

INFLUENCES OF SPATIAL AND TEMPORAL VARIABILITY OF SOUND SCATTERING
LAYERS ON DEEP DIVING ODONTOCETE BEHAVIOR

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAI'I AT MĀNOA IN PARTIAL FULFILLMENT OF THE
REQUIRMENT FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

ZOOLOGY (MARINE BIOLOGY)

August 2016

By

Adrienne Marie Copeland

Dissertation Committee:
Whitlow Au, Chairperson
Megan Donahue
Jeffrey Drazen
Paul Nachtigall
Jeffrey Polovina

© Copyright 2016 – Adrienne M. Copeland

All rights reserved.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Whitlow Au, for his support, supervision, and assistance throughout my doctorate research. He believed that a student fresh out of undergraduate could thrive in a PhD program and he continued to challenge me and for that I will be eternally grateful. I would like to thank my dissertation committee, Megan Donahue, Jeffrey Drazen, Paul Nachtigall, and Jeffrey Polovina for their priceless scientific input and guidance.

My research involved many moving parts and people so I want to thank everyone who contributed to the research. After Chapter II, III, and IV, I have acknowledged individuals who contributed to the data collection and analysis in that chapter. Specifically I want to thank my Au Laboratory colleagues past and present for their continued support and guidance throughout the data collection and defense process.

Furthermore I want to thank my family and friends for their continued support. Their reassurance and love encouraged me to enter a PhD program and ultimately complete one. This list could go on and on, so for anyone I may have missed, thank you all!

ABSTRACT

Patchiness of prey can influence the behavior of a predator, as predicted by the optimal foraging theory which states that an animal will maximize the energy gain while minimizing energy loss. While this relationship has been studied and is relatively well understood in some terrestrial systems, the same is far from true in marine systems. It is as important to investigate this in the marine realm in order to better understand predator distribution and behavior. Micronekton, organisms from 2 – 20 cm, might be a key component in understanding this as it is potentially an essential link in the food web between primary producers and higher trophic levels, including cephalopods which are primary prey items of deep diving odontocetes (toothed whales). My dissertation assesses the spatial and temporal variability of micronekton in the Northwestern Hawaiian Islands (NWHI), the Main Hawaiian Islands' (MHI) Island of Hawaii, and the Gulf of Mexico (GOM). Additionally it focuses on understanding the relationship between the spatial distribution of micronekton and environmental and geographic factors, and how the spatial and temporal variability of this micronekton relates to deep diving odontocete foraging. I used both an active Simrad EK60 echosounder system to collect water column micronekton backscatter and a passive acoustic system to detect the presence of echolocation clicks from deep diving beaked, sperm, and short-finned pilot whales. My results provide insight into what might be contributing to hotspots of micronekton which formed discrete layers in all locations, a shallow scattering layer (SSL) from the surface to about 200 m and a deep scattering layer (DSL) starting at about 350 m. In both the GOM and the NWHI, the bathymetry and proximity to shore influenced the amount of micronekton backscatter with locations closer to shore and at shallower depths having higher backscatter. We found in all three locations that some species of deep diving odontocetes were searching for prey in these areas with higher micronekton backscatter.

Beaked whales in the NWHI, short-finned pilot whales in the NWHI and MHI, and sperm whales in the GOM where present in areas of higher micronekton backscatter. These hotspots of backscatter may be good predictors of the distribution of some deep-diving toothed whale foragers since the hotspots potentially indicate a food web supporting the prey of the cetaceans.

TABLE OF CONTENTS

Acknowledgements.....	iii
Abstract.....	iv
List of Tables.....	viii
List of Figures.....	ix
Chapter I: Introduction.....	1
References.....	8
Chapter II: Influences of Spatial Variability of Sound Scattering Organisms in the Northwestern Hawaiian Islands (NWHI) on Deep-Diving Odontocete Foragers.....	12
Abstract.....	13
Introduction.....	14
Methods.....	16
Results.....	22
Discussion.....	35
Acknowledgements.....	41
References.....	42
Chapter III: Influences of Temporal Changes in Pelagic Scattering Layers on Short-Finned Pilot Whales Behavior.....	47
Abstract.....	48
Introduction.....	49
Methods.....	51
Results.....	55
Discussion.....	70
Acknowledgements.....	76
References.....	77
Chapter IV: Influences of Spatial Variability in Pelagic Scattering Layers on Sperm Whales Behavior.....	81
Abstract.....	82
Introduction.....	83
Methods.....	84
Results.....	89

