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UNIVERSITY OF CALIFORNIA, SAN DIEGO

**By the Light of the Moon:
North Pacific Dolphins Optimize Foraging with the Lunar Cycle**

A dissertation submitted in partial satisfaction of the
requirements for the degree
Doctor of Philosophy

in

Oceanography

by

Anne Elizabeth Simonis

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2017

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Co-Chair

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2017

EPIGRAPH

"All things make music with their lives."

—John Muir

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ABSTRACT OF THE DISSERTATION

By the Light of the Moon: North Pacific Dolphins Optimize Foraging with the Lunar Cycle

by

Anne Elizabeth Simonis

Doctor of Philosophy in Oceanography

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Simone Baumann-Pickering, Co-Chair

John A. Hildebrand, Co-Chair

The influence of the lunar cycle on dolphin foraging behavior was investigated in the productive, southern California Current Ecosystem and the oligotrophic Hawaiian Archipelago. Passive acoustic recordings from 2009 to 2015 were analyzed to document the presence of echolocation from four dolphin species that demonstrate distinct foraging preferences and diving abilities. Visual observations of dolphins, cloud coverage, commercial landings of market squid (*Doryteuthis opalescens*) and acoustic backscatter of fish were also considered in the Southern California Bight.

The temporal variability of echolocation is described from daily to annual timescales,

with emphasis on the lunar cycle as an established behavioral driver for potential dolphin prey. For dolphins that foraged at night, the presence of echolocation was reduced during nights of the full moon and during times of night that the moon was present in the night sky.

In the Southern California Bight, echolocation activity was reduced for both shallow-diving common dolphins (*Delphinus delphis*) and deeper-diving Risso's dolphins (*Grampus griseus*) during times of increased illumination. Seasonal differences in acoustic behavior for both species suggest a geographic shift in dolphin populations, shoaling scattering layers or prey switching behavior during warm months, whereby dolphins target prey that do not vertically migrate.

In the Hawaiian Archipelago, deep-diving short-finned pilot whales (*Globicephala macrorhynchus*) and shallow-diving false killer whales (*Pseudorca crassidens*) also showed reduced echolocation behavior during periods of increased lunar illumination. In contrast to nocturnal foraging in the northwestern Hawaiian Islands, false killer whales in the main Hawaiian Islands mainly foraged during the day and the lunar cycle showed little influence on their nocturnal acoustic behavior. Different temporal patterns in false killer whale acoustic behavior between the main and northwestern Hawaiian Islands can likely be attributed to the presence of distinct populations or social clusters with dissimilar foraging strategies.

Consistent observations of reduced acoustic activity during times of increased lunar illumination show that the lunar cycle is an important predictor for nocturnal dolphin foraging behavior. The result of this research advances the scientific understanding of how dolphins optimize their foraging behavior in response to the changing distribution and abundance of their prey.

Chapter 1

Introduction

1.1 The influence of light on behavior

Every day throughout the world's oceans, mesopelagic fish, squid and other invertebrates take part in the largest synchronized movement of biomass on the planet, known as diel vertical migration (DVM). Vertically migrating organisms are important prey for many fish, seabirds and marine mammals (Davison et al., 2015, Spear et al., 2007, Pauly et al., 1998) but they evade their more aerobic, visually oriented predators by residing in deep, dark, hypoxic waters during the day; only rising to the surface at night to forage under the cover of darkness (Barham, 1966, Netburn and Koslow, 2015, Lampert, 1993). One of the most significant factors affecting the magnitude, timing and distribution of vertical migrators is light, both solar and lunar (Boden and Kampa, 1967, Blaxter, 1974). Absolute light levels, the rate of change in light levels, and endogenous rhythms have been proposed as triggers for vertical migration (Benoit-Bird et al., 2009b, Ochoa et al., 2013). In addition to light and endogenous rhythms as cues, prey distribution, bioenergetics, tidal influence, predator avoidance and behavior of commensal species may also drive vertical migrations (see review in Neilson and Perry 1990). The most dramatic change of light in the ocean occurs between day and night, but the comparatively small differences related to the lunar

cycle also influence the behavior of vertical migrators.

The lunar cycle refers to the variation in lunar illumination due to the orbit of the Moon around the Earth, which occurs every 29.5 days. As the Earth rotates, the Moon travels by the same spot on the Earth every 24.8 hours, causing the Moon to rise above the horizon about 50 minutes later each day. The changing position of the Moon in relation to the Earth and the Sun causes varying fractions of the Moon's face to be illuminated in the night sky, as seen from Earth. Throughout the cycle from new to full moon, the brightness of the Moon varies on a nonlinear cycle due to the Moon's rough topography and high reflectance of lunar soils, with a full moon being about 10 times brighter than a new moon (Miller and Turner, 2009). On longer time scales, moon brightness may vary by about 30% due to the varying distance between Earth and the Moon (Miller and Turner, 2009). These changes in light levels may be perceived by marine organisms and in turn, influence their behavior, physiology and ultimately fitness.

The brightness of the moon influences the behavior of marine organisms in various ways, with effects that ripple throughout the food web. For mesopelagic fish and squid, the extent of vertical migration is reduced during nights of the full moon (Clarke, 1973, Roper and Young, 1975), but zooplankton are abundant in surface waters during these times due to the absence of their predators (Gliwicz, 1986b). A 9-year periodicity of especially bright lunar illumination increases the abundance of zooplankton, which in turn enhances the growth and survivorship of commercially important small pelagic fishes (Hernández-León, 2008). On shorter time scales (~hours to days), lunar dynamics of zooplankton abundance influence the downward flux of organic matter, with significant implications for biogeochemical cycling (Hernández-León et al., 2002). Optimal foraging theory suggests that the energy gained from prey should not exceed the energy spent while foraging (Pyke, 1984); therefore, both predators and their prey should be motivated to respond to changing light conditions in order to optimize their survival (Gliwicz, 1986a, Benoit-Bird et al.,

2009b).

For predators that access prey at depth, brighter moonlight conditions are associated with increased foraging costs; however, this may be offset by vertical packing of prey at depth, which results in higher densities of prey at depth and could ultimately increase foraging efficiency (Benoit-Bird et al., 2009a). Predators with thermal or aerobic limitations, such as marine mammals, may be limited to forage during new moons when prey are abundant near the surface. For example, juvenile Galápagos fur seals (*Arctocephalus galapagoensis*) lose biomass during nights of the full moon because they have not yet developed the diving ability to access prey at depth (Horning et al., 1999). Recreational fishermen also have varying success throughout the lunar cycle. Full moons are associated with low catch rates for mahi-mahi (*Coryphaena hippurus*) and yellowfin tuna (*Thunnus albacares*), but high catch rates for black marlin (*Makaira indica*; Lowry et al. 2007). Black marlin are physiologically limited to warm, surface waters, so when prey densities are low at the surface, they increase their foraging effort and become more vulnerable to fishing; In contrast, mahi-mahi and yellowfin tuna can cope with lower temperature and oxygen conditions at depth, and therefore track their mesopelagic prey to deeper waters during the full moon (Lowry et al., 2007). Tuna may be able to dive deeply, but they mainly rely on light to detect their prey and seem to be limited to forage during bright moonlight conditions (Musyl et al., 2003, Schaefer and Fuller, 2002, Wilson et al., 2005). Increased moonlight allows for visual predation, but can also decrease foraging efficiency if predators are more easily detected by prey. For dolphins, widespread nighttime foraging behavior (Evans, 1971, Norris et al., 1994, Soldevilla et al., 2010, Wiggins et al., 2013) suggests that there are significant costs to daytime foraging when prey are at depth; however, there are limited observations which describe how the moon may influence dolphin behavior. During nights of the full moon in nearshore waters of Hawai'i and New Zealand, Benoit-Bird et al. (2009b) observed an increase in the relative abundance of spinner (*Stenella longirostris*) and dusky

(*Lagenorhynchus obscurus*) dolphins, respectively, even though their mesopelagic prey was less abundant in surface waters during these times. Benoit-Bird et al. (2009b) suggested that the increase in dolphin relative abundance may be due to their enhanced ability to forage visually, a switch to non-foraging behaviors, or reduced foraging efficiency that required longer foraging efforts. The influence of the lunar cycle on the behavior of other dolphin species has not been described and is the focus of this study.

1.2 Passive acoustic monitoring

Many biological and anthropogenic sources produce characteristic acoustic signatures that can be recognized, and along with geophonic sources, these signals contribute to the overall soundscape of a habitat. Dolphins are especially good candidates for passive acoustic monitoring as they produce unique sounds during social communication, navigation, and foraging. Depending on the ambient noise level and species of interest, these acoustic signals can be classified to the species level and may be detected over ranges of thousands of meters (Soldevilla et al., 2008, Baumann-Pickering et al., 2013, 2015, Wiggins and Hildebrand, 2007). When combined with other data, such as in-situ or remotely sensed environmental parameters, long-term continuous acoustic monitoring can be an especially powerful tool to study the ecology and behavior of marine mammals and other acoustically active marine animals.

The ability of dolphins to navigate and forage through echolocation emerged 30 million years ago and it has evolved to be a primary sensory modality (Nummela et al., 2004, Fahlke et al., 2011, Branstetter et al., 2012). Echolocation, along with the ability to breath-hold and dive deeply, has allowed odontocetes to exploit foraging niches devoid of light where there may be little competition from other predators. Echolocation clicks are generated near the blow hole with a structure called the dorsal bursae complex, also known as the monkey lips (Cranford et al., 1996), before passing through a fatty melon

in the forehead which focuses the sound into a narrow beam (Au, 1993). The outgoing click from a dolphin has been shown to be very directional (-30 dB at $>30^\circ$ off axis of the clicks central beam for a bottlenose dolphin), with the frequency and amplitude of signals changing as they are received on the sides of the echolocation beam (Au, 1993, Au et al., 2012). Dolphins also have demonstrated some ability to control the source level and peak frequency of clicks depending on the echolocation tasks (Au, 1993, Au and Benoit-Bird, 2003), but the morphology of the dolphin head and sound generating mechanism is believed to have a significant influence on the outgoing signal (Cranford et al., 1996, Madsen et al., 2013, Macleod et al., 2007, Fahlke et al., 2011). The structural features of echolocation clicks arriving at a stationary receiver will vary due to the directional nature of the sound generator and changes in the heading of animals as they navigate and forage. For some species, there are consistent, distinct spectral and temporal features in echolocation clicks that can be used for species-level classification (Soldevilla et al., 2008, Baumann-Pickering et al., 2013, 2015).

The detection of echolocation clicks can indicate animal presence over long-term and continuous timescales, but dolphin behavior, instrument sensitivity and environmental conditions determine the spatial extent of passive acoustic monitoring. Echolocation clicks contain high frequency energy that is quickly attenuated as it travels through the water. From the surface to a bottom-moored recording instrument 1,000 m away, the transmission loss associated with spherical spreading and absorption for a signal at 30 kHz in 15°C water, is 66 dB (Urick, 1983). The directional beampattern of outgoing echolocation clicks will further limit the detection range for off-axis clicks. The expected detection range for a foraging group of dolphins will depend on many factors, including the number of individuals and orientation of the group; however, considering the behavior and transmission loss for shallow-diving dolphins (< 50 m), like common dolphins (*Delphinus delphis*), the expected detection range for a foraging group may vary from 1.5 to 5 km from a seafloor sensor at

1000 m (Frasier et al., 2016b). Therefore, passive acoustic monitoring is useful to investigate behavioral drivers in discrete locations over a large range of temporal scales.

1.3 Model species

1.3.1 Common dolphins

Common dolphins are one of the most widely distributed cetaceans and can be found in all temperate to tropical regions of the world. In the Southern California Bight (SCB), common dolphins are, by far, the most abundant cetacean (Barlow, 2016, Campbell et al., 2015). Two subspecies are recognized in the SCB including the short-beaked and long-beaked common dolphins, *D. d. delphis* and *D. d. bairdii*, respectively (Cunha et al., 2015). Their distribution within the SCB has been shown to vary on seasonal and inter-annual time scales, likely in response to shifting prey distributions and oceanographic conditions (Campbell et al., 2015). School sizes of tens to thousands of individuals have been observed, and have been shown to vary seasonally, with the largest group sizes in the SCB observed during winter months (Campbell et al., 2015).

Early tagging studies of common dolphins in the SCB showed that most foraging dives occurred within 30-60 m of the surface and dolphins rarely dove deeper than 200 m (Evans, 1971). There are distinct behavioral differences between night and day, where most foraging occurs at night and socializing and traveling occurs during the day (Henderson et al., 2011, Wiggins et al., 2013). Nighttime foraging behavior suggests diving abilities are not sufficient to reach the daytime depths of their prey, i.e. vertically migrating organisms.

Opportunistic feeding behavior of common dolphins observed around the world indicates that their diet represents prey that are locally available and energy-rich (Silva, 1999, Pusineri et al., 2007, Meynier et al., 2008, Spitz et al., 2010). Stomach content analyses confirm that vertically migrating fish and cephalopods are important prey items for common

dolphins in Southern California, but market squid (*Doryteuthis opalescens*), juvenile and adult small pelagic fish such as sardine (*Sardinops sagax*) or anchovy (*Engraulis mordax*) may be preferred when available (Evans, 1975, Osnes-Erie, 1999).

1.3.2 Risso's dolphins

Risso's dolphins (*Grampus griseus*) are found in a range of habitats around the world, ranging from tropical to cold-temperate, but peak densities are observed in continental shelf or slope waters in cool-temperate regions (Jefferson et al., 2014). Resident populations are found in coastal areas (Hartman et al., 2008, de Boer et al., 2013, Dohl et al., 1983), and in the Atlantic, males were shown to have higher site-fidelity than females (Hartman et al., 2015). In the California Current, sighting and stranding records indicate high decadal variability in Risso's dolphin distribution and abundance (Leatherwood et al., 1980, Dohl et al., 1983, Shane, 1995, Kruse et al., 1999). Inshore and offshore movements between winter and summer seasons have been reported for a resident population in southern California (Dohl et al., 1983, Barlow, 1995).

Risso's dolphins are a highly social species, forming stable, long-term associations between adults (Hartman et al., 2008) and often occurring in mixed-species associations with other marine mammals (Bacon et al., 2017). The collective searching ability of these social groups may improve the detection of solitary or widely distributed prey, and alloparental care provides protection for calves with limited diving abilities during maternal foraging dives (Bacon et al., 2017, Hartman et al., 2008).

Risso's are often labeled "deep-diving" dolphins due to the predominance of squid in their diet (Wurtz et al., 1992). Daytime tag records from adult Risso's dolphins offshore of Southern California indicate a mean dive depth of 128 m (range 20-566 m) and dive durations that range from 0.5 to 8.1 minutes (Arranz et al., 2016). Observations from passive acoustic recordings suggest that Risso's primarily forage at night (Soldevilla et al., 2010),

unlike that of other deep-diving odontocetes such as sperm and beaked whales which show little to no diel variation in foraging behavior (Davis et al., 2007, Baumann-Pickering et al., 2014).

Stomach content analyses from bycaught or stranded individuals confirm that squid are the primary prey for Risso's dolphins around the world (Orr, 1966, Blanco et al., 2006, Ozturk et al., 2007), although there may be significant differences in prey species between age-sex classes and between seasons (Cockcroft et al., 1993). Squid families *Loliginidae*, *Ommastrephidae*, *Onychoteuthidae*, *Histioteuthidae* represent preferred prey species as they are commonly found in stomach contents from Risso's dolphins globally (Wurtz et al., 1992, Cockcroft et al., 1993, Blanco et al., 2006). In California, market squid and jumbo squid (*Dosidicus gigas*) are known to be a part of Risso's dolphin diet (Orr, 1966, Kruse et al., 1999). Although squids seem to dominate the diet of Risso's dolphins, multiple authors have proposed that the dietary importance of squid may be overestimated due to the persistence of hard beaks in stomach contents (Cockcroft et al., 1993, Clarke and Pascoe, 1985). Few studies have sufficient sample sizes across seasons and populations to confidently describe the full range of foraging preferences for Risso's dolphins; however, stable isotope analyses from south Atlantic indicate that local foraging groups may coexist and prefer distinct prey types at different trophic levels (Riccialdelli et al., 2012). Additionally, in South Africa, epipelagic fish may be used as supplements to the diet, as Sekiguchi et al. (1992) observed stomach contents filled up to 24% by volume with anchovy (*Engraulis capensis*) and horse mackerel (*Trachurus capensis*). Further, in the Mediterranean and South Atlantic, teleost scales and other fish remains have also been documented from stranded individuals (Blanco et al., 2006). Nevertheless, the occasional records of fish as prey seem to be an exception to the consistent descriptions of almost exclusively cephalopod diets in Risso's dolphins around the world.

1.3.3 Pilot whales

Short-finned pilot whales (*Globicephala macrorhynchus*, referred to as pilot whales hereafter) are found in warm temperate and tropical waters around the world. They may be found in pelagic, offshore groups, as well as near oceanic islands and in coastal areas. Globally, pilot whale groups demonstrate a stable, matrilineal social structure, where offspring of both sexes remain with their mothers (Heimlich-Boran, 1993, Mahaffy et al., 2015, Alves et al., 2013). The presence of post-reproductive females, an unusual trait among vertebrates, suggests that older females contribute significant value to family groups, likely in the form of ecological knowledge about predator defense and foraging strategies (Kasuya and Marsh, 1984). Pilot whales are found throughout the Hawaiian Islands, and the west coast of the island of Hawai'i is a foraging hotspot and high use area for at least one population (Mahaffy et al., 2015, Baird et al., 2015, Abecassis et al., 2015).

Pilot whales are considered deep-divers among odontocetes. Time-depth recorders on tagged individuals document dives to depths greater than 1,000 m and regular dives to 700 m (Aguilar de Soto et al., 2008, Wells et al., 2013, Quick et al., 2017). In Florida and the Canary Islands, pilot whale dive behavior has been shown to be more consistent and shallower at night than during the day (Aguilar de Soto et al., 2008, Wells et al., 2013) suggesting that even with impressive diving abilities, they optimally schedule foraging to occur when vertically migrating prey are abundant in surface waters.

The extreme diving ability (Aguilar de Soto et al., 2008), reduced dentition and suction feeding abilities (Werth, 2000) of pilot whales suggest that they are squid-specialists, but diets show some variation between regions. Squid dominate the stomach contents from bycaught and stranded individuals examined in the California Current (Sinclair, 1992, Seagars and Henderson, 1985), but a variety of epipelagic fish and cephalopod species have been observed in Atlantic populations (Waring et al., 1990, Overholtz and Waring, 1991, Donovan et al., 1993). In Hawai'i, pilot whales are strongly associated with the deep

mesopelagic boundary community in a foraging hotspot along the western slope of the island of Hawaii (Abecassis et al., 2015).

1.3.4 False killer whales

False killer whales are wide-ranging, pelagic dolphins found in tropical and warm-temperate oceans (Baird, 2002). Throughout the Hawaiian archipelago, two resident populations are closely associated with the oceanic islands of the eastern main Hawaiian Islands (MHI) and the northwestern Hawaiian Islands (NWHI; Baird et al. 2008, 2012a, 2013). A third population of pelagic false killer whales is also recognized in waters greater than 40 km offshore of the islands (Carretta et al., 2011). The MHI population faces multiple threats, including elevated levels of persistent organic pollutants, reduced prey size and abundance due to competition with commercial fisheries, serious injury and mortality due to fishery interactions and retaliatory shooting related to fishery interactions (Baird, 2009). From 1994 to 2005, bycatch of false killer whales associated with depredation of longline fisheries exceeded sustainable levels (Carretta et al., 2016, Forney and Kobayashi, 2007) and the MHI population was designated as endangered in 2012 (77 FR 71260, 29 November, 2012).

Similar to pilot whales, false killer whales form matrilineal social groups that include post-reproductive females (Ferreira, 2009, Photopoulou et al., 2017) and strong, long-term associations form between individuals (Baird et al., 2008). In Hawai'i, small clusters of a few animals from larger groups of up to 40 individuals that may be spread over distances of 20 km (Baird et al., 2008).

There is little known about the diving behavior of false killer whales but short-term deployments of tags with time-depth recorders on false killer whales in Japan and Hawai'i indicate that most dives are within the upper 300 m, and nighttime dives are shallower and shorter than daytime dives (Minamikawa et al., 2013, Oleson et al., 2010).

In the South and Central East Atlantic, false killer whale stomach contents from

stranded animals have contained exclusively cephalopods, (Hernández-García, 2002, Andrade et al., 2001, Sekiguchi et al., 1992) or cephalopods combined with epipelagic or demersal-benthic fish depending on the habitat (Alonso et al., 1999, Botta et al., 2012). Occasionally, false killer whales have also been observed to take other marine mammals as prey (Perryman and Foster, 1980, Palacios and Mate, 1996, Rinaldi et al., 2006). In the main Hawaiian Islands, false killer whales have been documented feeding on at least 10 spp. of large pelagic fish including yellowfin (*Thunnus albacares*), albacore (*T. alalunga*) and skipjack tuna (*Katsuwonus pelamis*), broadbill swordfish (*Xiphias gladius*), mahi mahi (*Coryphaena hippurus*), ono (*Acanthocybium solandri*), and monchong (*Eumegistus illustrus*), that are also the targets of commercial and recreational fisheries (Baird, 2009).

1.4 Study areas

1.4.1 Southern California Bight

The Southern California Bight (SCB) is defined by the North American coastline south of 34°N (Point Conception) that curves eastward and terminates around 30°N in the south. The equatorward California Current dominates flow in the offshore waters of the SCB and brings cool, low salinity water into the region. The subsurface California Undercurrent, and the California Countercurrent are two poleward currents that bring warm, saline equatorial waters into the region. The SCB has a broad shelf, in which exists the California Borderlands, consisting of complex bathymetry forming many deep basins, ridges, and offshore islands, which interact with large-scale currents to form mesoscale eddies and energetic meanders. These mesoscale features aggregate zooplankton and fish larvae (Logerwell et al., 2001) creating foraging opportunities that attract predators, like sea birds and marine mammals (Croll et al., 2005).

Throughout the California Current System, equatorward winds intensify in the spring

and summer, and through Ekman transport surface waters are pushed offshore causing deep, cold, nutrient-rich water to upwell near the coast (Checkley and Barth, 2009). Seasonal upwelling stimulates primary productivity, which in turn supports higher trophic levels (Croll et al., 2005). In addition to wind-stress driven coastal upwelling, wind stress curl produces slower upwelling in offshore areas (Di-Lorenzo, 2003). The different rates of nutrient delivery in coastal and offshore habitats support distinct size classes of phytoplankton and consequently, distinct trophic assemblages (Rykaczewski and Checkley, 2008). The migration patterns and habitat ranges of many marine mammal species have evolved to strategically utilize the dynamic prey resources in the California Current System (Forney and Barlow, 1998).

On timescales longer than a year, the largest source of variation in the California Current System is associated with the El Niño Southern Oscillation (ENSO). Strong ENSO years bring higher sea surface temperatures, deeper mixed layers and reduced upwelling within the SCB (Hayward, 2000). Primary productivity is often suppressed, and subsequently, the geographic distribution of many zooplankton, fish, and marine mammals shifts northward (Hayward, 2000, McGowan, 1985). Related to ENSO, but on decadal scales, the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) are associated with varying strengths of the California Current that influence upwelling, primary productivity and zooplankton assemblages. The PDO is most closely linked with upwelling in northern California while the NPGO is most closely linked with upwelling in southern California (Di Lorenzo et al., 2008).

Southern California contains the most densely populated area of humans in the United States (U.S. Census Bureau, 2013) and as such, there are myriad human impacts on marine ecosystems in the SCB. Commercial shipping, recreational and commercial fishing and military activities introduce underwater noise, chemical and marine debris pollution, ship-strikes and increased risks of entanglement are just a few of these threats to marine

mammals. Anthropogenic impacts are reduced in the Channel Islands National Marine Sanctuary (CINMS), which encompasses the Channel Islands, including San Miguel Island, Santa Cruz Island, Santa Rosa Island, Anacapa Island, Santa Barbara Island, Richardson Rock and Castle Rock and extends six nautical miles offshore of each rock and island (<https://channelislands.noaa.gov/>).

