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy in
Marine Science and Conservation in the Graduate School
of Duke University

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ABSTRACT

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Abstract

Social structure is a key determinant of population biology and is central to the way animals exploit their environment. The risk of predation is often invoked as an important factor influencing the evolution of social structure in cetaceans and other mammals, but little direct information is available about how cetaceans actually respond to predators or other perceived threats. The playback of sounds to an animal is a powerful tool for assessing behavioral responses to predators, but quantifying behavioral responses to playback experiments requires baseline knowledge of normal behavioral patterns and variation. The central goal of my dissertation is to describe baseline foraging behavior for the western Atlantic short-finned pilot whales (*Globicephala macrocephalus*) and examine the role of social organization in their response to predators. To accomplish this I used multi-sensor digital acoustic tags (DTAGs), satellite-linked time-depth recorders (SLTDR), and playback experiments to study foraging behavior and behavioral response to predators in pilot whales. Fine scale foraging strategies and population level patterns were identified by estimating the body size and examining the location and movement around feeding events using data collected with DTAGs deployed on 40 pilot whales in summers of 2008-2014 off the coast of Cape Hatteras, North Carolina. Pilot whales were found to forage throughout the water column and performed feeding buzzes at depths ranging from 29-1176 meters.

The results indicated potential habitat segregation in foraging depth in short-finned pilot whales with larger individuals foraging on average at deeper depths. Calculated aerobic dive limit for large adult males was approximately 6 minutes longer than that of females and likely facilitated the difference in foraging depth. Furthermore, the buzz frequency and speed around feeding attempts indicate this population pilot whales are likely targeting multiple small prey items. Using these results, I built decision trees to inform foraging dive classification in coarse, long-term dive data collected with SLTDRs deployed on 6 pilot whales in the summers of 2014 and 2015 in the same area off the coast of North Carolina. I used these long term foraging records to compare diurnal foraging rates and depths, as well as classify bouts with a maximum likelihood method, and evaluate behavioral aerobic dive limits (ADL_B) through examination of dive durations and inter-dive intervals. Dive duration was the best predictor of foraging, with dives >400.6 seconds classified as foraging, and a 96% classification accuracy.

There were no diurnal patterns in foraging depth or rates and average duration of bouts was 2.94 hours with maximum bout durations lasting up to 14 hours. The results indicated that pilot whales forage in relatively long bouts and the ADL_B indicate that pilot whales rarely, if ever exceed their aerobic limits. To evaluate the response to predators I used controlled playback experiments to examine the behavioral responses of 10 of the tagged short-finned pilot whales off Cape Hatteras, North Carolina and 4 Risso's dolphins (*Grampus griseus*) off Southern California to the calls of mammal-eating

killer whales (MEK). Both species responded to a subset of MEK calls with increased movement, swim speed and increased cohesion of the focal groups, but the two species exhibited different directional movement and vocal responses. Pilot whales increased their call rate and approached the sound source, but Risso's dolphins exhibited no change in their vocal behavior and moved in a rapid, directed manner away from the source. Thus, at least to a sub-set of mammal-eating killer whale calls, these two study species reacted in a manner that is consistent with their patterns of social organization. Pilot whales, which live in relatively permanent groups bound by strong social bonds, responded in a manner that built on their high levels of social cohesion. In contrast, Risso's dolphins exhibited an exaggerated flight response and moved rapidly away from the sound source. The fact that both species responded strongly to a select number of MEK calls, suggests that structural features of signals play critical contextual roles in the probability of response to potential threats in odontocete cetaceans.

Dedication

This dissertation is dedicated to my parents, Richard and Tina Bowers, who have always supported me in all my endeavors.

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General Introduction

Short-finned pilot whales, *Globicephala macrorhynchus*, are common in deep tropical and sub-tropical waters across the globe. Pilot whales exhibit striking sexual dimorphism in body size with adult males having a mass up to three times that of adult females (Olson 2009). Short-finned pilot whales are a highly social, group-living species which typically occur in groups of approximately 15 individuals that sometimes coalesce into larger aggregations. For example, in line-transect surveys conducted by NOAA Fisheries off the southeastern U.S. in 1998, mean group size for this species was 16.6 (CV = 0.19) (Brown et al. 2004).

Social structure in group-living animals is defined by the nature and patterning of social interactions among members of a society, and social structure has far reaching implications for the ecology of individuals and populations (Whitehead 2008). Social structure is a key determinant of population biology (Wilson 1975) and is central to the way animals exploit their environment (Hoelzel, 1994; Baird & Dill, 1996). Thus, knowledge and integration of social structure is required for interpretation of behavioral patterns. This is particularly true for short-finned pilot whales which are unusual in several aspects of their social structure and life history.

Short-finned pilot whales are one of a very small number of mammalian species (including humans and killer whales) in which females exhibit reproductive senescence (Kasuya & Marsh 1984). Long post-reproductive lifespans are extremely rare in nature

and should only evolve when inclusive benefits outweigh the costs of foregone reproductive opportunities. Theoretical work suggests that kinship dynamics play a large role in determining the costs and benefits of reproductive senescence (Croft et al. 2015). The term kinship dynamics refers to the genetic relatedness of an individual to others in its social group that changes over the individual's lifespan as members enter and disperse from the group. For reproductive senescence to be favored, female local relatedness will need to increase with time. For most mammals, dispersal is male biased (Mabry et al. 2013), which leads to females being less closely related to offspring of the group over time (Cant & Johnstone 2008). Recent theoretical models suggest that there are two patterns of demography that can lead to increased group relatedness of females with age: (1) dispersal is female biased, and (2) neither sex disperses, but groups mate with other groups (Croft et al. 2015). Long term observations of short-finned pilot whale populations have found evidence for natal philopatry in both males and females (Heimlich-Boran 1993; Alves et al. 2013), although some field studies indicate that there may be some dispersal of male short-finned pilot whales (Mahaffy et al. 2015). Nevertheless, both theoretical and observational data suggests the social structure of this species is characterized by low levels of dispersal of female and (perhaps) male offspring from their natal group.

In well-studied populations near Tenerife, (Heimlich-Boran 1993), Madeira (Alves et al. 2013), and Hawaii (Mahaffy et al. 2015) individual short-finned pilot whales

exhibit long-term patterns of social association in mixed sex groups. Protracted maternal investment and long lifespans also contribute the investment and maintenance of social relationship (Wells 2014). Short-finned pilot whales exhibit one of the longest periods of parental care among marine mammals with mothers suckling calves for up to 13-15 years (Tyack 2009a). The long period of dependence likely leads to increased calf survival and facilitates the learning of social behaviors (Chivers 2009). It has been suggested that the long post-reproductive lifespans of females function to store cultural knowledge and/or provide alloparental care and potentially alloparental nursing (Kasuya 1995). Accumulated knowledge that is transferred through generations is thought to be one of the largest drivers in natal philopatry in observed in cetacean species, such as killer whales, *Orcinus orca*, sperm whales, *Physeter macrocephalus*, and pilot whales (Whitehead 2003). The extremely cohesive nature of the social structure of this species has been suggested as an explanation of its frequent mass strandings that often result in the death of all group members (Olson 2009).

The three main drivers for group living in animals are: 1) when susceptibility to predation is reduced by group living, 2) when access to resources is increased by group living 3) and when the distribution of resources promotes gregariousness (Gowans et al. 2007). Predation is an important driver of group living in cetacean species. The open ocean environment of short-finned pilot whales is largely devoid of refuge from predators and grouping may be one of the most effective anti-predator

strategies (Norris and Schilt 1988; Connor 2000). Deep waters may provide a refuge for sperm and beaked whales from predators, such as killer whales, that hunt at the surface (Tyack et al. 2011), but pilot whales, particularly small individuals, may not have the aerobic capacity to escape predators in this manner. Group living can lead to protection from predation through several methods including diluted predation risk, increased vigilance and anti-predator defense strategies (Bowen et al. 2002). Anti-predator defense can include a variety of tactics including herding, confusion, alarm calls, fleeing and or mobbing behavior (Marshall et al. 2012).

Mammal eating killer whales are the species most often implicated in predation on cetaceans. Killer whales are one of the most widely distributed cetaceans and represent a threat to most if not all marine mammals (Jefferson et al. 1991). Individual predation events are rare for marine mammals, but even occasional predation attempts can exert a significant selective force on social behavior, particularly amongst long-lived species (Isbell 1994; Connor 2000, Marino 2002). Short-finned pilot whales have been found in the stomach of killer whales (Jefferson et al. 1991) and killer whales have been observed attacking and killing long-finned pilot whales (*Globicephala melas*) (Bloch and Lockyer 1998; Donovan and Gunnlaugsson 1989). Playbacks of vocalizations of fish-eating killer whales, which are potential competitors, to long-finned pilot whales, *Globicephala melas*, resulted in increased group size and movement towards the sound source (Curé et al. 2012), suggesting that grouping in pilot whales may also function in

defense of resources. Curé et al. (2012) suggested this response either reflected an attraction to a shared food resource (herring) or a mobbing strategy to a potential threat or an aggressive action against a heterospecific species.

While there is evidence that predation is a driver for group living in pilot whales, it is less clear how or if group formation in short-finned pilot whales improves access to resources. Improved access to food resources can lead to the evolution of group behavior through defense of food resources, coordinated and cooperative foraging, and improved detection of prey items (Gowans et al. 2007). Gowans et al. (2007) noted it is unlikely that an odontocete living in a strongly three-dimensional environment would be able to defend a territory or large resource (Gowans et al. 2007). Records from acoustic tags indicate that short-finned pilot whales forage at depth with some foraging dives exceeding a 1000 meters and target single or few prey items (Soto et al. 2008). Jensen et al. (2011) suggested that short-finned pilot whales do not forage cooperatively due to evidence that calls at depth were used to maintain contact with group at the surface and the apparent lack of dive synchrony in the population (Soto 2006). It is possible that pilot whales coordinate search efforts which should lead to discovery of large food patches and minimize search time. A number of cetaceans, including pilot whales, fan out perpendicular to the direction of travel during foraging (Norris & Prescott 1961; Connor 2000). This behavior is often considered to reflect a cooperative effort to locate prey schools, but individuals targeting solitary prey items, which is

common in pilot whales, may spread out to reduce competition (Connor 2000). One of the universal costs of group living is resource competition (Alexander 1974), and Whitehead (Whitehead & Weitgart 2000) suggested groups that formed for anti-predator benefits ranks to offset some of these costs and does not necessarily reflect cooperative behavior.

Pilot whales, like all group living species, most certainly experience resource competition. For groups that exhibit natal philopatry, the degree to which both sexes maintain bonds to their natal group will be shaped by resource availability (Connor 2000). Baird (2000) argued that the difference in group sizes and level of natal philopatry between resident and transient killer whales in the Pacific Northwest is shaped by foraging strategy and resource competition. Resident killer whales travel in large groups that average eighteen individuals and exhibit natal philopatry in both males and females (Ford & Ellis 2014). Residents diet consists primarily of teleost fish, in particular pacific salmonids (Ford et al. 2011), and they do not appear to cooperatively heard or capture prey (Ford et al. 2011). Transient killer whales more often travel in smaller groups of two to six, with females dispersing from the group at sexual maturity and potentially males as well (Ford & Ellis 1999). Transient killer whales generally hunt in stealth to avoid detection by acoustically sensitive prey. This strategy likely constrains group size since large groups likely increase the detection hunt marine mammals, who are sensitive to sound which may make it unprofitable and it may be energetically efficient to have

small groups when hunting smaller marine mammals such as harbor porpoises or harbor seals

Resource availability will be strongly influenced by travel costs which is relatively low in the marine environment (Connor 2000). Williams (1999) found the energetic expenditure for a marine mammal to move over a given distance is similar to that of a terrestrial mammal that specializes in running or flying. This total cost of transport is comprised of maintenance cost and locomotion costs, and for marine mammals, most of the energy expenditure is due to increased maintenance cost resulting in relatively low locomotion costs (Williams 1999). Pelagic prey species (cephalopods and fish) are usually found in rare but profitable patches with large areas of habitat containing few if any food resources in between (Steele 1978). As group size increases, the amount of food per individual at each patch decreases, forcing the group to travel further to acquire sufficient food (Clutton-Brock & Harvey 1977; Terborgh & Janson 1986). While it is unclear if larger group sizes lead to larger home ranges or larger home ranges lead to larger groups, it is predicted that variation in home range should correlate with variation in group size. There is evidence that pilot whales range over large distances. Two individual short-finned pilot whales were satellite tracked following a mass stranding in Kudjoe Key, Florida and averaged rates of movement from 2-5 km a day and traveled approximately 900 kilometers over a 16 day period (Wells et al. 2013).

The large home ranges may also allow for more opportunities for individuals to interact with unrelated conspecifics and to avoid inbreeding in groups that exhibit natal philopatry. Dispersal from natal groups by members of one sex is typically thought of as an adaptation to avoid inbreeding (Greenwood 1980). For cetaceans who exhibit natal philopatry, large ranging patterns may allow for males to encounter mates while traveling with their mothers (Heimlich-Boran 1993). The large aggregations mentioned above may function as an opportunity for males to interact with females from other groups.

While the physical environment of the ocean would appear to put few limits on the movement and ranging patterns of cetaceans, restrictions may result from the composition of their group, particularly for size dimorphic species like short-finned pilot whales. Intraspecific variation in body size can result in divergent energetic and resource requirements, reproductive strategies, predator avoidance, activity budgets and social affinities (Ruckstuhl & Clutton-Brock 2005). In mammals, greater body size leads to the potential for greater energy stores which, in turn, allows animals to exploit patchier resources (Bowen et al. 2002). Ranging distances are strongly correlated with body size and there is an allometric relationship between the cost of transport and body size in marine mammals ($COT=7.94^*M-0.28$ (Williams 1999)). These differences may not be meaningful for daily activities but could be significant for migrations or large ranging patterns (Michaud 2005). Differences in body size can also lead to differences in

predation risk or tolerance of predation risk. Quite often these costs lead to size related segregation outside of breeding season and presents the question how do pilot whales overcome these costs and maintain group composition.

Environment

The Cape Hatteras study site is located approximately 40 km offshore of North Carolina's Outer Banks (Figure 1). The oceanographic setting off Cape Hatteras is driven by steep bathymetric gradients, the influence of the Gulf Stream and the confluence of southward flowing Middle Atlantic Bight water with northward flowing South Atlantic Bight water (Savidge & Bane 2001). This dynamic setting exhibits seasonal changes in temperatures and flow regimes, as well as significant oceanographic variability at shorter time scales due to high current velocities of the Gulf Stream and the continual advance of transient features such as Gulf Stream meanders and frontal eddies through the region (*e.g.*(Savidge 2004)). Dense aggregations of marine mammals and seabirds are distributed in a narrow region along the shelf break (Best et al. 2012(Roberts et al. 2016)) and commercial and recreational fishing vessels targeting large predatory fishes use this region year-round (National Marine Fisheries Service 2006). Many of these predators feed on squid that are associated with the Gulf Stream (Dawe et al. 2000), such as short-finned pilot whales (Mintzer et al. 2008). Short-finned pilot whales, common

dolphins, *Dephinus delphis*, offshore bottlenose dolphins, *Tursiops truncatus*, and beaked whales are all encountered frequently in this region.



Figure 1– Cape Hatteras Shelf Break Study Area

Approach

As mentioned above short-finned pilot whales exhibit natal-philopatry and maintain long-term stable associations with a lack of dispersal of females and potentially males from their natal group. This should influence how pilot whales exploit their environment, protect themselves from predators and leads to questions about how they overcome divergent costs, due to differences in body size, of maintaining group cohesion. The central objective of my dissertation is to understand the baseline foraging

behavior of short-finned pilot whales and to build upon that with an investigation into their response to predators. I use a suite of field and analytical tools to obtain comprehensive measurements of pilot whale behavior and to determine how this behavior changes in relation to both acoustic stimuli and environmental parameters.

Chapter 1 begins with an investigation of fine scale foraging patterns using multi-sensor acoustic tags and analysis of population level variation in foraging strategies. Specifically, I examine different foraging modalities with respect to sex and body size. In Chapter 2, I look at foraging over longer time scales, with respect to diurnal patterns and conduct a foraging-bout analysis. In this analysis, this I use fine-scale data from Chapter 1 to develop metrics that predict foraging in coarser, long-term tag data. In Chapter 3 I explore the response to predators by performing playbacks to short-finned pilot whales and Risso's dolphins.

Chapter 1: The Role of Size and Sex in the foraging Strategies of the Western Atlantic Short-finned Pilot Whales

Introduction

Body size is a fundamental trait that determines much of an animal's life history and ecological role (Peters 1983; Brown et al. 2004). Body size directly affects metabolism which, in turn, determines the energetic demands that organisms place on their environment for resources, and simultaneously sets powerful constraints on allocation of resources to components of fitness (Brown et al. 2004). Animals must feed to acquire energy, and body size affects how, upon what and where an animal forages (Peters 1983). Intraspecific variation in body size can result in divergent energetic and resource requirements, reproductive strategies, predator avoidance, activity budgets and social affinities (Ruckstuhl & Clutton-Brock 2005).

Size-related variation in feeding ecology has been observed in a diversity of taxa and ranges from minor differences in diet to segregation in time and space (Kamilar & Pokempner 2008). For example, monomorphic ungulates are more likely to occur in mixed sex groups and share habitat than sexually dimorphic species, which may segregate outside the breeding season (Mysterud 2000; Ruckstuhl & Neuhaus 2002). A number of hypotheses to explain size-related segregation have been advanced, particularly for ungulates, including differences in activity budgets, predation risk, forage selection, and intraspecific competition (Ruckstuhl 2007). I address each of these

hypotheses below. In most cases, it is likely that no single factor explains segregation, but that several factors may be operating in concert.

That differences in body size will lead to differences in energetic requirements and foraging behavior is the basis for the hypothesis of differential activity budgets between conspecifics. In mammals, greater body size leads to the potential for greater energy stores which, in turn, allows animals to exploit patchier resources (Bowen, Read, et al. 2002). For example, Northern elephant seals, *Mirounga angustirostris*, are one of the most dimorphic mammals, with adult males weighing 3 times more than adult females (Deutsch et al. 1994). As a result of this extreme dimorphism, male and female elephant seals have vastly different distributions at sea. Following the breeding season in central California, adult males move northwest to forage on demersal prey along the shelf break off the Aleutian Islands (Le Boeuf et al. 2000). In contrast, female northern elephant seals migrate shorter distances to the open, deep ocean and forage on mesopelagic prey (Le Boeuf et al. 2000). The larger mass and higher overall energy needs require male northern elephant seals to find prey patches that are denser, larger or composed of higher quality prey, whereas the females are able to forage efficiently on smaller, more ephemeral prey (Le Boeuf et al. 2000). Similar, but less extreme habitat segregation is observed in gray seals, *Halichoerus grypus*, in which the mass of adult males is 1.5 times that of adult females). Off the east coast of Canada, adult male gray seals range further than females and forage on the shelf while females foraging in the mid-shelf region

(Breed et al. 2006). Sperm whales, *Physeter macrocephalus*, show one of the greatest degrees of mammalian sexual dimorphism, with adult males weighing up to three times as much as adult females. This species provide an extreme example of sexual segregation in foraging habitat (Whitehead 2003). Female offspring remain in their natal groups, but juvenile males disperse to form bachelor schools and, with increasing size and age, become more and more solitary (Whitehead 2003). As adults, male sperm whales forage at high latitudes where they are spatially separated from females by thousands of kilometers, except during breeding (Whitehead 2003).

Segregation may also result from differential predation risk and/or predation risk tolerance. For example, male elephant seals forage closer to the coast than females, but at a cost of increased predation risk by white sharks and killer whales (Le Boeuf et al. 2000). Le Boeuf et al. (2000) speculated that the greater mass gain in males, relative to females, enhanced the probability of reproductive success in their extremely polygynous mating system and made this increased predation risk worthwhile. In cetaceans, dependent juveniles are more susceptible to predation due to their smaller body size and relative inexperience, so their presence often leads females to choose habitats that reduce predation risk and maximize offspring security (Wearmouth & Sims 2008).

Beluga whales, *Delphinapterus leucas*, seasonally segregate in the summer and fall with adult males selecting areas with high sea ice concentrations near the arctic circle and females and calves preferring open water near the mainland which provide refuge from

killer whale attacks and reduce the risk of polar bear predation (Loseto et al. 2007; Michaud 2005). In a similar manner, the year-round presence of female sperm whales and their young offspring in the tropics, where killer whales are less prevalent, may be a strategy to avoid predation (Dalheim & Heyning 1999). The same argument has been invoked to explain the general strategy of baleen whale migration to the tropics for calving (Corkeron & Connor 1999). Like northern elephant seals, male belugas and sperm whales might choose riskier, but more productive, waters to gain mass, because the added body mass aids them in contest competitions for access to females (Ralls & Mesnick 2009).

Differential choice of prey (sometimes termed forage selection) is often observed in dimorphic marine predators, in which the larger sex typically consumes larger items of the same prey, or a different diet all together (Bowen et al. 2002). Larger animals are capable of consuming a wider variety of food sources (Marshall et al. 2012). Dietary breadth in gray seals is related to body size, with males exhibiting significantly greater dietary breadth than females and juveniles (Tucker et al. 2007). Diving behavior in female gray seals also reflects a higher selectivity of prey than in males (Beck et al. 2003). In another sexually dimorphic species of pinniped, male Steller sea lions, *Eumetopias jubatus*, target larger prey items than females (Beck et al. 2007). In cetaceans, sex-related differences in diet have been observed in the following dimorphic species: belugas

(Lowry et al. 1985); bottlenose dolphins (Blanco et al. 2001); and sperm whales (Rice 1989).

Intraspecific competition may lead to sexual segregation, particularly under conditions of low food availability. At its extreme, intense feeding pressure from one sex may exclude the other sex from a particular foraging area. Scramble competition is unlikely to occur when predation forces females into poorer forage quality or when high quality food is abundant (Main 1998; Michaud 2005). Main (1998) suggested that the higher mobility and lack of parental care in sexually dimorphic species prompted adult males to avoid heavily exploited areas. This could explain the patterns described above in gray seals, in which females utilize smaller foraging ranges and males range further to avoid competition (Breed et al. 2006). Whitehead (2003) suggested that scramble competition was the best explanation for an observed influx of adult sperm whale males into the waters around the Galapagos soon after females left those waters.

In aquatic environments, larger animals also have the potential to dive to greater depths to partition resources and minimize the prospect of intraspecific competition. The diving ability of air-breathing vertebrates is often characterized by aerobic dive limit (ADL). ADL is shaped by several factors, but in simplest terms, an animal's breath-hold duration is determined by its oxygen stores and the rate at which those stores are consumed. In marine mammals, which store most of their oxygen in blood and muscle tissues, oxygen stores scale with $M^{1.0}$, but the rate at which oxygen is consumed scales

with $M^{0.75}$ (Weise et al. 2010). This differential allometric scaling of O₂ stores and consumption provides a significant advantage in diving duration (and thus the ability to exploit increasing depth) to larger bodied animals. Schreer and Kovaks (1997) found strong allometric relationships between maximum depth, dive duration and body size in breath-hold diving vertebrates. Sexual segregation in dive depth has been reported in diving birds (cormorants and penguins) and appears to be driven by size dimorphism (Catry et al. 2005). Male gray seals and California sea lions, *Zalophus californianus*, forage at greater depths than their female counterparts (Breed et al. 2009; Weise et al. 2010). Male and female southern elephant seals, *Mirounga leonina*, from Marion Island utilize the same geographic locations and appear to partition resources through targeting different foraging depths (McIntyre et al. 2010).

Sexual dimorphism in short-finned pilot whales, *Globicephala macrorhynchus*, is pronounced, with females reaching close to 4 meters in length and weighing approximately 700 kg whereas males can grow up to 5.5 meters and weigh over 2000 kg. Short-finned pilot whales are highly social and are one of a very small number of mammalian species (including humans and killer whales) in which females exhibit reproductive senescence (Kasuya & Marsh 1984). Theoretical models indicate that reproductive senescence can be adaptive if (1) neither sex disperses, but groups mate with other groups, or (2) females disperse (at least more than males) (Croft et al. 2015). Long-term observations of short-finned pilot whales suggest that males and females

exhibit philopatry to their natal groups (Heimlich-Boran 1993; Alves et al. 2013). Thus, the social structure of this species is characterized by a lack of dispersal of both male and female offspring from their natal group, although some field studies indicate that there may be some dispersal of male short-finned pilot whales (Mahaffy et al. 2015). In well-studied populations near Tenerife, (Heimlich-Boran 1993), Madeira (Alves et al. 2013), and Hawaii (Mahaffy et al. 2015) individual short-finned pilot whales exhibit long-term patterns of social association in mixed sex groups.

Sexually dimorphic species that form stable, mixed-sex groups are unusual amongst mammals. Resident killer whales in the Pacific Northwest are dimorphic and have a similar social structure to short-finned pilot whales, in which neither sex disperses from their natal group, but exhibit segregation within groups in which adult males forage on the periphery of females in deeper water (Beerman et al. 2015) and tend to dive deeper (>30 m) and more frequently than females (Baird et al. 2005). The deep water habitat of short-finned pilot whales allows for the possibility of segregation in foraging depth, in which larger-bodies males forage in deeper waters than females. The three-fold difference in body mass should result in significantly greater ADL in adult male pilot whales relative to their adult female counterparts.

Quick et al. (2016) examined the diving behavior of 20 short-finned pilot whales off North Carolina, USA and described variation in foraging patterns exhibited by these animals. Multiple foraging events (as reflected by feeding buzzes) were observed during

each foraging dive and the number of feeding events increased with depth (Quick et al., 2016). This pattern of foraging was quite different from that observed in Tenerife, in which short-finned pilot whales often target single, large prey items during prolonged chases (Soto et al. 2008). Quick et al. (2016) suggested the variation in the number of foraging events might reflect variation in foraging success or perhaps reflect the size and caloric value of prey targeted by different whales, and that variation in foraging strategies might be shaped by ecological factors and physiological limitations related to body size. Very little is known of the prey of this population of whales. In the only study of diet of short-finned pilot whales in this region, the stomachs of 11 whales that mass stranded near Cape Hatteras in January 2005 contained a diverse assemblage of small-bodied meso- and bathypelagic cephalopods (Mintzer et al. 2008). Nevertheless, it is possible that pilot whales target prey of varying size and energetic value in this region and that some of this variation might be structured by dive depth capabilities of individuals.

Analysis of dive patterns can allow us to infer information on diet (Tinker et al. 2007), but with unknown accuracy. The ability to identify the timing and location of prey capture, together with an analysis of the kinematics of foraging events, can provide further insight into prey selection. Foraging on mobile prey requires that predators expend energy in the pursuit, capture and handling of the prey item (Spitz et al. 2012) and differences in the mobility of the prey item should be reflected in the kinematics

around each feeding attempt. This type of data integration has led to novel observations of the foraging sprints of short-finned pilot whales *Globicephala macrorhynchus* in the Canary Islands (Soto et al. 2008) described above, circling behavior around patches of prey which potentially functions to herd prey by Blainville's beaked whales *Mesoplodon densirostris* (Johnson et al. 2008), and long-range prey detection by sperm whales (Watwood et al. 2006). Furthermore, the concurrent use of acoustics and accelerometers can be used to identify successful foraging attempts (Ydesen et al. 2014; Wisniewska et al. 2014).

In the present chapter I describe the foraging behavior of 40 short-finned pilot whales from diving records obtained off Cape Hatteras (including the 20 animals examined by Quick et al. 2016). I calculate Aerobic Dive Limits (ADL_C) for individuals to assess the influence of size on diving capacity. I then use a Bayesian mixed effects regression model to investigate the role of size and kinematics including speed and dynamic acceleration in the tactics used by whales to capture prey at different depths in the water column. I use these observations to explore the role of body size in structuring the foraging habitat of these whales and to test the hypothesis that larger-bodied whales forage at greater depth.