Discussion.....	97
Acknowledgements.....	101
References.....	103
Chapter V: Discussion and Conclusions.....	106
References.....	111

LIST OF TABLES

2.1	Generalized additive model (GAM) results of environmental and geographic forcing in the Northwestern Hawaiian Islands (NWHI).....	24
2.2	Summary of Z-score and associated p-values for odontocete presence.....	34
3.1	Summary of the temporal and spatial data collected for this chapter.....	57
4.1	Summary of sperm whale sightings and acoustic detections in Gulf of Mexico (GOM).....	92
4.2	GAM results of the environmental and geographic forcing in GOM.....	96

LIST OF FIGURES

2.1	Sampled area in the Northwestern Hawaiian Islands (NWHI).....	17
2.2	Median nautical area scattering coefficient (NASC) for shallow (SSL) and deep scattering layers (DSL).....	20
2.3	Map of the NASC throughout the NWHI.....	23
2.4	Generalized Additive Model (GAM) of the environmental and geographic forcing.....	24
2.5	“Hotspots” of the daytime and nighttime backscatter for the SSL and DSL.....	26
2.6	Frequency distribution of the bathymetry of the SSL and DSL “hotspots”.....	27
2.7	Map of the depth of the DSL maximum of daytime NASC.....	28
2.8	Vertical distribution of NASC for selected “hotspot” locations.....	29
2.9	Frequency distribution of the bathymetry of locations echolocation was detected.....	30
2.10	Comparison between bathymetry at “hotspot” and echolocation detected locations.....	32
2.11	Map of the SSL and DSL “hotspots” and echolocation detections.....	33
3.1	Map of sample locations in the leeward waters of Island of Hawaii.....	52
3.2	Pictorial representation of the 500 by 500 meters fine scale sampling design.....	53
3.3	Median NASC values for SSL and DSL for 38 and 70 kHz frequencies.....	56
3.4	The 38 kHz backscatter for each location: PW0, PW1, PW2, and PW3.....	58
3.5	Results of the mixed effects model for 38 and 70 kHz frequencies.....	61
3.6	GAM results comparing the vertical distribution of NASC for echolocation and control samples.....	63
3.7	Frequency distribution of NASC values from 900 – 1060 m for control and echolocation samples.....	63
3.8	Mean of the volume backscattering strengths (dB) difference between the 70 and 38 kHz frequency across depth for each location.....	65
3.9	GAM smooth functions of the mean of the volume backscattering strengths (dB) difference of the 70 and 38 kHz frequency across depth for each location.....	66
3.10	Index of aggregation of backscatter from surface to depth for the 38 kHz and 70 kHz frequencies.....	68
3.11	Index of aggregation of backscatter for DSL for the 38 kHz and 70 kHz frequencies....	69
3.12	Ocean surface currents in the sample area over the dates sampled.....	74
4.1	Map of sea surface height & currents of sampled location in Gulf of Mexico (GOM)....	86

4.2	Map of NASC and sightings/acoustic detections of sperm whales in GOM.....	91
4.3	Frequency distribution of NASC values for the daytime and nighttime.....	92
4.4	Frequency distribution of bathymetry for ship and whale samples day and night.....	93
4.5	Frequency distribution of percent slope for ship and whale samples day and night.....	94
4.6	Frequency distribution of NASC for ship and whale samples day and night.....	95
4.7	GAM smoother for NASC relative to the bathymetry and a histogram of the number of locations of sperm whales.....	96
4.8	Generalized Additive Model (GAM) of the environmental and geographic forcing.....	97
4.9	Comparison between the map of locations in Davis et al 2002 and current study.....	102

CHAPTER I

INTRODUCTION

The optimal foraging theory (Stephens & Krebs 1986) (OFT) predicts that mobile organisms will select locations to forage by minimizing the cost and maximizing the gains (Schoener 1971), which suggests that they will search for food in areas with a high density of prey in order to minimize the time investment required. OFT is hard to evaluate for many mobile marine animals. Patchiness or heterogeneity of the environment and organisms is common in both terrestrial and marine ecosystems, and can exist on a wide range of spatial and temporal scales (Steele 1978, Delcourt et al. 1983). It is important to understand the spatial and temporal variability of these patches because they can influence behaviors and distributions of mobile organisms. It can be hard to assess these variables because they can exist over large spatial and temporal scales. Recent technological advances have allowed for better spatiotemporal measurements which were not previously possible (Porter et al. 2005).