1.4.2 Hawaiian Archipelago

The Hawaiian Archipelago is the most remote island chain in the world, located more than 1,000 miles from the nearest foreign country (Kiribati) and more than 2,000 miles from the nearest continent (North America). The volcanic island chain consists of a string of islands and reefs, spanning more than 1,500 miles from the island of Hawai'i in the south, to Kure Atoll in the north. The Hawaiian Islands lie within the clockwise rotating North Pacific subtropical gyre, and extend from the North Equatorial Current in the south, to the edge of the eastward flowing North Pacific Current in the north. The subtropical gyre is characterized by oligotrophic conditions, with low concentrations of chlorophyll *a* and persistent stratification of the upper ocean waters. Sea surface temperature varies from 25-30°C, with mixed layers typically around 100 m thick (Stevenson and Niiler, 1983). When the northeastern trade winds interact with the Hawaiian island topography, eddies, internal waves, local upwelling and Taylor columns may form, which all have important effects on marine ecosystems (Boehlert and Genin, 1987). These interactions lead to enhanced primary production near the islands compared to the open ocean environment, a feature known as the "Island Mass Effect" (Doty and Oguri, 1956). Even with winter storms to promote mixing, the maximum mixed-layer depth remains shallower than average nitracline depths, creating nutrient limited primary production in surface waters (Dore and Karl, 1996, Dore et al., 2002). This mid-latitude region of low-surface chlorophyll is separated from the productive, high-chlorophyll region of the subpolar gyre by a basin wide Transition Zone Chlorophyll

Front (TZCF) observable from satellite sensors (Chavez et al., 1999, Polovina et al., 2001). This front provides important foraging habitat for large-pelagic species, which have been shown to track the front as it seasonally migrates up to 1000 km north and south (Polovina et al., 2001).

Near the islands, the greatest source of variation on a diel timescale is the horizontal and vertical movement of the mesopelagic community. As nighttime progresses, the mesopelagic boundary community vertically expands into two distinct layers while also moving closer to shore (Benoit-Bird et al., 2001). The extent of this movement peaks at midnight, after which organisms retreat to their original daytime positions in deeper, offshore waters (Benoit-Bird et al., 2001). On timescales of less than one year, cold-core eddies are the source of significant variation in the physical conditions of the upper ocean, influencing the distribution and abundance of a range of planktonic organisms to apex predators (Patzert, William C., 1969, Seki et al., 2001, 2002). The most significant source of inter-annual variation includes El Niño and La Niña events, which occur on cycles with periods of 3-7 years. During an El Niño event, the easterly trade winds weaken, causing a weakening of the westward equatorial current, deepening of the thermocline and increased stratification in the central and eastern Pacific.

The southern islands of Ni'ihau, Kaua'i, O'ahu, Moloka'i, Lna'i, Kaho'olawe, Maui and Hawai'i are home to the majority of the 1.4 million Hawaiian residents, although there are small military and scientific outposts on some of the northwestern islands (U.S. Census Bureau, 2013). Human activity around the islands includes commercial shipping, recreational and commercial fishing, and military activity. Longline fisheries represent the greatest threat to dolphins (Forney et al., 2011), and include a deep-set fishery targeting tunas and a shallow-set fishery targeting swordfish (WPRFMC, 2013). Anthropogenic threats are reduced in the Northwest Hawaiian Islands due to the designation of the Papahānaumokuākea Marine National Monument, one the of largest marine conservation areas in the world

(<http://www.papahanaumokuakea.gov/>). The Hawaiian Islands Humpback Whale National Marine Sanctuary also offers additional protection to cetaceans and their habitat around the Main Hawaiian Islands (<https://hawaiihumpbackwhale.noaa.gov/>).

1.5 Data sources

1.5.1 Passive acoustic recordings

The passive acoustic recordings used in this study were all collected using seafloor-moored High Frequency Acoustic Recording Packages (HARPs; Wiggins and Hildebrand 2007). HARPs recorded at sampling rates of 200 or 320 kHz with 16-bit quantization. The hydrophone was positioned about 30 m above the seafloor and was an omni-directional sensor (ITC-1042, International Transducer Corporation, Santa Barbara, CA) which had an approximately flat (± 2 dB) sensitivity from 10 Hz to 100 kHz of -200 dB re 1V/ μ Pa. Each system contained a custom-built preamplifier board and bandpass filter (Wiggins and Hildebrand, 2007). The calibrated preamplifier response was accounted for during analysis.

1.5.2 Active acoustic recordings

Acoustic backscatter of potential dolphin prey species was available at one site in the Southern California Bight (near Point Conception, California at 34° 18.45'N, 120° 48.39'W) during 2011-2014. Two customized Simrad ES10 190 kHz echosounders were mounted at 150 m depth on an interdisciplinary biogeochemical mooring (CCE-2; http://mooring.ucsd.edu/index.html?/projects/cce/cce2_data.html). Prior to deployment, each transceiver-transducer pair was calibrated using a 38.1-mm diameter sphere made from tungsten carbide with 6% cobalt binder (Demer et al., 2015). Every 30 minutes, two multiplexed transducers transmitted three 1024 μ s pulses towards the sea-surface, sampling the upper 150 m, and then three more towards the seabed, sampling from 150 to 300 m depth.

Samples at ranges surrounding the transmit pulses and echoes from other components of the mooring were removed. Then, echoes from large scatterers (body length $\gg$ wavelength, ~ 7.9 mm), i.e. putative fish and squid, were retained if their variance-to-mean ratio (VMR), calculated from samples at equivalent range across each 3-transmission ensemble, were between -40 and -23 dB, determined empirically (Demer et al., 2009). Finally, nautical area backscattering coefficients (sA ; $m^2 \text{ nmi}^{-2}$) were calculated for each 10-m depth and 30-minute interval.

1.5.3 Commercial squid catch

Southern California market squid landing receipts from all fishing blocks south of Point Piedras Blancas were taken from the California Department of Fish and Wildlife database during 2009-2015 (California Department of Fish and Wildlife, 2015). Catch data should be viewed with some caution as stocks may be depleted with little decline observed in catch rates, especially for fisheries that target aggregations, such as those for market squid (Jensen et al., 2012). Catch data alone should not be used as a proxy for biomass (Jensen et al., 2012), so the catch per unit effort (CPUE) was defined as the weight of landings per day, divided by the number of seine vessel receipts. The CPUE provides an index for squid abundance by measuring the amount of time required to make the landings.

1.5.4 Visual sightings of dolphins

Marine mammal visual observations were collected on quarterly California Cooperative Oceanic Fisheries Investigations (CalCOFI; <http://calcofi.org>) surveys using standard line-transect marine mammal survey protocols (Buckland et al., 1993, Barlow, 1995). Two experienced marine mammal observers used 7x50 Fujinon binoculars to record all marine mammals encountered during daylight hours while transitioning between CalCOFI stations. The species, group size, reticle of cetacean position relative to the horizon, relative angle

from the bow, latitude, longitude, ship heading, behavioral state, sighting cue, sea state, swell height, visibility and comments were noted for each sighting. Sightings were classified as “on-effort” when two observers were actively searching in Beaufort sea state 0-5, with the vessel traveling at least 11 km/h and visibility was greater than 1 km. Only “on-effort” sightings were included in this analysis.

1.6 Dissertation outline

The goal of this study is to understand how four dolphin species with distinct habitat preferences and foraging strategies optimize their behavior with respect to the lunar cycle. Chapters 2-4 are intended to stand alone as publishable articles and the reader may encounter some redundancy in the introduction and methods for each chapter.

In Chapter 2, I document lunar patterns in common dolphin foraging in the Southern California Bight. Assuming high rates of echolocation are indicative of foraging behavior, common dolphins show reduced rates of foraging during nights surrounding the full moon and during times of night when the moon is present in the night sky, especially during cooler months. I hypothesize that during these times, mesopelagic prey were beyond the range of shallow-diving dolphins. In warmer months of the spring and summer, more consistent foraging is observed throughout the lunar cycle and may represent geographic shifts of Eastern Tropical Pacific common dolphin populations into the Southern California Bight, shoaling scattering layers or prey switching behavior during the warm months, whereby dolphins target preferred small pelagic fish, not associated with the deep scattering layers, which are only seasonally available.

In Chapter 3, I studied how Risso’s dolphins in the Southern California Bight optimized their foraging with the lunar cycle. This chapter builds on the previous chapter by including measures of potential prey. Foraging activity of Risso’s dolphins was identified from passive acoustic recordings and visual sightings were used to show seasonal differences

in their geographic distributions. Likely prey was considered through the analysis of active acoustic backscatter and catch records from the Southern California commercial market squid fishery. Variation in Risso's dolphin acoustic activity corresponded to the annual catch per unit effort of market squid, and the distribution of Risso's dolphins in winter months closely matched that of spawning squid aggregations. I documented the highest rates of nocturnal dolphin foraging before the moon rose and during the darkest nights of the lunar cycle, when vertically migrating organisms were most abundant in surface waters. In spring and summer months, foraging also occurred during nights surrounding the full moon, when fish were present in the upper 300 m. It is likely that squid were associated with epipelagic fish, therefore the data in this chapter cannot confidently discriminate between full moon foraging effort for fish and squid.

In Chapter 4, I compare how the lunar cycle is related to the acoustic activity of two dolphins with distinctly different foraging strategies in the Hawaiian archipelago. Pilot whales are deep-diving odontocetes and squid specialists while false killer whales are shallow divers with more varied diets, but the nocturnal foraging behavior of each is reduced during the nights of the full moon and during the times that the moon is present in the night sky. There was significantly more echolocation activity from false killer whales during the day in the main Hawaiian Islands compared to the northwest Hawaiian Island location. Different temporal patterns in false killer whale acoustic behavior between the main and northwestern Hawaiian Islands can likely be attributed to distinct populations or social clusters with dissimilar foraging strategies and may be related to varying fishing pressure and environmental conditions.

Chapter 2

Lunar cycles affect common dolphin (*Delphinus delphis*) foraging in the Southern California Bight

2.1 Abstract

In the Southern California Bight, common dolphins (*Delphinus delphis*) are the most abundant dolphin and prey upon small pelagic fish, mesopelagic fish, and cephalopods. Mesopelagic fish and many cephalopods are available throughout the year, and they form deep scattering layers, some of which characteristically undergo strong diel vertical migrations. The extent of vertical migration depends on the degree of sea surface solar and lunar illumination. At their daytime depth, mesopelagic prey are beyond the range of shallow-diving dolphins, limiting their access to the prey field. Autonomous acoustic recorders monitored dolphin echolocation at two offshore recording locations 2009-2014. Manual and automated classification techniques were used to identify periods of high echolocation activity indicative of common dolphin foraging. Clear lunar patterns existed in cool

months when echolocation activity was highest during the darkest periods of the night and lunar month, indicating times when dolphins were foraging, possibly on mesopelagic prey. Echolocation was more abundant during warm months, but diel and lunar patterns in echolocation were weaker. Generalized additive mixed models show that the observed patterns in echolocation activity are correlated with lunar day and position of the moon in the night sky. Seasonal patterns may represent geographic shifts in common dolphin populations, shoaling scattering layers or prey switching behavior during the warm months, whereby dolphins target preferred small pelagic fish not associated with the deep scattering layers. Overall, dolphin foraging activity declined from 2009 to 2014 during warm months, which may be related to a declining abundance of small pelagic fish.

2.2 Introduction

Common dolphins (*Delphinus delphis*) are one of the most widely distributed cetaceans and, by far, are the most abundant cetacean predator in the Southern California Bight (SCB; Evans 1975, Barlow et al. 2008, Campbell et al. 2015). Two subspecies are recognized in the SCB: the short-beaked and long-beaked common dolphins (*D. d. delphis* and *D. d. bairdii*, respectively; Cunha et al. 2015). School sizes of tens to thousands of individuals have been observed, and have been shown to vary seasonally, with the largest group sizes in the SCB observed during winter months (Campbell et al., 2015). Common dolphin distribution in the region is also known to vary on seasonal and inter-annual time scales, likely related to shifting prey distributions and oceanographic conditions (Campbell et al., 2015). Opportunistic feeding behavior of common dolphins observed around the world suggests that their diet represents prey that are locally available and energy-rich (Silva, 1999, Pusineri et al., 2007, Meynier et al., 2008, Spitz et al., 2010). Therefore, the foraging behavior of common dolphins may indicate the distribution and relative abundance of dolphin prey. The objective of this study is to identify patterns in common dolphin

foraging behavior and consider how they may relate to potential prey.

Early tagging studies of common dolphins in the SCB showed that most deep foraging dives are made to 30-60 m and occur at night; only rarely did dolphins dive deeper than 200 m (Evans, 1971). Recent studies in the same region have shown distinct diel behavioral patterns of common dolphins where foraging mainly occurs at night and travel and social behavior occurs during the day (Henderson et al., 2011, Wiggins et al., 2013). The observed diving behavior suggests that the dolphins nocturnally feed on mesopelagic organisms, which migrate to the epipelagic zone (surface-200 m) at dusk.

Stomach content analyses confirm that vertically migrating fish and cephalopods are important prey items for common dolphins in Southern California (Evans, 1975, Osnes-Erie, 1999) but market squid (*Doryteuthis opalescens*), juvenile and adult small pelagic fish such as sardine (*Sardinops sagax*) or anchovy (*Engraulis mordax*) may be preferred when available (Evans, 1975). Adult anchovy and sardine are most abundant in the SCB during winter and spring months, respectively (Lo et al., 2011, MacCall et al., 2016); however, populations of both fishes have been shown to dramatically fluctuate in abundance with characteristic periods of about 60 years (Baumgartner et al., 1992). Osnes-Erie (1999) found no significant difference in variation of the diet of common dolphins between seasons in California from 1975 to 1994; however, the diet analysis was done at the species-level of prey items and an alternative analysis based on functional group (e.g. mesopelagic vs. small pelagic fishes) may yield different results. The ability of common dolphins to cope with large fluctuations in prey availability on seasonal and decadal timescales suggests that they are opportunistic and can adjust foraging strategies depending on local conditions.

Many mesopelagic fish and cephalopods undergo a diel vertical migration, from depth (normally below 300-400 m) during the day (Longhurst, 1976) to the epipelagic zone at night where they feed (Barham, 1966, Bianchi and Mislan, 2016, Klevjer et al., 2016). Mesopelagic organisms often associate and migrate in distinct layers, called deep scattering

layers (DSLs) due to their high acoustic reflectance, which produces layers of detections when observed with active sonar systems. It appears that mesopelagic fish seek refuge in dark waters and at the edges of deep oxygen minimum zones, which are inaccessible or unsuitable for their more aerobic and visually oriented predators (Seibel, 2011, Netburn and Koslow, 2015). Both absolute light levels, as well as the rate of change in light levels, have been proposed as triggers for changes in the behavior of vertical migrators, and there also seems to be an endogenous rhythm component to vertical migration (Benoit-Bird et al., 2009a, Ochoa et al., 2013). Lanternfish (family: *Myctophidae*), in particular, play an important role in SCB ecosystems (Davison et al., 2015), are abundant in DSLs, and are known to occur at much lower densities in the epipelagic zone during nights surrounding the full moon versus dark nights of the new moon (Clarke, 1973). However, during full moon periods, fish density may increase at certain depths as organisms become more tightly packed vertically (Benoit-Bird et al., 2009a). In addition to light and endogenous rhythms as cues, prey distribution, bioenergetics, tidal influence, predator avoidance and effects of commensal species may also drive vertical migrations (see review in Neilson and Perry (1990)).

Optimal foraging theory suggests that predators will minimize the cost of pursuing prey to maximize the energy gained while foraging (Pyke, 1984). As such, marine predators that eat mesopelagic prey will likely track the dynamics of DSLs and adjust their response to nocturnal light conditions to maximize foraging efficiency. During full moon periods, when the vertical migration of prey is suppressed, the foraging efficiency of juvenile Galápagos fur seals is reduced and as a result they lose weight (Horning et al., 1999). Hervé Glotin (unpublished data) observed that sperm whales in the Mediterranean spend more time foraging during full moon periods. This may be related to increased density of their prey at shallower depths as a response to moonlight. Lowry et al. (2007) showed that catch rates in sports fisheries were well-correlated with lunar cycles. Black marlin (*Makaira indica*) are

physiologically limited to warmer surface waters and cannot access DSL prey during the full moon. This may make them more likely to increase their foraging effort in response to lower densities of prey (Lowry et al., 2007) and results in a positive correlation between full moon and catch rate. In contrast, fish like mahi-mahi (*Coryphaena hippurus*) and yellowfin tuna (*Thunnus albacares*) are able to track the vertical movements of their prey and are more abundant in surface waters during the new moon. In all of these cases, the association of altered behavior during different lunar periods is attributed to the ability of these predators to access their prey.

Dolphins use echolocation to forage and navigate, which creates an opportunity for passive acoustic monitoring to be a useful indicator of odontocete presence and behavior, on timescales of hours to years (Henderson et al., 2011, Wiggins and Hildebrand, 2007). Dolphin behavior, in addition to instrument sensitivity and environmental conditions, determine the spatial extent of passive acoustic monitoring. The source level of common dolphin echolocation clicks has been measured in captivity (145-170 dB re: 1 μ Pa; (Evans, 1973, Fish and Turl, 1976); however, source levels measured from dolphins in highly reverberant tanks may be up to 60 dB lower than those observed in open-water environments (Au et al., 1974, Au and Snyder, 1980). Source levels for free-ranging common dolphins may be similar to the source levels measured in open-ocean environments for other dolphins with similar body sizes, including white-beaked (*Lagenorhynchus albirostris*), spinner (*Stenella longirostris*) and spotted (*Stenella attenuata*) dolphins (190-220 dB re: 1 μ Pa; (Rasmussen et al., 2002, Schotten et al., 2004). Echolocation behavior is dependent on the task, and dolphins may decrease the source level of their clicks with decreasing target range (Au and Benoit-Bird, 2003). Given the high frequency energy content of echolocation clicks, attenuation from the source to the receiver can be significant. From the surface to a bottom-moored instrument 1,000 m away, the transmission loss associated with spherical spreading and absorption for a signal at 30 kHz in 15°C water, is $\sim$ 66 dB (Urick, 1983). The directional beam pattern

of outgoing echolocation clicks (-30 dB at $>30^\circ$ off axis of the clicks central beam for a bottlenose dolphin; Au 1993) will further limit the detection range for off-axis clicks. Individuals in actively foraging groups of common dolphins in the SCB have been observed to change direction frequently while consistently echolocating, resulting in a constant stream of clicks that arrive to the receiver while a group is actively foraging nearby (Wiggins et al., 2013). Traveling behavior is captured in the acoustic record as a more fleeting and compact bout of click detections, while socializing behavior would be associated with many fewer click detections (Wiggins et al., 2013). The expected detection range for a foraging group of dolphins will depend on many factors, including the number of individuals and orientation of the group; however, considering the behavior and transmission loss for shallow-diving dolphins, like common dolphins, the expected detection range for a foraging group may vary from 1.5 to 5 km from a seafloor sensor (Frasier et al., 2016b). Variation in daily, monthly and seasonal acoustic activity provides information about how dolphins exploit available resources.

In this study passive acoustic recordings are analyzed to monitor the echolocation behavior of common dolphins in the SCB from 2009 to 2014. Based on the behavior of other predators that feed on DSL organisms, we hypothesize that common dolphin foraging ability will be impeded and that echolocation behavior will be depressed during full moon periods of the lunar cycle. We identify patterns in echolocation activity at daily and monthly timescales in cool seasons (November-April) and warm seasons (May-October). A relationship between dolphin acoustic behavior and the lunar cycle is explored between different seasons through a regression analysis. We consider how the patterns in acoustic behavior may relate to dolphin foraging, local light conditions and the behavior of locally available prey.

2.3 Methods

2.3.1 Passive acoustic data collection

Autonomous high-frequency acoustic recording packages (HARPs; Wiggins and Hildebrand 2007) were deployed at two locations in the SCB (Figure 2.1) with the hydrophone positioned about 30 m above the seafloor. One recorder was placed at “Site 1” at a depth of 1300 m, 50 km southwest of San Clemente Island ($32^{\circ} 50.550$ N $119^{\circ} 10.266$ W) and the other was at “Site 2” at a depth of 900 m, 58 km west of San Clemente Island ($32^{\circ} 22.186$ N $118^{\circ} 33.769$ W). These instruments were part of an earlier, long-term acoustic monitoring project throughout the SCB and were chosen for this analysis based on the concurrent multi-year time series and the year-round presence of common dolphins at each location. There were multiple deployments from January 2009 to December 2014. All HARPs continuously collected recordings at a sampling rate of 200 kHz with 16-bit quantization, although there were gaps in coverage due to equipment servicing (see horizontal bars on top of each panel in Figure 2.4). The hydrophone used was an omni-directional sensor (ITC-1042, International Transducer Corporation, Santa Barbara, CA), which had an approximately flat (± 2 dB) hydrophone sensitivity from 10 Hz to 100 kHz of -200 dB re $V/\mu\text{Pa}$. Each system contained a custom-built preamplifier board and bandpass filter (Wiggins and Hildebrand, 2007). The calibrated system response was accounted for during analysis.

2.3.2 Acoustic data analysis

Signal processing was performed using the custom software program *Triton* (Wiggins and Hildebrand, 2007) and other MATLAB custom routines. Individual echolocation signals were automatically detected using a computer algorithm with a two-step approach (Soldevilla et al., 2008, Roch et al., 2011) and a minimum peak-to-peak received level threshold was

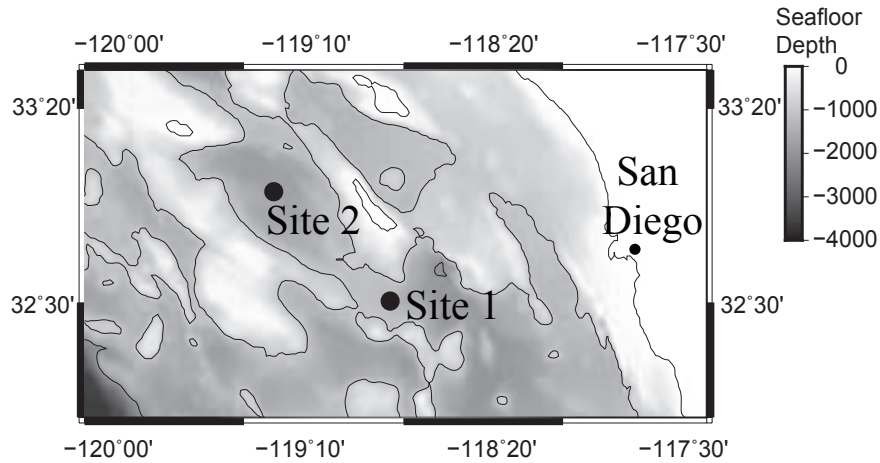


Figure 2.1: Recording locations for common dolphins. Map of Southern California Bight with two recording locations marked. 1000 m contour lines are drawn.

set to 120 dB re: 1 μ Pa. This received level was defined based on a manual review of the detection data to determine the received level at which echolocation clicks were no longer reliably detected. Long-term spectral averages (LTSAs) were calculated to visually inspect long-term recordings. LTSAs are similar to spectrograms, but each time bin contains an average of 500 non-overlapped Hann-windowed 10 ms frames whose spectra have been averaged with the Welch (1967) resulting in 5 s time bins with 100 Hz resolution. Trained analysts manually screened 1 hour windows of LTSAs and identified acoustic encounters of echolocation in the HARP data while recording the presence of species-specific echolocation signals of Pacific white sided (*Lagenorhynchus obliquidens*) and Rissos (*Grampus griseus*) dolphins based on the click descriptions described in Soldevilla et al. (2008), in order to exclude these species from this analysis. Acoustic encounters with Cuviers (*Ziphius cavirostris*) and unidentified beaked whale species were classified according to the methods outlined in Baumann-Pickering et al. (2013) and excluded from this analysis.

There is an offshore population of bottlenose dolphins consistently present in the Southern California Bight (Forney and Barlow, 1998) whose echolocation clicks cannot

currently be distinguished from common dolphins. The most recent 2014 abundance estimates for Southern California suggest population sizes of approximately 624,503 (CV=0.15) and 52,331 (CV=0.39) for short and long-beaked common dolphins, respectively and 5,585 (CV=0.42) for bottlenose dolphins (Barlow, 2016). From 1991 to 2014 in the California Current, the mean group size was 190 and 482 for short and long-beaked common dolphins and 13.3 for bottlenose dolphins (Barlow, 2016). Also, sightings of offshore bottlenose dolphins in the SCB are typically concentrated in nearshore areas around the Channel Islands (Hamilton et al., 2009) and would not be within the acoustic detection range of the HARPs used in this study. The low density, small group sizes and known distribution of bottlenose dolphins in the SCB indicate that the probability of detecting clicks that exceed the thresholds used in this study that are not attributable to common dolphins is low. Consequently, any misclassification of acoustic encounters are unlikely to bias the overall observed patterns. See Discussion for consideration of other potentially confounding species.