Materials and Methods

Data Collection

Thirty-nine short-finned pilot whales were tagged along the shelf break off Cape Hatteras (approximately 35°N and 75°W) in the summers (May to September) of 2008–2014 (Table 1). Two of the tags were deployed concurrently on a pair of large, strongly associated animals. Larger, well-marked whales were selected for tagging and adult females accompanied by dependent calves were avoided. DTAGs were secured to the dorsal fin or dorsal surface of whales with four 6-cm diameter suction cups, using a hand-held carbon fiber pole from a small rigid-hulled inflatable boat (RHIB). The tags sampled acoustic data at 96 kHz on two channels using a 16-bit analogue-to-digital converter. The tags sampled the pressure sensor, accelerometers and magnetometers at 50 Hz to generate measurements of the depth and orientation of the tagged whale. The RHIB followed tagged whales from a distance of approximately 100 m and recorded surface behavior and range and bearing from the RHIB to create a track of positions during the tag record. The VHF beacon in the DTAG was used to locate the tagged whale after long dives and to relocate the tag after it jettisoned from the whale. In several cases, whales were tracked overnight from a larger research vessel. Each tagged whale was identified with a code that included the initials of the scientific name, year, Julian day and sequential deployment of the day and is referred to as Tag ID.

Digital images of all tagged whales and their associates were collected and small samples of skin were obtained from 19 tagged whales for determination of sex using a crossbow and modified biopsy tip (Table 1). These biopsy samples were obtained soon after the tag was released or just before the tag was programmed to come off the whale.

Data Analysis

Fifteen deployments were part of experiments that measured the behavioral response to the playback of various sounds. Each of these experiments included a pre-exposure period lasting up to two hours, used as baseline information for that whale. I included data from the baseline periods from these 15 deployments and excluded any post-baseline data, as well as any records lasting less than 30 minutes. I followed previous investigators by defining a dive as any submergence greater than 20 m (Soto et al. 2008).

I manually audited the acoustic recordings in MATLAB (MATLAB 2012) by carefully listening to the recording along with visual inspection of the spectrogram. I marked all potential foraging buzzes, and pulsed sounds that were associated with continuous echolocation clicks (Soto et al. 2008) along with the start and end of echolocation clicks. Following the audit, I employed a supervised click detector (Arranz et al. 2011) to identify clicks with a low-frequency energy (1-5kHz), indicative of clicks originating from the tagged animal. These clicks were then displayed with their angle of

arrival (based on difference in time of arrival to the two tag hydrophones). After establishing angle of arrival for the click sequences on each dive, I assessed and removed any buzz that appeared to be produced by another whale (Figure 2). I then fit a mixed Gaussian distribution to the log of the inter-click intervals (ICI) and used the equal posterior probability value as the boundary between buzz and regular clicks (Figure 3). Finally, I computed buzz durations as the time from the first to the last click in the buzz with an ICI less than 22 ms (Teloni et al. 2008); (Wisniewska et al. 2014).

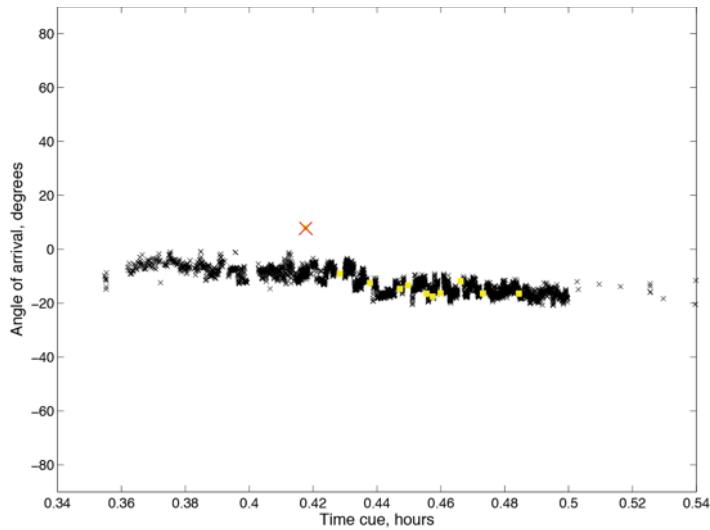


Figure 2 – Angle of arrival of clicks and buzzes. Black crosses represent clicks, yellow squares are buzzes. The red cross over the yellow square represents a discarded buzz, presumably made by another whale.

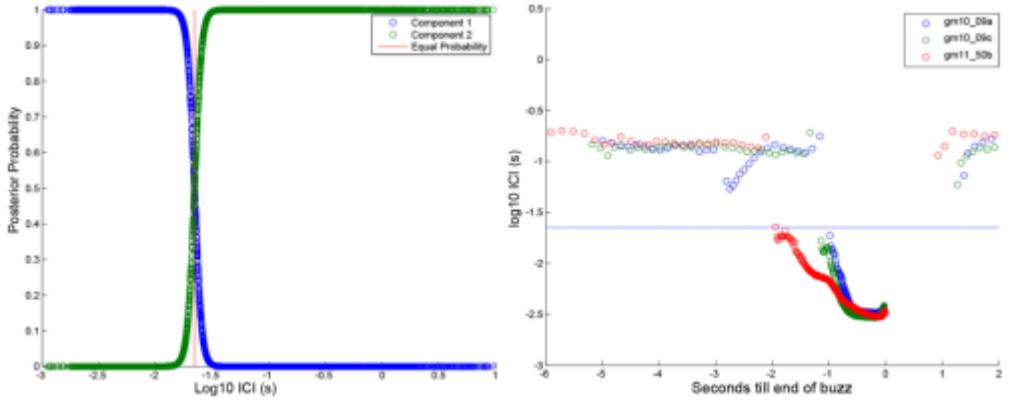


Figure 3 – Left: Posterior probabilities for the two components of the mixed Gaussian distribution fit from the log transformed ICIs. The equal probability is highlighted with a vertical line and represents the boundary between buzz and regular clicks. **Right:** Examples of buzzes from three different animals with ICIs plotted against time till end of the buzz. The blue dashed line represents the boundary between buzz and regular clicks.

I aligned the marked times of each foraging buzz with the depth and accelerometer records, and categorized all dives containing a buzz as a foraging dive. I used a variety of measures to evaluate the kinematics around each foraging buzz. Using the accelerometer data I computed indices of movement including mean specific acceleration (MSA) and overall dynamic body acceleration (ODBA) following procedures outlined in prior studies (Simon et al. 2009; Qasem et al. 2012). To estimate speed I used low frequency flow noise computed from the tag acoustic recordings (Goldbogen 2006; Soto et al. 2008). I computed low frequency flow noise for each tag (noise power at 500 Hz band-pass filtered with a 2-pole Butterworth filter) for continuous periods on the descent phase with a pitch greater than 60 degrees in 5-

second bins. I estimated velocity on these descents by dividing rate of change of depth by the sine of the pitch angle and fit the values to the function:

$$\text{Vertical Velocity} \sim m(20 \log(\text{noise power})) + b \quad (1)$$

I fit this function to every whale that performed a feeding buzz and computed the average speed, MSA and ODBA for the duration of and 4 seconds preceding each foraging buzz.

Body Length

I used the known dimensions of the DTAG to estimate the length of the base of the dorsal fin (DBL) in digital images. I adapted methods for DBL measurement from (Durban & K. M. Parsons 2006) and (Rowe & Dawson 2008). I defined DBL as the length between the anterior and posterior insertions of the dorsal fin (Figure 4), and I defined the anterior insertion as the beginning of the dorsal fin crease on the leading edge, which is the midpoint of the curve at the anterior edge of the fin. I defined the posterior insertion as the point where the plane of the back deviates from the plane of the dorsal fin (solid black line in Figure 4). I determined height (h) by drawing a line parallel to the base of dorsal fin, which just touches the top of the fin, then extending a line perpendicular to the two parallel lines (Figure 4). The measurements were made in Adobe Photoshop using the measurement tool (Figure 4). I then used a large

morphometric data set from this species (Yonekura et al. 1980) to predict total body length (TL) with equation (2).

$$DBL = 0.209(TL) - 4.246 \quad (2)$$

The value of 395 cm represents both the maximum length of adult females and the minimum length of adult males (Kasuya & Matsui 1984). Therefore, I categorized whales as either large or small using 395 cm as a separator.

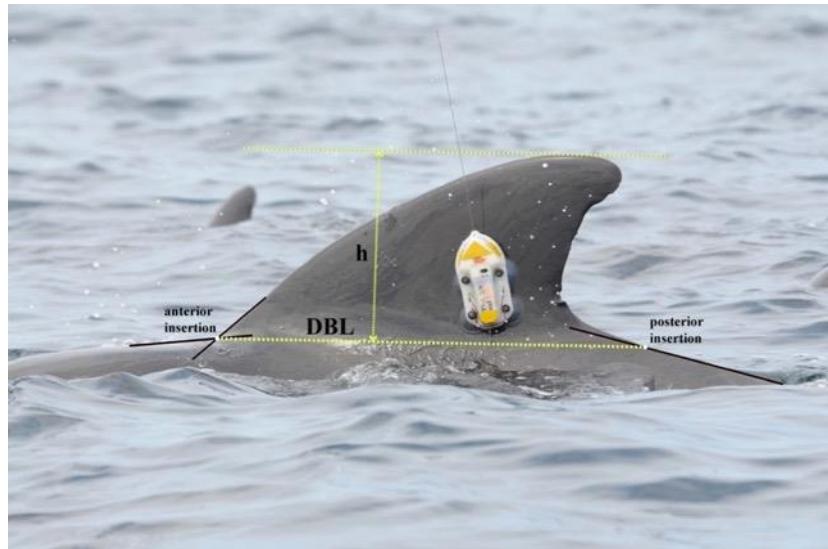


Figure 4 – Example of dorsal fin measurement on Gm08_143a

Jerk

To assess foraging success I examined the jerk signal (differential of acceleration) associated with each buzz. Prey engulfment by many marine mammals is accompanied by a rapid change in acceleration, in both raptorial and suction feeders, which likely reflects movements of the muscular in the gular region (Johnson et al. 2004; Ydesen et al.

2014; Wisniewska et al. 2014). To calculate the jerk signal, I used accelerometer data (sampled at 50 Hz) from the DTAG and calculated the 2-norm of the 3-axis differential of acceleration. To assess whether jerks could be used to identify capture events, I separated the jerk signal into three time windows (before, during and after a feeding buzz) of three seconds each. I first examined animals with DTAGs mounted forward of the dorsal fin, which would most likely capture a rapid change in the gular region and assessed jerk signals for buzzes that were isolated (>10 seconds from another buzz), closely prior to another buzz (<4 seconds), and closely following another buzz (<4 seconds), but without another following buzz. I built a distribution of non-buzz jerk signals from periods at least four second prior to buzzes. I compared maximum jerk (during a buzz), rms jerk value for the buzz, 95th percentile control jerk value, and position of the max jerk relative to the end of the buzz to look for a significant change in jerk value.

Calculated Aerobic Dive Limit (ADL_c)

Aerobic dive limit is defined as the post-dive onset of blood lactate accumulation (Kooyman 1980). Calculated aerobic dive limit (ADL_c) is determined by dividing total body oxygen stores by the diving metabolic rate (dMR) and is based on the findings that these values are quite close to the inflection point of the lactate concentration – dive duration curve (Kooyman 1980, 1983). Velten et al. (2013) estimated the mass-specific

total body oxygen (TBO) stores in short-finned pilot whales to be 68.3 ml O₂/kg. dMR has only been measured in a few species and is the least documented value in the ADL_c equation (Ponganis 2015), so I evaluated ADL_c with several possible values of the dMR including standard metabolic rate (SMR), 2*SMR, total cost of transport (COT_{TOT}), and COT_{TOT} with stroke glide efficiency. SMR is the resting metabolic rate per unit mass and is based on the Kleiber equation (Equation (3), (Kleiber 1975)),

$$SMR = 10.1mass^{0.75} \quad (3)$$

A value twice the allometrically predicted resting metabolic rate (2*SMR), based on Weddell seal and penguin data (Kooyman, 1980; Ponganis 2010), is commonly used to estimate dMR (Ponganis, 2015). COT_{TOT} (Equation (4); J kg⁻¹ m⁻¹) is a combination of maintenance and locomotor costs (Williams 1999) and is multiplied by the animals swim speed (using 4.8 kcal⁻¹ O₂ and a conversion factor of 4.187*10³ J kcal⁻¹) to calculate the dMR

4.

$$COT_{TOT} = 7.94mass^{-0.29} \quad (4)$$

COT_{TOT} likely over estimates dMR ((Velten et al. 2013), so I calculated COT_{adj} by applying a 27.7% reduction to the COT_{TOT}, which Williams et al. (Williams et al. 2000) estimated as the average metabolic savings Weddell seals achieved via stroke glide swimming.

Model

I used both physiological and behavioral factors to predict foraging depth for pilot whales. My goal was to apply a cost to each feeding event, using information from the DTAG to understand the pattern of buzzes in the water column. I built Bayesian linear models which predicted depth based on body size (small or large) of the animal and a cost metric for each feeding event. I evaluated a linear regression, linear mixed effects model with random intercepts and fixed slopes, and linear mixed effects model with random intercepts and random slopes and used deviance information criterion (DIC) to decide on the final model structure (see Appendix A). The best model was the Bayesian linear mixed model with random intercepts and random slopes. Mixed effects models are effective for longitudinal data, including repeated measurements from the same individual made at different points in time (Matthiopoulos 2011). Mixed effects models account for within-subject correlation, different group-level sample sizes and can prevent over-fitted models (Gelman & Hill 2007). The cost metric is a proxy for the energy expenditure of each feeding event, and I used several variables to estimate cost, including ODBA, MSA, speed, and buzz duration. I made a separate model for each cost metric and used deviance information criterion (DIC) to decide on the final model. I included subject specific random effects to account for subject specific variation and to account for the complex patterns of measurement inherent in this type of study. The model structure is:

$$y_{ij} \sim N(\theta_{ij}, \sigma^2) \quad (5)$$

$$\theta_{ij} = X_{ij}\beta + Z_{ij}\alpha_j \quad (6)$$

$$\alpha_j \sim MVN(\mathbf{0}, \Sigma) \quad (7)$$

Y_i is the response variable, which is depth for all models, X is the design matrix of predictor variables, β are the coefficients associated with each fixed predictor, and α_j is a vector of coefficients associated with the random effect (individual). The random effects slopes and intercepts are correlated with a multivariate normal distribution structure (Equation (7)), where Σ is the variance-covariance matrix. Σ is modeled as a wishart with a non-informative priors on each variance term and non-informative truncated normal (-1,1) on the correlation between variance terms in the off-diagonals. I used uninformed priors on all predictors and allowed a Gibbs sampler to model the data. All continuous predictors were centered and standardized. All analyses were performed in R version 3.0.3 and JAGS version 3.4.0.

Results

I obtained more than 209 hours of data, encompassing 330 dives, 227 foraging dives and 2556 individual foraging buzzes from the 40 pilot whale DTAG records (Table 1). Tag records ranged from 1:49 to 18:14 hours, with four of the tag records collecting data overnight. The estimated standard lengths of the 40 animals ranged from 2.9 to 5.1 meters (Table 1). Of the 19 tagged whales for which sex was determined, 11 were males (65.5 hours of data) and 8 were females (51.3 hours of data).

In general, the duration of dives increased with the maximum depth of dive, as observed in other studies of deep diving cetaceans (Soto et al. 2008). The number of buzzes per dive ranged from 1 to 52, with almost all (97%) foraging dives exhibiting more than a single buzz. In addition to dive duration (Figure 5), the number of buzzes (Figure 6), and rate of feeding buzzes (Figure 7) also increased with depth of dive. The distribution of the depth of buzzes across the population was slightly bi-modal with a break near 600 meters (Figure 8). Individual whales foraged in multiple areas of the water column (Figure 9), and were capable of switching between deep and shallow foraging dives during a single tag record.

Table 1 – DTAG deployment times, durations, sex and size including length of the base of the dorsal fin (DFB), the estimated body length calculated with Equation 2, and total identified feeding attempt buzzes. Tag ID is based on species, year and Julian day.

Date	Tag ID	Time On (local)	Time Off (local)	Total Time (hh:mm)	Sex	DBL (cm)	Body Length (cm)	Total Feeding buzzes
22-May-08	Gm08_143a	14:28	17:42	3:14		100	496	44
22-May-08	Gm08_143b	18:18	22:49	4:31		83	416	24
26-May-08	Gm08_147a	15:02	17:20	2:18		71	358	0
30-May-08	Gm08_151a	8:46	9:52	1:06		72	365	8
30-May-10	Gm08_151b	13:14	6:00	16:46		83	419	25
4-Jul-10	Gm10_185b	14:30	20:20	5:50	F	73	369	37
5-Jul-10	Gm10_186a	11:10	11:40	0:30		70	357	0
5-Jul-10	Gm10_186b	14:32	16:28	1:56	F	78	394	0
6-Jul-10	Gm10_187a	8:43	10:55	2:12		95	475	12
6-Jul-10	Gm10_187b	12:53	6:15	17:22	M	86	431	271
27-Jul-10	Gm10_208a	14:50	23:40	8:40	F	69	352	96
28-Jul-10	Gm10_209a	8:54	10:12	1:12	M	91	456	35
28-Jul-10	Gm10_209c	13:19	19:45	6:26	M	83	419	22
23-Sep-10	Gm10_266a	18:35	12:49	18:14		106	530	578
24-Sep-10	Gm10_267a	15:19	9:03	17:44	M	104	521	464
27-May-11	Gm11_147a	9:03	13:33	4:29	F	52	270	13
28-May-11	Gm11_148a	10:29	14:15	3:45	M	77	389	78

29-May-11	Gm11_149b	10:33	14:50	4:17	M	72	364	72
29-May-11	Gm11_149c	10:59	14:50	3:50		89	447	10
30-May-11	Gm11_150a	10:54	15:10	4:16		61	312	0
30-May-11	Gm11_150b	11:11	13:51	2:40		79	398	36
4-Jun-11	Gm11_155a	10:10	14:38	4:27		73	369	0
5-Jun-11	Gm11_156a	13:32	16:29	2:56		71	359	15
7-Jun-11	Gm11_158b	11:51	16:35	4:43	F	73	371	0
14-Jun-11	Gm11_165a	10:02	13:11	2:09	M	98	489	97
4-May-12	Gm12_125a	6:40	10:31	3:51	M	103	514	36
4-May-12	Gm12_125b	12:56	16:37	3:41		103	513	34
12-May-12	Gm12_133a	8:48	2:17	17:29	F	60	307	0
9-Jun-12	Gm12_161a	9:28	11:46	2:18	M	76	384	129
10-Jun-12	Gm12_162a	9:30	12:25	2:55	M	96	479	65
11-Jun-12	Gm12_163a	8:18	10:07	1:49		61	311	20
11-Jun-12	Gm12_163b	11:20	14:49	3:29	M	95	476	3
20-Jun-12	Gm12_172a	9:52	14:04	4:12	F	73	369	37
2-Sep-12	Gm12_246a	9:10	12:58	3:48	F	57	292	0
25-May-14	Gm14_145a	10:30	14:43	4:13		57	294	34
16-Jun-14	Gm14_167a	9:57	14:32	4:35		86	432	16
27-Jun-14	Gm14_178a	12:09	16:38	4:29		92	463	57
27-Jun-14	Gm14_178b	12:22	15:53	3:31		92	460	66
7-Oct-14	Gm14_279a	12:42	15:52	3:10		95	472	122
8-Oct-14	Gm14_280a	12:31	15:12	2:41		72	362	0

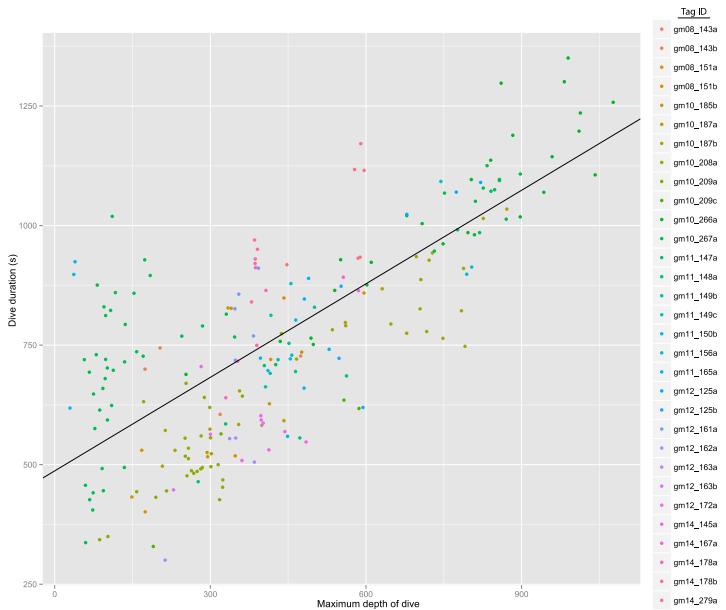


Figure 5 – Duration of dive vs maximum depth of dive, depicting an increasing trend of dive duration with increasing depth ($y=0.63x+484$, $r^2=0.54$).

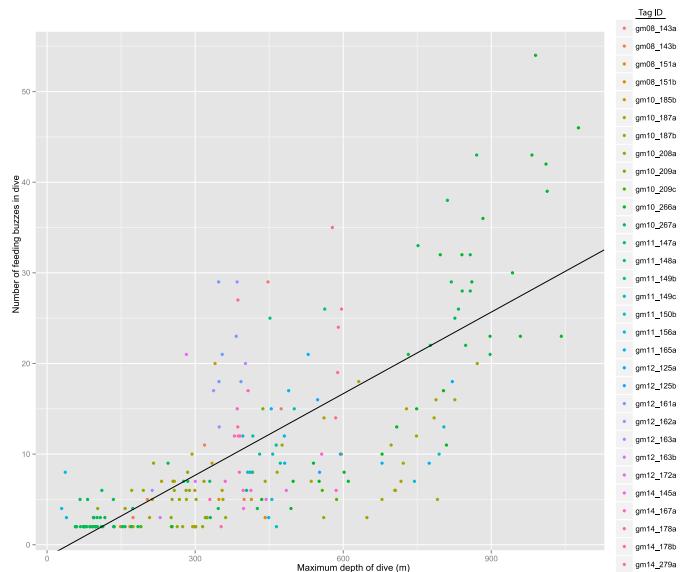


Figure 6 – Total feeding buzzes in dive vs maximum depth of dive. The number of buzzes per dive increases with increasing depth ($y=0.03x-1.33$, $r^2=0.51$) across the population.

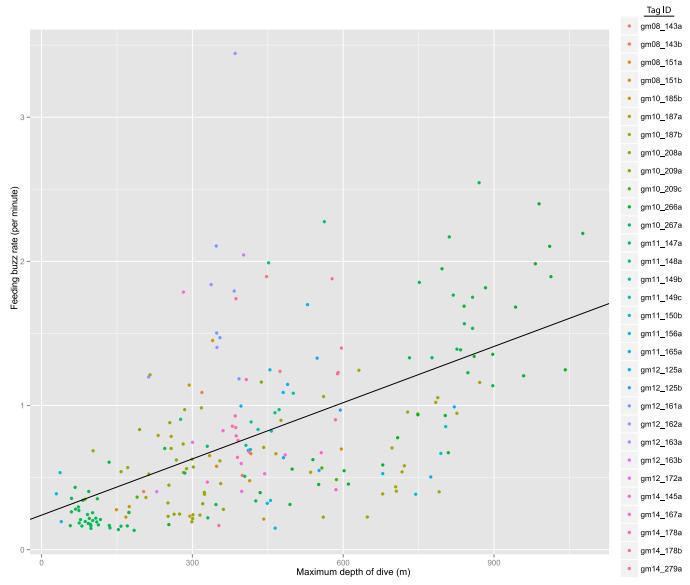


Figure 7 – Feeding buzzes per minute vs maximum depth in dive. The feeding buzz rate (per minute) increases with increasing depth ($y=0.0013x+0.24$, $r^2=0.32$) across the population

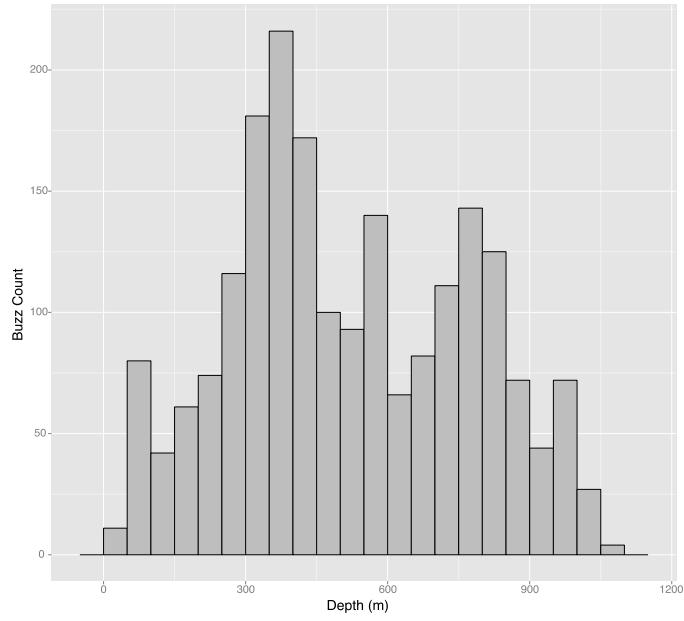


Figure 8 – Histogram of foraging buzz depths.

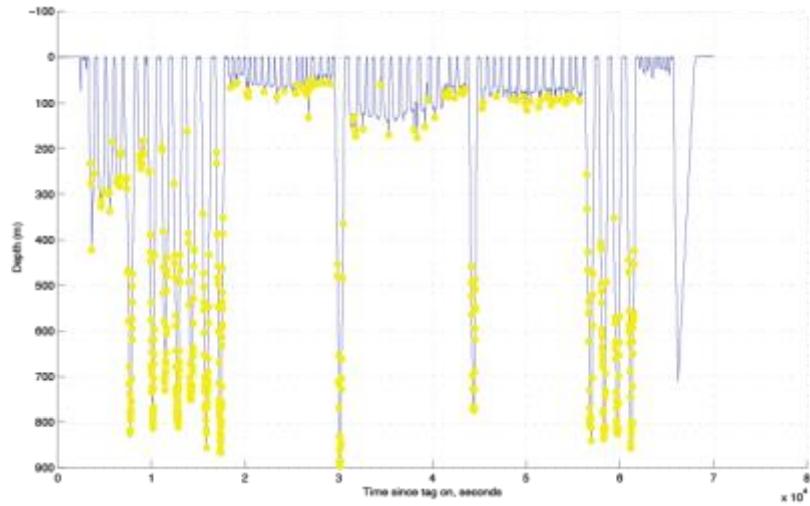


Figure 9 - Dive profile for Gm10_267a, yellow circles indicate buzzes. The individual varied its foraging activity between deep and shallow dives.