Patchiness in prey fields has been seen to affect the distribution of many predators including fish (Thompson et al. 2001) and marine mammals (Benoit-Bird & Au 2003, Benoit-Bird et al. 2004, Friedlaender et al. 2006) suggesting mobile predators do seek out areas with higher densities of their prey to maximize their energy gains. The density of the prey can be difficult to assess but there are links between the density of phytoplankton and top predators in some cases. The density of phytoplankton in the marine environment is patchy and can be influenced by an array of oceanic conditions including the availability of nutrients, with areas closer to land having higher densities of phytoplankton due to higher levels of nutrients in the water (termed the Island Mass Effect (Doty & Oguri 1956)) (Gilmartin & Revelante 1974, Gove et al. 2016). Higher densities of phytoplankton can result in greater densities of predators. Woodworth et al. (2012)

demonstrated an increase in the number of melon-headed whales and Seki et al. (2001) demonstrated an increase in the number of billfish near eddies in Hawaiian waters due to the upwelling of nutrients which increased the availability and higher concentrations of their prey. For some species, the patchiness of prey can be assessed and has been seen to influence the distribution of marine mammals. Pinnipeds, specifically the Antarctic fur seals (*Arctocephalus gazelle*), change the temporal variability of their dives in relationship to the spatial pattern of their prey (Boyd 1996). Humpback whales, *Megaptera novaeangliae*, and minke whales, *Balaenoptera acutorostrata*, in the Western Antarctic Peninsula, distribute themselves in areas with higher zooplankton backscatter (Friedlaender et al. 2006). Spinner dolphins, *Stenella longirostris*, in Hawaiian waters (Benoit-Bird & Au 2003) and dusky dolphins, *Lagenorhynchus obscurus*, off New Zealand (Benoit-Bird et al. 2004) also appear to distribute themselves in relation to higher densities of their micronekton prey.

Limited studies have examined the relationship between top predators and marine food webs. Before 1999, only a handful of oceanic studies looked at this relationship (Baum & Worm 2009) leading scientists to believe that top down control was very rare. Studies of odontocete, toothed whales, relationships to the food web are even more uncommon. Estes et al. (1998) found a link between killer whales and coastal primary producers in western Alaska. Killer whales increased their predation of sea otters, leading to a decline in sea otter populations, which led to an increase in the sea otter's primary prey species of sea urchins, ultimately resulting in a decline in total kelp density (Estes et al. 1998). It is important to analyze the food web dynamics because marine mammals can consume prey from a variety of trophic levels (Pauly et al. 1998). Marine mammals consume large quantities of fish, squid, and zooplankton which might have consequences on the ecosystem (Kenney et al. 1997). Therefore, a better understanding of the

relationship between odontocetes and their prey might lead to a better understanding of ecosystem dynamics.

The understanding of odontocete behavior has vastly increased with tagging research, specifically, Deep Towed Acoustics/Geophysics System (DTAGs) (Johnson & Tyack 2003). Based on data from tagged whales we know that some species of odontocetes, including Blainville's beaked whales, *Mesoplodon densirostris*, and Cuvier's beaked whales, *Ziphius cavirostris*, (Johnson et al. 2004, Madsen et al. 2005, Tyack et al. 2006), sperm whales, *Physeter macrocephalus* (Miller et al. 2004), and short-finned pilot whales, *Globicephala macrorhynchus* (Aguilar de Soto 2006, Aguilar Soto et al. 2008) dive into and below the Deep Scattering Layer (DSL) to feed. These species have been recorded to dive down below the start of the DSL at about 300 – 400 meters. Some species, including beaked whales, do not begin echolocating until they have descended beyond 250 – 475 m and then are detected almost continuously at depth (Johnson et al. 2004) indicating that they are not searching for prey in the surface waters. Diving this deep is costly in transport time (Tyack et al. 2006). While deep diving species can utilize gliding to conserve energy (Tyack et al. 2006), some species including short-finned pilot whales can perform sprints at depth with speed ranging from 4 to 9 m s⁻¹ (Aguilar Soto et al. 2008) increasing energy expenditure. The patchiness of prey might influence the location and variability of these costly deep dives.