Acoustic features including the mean spectra and inter-click intervals have been shown to be distinct between encounters of different dolphin species (Madsen et al., 2004a, Frasier, 2015) and both features are used here to classify encounters of common dolphins. Click detections were divided into 30-minute time periods and further inspected. First, the mean spectrum of all click detections within each 30-minute time period was manually reviewed to identify false or anomalous detections. Any spectra with dominant low frequencies (<20 kHz), narrowband or anomalous energy content were further inspected. Encounters with anomalous characteristics were reviewed using an LTSA, along with plots of peak-to-peak received level, inter-click-interval and mean spectrum (Figure 2.2) to determine correct and false detections of echolocation activity that could be attributed to common dolphins.

There was a predominant mode in inter-click intervals around 50 ms during acoustic encounters with dolphins (Figures 2.2 and 2.3 B). Thirty-six 30-minute time periods ($<1\%$

of total time periods with detections) contained dolphin echolocation concurrent with false detections from ship noise or mid-frequency active sonar. In these cases, it was prohibitively time consuming to separate the echolocation clicks from the other signals. An analyst estimated the click metrics for these time periods. To verify that the spectral content of all detections was similar, the mean click spectra from 30-minute time periods were plotted as spectrograms and arranged by increasing peak frequencies (a random sample of 10% of all time periods is plotted in Figure 2.3 A). Intense low frequency energy (<20 kHz) in time periods with verified echolocation detections was reviewed and verified as being attributable to concurrent delphinid whistles and echolocation. Given the elimination of known signals, the consistent features of detected echolocation clicks and the known distribution of dolphin species in the SCB, the detections considered in this analysis can confidently be attributed to common dolphins.

2.3.3 Regression analysis

To infer behavior from the acoustic record, the actual number of echolocation clicks received is not as diagnostic as the presence of echolocation bouts. Our definition for the presence or absence of echolocation in each 5-minute time period is based on a minimum number of click detections. The mode of observed inter-click intervals was 50 ms, likely reflecting a typical inter-click interval used by common dolphins. Considering that dolphins are frequently changing direction while foraging along with the highly directional nature of echolocation clicks, it is unlikely that all echolocation clicks from nearby dolphins will be detected at the receiver. Two sets of thresholds were used in our analysis of echolocation clicks as a proxy for foraging behavior. In both cases, thresholds were motivated by the 6000 clicks that a dolphin would produce while clicking continuously over 5 minutes with a 50 ms inter-click interval, with the assumption that at least one of the dolphins would be detectable at any given time. As there are still large differences in detectability of off-axis

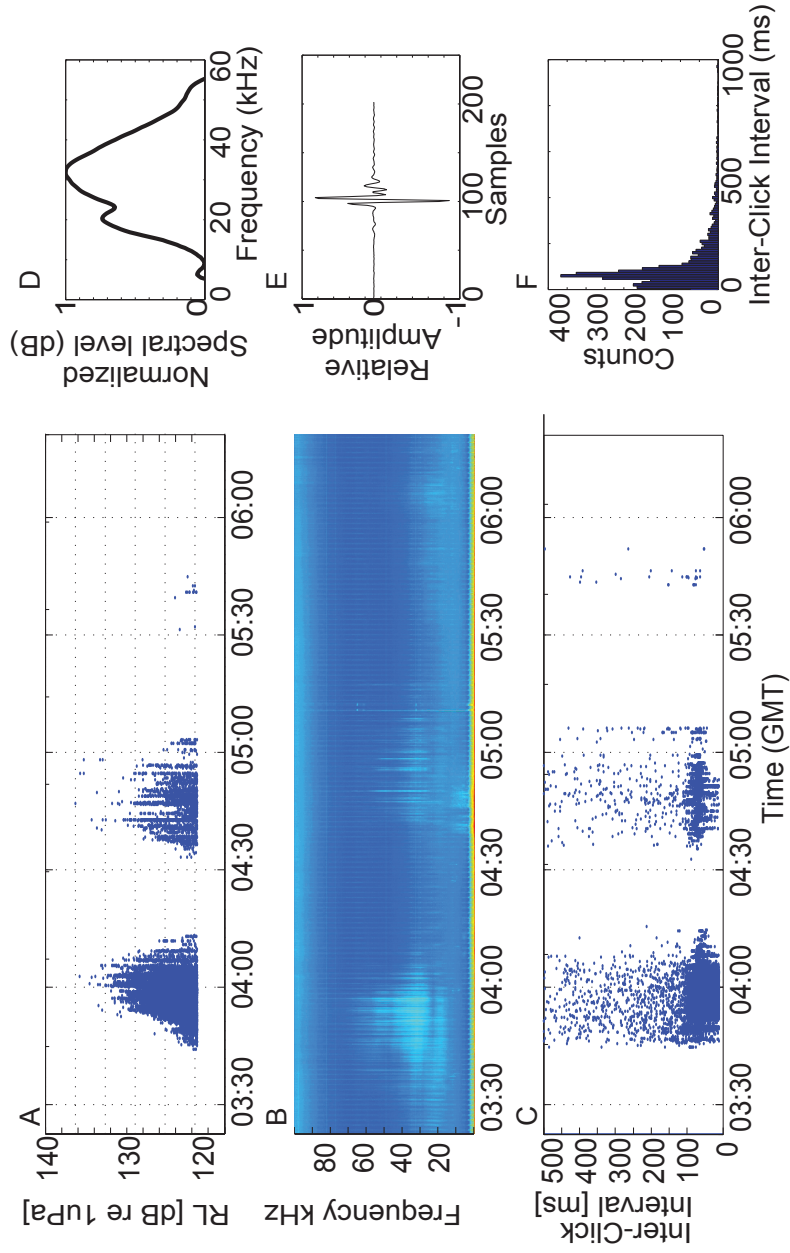


Figure 2.2: Display summary for classification of acoustic encounters. Display used to review echolocation click detections. Peak-to-peak received level (A), long-term spectral average (B) and inter-click interval (C) are plotted against time. Also shown are the mean spectrum (D), mean click waveform (E) and histogram of all inter-click intervals (F).

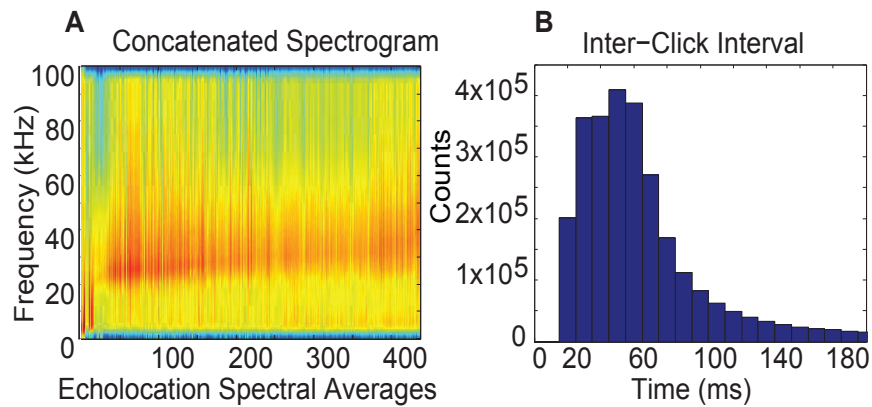


Figure 2.3: Concatenated spectrogram and inter-click intervals of common dolphin encounters. Concatenated spectrogram of mean spectra from 10% random sample of 30-minute time periods sorted by peak frequency (A) and histogram of inter-click intervals (B) across all detections show consistent spectral and temporal characteristics. Intense low frequency energy (<20 kHz) was confirmed from concurrent delphinid whistles and echolocation.

echolocation clicks for animals that are not close to the hydrophone, we considered both lenient 10% (600 clicks) and strict 100% (6000 clicks) thresholds.

Predictor variables were chosen to consider the explanatory effects of various components of the lunar cycle that are known to influence behavioral dynamics of DSLs and may influence the acoustic behavior of dolphins (Table 2.1). Predictors included categorical factors such as the recording location (site), calendar month and year, occurrence before, during or after the moon was visible in the night sky (moon presence), as well as continuous predictors such as lunar day (0-29, with day 15=full moon) considered as a cyclical predictor, normalized time between sunset and sunrise [0, 1], and apparent magnitude of moonlight. Moon presence accounts for the relative differences in timing of moonrise and sunset throughout the lunar cycle. For nights when the moon was never present in the night sky, the “moon presence” predictor for all times of the night was labeled as “before.” Lunar magnitude and lunar day were never combined in a single model due to the high correlation of these predictors. Nighttime cloud cover metrics were included when available. Interactions between the predictors were also considered.

In addition to variance in illumination from the moon, cloud cover may reduce localized light levels. Low level marine stratus clouds are a highly persistent feature in the SCB during warmer months and have higher albedo than thin, high clouds, therefore low level clouds were used to best track cloud conditions with potential to reduce surface light levels (Iacobellis and Cayan, 2013, Schwartz et al., 2014). Using methods described by Clemesha et al. (2016), remotely sensed low cloud cover was estimated at 30-minute intervals during May - September on a 4 km by 4 km grid. Cloud coverage data were not available for the entire year as these methods cannot reliably estimate cloud cover during October - April. At each grid cell, low clouds were assessed as present or absent. Clouds were considered to be present if low clouds were detected in at least 2 of the 4 grid cells surrounding each HARP location.

To predict the presence of echolocation in a 5-minute time period, we used generalized additive mixed models (GAMMs), which can account for lack of independence in time series measurements. GAMMs were built using various predictors during both cool (November - April) and warm (May - October) seasons across multiple years. Each year was divided into separate cool and warm seasons based on deviations from the mean sea surface temperature at the pier of Scripps Institution of Oceanography (SIO Shore Stations program; www.shorestation.ucsd.edu). Scatterplots, histograms and boxplots of each explanatory variable were checked for extreme values and severe non-normality, which would violate model assumptions (Zuur et al., 2009). GAMM analysis was carried out using the “mgcv” package (Wood, 2004) in the R statistical software, version 3.3.0 (Wood 2006, R Development Core Team 2016). The mgcv parameter gamma was set at 1.4 as recommended by Wood2006GeneralizedR to avoid overfitting. To simplify analysis due to the different patterns observed in each season, separate models were built for cool and warm seasons, as opposed to including a monthly or seasonal interaction factor with each predictor. Due to the binary nature of the data (presence or absence of echolocation), we

used a binomial distribution with a logistic link function. The link function contains an intercept and multiple smoothing functions, describing non-linear effects of lunar and seasonal cycles on echolocation behavior. The smoothing functions for continuous predictors were estimated by cubic regression splines (cyclic cubic regression splines for periodic predictors like lunar day) and the optimal level of smoothing was estimated using cross-validation (Wood, 2006).

Various models were fitted using different subsets of the explanatory variables. All were fit in a step-wise fashion, dropping predictors individually and selecting the model with the maximum log-likelihood. Models for warm seasons were fitted with and without cloud cover as a factor. Remotely sensed cloud coverage estimates for each recording location were available at 30-minute intervals for select warm months (May - September) only. When included, the presence or absence of clouds was considered as a factor with an interaction effect with lunar day. For the partial warm season datasets including cloud cover, the same model selection process was conducted. Model performance was also assessed with a four-fold cross-validation procedure in which four models were trained on 75% of the data and predictions on the remaining 25% were combined and compared to observations.

Table 2.1: Predictors used in model selection and analysis of nighttime common dolphin echolocation activity.

Predictor	Type	Description
recording location	categorical	Site 1 or 2
month	categorical	Calendar month (January =1, December=12)
year	categorical	Calendar year (2009,2010, etc.)
moon presence	categorical	Occurrence before, with or after the moon is present in the sky over the course of one night
cloud presence	categorical	Presence or absence of cloud cover. Data available May-September 2009-2014.
lunar day	cyclic	Lunar Day [1,29] 1=New Moon 15=Full Moon
normalized time of night	continuous	Normalized time of night [0,1] between sunset and sunrise
apparent lunar magnitude	continuous	Brightness of the moon on the apparent magnitude scale. New moon = 0 Full moon = -12.9

2.4 Results

The majority (62%) of 5-minute observation periods at both recording locations contained no detected echolocation clicks. For click-positive observation periods, the median number of detections was 284 with a range of 1 to 58,977. The median peak-to-peak received level for detections in each 5-minute bin had a range of 120–149 dB re: 1 μ Pa, with a mean and standard deviation of 126 ± 3 dB re: 1 μ Pa. Deeper diving dolphins may result in higher received levels in click detections, so the distribution of the 90th percentile of received levels within each 5-minute time period was investigated throughout the lunar month and between seasons using two-sample Kolmogorov-Smirnov tests (ks-test). Within cool months, there were significant differences in the distribution of the 90th percentiles of received levels of dolphin clicks in 5-minute time periods from the 3 days around the new and full moons (Kolmogorov-Smirnov tests (ks-test) p-value $< 2.2e-16$), and the mean values was ~ 1.5 dB higher during the full moon (full moon mean = 128.8 ± 3 dB re: 1 μ Pa, new moon mean = 127.3 ± 3 dB re: 1 μ Pa). In the warm season, the mean value of the 90th percentiles of 5-minute time periods was also higher during nights of the full moon by ~ 1 dB (full moon mean = 127.9 ± 3 dB re: 1 μ Pa, new moon mean = 127.1 ± 3 dB re: 1 μ Pa) and the ks-test indicated there were significant differences in the distributions (ks-test p-value $< 2.2e-16$).

At both sites, temporal patterns and the relationship of echolocation presence with explanatory variables using both the 600-detection and 6000-detection thresholds were similar; as such, only the 600-detection threshold is presented here. Distinct diel, lunar, and seasonal patterns of common dolphin echolocation activity were observed throughout the recording period (Figures 2.5 and 2.6) and were similar at both sites. Throughout the year, echolocation activity showed a diel pattern, with most echolocation occurring at night (Figure 2.5). Nighttime echolocation was lowest during crepuscular periods and most abundant at the midpoint between sunrise and sunset (Figure 2.6). From 2009 to 2011,

there was also a seasonal pattern at both sites, with reduced echolocation activity during May through June (week 18-24; Figures 2.4 and 2.6) and elevated echolocation activity was observed in August and September (week 31-39). In the years 2012 and 2013, there was not sufficient recording effort at both locations to determine seasonality. Echolocation activity during 2014 was much lower than all previous years and diel, lunar, and seasonal cycles of echolocation were not apparent (Figures 2.4 and 2.6).

Throughout the year at both sites, nighttime echolocation activity was reduced during the nights directly before, during and after the full moon (Figures 2.5 and 2.6). This lunar pattern was most obvious and consistent during cool months, although there were also occasional warm months in which echolocation activity was depressed during full moon periods (Figures 2.5 and 2.6). During the cool season, echolocation was also depressed at times when the moon was present in the night sky, but not necessarily full (Figure 2.6).

At both sites during May-June, echolocation was lower than later warm months (July-September) and overall, echolocation activity was reduced in each successive warm season from 2010 to 2014 (Figure 2.6). Compared to cool months, echolocation was more consistent throughout the lunar cycle during the warm season; however there were some warm months that showed a decrease in echolocation around the nights of the full moon, especially at site 2 (Figure 2.6). During warm months with available cloud cover data (May to September 2009-2014), the long-term average nighttime cloudiness was 58% for site 1 and 54% for site 2. Although the reduction of echolocation near full moon nights was not strong in warm months, when clouds were present there was more echolocation activity on nights surrounding the full moon than during the nights near the new moon, suggesting a behavioral response to surface light conditions (Figure 2.7).

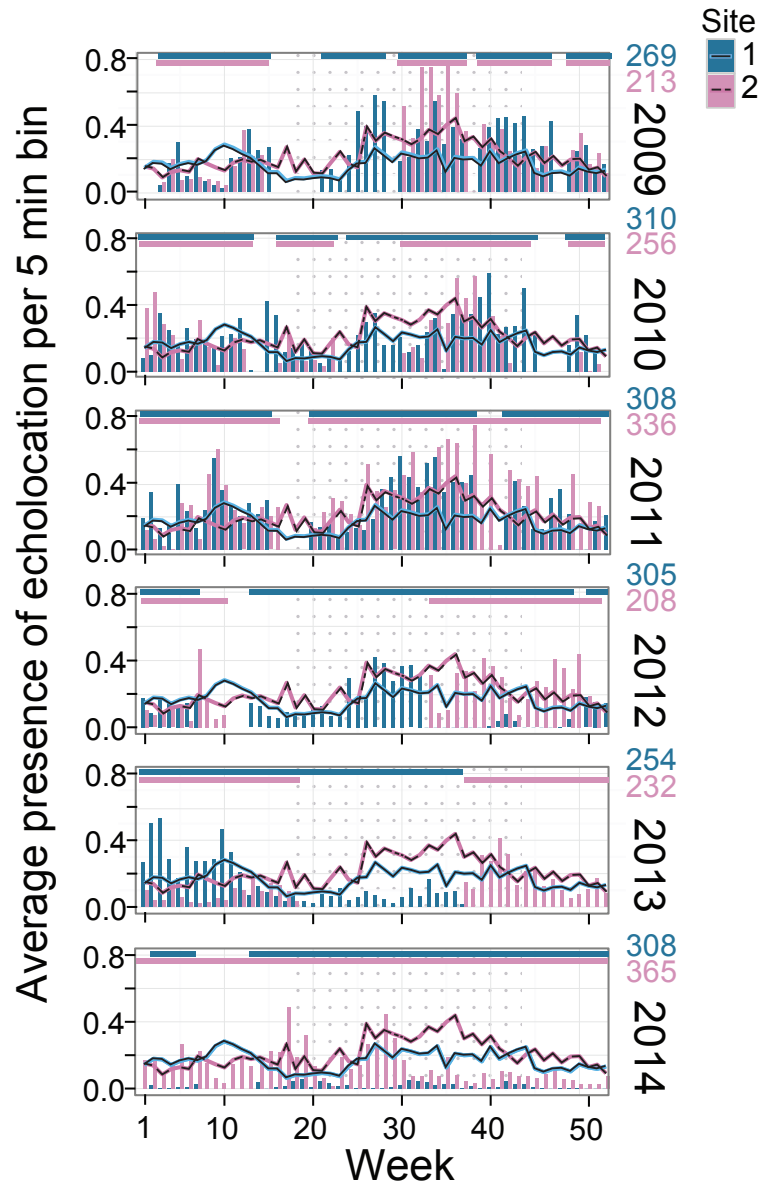


Figure 2.4: Weekly presence of common dolphin echolocation. Vertical bars indicate the average weekly presence of echolocation in 5-minute time periods for Site 1 (blue) and Site 2 (pink). Lines show weekly value averaged across years 2009-2014 for Site 1 (solid black and blue) and Site 2 (dashed black and pink). Colored, horizontal bars on top of each panel show recording periods and the associated colored numbers on the right are the total annual number of days with recordings for each site. Weeks in the warmer months of the year (May - October) are indicated by dotted background.

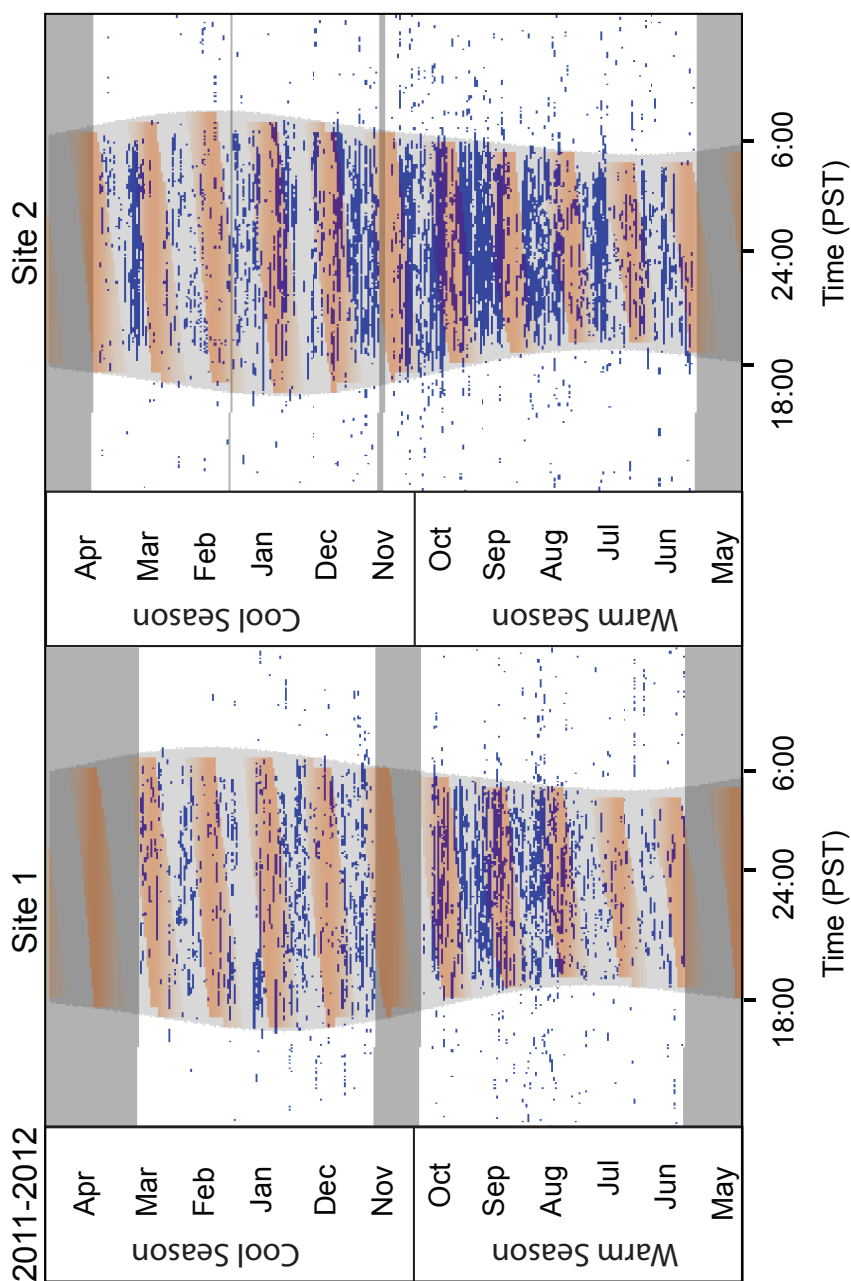


Figure 2.5: 24 hour record of common dolphin echolocation activity over one year. One year (May 2011 - April 2012) of common dolphin echolocation activity (blue shading) at Site 1 (left) and Site 2 (right). Detections are plotted in 5-minute time periods across an entire day, centered on midnight, with light gray shading indicating nighttime periods. Presence indicates a minimum of 600 detections per 5-minute period. Nighttime lunar illumination is shaded orange and acquired in 5-minute bins. Dark gray horizontal boxes indicate periods of no recordings.