Cost Metrics

The regression values for speed estimation had a strong fit with an average r^2 value of 0.82 , similar to values from other studies (Goldbogen et al. 2008). Foraging animals averaged a swimming speed of 1.5 m/s during dives and increased their speed to 2.7 m/s during feeding buzzes, with some animals nearing 5 m/s during a feeding buzz (Table 2). Speed during and before buzzes varied considerably across animals, but was significantly less than values found in the Tenerife population (Soto et al. 2008). Long buzzes (>5 sec in duration), indicative of a prolonged chase (Teloni et al. 2008), occurred primarily at depths less than 600 meters (Figure 10). Variation in MSA (Figure 12) and ODBA (Figure 13) was also higher at shallower depths, although some of this variability is likely due to the influence of tag position on these measurements (Qasem et al. 2012). The pair of animals with concurrent tag deployments appeared to dive and

surface in synchrony, foraged at similar depths, and exhibited similar ODBA values for each feeding buzz (Figure 14).

Table 2 – Tag IDs, regression parameters from Equation 1 including goodness of fit (r^2), and average swim speeds, average buzz speed, and max buzz speed for the 31 pilot whales that performed feeding buzzes.

Tag ID	r^2	m	b	Average swim speed	Average buzz speed	Max buzz speed
Gm08_143a	0.74	-0.109	7.291	1.3	2.5	3.1
Gm08_143b	0.71	0.009	6.062	1.2	2.2	3
Gm08_151a	0.86	-0.057	4.191	1.4	3	3.7
Gm08_151b	0.63	-0.042	4.033	1.2	2.7	3.1
Gm10_185b	0.86	0.034	2.326	1.1	3.4	3
Gm10_187a	0.84	-0.042	3.185	1.15	2	3.7
Gm10_187b	0.64	-0.073	5.716	2	3.1	4.4
Gm10_208a	0.87	-0.113	7.452	1.56	2.8	3.6
Gm10_209a	0.96	-0.102	6.733	2	3.6	4.6
Gm10_209c	0.78	-0.044	4.535	1.5	3	3.5
Gm10_266a	0.96	-0.107	7.306	1.6	2.4	3.6
Gm10_267a	0.95	-0.082	5.877	1.5	2.3	2.9
Gm11_147a	0.69	-0.160	9.595	1.6	2.6	3.1
Gm11_148a	0.86	-0.069	4.917	1.5	2.6	3.1
Gm11_149b	0.91	-0.282	13.587	1.7	4	4.6
Gm11_149c	0.81	-0.109	6.152	1.8	2.1	2.2
Gm11_150b	0.89	-0.178	9.485	1.8	2.2	2.5
Gm11_156a	0.97	-0.054	5.576	1.8	4.4	4.8
Gm11_165a	0.99	-0.137	8.550	1.6	2.4	2.8
Gm12_125a	0.88	-0.110	5.747	1.6	2.4	2.9
Gm12_125b	0.72	-0.272	11.565	1.6	2	2.4
Gm12_161a	0.97	-0.132	7.751	1.8	3.7	4.3
Gm12_162a	0.25	0.173	2.599	1.6	3.4	3.9
Gm12_163a	0.94	-0.081	4.966	1.3	2.3	2.5
Gm12_163b	0.52	-0.028	3.489	1.1	2.6	2.6
Gm12_172a	0.91	-0.199	10.423	1.6	2.6	3
Gm14_145a	0.88	-0.011	3.422	1.2	2.2	2.6
Gm14_167a	0.96	-0.145	8.496	1.5	2.2	2.7
Gm14_178a	0.91	-0.021	3.249	1.5	2.4	3

Gm14_178b	0.78	-0.044	4.503	1.4	2.1	2.3
Gm14_279a	0.77	-0.059	5.244	1.8	2.3	2.6
AVERAGE	0.82	-0.085	6.259	1.5	2.7	3.2



Figure 10 - Buzz duration plotted at the depth of each feeding buzz. Longer buzz durations indicate a chase and the color indicates the individual animal.

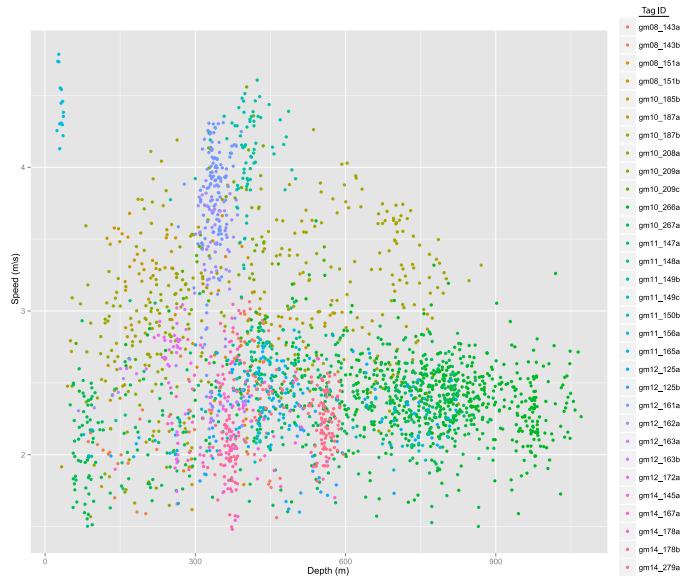


Figure 11- Estimated speed from flow noise for each feeding buzz plotted at the depth of the feeding buzz. Color indicates the individual animal.

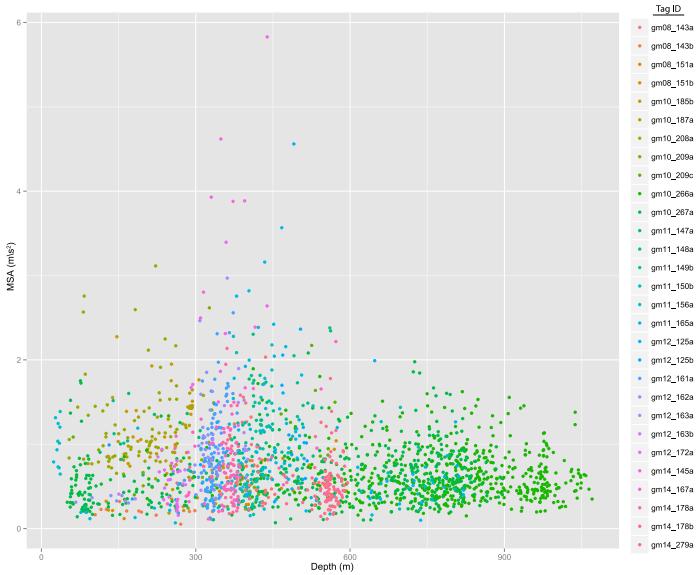


Figure 12 – Mean specific acceleration (MSA) for each feeding buzz plotted at the depth of each feeding buzz. Color indicates the individual animal.

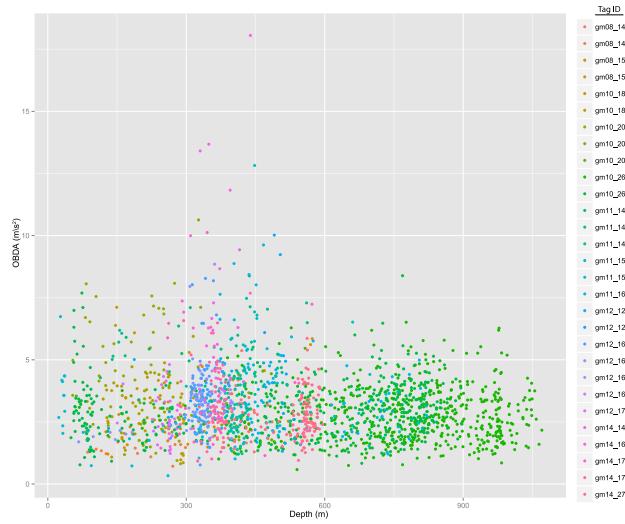


Figure 13 – Overall dynamic body acceleration (ODBA) for each feeding buzz plotted at the depth of each feeding buzz. Color indicates the individual animal.

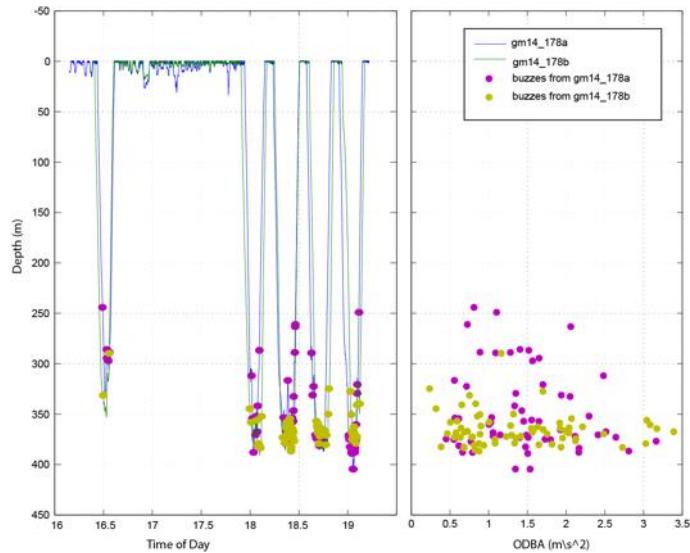


Figure 14- Simultaneous deployment of DTAGs on two pilot whales in a single group. At left is a time-aligned dive profile of the two animals with buzzes highlighted as blue and orange dots. On the right is the corresponding mean ODBA values for each buzz.

The estimated lengths of each of the animals fell within reported ranges for male and female short finned pilot whales (Yonekura et al. 1980). The average tag

deployment duration was similar for both sexes (Table 3), but the buzz rates for males (19.4 buzzes per hour) was five times greater than for females (3.5 buzzes per hour). There was a similar skew in foraging rates based on size, rather than sex, but this was not as pronounced (Table 4). There were marked differences in the foraging depths for male and female whales (Figure 15) and for large and small animals (Figure 15). Density plots indicate that females focused most of their foraging effort around 250 meters. Males foraged throughout the water column, but with most of their effort in waters deeper than 250 meters (Figure 16). Again there is a similar pattern with large and small animals, with smaller animals concentrating their foraging effort in shallower waters and larger animals foraging across a greater range of depths, but with more of their effort in deeper waters (Figure 17). The average speed during feeding buzzes was very similar for the two sexes with males averaging 2.83 ± 0.04 m/s and females averaging 2.84 ± 0.07 m/s. There was a slight difference in speed during buzzes between large and small animals with large animals averaging 2.67 ± 0.06 m/s and small animals averaging 2.91 ± 0.26 m/s.

Table 3 – Number of foraging dives (dives including buzzes), number of buzzes, total hours data, and number of animals for males, females and unknown sex.

Sex	Number of Foraging Dives	Number of Buzzes	Hours of Data	Number of Animals	Average Tag time (hours)	Buzz Rate per hour
Female	39	183	51.3	8	6.4	3.6
Male	112	1272	65.5	11	5.9	19.4
Unidentified	76	1101	92.4	21	4.6	11.9
Total	227	2556	209.2	40	5.4	12.2

Table 4 – Number of foraging dives (dives including buzzes), number of buzzes, total hours data, and number of animals in each size class

Size	Number of Foraging Dives	Number of Buzzes	Hours of Data	Number of Animals	Average Tag time (hours)	Buzz Rate per hour
Small (<395 cm)	71	564	89.9	21	4.5	6.1
Large (>395 cm)	156	1992	109.3	19	5.8	18.2
Total	227	2556	209.3	40	40	12.2

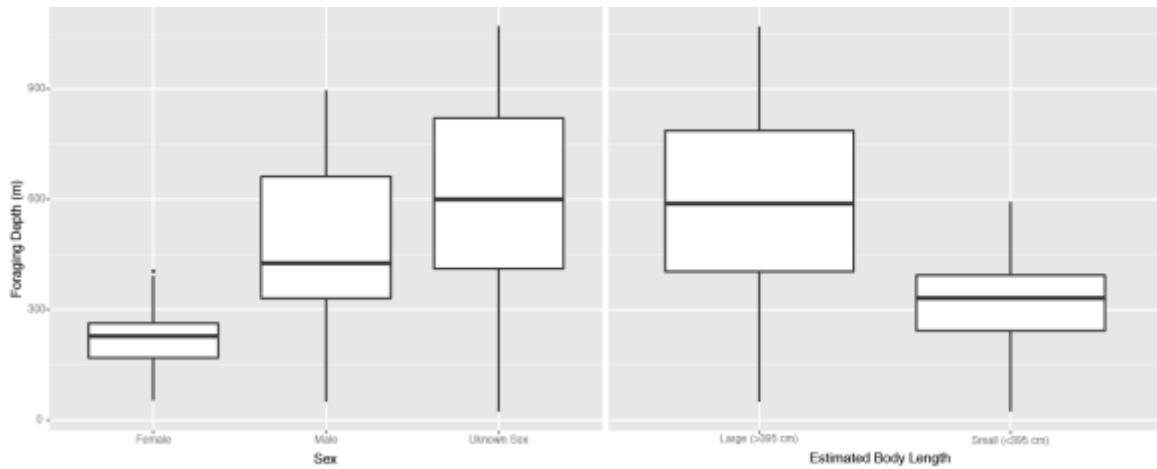


Figure 15 – Feeding buzz depths of different sex and size classes.

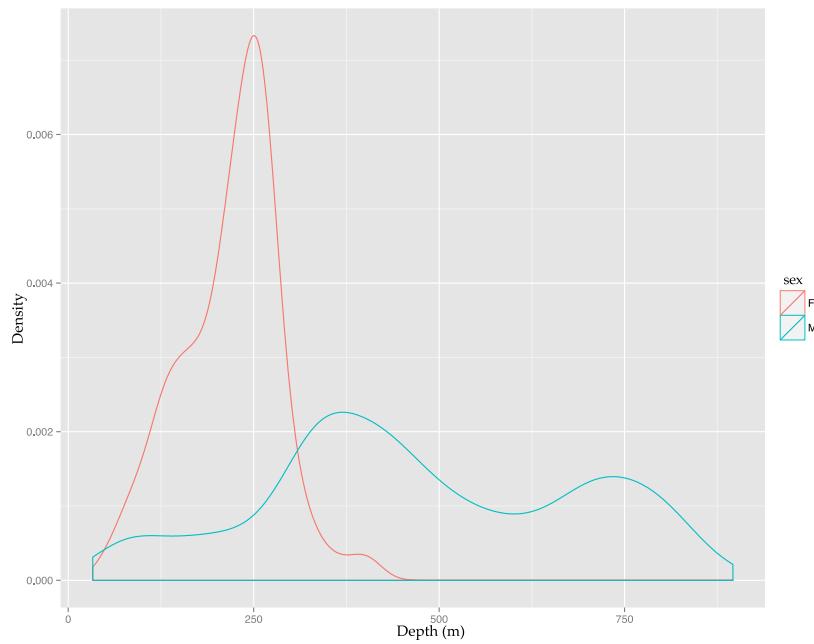


Figure 16 – Density plot of feeding buzz depths for females (red) and males (blue).

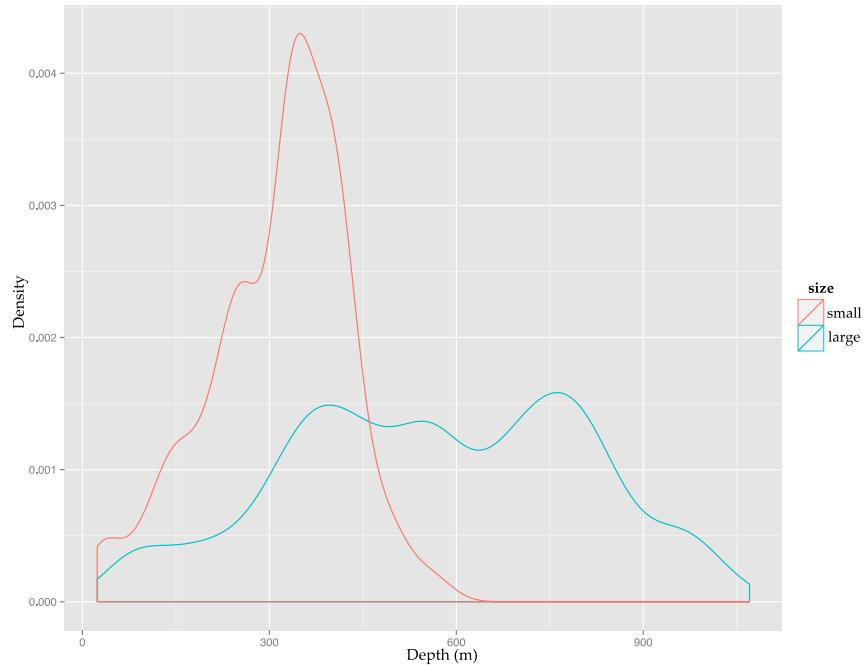


Figure 17 – Density plot of feeding buzz depths for small animals (<395 cm, red) and large animals (>395 cm, blue).

ADL_c

The calculated dive limits varied across body sizes and with the different values of metabolic rates used to estimate this parameter. The ADL_c values for large males (550 cm) was approximately 5 minutes longer than the ADL_c values of large females (395 cm, Table 5). The ADL_c values with 2*SMR and COT_{adj} dMR were similar for smaller animals but deviated for animals of larger mass (Table 5). Use of 2*SMR is slightly more conservative and appeared to fit the data well. For example, the largest pilot whale tagged was Gm10_266a, with an estimated standard length of 530 cm. The ADL_c of this whale at 2*SMR was 21.8 minutes and the 95th percentile dive duration for the same animal was 21.9 minutes. Observations from other studies suggest that diving animals rarely exceed their ADL (Ponganis 2015), and the dive duration below which 95-97 percent of dives occur has been used to estimate this parameter (Burns & Castellini 1996; Hindle et al. 2011). If 2*SMR is an appropriate value of dMR, the pilot whales in this study rarely exceeded their ADL (Figure 18 and Figure 19).

Table 5 – Calculated aerobic dive limits for different size classes and metabolic rates. Mass was calculated using the length to mass equation from Kasuya & Matsui (1984).

Length (cm)	Mass (kg)	ADL _c COT _{adj}	ADL _c 2*SMR
550	1942.13	24.34	22.39
470	1233.61	21.33	19.98
395	746.77	18.44	17.62
360	571.27	17.06	16.48

280	276.51	13.82	13.74
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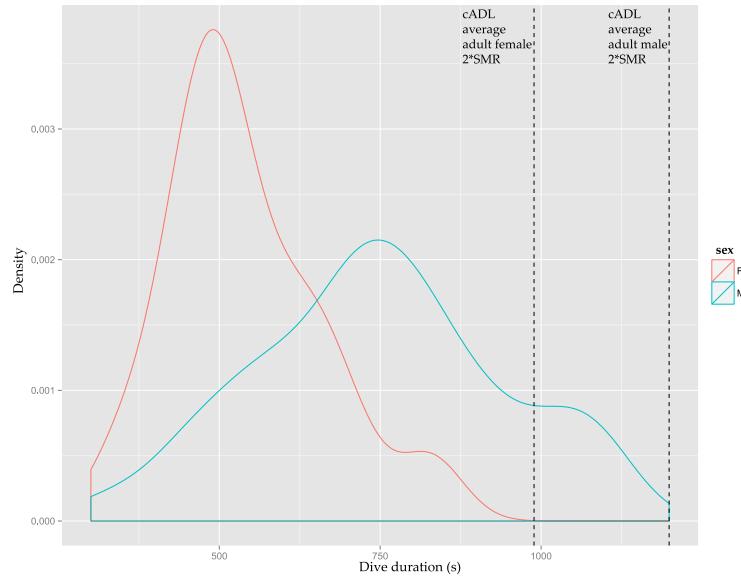


Figure 18 – Density plot dive durations for males (blue) and females (red).
Dashed lines represent at the ADL_c (2*SMR) for average adult males (460 cm) and females (360 cm).

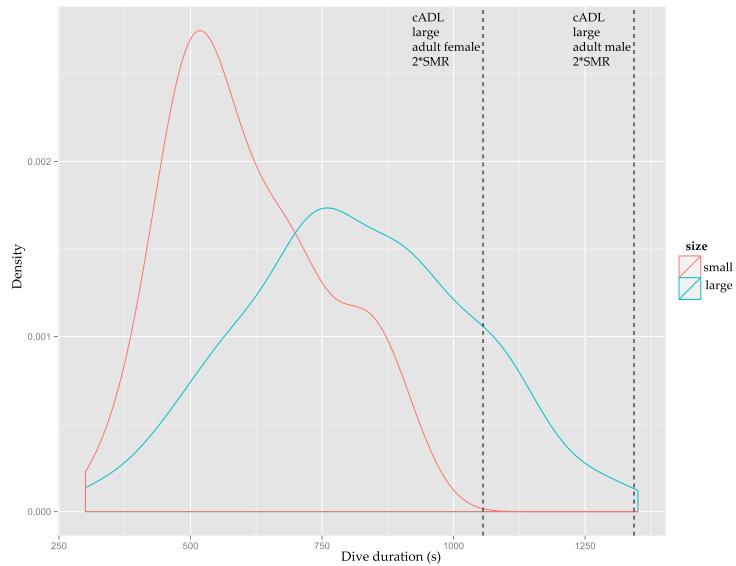


Figure 19 – Density plot of dive durations for large (>395 cm) and small (<395 cm) animals. The dashed lines represents the ADLc (2*SMR) for large adult males (550 cm) and females (395 cm).

Jerk

Values of the peak jerk signal varied significantly across and within animals in both magnitude and location relative to the end of each buzz. Jerk signals from isolated buzzes, buzzes followed closely by another buzz, and buzzes closely preceded by another buzz did not deviate from one another in terms of maximum magnitude (ratio to 95th percentile of the pre-jerk distribution) (Figure 20). (Ydesen et al. 2014) found a significant difference between the rms jerk values of before and during a prey capture. Most (94%) rms jerk signals (200 ms window) during buzzes were greater than the 95th percentile of the pre-jerk distribution, and, assuming this is an acceptable metric of capture success, indicates that most feeding buzzes result in captures.

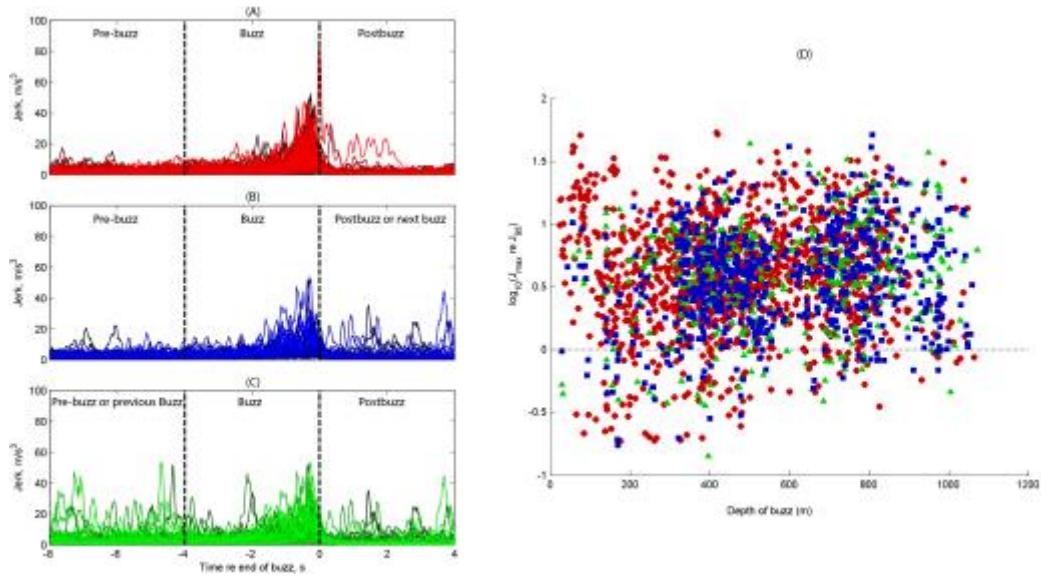


Figure 20 – A,B and C) Jerk values plotted before, during and after for each buzz. Red indicates feeding buzzes that were isolated with no other buzz within 10 seconds of the buzz, blue indicates feeding buzzes that were followed by another buzz within 4 seconds, and green indicates feeding buzzes that were preceded by another feeding buzz (<4 seconds), but not followed by another buzz. **D)** Log ratio the log ratio of max rms jerk value (200 ms window) over the 95th percentile pre-buzz jerk (non-buzz) values plotted at the depth of each buzz. Values below zero (dashed line) represent jerks that were lower than

Model

I modeled the depth of foraging buzzes with four models using different cost metrics, including ODBA, MSA, speed and buzz duration, with each cost metric modeled as both a fixed and random effect. Model 1, which featured ODBA, produced the lowest DIC (Table 6). Models employing MSA, ODBA and speed all resulted in a non-significant relationship with depth, while size was a significant predictor of foraging depth in all models (Table 7). The only cost metric that had a significant

relationship with depth was buzz duration (Table 8), which had a decreasing trend with depth.

Table 6 – DIC values for each model. X represents the fixed effects design matrix, Z is the random effects design matrix, and y represents the response variable.

Model	y	X	Z	DIC
model 1	depth	size, ODBA	ODBA	281949
model 2	depth	size, MSA	MSA	303017
model 3	depth	size, Speed	speed	300086
model 4	depth	size, Buzz duration	Buzz duration	293238

Table 7 – Fixed effects β values for model 1, if the range of values crosses zero it is equivalent to no effect

percentile	Intercept	Size (small)	ODBA
2.50%	379.33	-235.81	-0.33
50%	439.28	-138.2	9.65
97.50%	498.597	-39.43	20.29

Table 8 - Fixed effects β values for model 4, if the range of values crosses zero it is equivalent to no effect

percentile	Intercept	Size (small)	Buzz duration
2.50%	379.33	-229.13	-21.12
50%	439.28	-114.1	-11.89
97.50%	498.597	-3.12	-3.46

Discussion

The results of this study indicate that size and sex influence the diving behavior of short-finned pilot whales. The range of foraging depths of short-finned pilot whales appears to be constrained by body size and results in the potential for segregation of foraging habitat between different sex and size classes. Males and large animals foraged throughout the water column with most of their foraging effort at greater depths than where female and small animals foraged. Males and large animals also had foraging rates several times greater than females and small animals. The cohesive nature of short-finned pilot whale social structure likely limits adult males' ability to segregate geographically, but the differences in body size enable adult males to segregate from other members of their group by exploiting foraging patches at greater depth. The potential segregation of foraging habitat is likely facilitated by greater dive capacity and promoted by the combination of differences in activity budgets, predation tolerance and reduced intraspecific competition.

The variance in foraging depth and kinematics indicates western Atlantic short-finned pilot whales are opportunistic foragers that appear to flexibly alter foraging depth and strategies. Buzz frequency, slower speeds and the relatively weak jerk signals indicate that western Atlantic short-finned pilot whales are foraging on multiple small prey items. This pattern of foraging is different from that observed in Tenerife, Canary Islands where tagged animals often made downward directed sprints, presumably in

pursuit of large prey items (Soto et al. 2008). The weak jerk signals might be a product of tag placement, with most tags placed further back on the animal and might not have picked up on movements in the gular region. Also, the smaller prey items that these animals are assumed to be foraging on (Mintzer et al. 2008) might not elicit a large or distinct jerk signal during foraging. While the dietary segregation can result from habitat segregation, the results from my model imply that males and females, large and small animals, had similar kinematics around each foraging attempt. The results of stable isotope analysis from the same population indicate that both sexes forage in the same food web and are operating at the same trophic level (Unpublished Data).

In the only other large-scale published study, Soto et al. (2008) used DTAGs to study the foraging behavior of 23 short-finned pilot whales off Tenerife, in the Canary Islands. In general, their observations were similar to mine, with foraging dives reaching depths of 1,018 m and lasting up to 21 minutes. These authors focused their attention on a subset of foraging dives during daylight hours that involved high speed sprints presumably in pursuit of large squid. Their results also indicated a differences between day time and night time diving behavior, with night being much more centered on the deep scattering layer with more buzzes than daytime dives. Given the high level of variation observed in other aspects of the behavior of this species, I predict that differences in foraging strategies among populations of short-finned pilot whales will most likely reflect variation in the environment and prey fields.