From stomach contents of stranded marine mammals, many deep diving odontocetes preferentially feed on certain species of larger cephalopods and occasionally fish that are found at these deep depths (Clarke 1980, Seagars & Henderson 1985, Sinclair 1992, Clarke & Goodall 1994, Clarke 1996a, Gannon et al. 1997, Clarke & Young 1998, Pauly et al. 1998, Santos et al. 2001, Ohizumi & Kishiro 2003). While the distribution of these highly mobile larger

cephalopods can be hard to study directly, the less mobile micronekton these cephalopods feed on (Clarke 1996b, Phillips et al. 2001, Ohizumi 2002, Markaida & Sosa-Nishizaki 2003, Parry 2006) might be used as a proxy to understand how the patchiness of prey could affect the distribution of cephalopods and subsequently odontocetes. Micronekton are organisms ranging in size from 2 cm – 20cm, including small fish, crustaceans, and cephalopods (Brodeur & Yamamura 2005). Patchiness in distribution of micronekton is an important area to study because they appear to be an essential link in the food web linking primary producers with higher trophic levels (Roger & Grandperrin 1976, Choy et al. 2013, Young et al. 2015, Choy et al. 2016).

During the daytime, a majority of the micronektonic biomass is located in the DSL at depths greater than 400 meters (Maynard et al. 1975) making it difficult to study their distribution. The scientific echosounder is one important tool used to quantitatively assess the spatial and temporal variability of micronekton in the ocean and the relationship to marine mammals (Benoit-Bird & Au 2003, Benoit-Bird et al. 2004, Benoit-Bird & Au 2009). Echosounders emit sounds at a specific frequency into the water column and receive echoes back (often referred to as backscatter) from objects and organisms. Varying the frequencies of the echosounder (e.g. 38 kHz and 70 kHz) can provide different information about the environment. The higher frequency has better resolution and is able to sample smaller organisms, but attenuates more quickly than lower frequencies so it cannot sample as deep. The lower frequency is able to sample deeper due to less attenuation of the signal, but is only able to sample larger organisms. Both frequencies are able to sample at least a portion of the DSL within the mesopelagic zone.

Acoustics can also be used to study the distribution of the deep diving odontocetes. The whales echolocate at depth and the presence of echolocation clicks indicates that these deep divers are

surveying the environment and searching for prey (Norris et al. 1961, Au 1993) allowing for the use of underwater hydrophones to detect the presence of and indicate foraging behavior of these deep divers. Additionally, an array of hydrophones can be used to determine the bearing and distance of the clicking whale in reference to the array by accounting for the different arrival times of the clicks at each hydrophone. Different species of deep divers can be identified by examining the characteristics of their clicks. Sperm whales have lower frequency clicks with peak intensity at frequencies below 10 kHz (Møhl et al. 2003) that humans can hear with recording equipment and visually identify on spectrographic instruments. Short-finned pilot whales click at higher frequencies similar to false killer whales, requiring visual confirmation of species or confirming the presence of two distinct spectral peaks at 12 and 18 kHz which are only present in short-finned pilot whales (Baumann-Pickering et al. 2015). Beaked whales have unique frequency modulated clicks with peaks in the 30 – 40 kHz range (Zimmer et al. 2005, Baumann-Pickering et al. 2013)

The greatest mystery involving the foraging of deep diving odontocetes is how these animals “know” where “hotspots” of micronekton exist since some species do not start echolocating until they reach a certain depth regime. Diving so deep does not appear to follow the OFT predications because it requires large amounts of time and energy and it seems that the deep divers cannot afford to have many if any unsuccessful dives. So is it high density of their prey at depth that is driving this behavior? Using active and passive acoustics we are able to assess the temporal and spatial variability of the micronekton and compare it to the presence of foraging deep-diving odontocetes. There is currently a lack of comprehensive knowledge on the relationship between micronekton distribution and odontocete presence. I used data from the Gulf of Mexico (GOM), the Northwestern Hawaiian Islands (NWHI), and the Island of Hawaii