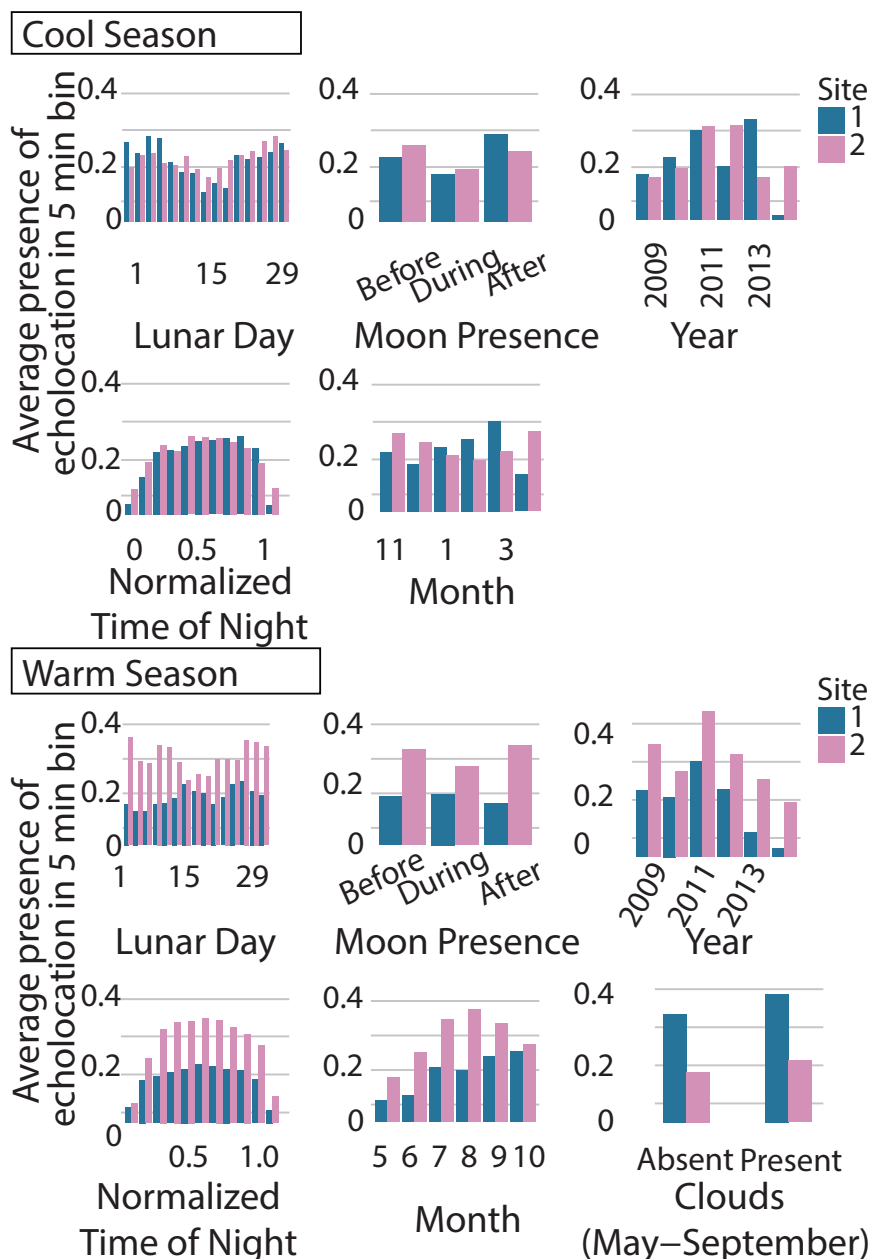


Figure 2.6: Nighttime observations of common dolphin echolocation. Nighttime observations (2009-2014) of the presence of echolocation per 5-minute time period shown with explanatory variables including lunar day, presence of the moon, year, normalized time of night and month. Cloud coverage data is only available for May - September each year. Two-day averages are shown for lunar day for ease of visibility. Lunar cycle begins with new moon at day 1 and full moon at day 15. Blue and pink bars show averages for sites 1 and 2, respectively, in cool (November - April; top panels) and warm (May - October; bottom panels) months.

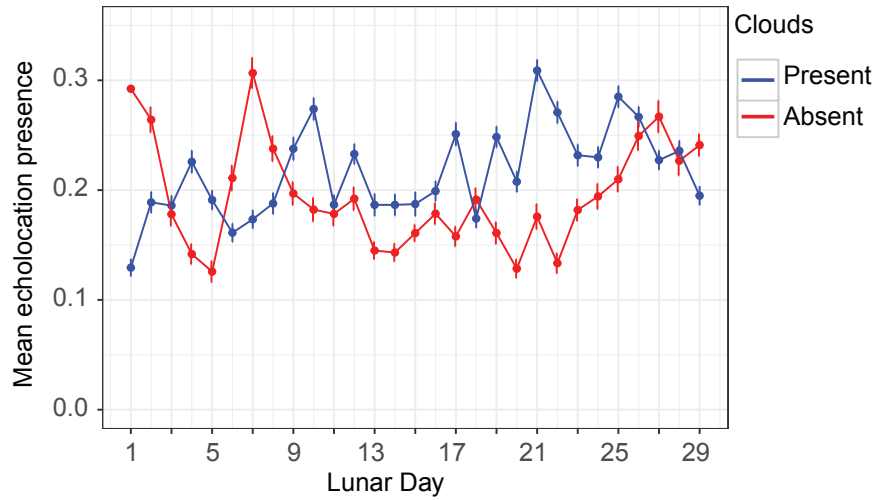


Figure 2.7: Nighttime observations of common dolphin echolocation with cloud cover. Mean presence and standard error of echolocation throughout the lunar month (Lunar Days 1 and 29 = new moon) for times with clouds absent (red solidline) and clouds present (blue dashed line).

2.4.1 Regression analysis

The regression analysis was designed to identify drivers of the observed lunar patterns and did not incorporate the dynamics of large-scale environmental conditions that might induce geographic shifts in dolphin distributions. Consequently, the anomalously low observations of echolocation in 2014 were not included in the GAMMs.

An examination of the autocorrelation function (ACF) plot of the residuals indicated that there was significant autocorrelation remaining in the residuals. To account for first and second order autoregression, respective AR(1) and AR(2) models for the residuals were included in two additional GAMM fits. The second order autoregression model had the lowest AIC and the ACF values of the residuals for the first 5 time lags were not significant at the 95% confidence level and therefore this model was chosen as the final model. The parameter estimates were similar to the original model, but the standard errors were adjusted and are slightly larger. Visual inspection of the histogram and normal quantile plot of the residuals indicate that the residuals are approximately normal, with the exception of some

deviation in the tails of the distribution.

For both warm and cool seasons, the best GAMMs included explanatory variables for lunar day, normalized time of night, month, year, site and presence of the moon (Table 2.2, Figure 2.8). Reduced moonlight conditions due to cloud coverage was considered as an interaction effect between lunar day and cloud coverage. For warm months with available cloud coverage data, this interaction improved model fit. During the cool season, the smoothing function for lunar day reflected reduced echolocation during the nights of and around the full moon, during the hours immediately after sunset and before sunrise and while the moon was present in the night sky (Figure 2.8: A1, A2, A6).

The smoothing functions for the warm season show a weaker and less obvious relationship between echolocation, lunar day, and moon presence (Figure 2.8: B1, B6), however there is a progressive increase in echolocation activity from May to October (Figure 2.8: B3). Similar to the cool season, echolocation was reduced in the hours following sunset and before sunrise (Figure 2.8: B2). The smoothing function for the interaction between cloudiness and lunar day shows reduced echolocation during nights surrounding the full moon, in the absence of clouds (Figure 2.9 C1).

2.4.2 Predictive ability

Contiguous 5-minute observation periods were grouped by night and nights were randomly assigned to four testing and training datasets. A four-fold cross-validation procedure trained four models on 75% of the data and then made predictions on the remaining 25% of the dataset. Peaks in predicted echolocation activity closely tracked periods of observed echolocation around nights of the new moon and during dark periods of the night before or after the moon was present in the night sky (Figures 2.10, 2.11, 2.12 and 2.13). In both warm and cool seasons, the highest predicted echolocation was during the last quarter of the lunar month, when there were extended periods of darkness after sunset before the

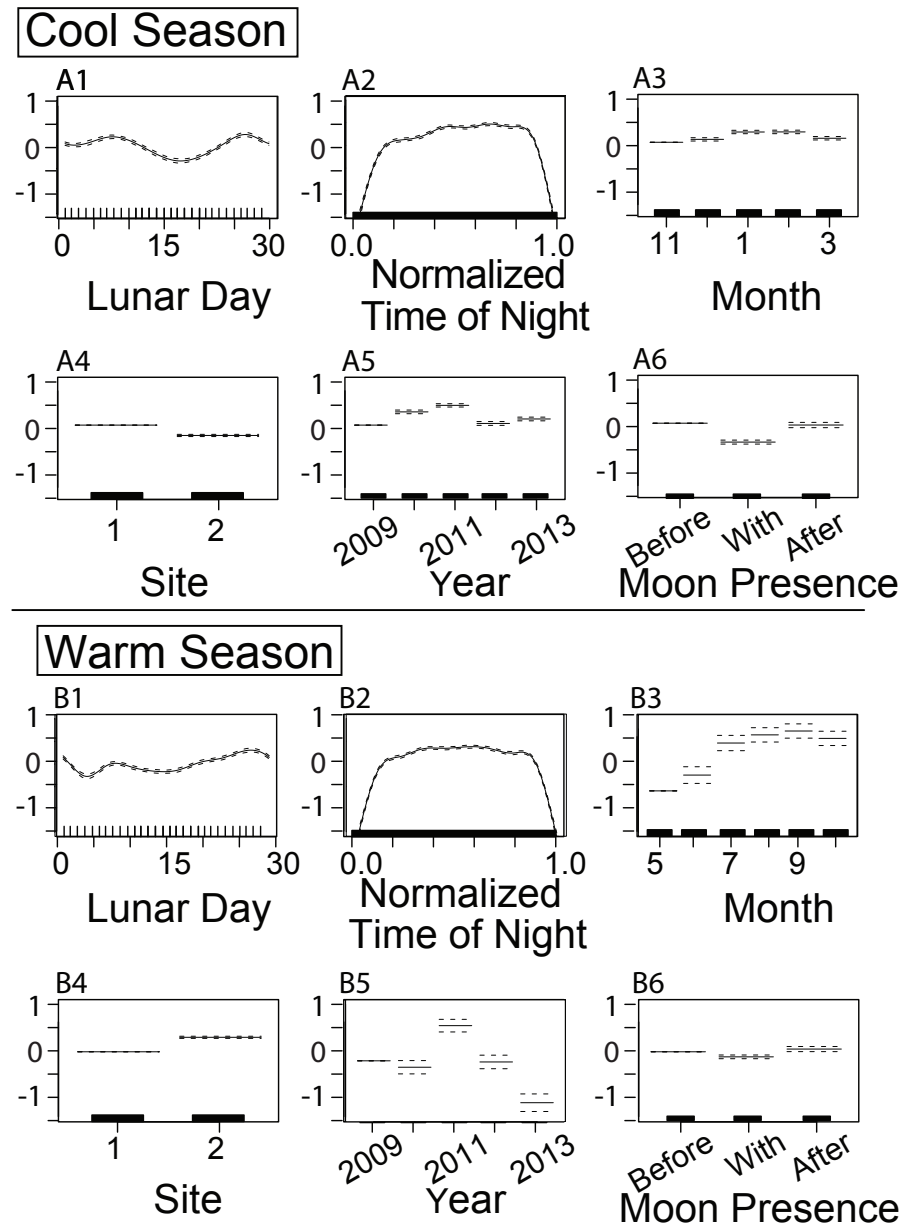


Figure 2.8: GAMMs for nighttime common dolphin echolocation in cool and warm seasons. Estimated smoothing curves (A1, A2, B1, B2) and factors (A3-A6, B3-B6) of nighttime GAMM for cool (top panel) and warm (bottom panel) seasons. Zero on the vertical axes corresponds to no effect of the explanatory variable. Dashed lines indicate 95% confidence limits. Ticks above the x-axis indicate locations of observations.

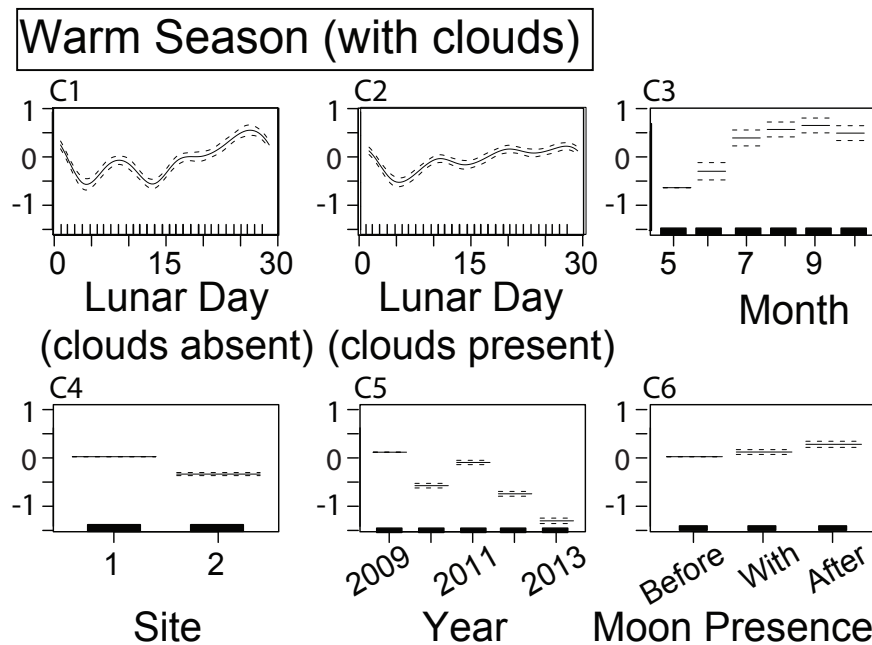


Figure 2.9: GAMMs for nighttime common dolphin echolocation in warm season with cloud coverage. Estimated smoothing curves (C1, C2) and factors (C3-C6) of nighttime GAMM model for warm season with available cloud coverage data (May-September). C1 and C2 show the interaction of lunar day with cloud absence and presence, respectively. Zero on the vertical axes corresponds to no effect of the explanatory variable. Dashed lines indicate 95% confidence limits. Ticks along the x-axis indicate locations of observations.

moon rose in the night sky (Figure 2.10). The predicted values in cool months followed a strong lunar cycle with lowest abundance of echolocation predicted in nights surrounding the full moon and while the moon was present in the sky (Figure 2.12). Predictions for warm months showed a weaker association with the lunar cycle and presence of moon in the sky (Figure 2.11). For times during the warm months with available cloud cover data, predictions of more abundant echolocation were associated with cloud coverage (Figure 2.13) which reflects observations. Predictions more closely followed observations for cool seasons than warm seasons.

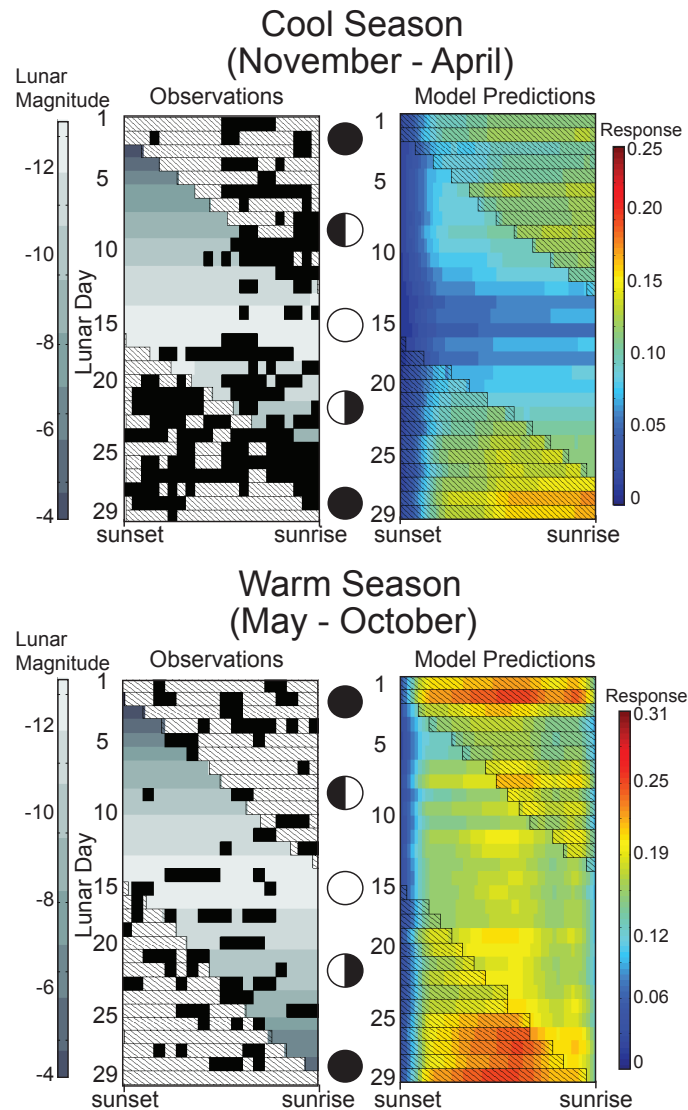


Figure 2.10: GAMM cross-validation for common dolphins. Nighttime echolocation observations and model predictions from cross-validation are shown for example lunar months from cool (12/16/2009 - 1/14/2010 Site 2; top panel) and warm (6/01/2011 - 6/30/2011, Site 1; bottom panel) seasons. For both sites, predictions and observations are comparable among months for each season. Hatched areas indicate times of the night before or after the moon is present in the night sky. Black boxes indicate time periods that have met or exceeded the detection threshold to indicate the presence of echolocation. Blue-gray shading indicates lunar magnitude (left panel) and cool to hot colors indicate prediction values of 4-fold cross-validation of GAMM (right panel). Lunar cycle begins with new moon at day 1 and has a full moon at day 15. Central shaded circles indicate moon phase.

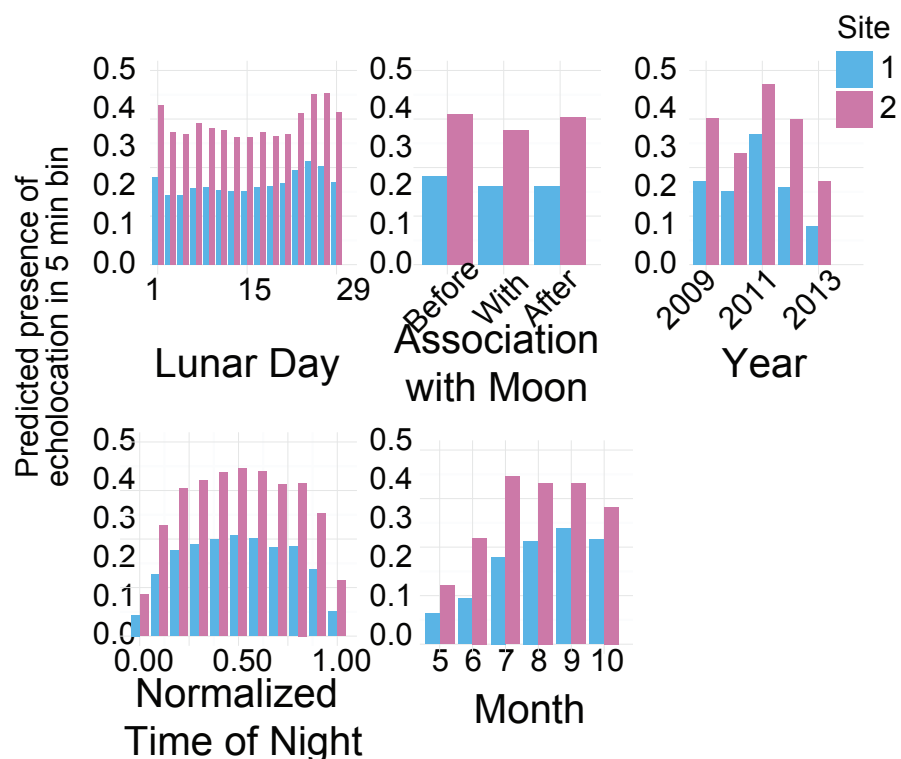


Figure 2.11: GAMM predictions for common dolphin echolocation in warm season. Predictions from GAMM for warm seasons plotted against predictors included in the model. Lunar cycle begins with new moon at day 1 and full moon at day 15. Blue and pink bars show averages for sites 1 and 2 respectively, in warm period (May-October) of the year.

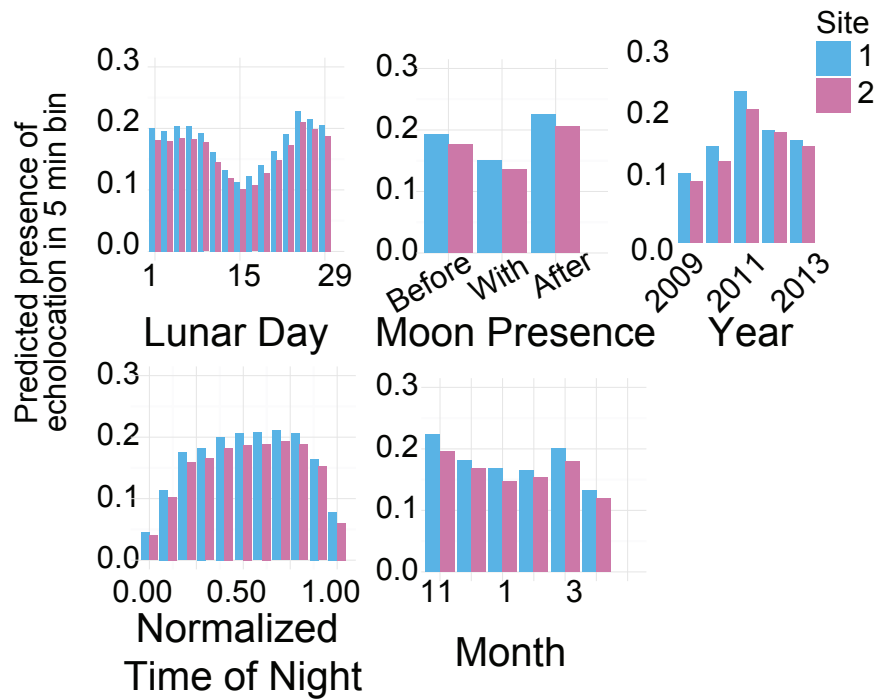


Figure 2.12: GAMM predictions for common dolphin echolocation in cool season. Predictions from GAMM for cool season plotted against predictors included in the model. Lunar cycle begins with new moon at day 1 and full moon at day 15. Blue and pink bars show averages for sites 1 and 2 respectively, in cool period (November - April) of the year.

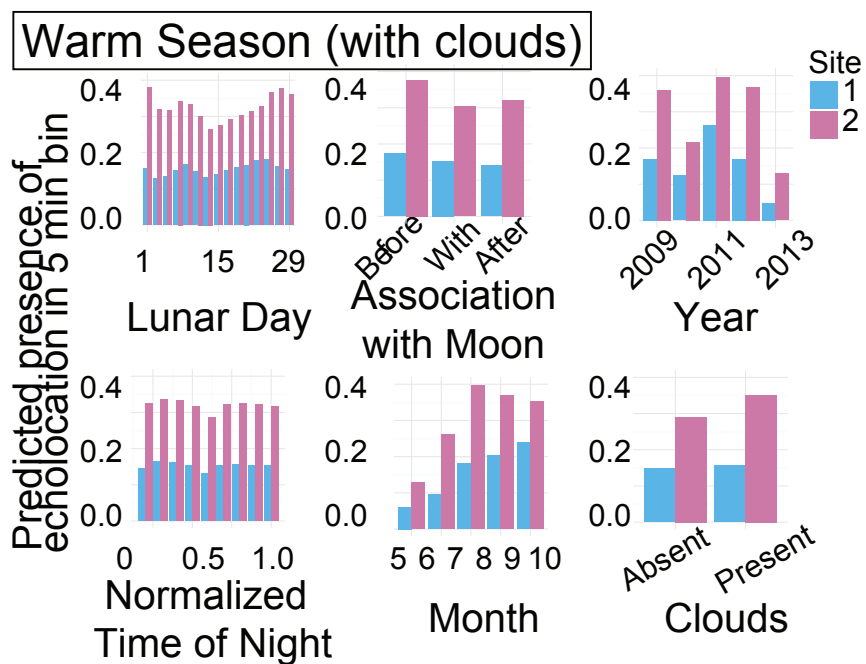


Figure 2.13: GAMM predictions for common dolphin echolocation in warm season with cloud coverage. Predictions from GAMM for warm season with available cloud coverage data (May - September), plotted against predictors included in the model. Lunar cycle begins with new moon at day 1 and full moon at day 15. Blue and pink bars show averages for sites 1 and 2, respectively.