While I cannot fully define the activity budgets for short-finned pilot whales, I can make an assessment of time devoted to foraging. Males and large animals made longer and deeper dives than females and smaller animals. The larger body mass of adult males resulted in ADLc values that were nearly an additional five minutes longer than that of an average adult female (Table 5). It appears that this population of short-finned pilot whales, like most breath hold divers, rarely if ever exceed their aerobic dive limits (Ponganis 2015). A considerable amount of time and energy is spent in transit to deep foraging depths and the extra time at depth should confer an energetic advantage by reducing the number of transits from the surface to capture prey. I observed stark differences in the feeding budgets between males and females (Table 3) and between large and small animals (Table 4), including buzz rates for that were five times higher for males than females. The larger size of males lead to greater overall metabolic requirements. Using the equation $FMR = 406 * M_b^{0.75}$, (Williams et. al., 2001) the field metabolic needs of an average adult male is approximately 1.8 times greater than that of an average adult female. The presence of dependent calves and small independent juveniles could limit the foraging depths and durations of adult females. Short-finned pilot whales have a remarkably long period of dependency and some calves appear to nurse into their teens (Williams et al. 2008). Calves and juveniles will have restricted dive capacities ((Kasuya & Marsh 1984; Tyack 2009a)) and solitary calves are vulnerable to predation at or near the surface by sharks and killer whales (Best et al. 1984). Bernard

and Hohn (1989) suggested that by feeding at the surface on flying fish, as opposed to the deeper squid preferred by others, female spotted dolphins, *Stenella frontalis*, avoid leaving their vulnerable calves unattended. In a similar way, pilot whale females might limit daytime foraging since they are presumably subject to higher predation pressure at the surface during daytime hours (Best et al. 1984).

It is difficult to measure the influence of predation on short-finned pilot whales both due to the inherent rarity in predation events and the limited ability to observe deep diving cetaceans that live far from shore. Pilot whales have been found in the stomachs of killer whales (Baird et al. 2008), and one of the most important factors promoting the evolution of sociality in cetaceans is protection from predators via dilution of predation risk, increased vigilance and social anti-predator defense (Jefferson et al. 1991). Short-finned pilot whales make calls during ascents from deep dives to maintain social ties at the surface (Connor 2000), and closely related long-finned pilot whales synchronize their foraging bouts (Jensen et al. 2011). In the single simultaneous deployment, ascents and descents were strongly synchronized between two pilot whales of different sizes ((Visser et al. 2014)). Pilot whales are at risk to predation at the surface (Jefferson et al. 1991), so the maintenance of group cohesion between dives appears to be a form of social predator defense. This hypothesis appears to be supported by a series of recent playback studies in which closely related long-finned pilot whales (*Globicephala*

melas) rapidly congregated at the surface when exposed to the sounds of killer whales (Jefferson et al. 1991).

The social structure of pilot whales likely provides some measure of protection from predation risk, at a certain point the benefits of group living are exceeded by costs, mainly feeding competition (Curé et al. 2012). For groups that exhibit natal philopatry, the degree to which both sexes maintain bonds to their natal group will be shaped by resource availability (Marshall et al. 2012). Resident killer whales appear to reduce competition between males and the other members of their maternal group through small-scale segregation (Beerman et al. 2015). While it is unclear to what degree short-finned pilot whales exhibit natal philopatry, they do form long-lasting, stable associations and are found in mixed sex and age groups (Beerman et al. 2015). Male short-finned pilot whales, whose short-term movement patterns are constrained by the need to remain within a social group, will experience significantly less intra-specific competition for resources at greater depths, foraging areas that cannot be reached by smaller-bodied females and juvenile whales. Feeding buzz rates increased with the depth of dive and buzz duration decreased with depth ((Mahaffy et al. 2015; Alves et al. 2013)), indicating longer (and more expensive) chases at shallower depths. This may be reflection of prey as cephalopods in the upper water column tend to be fast with high muscle mass and metabolic rates (Seibel 2007), while deep-living cephalopods tend to be sit and wait predators that are less active swimmers (Seibel 2007). It's unclear if this is

the case because the speed and kinematics around each foraging buzz did not change with depth. It is possible that these differences might be the result of differences in prey density, which determines how many prey a diving predator will encounter in a patch, and has been shown to determine consumption rates and efficiency (Seibel 2007).

Habitat structure has also been shown to mediate the foraging success of predators (Beyer 1995; Goundie et al. 2015; Goldbogen et al. 2015) and large males might use the sea floor as a boundary to limit prey escape behavior.

What makes this system unique is the drivers that normally force sexually dimorphic species to segregate appear to work in concert to facilitate cohesion in short-finned pilot whales. Predation risk promotes cohesion at the surface as a form of social defense strategy while the large size of adult males provides the capacity to feed over a greater range of depths, potentially limiting intraspecific competition. While differences in body size lead to differences in energy requirements, feeding rates and dive capacities, pilot whales appear to overcome the costs to synchrony by coordinating their foraging bouts (Cermak 2002; Warfe & Barmuta 2004) and making calls at depth to maintain social ties with the group (Visser et al. 2014).

The findings of this study provide strong support for the hypothesis that pilot whale size classes segregate their foraging habitat by diving to different depths. A clearer picture of short-finned pilot whale group dynamics is required to put these findings into a context. Many of these gaps can be filled with synoptic tag data within a

group. Confirmation of segregation of foraging depths will require concurrent deployment of tags on dissimilar sized pilot whales within a group. Satellite-linked time-depth recorders (SLTDRs) will also provide a clearer picture of the activity budgets, degree of foraging segregation, bout synchrony and the level to which adult males are constrained geographically by their social group by providing continuous dive and movement data over several weeks to months.

Chapter 2: A Multi-scale Approach to Understanding the Temporal Variation in the Foraging Patterns of Short-Finned Pilot Whales

Introduction

The impact of anthropogenic disturbance on measures of fitness, such as survival and reproductive success, requires an understanding of natural patterns of variation in behavioral states (Viviant et al. 2014). Understanding when and why animals move from one state to another, is an important first step to developing a baseline of these natural patterns. Investigation of variation in behavioral patterns, and of transitions between states, often requires a researcher to define *bouts*, which are periods in which a particular behavior is engaged in frequently, although not necessarily continuously (Bart et al. 2009). Diving vertebrates, which must return to the surface for oxygen at the end of every dive, typically forage in bouts of dives interspersed with periods of other behaviors such as traveling, resting, or socializing (Boyd 1996; Mori et al. 2001; Luque & Guinet 2007). Analysis of the duration of foraging bouts, and of variation in this parameter, requires sampling periods that are longer than typical bout duration and the ability to differentiate foraging dives from other subsurface behaviors. Studies of bout analysis in cetaceans have lagged behind those of other diving species, such as pinnipeds, due to the difficulties associated with studying these fully aquatic animals in the marine environment for periods of time sufficient to characterize bout behavior (Hooker & Baird 2001).

The use of a new generation of animal-borne tags is overcoming many past difficulties and is revolutionizing our understanding of cetacean movement and foraging patterns. Biologging devices now available for use with cetaceans range from archival tags that yield high-resolution data on fine-scale behavior and acoustics (Johnson & Tyack 2003) to satellite-linked sensor packages that provide positional data over very large spatial and long temporal scales (Goldbogen, Friedlaender, et al. 2013; Schorr et al. 2014). Acquisition of data from these tags is constrained by storage space in archival tags and battery life and the bandwidth required to transmit data in satellite-linked tags. As a result, researchers must consider important tradeoffs between data resolution and tag longevity when planning a field program. High-resolution data are often required to accurately define behavioral state (Whitehead 2008), but it is impossible to store such data for long periods or to transmit them over bandwidth-limited satellite systems. In such circumstances, the use of archival tags (and the necessity to recover the tags) is essential. Many species of cetaceans range over great distances (Hooker & Baird 2001), so investigation of foraging patterns in the medium to long-term requires some mode of data telemetry. Satellite-linked time-depth recorders (SLTDRs) relay summarized and compressed data (location, temperature, depth, and dive metrics) through the ARGOS satellite system and can transmit for many months. As a result of these limitations, researchers must often decide between high-resolution behavioral inferences made over short periods, or collection of summarized data over

much longer periods. There have been recent calls to merge these different modalities to address complex questions of behavioral response over more time scales that are relevant to the questions being addressed (Goldbogen, Friedlaender, et al. 2013).

Cetaceans dive for many reasons including foraging, horizontal movement (Fish 2006), predator avoidance (Tyack et al. 2006), and management of blood and tissue gases (Hooker et al. 2012). In studies of pinniped diving behavior, researchers typically assign each dive to a behavioral category using metrics such as dive shape and/or bottom duration (Le Boeuf et al. 1988; Baechler et al. 2002), assuming that these aquatic predators will maximize profitable foraging time at the bottom of each dive.

Simultaneous deployments of additional sensors such as stomach-temperature loggers (Austin et al. 2006), accelerometers for 3D movement (Harcourt et al. 2000; Gallon et al. 2013; Shepard et al. 2008), accelerometers to measure jaw movement (Liebsch et al. 2007; Wilmers et al. 2015), and video cameras (Wilson et al. 2015, Davis et al., 1999 & 2003, Bjorge 1995) have been used to ground truth these classification systems. Pinnipeds are well suited for such studies since they return to shore periodically (Ropert-Coudert et al. 2009), facilitating the deployment and retrieval of multiple archival tags, sometimes on a single individual.

Unfortunately, it is difficult to deploy multiple tags on individual cetaceans. Instead, the predictive power of dive metrics generated from summarized, long-term data can be tested with the use of high resolution tag data collected during shorter

deployments (Viviant et al. 2014). The fine-scale foraging behavior of several species of toothed whales has been described with the use of archival, high resolution, multi-sensor DTAGs (Johnson et al. 2009). Toothed whales echolocate to find prey using low repetition clicks and produce rapid click trains, often referred to as foraging buzzes, in the terminal phase of prey capture attempts (Johnson et al. 2009). DTAGs provide detailed records of the three-dimensional movement and recordings of the animal's acoustic environment, including echolocation produced during foraging (Johnson & Tyack 2003). Therefore, records of foraging buzzes, integrated with depth and three-dimensional movement have been used to examine the foraging strategies of several odontocete species (Johnson et al. 2004; Soto et al. 2008).

Long sampling periods may also allow for inference into the physiological limits to foraging behavior. Breath-hold diving animals must balance the competing costs of energy gain and oxygen consumption and the patterns of foraging behavior will likely be mediated by these two competing needs. Marine mammals seldom exceed their aerobic dive limit (ADL), the maximum length of period an animal can stay submerged without generating lactic acid through anaerobic metabolism (Ponganis 2015). However, Hazen et al. (2015) recently showed that blue whales, *Balaenoptera musculus*, will incur an oxygen debt when prey density is particularly high. Nevertheless, most dives should be shorter in duration than the ADL, and researchers have taken advantage this pattern to infer a behavioral aerobic dive limit (ADL_B) as the dive duration below which 95-97% of

dives occur (Hindle et al. 2011). Any oxygen debt incurred by very long dives should be reflected in subsequent surface resting periods, so an analysis of minimum inter-dive intervals in relation to dive durations can also been used to estimate ADL_B (Horning 2012).

Air breathing predators that feed on vertically migrating prey should act to minimize transport costs by foraging during periods when prey patches are near the surface. Diel vertical migration (DVM) is a common feature in the world's oceans and is characterized as a regular pattern of vertical movement from shallow depths at night to deeper depths during daylight hours (Hays 2003). It is hypothesized that organisms employ DVM to reduce predation risk to visual predators (Bollens et al. 1992). Some echolocating odontocetes are known to take advantage of DVM to feed at night when prey is near the surface. In Hawaiian waters, Spinner dolphins, *Stenella longirostris*, forage on prey that make both vertical and horizontal diel migrations (Benoit-Bird & Au 2003). The dolphins rest in shallow waters during the day and at night track their preys' horizontal movement and exploit the vertical areas within the boundary layer that has the highest density of prey (Benoit-Bird & Au 2003). In the Canary Islands, short-finned pilot whales, *Globicephala macrocephalus*, spent more time foraging at night in shallow waters based on acoustic recordings of echolocation clicks and depth sensor (Soto 2006). Long-finned pilot whales, *Globicephala melas*, in the Ligurian sea made their deepest dives just before sunset (Baird et al. 2002). Pantropical spotted dolphins, *Stenella attenuata*,

forage more at night than during the day and make their deepest dives just before sunset, presumably to meet the rising diel migrants (Baird et al. 2001).

Here I describe the foraging patterns of short-finned pilot whales off Cape Hatteras, North Carolina by combining DTAG and SLTDR records. The specific goals of this study were to: (1) use acoustic records from the DTAG to separate foraging from non-foraging dives, and then to evaluate the predictive power of various dive metrics to predict foraging behavior in short-finned pilot whales; and (2) classify dives from SLTDR records as foraging or non-foraging using the results of (1). My intent was to combine these two types of data to analyze long-term foraging patterns and, particularly, to determine pattern and variation in foraging bouts, evaluate the potential for diurnal variation in foraging behavior, and calculate ADL_B for short-finned pilot whales, specifically to examine whether aerobic capacity contributes to the cessation of foraging bouts.

The study area off Cape Hatteras is a particularly dynamic region. Located on the continental shelf break where the Gulf Stream and Labrador Currents converge, the area experiences significant variation in temperature and flow regimes, as the Gulf Stream meanders east and west and produces a constant stream of transient features, such as frontal eddies that influence the region (Savidge 2004). The area attracts dense concentrations of marine mammals and seabirds, particularly along the shelf break (Best et al. 2012;(Roberts et al. 2016), and commercial and recreational fishing vessels target

tunas and other large predatory fishes in this region year-round ([NMFS 2006](#)). The diet of short-finned pilot whales in this region has been described in a single study, which examined the stomach contents of 27 mass-stranded whales. These whales stranded near Cape Hatteras in January 2005 and their stomachs contained a diverse assemblage of small-bodied meso- and bathypelagic cephalopods ([Mintzer et al. 2008](#)). At least some of these prey species undertake diel vertical migrations. Based on these observations, I predicted that pilot whales off Cape Hatteras would feed mostly at night when the Deep Scattering Layer (DSL) rises towards the water's surface, making prey more accessible to these air-breathing predators.

Materials and Methods

Instrument Deployment

Forty DTAGs and six Low Impact Minimally Percutaneous Electronic Transmitter (LIMPET) SLTDR tags were deployed on short-finned pilot whales (

Table 9) along the shelf break off Cape Hatteras (Figure 21). All tags were deployed in the months of May through September with DTAGs deployed from 2008 to 2015 and SLDRs deployed only in 2014 and 2015. Larger, well-marked whales were selected for tagging and adult females accompanied by dependent calves were avoided (Figure 22).

DTAGs were secured to the dorsal fin or dorsal surface of whales with four 6-cm diameter suction cups, by a researcher using a hand-held carbon fiber pole from a small rigid-hulled inflatable boat (RHIB). The DTAGs sampled acoustic data at 96 kHz on two channels using a 16-bit analogue-to-digital converter and sampled the pressure sensor at 50 Hz to generate measurements of the depth. The LIMPET tags were deployed with a Dan-Inject CO₂ rifles and attached to the dorsal fin of each whale. The LIMPET tags used Wildlife Computers SPLASH10-292B sensors, which transmit continuous records of summarized and compressed data on temperature, depth and light for 14 days, before adopting a transmission duty cycle for the remainder of the deployment (Schorr et al. 2014). This 14-day period of continuous transmission afforded an opportunity to examine the diving behavior of these tagged whales and, particularly, the duration of foraging bouts.

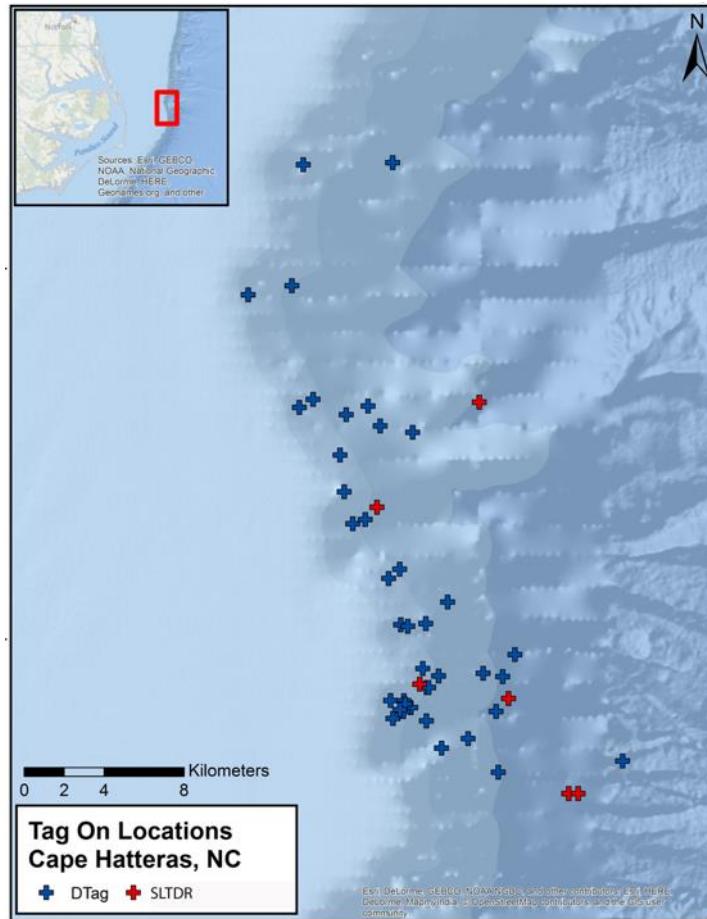


Figure 21 - Tagging locations for DTAGs and SLTDRs on short-finned pilot whales off Cape Hatteras, North Carolina.

Table 9 - Deployments of SLTDRs on short-finned pilot whales off Cape Hatteras, North Carolina

Deployment Date	Tag ID	Duration
5/14/14	Gm_Tag085	14 days
6/11/14	Gm_Tag093	14 days
9/11/14	Gm_Tag098	14 days
9/11/14	Gm_Tag100	14 days
5/16/15	Gm_Tag123	6 days

5/19/15 Gm_Tag127 14 days



Figure 22 - Images of LIMPET and DTAGs deployed on pilot whales GmTag087 and Gm12_161a off Cape Hatteras, North Carolina.

Data Processing

I manually audited the acoustic recordings on the DTAG records in MATLAB (MATLAB 2012) by carefully listening to the recording along with visual inspection of the spectrogram. I marked all potential foraging buzzes, and pulsed sounds that were associated with continuous echolocation clicks (Soto et al. 2008) along with the start and end of echolocation clicks for each dive. Following the audit, I employed a supervised click detector (Arranz et al. 2011) to identify clicks with low-frequency energy (1-5kHz), indicating that they originated from the tagged animal. These clicks were then displayed with their angle of arrival (based on difference in time of arrival to the two tag hydrophones). After establishing angle of arrival for the click sequences on each dive, I removed any buzz that appeared to be produced by another whale. I then fit a mixed Gaussian distribution to the log of the inter-click intervals (ICI) and used the equal posterior probability value as the boundary between buzz and regular clicks. Finally, I

computed buzz durations as the time from the first to the last click in the buzz with an ICI less than 22 ms (Teloni et al. 2008).

I classified a *dive* as any submergence with a maximum depth of 20 m or more and identified *foraging dives* by the presence of at least one foraging buzz produced by the focal animal during the dive. For each dive I extracted metrics of *maximum depth*, *duration*, *shape*, and *post-dive duration* to use as potential predictors of foraging behavior. To describe dive shape I used a Wildlife Computers algorithm based on time spent at 80% of the maximum depth of the dive. I defined these metrics as follows:

$$\begin{aligned} D &= \text{Duration of Dive} \\ T &= \text{Time spent at 80\% of maximum} \\ &\quad \text{depth} \\ V &\text{ shape if } T < 0.2*D \\ U &\text{ shape if } 0.2*D \leq T < 0.5*D \\ \text{Square} &\text{ shape if } T \geq 0.5*D \end{aligned} \tag{1}$$

For each tag deployment I determined the time of sunset and sunrise each day with the function *suncycle* in MATLAB, which uses the Naval Observatory classification system. I used these times to create a factor level for each dive as either daytime or nighttime determined by the starting time of the dive since several dives spanned both levels.

Analysis

I carried out all analysis using R statistical software (R Core Team 2014). I employed two different decision tree methods to discriminate between foraging and non-foraging dives with the DTAG data using the following predictive variables: *maximum depth; duration; shape; post-dive duration; and day/night.* Before running each decision tree, I split the data set into training and testing sets to assess the predictive accuracy of each method. To understand the relative contribution of each variable, I used the non-parametric Random Forest (RF) method. RFs improve statistical prediction by generating a large number of bootstrapped decision trees (based on random samples of variables) and adopting a final result by combining the results across all the trees (Liaw & Wiener 2002).

RFs are powerful classifiers, but it can be difficult to follow a single dive through the forest and arrive at the reason(s) for its classification because there are thousands of trees and only one set of predictors (Murray & Rosauer 2011). To aid in the interpretation of the RF results and to provide applicable classification values for other researchers, I employed a Conditional Inference Tree using the function ctree (Hothorn et al. 2012) in the package partykit (Hothorn & Zeileis 2014). A Conditional Inference Tree uses a significance test to select variables rather than simply selecting the variable that maximizes an information measure. This statistical approach ensures an appropriately

sized tree is grown and requires no pruning. I fit the models with a training dataset and determined classification error with an independent validation set.

I restricted my analysis of bouts to continuous dive records from the SLTDR tags, generated during the first 14 days of each record (one tag transmitted for only six days). I categorized dives as foraging or non-foraging based on the results of the decision tree analysis described above and conducted an analysis of diving and foraging bouts. I determined Bout Ending Criteria (BEC) for each record following the methods described in Luque and Guinet (2007) using the R package DiveMove (Luque 2007). DiveMove uses maximum likelihood estimation of the distribution of the absolute difference in inter-dive duration (t), which is the time elapsed between one foraging dive and the following one. The distribution of t is assumed to be a mixture of two random Poisson processes. These processes are composed of a fast process, representing the short time scale of an individual dive, and a slow process, representing the time scale over which bouts are characterized (Sibly et al. 1990). I removed isolated dives from the analysis and included only bouts consisting of at least three dives.

To estimate ADL_B I analyzed the minimum surface intervals in relation to dive durations using the SLTDR data. Following Horning et al. (2012), I used constraint line analysis of scattergrams of dive durations and inter-dive intervals to find an inflection point where surface intervals begin to increase with increasing dive durations. There was no inflection point between dive durations and inter-dive intervals and I could not

determine a ADL_B using this method. Therefore, I determined the ADL_B as the dive duration below which 95-97% of the dives occur (Burns & Castellini 1996; Hindle et al. 2011). This is based on the original observations by Kooyman et al. (1980) that 93-97% of dives by Weddell seals do not exceed their measured aerobic dive limit. I compared the ADL_B values to calculated aerobic dive limits (ADL_C) following methods outlined in Chapter 1. For ADL_C values I used two times standard metabolic rate (2^*SMR) based on estimated body size of each tagged animal, which I determined using photos of the dorsal fins and known dimensions of the tags following the methods described in Chapter 1.

Results

The individual DTAG records ranged from 1 to 18 hours in duration and the entire dataset consisted of more than 209 hours of data, including 330 dives and 227 foraging dives. The Random Forest Analysis indicated that the two most important predictors of foraging were dive duration and maximum depth; dive shape and day/night had little predictive power. Classification error was similar in both models (Table 12), so I opted for the simple classification using the conditional inference tree, and thus defined a foraging dive as any submergence with a duration of more than 400.6 seconds.

I applied the predictors identified from the conditional inference tree to the six SLTDR dive records and defined 2,783 of the 3,572 dives (78%) as foraging dives. Foraging dives primarily occurred along the shelf-break off the coast of North Carolina

and southern Virginia (Figure 25). Mean foraging bout period across all whales was 2.94 hours, with a mean of 8.2 dives per bout, and a maximum bout duration of 14.34 hours (Figure 26 and Figure 27, Table 14). The post-dive surface duration varied relative to bout duration, and there did not appear to be any discernable pattern of increased minimum post-dive surface duration with increasing bout length (Figure 28 and Figure 29).

The mean length of dive bouts to be 5.06 hours, with an average of 12.4 dives per bout and maximum bout duration of 40.8 hours (Table 15). There was no discernable relationship between bout duration and post-dive duration. Nor was there any diurnal pattern in dive behavior, or any significant diel differences in the number dives per hour, foraging dives per hour, or mean maximum depth of foraging dives (Figure 31, Table 16). Minimum inter-dive intervals did not increase with increasing dive durations in any of the six SLTDR dive records (Figure 32). ADL_B and ADL_C values were in close agreement with each other across animals (Table 17) and the ADL_B determined at the 97th percentile of dive durations was smaller than the ADL_C for five of the six animals.

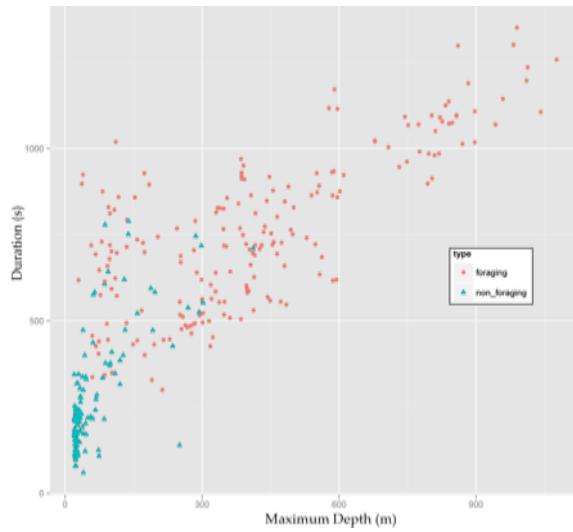


Figure 23 – Results of DTAG analysis, plot of maximum depth vs. duration with blue triangles representing non-foraging dives and red circles representing foraging dives.

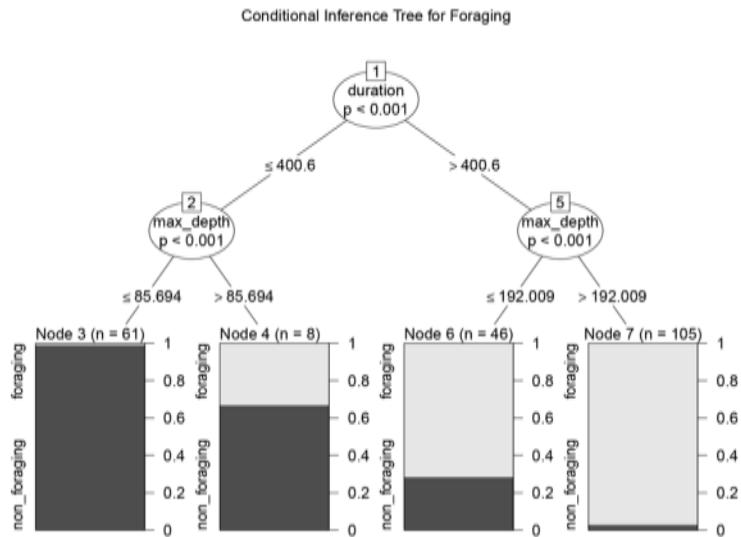


Figure 24 - Classification tree produced by analysis of predictors of foraging dives. Bar plots in the non-branching nodes indicate the relative dropouts with particular combinations of relative predictors.