Table 2.2: GAMM estimates of predictors for common dolphin echolocation in cool and warm seasons. GAMM estimates of predictors for nighttime echolocation periods during cool (Nov-Apr) and warm (May-Oct) seasons of 2009-2013. Estimates for predictors in warm months with available cloud cover data (May-September) are also shown. Only estimates from the best models are shown here. Data from 2014 were not included due to the anomalously low number of observations. The selected explanatory variables in each model were identified as smooth functions or factors along with their estimated degrees of freedom in parentheses and approximate p-value significance. The number of observations for each model are denoted by n. All terms in bold = *p<0.05, ** p<0.01, ***p<0.001

	Cool Season n=188,450	Warm Season n=163,342	Warm Season (with clouds) n=95,514
<u>Smooth Functions</u>			
Normalized Time of Night	7.97 (9.00)***	8.57 (9.00)***	
Lunar Day	5.56 (8.00)***	6.81 (8.00)***	
Lunar Day: Cloud=0			5.07 (8.00)***
Lunar Day: Cloud=1			2.58 (8.00)*
<u>Factors</u>			
month 6		0.38 (0.10)***	0.40 (0.10)***
month 7		1.16 (0.09)***	1.18 (0.10)***
month 8		1.36 (0.09)***	1.3 (0.09)***
month 9		1.46 (0.09)***	1.41 (0.09)***
month 10		1.28 (0.09)***	
month 11	0.32 (0.07)***		
month 12	0.25 (0.25)***		
month 2	0.14 (0.06)*		
month 3	0.29 (0.07)***		
month 4	0.20 (0.08)*		
Site 2	-0.16 (0.04)***	0.47 (0.04)***	0.61 (0.05)***
year 2010	0.40 (0.07)***	-0.11 (0.06)	-0.41 (0.08)***
year 2011	0.95 (0.07)***	0.62 (0.06)***	0.50 (0.07)***
year 2012	0.76 (0.07)***	-0.02 (0.06)	0.03 (0.07)
year 2013	0.61 (0.07)***	-0.74 (0.08)***	-1.33 (0.11)***
Moon Presence (During)	-0.23 (0.05)***	-0.04 (0.05)	-0.21 (0.06)***
Moon Presence (After)	-0.07 (0.07)	0.12 (0.07)	-0.34 (0.07)***

2.5 Discussion

Common dolphin echolocation activity showed consistent diel, lunar, and seasonal patterns from 2009 to 2013 at two deep, offshore locations. The observed patterns in common dolphin foraging corresponded to behavioral patterns of mesopelagic and small pelagic organisms, during cool and warm months respectively. Echolocation activity was

predominantly nocturnal, confirming the findings of previous acoustic studies that showed nighttime being an important foraging time for common dolphins (Henderson et al., 2011, Wiggins et al., 2013). The acoustic record also indicated reduced echolocation activity between April and June, similar to the low regional abundance of common dolphins observed in visual surveys during this time, reported by Campbell et al. (2015). There was a clear and significant relationship between echolocation activity and the lunar cycle during cool months and a weaker yet still significant relationship in warm months.

During cool months at both recording locations, the lowest rates of nocturnal echolocation were observed during nights of and around the full moon, when the moon is brightest and present in the night sky during most of the night. Low rates of echolocation may indicate horizontal or vertical shifts, reduced local foraging behavior or a switch in foraging behavior from acoustic to visual predation. The most consistent periods of echolocation were associated with the darkest times of the night and the darkest nights of the lunar cycle. During cool months, when echolocation was observed in the presence of moonlight, it most often occurred on nights near the new or quarter moon periods, when moonlight conditions are dimmer than full moon nights (Figure 2.10). Model predictions highlighted a maximum in echolocation activity during the last quarter of the lunar month when there is an extended period of darkness after sunset, before the moon is present in the night sky. During these nights, mesopelagic prey may migrate toward the surface in the darkness until they are suddenly vulnerable to predators when the moon rises, as observed in freshwater zooplankton (Gliwicz, 1986b). Increased dolphin foraging activity during these nights might compensate for reduced opportunities during nights around the full moon or potentially relate to a lunar-mediated behavioral response of their prey.

Vertical or horizontal movements away from the HARP during full moon periods would impact detectability of echolocating dolphins, which could explain the lunar patterns observed here. There were small, but significant differences between the received level

of echolocation clicks between nights surrounding the new and full moons throughout the year. Given a bottom moored instrument at a depth of 1000 m, the transmission loss due to absorption and spherical spreading for a signal at 30 kHz in 15°C water would be about 3 dB greater for a dolphin foraging at 50 m depth compared to at 100 m (Urick, 1983). However, received levels are also influenced by the orientation of the animal and the echolocation task being performed. The slight (~ 1 -1.5 dB) difference in received levels between nights of the new and full moons, could be due to the lower transmission losses associated with dolphins diving deeper or nearer to the HARP; however, this difference could also result from a different orientation of the animal or echolocation task being performed. The current data cannot determine the depth, orientation or horizontal distance of dolphins from the recorder.

Although diel, lunar and seasonal patterns were similar between the two locations, the “Site” improved model fit, indicating that there are differences between common dolphin acoustic behavior at the two recording locations. During warm months, the lunar day and presence of the moon in the sky showed a significant but weak influence on echolocation, especially at site 2 (Table 2.2, Figure 2.6). Site 1 was slightly deeper with steeper local bathymetry compared to site 2, but there are no known differences in community composition between these two locations.

During the warm season, observations of higher levels of echolocation on nights with clouds present (Figures 4 and 5) corroborates earlier observations in the SCB of tagged common dolphins that continued to forage during daylight hours on cloudy days (Evans, 1974). Low-level marine stratus clouds are a highly persistent feature alongshore and offshore of the California coastline (Iacobellis and Cayan, 2013) and may contribute to increased foraging opportunities for dolphins during both nighttime and daytime periods by reducing epipelagic light conditions and encouraging vertical migrants to stay near the surface. As cloud coverage does not follow the same predictable cycle of light levels

associated with the lunar cycle, these observations suggest that dolphins, and possibly their prey, may be responding to unpredictable short-term changes in light conditions. If reliable analysis methods become available for assessing cloud coverage in cool months, it may be useful to observe if increased cloudiness provides dolphins with enhanced opportunities to prey upon vertically migrating organisms throughout the year.

Common dolphin nocturnal echolocation becomes more consistent throughout the lunar cycle, showing little variation between nights of the new and full moon, during the transition from cool to warm seasons in the SCB, when strong coastal upwelling begins. Increased upwelling stimulates primary productivity, which affects the water transparency and dissolved oxygen concentrations. The extent and variation of vertical migration of DSLs varies with dissolved oxygen concentration (Netburn and Koslow, 2015), as well as water transparency (Isaacs et al., 1974), and has been shown to vary across seasons (Urmy et al., 2012), latitude (Tont, 1976, Hazen and Johnston, 2010), and in regions of high productivity (Isaacs et al., 1974, Kaartvedt et al., 1996). In years of low oxygen, the decline of midwater fish abundance may be attributed to increased vulnerability to predation as DSLs move into more illuminated waters (Koslow et al., 2011). The largest declines in midwater oxygen in the SCB are observed during July–September (Bograd et al., 2008), which closely corresponds to the months where we observed consistent nocturnal echolocation throughout the lunar month. The consistent echolocation throughout warm season lunar cycles could indicate that shoaling DSLs are more accessible to dolphin predation, but it could also indicate that dolphins are pursuing alternative, non-vertically migrating prey as mesopelagic fish abundance declines. Future studies are encouraged to track the vertical and horizontal movements, abundance and community composition of DSLs across seasons and in varying conditions of hypoxia.

The seasonal shift in foraging behavior during nights of the full moon may reflect seasonal prey-switching behavior. In the Atlantic, common dolphins are known to choose

energy-rich prey over low quality prey, even when low quality prey are abundant in the environment (Spitz et al., 2010). Coastal pelagic fish species (CPS) are a preferred prey for common dolphins in the Pacific (Fitch and Brownell Jr., 1968, Evans, 1975, Osnes-Erie, 1999) and are known to respond to the onset of the upwelling season and changing oceanographic conditions. Spawning aggregations of Pacific sardine are present in offshore areas of the SCB (Checkley et al., 2000) during spring months (March-May), although the geographic distribution of spawning aggregations may shift from inshore to offshore areas from year to year (Zwolinski et al., 2012, Hill et al., 2015). CPS species vertically migrate from depths of 15-70 m during the day, to form loose surface aggregations at night (Cutter and Demer, 2008). Even during the day, CPS would be well within the normal preferred foraging depths of common dolphins, which may explain the shift to more prevalent daytime echolocation activity during warm months. Further, the highest commercial catch rates of Pacific sardine and other CPS including northern anchovy are recorded during summer months (Hill et al., 2015), corresponding with a diminished relationship between lunar cycles and dolphin echolocation. The results from the acoustic record we present here may be attributable to prey switching behavior between oceanographic seasons, with dolphins depending on organisms associated with the DSL during cool months and switching to incorporate more abundant and energy rich CPS in warm months.

There also seems to be a link between declining abundance in local CPS and reduced echolocation activity during warm seasons from 2010 to 2013. There was no associated decline observed in cool months during these years and common dolphin abundance in the California Current was at a record high in 2014 (Barlow, 2016). Considering survey years between 1951-2011, anchovy abundance in Southern California has been more than one standard deviation below the mean since 2005, and the lowest abundance ever recorded occurred in 2011 (Wells et al., 2014, MacCall et al., 2016). The sardine stock biomass estimates have been decreasing throughout the California Current since 2007 and recruitment

in 2010 and 2013 was the weakest in recent history (Hill et al., 2015). The lack of CPS in Southern California waters may have driven the dolphins to seek alternative foraging grounds during warmer months. Future studies that concurrently measure dolphin activity and prey distribution and abundance are needed to determine how common dolphins respond to seasonal changes in oceanography and prey availability. Echolocation activity throughout 2014 was so low that this time period was not included in regression analyses. During 2014, the normally vigorous upwelling season was the weakest and shortest observed since the 1990s (Peterson et al., 2015) and surface waters were anomalously warm due to the presence of the “blob” (Hartman et al., 2015). In 2014 there was also an influx of anomalous “warm water” marine mammals, tropical sea birds and turtles to the SCB (Barlow, 2016). The community composition of lower trophic levels also shifted from a cold-water to a warm-water assemblage ((Peterson et al., 2015) and there was a lack of evidence of spawning for record low Pacific sardine populations in 2014-2015 (Hill et al., 2015). The dramatic shifts in dolphin echolocation activity may be linked to the anomalous physical and biological characteristics of the California Current and merits further investigation. Different acoustic behavior between seasons is not attributed to other dolphin species observed in the California Current, such as bottlenose, northern right whale (*Lissodelphis borealis*) or striped dolphins (*Stenella coeruleoalba*). Although these species are not currently acoustically recognizable, northern right whale and striped dolphins are rarely observed at the recording locations and there are very few bottlenose dolphins sighted in offshore areas (Hamilton et al., 2009). Common dolphins are by far the most abundant cetacean at the recording locations (Barlow et al., 2008, Campbell et al., 2015, Barlow, 2016) and any falsely classified detections would be unlikely to bias the overall observed patterns. While it is unlikely that other dolphin species are represented in the acoustic record presented here, a seasonal geographic shift in common dolphin populations could introduce dolphins with alternative foraging preferences to this study area. Warm water conditions are associated with large scale northward shifts

of common dolphin populations, with populations from the eastern tropical Pacific and the Pacific coast of Mexico possibly moving into California waters (IATTC, 1997, Carretta et al., 2016). The seasonal difference in foraging behavior described here may reflect the combined foraging effort of converging populations with varying preferences for vertically and non-vertically migrating prey. Here we report a relationship between common dolphin echolocation activity and the lunar cycle throughout the year at two offshore locations in the SCB. The relationship between echolocation and the lunar cycle is strongest during cooler months and seems to match the expected vertical migration of organisms within deep scattering layers. We believe that the strong relationship between lunar cycles and echolocation behavior corresponds to the importance of mesopelagic prey during cooler months. Seasonal differences in acoustic behavior may be related to dynamic upwelling and dissolved oxygen conditions, the migration of CPS, geographic shifts in common dolphin populations and changes in the foraging strategies of dolphins. While some behaviors linked to the lunar cycle may be based on an endogenous rhythm, the dolphins also demonstrated a response to unpredictable changes in the light environments due to cloud cover. The ability to respond to changes in oceanographic conditions and community composition on seasonal timescales may buffer dolphin populations from the dramatic historical cycles observed in CPS populations.

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Chapter 3

Optimal foraging of a marine top predator tied to the lunar cycle

3.1 Abstract

The energetic cost of foraging should not exceed the energy gained from prey. In the ocean, many fish, seabirds and marine mammals forage on squid that seek refuge from predators in dark, cold, and hypoxic waters during the day. Diving to access this prey can be costly, especially for warm-blooded mammals that breathe at the surface. However, vertical migration is a widespread behavior among squid, in which they rise to the surface at night to feed. The extent of vertical migration is affected by sunlight and moonlight, and we hypothesize that predators will minimize their energetic costs by foraging when prey is nearest to the surface throughout the lunar cycle. Multiple lines of evidence were examined that suggest that Risso's dolphins, *Grampus griseus*, use a foraging strategy that reduces energetic effort by synchronizing foraging effort to prey behavior forced by the lunar cycle, enabling feeding at shallower depths. Supporting evidence includes records of foraging activity in passive acoustic recordings collected during 2009-2015 from three locations in the Southern California Bight. The highest rates of dolphin foraging are before the moon

risers and during the darkest nights of the lunar cycle. In spring and summer months, foraging also occurs during nights surrounding the full moon, when both vertically migrating and non-migrating fish are present in the upper 300 m. This is further supported by visual observations of Risso's dolphins, catch records from the local squid fishery, and acoustic backscatter measures of fish in the water column. Our data support previous observations that Risso's are squid-specialists, with strong spatial and temporal overlaps with the squid fishery and nocturnal foraging that corresponds with the vertical migration of squid. We hypothesize that Risso's dolphins minimize their energetic costs by foraging when their prey is nearest to the surface throughout the lunar cycle.

3.2 Introduction

Long-term trends in lunar illumination have been linked to natural cycles of variability in commercially important fish populations (Hernández-León, 2008). On shorter time scales (~hours to days), lunar cycles elicit behavioral changes in vertically migrating organisms that have important implications for biogeochemical cycling (Hernández-León et al., 2002), the body mass of top predators (Horning et al., 1999) and catch rates for both commercial and recreational fisheries (Lowry et al., 2007, Masuda et al., 2014). In the open-ocean environment, resources may be sparse, fleeting and mobile, and understanding the drivers of animal behavior is one of the central tenets of ecology. Predators must optimize the energy from prey consumption with the energy they expend while foraging (Norberg, 1977). Diving predators adjust their foraging behavior based on the distribution, abundance, and quality of prey (Thompson and Fedak, 2001, Spitz et al., 2010, Houston and Carbone, 1992). As a consequence, variation in predator behavior can be informative of the availability of prey.

Cephalopods, especially squid from the families *Ommastrephidae* and *Loliginidae*, are well represented in the diets of fishes, seabirds and marine mammals in all oceans

of the world (Logan et al., 2013, Staudinger et al., 2013, Ménard et al., 2013, Rodhouse et al., 2013). Market squid, *Doryteuthis opalescens*, is a centrally important prey species in the pelagic food webs of California (Morejohn et al., 1978) and also the focus of the most productive Californian fishery, in terms of profit and landed biomass since the 1980s (Vojkovich, 1998). Throughout most of the year, market squid are found in open coastal waters offshore of California (Recksiek and Frey, 1978) but from December through March, adults migrate from their pelagic and upper slope feeding grounds (Miller et al., 2008) to nearshore, shallow waters (less than 90 m) to spawn (Zeidberg et al., 2006)).

Light influences the widespread vertical migratory behavior of fish, squid, and other invertebrates (Roper and Young, 1975, Mäthger, 2003, Hernández-León et al., 2002). For market squid, spawning aggregations form near the seabed (20-90 m) during the day that rise to disperse throughout the water during the night (Forsythe et al., 2004), but vertical migration behavior outside of neritic spawning grounds is not well understood due to our inability to capture or observe them. Oceanic squid from the families *Ommastrephidae* and *Histioteuthidae* exhibit a pronounced diel vertical migration, with some species migrating from depths of 500-1000 m during the day to mid-water depths or the sea surface at night to feed on micronekton (Gilly et al., 2006, 2012, Roper and Young, 1975). Bright moonlight conditions may reduce the extent of vertical migration in some species (Baker, 1960, Roper and Young, 1975, Gilly et al., 2006). Commercial catch rates of squid can also be strongly affected by the lunar cycle; in the Japanese fishery for common squid (*Todarodes pacificus*), landings increase during nights surrounding the new moon (Masuda et al., 2014). Additionally, the timing of moon rise can be an important predictor where reduced catches are observed on nights when the moon rises after midnight and interferes with the illumination strategy used by fishermen (Masuda et al., 2014). Some large game fish that forage on vertically migrating prey, such as mahi-mahi (*Coryphaena hippurus*) and yellowfin tuna (*Thunnus albacares*), will adjust their depth in different light conditions to

maximize their foraging efficiency (Lowry et al., 2007), but predators with limited diving abilities may rely on different strategies to access prey throughout the lunar cycle.

Risso's dolphins, *Grampus griseus*, are described as squid-specialists among odontocetes (Orr, 1966, Ozturk et al., 2007). Globally, they appear to prefer squid from the families *Loliginidae*, *Ommastrephidae*, *Onychoteuthidae*, *Histioteuthidae*, judging from dominant representation in samples of their stomach contents (Wurtz et al., 1992, Cockcroft et al., 1993, Blanco et al., 2006), although significant differences in diet between seasons and age-sex classes were detected in the stranding record from South Africa (Cockcroft et al., 1993). Off California, Risso's dolphins have been reported to feed on market squid and jumbo squid (Orr, 1966, Kruse et al., 1999), and the distributions of Risso's dolphins overlap spatially and temporally with the neritic spawning grounds of market squid (Soldevilla et al., 2010). Although cephalopods seem to dominate their diets, few studies have sufficient sample sizes across seasons and populations to confidently describe the full range of foraging preferences for Risso's dolphins. Off South Africa, Risso's dolphins may supplement their diet with epipelagic fish (Sekiguchi et al., 1992), as revealed from stomach contents which were comprised of up to 24% by volume of anchovy (*Engraulis capensis*) and horse mackerel (*Trachurus capensis*). In the North Pacific, both market squid and epipelagic fish, commonly eaten by several delphinid species, have higher protein concentrations and energy content (calories/100 g) than mesopelagic squid (Sidwell et al., 1974, Sinclair et al., 2015). Therefore, during times when market squid are less available, it may be energetically advantageous to forgo abundant, but energy-poor, mesopelagic organisms and select energy-rich small pelagic fish (Spitz et al., 2010). Notwithstanding the potential advantages of prey switching, the occasional records of fish as prey seem to be an exception to consistent descriptions of primarily cephalopod diets for Risso's dolphins around the world.

Risso's dolphins are often considered deep-diving odontocetes, partially owing to the known distribution and behavior of squid in their diet (Wurtz et al., 1992). Short-term

acoustic tags with time-depth recorders have shown that adult Risso's dolphins offshore of Southern California conduct daytime dives to a mean depth of 128 m (range 20-566 m) and their dives last from 0.5 to 8.1 minutes in duration, with prey-capture attempts occurring over a large range of depths (Arranz et al., 2016). These dive records were collected exclusively during daylight hours, which would be when the most extreme dive behavior would be expected, given the assumed vertical migration of their cephalopod prey (Roper and Young, 1975). All odontocetes are believed to use echolocation for navigation and foraging (Au, 1993), and recordings of echolocation click behavior indicate that Risso's dolphins primarily echolocate, and thereby forage, at night (Soldevilla et al., 2010). Risso's dolphin groups range in size from tens to hundreds of individuals (Kruse et al., 1999, Leatherwood et al., 1980). Adults form long-term stable associations comprised of pairs or clusters (Hartman et al., 2008). These stable social structures may be adaptations for cetaceans with cephalopod diets, because collective searching may improve the detection of solitary or widely distributed prey, and alloparental care provides protection for calves with limited diving abilities during maternal foraging dives (Hartman et al., 2008). The facility of accessing vertically migrating prey may change throughout the lunar cycle and we hypothesize that Risso's dolphins will minimize their energetic costs by foraging when prey is nearest to the surface throughout the lunar cycle. Underwater sound was continuously recorded during 2009-2015 at three locations in the Southern California Bight to observe patterns in the foraging behavior of Risso's dolphins (Figure 3.1). The study area includes Point Conception (PC), located 30 km offshore the headlands of the SCB, which is characterized by strong winds and high primary productivity (Brink et al., 1984, Dugdale and Wilkerson, 1989) and further south, the sites at Santa Monica (SM) and Catalina Basin (CB) lie 20 and 60 km offshore from Los Angeles, respectively. Acoustic behavior was compared to visual observations of Risso's dolphins from quarterly cruises over the same period, the landings of the southern California commercial squid fishery, and mooring-based

acoustic backscatter measures of fish. Patterns in echolocation activity were identified at daily, monthly, seasonal and inter-annual timescales, which show how a marine top predator, the Risso's dolphin, optimizes its foraging behavior to respond to available prey.

3.3 Methods

3.3.1 Passive acoustic data collection

Autonomous high-frequency acoustic recording packages (HARPs; Wiggins and Hildebrand 2007) were deployed on the seafloor at three locations in the SCB (Figure 3.1, Table 3.1). Each system contained a custom-built preamplifier board and bandpass filter (Wiggins and Hildebrand, 2007). The calibrated response of the preamplifier was accounted for during analysis. Acoustic data were continuously collected with a sampling rates of either 200 kHz or 320 kHz and 16-bit quantization from 2009-2015. There were several gaps in coverage due to equipment servicing (Figure 3.1). Signal processing was performed using the custom software program *Triton* (Wiggins and Hildebrand, 2007) and other MATLAB custom routines. Human analysts visually inspected the recordings using long-term spectral averages (LTSAs) to identify the start and end time of acoustic encounters of Risso's dolphins based on the click descriptions from (Soldevilla et al., 2008). Individual echolocation signals were automatically detected using a two-step approach (Soldevilla et al., 2008, Roch et al., 2011) and a minimum peak-to-peak received level threshold was set to 120 dB re: 1 μ Pa. This received level was defined based on a manual review of the detection data to determine the received level at which echolocation clicks were no longer reliably detected. Echolocation activity that may indicate foraging behavior, was based on a minimum number of detections (2700 in 5 minutes) that would be expected if a single Risso's dolphin were echolocating within the detection range of the instrument at the modal click rates that have been reported for free-ranging Risso's dolphins (Arranz et al., 2016,

Frasier, 2015). Presence or absence of echolocation activity based on these thresholds was coded for 5-minute time periods, every night, between sunset and sunrise.

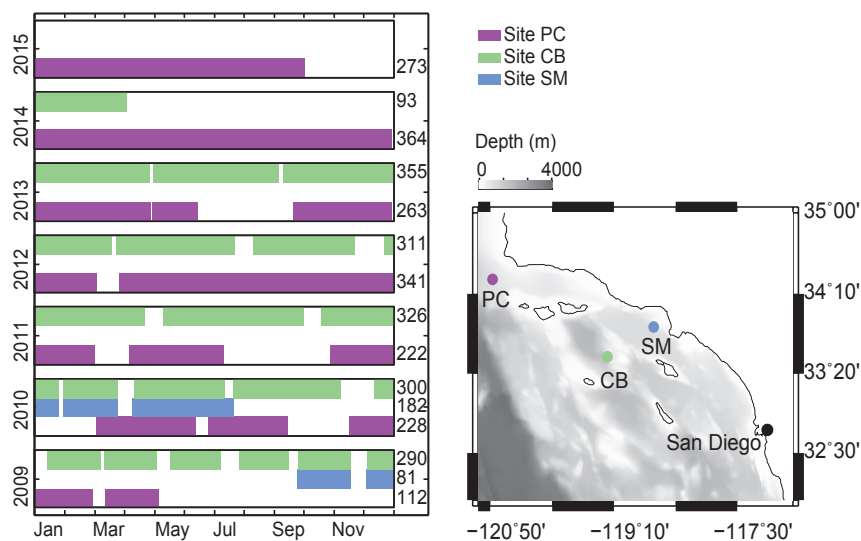


Figure 3.1: Left: Horizontal bars indicate days with recording effort from 2009 to 2015 at three recording locations including Point Conception (PC, purple), Catalina Basin (CB, green) and Santa Monica Bay (SM, blue). The numbers to the right of the horizontal bars indicate the total number of days with recordings in each year. Right: Map of the study area.

Table 3.1: Recording locations and depths of instrument deployments. Number of instruments deployed at each site shown by n.

Location	n	Mean Depth (m)	Depth range (m)
Point Conception (PC)	22	780	600-915
Santa Monica Bay (SM)	4	910	660-1120
Catalina Basin (CB)	18	678	670-690

3.3.2 Active acoustic data

Acoustic backscatter was sampled near Point Conception, California at 34° 18.45' N, 120° 48.39' W, from 2011 to 2014 with a customized Simrad ES10 190 kHz echosounder mounted at 150 m depth on an interdisciplinary biogeochemical mooring (CCE-2; http://mooring.ucsd.edu/index.html?/projects/cce/cce2_data.html). Prior to deployment, each

transceiver-transducer pair was calibrated using a 38.1-mm diameter sphere made from tungsten carbide with 6% cobalt binder (Demer et al., 2015). Every 30 minutes throughout most of the deployment period, two multiplexed transducers transmitted three 1024 μ s pulses towards the sea-surface, sampling the upper 150 m, and then three more towards the seabed, sampling from 150 to 300 m depth. Only data collected at night were analyzed. Samples at ranges surrounding the transmit pulses and echoes from other components of the mooring were removed. Then, echoes from large scatterers (body length $\gg$ wavelength, ~ 7.9 mm), i.e. putative fish and squid, were retained if their variance-to-mean ratio (VMR), calculated from samples at equivalent range across each 3-transmission ensemble, were between -40 and -23 dB, determined empirically (Demer et al., 2009). Finally, nautical area backscattering coefficients (NASC; $\text{m}^2 \text{nmi}^{-2}$) were calculated for each 10-m depth and 30-minute interval.

3.3.3 Commercial squid landings

Southern California market squid landing receipts from all fishing blocks south of Point Piedras Blancas were taken from the California Department of Fish and Wildlife database during 2009-2015 (California Department of Fish and Wildlife, 2015). Catch data should be viewed with some caution as stocks may be depleted with little decline observed in catch rates, especially for fisheries that target aggregations, such as those for market squid (Jensen et al., 2012). Catch data alone should not be used as a proxy for biomass (Jensen et al., 2012), so the catch per unit effort (CPUE) was defined as the weight of landings per day, divided by the number of seine vessel receipts. The CPUE provides an index for squid abundance by measuring the amount of time required to make the landings.

3.3.4 Visual sightings of dolphins

Marine mammal visual observations were collected on quarterly California Cooperative Oceanic Fisheries Investigations (CalCOFI; <http://calcofi.org>) surveys using standard

line-transect marine mammal survey protocols (Buckland et al., 1993, Barlow, 1995). Two experienced marine mammal observers used 7x50 Fujinon binoculars to record all marine mammals encountered during daylight hours while transitioning between CalCOFI stations. For each sighting, the species, group size, declination angle relative to the horizon measured with binocular reticles, azimuth relative to the bow, latitude, longitude, ship heading, behavioral state, sighting cue, sea state, swell height, visibility and comments. Sightings were classified as on-effort when two observers were actively searching in Beaufort sea state 0-5, with the vessel traveling at least 11 km/h and visibility greater than 1 km. Only on-effort sightings were included in this analysis.

3.3.5 Regression analysis

All regression analysis was conducted in R 3.3.0 (Wood, 2006, R Development Core Team, 2016). The relative time difference between moonrise and sunset throughout the lunar cycle is considered as a categorical predictor for “moon presence”. Times are labeled as occurring before, with, or after the moon was visible. For nights when the moon was never present in the night sky (around the new moon), all times of the night were labeled as “before”. The presence of low marine stratus clouds was considered at each site, but the methods limited the analysis to only include the months of May through October (Clemesha et al., 2016). The presence of fish was considered for increasing depth ranges from the surface to 300 m, in 100 m increments. NASC thresholds for presence of fish were tested at increments of 50, from 50 to 300. The presence of fish and cloud coverage were considered as interaction effects with the smooth for the cyclical lunar day (new moon at day 1 and 29). Julian day is also a cyclical predictor. Location, presence of the moon and year were considered as factors. Scatterplots, histograms and boxplots of each explanatory variable were checked for extreme values, and severe non-normality, which would violate model assumptions (Zuur et al., 2009). Generalized additive mixed models (GAMMs; mgcv

package (Wood, 2006, R Development Core Team, 2016) were constructed to account for correlation between adjacent observations. The restriction to nocturnal observations resulted in many short time series separated by daylight hours, so nightly blocks were used in the correlation structure. The autocorrelation function (ACF) plot of the residuals was examined to assess any remaining correlation in the data. The fixed-effects structure was simplified through a backwards, step-wise procedure, selecting the best model with the minimum Akaike Information Criterion (AIC; Akaike 1974) that retained significant predictors.

3.4 Results

3.4.1 Primarily nighttime foraging

Throughout the year, at all recording locations, echolocation of Risso's dolphins was predominantly detected during the night (Figure 3.2, Table 3.2). A chi-squared test of independence between echolocation and diel period (day versus night) was significant at each location ($p < 0.001$; Table 3.2). For periods with echolocation, the mean and standard deviation (sd) of the number of click detections per 5 minute bin was 1209 ± 2501 clicks, with a range of 1 to 48,512 clicks. The median peak-to-peak (p-p) sound pressure level detected in 5 minute bins ranged from 120 to 161 dB p-p re: $1 \mu\text{Pa}$ with a mean $\pm$ sd of 125 ± 3 dB p-p re: $1 \mu\text{Pa}$.

3.4.2 Predator presence and distribution follows squid

There were temporal and spatial overlaps between the presence of Risso's dolphins and the Southern California commercial squid fishery. Visual observations indicate a shift in Risso's dolphin distribution to more coastal regions during fall and winter months (Figure 3.3), corresponding to the neritic spawning habitat of market squid during the same time of year. Group sizes were smaller in fall and winter months (mean $\pm$ sd = 20 ± 48)

than during spring and summer months (mean $\pm$ sd = 57 ± 197) when Risso's dolphin distribution extended to a broader, more offshore region of the Southern California Bight (SCB). Echolocation activity was also positively correlated with squid catch per unit effort (CPUE) on an annual basis at site PC ($r=0.92, df=3, p=0.03$; Pearson correlation statistical criteria) but not at site CB ($r=0.18, df=3, p=0.77$). The single year of data at site SM prevented a correlation analysis. Maximum squid landings and CPUE occurred during winter months, yet there were no consistent seasonal trends in echolocation activity (Figure 3.2).

3.4.3 Fish backscatter is seasonal and responds to lunar cycle

Acoustic backscatter from mesopelagic and small pelagic fish was available from site PC in 2011-2014. The highest nautical area backscattering coefficient (NASC; $m^2 \text{ nmi}^{-2}$) values were consistently observed during April-June (weeks 15-25) of each year. Throughout each year, NASC values were higher during nights of the new moon compared to nights of the full moon (Figure 3.4). Echolocation activity of Risso's dolphin was higher during nights with elevated NASC values in the upper 300 m both during new and full moon periods (Figure 3.6).

3.4.4 Lunar cycle influences optimal foraging strategy

At all three recording locations, echolocation was ~ 2 fold less during full moon nights compared to new moon nights (Figure 3.5). The presence of echolocation during the 4 nights surrounding new or full moon was significantly different from each other at each recording location (Kruskal-Wallis test, $p < 0.005$). The degree to which echolocation was less during full versus new moons varied between sites throughout the year. More consistent echolocation during nights of the full moon was observed during spring and summer months. At night, echolocation occurred more often before moonrise (Figure 3.5). Occurrences of echolocation before, during, and after the moon was present were significantly different at

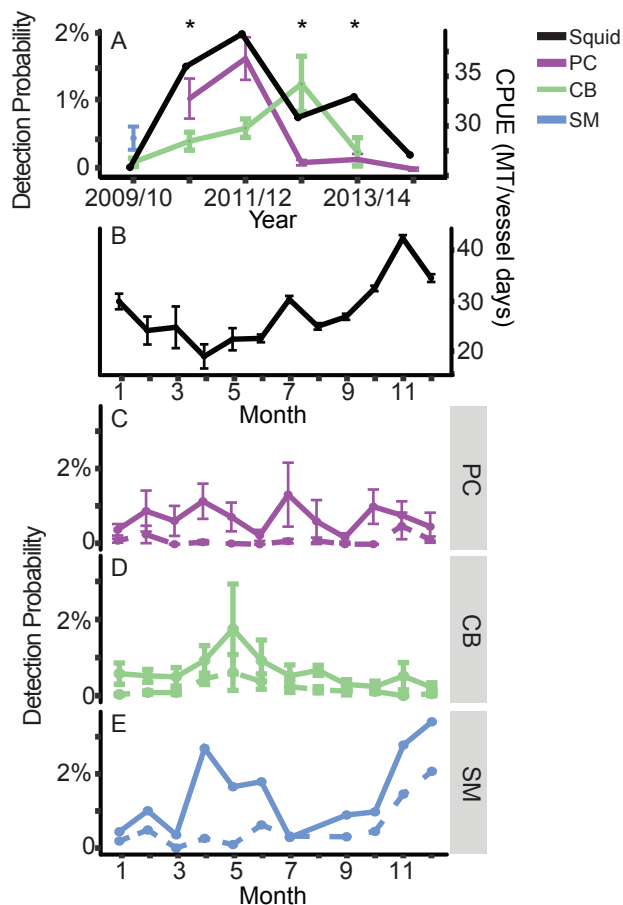


Figure 3.2: Squid landings and Risso's dolphin echolocation. (A) Annual squid catch per unit effort (CPUE; based on fishing season April-March) and (B) average monthly CPUE from the Southern California commercial squid fishery 2009-2014 (black lines, right axis). Asterisks indicate years with early closures of the squid fishery due to projected landings meeting the seasonal catch limit. The fishery operates April-March, but was closed early in 2010 (December), 2011(November), 2012 (November), and 2013 (October). (A) shows annual probability of detecting Risso's dolphin echolocation (colored lines/points). (C-E) contrasts echolocation behavior between the day (dashed lines) and night(solid lines) on a monthly scale. Standard error bars are shown.

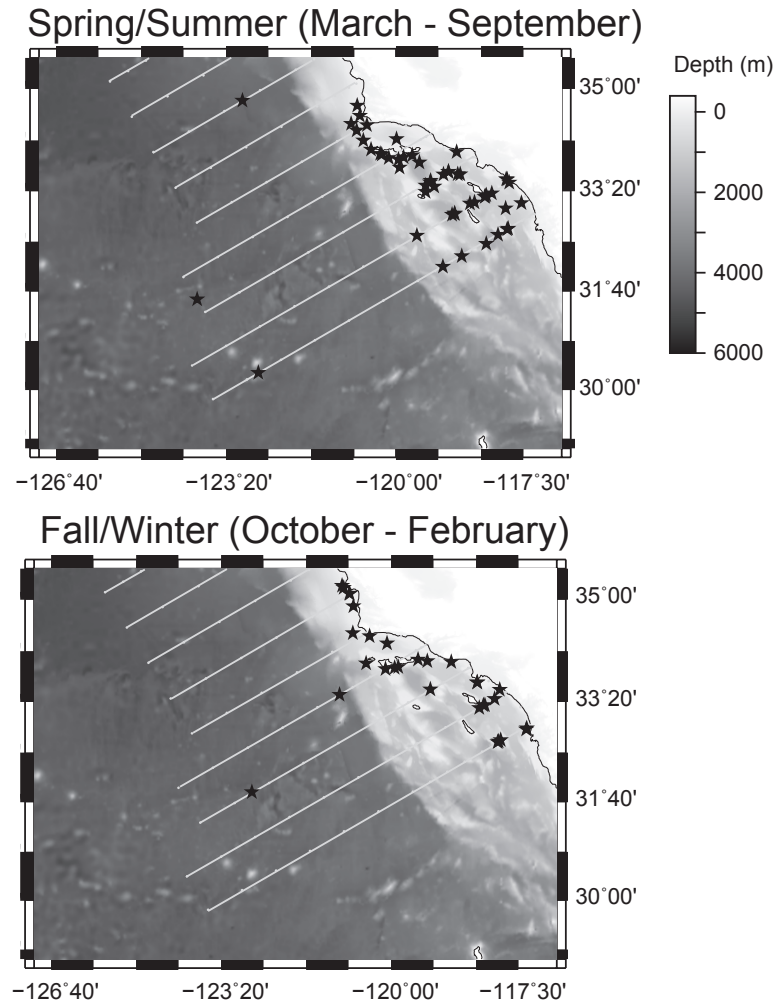


Figure 3.3: Visual observations of Risso's dolphins in the Southern California Bight. Map of the Southern California Bight with California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey lines (gray). On-effort visual observations (black stars) of Risso's dolphins from spring/summer (top) and fall/winter (bottom) cruises from 2005 to 2016. Risso's dolphins were sighted at least once in 76% (16/21) of all spring/summer cruises and 88% (14/16) of all fall/winter cruises.

Table 3.2: Day and nighttime detection probability for Risso's dolphin echolocation. Probability of detecting Risso's dolphin echolocation during day and nighttime periods. Number of 5-minute observation periods at each site shown by n. χ^2 p-value indicates the significance of a Chi-square test of independence between echolocation presence and diel period (day versus night) using one degree of freedom.

Location	n	Probability of Detection		χ^2
		Day	Night	
Point Conception (PC)	770,778	0.7%	3.9%	$p < 0.001$
Santa Monica Bay (SM)	74,608	0.5%	4.9%	$p < 0.001$
Catalina Basin (CB)	499,758	1.3%	4.5%	$p < 0.001$

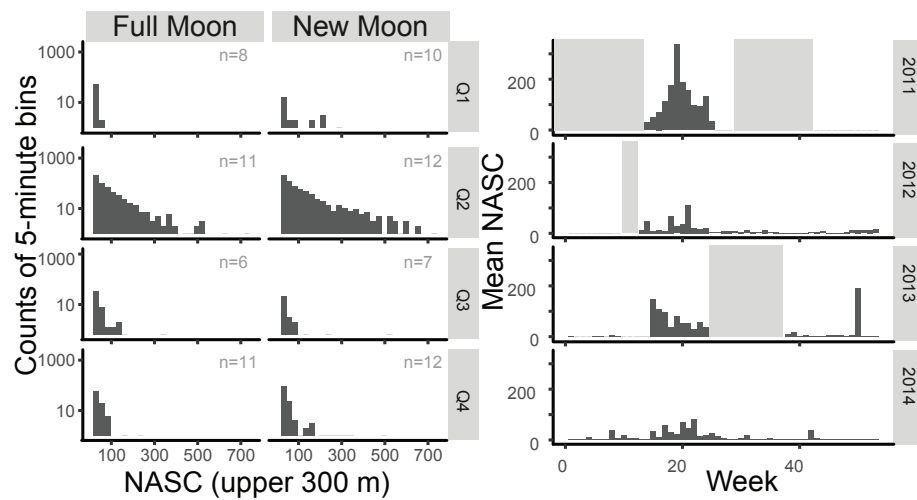


Figure 3.4: Acoustic backscatter during nights of the new and full moon. Histograms of acoustic backscatter as the Nautical Area Scattering Coefficient (NASC; $\text{m}^2 \text{nmi}^{-2}$) in the upper 300 m and in 30-minute bins at the Point Conception (PC) recording location. Left panels: Data shown are for the four nights surrounding the full and new moon during four quarters of the year (Q1-Q4). The number of months with available data for each lunar phase is shown by n= in each subplot. Right panels: Mean NASC is shown by week for 2011-2014. Gray boxes indicate times with no data.

sites PC and CB (Kruskal-Wallis test, $p < 0.005$), but not at site SM (Kruskal-Wallis test, $p = 0.15$).

3.4.5 Models confirm lunar relationship with foraging activity

Generalized additive mixture models (GAMMs) were applied to quantify the observed seasonal lunar patterns in nocturnal dolphin echolocation activity at all recording locations. In a model including data from all recording locations, the most important predictors included lunar day, the presence of the moon, Julian day and recording location (Table 3.3). The minimum probability of detecting echolocation was estimated surrounding the nights of the full moon (Lunar Day 14 or 15) and during times when the moon was present in the night sky (Figure 3.7). Overall, the probability of detecting echolocation was about 10% lower during nights of the full moon compared to nights of the new moon and during times when the moon was present in the night sky, the probability of detecting echolocation was about 25% lower than times before the moon rose (Table 3.3, Figure 3.7). Although observations indicated varying seasonal patterns at each site, a single predictor for all sites was retained that showed a seasonal cycle with maximum echolocation activity between April and May (Julian days 100–150). The greatest level of echolocation activity was predicted at Site SM.

At site PC, an additional site-specific model was constructed which considered the presence of fish from the acoustic backscatter data. Fish presence was retained in the best model, based on NASC values of $50 \text{ m}^2 \text{ nmi}^{-2}$ or greater in the upper 300 m, as an interaction effect with lunar day. When fish were absent, a minimum in echolocation activity was estimated during the nights of and following the full moon (Figure 3.7). Conversely, when fish were present, echolocation was not reduced around nights of the full moon but rather following the new moon (Figure 3.7). The presence of the moon had a much stronger effect for the model for site PC than for all sites combined, shown by decrease in the

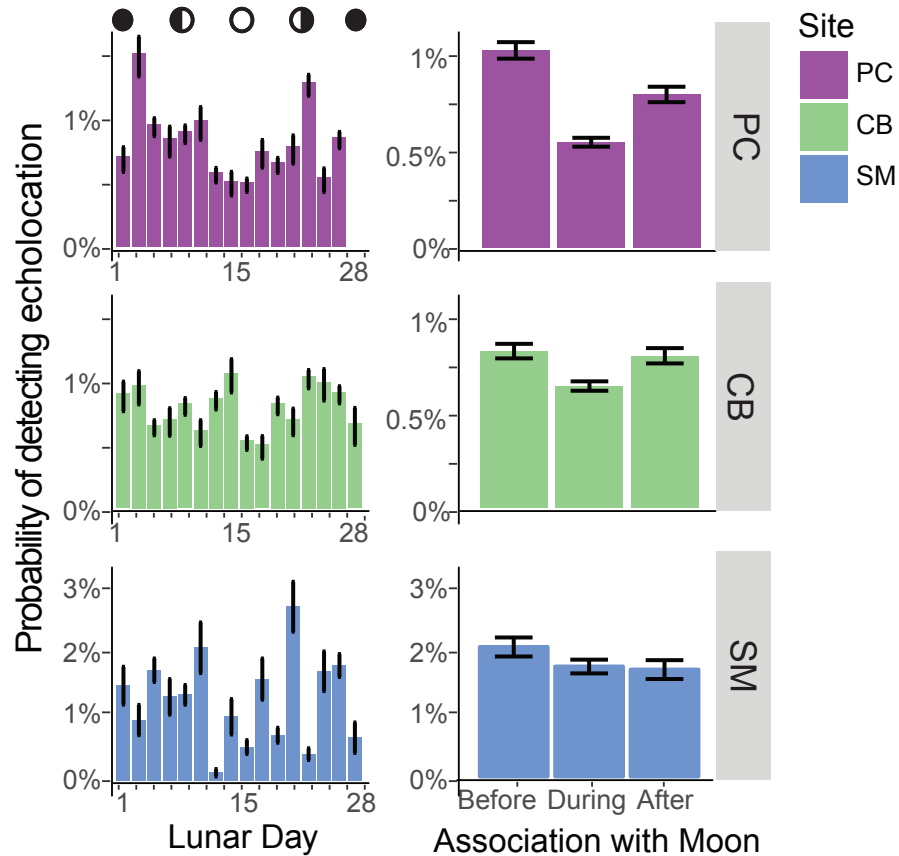


Figure 3.5: Nighttime observations of Risso's dolphin echolocation. Nighttime echolocation of Risso's dolphin at three locations in the Southern California Bight: Point Conception (PC, purple), Catalina Basin (CB, green) and Santa Monica Bay (SM, blue). Probability of detecting echolocation is plotted for all lunar days (Full Moon = Lunar Day 15, circles indicate quarterly moon phases), and for times before, during and after the moon was present in the night sky. Standard error bars are shown.

probability of detecting echolocation during times when the moon was present by about 80% (Table 3.3).

For all models, the inclusion of a first order autoregressive structure in the random effects improved the model fit. Visual inspection of the histogram and normal plot of the residuals indicate that the residuals are approximately normal, with some deviation in the tails of the distribution. Although autocorrelation was reduced with a first order autoregressive structure in the random effects portion of the model, the autocorrelation function still showed significant autocorrelation in lags 3 through 6, e.g. 15-30 minutes, at the 95% confidence level.

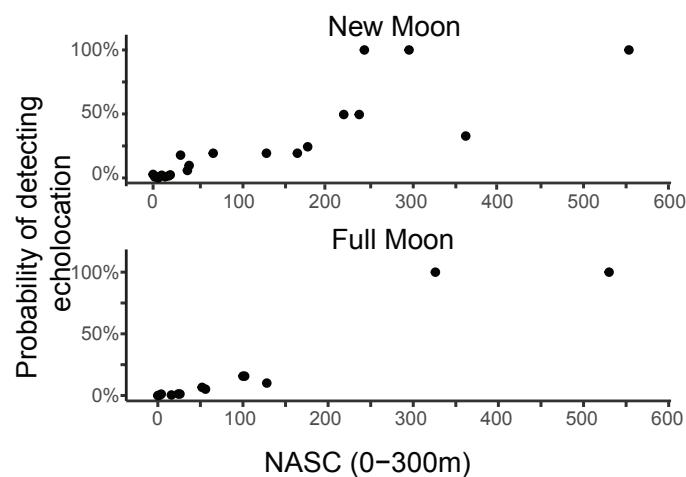


Figure 3.6: Risso's dolphin echolocation with acoustic backscatter. Probability of detecting Risso's dolphin echolocation with acoustic backscatter as Nautical Area Scattering Coefficient (NASC) in the upper 300 m during the four nights surrounding the new (top) and full (bottom) moon at the Point Conception (PC) recording location.

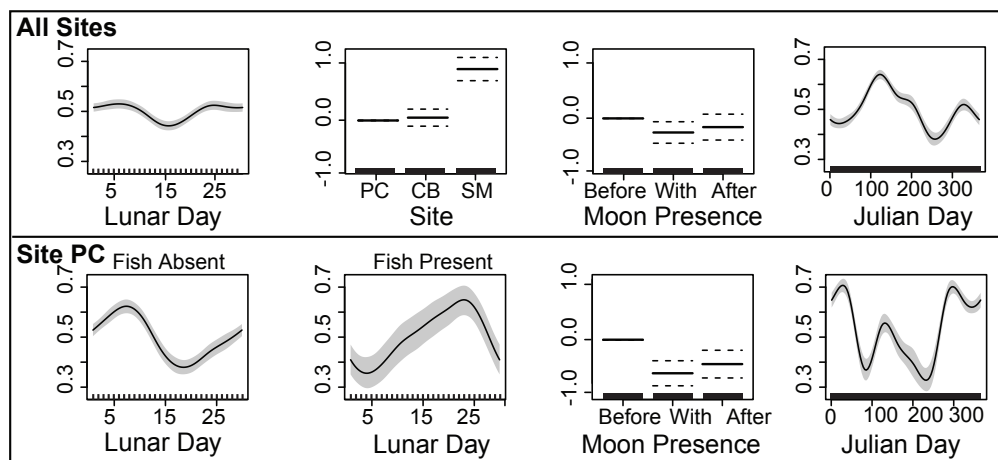


Figure 3.7: GAMM estimates of predictors for Risso's dolphin echolocation. Estimated smoothing curves and factors of GAMM for nighttime echolocation of Risso's dolphins for all sites combined (top row), and at site PC (bottom row) with acoustic backscatter as an indicator of potential prey (2011-2014). Zero on the vertical axis corresponds to no effect of the explanatory variable. Shaded or dashed regions indicate 95% confidence limits. Ticks above the x-axis indicate locations of observations.

Table 3.3: GAMM estimates of predictors for Risso’s dolphin echolocation. GAMM estimates of predictors for nighttime echolocation in 5-minute bins from all sites (2009-2014) and from site PC (2011-2014) where acoustic backscatter of potential prey was available. Only estimates from the best models are presented here. Smooth terms are shown with degrees of freedom and factors are indicated with standard error in parentheses. The number of observations is denoted by n. All terms in bold indicate significant predictors = * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

	All Sites n=528,977	Site PC with backscatter n=29,049
<u>Smooth Functions</u>		
Lunar Day	3.25 (8)***	
Julian Day	6.08 (8)***	6.86 (8)***
Lunar Day:Fish Absent		3.42 (8)***
Lunar Day:Fish Present		2.32 (8)*
<u>Factors</u>		
Moon Presence (During)	-0.25 (0.10)***	-0.80 (0.15)***
Moon Presence (After)	-0.15 (0.11)	-0.58 (0.16)***
Site CB	0.05 (0.08)	
Site SM	0.91 (0.10)***	

3.5 Discussion

Risso’s dolphins are considered deep-diving odontocetes; however, recent observations from the animals in the SCB tagged with time-depth recorders suggest moderate diving abilities compared to other odontocetes (Arranz et al., 2016). If extreme diving is not an option for Risso’s dolphins, strategic foraging while prey are more abundant in surface waters would be expected. The nocturnal foraging behavior reported here and by previous authors (Soldevilla et al., 2010) supports the hypothesis of moderate diving abilities. Further, we now report that foraging may be optimized to occur during the darkest times of the lunar cycle. As expected for vertically migrating organisms, the presence of fish in the upper 300 m increased during dark nights of the new moon, and likely would be associated with other

mesopelagic species not observed in the acoustic backscatter, such as squid. Conversely, on nights of the full moon the presence of fish decreased, as did echolocation activity, potentially indicating an increased energetic cost of foraging for the dolphins when their prey remained at depth. The time between sunset and moonrise is the longest during the last quarter of the lunar cycle and during this time of darkness, vertically migrating species rise to the surface in apparent safety before they become vulnerable to visual predators when the moon rises (Gliwicz, 1986a, Hernández-León et al., 2002). The increase in dolphin foraging during the hours before the moon rose in the last quarter of the lunar cycle may offset the higher cost of accessing deeper prey during times when the moon illuminates surface waters. Our observations of reduced echolocation during the full moon could also indicate that the dolphins have moved out of the detection range of the recorder (1.5 - 5 kilometers, Frasier et al. 2016a), that they switched to visual predation, or that they more efficiently accessed denser patches of prey at depth (Benoit-Bird et al., 2009b), thereby reducing their total time spent foraging. The decision to forgo or alter foraging during nights of the full moon could be strategic for Risso's dolphins given that prey may be easier to access during darker nights.