Table 10 – Confusion matrix for Random Forest Analysis showing the classification error for the two dive categories.

Prediction Reference	Foraging	Non-foraging	Classification error
Foraging	52	1	0.018
Non-foraging	4	28	0.125

Table 11 – Confusion Matrix for Conditional Inference Tree showing the classification error for the two dive categories.

Prediction Reference	Foraging	Non-foraging	Classification error
Foraging	51	2	0.038
Non-foraging	3	29	0.094

Table 12 – Comparison of overall accuracy and statistics between the two classification methods.

Test Statistics	Random Forest	Conditional Inference Tree
Accuracy	0.941	0.941
95% CI	0.868, 0.981	0.868, 0.981
Kappa	0.872	0.868

Table 13 – Variable importance determined in Random Forest Analysis. The mean decrease accuracy reflects the reduction in accuracy if the variable was removed from a decision tree.

Variable	Foraging	Non-Foraging	Mean decrease Accuracy	Mean Decrease Gini
Duration	54.7	85.5	88.1	63.4
Max Depth	46.6	49	64.1	46.6
Post-Dive Duration	30.5	-3.6	26.4	14.5
Shape	5.7	13.3	12.9	3
Daytime/Nighttime	-1.4	2.2	-0.1	1

Table 14 – Foraging bout analysis, including bout ending criterion (BEC), average bout duration, maximum bout duration, average number of dives in the foraging bout, maximum number of foraging dives in a bout and the percent of the tagged animal's time spent in foraging bouts.

Animal ID	Tag Period	BEC (sec)	Avg Bout Duration (Hrs)	Max Bout Duration (Hrs)	Avg. No of Foraging Dives	Max No. of Foraging Dives	Percent Time in Foraging Bouts
GmTag085	5/14/14-5/28/14	978.2	2.71	10.79	8.1	29	59
GmTag093	6/11/14-6/17/14	1231.8	2.25	6.82	6.9	17	54
GmTag098	9/11/14-9/25/14	808.6	3.04	9.36	8.2	34	67
GmTag100	9/11/14-9/25/14	772.6	2.8	8.83	7.2	34	61
GmTag123	5/16/15-5/23/15	1257	3.17	10.03	8.1	31	58
GmTag127	5/19/15-6/2/15	984.3	3.68	14.34	10.9	45	67
Across all Animals	-	1005.4	2.94	14.3	8.2	45	61

Table 15 – Dive bout analysis including bout ending criterion (BEC), average bout duration, maximum bout duration, average number of dives in the bout and maximum number of dives in a bout

Animal ID	Tag Period	BEC (sec)	Avg Bout Duration (Hrs)	Max Bout Duration (Hrs)	Avg. No of Dives	Max No. of Foraging Dives
GmTag085	5/14/14-5/28/14	732.6	4.26	31.1	15.21	155
GmTag093	6/11/14-6/17/14	179.9	4.3	29.4	12.73	64
GmTag098	9/11/14-9/25/14	450	4	26.6	12.8	165
GmTag100	9/11/14-9/25/14	432.8	3.6	29	12.4	149
GmTag123	5/16/15-5/23/15	854	7.8	35.2	13.3	55
GmTag127	5/19/15-6/2/15	601.6	6.4	40.8	8.1	211
All Tags	-	541	5.06	40.8	12.42	211



Figure 25 – Foraging dive locations for each SLTDR deployment during the tag's continuous period. Each point represents the location at the beginning of each foraging dive.

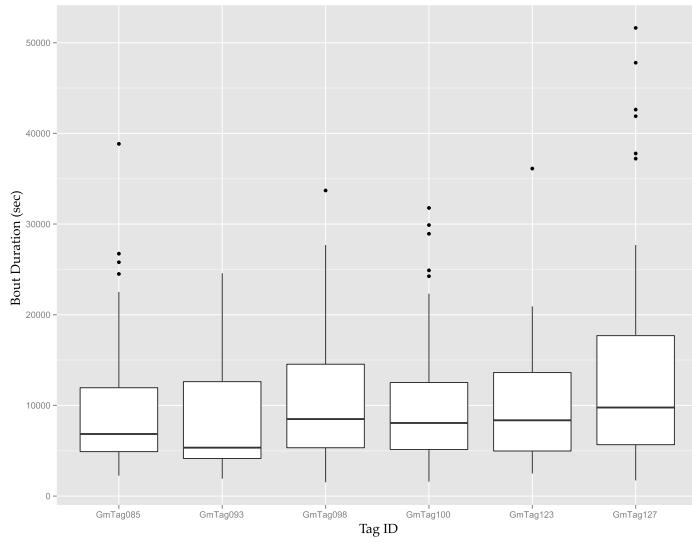


Figure 26 – Foraging bout durations for each SLTDR deployment

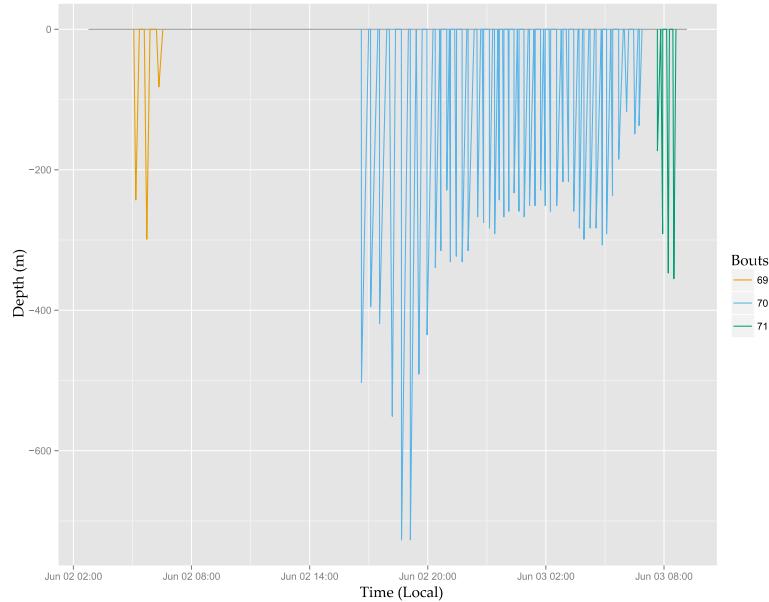


Figure 27 – Dive record from Gm127 showing the longest foraging bout (bout 70 in blue) which lasted for 14.34 hours and was followed by 44.7 minute period at the surface.

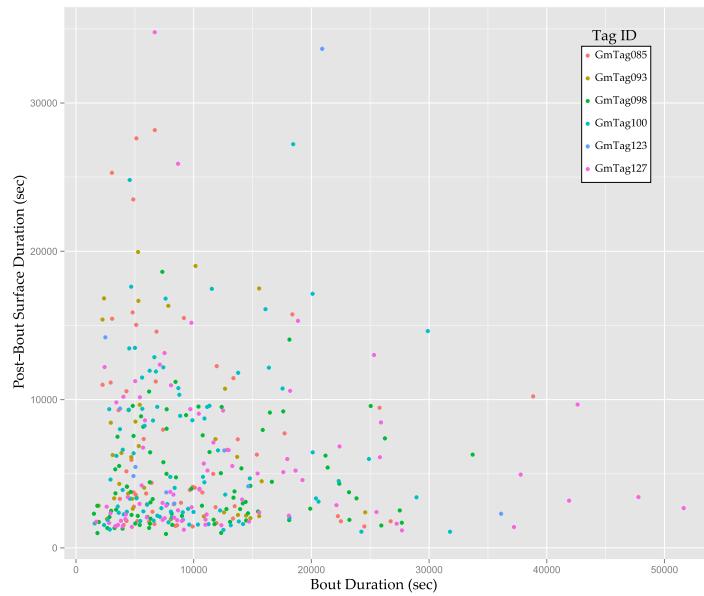


Figure 28 – Surface durations following foraging bouts.

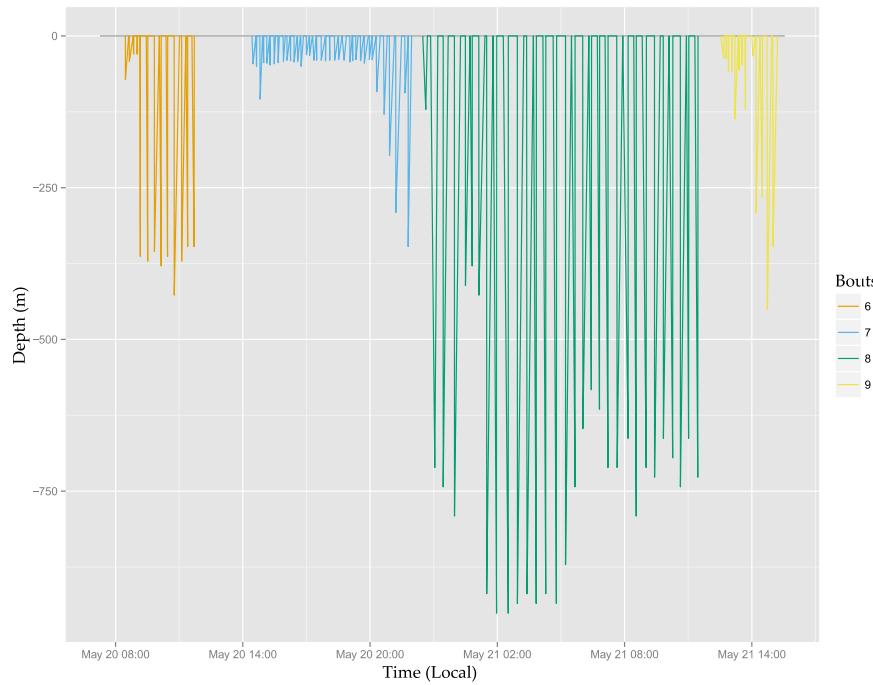


Figure 29 – Dive record of pilot whale GmTag127 covering approximately 33 hours and containing 4 foraging bouts which are highlighted by shading. Bouts 7 & 8 cover approximately 21.3 hours and were separated by 19.7 minutes.

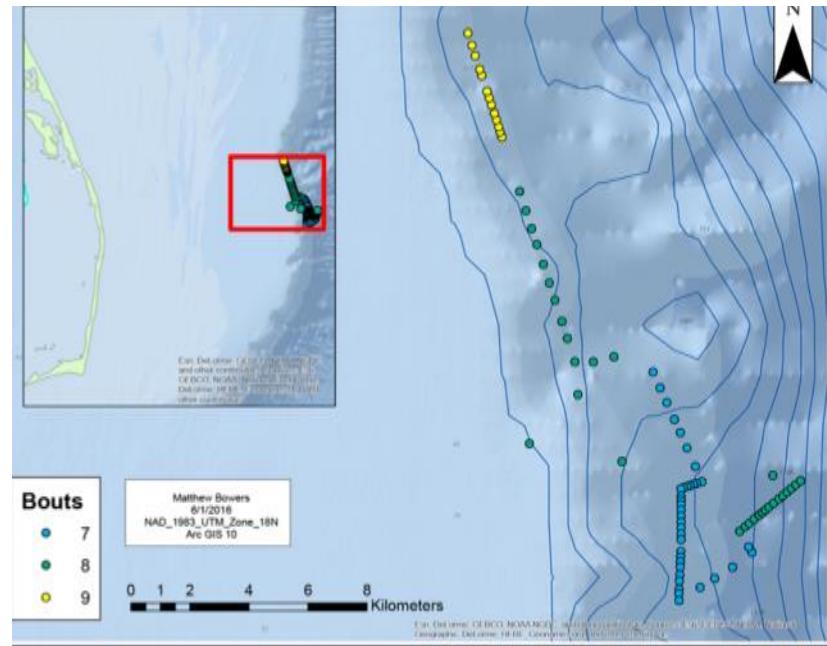


Figure 30 – Locations of foraging bouts 7, 8 and 9 (dive record in Figure 29) from GmTag127. Each dot represents the location at the beginning of the foraging dive.

Table 16 - Diel variation in foraging rates, dive rates, and average depths

Animal ID	Nighttime Hours total	Daytime Hours total	Nighttime Foraging dives (Dives/hour)	Daytime Foraging Dives (Dives/hour)	Nighttime Dive Rate (Dives/hour)	Daytime Dive Rate (Dives/hour)	Avg Nighttime Foraging Depth (m)	Avg Daytime Foraging Depth (m)
GmTag08 5	137.17	172.84	1.77	1.49	2.77	3.11	479.50	411.82
GmTag09 3	55.55	69.88	2.03	2.32	5.38	4.08	323.91	410.57
GmTag09 8	147.46	159.18	1.70	1.82	3.72	4.01	545.01	513.53
GmTag10 0	145.63	152.92	1.52	1.51	4.45	3.95	494.61	636.60
GmTag12 3	73.85	97.70	2.21	1.77	2.72	2.16	468.29	451.14
GmTag12 7	137.12	191.29	2.00	2.12	2.49	2.35	342.71	359.05

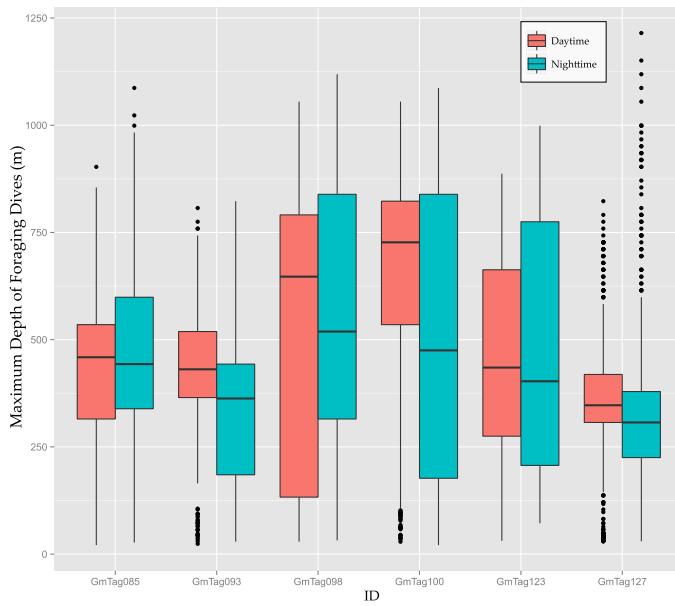


Figure 31 - Box and whisker plot of depth of foraging dives during day and night

Table 17 – Estimated body lengths, ADL_B determined at both the 95th and 97th percentile of dive durations, the maximum dive duration, and the ADL_C determined at two times standard metabolic rate for the six pilot whales tagged with SLTDRs. * indicates poor photo quality and a conservative (minimum) estimate of size.

Tag ID	Estimated Body Length (cm)	ADL_B , 95th Percentile Dive Duration (min)	ADL_B , 97th percentile dive duration (min)	Maximum Dive duration (min)	ADL_C at 2*SMR (min)	Number of dives in the record
GmTag085	438*	16.65	18.02	20.00	18.99	594
GmTag093	408*	15.11	16.25	18.60	18.04	297
GmTag098	563	21.25	21.93	26.00	22.97	832
GmTag100	544	21.04	21.84	24.20	22.21	676
GmTag123	473	18.18	18.54	19.53	20.07	336
GmTag127	481	18.97	20.47	23.90	20.32	1019

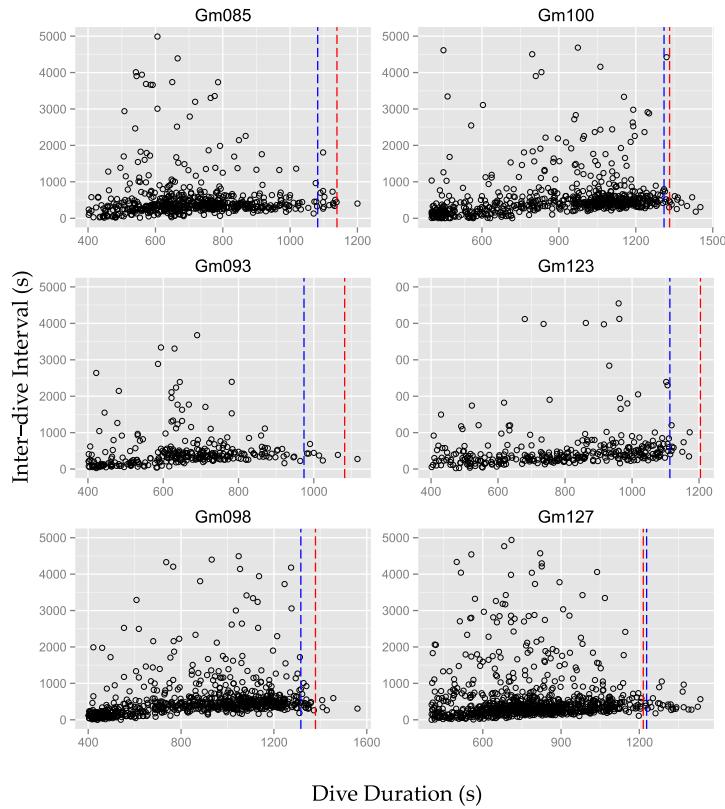


Figure 32 – Dive durations plotted against inter-dive intervals for the six animals tagged with SLTDRs. Blue dotted lines indicate ADL_B at the 97th percentile of dive durations. Red dotted lines represent the ADL_C at 2*SMR

Discussion

The multi-scale approach employed here provided considerable insight into pattern and variation of the foraging behavior of short finned pilot whales off Cape Hatteras. Studies of pinnipeds have used high-resolution data to assist in the classification of sub-surface behavior (Austin et al. 2006; Gallon et al. 2013; Viviant et al. 2014), but this is the first study, to my knowledge, to attempt such validation with

cetaceans. Dive duration was an excellent predictor of foraging behavior in short-finned pilot whales, with a classification error of only 6%, similar to or better than other studies (Austin et al. 2006; Viviant et al. 2014). Other traditional metrics, such as dive shape, were poor predictors of foraging behavior in pilot whales. BEC varied across animals, but the duration of foraging bouts and the number of dives within a foraging bout were fairly consistent. Maximum durations of foraging and dive bouts were similar, but dive bouts were, on average, longer than foraging bouts. Short-finned pilot whales appear to forage in bouts of relatively long duration, during which they rarely, if ever, exceed their aerobic diving capacity. There was no discernable pattern in surface durations following foraging bouts, suggesting that factors other than oxygen, such as prey availability, digestive capacity, or management of other blood tissue gases limit the duration of foraging bouts.

Other studies of marine mammals have also employed dive duration as an indicator of foraging behavior (Lesage et al. 1999; Costa & Gales 2000; Baechler et al. 2002; Austin et al. 2006). Diving vertebrates should engage in foraging tactics that respond to the availability and quality of prey species (Bowen, Tully, et al. 2002). Thus, diving whales should lengthen their dives when they encounter a profitable prey patch. Optimal foraging theory predicts that animals should behave in a way that will maximize their net energy gain, and diving mammals may exceed their aerobic limits to maximize foraging time on particularly profitable patches (Costa et al. 2004; Hazen et al.

2015). While pilot whales do appear to increase their dive durations for foraging, they do not regularly exceed their aerobic capacity. While exceeding the ADL may increase the duration of a single dive, the total accumulated time spent underwater in a bout of dives will be reduced, due to the required surface time to clear the lactic acid (Costa et al. 2004). Considering pilot whale foraging bouts are relatively long, it maybe that they optimize energy intake over the temporal scale of the bout rather than individual dives.

It is less clear why some of the other dive metrics, particularly dive shape, were less useful in predicting foraging behavior. Buzzes on the DTAG records occurred over a large range in depths, which on average was between 65% and 100% of the maximum dive depth. Shape is determined by time spent at depths greater than or equal to 80% of the maximum depth of the dive, indicating that some of the parameters for determining shape might need to be tweaked to accurately capture foraging. Some of the tagged whales were diving to the sea floor with most of the foraging dives occurring along the continental shelf break (Figure 25), and it is possible that variation in depth and topography in this area led to complex dive shapes that precluded simple classification.

As in other aspects of their ecology, short-finned pilot whales have demonstrated considerable variation in foraging behavior. The whales made foraging dives to depths of 29-1215 meters and that lasted from 6.5 to 26 minutes. This range of depth and duration implies considerable plasticity in foraging strategies and supports previous observations that this species forages on a range of prey items off Cape Hatteras.

Foraging performance is ultimately constrained by physiological limits, including digestive capacity, gas management and thermal balance (Costa et al. 2004; Rosen et al. 2007; Hooker et al. 2009). Repeated breath-hold dives with short inter-dive intervals can lead to nitrogen saturation in the blood and body tissues (Paulev 1967), resulting in the potential for decompression sickness (Hooker et al. 2012). Management of blood and tissue gases may be reflected in the maximum observed duration of foraging bouts, which ranged from 6.8 to 14.3 hours for individual whales (Table 14). Quick et al. (2016) suggested the shallow non-foraging dives potentially aid in efficient movement or to help maintain contact with other individuals through improved propagation of calls. These short dives, which regularly occur between foraging bouts, may also function to reduce saturation of blood and tissue gases (Fahlman et al. 2014).

The ADL_B values were less than the ADL_C for 5 of the 6 animals and inter-dive intervals did not increase with increasing dive durations. The dives that exceeded the ADL_C were usually preceded and followed by dives that were significantly shorter. For example, the 26-minute dive by Gm098 was preceded by a 22 minute dive and followed by dives with durations of 17.5, 17 and 18 minutes. Perhaps pilot whales manage oxygen debt by limiting dive durations on subsequent dives rather than extending surface intervals. This may explain why long bouts were followed by relatively short surface intervals (Figure 28) and why there was no marked increase in inter-dive intervals following long dives (Figure 32). This would suggest that short-finned pilot whales

rarely if ever exceed their aerobic dive limit and support the concept that likely oxygen debts do not contribute to the end of bouts. The purpose of the periods separating bouts might be elucidated through examination of the geographic movement during these surface intervals. In one case, an animal foraged for over 22 hours with only a 20 minute surface interval separating two bouts (Figure 29). Examination of this 20 minute interval (Figure 30) suggests the individual is resting as it did not move a great distance to resume foraging. It is unknown what factor or factors ultimately limit the duration of foraging bouts in this species. This will require further study of pilot whale diving physiology and digestive capacity, as well a more complete understanding of the distribution and availability of their prey.

There were no diel patterns in foraging rates or foraging depth on DTAG or SLTDR records, suggesting that short-finned pilot whales do not feed exclusively on DSL organisms off Cape Hatteras. I was surprised by this observation and remain puzzled that pilot whales do not take advantage of diel variation in the availability of potential prey items in the DSL. The decisions made by foraging pilot whales are complex and may involve tradeoffs between energy expenditure and return that are difficult to elucidate without direct measurements of the availability of prey at various depths. Nevertheless, these observations do not preclude the possibility that pilot whales forage in the deep scattering layer. In fact, the relatively large variance in

nocturnal foraging depths (Figure 31) is consistent with the hypothesis that they do, on occasion, take advantage of this resource.

It is difficult to compare these results with those of pilot whales elsewhere, because there are so few published observations of the foraging behavior of this species. In the only other large-scale published study, Soto et al. (2008) used DTAGs to study the foraging behavior of 23 short-finned pilot whales off Tenerife, in the Canary Islands. In general, their observations were similar to ours, with foraging dives reaching depths of 1,018 m and lasting up to 21 minutes. These authors focused their attention on a subset of foraging dives during daylight hours, in which tagged animals made downward directed sprints in pursuit of large prey items. Soto et al. (2008) reported some apparent diel variation in foraging behavior, with deeper dives made during daylight hours, but with more foraging buzzes in foraging dives made at night. Given the high level of variation observed in other aspects of the behavior of this species, I predict that differences in foraging strategies between and among populations of short-finned pilot whales will most likely reflect variation in the environment and prey fields.

Definition of foraging bouts, as described here, has important implications for understanding the effects of disturbance on this species. In many mammals, cessation of foraging is considered to be an important response to anthropogenic disturbances, because it has obvious consequences for the fitness of the individual (Southall et al. 2008). The present study provides empirical observations of the start and end of foraging

behavior under undisturbed conditions and identified important predictors of foraging behavior. Future behavioral response studies with short-finned pilot whales will benefit from this information, because we can now predict the probability that an animal will cease foraging in an undisturbed state. This baseline information can then be compared to changes in behavioral state that are observed following a particular stimulus to determine the probability that a cessation in foraging was caused by said stimulus. Few prior studies have attempted to analyze the foraging bouts of cetaceans because of limited data records (particularly with DTAGs) or difficulties in defining foraging dives. The multi-scale approach employed here overcame the limitation of data records by examining long (14 day) periods for individual whales monitored by SLTDRs. In addition, I developed a simple and systematic method of using dive metrics generated from DTAG data to distinguish foraging from non-foraging dives in long-term SLTDR records.

Chapter 3: The divergent response of Short-finned pilot whales and Risso's dolphins to the Calls of Mammal Eating Killer Whales

Introduction

Cetacean mass stranding and mortality events linked to naval mid-frequency active sonar (MFAS) have raised considerable conservation concern (Fernández et al. 2005; Hohn et al. 2006; Cox et al. 2006; E. C. M. Parsons et al. 2008; D'Amico et al. 2009). Certain species of beaked whales appear to be particularly sensitive to such sounds (Cox et al. 2006; D'Amico et al. 2009 Fernández et al. 2005; Hohn et al. 2006; Parsons et al. 2008). Beaked whales have garnered most of this attention, but other cetacean species have stranded coincident with naval exercises (Hohn et al. 2006; Nowacek et al. 2007). A considerable body of research (e.g. Southall et al. 2012; Goldbogen et al. 2013; DeRuiter et al. 2013; Miller et al. 2014; Antunes et al. 2014) has been devoted to understanding the impact of MFAS using controlled exposure experiments, but the underlying drivers of such responses have remained obscure, in part because MFAS signals are produced at frequencies lower than the best hearing of many toothed whales (e.g., Tyack et al., 2011) and above those of many baleen whales (Goldbogen, Southall, et al. 2013). Zimmer and Tyack (2007) first noted the similarities between the acoustic signals used in MFAS and the social sounds made by mammal-eating transient killer whales (*Orcinus orca*). This led to the hypothesis that the strong aversive responses may reflect an anti-predatory

behavior in which animals are responding to sonar signals they perceive as killer whale sounds (Tyack 2009a; Tyack et al. 2011).

If some odontocetes categorize (or respond to) MFAS as if they were the calls of a predator, it should be possible to predict their responses based on knowledge of their anti-predator strategies, if known, or to make inferences into these strategies based on knowledge of their social behavior. Once a predator is detected, potential prey may respond by moving away (flight), through group or individual defense (fight), or some combination of these strategies (Stanford 2002). The results of several controlled exposure experiments (CEEs) on free-ranging cetaceans, primarily using anthropogenic sources of sound, have supported the anti-predator hypothesis. For example, a Cuvier's beaked whale responded to simulated MFAS by stopping vocalization, rapid directed movement away from the sound source, an extended dive duration with slow ascent, with some of these behavioral changes lasting well after the end of the exposure (DeRuiter et al. 2013). The apparent flight response observed in beaked whales may place individual animals under physiological risk in certain exposure circumstances (Tyack et al. 2011; Fahlman et al. 2014). Avoidance responses to simulated MFAS have been recorded in several other species of cetaceans (Stimpert et al. 2014; Miller et al. 2014; Goldbogen, Southall, et al. 2013), but the strength and duration of these responses, relative to exposure, varies across and within species. Importantly, not all species exhibit a flight response. In particular, pilot whales typically do not exhibit silencing and

avoidance behavior after exposure to MFAS or the sounds of predators (Tyack 2009b; Miller et al. 2012). The response of short-finned pilot whales to simulated MFAS signals in the Bahamas BRS (Southall et al. 2008) was more reminiscent of a social defense strategy, which included elevated vocalization rate and increased group cohesion (Tyack 2009b). Taken together, these results suggest that sociality (and specifically the social nature of anti-predator behavior) might mold the response of cetacean species to MFAS signals.

Protection from predators is one of the most important factors promoting the evolution of sociality in mammals (Connor 2000). Group living can provide protection to an individual in a variety of ways. Detection of predators is more effective in larger groups, and an individual in a large group has a decreased probability of being attacked than an individual in small group (Stanford 2002). Increased vigilance and diluted predation risk is often cited as a factor promoting sociality in birds and primates (Rubenstein 1978). Anti-predator defense can include a variety of behavioral tactics including herding, confusion tactics, alarm calls, fleeing and or confronting the predator with mobbing behavior (Rubenstein 1978). Increasing group cohesion may lead to predator confusion (Milinski 1984), and fleeing in a coordinated manner can make it more difficult for a predator to target any one individual from the group (Alcock 2005). Alarm calls, such as vocalizations emitted in the presence of danger (Caro 2005) can serve a variety functions, including conveying information about the identity of a

predator and location (Seyfarth, Cheney & Marler 1980a), and/or signaling awareness of the predator (Zuberbühler et al. 2009). Alarm calls can also be used to recruit conspecifics to engage in mobbing behavior in both mammals and birds (Curio et al. 1978; Tamura 1989).

Actual predation events are extremely rare for long-lived mammals and particularly difficult to observe with marine mammals. Consequently, many researchers have conducted playback studies with predator sounds to test the response of these animals to the risk of predation. Most playback experiments involving marine mammals have used killer whale calls as the experimental stimulus. Killer whales occur in several ecotypes, which specialize on different prey types, and may act as either predators or potential competitors of other marine mammals. Playbacks of the calls of fish-eating killer whales to long-finned pilot whales (*Globicephala melas*) resulted in increased group size and movement towards the sound source (Curé et al. 2012). In contrast, harbor seals (*Phoca vitulina*) responded strongly to the calls of mammal-eating killer whales and unfamiliar fish-eating killer whales. Interestingly, however, the harbor seals did not respond to the calls of familiar fish-eating killer whales, suggesting that they are capable of discriminating between the calls of different ecotypes of killer whales (Deecke et al. 2002). This suggests that harbor seals successfully categorized the calls of different killer whale ecotypes, based on the perceived risk of predation, and responded appropriately. Solitary male sperm whales (*Physeter macrocephalus*) stopped foraging and increased

vocalization rates in response to the sounds of mammal-eating killer whales (Curé et al. 2013). Humpback whales (*Megaptera novaeangliae*), which were predicted to respond to killer whales by aggression (Ford & Reeves 2008), responded to playbacks of mammal-eating killer whale with strong avoidance behavior (Curé et al. 2015). Behavioral context is critical in such experiments and, in the latter case, the observed flight response may have occurred because the humpback whales perceived the predator as a distant threat (Curé et al. 2015).

In this chapter I report the results of an experiment designed to identify potential anti-predator responses of odontocete cetaceans by performing playbacks to two closely related species with different patterns of social organization. The experiment measured individual and social response of short-finned pilot whales (*Globicephala macrorhynchus*) off North Carolina and Risso's dolphins off California (*Grampus griseus*) to the sounds of mammal eating killer whales.

There are no published accounts of killer whales preying on the two focal species, but both have been found in the stomachs of killer whales (Jefferson et al. 1991). Killer whales have been observed attacking and killing long-finned pilot whales (Bloch & Lockyer 1988) (Donovan & Gunnlaugsson 1989). Even rare predation attempts can exert a significant selective force on social behavior, particularly amongst long-lived species such as primates and marine mammals (Isbell 1994; Connor 2000; Marino 2002).

Short-finned pilot whales are highly social odontocetes found in tropical and subtropical waters throughout the world. These pilot whales typically occur in small, stable social groups that frequently coalesce into larger aggregations. Like humans and killer whales, female short-finned pilot whales exhibit reproductive senescence (Kasuya & Marsh 1984). The evolution of such an unusual trait reflects permanent social bonds amongst related individuals and females, at least, are believed to exhibit philopatry to their natal group (Heimlich-Boran 1993; Alves et al. 2013). The extremely cohesive nature of their social structure has been suggested as an explanation of frequent mass strandings of this species that may result in the death of all group members (Olson 2009). Field observations in Hawaii suggest that adult males may disperse from their natal groups (Mahaffy et al. 2015). Closely related long-finned pilot whales, whose social structure has been better studied, live in permanent family groups from which neither males nor females disperse (Amos et al. 1993; de Stephanis et al. 2008).

Risso's dolphins (*Grampus griseus*) are closely related to pilot whales and are classified together in the sub-family Globicephalinae (Leduc 2009). Like pilot whales, they are medium-sized odontocetes found in tropical, subtropical and temperate waters throughout the globe. The social structure of Risso's dolphins has not been as well studied as that of pilot whales, but their social organization is characterized by more fluidity. In Tenerife, both male and female Risso's dolphins leave their natal pods (Visser 2014), and genetic analysis of Risso's dolphin groups show low overall levels of

relatedness (Gaspari 2004). The structure of the Tenerife population shows similarities to the fission-fusion model of social organization, with some individuals exhibiting no stable patterns of association (Visser 2014). However, most of the population is organized into pods, with loose associations of sub-adults and more stable relationships among pairs or clusters of older animals (Visser 2014). These groups are stratified by sex and maturity, with stronger associations among adult males and females (Hartman et al. 2008; Visser 2014).

I hypothesize that Pilot whales and Risso's dolphins will display differential responses to acoustically threatening sounds based on the knowledge of the social behavior of the two species. Specifically, I predicted that the pilot whales would respond to the calls of a predator by increasing social cohesion and vocalization rate. In contrast, I predicted that Risso's dolphins would move away from the sound source and reduce their vocal activity.

Materials and Methods

The field experiments were designed to present realistic scenarios in which focal animals would detect the presence of a predator at a moderate (hundreds of meters) distance. Consequently, the representative source levels were based on field measurements of killer whale social calls, instead of trying to maximize the received level of sounds on experimental animals. The positive and neutral control stimuli were

deliberately balanced in terms of sound output to ensure that any differential responses were not a function of relative sound level. In addition, the stimuli were of very short duration, to provide a cue that was just sufficient to elicit the natural response(s) of the focal animals and to reduce the likelihood that they would determine that no predator was actually present.

Field Sites

Playback experiments were conducted with pilot whales off Cape Hatteras, 50 km east of Oregon Inlet, North Carolina, and with Risso's dolphins off the coast of Southern California near Catalina island. All playbacks were performed in a Beaufort Sea States of 0- 3 so that it was possible to observe behavioral responses at the surface.

Sound Source

Stimuli were presented to focal animals and their groups through a custom sound source built by Applied Physical Sciences Corporation (APS), using the following design parameters: (1) sufficiently lightweight to deploy by hand using a small davit arm; (2) powered independently of ship AC power; and (3) capable of transmitting a flat frequency response from 0.5-10 kHz. The resulting Lightweight Broadband Underwater Sound Source (LWBBUSS) included four free-flooded ring transducers in a small housing, with a total weight of <20 kg, that was easily deployed by hand. The

requirement for flat response across such a broad frequency range resulted in a source design using four individual transducer elements (lightweight free-flooded rings), each with a resonant frequency response in different regions of the specified operating band (measured at the Navy's Dodge Pond test facility – see **Error! Reference source not found.**). To minimize extraneous electrical noise in the playback signals, the system was powered in the field by devoted 12V batteries and AC power was supplied from a pure sine wave inverter (Magnum Energy MS2012).

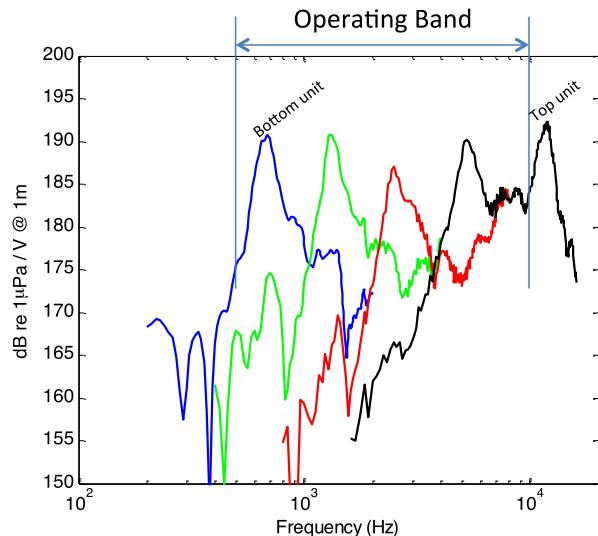


Figure 33- Transmit voltage response for each of four elements prior to frequency compensation, showing differential resonance frequencies across the requested operating band (0.5-10 kHz).

The LWBBUSS was controlled by a custom data acquisition board set and amplifier configuration designed and built by APS. Each of the transducer elements had a differential frequency response and a flat transmission across the 0.5-10 kHz band was

required, so we used a virtual cross-element filtering network to generate signals sent to the amplifier for each transducer such that the effective output of the system was flat over the frequency band. The transmitted voltage frequency response calibration curves for the four transducers shown in Figure 33 were used to deliver appropriately frequency-weighted input signals to each amplifier that retained the original signal phase. A band-pass filter (0.2-16 kHz) was applied to the input signal to provide some filtering of out-of-band noise. The result of this frequency compensation across the different transducer elements was that the transmitted spectrum of test signals (sent to the amplifier elements) was sufficiently controlled across all elements to ensure flat (+/- 2 dB) transmission across the operating band (Figure 34).

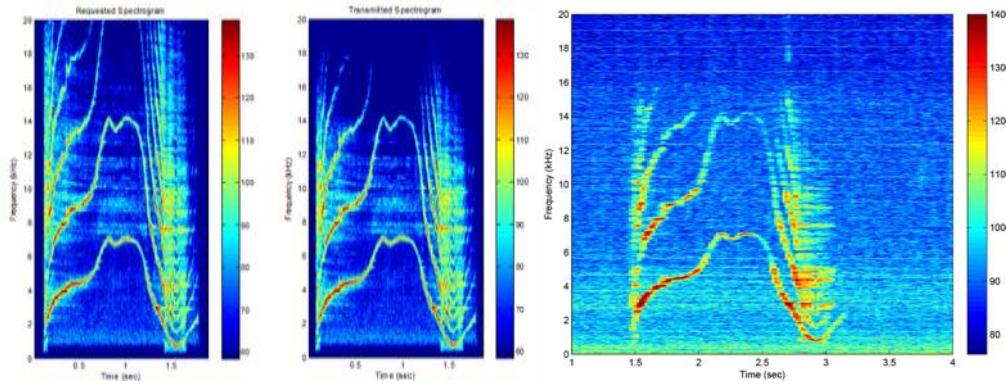


Figure 34- Exemplar Gm-03 requested from the control software (left), filtered and transmitted to the transducer elements (middle) and received at 1 m with a calibrated hydrophone (right).

Output levels were confirmed relative to requested and transmitted stimuli in the field by measuring calibration tones and test stimuli 1 m from the LWBBUSS.

Transmitted tonal signals were measured 1 m from the central axis of the LWB USS with calibrated hydrophones (B&K 8103, HTI-96-min). Calibration measurements (in RMS dB re 1 μ Pa units of sound pressure level, hereafter dB SPL) were made with an oscilloscope (LeCroy Waverunner 6030A), MATLAB custom software and SpectraPlus (Pioneer Hill) measurement software. Results using tonal stimuli confirmed system performance within specifications described above for signals within the specified operating band (see examples in Figure 35).

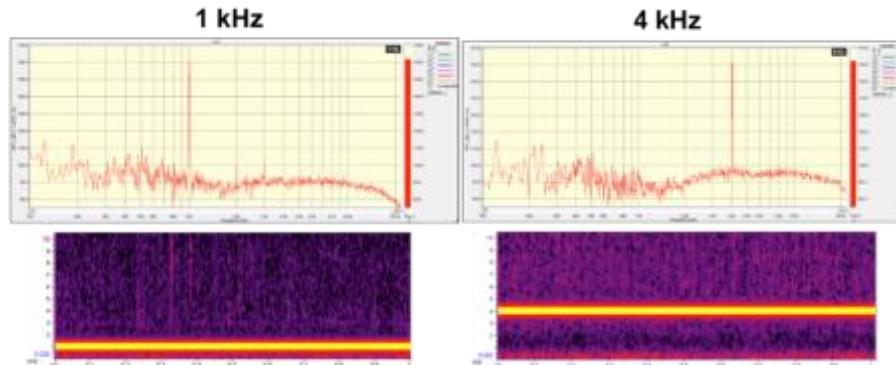


Figure 35-Tonal calibration stimuli at 1 kHz (left) and 4 kHz (right) measured at 1m from the LUWBUSS. Requested source levels were 160 dB re 1 μ Pa-m. Measured source levels were 160.4 and 161.6 dB re 1 μ Pa-m for 1 and 4 kHz respectively.

Playback Stimuli

The calls of mammal-eating killer whales constituted the *experimental stimulus*. Good quality recordings of the calls of mammal-eating killer whales are relatively rare, so representative exemplars from the population of mammal-eating killer whales in the Pacific Northwest and Northeast Atlantic (Shetland, UK) were used (see Deecke et al.

2006; Deecke et al. 2011). Conspecific calls were used as *positive controls* in both field trials. In the pilot whale trials, calls were used that are produced during ascent to the surface from foraging dives in a different population (Jensen et al. 2011), but I expected that focal animals would respond to these exemplars with less urgency than to the calls of predators, or perhaps not at all (*sensu* (Deecke et al. 2006). The humpback whale (*Megaptera novaeangliae*) calls were *true controls* – I did not expect focal pilot whales or Risso’s dolphins to respond to these familiar, non-threatening exemplars in any way. The use of a true control allowed me to assess whether there were any artifacts created by the sound source or field protocol that could influence the response of the focal animal to the experimental stimuli (i.e. artifacts that might elicit a response due to the novel nature of the stimulus, regardless of its behavioral context).

Thus, in each playback trial, a focal animal was presented with three sets of acoustic stimuli or *exemplars*: (1) calls of mammal-eating killer whales recorded from DTAGs off the Pacific coast of the U.S. and Canada (the sound of potential predators, Figure 36); (2) pilot whale social sounds recorded using DTAGs in Tenerife, Spain or Risso’s dolphins recorded with DTAGs off the coast of Southern California (the sound of conspecifics, Figure 37 and Figure 39); and (3) humpback whale social sounds recorded with DTAGs from the Stellwagen Bank National Marine Sanctuary, off Cape Cod, Massachusetts (true controls, Figure 38). Due to the limited availability of recordings,

the conspecific calls used in Southern California came from the same population of Risso's dolphins.

All exemplars were generated from high signal to noise recordings and normalized to have an equivalent maximum RMS voltage using a 200 ms RMS window. SpectraPlus and MATLAB tools were used to measure the relative broadband RMS levels of the signal and normalized using Adobe Audition to ensure output levels were balanced across all test stimuli. Test signal levels again were then confirmed in SpectraPlus and MATLAB to ensure that relative output levels were within 1 dB across all test stimuli. Each exemplar was then transmitted through the LUWBUSS software to ensure that signals sent to the transducer elements retained signal integrity in both time and frequency domains across the operating frequency band.

Each playback trial consisted of three discrete playback sequences involving seven identical exemplars from one of the three species (killer whale, humpback whale, and conspecific (Risso's/pilot whale). Each playback sequence was spaced 30 minutes apart and included seven repetitions of the same exemplar. Each exemplar (calls of killer, pilot whales or Risso's dolphins, and humpback whales) was unique and used only once in trials with each focal species, to avoid pseudo-replication (Deecke 2006). That is, I used the same set of exemplars for both Risso's dolphins and pilot whales, but the same exemplars were not used for multiple subjects within the same species.

I selected exemplars randomly without replacement using 'randperm' in MATLAB, with one important exception. In the last year of the experiment, I restricted the selection of killer whale calls to biphonic signals, because of the strong response observed to these call types by both focal species in prior trials (see below).

Thus, each stimulus set consisted of seven repeated exemplars with a four-second interval between each call. I selected the sequence in which stimuli sets were presented (*e.g.* pilot whales, followed by killer whales, followed by humpback whales) randomly using 'randperm' in MATLAB (MATLAB 2012). Each exemplar was relatively short in duration (~0.5-1 sec) and the entire presentation of an exemplar set lasted no more than 34 seconds. Spectrograms of all exemplars were generated in MATLAB and are shown below (Figure 36 to 39).

The requested source levels for all exemplars were normalized to 168 dB re 1 μ Pa-m as described above. This source level was chosen to match naturally occurring source levels for killer whales and used balanced levels for playbacks of other species to ensure that all stimuli were presented at equivalent levels, to avoid cues based solely on level (Deecke 2006). Finally, each playback trial occurred at a predetermined time and not in a contextual fashion. Thus, each trial began regardless of the focal animal's particular behavioral state (resting or foraging, for example).

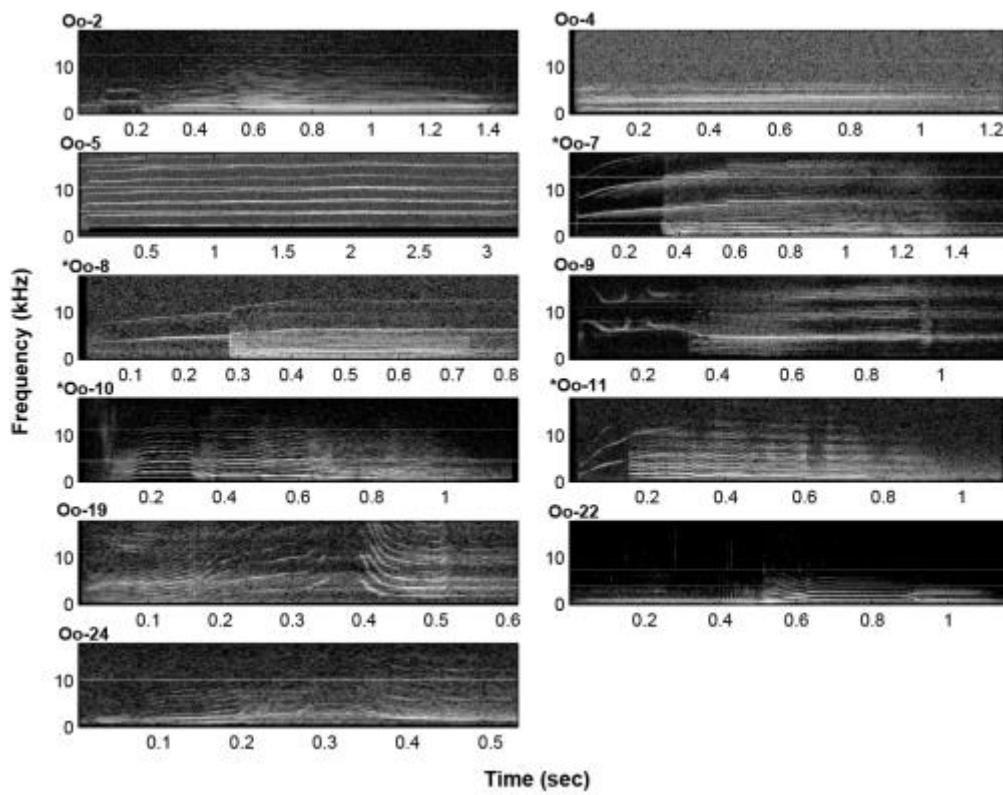


Figure 36 - Spectrograms of calls from mammal-eating killer whales used in playback experiment with short-finned pilot whales and Risso's dolphins *denotes that a strong response was observed during field trials.

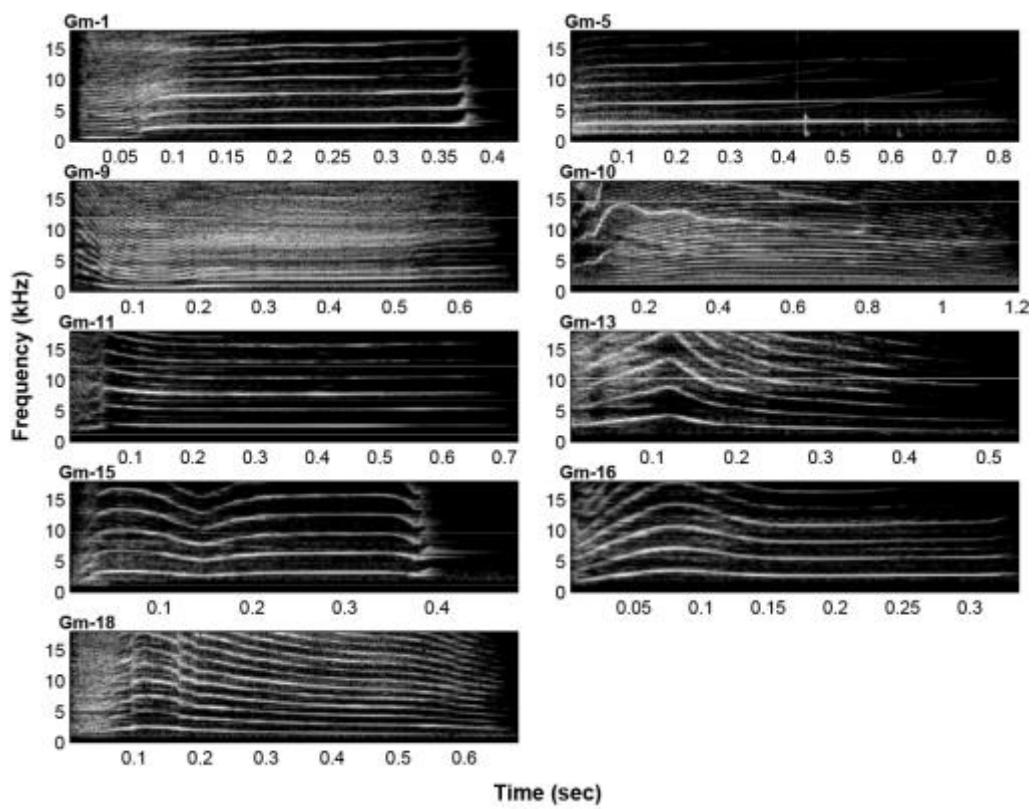


Figure 37 - Spectrograms of short-finned pilot whale calls from Tenerife used in playback experiment with short-finned pilot whales off Cape Hatteras.

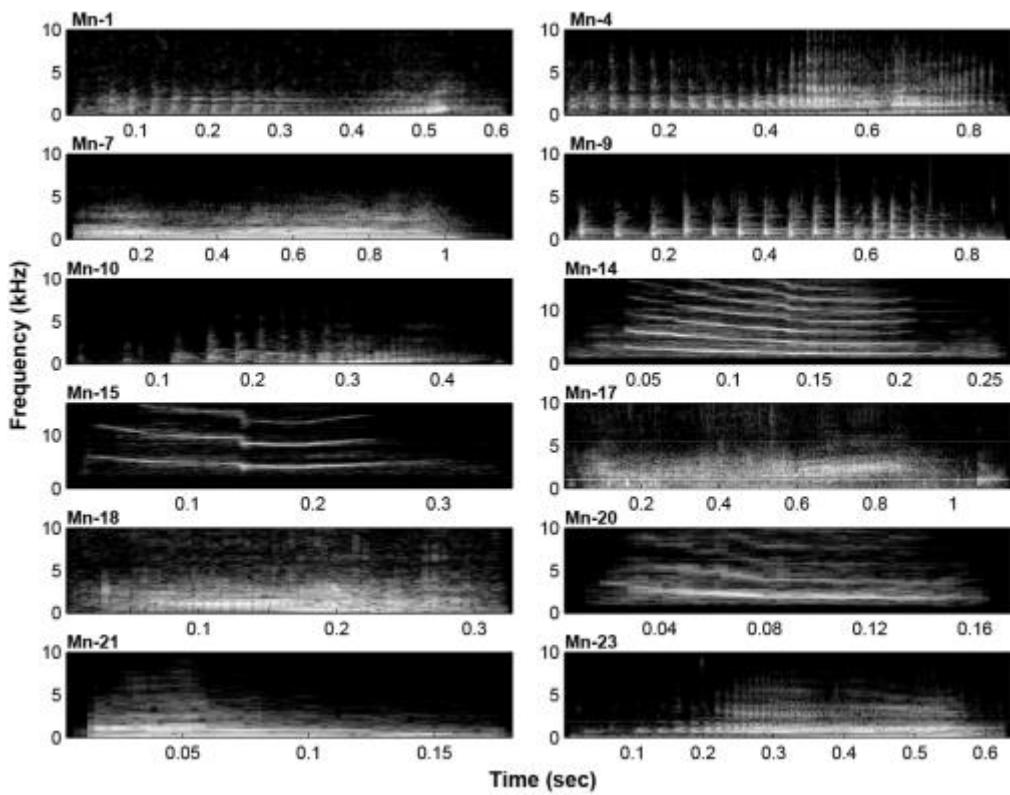


Figure 38 - Spectrograms of humpback social sounds from Stellwagen Bank used in playback experiment with short-finned pilot whales and Risso's dolphins.

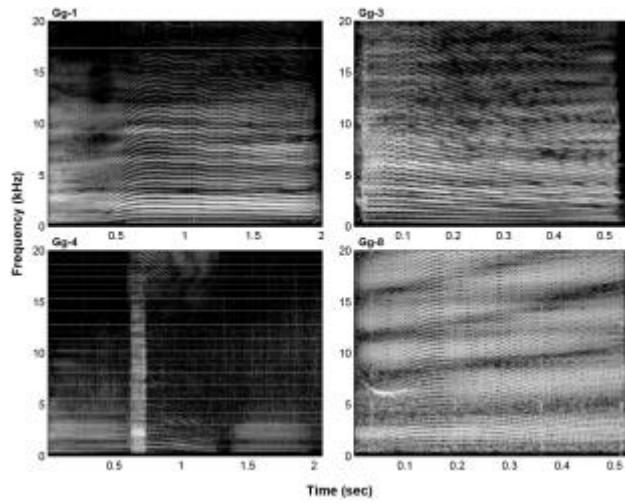


Figure 39 - Spectrograms of Risso's dolphin calls from southern California used in playback experiment with Risso's dolphins off Catalina Island.

Experimental Protocol

Two vessels were employed in each field trial: a *Source Vessel* (SV) and a small Rigid-Hulled Inflatable Boat as the *Observation Vessel* (OV). The OV approached each group and selected a large well-marked pilot whale or Risso's dolphin and attached a Version 2 or 3 DTAG (Johnson and Tyack, 2003), to the dorsal fin or dorsal surface with an anticipated deployment time of four hours. Females with dependent calves were avoided and, as a condition of the project's permits, playbacks were not performed to groups of either species that contained neonates.

Once the focal whale was tagged, photographs of the tag attachment were obtained and the quality of VHF signals received from the tag was assessed. The experiment began with a 60-minute *pre-exposure* period of observation. During this period, the SV remained several kilometers away from the focal animal, with all active acoustic sources turned off. Observers on the OV recorded the behavior using a point sampling protocol (Altmann, 1973) designed to provide information on the behavioral state of the tagged animal, including several measures of social cohesion for the focal group.