The spatial and temporal overlap between the presence of Risso's dolphins and the market squid fishery support widespread observations of squid as important and preferred prey for Risso's dolphins (Orr, 1966, Ozturk et al., 2007, Cockcroft et al., 1993). In the SCB, the average acoustic presence of Risso's tracked annual market squid CPUE, and the geographic extent of visual sightings contracted to coastal areas during the peak of the market squid fishing season, in autumn and winter months. The recording locations included in this study are located deeper (600-1000 m) than spawning aggregations of squid are generally found (<90 m, Zeidberg et al. 2006), but the behavior of market squid outside of SCB coastal habitats is not well understood due to the difficulty in observing oceanic squid. The prevalence of Risso's foraging behavior at night and during the darkest periods of the lunar cycle suggest that market squid are easier for Risso's dolphins to capture during

the night, possibly because they vertically migrate from depth during the day to the surface at night, or their ability to detect and avoid predators is reduced in the darkness. Further, the reduced group sizes of Risso's dolphins in autumn and winter months may suggest that coordinated foraging is less important when feeding on spawning aggregations of market squid. The geographic distribution of Risso's dolphins shifts seasonally but the movement or varied foraging strategies described here cannot be ascribed to any particular population or age/sex class. The changes that we observed in geographic extent, group size and acoustic behavior suggest that Risso's dolphins may optimize their foraging behavior for distinct prey that are seasonally available.

During spring and summer months, increases in the presence of fish in surface waters resulted in consistent echolocation behavior, even during nights of the full moon. The analysis of acoustic backscatter data, including the VMR and threshold processing steps, were designed to retain backscatter from large organisms (relative to the 190 kHz pulse) and omit backscatter from zooplankton. As such, the NASC values represent integrated energy from the backscatter of all fish in the sampled water volume but are limited in the ability to interpret the density or species of fish that are present. Additionally the context of these observations, e.g. fish behavioral state, species present, oceanographic conditions, and other seasonal effects, could impact the backscatter dynamics. This shift occurred during April-June every year, coinciding with times of increased primary productivity in the SCB, when market squid were not abundant. There have been reports of Risso's dolphins foraging on fish in South Africa (Sekiguchi et al., 1992), but this is the first indication that Risso's dolphins may seasonally forage on species other than squid in the California Current System. With the current data, it is not possible to discern if the dolphins were preying on the available fish or other organisms (such as squid) associating with the fish, but the dolphins responded to a shift in the community by increasing their echolocation activity when potential prey were abundant in shallow waters throughout the lunar cycle.

The regression analysis showed that the lunar day, presence of the moon in the night sky and seasonal cycles were all significant predictors of echolocation activity. Although seasonal cycles varied at each site from year to year, the best performing model did not include any interaction effects with year or site and Julian day, but rather predicted an overall maximum in echolocation during spring and summer months. The temporal correlation of adjacent observations each night was accounted for in the random effects structure of our model, but there was still residual autocorrelation in our residuals. This suggests that there likely are other predictors to describe the presence of echolocation that we have not accounted for here. Our models were designed to quantify the effect of the lunar cycle on echolocation rather than predict echolocation behavior in all conditions. As such, we did not incorporate the complex suite of predictors that might be associated with prey and predator distributions. More complex ecological models that include predictors based on the lunar cycle as well as environmental conditions would likely improve model fit.

The increasing demand to predict ecosystem response to climate change and for fisheries management is associated with a need to understand the complexities of trophic interactions at multiple scales. Our results show that the passive acoustic record can be useful in tracking temporal variability in the predation pressure exerted by marine top predators, especially odontocetes for which traditional biological sampling may present challenges. Although Risso's dolphins are often described as deep-diving odontocetes, our observations suggest that there may be energetic advantages to foraging at different times of the night and lunar month. Especially for squid-specialists like Risso's dolphins, adjusting the timing of foraging may result in larger energetic gains than switching to alternate prey types, but differences in prey preferences between seasons and possibly among populations merits further investigation. The complementary use of telemetry and biochemical tracers is encouraged in future studies of how behavior and prey quality may change over monthly, seasonal and annual timescales. Understanding the spatial and temporal variability in

foraging behavior is necessary to promote healthy populations of predators and manage productive marine ecosystems.

3.6 Acknowledgements

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Chapter 3, in part, is currently being prepared for submission for publication of the material. Simonis, Anne E., Demer, David A., Krumpel, Anna, Kim, Ella B., Debich, Amanda J., Roch, Marie A., Hildebrand, John A. and Simone Baumann-Pickering. Optimal foraging of a marine top predator tied to the lunar cycle. The dissertation author was the primary investigator and author of this material.

Chapter 4

Lunar patterns in acoustic activity of short-finned pilot whales (*Globicephala macrorhynchus*) and false killer whales (*Pseudorca crassidens*) throughout the Hawaiian Islands

4.1 Abstract

In the oligotrophic subtropical gyre, the mesopelagic boundary community of the Hawaiian Islands is a critical prey resource for large, diving predators. Around the islands, the vertical and horizontal movement of mesopelagic organisms is influenced by light, both solar and lunar which may in turn, influence the behavior of their predators. Here a comparison is made between the acoustic behavior of two dolphin species with different diving behavior, false killer whales (*Pseudorca crassidens*) and short-finned pilot whales

(*Globicephala macrorhynchus*). Variability in echolocation is documented at three locations during 2009-2014 in the main and northwestern Hawaiian Islands from daily to annual timescales, with emphasis on the lunar cycle as an established behavioral driver for some dolphin prey. The echolocation from pilot whales at all locations and false killer whales at Pearl and Hermes Reef in the northwest Hawaiian Islands was mainly detected at night with peaks during crepuscular periods. Conversely, for false killer whales in the main Hawaiian Islands (Kaua'i and Hawai'i) echolocation was mainly detected during the day. Low levels of echolocation prevented investigation of lunar cycles for false killer whales at Hawai'i, and pilot whales at Kaua'i and Pearl and Hermes Reef. Both species showed low levels of nighttime echolocation during full moon phases and during times that the moon was present in the night sky. Generalized additive mixed models show that lunar covariates were important in predicting nighttime echolocation activity for both species, although not at Kaua'i where echolocation occurred mainly during the day. The prevalence of nighttime versus daytime false killer whale acoustic behavior in the northwest and main Hawaiian Islands, respectively, can likely be attributed to distinct populations or social clusters with different foraging strategies. The dissimilar fishing pressure and environmental conditions in each habitat may be relevant to false killer whale foraging behavior.

4.2 Introduction

Every day throughout the world's oceans, mesopelagic fish, squid and invertebrates take part in the largest synchronized movement of biomass on the planet, known as diel vertical migration (DVM). During the day, these organisms reside in deep waters, where darkness and hypoxia provide refuge from their more aerobic, visually oriented predators, but at night they rise to the surface to actively forage (Barham, 1966, Netburn and Koslow, 2015). One of the most significant factors affecting the magnitude, timing and distribution of vertical migrators is light, both solar and lunar (Boden and Kampa, 1967, Blaxter, 1974).

On nights of the full moon, many fishes and cephalopods are found at lower densities at the surface than during the darker nights of the new moon (Baker, 1960, Benoit-Bird et al., 2009b, Clarke, 1973, Musyl et al., 2003, Roper and Young, 1975). In island habitats, diel migration may also have a horizontal component, with organisms found further offshore during times of increased illumination (Benoit-Bird et al., 2001, Benoit-Bird and Au, 2006). The variation in vertical migration behavior throughout the lunar cycle has been shown to have important implications for biogeochemical cycling (Hernández-León et al., 2002), catch rates in both commercial (Hernández-León, 2008, Masuda et al., 2014) and recreational (Lowry et al., 2007) fisheries, and the foraging success of marine mammals with limited diving abilities (Horning et al., 1999). The objective of this study is to investigate the acoustic behavior of two large marine predators with distinct foraging strategies on hourly to annual timescales, with emphasis on the lunar cycle as an established behavioral driver for some dolphin prey.

Diving to forage at depth can be costly, and optimal foraging theory suggests that predators will optimize the balance of energy spent and gained while foraging. Dolphins are diving predators, tied to the surface to breath, but they have evolved various strategies to access prey. These adaptations may be behavioral (e.g. foraging at night, cooperatively foraging, selecting energy-rich prey) or physiological (e.g. higher myoglobin concentrations to support deeper or longer dives). Short-finned pilot whales (*Globicephala macrorhynchus* hereafter referred to as pilot whales) and false killer whales (*Pseudorca crassidens*) are two large members of the dolphin family (*Delphinidae*) that demonstrate distinct foraging and diving behavior. Pilot whales are considered deep-diving squid-specialists (Sinclair, 1992, Seagars and Henderson, 1985), capable of diving deeper than 1,000 m (Wells et al., 2013, Quick et al., 2017) and sprinting at speeds up to 9 m/s in order to pursue large, muscular squid (Aguilar de Soto et al., 2008). Conversely, false killer whales generally remain in the upper 300 m of the ocean and diets include cephalopods, epipelagic or benthic-demersal

fish and occasionally even marine mammals (Alonso et al., 1999, Ortega-Ortiz et al., 2014, Baird, 2009, Rinaldi et al., 2006). Both pilot and false killer whales live and forage in highly social groups (Mahaffy et al., 2015, Baird, 2009), and the presence of post-reproductive females indicates that ecological knowledge may be important for group survival (Kasuya and Marsh, 1984, Ferreira, 2009). Ecological knowledge may include tactics to avoid predators or alternative foraging strategies that post-reproductive females teach to their kin. As such, the foraging preferences of pilot and false killer whales may be strongly influenced by socially learned behaviors, in addition to the distribution and abundance of locally available prey.

In an otherwise nutrient depleted oligotrophic gyre, the Hawaiian archipelago offers a rich network of regions of enhanced productivity, which support a diverse array of top predators, including both pilot and false killer whales. A resident population of pilot whales inhabits the western slope waters of the island of Hawaii (Mahaffy, 2012), where the deep mesopelagic boundary community likely provides plentiful prey resources for pilot whales (Abecassis et al., 2015). Two resident populations of false killer whales are found in the insular main Hawaiian islands (MHI) and northwestern Hawaiian islands (NWHI; Baird et al. 2008, 2012a, 2013) and a third population is recognized in waters greater than 40 km offshore of the islands (Baird et al., 2013, Carretta et al., 2011). False killer whales in the MHI are considered an endangered population and one of their principal threats is negative interactions with longline fisheries (Forney and Kobayashi, 2007). Individuals from the MHI population have been described predominantly as daytime foragers, due to many observations of predation on large pelagic fish, including yellowfin (*Thunnus albacares*), albacore (*T. alalunga*) and skipjack tuna (*Katsuwonus pelamis*), broadbill swordfish (*Xiphias gladius*), mahi mahi (*Coryphaena hippurus*), ono (*Acanthocybium solandri*), and monchong (*Eumegistus illustrus*), but daytime observations are biased due to largely visual survey effort (Baird, 2009). A collection of 29 satellite tags on 27 individual false killer whales in

the MHI population showed that individuals frequent discrete habitats, which may indicate foraging specialization between social clusters (Baird et al., 2015). Small boat surveys and tagging efforts have been used to describe site fidelity and social behavior for both pilot and false killer whales around the Hawaiian Islands, but these methods are limited in their geographic scope and ability to document nighttime activity or longer-term patterns in habitat use and foraging behavior. Especially for the endangered MHI population of false killer whales, improving the understanding of foraging behavior on both short and long timescales could be useful for managers looking to mitigate negative interactions with fisheries.

Most dolphins use echolocation while foraging, making passive acoustic monitoring an effective method to document their presence and behavior on timescales of hours to years (Henderson et al., 2011, Wiggins et al., 2013). Especially for animals that are acoustically active at depth, during the night, or in remote habitats, passive acoustic monitoring is a valuable tool to study behavioral ecology. Species-level classification of echolocation signals is possible for pilot and false killer whales, due to distinct spectral and temporal features in their echolocation clicks (Baumann-Pickering et al., 2015). The source levels of echolocation clicks for pilot whales have not been described, but are likely very similar to those of long-finned pilot whales (*Globicephala melas*, 203 dB re 1 μ Pa pp; Eskesen et al. 2011). Source levels of false killer whale echolocation clicks have been reported at 201-225 dB re 1 μ Pa pp; Madsen et al. 2004b, Thode et al. 2016). For echolocation clicks traveling 700 m from the surface to a bottom mounted recording instrument, there is high transmission loss (-58 dB at 20 kHz at 20°C; Urlick 1983) due to spherical spreading and absorption. The directional beampattern (-20 dB at >20° off axis central echolocation beam for a false killer whale; Au et al. 1995) further limits the detection range for outgoing clicks. As such, the detection range for echolocation clicks using a bottom moored acoustic recorder is generally 1.5-5 km for groups of foraging dolphins, with effective range determined by the instrument

sensitivity, environmental conditions and the behavior of dolphins (Frasier et al., 2016b). Therefore, passive acoustic monitoring is useful to investigate behavioral drivers in discrete locations over a large range of temporal scales.

Continuous, long-term acoustic recordings were collected at three recording locations in the Hawaiian archipelago to document the presence of pilot and false killer whale echolocation. The temporal variability of echolocation is described at daily, weekly, monthly and annual timescales, with emphasis on the lunar cycle, an established driver in the behavior of potential dolphin prey species. The acoustic behavior of false killer whales is examined at two different locations, which likely represent animals from the insular main and northwest Hawaiian Island populations. Drawing from the concepts of optimal foraging theory, it is hypothesized that both species of dolphins will echolocate, and therefore forage, at times when their prey are more abundant in surface waters.

4.3 Methods

4.3.1 Passive acoustic data collection

Autonomous high-frequency acoustic recording packages (HARPs; Wiggins and Hildebrand 2007) were deployed on the seafloor 15 km southeast of Pearl and Hermes Reef (PHR), 12 km west of Kaua'i, and 15 km west of the island of Hawai'i (Figure 4.1). The deployment depths varied between 620-814 m (Table 4.1). Each system contained a custom-built preamplifier board and bandpass filter to minimize ambient noise and amplify signals of interest (Wiggins and Hildebrand, 2007) and the calibrated pre-amplifier response was accounted for during analysis. Acoustic data were collected with a sampling rate of 200 kHz and 16-bit quantization. HARPs either recorded continuously or on a duty cycle, collecting acoustic data for 5 minutes within periods of 8-20 minutes depending on the deployment (Table 4.1).

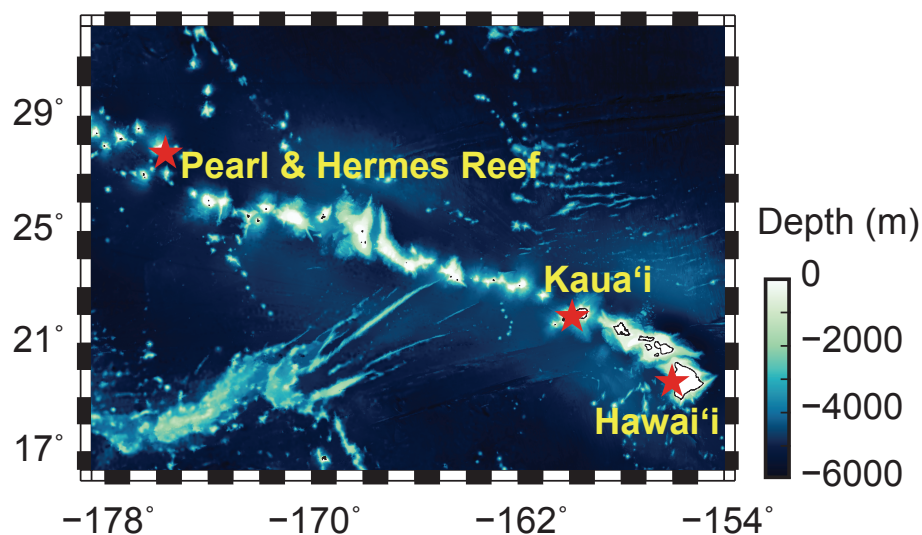


Figure 4.1: Map of recording locations for pilot and false killer whales. Map of the Hawaiian archipelago with the HARP recording locations marked by stars.

Table 4.1: Recording effort for pilot and false killer whales. Recording effort for HARPs at all locations. The duty cycle for each instrument is reported as duration recording cycle/duration of active recording in minutes.

Location	Recording Period	Recording Days	Duty Cycle(min)	Depth (m)
Hawai'i	4/23/09 - 8/18/09	117	15/5	620
	10/25/09 - 12/15/09	51	continuous	620
	5/1/10 - 6/17/10	47	continuous	620
	9/30/10 - 1/17/11	109	8/5	652
	Total	324		
Kaua'i	10/3/09 - 5/12/10	221	20/5	706
	6/4/10 - 8/21/10	78	continuous	720
	Total	299		
Pearl and Hermes Reef	10/20/09 - 05/24/10	216	20/5	753
	06/01/10 - 9/18/10	109	continuous	752
	4/12/11 - 7/29/11	108	continuous	550
	8/15/11 - 1/7/12	145	8/5	814
	9/12/14 - 7/16/15	307	20/5	780
	Total	885		

Signal processing was performed using the custom software program *Triton* (Wiggins and Hildebrand, 2007) and other MATLAB custom routines. Individual echolocation signals were automatically detected using a two-step approach (Soldevilla et al., 2008, Roch et al., 2011) and a minimum peak-to-peak received level threshold was set to 120 dB re: 1 μ Pa. This threshold was defined based on a manual review of the detection data to determine the received level at which echolocation clicks were no longer reliably detected. Individual echolocation click detections were digitally filtered with a 10-pole Butterworth band-pass filter, with a pass band between 5 and 95 kHz. The filtering for each detection was based on 800 sample points centered on the echolocation signal. The spectrum of each detected signal was calculated using 2.56 ms (512 samples) of Hann-windowed data. The spectral features used for species classification including peak and center frequency were calculated using methods from Au (1993). Click duration was calculated from the Teager-Kaiser energy detector output (Kaiser, 1990) and inter-click intervals were recorded as the duration between the start times of subsequent detections.

4.3.2 Acoustic species-classification

Acoustic encounters of pilot and false killer whales were manually identified through visual inspection of 1-hour windows of long-term spectral averages (LTSAs) of acoustic data based on the species-specific features described by Baumann-Pickering et al. (2015). To verify the species-classification of acoustic encounters, two experienced analysts (SBP and AES) independently reviewed spectral and temporal features of all click detections within each encounter. Cases of overlapping acoustic encounters of different signal types prevented the use of a precise detection threshold to indicate the presence of each species. The received level, inter-click interval, peak and center frequency and mean spectra of all detections were examined and encounters were considered for further analysis only if the classification decisions of both analysts matched.

4.3.3 Regression analysis

The presence or absence of echolocation activity for each species was coded as 0 or 1 in 5-minute bins. For duty-cycled data, only times with active recording were included. The probability of detecting echolocation was explored at hourly, daily and weekly timescales and defined as the number of click-positive time periods divided by the total number of bins in that time. A chi-square test of independence was used to identify significant relationships between diel period (day versus night) and the presence of echolocation. Nighttime periods were defined as the time between civil dusk and civil dawn. Predictor variables were chosen to explore the explanatory effects of various components of the lunar cycle that are known to affect vertical migration of mesopelagic fish and squid that may influence the acoustic behavior of dolphins. Predictors included categorical factors such as the year, occurrence before, during or after the moon was visible in the night sky (moon presence), as well as continuous predictors such as normalized time between sunset and sunrise [0,1], Julian day [1,365] and lunar day [1,29]. Lunar days 1, 28, and 29 occurred during the new moon and lunar days 14-15 corresponded to nights of the full moon. Both Julian day and lunar day were considered as cyclical predictors. Throughout the lunar cycle, the moon rises about 50 minutes later every night, so the predictor “moon presence” accounted for the relative difference between sunset and moonrise. During the nights when the moon was never present in the night sky, the moon presence was labeled as “before.” Interactions between lunar predictors (lunar day and moon presence) with temporal predictors (month and year) were also considered to examine dynamics in the lunar pattern over time.

To quantify the potential nonlinear functional relationships between echolocation activity and various predictors associated with the lunar cycle, generalized additive mixed models (GAMMs) were constructed using the “mgcv” package (Wood, 2006) in the open source R software version 3.3.0 (R Development Core Team, 2016). GAMMs were chosen as the preferred method to analyze the time series data because they offer an option to

incorporate autocorrelation into the error structure (Zuur et al., 2009). Separate models were built for each recording location to describe species and site-specific behaviors. To investigate how the lunar cycle and associated light dynamics may influence the acoustic behavior of each species, only nighttime observations were considered, resulting in many short time series of observations separated by daylight hours. Autocorrelation was considered between 5-minute observation periods, subsequent nights, months and years. First, a “beyond optimal” model was built that contained all explanatory variables to identify the best random effects structure. The model was then simplified through a stepwise procedure, dropping individual predictors and selecting the model with the minimum Akaike Information Criterion (AIC; Akaike 1974). Non-significant predictors ($p > 0.1$) were then dropped from the resulting model.

4.4 Results

4.4.1 Behavior varies by habitat

At all recording locations echolocation was detected during all hours of the day, but the relationships between diel periods and echolocation activity of pilot and false killer whales varied by habitat. For pilot whales at all locations, echolocation was detected more often at night, with peaks during crepuscular periods (Figure 4.2). A chi-squared test of independence between pilot whale echolocation and diel period (day versus night) was highly significant ($p < 0.001$) at Kaua'i and Hawai'i, but less so at PHR ($p = 0.01$) where there was very little pilot whale echolocation detected overall (Figure 4.2, Table 4.2). For false killer whales, echolocation was mainly detected during the day at Kaua'i and Hawai'i, and during the night at PHR (Figure 4.2). A chi-squared test of independence between echolocation and diel period was highly significant ($p < 0.001$) at Kaua'i and PHR, and not significant at Hawai'i ($p = 0.09$) where there was very little false killer whale echolocation

overall (Figure 4.2, Table 4.2).

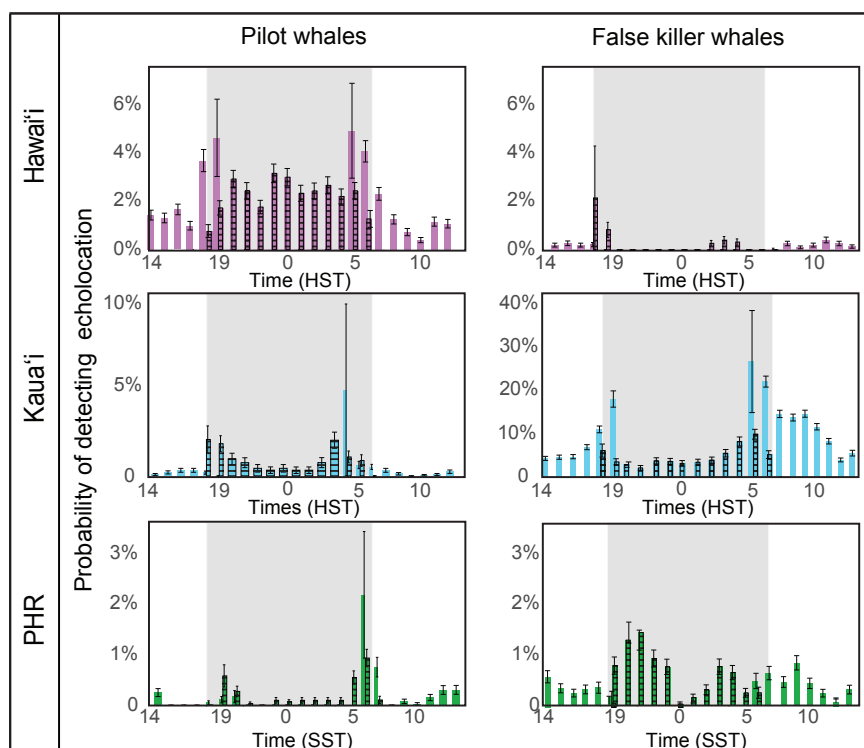


Figure 4.2: Hourly probability of detection for pilot and false killer whale echolocation at Hawai'i (top), Kaua'i (middle) and Pearl and Hermes Reef (bottom). HST: Hawai'i Standard Time. SST: Samoa Standard Time. Dashed bars and gray shading indicate hours of nighttime observations.