Following the pre-exposure period, the operator on the SV contacted observers on the OV to ensure that no neonatal animals were in the group. Once experimental and required mitigation conditions were met, the SV moved into a position approximately 200-500 m (but not directly ahead of) from the tagged whale. The operator on the SV

deployed the sound source, confirmed no animals were in proximity to the sound source, and conducted the first playback trial (described above). Observers on the OV were blind to the playback sequence and identity of the exemplar, to avoid any potential for observer effects (Deecke 2006). The initial playback was followed by a 30-minute period of observation before the process was repeated for a second and then again for the third set of exemplars. After the final playback, behavioral observations continued until the tag jettisoned from the whale. A remote biopsy was attempted to obtain sample of skin from focal pilot whales (but not for Risso's dolphins, due to permit issues) immediately after the tag was recovered. The biopsy samples allowed for the determination of the sex of the focal whale.

Processing Received Stimuli

I isolated playback signals on the DTAG records and analyzed these signals in several steps. After locating and isolating individual stimuli, I ran custom MATLAB scripts on each stimulus signal. These scripts account for the gain settings and calibrations of individual DTAGs and calculate the received levels (RL) and signal to noise ratio (SNR) for each of the playback stimuli (Table 18). I generated maximum received levels from measurements made in 200 ms windows during the duration of the playback. Importantly, I used transient elimination algorithms on all signals, which excludes energy from short, intense sounds such as echolocation clicks and allows for

accurate calculation of the RLs (as described in Tyack et al., 2011). I calculated levels for a single broadband value, resulting in 19 RL 1/3-octave measurements and a single broadband measurement. A high-pass filter on the DTAGs ensured that low-frequency flow noise did not contribute to this measurement. I present all measurements in (RMS) units of dB re: 1 μ Pa calculated with the 200 ms window.

Analysis of Movement

I first assessed each playback qualitatively by plotting tag data including the acoustics spectrogram, flow noise (noise power at 500 Hz band-pass filtered with a 2-pole Butterworth filter), overall dynamic body acceleration (ODBA), depth and heading for the 30 seconds before during and after each playback (Figure 40 and Figure 41). I chose 30-second time bins to match the duration of the playbacks. Flow noise and ODBA were calculated following procedures outlined in prior studies (Simon et al. 2009; Qasem et al. 2012). After observing a strong pattern of heading changes and increased ODBA associated with playbacks of biphonic calls (containing two fundamental frequencies) from mammal eating killer whale calls, I decided to group killer whale calls into monophonic and biphonic calls for further analysis.

I estimated mean ODBA in 30-second time steps and evaluated it against four treatments: baseline, before, during and after for each call type with a Gaussian General Estimating Equation (GEE) using the geepack package (Højsgaard et al. 2006) in R

statistical software (R Core Team 2014). GEEs are used to determine population-averages when the responses are not independent. To deal with the repeated measures in the experimental design I specified a blocking unit (focal ID), which allows for within-subject correlation of residuals, but assumes independence between blocking units. Data from the concurrently tagged animals (Gm14_178a & b) were placed in the same blocking unit and were not assumed to be independent. GEEs have been used in a number of other playback experiments with cetaceans to test stimulus effects (Curé et al. 2012). I ran models with an independent and autoregressive correlation structure and used the ANOVA method to compare each model by Wald tests. In each case the independent correlation structure was determined to be a better model. Each treatment was compared to the baseline using 95% confidence intervals derived from a parametric bootstrap of 10,00 iterations on the fit parameters of the GEE. For the bootstrap I assumed a multivariate normal distribution with means equal to the estimated parameters from the model and the variance-covariance matrix from the fit model.

I estimated the focal animal's position and heading at each available surfacing using range and bearing from the OV, combined with estimates of the vessel's position from an on-board GPS unit. I interpolated the path of the focal animal for the duration of the experiment by creating straight-line tracks between each of these points. Using this interpolated path, I calculated the distance between the focal animal and the sound source immediately prior to the playback and for the 30 minutes following each

playback. I then determined the bearing between the focal animal and the sound at the time of the playback using this track. I then evaluated whether the animal changed its heading relative to the source by running a circular two sample t-test on the heading data collected on the DTAG for the 2 minutes before and after each playback (Berens 2009).

Analysis of Social Calls

I estimated call counts on the DTAG record in the baseline period (10 minutes before any stimulus) and for five minutes before and after each stimulus. I did not analyze call counts during the playbacks due to the high levels of background noise (flow-noise and splashing) which occurred on a number of the playbacks. I identified feeding buzzes and clicks following methods described in (Soto et al. 2008). I incorporated all calls that were not feeding buzzes or clicks, which included whistles, burst pulses, social buzzes, and rasps. These calls were binned into 30-second time steps and I analyzed with a Poisson GEE using the geepack package (Højsgaard et al. 2006) in R statistical software (R Core Team 2014). I ran models with an independent and autoregressive correlation structure and used the Anova method to compare each model by Wald tests. In each case the independent correlation structure was determined to be a better model. Each treatment was compared to the baseline using 95% confidence

intervals derived from a parametric bootstrap following the same procedures described above.

Analysis of playback stimuli

Due to the limited number of responses to playbacks I analyzed each exemplar for nonlinear components including biphonation, deterministic chaos, subharmonics and frequency jumps (Fitch et al. 2002). Furthermore, each of the killer whale exemplars were run through ARTwarp classification system (see (Deecke 2003; Deecke & Janik 2006)) to determine if certain call types were eliciting a response. *Biphonation* occurs when a call has two overlapping, independently modulated components (Filatova et al. 2012), both of which can exhibit harmonics. The modulations of these two components are not linked and thus act as two overlapping, coincident but unrelated calls. When two independent sources are responsible for production of the sounds, they are referred to as *two-voiced calls* (Zollinger et al. 2008). The mechanism of production of these calls in killer whales is not understood, so I refer to them as biphonic calls (Filatova et al. 2012). *Frequency jumps* represent a break in the F_0 (fundamental frequency) in which the vibration rate increases or decreases abruptly and is qualitatively different from continuous, smooth modulation (Tyson et al. 2007). Frequency jumps represent regime instability, i.e., an abrupt, unpredictable transition from one regime of vocal fold oscillation to another (Wilden et al. 1998; Brown et al. 2003). *Subharmonics* occur when

there are additional visible spectral components that occur at fractional integers of an identifiable F_0 (i.e. $F_0/2$, $F_0/3$ and so on) and are visible on a spectrogram (Tyson et al. 2007). The result is energy can appear at evenly spaced intervals below F_0 and between adjacent harmonics throughout the frequency spectrum (Riede et al. 2004). *Deterministic chaos* refers to periods of non-random, irregular noise that is produced by desynchronized coupled oscillators (Fitch et al. 2002). It is characterized by having a relatively broad frequency band with some residual periodic energy related to the harmonic components (Brown et al. 2003; Tyson et al. 2007).

Nonlinear components were identified through power analysis and visual inspection of spectrograms following previously applied methods (Tyson et al. 2007). The calls were analyzed in MATLAB using fast Fourier transformations (FFT), with 2048 points FFT order, hanning windows, and a 75% overlapping of successive windows. Identification of deterministic chaos was done using the Openstool package (Version 1.2; Merkwith et al. 2009) in Matlab and were analyzed in a similar manner to Tyson et al. (2007). I determined the presence of chaos by calculating Lyapunov exponents for each exemplar where positive exponents are an indication for deterministic chaos (Edoh et al. 2013). I used to the method of surrogate data to test the null hypothesis that the signals were produced by a stationary, linear, random Gaussian process (Thieler et al. 1992; Tyson et al. 2007). If Lyapunov exponents are significantly different between the test signal and the surrogate data, then the null hypothesis can be rejected. Surrogate

data for each call was produced using the surrogate1 function and follows the approach used by Thieler et al. (1992) which creates the surrogate signal by phase-randomizing the data. To identify deterministic chaos in the signal I calculated the Lyapunov exponents in both the original and surrogate data using the largelyap function. The largelyap function requires an embedding delay which was calculated using the amutual function and an embedded dimension which was determined using the cao function. I then performed paired t-tests on the Lyapunov exponents from the surrogate and original data where significant differences ($P \leq 0.05$) indicate the presence of chaos (Theiler et al. 1992).

Results

Maximum received levels of the various playback exemplars ranged from 102-137 dB (Table 18). In three of 41 exemplars, signals were not detected on the DTAG at the time they were presented. The degree of variation observed in received levels was expected, given that natural source levels were used, and due to propagation effects and the tagged whale's range from the source and position in the water column (Madsen et al. 2006). Furthermore, the received level recorded on the tag can be affected by the orientation of the animal relative to the source. For example, the received level can be reduced if the animal's body or the body of another whale is shadowing the tag.

Table 18- Maximum RMS (dB re: 1uPa) broadband received levels (Max RL) for all playbacks. X denotes playback exemplars that were not detected on the tag acoustic record. A J denotes that the DTAG jettisoned before the call was played. An asterisk denotes potential shadowing of the signal by the tagged individuals body (determined by tag position on the animal and the animals orientation relative to the source). Estimated distance is distance at the beginning of the playback between the sound source and the tagged animals location determined from a straight line pseudo-tracks between focal follow points.

ID	Humpback Exemplar		Conspecific Exemplar		Killer Whale Exemplar	
	Est. distance (m)	Max RL (dB)	Est. distance (m)	Max RL (dB)	Est. distance (m)	Max RL (dB)
Gm12_125a	600	X*	300	125*	400	129*
Gm12_125b	450	102*	250	133	200	137
Gm12_133a	400	118	250	119*	450	110*
Gm12_162a	450	120	500	117*	500	122
Gm12_172a	550	X*	500	124	250	135
Gm12_246a	300	125	450	122	350	118*
Gm14_145a	300	112	300	120	350	120
Gm14_167a	300	122	250	111*	300	125
Gm14_178a	200	127	250	121*	300	127
Gm14_178b	-	126	-	X	-	121
Gg13_227b	-	J	400	118	400	123*
Gg13_228b	300	121*	400	127	400	124
Gg13_231c	300	115*	400	121	350	129
Gg14_222a	300	127	300	115*	350	119*

In total, nine complete playback sequences were completed that included presentation of all three sets of stimuli to pilot whales (Table 19). Three complete playback sequences and one partial sequence (two playbacks) were conducted with Risso's dolphins (Table 20). Seven of the exposed animals (five pilot whales and two

Risso's dolphins) displayed strong and unequivocal responses to the calls of mammal-eating killer whales, while the other seven did not. The response of both species included increases in speed, heading variance, and ODBA (Figure 40 and Figure 41). After the playback, pilot whale call rates increased and the focal pilot whales and their groups made directed movement towards the sound source. Risso's dolphins made no measurable change in call counts but made rapid directed movement away from the sound source.

Of these seven strong responses, four of the five pilot whales and one of the two Risso's dolphins occurred in response to biphonic calls of mammal-eating killer whales. One monophonic killer whale call (Exemplar Oo-10, Figure 36) also elicited a strong response during playbacks to both species. There was no measurable response to any of the humpback or conspecific calls. There were no correlations between the strong reaction and RL, estimated distance between the focal animal and sound source, or sequence of presented calls.

Table 19 - Playback calls, stimulus order, and group context for each pilot whale playback trial.

Pilot Whales ID	Humpback Exemplar	Conspecific Exemplar	Killer Whale Exemplar	Stimulus Order	Group Context
Gm12_125a	Mn-9	Gm-5	OO-11	H-C-K	5 animals, consisting of two subgroups of 3 and 2 animals.
Gm12_125b	MN-10	Gm-1	OO-5	P-C-H	10 animals that increased to 14.
Gm12_133a	Mn-1	Gm-9	OO-24	H-C-K	Solitary animal joined up with 4 others before the playback, 2 of which were a mom/calf pair.
Gm12_162a	Mn-21	Gm-18	OO-19	K-H-C	10 whales, spread out, mostly mom/calf pairs
Gm12_172a	Mn-17	Gm-15	OO-9	C-H-K	14 whales, spread out, decreased to 9 before the playbacks
Gm12_246a	Mn-7	Gm-11	OO-22	C-H-K	16 whales, fairly tight, consisting of multiple mom/calf pairs
Gm14_145a	Mn-4	Gm-16	OO-10	H-C-K	15 whales, several sub-adults and at least 2 mom/calf pairs
Gm14_167a	Mn-15	Gm-10	OO-7	K-C-H	22 whales, consisting of two subgroups of 14 and 8 that split and joined throughout the playback
Gm14_178a					10 whales, joined a large aggregation of several hundred during the experiment
Gm14_178b	Mn-14	Gm-13	OO-8	H-C-K	

Table 20- Playback calls, stimulus order, and group context for each Risso's dolphin playback trial.

Risso's Dolphin ID	Humpback Exemplar	Conspecific Exemplar	Killer Whale Exemplar	Stimulus Order	Group Context
Gg13_227b	X	GG-1	OO-2	C-K	12-16 whales in scattered formation with high activity.
Gg13_228b	Mn-23	GG-3	OO-10	K-C_H	14-16 whales in a relatively tight formation, slow travel
Gg13_231c	Mn-18	Gg-8	OO-4	H-K-C	10 whales in tight formation with another subgroup of 10 nearby, slow travel
Gg14_222a	Mn-20	Gg-4	OO-11	C-H-K	5-7 whales with 15-20 more whales scattered in the area, traveling with low activity level

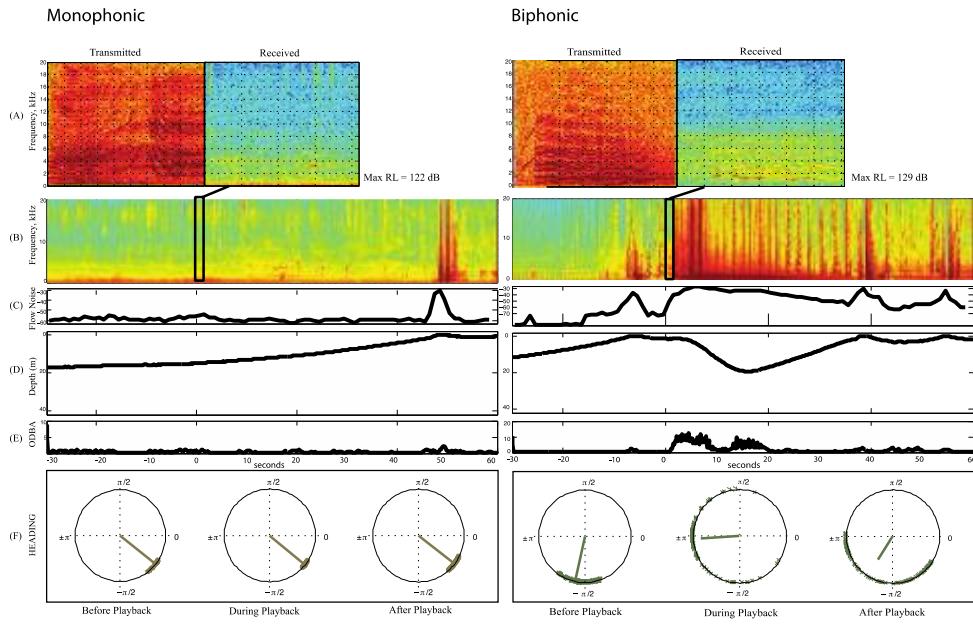


Figure 40 - Examples of a lack of reaction (left) and a strong reaction (right) of short-finned pilot whales to playbacks of monophonic and biphasic mammal-eating killer whale calls. The reactions included increased flow noise, ODBA and heading variance. Each panel displays a 30-second period before, during and after presentation of a killer whale call and provides values for: (A) transmitted and received signals; (B) spectrogram of the acoustic record; (C) flow noise, which is a proxy for the speed of the tagged animal; (D) depth profile of the tagged animal; (E) ODBA, which is a proxy for movement of the tagged animal; and (F) circular plots of heading of the tagged animal.

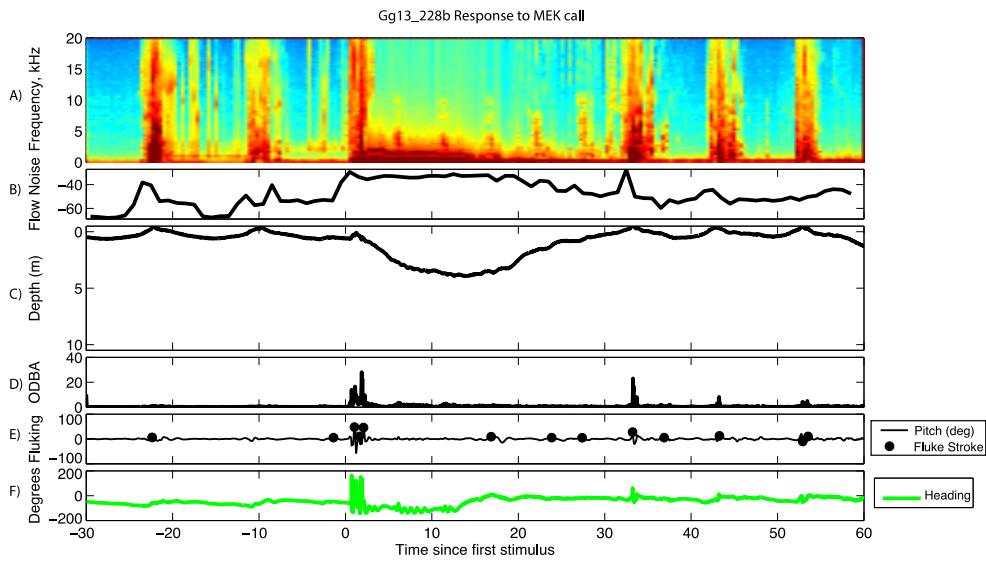


Figure 41 - Response of Risso's dolphin Gg13_228b to playback of a mammal-eating killer whale call. Similar to the response seen in pilot whales, I observed an increase in flow noise, ODBA and heading variance during presentation of the killer whale call. The figure displays the 30 seconds before, during and after the playback and displays: (A) spectrogram of the acoustic record; (B) flow noise, which is a proxy for the speed of the tagged animal; (C) depth profile of the tagged animal; (D) ODBA, which is a proxy for movement of the tagged animal; (E) pitch and fluke strokes by the tagged animal; and (F) heading of the tagged animal

Observational data

A large number of values were missing from the surface behavioral observations, as the focal animals were often submerged and thus unavailable, so I was unable to perform any robust statistical analysis on the observational data. Nevertheless, I used these observations to provide a qualitative description of the response of focal animals and their groups to the playbacks. Following the playback of biphonic killer whale call to pilot whale Gm12_125a, for example, two sub-groups of whales moved quickly to

coalesce into a single, very tight group, with almost all whales in physical contact. The group then dove in unison, moving towards the sound source. There was a similar response following the playback to pilot whale Gm14_145a; the focal group contracted, with almost all of the whales in physical contact. The group then moved in a coordinated and directed manner towards the sound source. In contrast, playbacks of most monophonic killer whale calls evoked little or no obvious response from the focal animal or its group.

There were strong responses following the playbacks of killer whale calls to Risso's dolphins Gg13_228b and Gg14_222a, in which sub-groups clustered together into a tight formation over the course of several minutes following exposure, before making extremely strong directional movement (leaping at high speed) away from the sound source for distances up to 7 miles. In both cases, the DTAG was shed before or at the commencement of this rapid directional travel. According to those experienced with this species in southern California, this behavior was extraordinary and observed only after these playbacks of these two exemplars.

DTAG data

The general estimating equations (GEEs) for pilot whales demonstrated a number of clear aspects of the behavioral response observed during playbacks of biphonic killer whale calls. Measured ODBA levels for pilot whales were significantly

higher during the playbacks of calls categorized as biphonic than calls categorized as monophonic calls (Figure 42). This suggests rapid and variable movement by the tagged animals during exposure to this call type, behavior that would be consistent with either a rapid orienting response. No other playback elicited a significant response relative to baseline values. The relatively large confidence interval observed during playbacks of monophonic calls is most likely due to the exemplar (Oo-10) that resulted in a strong response. I observed similar responses in ODBA in playbacks of the exemplars (Oo-10 & 11) to Risso's dolphins. I did not apply the GEE to the Risso's data due to the small sample size.

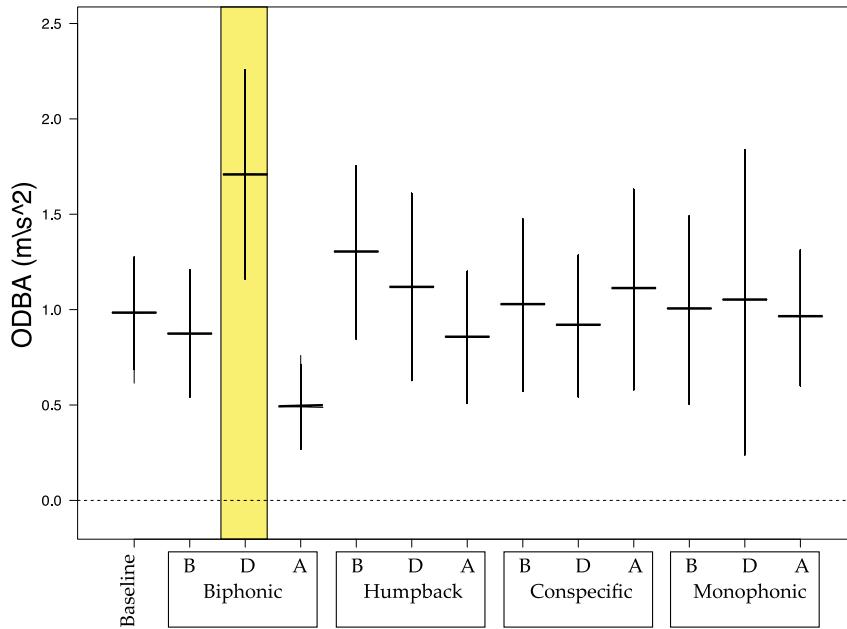


Figure 42 - Parameter estimates, together with with 95% confidence intervals (CI) of Gaussian GEE for ODBA for before, during and after playbacks of various exemplars to short-finned pilot whales. Horizontal lines represent parameter estimates and vertical lines represent the 95% CI derived from parametric bootstrap of the fit parameters of the GEE. ODBA levels during the playback of biphonic mammal-eating killer whale calls (highlighted in yellow) were significantly higher than baseline levels. No other period (before, during or after) for any other stimulus were found to be significantly different from baseline levels.

As noted above, I used social call counts (vocalizations of focal species recorded on the tags) as a metric of potential changes in social cohesion. For pilot whales, call counts following playbacks of biphonic killer whale calls were significantly higher than baseline levels (Figure 43); there was no difference from baseline levels from playbacks of any other call types. I did not apply the GEE to call counts for Risso's dolphins due to

the small sample size. I did not observe any patterns in call counts for Risso's dolphins in any playback condition (Figure 44).

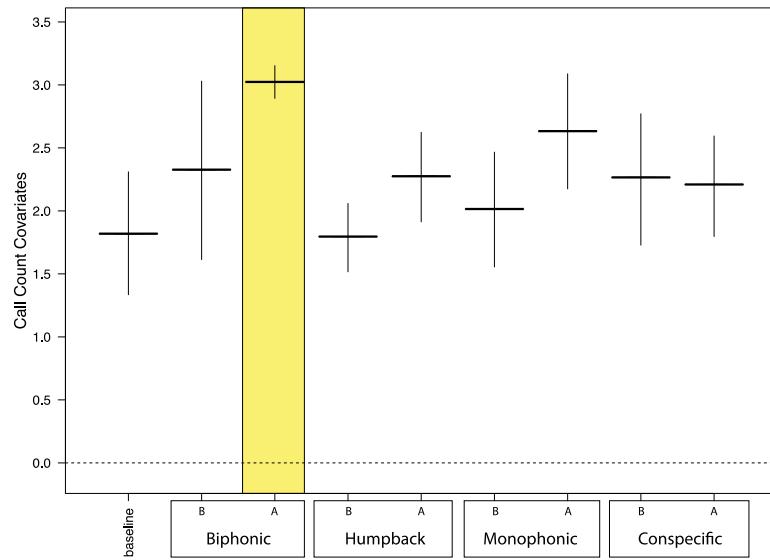


Figure 43 - Parameter estimates of Poisson GEE of pilot whale call counts before and after playbacks of each stimulus type. Horizontal lines represent parameter estimates and vertical lines represent the 95% CI derived from parametric bootstrap of the fit parameters of the GEE. Call counts following the playback of biphasic mammal-eating killer whale calls (highlighted in yellow) were significantly higher than baseline or before levels.

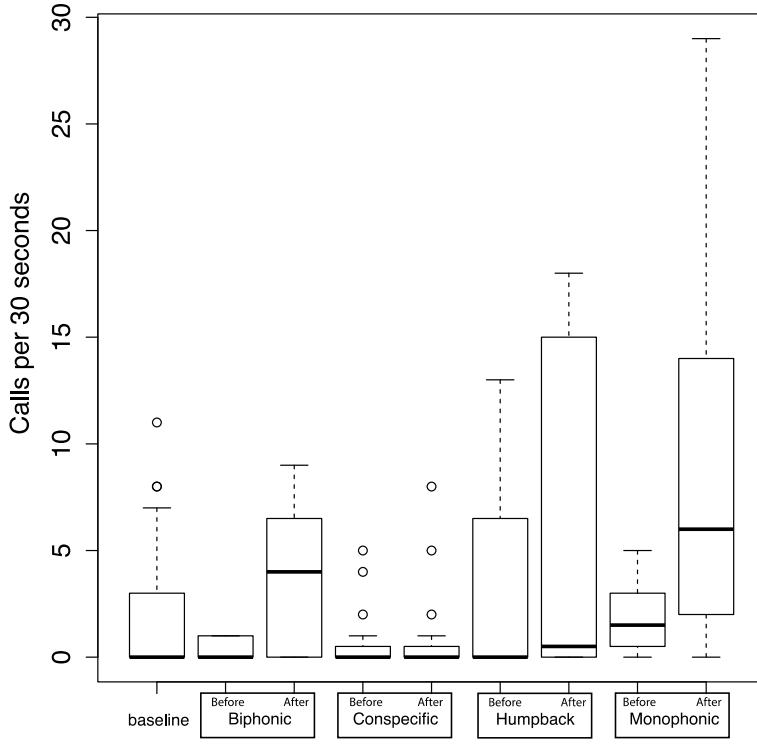


Figure 44 – Risso’s dolphin call counts before and after playbacks of each stimulus type. There were no discernable patterns in call counts following playbacks of any of the stimulus types relative to baseline levels.

Below I present ODBA values from individual focal animals for each playback trial involving killer whale calls for pilot whales (Figure 45) and Risso’s dolphins (Figure 46). Playbacks highlighted in yellow involved biphasic killer whale calls. In each case I observed an increase in ODBA during the playback followed by a decrease after the playback. The single playback in green involved exemplar Oo-10, which elicited a similar reaction in ODBA for both pilot whales and Risso’s dolphins. This pattern of increased ODBA during playbacks was not observed in playbacks of any of the other exemplars.

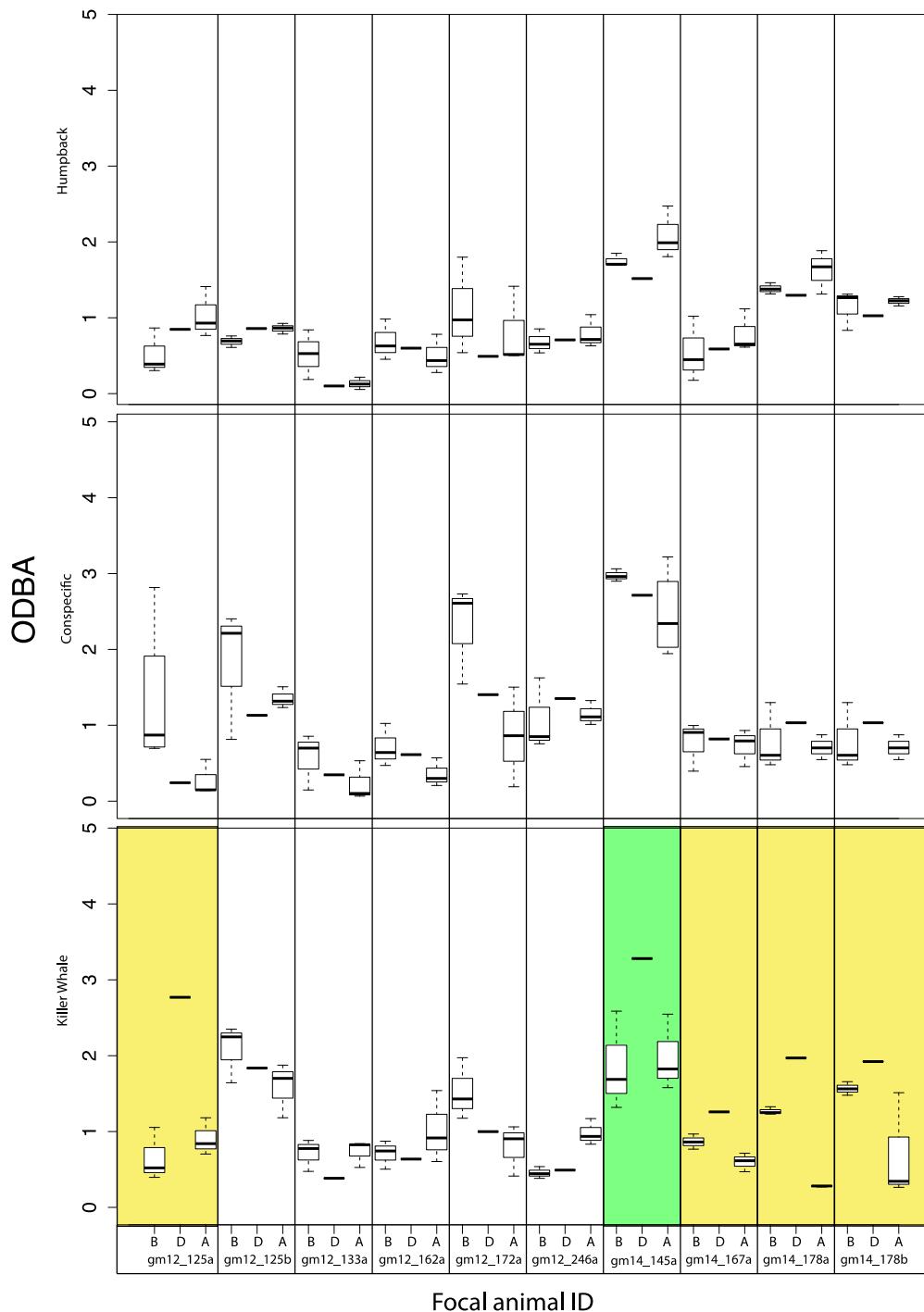


Figure 45 - Boxplots of ODBA values for 30-second time bins (before, during and after) for three playback stimuli for each tagged pilot whale. Highlighted in yellow are the playbacks of biphonic killer whale calls and in green is the single

monophonic call (Oo-10) that elicited a response. All five animals exhibited an increase in ODBA during the playback followed by a reduction in ODBA.

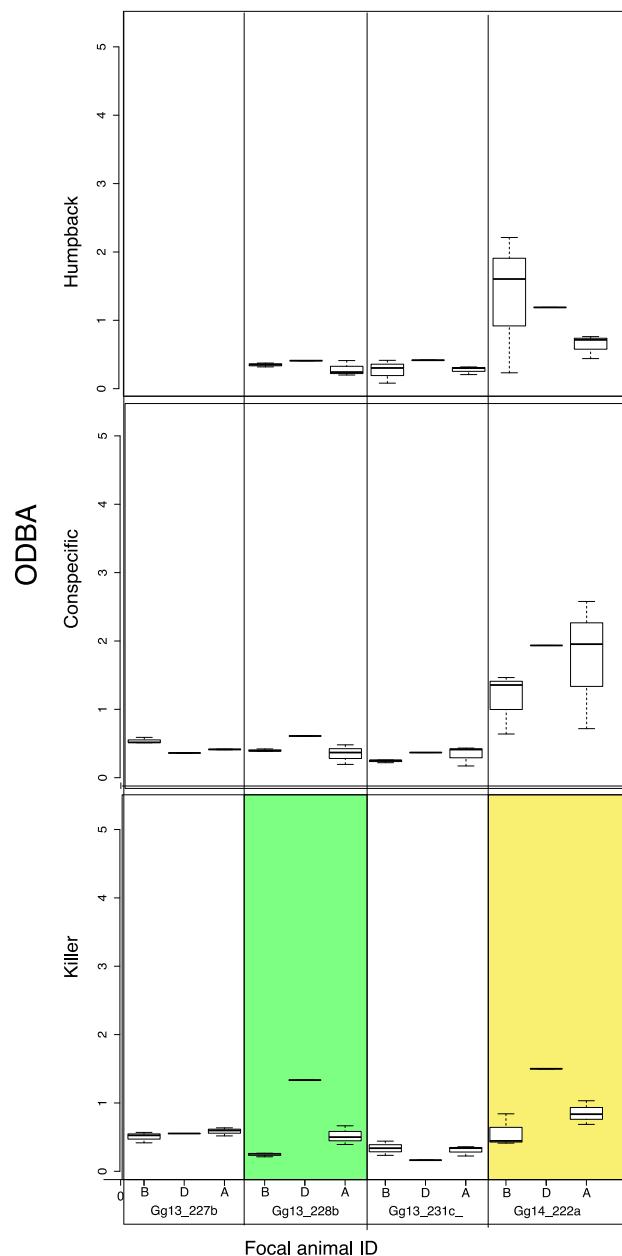


Figure 46 - Boxplots of ODBA values for 30-second time bins (before, during and after) for three playback stimuli for each tagged Risso's dolphin. Highlighted in yellow is the playback of a biphonic killer whale call and in green is the single

monophonic call (OoO-10) that elicited a response. Risso's dolphins displayed a similar response to pilot whales, which included an increase in ODBA during the playback followed by a reduction in ODBA.

I analyzed individual responses to playback trials in terms of physical movement towards or away from the sound source using the estimated heading of focal pilot whales ([Table 21](#)) and Risso's dolphins ([Table 22](#)). In both species, I observed no significant difference in terms of distance to the source for playbacks of conspecific calls or humpback whale social sounds. Conversely, playbacks of killer whale calls resulted in significant differences in animal-source distance, with a significant change in tagged animal heading, but only for playbacks from a subset of MEK calls. It is important to note that the significant differences measured in responses in these conditions indicated movement *toward* the sound source for pilot whales ([Table 21](#)), but movement *away* from the sound source in Risso's dolphins ([Table 22](#)).

Table 21- Distance between focal pilot whale and sound source during playback trials. Minus sign (-) indicates decreasing distance between sound source and focal animal and a plus sign (+) indicates increasing distance between sound source and the focal animal. Red indicates a significant change in heading, as determined using a two-

sample circular t-test on the heading data collected on the DTAG for two minutes before and after each playback.

Playback	Distance to Sound Source Following Playback		
	Pilot Whale	Humpback Whale	Killer Whale
GM12-125a	+	+	-
GM12-125b	+	+	-
GM12-133a	+	+	+
GM12-162a	+	+	+
GM12-172a	+	+	+
GM12-246a	-	-	-
GM14-145a	-	+	-
GM14-167a	+	-	-
GM14-178a	-	-	-

Table 22- Distance between focal Risso's dolphin and sound source during playback trials. Plus sign (+) indicates increasing distance and a minus sign (-) indicates decreasing distance between the sound source and the focal animal. Red indicates a significant change in heading, as determined using a two-sample circular t-test on the heading data collected on the DTAG for the two minutes before and after each playback.

Playback	Distance to Sound Source Following Playback		
	Pilot Whale	Humpback Whale	Killer Whale
Gg13-227b	-	-	-
Gg13-228b	-	-	+
Gg13-231c	-	-	-
Gg14-222a	-	-	+

I analyzed heading data to investigate potential changes of the orientation of focal animals relative to the sound source for 30 seconds before and 30 seconds after playback of each exemplar. An example of this analysis is provided below for exemplar Oo-10 that was presented to both a pilot whale and Risso's dolphin (Figure 47). The

same divergent pattern of response in terms of spatial orientation to the sound source described above is evident here. Both animals made changes to their heading, but the pilot whale oriented towards the sound source and the Risso's dolphin oriented away from the sound source.

Heading Before and After Exposure to MEK Call Oo-10

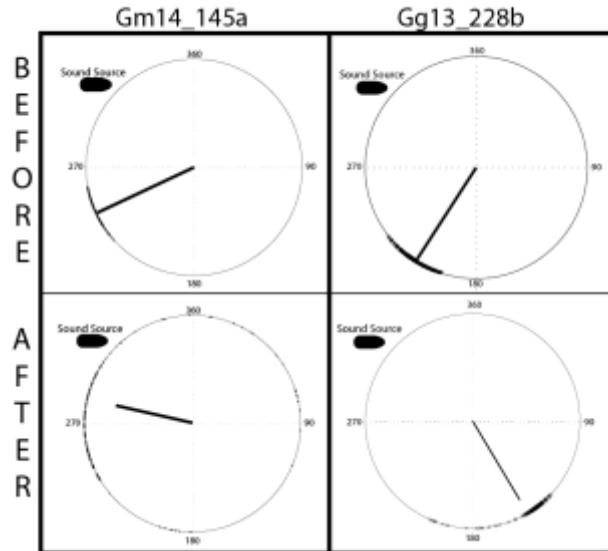


Figure 47 - Circular plots of heading relative to the sound source for 30 seconds before and after playbacks of killer whale exemplar Oo-10 to a pilot whale (left) and a Risso's dolphin (right). Bearing of the sound source to the focal animal was determined using known location of the sound source and the estimated heading of the focal animal as reconstructed from the focal follow points.

Playback Stimuli

Several killer whale exemplars had multiple non-linear components (Table 23) including all four exemplars that elicited a response (Oo-7,8,10,11). The four exemplars

that elicited a response all included deterministic chaos and another non-linear component. Only one call (Oo-2) contained deterministic chaos and did not elicit a reaction. Two of these calls (Oo-7,8) had the same ARTwarp classification. There were no calls from humpbacks, or conspecifics that contained deterministic chaos.

Table 23 – ARTwarp classification of the killer whale exemplars and identification of nonlinear components in all of the exemplars including biphonation, chaos, subharmonics and frequency jumps. Artwarp classification was determined following methods in Deecke & Janik (2006). The set of letters prior to each number indicates the population of killer whales with WCT indicating west-coast transient and NASH indicating North Atlantic Shetland. A checkmark (✓) indicates the presence of the non-linear component from that column.

Exemplar	ARTwarp Classification	Biphonation	Chaos	Subharmonics	Frequency Jumps
Oo-2	WCT08		✓		
Oo-4	WCT11			✓	
Oo-5	Whistle/variable				
Oo-7	WCT03	✓	✓	✓	✓
Oo-8	WCT03	✓	✓		✓
Oo-9	Whistle/variable			✓	✓
Oo-10	WCT02iii		✓		✓
Oo-11	WCT04	✓	✓	✓	
Oo-19	NASH03i				
Oo-22	WCT02iii				
Oo-24	NASH06				
Gm-1			✓		
Gm-5				✓	
Gm-9					
Gm-10		✓			
Gm-11				✓	✓
Gm-13				✓	
Gm-15					
Gm-16				✓	

Gm-18	
Mn-1	
Mn-4	
Mn-7	
Mn-9	
Mn-10	
Mn-14	✓
Mn-15	✓
Mn-17	
Mn-18	
Mn-20	
Mn-21	
Mn-23	
Gg-1	
Gg-3	
Gg-4	
Gg-8	

Discussion

Short-finned pilot whales and Risso's dolphins reacted strongly but divergently to playbacks of a subset of calls from mammal-eating killer whales. Four calls, exemplars Oo-7, Oo-8, Oo-10, and Oo-11 elicited strong responses in short-finned pilot whales and Oo-10 and Oo-11 also elicited strong responses in Risso's dolphins. Neither focal species responded to playbacks of majority of the killer whale calls or to any of the calls of conspecifics or humpback whales. The lack of response to the humpback whale and conspecific calls suggests that there were no artifacts in the playback trials. Oo-7,8 and 11 were categorized as biphonic and the GEE showed that pilot whales increased ODBA

and call counts during and/or after playbacks involving these calls. The response in both species involved increased speed, heading variance and ODBA. In both species, the response included increased cohesion of the focal groups, but there were clear interspecies differences in their vocal and movement responses. After exposure to this subset of killer whale calls, pilot whales increased vocalization rates and approached the sound source. Conversely, Risso's dolphins did not change their vocal behavior, and moved in a rapid, directed manner away from the source.

I acknowledge that the samples sizes for both species are small and that the playback exemplars used do not represent the full range of signals produced by these species. Nor do I fully understand the behavioral contexts in which the calls of mammal-eating killer whales were originally produced. Nevertheless, given these caveats and within the conditions tested here, I observed clear responses that followed my predictions based on the social behavior of the two focal species. Both short-finned pilot whales and Risso's dolphins responded more strongly to certain sounds of potential predators than those of conspecifics and neutral stimuli. There has been very little prior research exploring the responses of odontocete cetaceans to killer whale calls, so these results provide both answers and questions about the acoustic ecology of these animals.

Other mammalian prey have the capacity to recognize and discriminate among predators (Seyfarth, Cheney & Marler 1980a; Seyfarth, Cheney & Marler 1980b; Seyfarth & Cheney 1990; Deecke et al. 2002; Hettena et al. 2014), but it is not always apparent

which cues are used for recognition and discrimination. It may be that the structural features of the calls and/or the context in which they were produced allows pilot whales and Risso's dolphins to identify them as potentially threatening. Stimuli Oo-7 and Oo-8 were categorized as the same call type with ARTwarp classification (Table 23). While Oo-10 and Oo-11 were categorized as different call types, they share some similarities including fairly rapid frequency modulation within a relatively small frequency band; in the spectrogram these modulations create a series of plateaus. The four exemplars that elicited a response were recorded on two different days from two different groups. It is possible that these calls were produced under the same context. Exemplars Oo-10 and Oo-11 were recorded on 7-27-2005 from the same group and may have been produced by the same individual. Exemplars Oo-7 and Oo-8 were recorded on 7-13-2005 and may have been produced by the same individual. Several calls that did not elicit a response were also recorded on 7-13-2005 (Oo-2, Oo-4, Oo-5 and Oo-9).

There are many features in these calls beyond those described as 'nonlinear'. Biphonation and other non-linear phenomena such as sub-harmonics, frequency jumps and deterministic chaos are commonly found in alarm calls, and are known to elicit strong reactions in mammals (Fitch et al. 2002; Tyson et al. 2007). The unpredictability of non-linear phenomena in alarm calls may function as a way to prevent habituation (Fitch et al. 2002; Blesdoe & Blumstein 2014). A common example of a human alarm call containing non-linear properties is a baby screaming, which is well known as a difficult

signal to ignore. In both mammal and bird species, the addition of non-linearities to calls, synthesized non-linear sounds, and unfamiliar non-linear biological calls have been shown to provoke reactions in animals (Blumstein & Récapet 2009; Blesdorff & Blumstein 2014). All of the stimuli that elicited a response contain at least two 'nonlinear' features and some contain three (e.g., Oo-7 exhibits frequency jumps, biphonation and deterministic chaos) and all four contain deterministic chaos. Killer whale exemplar Oo-2, which did not elicit a response, also was identified as containing deterministic chaos, but did not contain any other nonlinear components. Perhaps it is the presence of deterministic chaos and an additional nonlinear feature(s) or other features unique to killer whales that elicited such strong responses.

Three of the four calls that elicited a response were classified as biphonic and while it is too early to say that biphonation is a feature in killer whale calls that elicits a response, it does merit further investigation. Biphonic calls have been described in all mammal-eating killer whale populations studied to date (Tyson et al. 2007), and their behavioral and contextual usages imply that they function as group identifiers among pods (Filatova et al. 2009). The upper frequency component of these calls is more directional than the lower frequency component, which might allow a receiver to localize the caller based on the relative intensities of the two components in the call (Miller 2006). Biphonic calls tend to have higher source levels than monophonic calls, further supporting the idea that these calls are used for group communication (Miller

2006). Thus, these calls may reflect the presence of a large numbers of killer whales in the area possibly following cooperative prey capture events, which could explain the strong reactions observed here in pilot whales and Risso's dolphins.

Pilot whale calls share some characteristics with those of killer whales including biphonation and other non-linear phenomena (Sayigh et al. 2012). For example, the exemplar Gm-10 was biphasic, but did not include any other non-linear phenomena. Several pilot whale calls included subharmonics (Gm-1,5,11,13 and 16) and Gm-11 contained both subharmonics and frequency jumps. The lack of response of pilot whales to these calls supports my contention that the behavior following playbacks of killer whale calls was an anti-predator response. There is a large body of literature supporting the concept of an innate identification of predators (see (Hettenga et al. 2014) for review), and the results of this study suggest that both pilot whales and Risso's dolphins can identify particular calls of potential predators which may indicate potential danger based on structural features in the calls.

There were no clear aspects of group size, group composition, or behavioral context that predicted the reactions observed in pilot whales or Risso's dolphins (Table 19 and Table 20). Received level, potential reduced received levels based on the orientation of the tag relative to the sound source and distance from the sound source and the animal did not correlate with strong responses (Table 18). Given the evidence, the responses appeared to result from a differential categorization of calls that reflected

the potential risk of predation. In both focal species, these responses occurred in a manner that is consistent with their patterns of social organization. Pilot whales, which live in relatively permanent groups characterized by strong social bonds, responded by increasing social cohesion. Risso's dolphins, with a social structure that has less permanence in social affiliations and is characterized by more fluidity, displayed an exaggerated flight response, moving rapidly away from the sound source, in a coordinated manner.

These results do not unequivocally demonstrate that the two focal species have a completely stereotyped anti-predator response or that in all cases the sole determinant of the probability of a response to killer whale calls is the presence or absence of biphonic calls. Nor do these results prove that the strong responses observed to other external stimuli, including MFAS, are necessarily the result of animals categorizing those sounds in the same general class as the calls of predators. However, the responses of both species to signals that share specific call structure is striking, particularly given the small number of playback trials. It is also striking that these calls were produced on the same days within the same groups and potentially under the same context. These findings suggest that these animals are performing some type of cognitive categorization, such that social organization of each species modulates the nature of responses that do occur.

Conclusions

Short-finned pilot whale social structure appears to have wide ranging implications from foraging strategies to protection from predators. The high resolution movement and acoustic data acquired from DTAGs provided a window into short-finned pilot whale foraging behavior and allowed me to assess the different individual and social response of pilot whales and Risso's dolphins to the sounds of predators. This information combined with genetic data and photogrammetry allowed me to identify potential habitat segregation due to differences in body sizes in short-finned pilot whales. I used this fine scale foraging to inform SLTDR data, thus I was able to put these fine scale observations into a longer term context.

Analysis of both fine and course scale foraging behavior allowed me to examine the influence of social structure, environment and physiological limits on the foraging strategies of short-finned pilot whales. Drivers that normally force sexually dimorphic species to segregate appear to work in concert to facilitate cohesion in short-finned pilot whales. Predation risk promotes cohesion at the surface as a form of social defense strategy while the large size of adult males provides the capacity to feed over a greater range of depths, potentially limiting intraspecific competition. While differences in body size lead to differences in energy requirements, feeding rates and dive capacities, pilot whales appear to overcome the costs to synchrony by coordinating their foraging

bouts (Visser et al. 2014) and making calls at depth to maintain social ties with the group (Jensen et al. 2011).

Most foraging dives contained multiple feeding buzzes and feeding attempts did not coincide with large bursts of speed which would suggest this population of short-finned pilot whales are foraging on multiple (small) prey items. It is unclear whether large and small individuals were foraging on different prey items. Kinematics including ODBA and speed around prey capture attempts did not differ by depth, but pilot whales on average had longer pursuits during prey capture attempts at shallower depths. I observed no diel patterns in foraging rates or depth on DTAG or SLTDR records, which contradicted my initial predictions based on observed prey types in the stomachs of stranded pilot whales off Cape Hatteras (Mintzer et al. 2008) and from observations of the foraging behavior of closely related odontocete cetaceans (Baird et al. 2002; Soto et al. 2008). ADL_C and ADL_B values both implied that this population of pilot whales rarely if ever exceed their aerobic dive limits when foraging for food. Optimal foraging theory predicts that animals should behave in a way that will maximize their net energy gain and diving mammals may meet or exceed their aerobic limits to maximize foraging time on particularly profitable prey patches (Costa et al. 2004; Hazen et al. 2015). Considering pilot whale foraging bouts are relatively long, it may be that they optimize energy intake over the temporal scale of the bout rather than individual dives. This fits with recent

work that suggests dive durations will increase with short-term dive-scale patch quality but decrease with long-term, bout-scale patch quality (Watanabe et al. 2014).

It is difficult to compare my results with those of pilot whales elsewhere because there are so few published observations of the foraging behavior of this species. In the only other large-scale published study, Soto et al. (2008) used DTAGs to study the foraging behavior of 23 short-finned pilot whales off Tenerife, in the Canary Islands. In general, their observations were similar to mine, with foraging dives reaching similar depths and having similar durations. Soto et al. (2008) reported some apparent diel variation in foraging behavior, with deeper dives made during daylight hours, but with fewer foraging buzzes than foraging dives made at night. These authors focused their attention on a subset of foraging dives during daylight hours, in which tagged animals made downward directed sprints, presumably in pursuit of large prey items. Soto et al. (2008) estimated foraging sprints short-finned pilot whales may use anaerobic pathways during foraging due to the eightfold increase in power compared to the mean swim speed. They posited the short dive durations (relative to other deep diving marine mammals) are a result of energy expended during these sprints. These differences may explain why I observed such long bouts, with few instances of dives exceeding aerobic limits in the Western Atlantic population of short-finned pilot whales. While it may be beneficial to exceed aerobic limits when pursuing highly calorific prey items as seen in

Tenerife, there is most likely minimal benefit to exceeding aerobic limits in pursuit of an additional single small prey item.

Lastly the study of the response of short-finned pilot whales and Risso's dolphins to the calls of mammal eating killer whales advances the concept that cetacean social structure mediates the response to a potential predator or threat. Short-finned pilot whales and Risso's dolphins reacted to the sound of mammal-eating killer whales in a manner that is consistent with their social organization. Pilot whales increased social cohesion, increased their vocal activity, and oriented towards the sound source. In contrast, Risso's dolphins did not change their vocal activity and moved strongly away from the source. Both pilot whales and Risso's dolphins responded to a select number of MEK calls, suggesting that recognition of predators might be specific to certain calls and or components within a call. Both species appear capable of discriminating amongst different killer whale calls and this is the first demonstration, to my knowledge, of such an ability in cetaceans. This suggests that structural features of these signals play critical contextual roles in determining the probability of response to potential threats in odontocete cetaceans.

Data Gaps and Future Work

My analysis of fine scale foraging data provided strong support for the hypothesis that pilot whale size classes segregate their foraging habitat by diving to

different depths. Confirmation of segregation by foraging depth will require concurrent tag deployments on multiple animals of different sizes. Deployment of multiple SLTDRs on different sized animals in a group will provide both synoptic records of dive depth and an understanding of the movement patterns and cohesive nature of the group. Furthermore, my analysis of foraging behavior and capture success was hampered by the unknown effect of tag placement on jerk signal and other kinematics. Future work might benefit from an analysis of the influence of tag placement on the measures of kinematics and might be accomplished through studies involving captive trained animals.

The results of the multi-scale study provided further insights into the pattern and variation of pilot whale foraging behavior. This study, which applied high resolution behavioral data and analysis to low-resolution data, can be useful in many applications. For the past two decades, there has been considerable interest in science and management of the impact of anthropogenic sounds on marine mammals (National Research Council 2005; Southall et al. 2008). In many mammals, cessation of foraging is considered to be an important response to anthropogenic disturbances, because it has obvious consequences for the fitness of the individual (Southall et al. 2008). Understanding when and if anthropogenic disturbance coincides with, and is the potential cause for the cessation of foraging will require an understanding of the natural patterns of foraging. While this study used short-finned pilot whales, there is a large

opportunity to test this method with cetacean species where fine scale, accurate foraging data is available. About 980 DTAGs have been deployed on 20 species of cetaceans, 13 of which are odontocetes (Sound and Movement Tags). This large body of data could yield species and population specific predictors of foraging and would help inform future studies.

The results of the playback study in chapter 3 suggests the structural features of MEK calls play critical contextual roles in determining the probability of response to potential threats in odontocete cetaceans. Future work should consider the relative importance of particular aspects of calls of mammal-eating killer whales, such as deterministic chaos, frequency jumps, subharmonics and biphonation in eliciting behavioral responses. This research should examine the potential importance of frequency modulation patterns and order relative to tonal elements and the extent to which reverberation may indicate a spatial context (e.g. distance to the source) in ways that mediate potential behavioral responses.

A straightforward approach to this problem would be to conduct playback experiments, similar to those described in chapter 3 with mammal-eating killer whale calls that have been digitally manipulated. The calls should be manipulated in a manner that would facilitate identification of the specific feature(s) of the calls that elicit the strong responses I observed. For example, calls of mammal-eating killer whales could be manipulated to remove certain frequency components or to manipulate the chaotic

portion of the stimulus. In such work, careful consideration should be given to the exact type of signal manipulation and appropriate controls to ensure that field experiments provide the greatest power possible to determine which specific aspects of these signals evokes a response in focal animals. The playback should be presented under the appropriate behavioral context in which the animal would experience it. Lastly great care should be taken in considering what behavioral variables, including broad contextual variables, are collected and at what frequency.

Appendix A

Table 24 – DIC values for each model type and for each cost metric used in each model. For all cost metrics, the Random Slope, Random intercept model had the lowest DIC values.

Cost Metric	Bayesian Linear Regression	Fixed Slope, Random Intercept	Random Slope, Random Intercept
ODBA	519564	451285	281949
MSA	541893	473193	303017
Speed	540956	472010	300086
Buzz Duration	531152	465319	293238

Table 25 - β values for Bayesian linear regression with ODBA as the cost metric, if the range of values crosses zero it is equivalent to no effect

Bayesian Linear Regression			
percentile	Intercept	Size (small)	ODBA
2.50%	566.22	-252.87	-3.96
50%	566.88	-251.45	-3.39
97.50%	567.54	-250.03	-2.83

Table 26 - Fixed effects β values for fixed slope random intercept model with ODBA as the cost metric, if the range of values crosses zero it is equivalent to no effect

Random Intercept, Random Slope			
percentile	Intercept	Size (small)	ODBA
2.50%	382.55	-236.81	-0.59
50%	442.15	-139.76	9.95
97.50%	503.7	-41.72	19.82

Table 27 - β values for Bayesian linear regression with buzz duration as the cost metric, if the range of values crosses zero it is equivalent to no effect

Bayesian Linear Regression			
percentile	Intercept	Size (small)	Buzz duration
2.50%	510.83	130.56	-46.26
50%	511.4	131.14	-45.66
97.50%	511.98	131.72	-45.08

Table 28 - Fixed effects β values for fixed slope random intercept model with buzz duration as the cost metric, if the range of values crosses zero it is equivalent to no effect

Fixed Slope, Random Intercept			
percentile	Intercept	Size (small)	Buzz duration
2.50%	294	127	-46.85
50%	509.29	127.61	-46.23
97.50%	641.26	128.26	-45.7

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