Table 4.2: The probability of detecting echolocation during day and nighttime periods. Total number of 5-minute observations in each recording location shown by N. X^2 p-values indicate significance of relationship between echolocation and diel period using one degree of freedom for observations in day and nighttime periods.

Location	N	Probability of Detection					
		Pilot whales			False killer whales		
		Day	Night	X^2	Day	Night	X^2
Hawai'i	55,856	1.7%	2.9%	<0.001	0.2%	0.1%	0.09
Kaua'i	31,871	0.3%	1.2%	<0.001	9.3%	4.5%	<0.001
Pearl and Hermes Reef	91,113	0.1%	0.2%	0.01	0.3%	0.6%	<0.001

4.4.2 Lunar cycle influences echolocation of both species

Lunar patterns were evident in the echolocation activity of pilot whales at Hawai'i and false killer whales at PHR and Kaua'i. At these locations, the lowest levels of nighttime echolocation for pilot and false killer whales were observed during full moon phases and during times that the moon was present in the night sky (Figure 4.3). Pilot whale echolocation near Kaua'i showed no clear association with the moon and due to low levels of nighttime detections, lunar trends were not investigated for false killer whales at Hawaii (n=26 observation periods in 2 days) and pilot whales at PHR (n=80 observation periods across 12 days). Echolocation of both species was reduced at the midpoint between sunrise and sunset at Kaua'i, but conversely there was a maximum of pilot whale echolocation at this time near Hawai'i (Figure 4.3)

The relationship between echolocation and lunar predictors was analyzed further through a GAMM analysis. At all locations, the most significant autocorrelation existed within observations of the same night and a first order autocorrelation structure on nightly blocks was selected for in all models. The best GAMMs for pilot whales at Hawai'i and false killer whales at PHR selected lunar day as a significant predictor, whereby echolocation decreased by about 30% during the full moon phase (Figure 4.4). Lunar predictors were not selected in the GAMMs for either species at Kaua'i. The Kaua'i model for false killer whale echolocation included the normalized time of night (Figure 4.4), and for pilot whales, the intercept only (not shown). Julian day and year were not included as important predictors for any model.

4.4.3 Kaua'i and Hawai'i are important habitats

On timescales of weeks to years, there were consistent detections of pilot whales at Hawai'i and false killer whales near Kaua'i, but both species were infrequently detected near PHR (Figures 4.6, 4.5, 4.7). Pilot whales were detected nearly every week of active recording

near Hawai'i, including 27% (87/324) of all recording days (Figure 4.6), but their acoustic activity was more sporadic near Kaua'i, with only 10% (34/321) of recording days containing detections of echolocation (Figure 4.5)). Conversely, false killer whale echolocation was detected on 2% (7/324) of recording days near the Hawai'i location (Figure 4.6), but on 27% (88/321) of recording days near Kaua'i (Figure 4.5). Weekly encounters of false killer whale echolocation at Kaua'i were split by a gap between December 2009 and June 2010, during which there were detections on five days (Figure 4.5). At PHR, pilot and false killer whale acoustic activity was less consistent compared to the MHI locations, with 2% (17/885) and 4% (38/885) of recording days containing detections for each species, respectively (Figure 4.7). No acoustic recordings were collected from PHR in 2012 and 2013, but after recording resumed in 2014 through 2015, there were no pilot whale detections and detection rates for false killer whales were much lower than previous years (Figure 4.7).

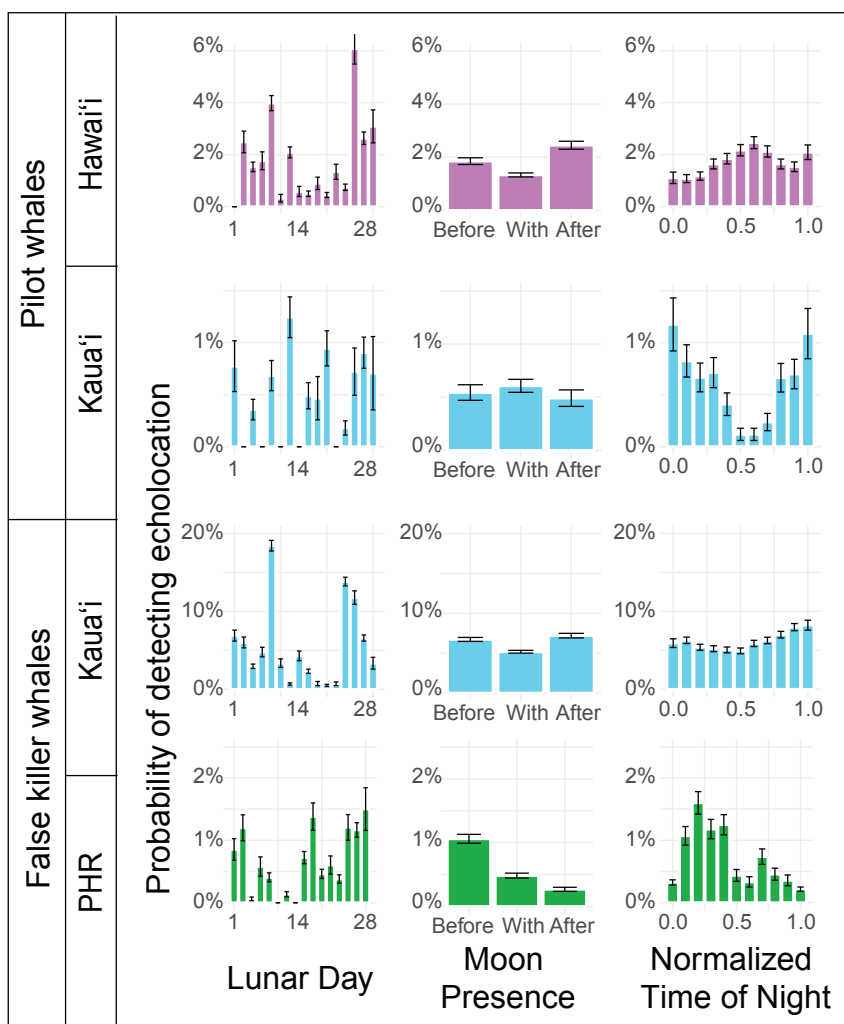


Figure 4.3: Nighttime observations of pilot and false killer whale echolocation. Probability of detecting nighttime echolocation of pilot and false killer whales at Hawai'i (top), Kaua'i (middle) and Pearl and Hermes Reef (bottom) shown with explanatory variables including lunar day, presence of the moon, normalized time of night. Two-day averages are shown for lunar day for ease of visibility. Lunar cycle begins with new moon at Day 1 and full moon at Day 14

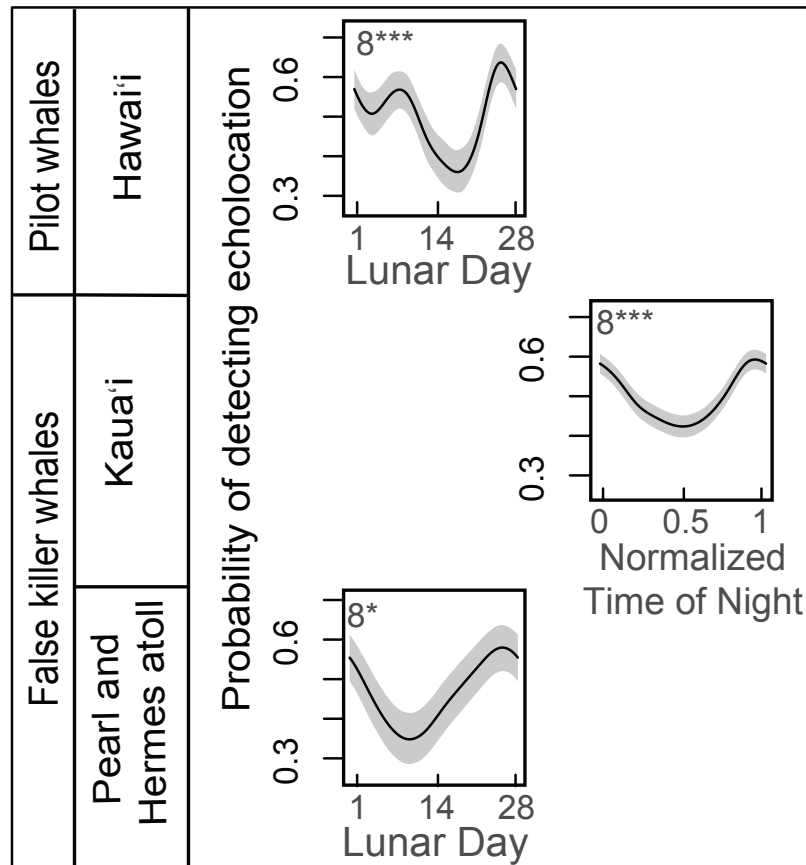


Figure 4.4: GAMM estimates of predictors for pilot and false killer whale echolocation. Estimated smoothing curves of GAMMs for nighttime echolocation of pilot whales at Hawai'i (top), and false killer whales at Kaua'i (middle) and Pearl and Hermes Reef (bottom). Shaded region indicates 95% confidence limits, Degrees of freedom shown in upper left corner of each smooth. * $p < 0.05$, *** $p < 0.001$. Number of 5-minute observations: Hawai'i=35,225, Kaua'i=34,382, Pearl and Hermes Reef=79,565. Lunar cycle begins with new moon at Day 1 and full moon at Day 14. Normalized time of night where sunset=0, sunrise=1

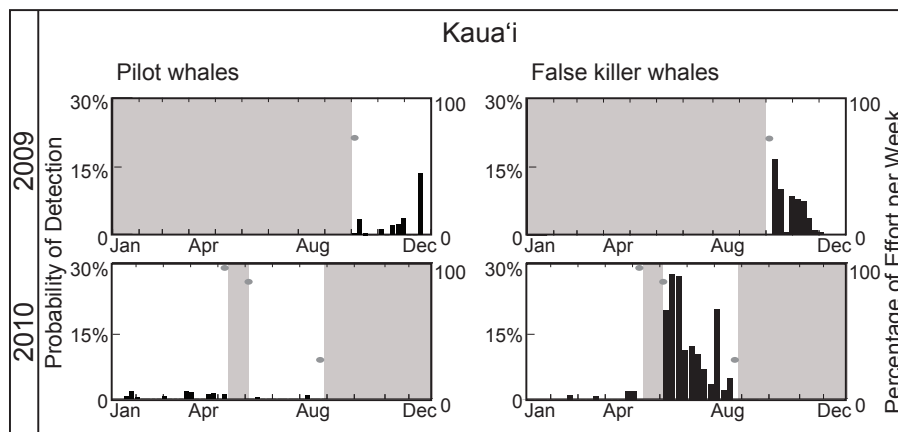


Figure 4.5: Kaua'i weekly observations of pilot and false killer whale echolocation. Black bars show weekly probability of detecting echolocation from pilot whales (left) and false killer whale (right) at Kaua'i from 2009 to 2010. Bars include day and nighttime observations. For weeks with partial effort, the percentage of effort per week (right y-axis) is shown by gray circles. Shaded regions indicate times of no effort.

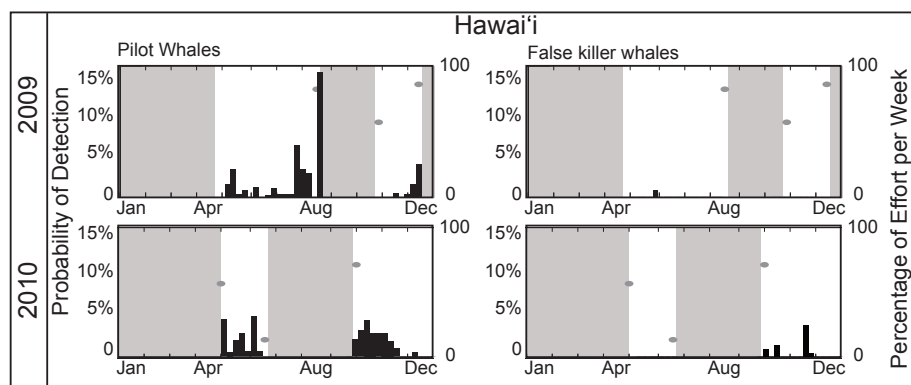


Figure 4.6: Hawai'i weekly observations of pilot and false killer whale echolocation. Black bars show weekly probability of detecting echolocation from pilot whales (left) and false killer whale (right) at Hawai'i from 2009 to 2010. Bars include day and nighttime observations. For weeks with partial effort, the percentage of effort per week (right y-axis) is shown by gray circles. Shaded regions indicate times of no effort.

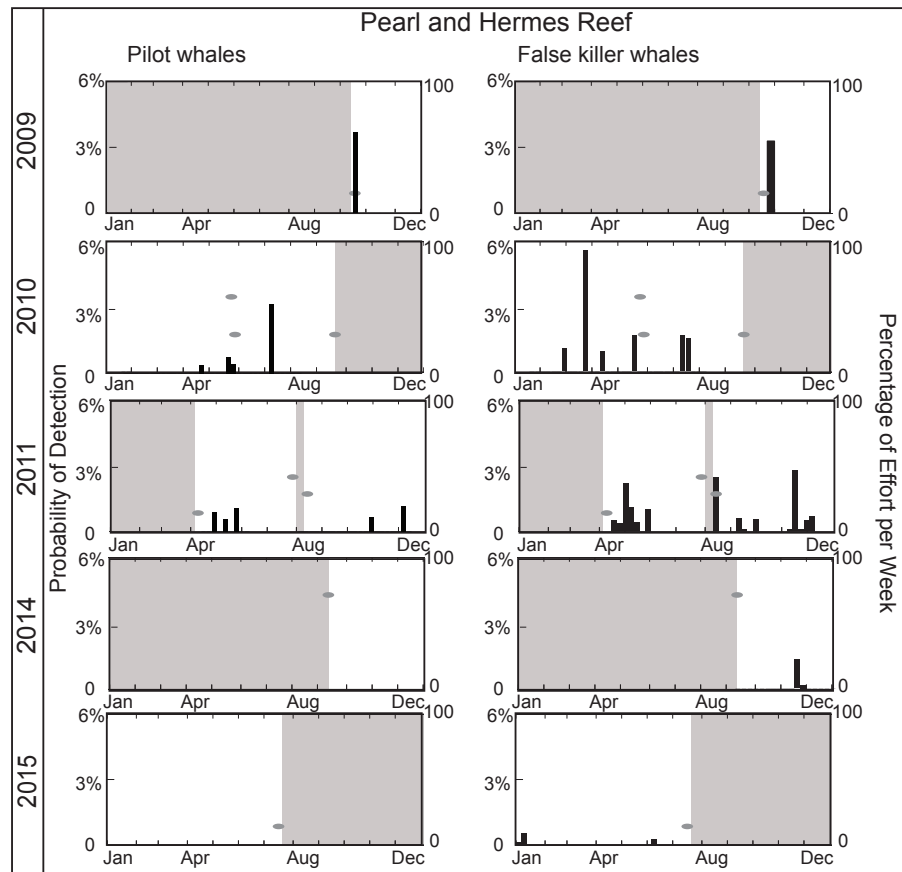


Figure 4.7: Pearl and Hermes Reef weekly observations of pilot and false killer whale echolocation. Black bars show weekly probability of detecting echolocation from pilot whales (left) and false killer whale (right) at Pearl and Hermes Reef from 2009 to 2011 and 2014 to 2015. Bars include day and nighttime observations. For weeks with partial effort, the percentage of effort per week (right y-axis) is shown by gray circles. Shaded regions indicate times of no effort.

4.5 Discussion

The opposing peaks in false killer whale echolocation during the day and at night in the main and northwestern Hawaiian Islands, respectively, suggest that different populations or social clusters utilize distinct foraging strategies, or that different types of prey are pursued at each location. Detections of false killer whales at PHR likely can be attributed to the NWHI population based on the known range for this population, but Kaua'i lies at the edge of a region of overlap for the insular MHI and NWHI populations (Baird et al., 2013) and echolocation activity there could plausibly be attributed to either population. There were few false killer whale detections overall at Hawai'i and the relationship between echolocation and diel period was not significant; but similar to Kaua'i, more detections occurred during the day (Figure 4.2). Daytime observations of echolocation in the MHI support visual observations of daytime foraging on large pelagic fish within the range of the MHI population (Baird, 2009). Many species of pelagic fish are restricted to warmer, surface waters during the day, although regular, deep (>300 m), daytime excursions are common for large tuna and a large fraction of daylight hours may be spent at depth (Musyl et al., 2003, Brill et al., 1999). These daytime dives cease when large fish associate with buoys or fish aggregating devices (FADs; Musyl et al. 2003), which are common in the Hawai'i nearshore and pelagic fisheries. There are many permanent FADs installed along the coast of Kaua'i (<http://www.himb.hawaii.edu/FADS/>), and many temporary devices are undocumented. These FADs likely support abundant large fish in surface waters throughout the day, making them accessible to false killer whales. In contrast, although marine debris may act as unintentional FADs near PHR, fishing is prohibited within the Papahānaumokuākea Marine National Monument and consequently, large fish there likely dive throughout the day and remain at the surface at night to pursue mesopelagic prey, making them most abundant in surface waters at night. Further, the fishing pressure in the MHI can cause changes in fish size distribution (Friedlander and DeMartini, 2002) and there are additional environmental

differences between these two habitats that may be relevant to false killer whale foraging (Lumpkin, 1998, Seki et al., 2001, 2002). To understand differences in prey preferences and foraging behavior of false killer whales between PHR and Kaua'i, future studies will need to incorporate the additional analyses of biogeochemical tracers, movement data or direct observations of predation.

Throughout the Hawaiian Archipelago, variation in the acoustic behavior of pilot and false killer whales suggests that both species are influenced by the lunar cycle. Detections of echolocation were reduced during nights of the full moon and during times that the moon was present in the night sky for pilot whales and false killer whales, especially at Hawai'i and PHR where echolocation predominantly occurred at night (Figure 4.2, Table 4.2). Under the assumption that echolocation is linked to foraging behavior, this indicates that both species strategically alter their foraging behavior with the lunar cycle. For pilot whales and false killer whales at PHR, echolocation was mainly detected at night and during the darkest periods of the lunar cycle, corresponding to times when vertical migrators are more abundant in surface waters (Clarke, 1973, Benoit-Bird et al., 2009b). The deep mesopelagic boundary community is known to be an important source of prey for pilot whales off the west coast of Hawai'i (Abecassis et al., 2015) and false killer whales may be targeting similar prey at PHR given the similarities in observed patterns of echolocation. However, the depth distribution of yellowfin and bigeye tuna has also been shown to track that of their vertically migrating prey throughout the lunar cycle (Schaefer and Fuller, 2002, Wilson et al., 2005), which may in turn impact their availability for false killer whales.

While the lunar cycle had a significant relationship with behavior, reduced echolocation does not necessarily mean reduced foraging. In nearshore habitats of O'ahu, the mesopelagic prey field was found at shallower depths during the new moon, but the relative abundance of spinner dolphins (*Stenella longirostris*) was higher during nights of the full moon (Benoit-Bird et al., 2009b). Spinner dolphins have been shown to cooperatively forage

on mesopelagic prey (Benoit-Bird and Au, 2003), but the fine-scale foraging strategies of pilot and false killer whales are unknown. Distinct foraging strategies between these different species may explain a seemingly opposite response to the reduced vertical migration of mesopelagic prey during the full moon. Alternatively, if all of these dolphin species reduce their echolocation activity when visual predation becomes possible, the results reported here support the hypothesis presented by Benoit-Bird et al. (2009b), in which dolphins switch to visual predation during nights of the full moon. Another possibility is that the reduction in pilot and false killer whale echolocation during the full moon could be attributed to the movement of echolocating animals out of the HARP detection range.

A shift in the horizontal extent of the vertical migrators around the islands may attract dolphins to areas further offshore and subsequently, beyond the detection range of the HARP. On a daily cycle, the Hawaiian mesopelagic boundary community can horizontally migrate 11 km to nearshore waters (Benoit-Bird and Au, 2006) and spinner dolphins have been shown to track the horizontal movement of associated prey on scales of tens of meters to several kilometers (Benoit-Bird et al., 2001). The recording locations in this study were 12-15 km offshore, where the horizontal and vertical migration of mesopelagic prey is not well documented, but tagging studies of pilot whales show deeper dives and offshore movements during periods with a full moon (Owens, pers. comm.). The small detection range (1.5-5 km) of the HARP does not imply exclusion over a larger range. The single acoustic sensor on the HARP prevented the localization of dolphin movement, but increased echolocation during darker times of the night and lunar month suggest that both pilot and false killer whales optimize their foraging behavior at these locations with the presumed vertical response of mesopelagic prey to the lunar cycle.

Neither species was consistently detected at the same site, yet both demonstrated some association with the lunar cycle. If foraging preferences are indeed distinct between pilot and false killer whales, this suggests that the lunar cycle has a significant influence on

the behavior of multiple trophic levels, leading to a pervasive response in the ecosystem. Another possibility is that the contrasting detection rates at each location is a signal of competitive exclusion, whereby one species prevents the other from occupying the same habitat.

Consistent detections of echolocation for pilot whales and false killer whales at Hawai'i and Kaua'i respectively, indicate that these may be important habitats for each species. Kaua'i was not previously included in a description of biologically important areas for MHI false killer whales based on satellite tag records deployed on individuals near Hawai'i and Oah'u; however, data were only available from two of three known social clusters that are present in the MHI (Baird et al., 2012a). The consistent acoustic presence of false killer whales near Kaua'i over periods of multiple months may indicate that the western coast of Kaua'i is a biologically important area for the third MHI social cluster or the insular NWHI population. The Hawai'i location lies just south of a biologically important area for false killer whales along the northwest coast of Hawai'i (Baird et al., 2015), and the low level of acoustic detections reported here suggest that the southwestern (Kona) coast is not a preferred habitat.

The consistent level of pilot whale echolocation activity at the Hawai'i location provides further support for the designation of this area as a biologically important area and foraging hotspot that may warrant additional protections (Mahaffy, 2012, Baird et al., 2015, Abecassis et al., 2015). Pilot whales have been observed throughout the main and northwest Hawaiian Islands (Bradford et al., 2017, Baird et al., 2012b), however the low levels of echolocation in the detection area surrounding the the Kaua'i and PHR recording locations, suggest that these habitats are not preferred habitats.

The uneven acoustic survey effort across all years prevents a clear analysis of seasonality, however during 2014 and 2015, detection rates of both species at PHR were much lower than previous years. Beginning in the boreal winter of 2013-2014, strong

positive temperature anomalies known as “The Blob” were present throughout the northeast Pacific Ocean that persisted through 2015 (Peterson et al., 2016). The anomalous winter winds in 2014 moved the North Pacific Transition Zone further north than usual and reduced primary productivity in the NE Pacific, which may have caused a displacement in large predators away from the subtropics (Whitney, 2015). The low levels of false killer whales at PHR in 2014 and 2015 may be associated with this anomalous event.

4.5.1 Conclusions

Temporal patterns at hourly, diel and lunar timescales are present in the echolocation activity of pilot and false killer whales at three locations in the main and northwestern Hawaiian Islands. Although both species have distinct diving abilities and potentially different prey preferences, their echolocation activity is reduced during nights of the full moon and times when the moon is present in the night sky. The timing of foraging behavior suggests that both species account for the shifting vertical and horizontal distribution of prey throughout the lunar cycle by foraging when prey are more abundant in shallow waters. Significantly different levels of false killer whale echolocation during the night and day occur at Kaua'i and PHR, which suggests differences in prey preferences or foraging strategies between false killer whale populations or social clusters. Daytime foraging may be driven by fishing activity in the main Hawaiian Islands and merits further investigation.

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Chapter 4, in part, is currently being prepared for submission for publication of the material. Simonis, Anne E., Oleson, Erin M., Hildebrand, John A., and Simone Baumann-Pickering. Lunar patterns in acoustic activity of short-finned pilot whales and false-killer whales in Hawaiian waters. The dissertation author was the primary investigator and author of this material.

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