in the Main Hawaiian Islands (MHI) to analyze the micronekton distribution along the shelf and pelagic waters and compare it to the sightings and echolocation detections of deep-diving odontocetes. This dissertation will further the understanding of the relationship between deep diving odontocete foraging and lower trophic levels. We hypothesize that the prey of the cetaceans will be attracted to areas with higher densities of micronekton. Chapters II and IV of this dissertation focus on the spatial variability of the micronekton layers in the NWHI and the GOM where there is a substantial population of deep diving odontocetes but very limited studies on the patchiness of the micronekton and how that relates to whale distribution. There were three gaps in our understanding that we wanted to address. First we wanted to determine if there was patchiness in micronekton, as examined using acoustic backscatter, and what oceanographic and geographic features explained this variability. We hypothesize based on very limited studies in other parts of the world that the micronekton distribution would be patchy with increased backscatter in areas closer to shore, at shallow depths, higher chlorophyll-a, and higher sea surface temperature (SST) (Hazen & Johnston 2010, Escobar-Flores et al. 2013). The second objective was to determine if there was patchiness in the presence of odontocete foragers. We hypothesize that they will be found at very specific depth habitats based on the differences in dive behavior (Tyack et al. 2006, Watwood et al. 2006, Aguilar Soto et al. 2008) and past studies of sighting locations in the MHI (Baird et al. 2013) and GOM (Davis et al. 2002). Our final objective is to determine the relationship between the micronekton biomass and foraging whales. We hypothesize that the whales will be searching for food in areas with higher micronekton backscatter (Benoit-Bird & Au 2003, Benoit-Bird et al. 2004, Hazen & Johnston 2010, Hazen et al. 2011, Abecassis et al. 2015) because more micronekton will attract more prey for the whales feed on.

Chapter III of this dissertation will assess the temporal variability of the micronekton backscatter and how it relates to deep diving odontocete foraging in the MHI. We were interested in addressing if there was temporal variation in the horizontal and vertical structure of micronekton, if there was temporal variability of the scattering layer composition, and how these parameters related to whale foraging. We hypothesized that the micronekton distribution would vary temporally with higher values and larger organisms present during whale foraging.

It is critically important to understand the environmental and geographic parameters that might affect the distribution of micronekton in pelagic waters because they appear to be an important link in the food web connecting lower and higher trophic levels. A better understanding of what might affect the distribution of the prey of marine mammals may help to better predict the locations of marine mammals, and therefore help conservation organizations which must know the locations of the animals.

References

- Abecassis M, Polovina J, Baird RW, Copeland A, Drazen JC, Domokos R, Oleson E, Jia Y, Schorr GS, Webster DL, Andrews RD (2015) Characterizing a foraging hotspot for short-finned pilot whales and Blainville's beaked whales off the west side of the Island of Hawai'i with tagging and oceanographic data. *PLoS One* 10:1-22
- Aguilar de Soto N (2006) Acoustic and diving behaviour of the short finned pilot whale (*Globicephala macrorhynchus*) and Blainville's beaked whale (*Mesoplodon densirostris*) in the Canary Islands. Implications on the effects of man-made noise and boat collisions. Doctoral thesis, La Laguna University, La Laguna,
- Aguilar Soto N, Johnson MP, Madsen PT, Diaz F, Dominguez I, Brito A, Tyack P (2008) Cheetahs of the Deep Sea: Deep Foraging Sprints in Short-Finned Pilot Whales off Tenerife (Canary Islands). *Journal of Animal Ecology* 77:936-947
- Au WW (1993) *The Sonar of Dolphins*. Springer
- Baird R, Webster DL, Aschettino JM, Schorr GS, McSweeney DJ (2013) Odontocete Cetaceans Around the Main Hawaiian Islands: Habitat Use and Relative Abundance from Small-Boat Sighting Surveys. *Aquatic Mammals* 39:253-269
- Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology* 78:699-714
- Baumann-Pickering S, McDonald MA, Simonis AE, Solsona Berga A, Merkens KP, Oleson EM, Roch MA, Wiggins SM, Rankin S, Yack TM, Hildebrand JA (2013) Species-specific beaked whale echolocation signals. *J Acoust Soc Am* 134:2293-2301
- Baumann-Pickering S, Simonis AE, Oleson EM, Baird RW, Roch MA, Wiggins SM (2015) False killer whale and short-finned pilot whale acoustic identification. *Endangered Species Research* 28:97-108
- Benoit-Bird KJ, Au WWL (2003) Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology* 53:364-373
- Benoit-Bird KJ, Au WWL (2009) Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *J Acoust Soc Am* 125:125-137
- Benoit-Bird KJ, Wursig B, Mcfadden CJ (2004) Dusky Dolphin (*Lagenorhynchus Obscurus*) Foraging in Two Different Habitats: Active Acoustic Detection of dolphins and their Prey. *Marine Mammal Science* 20:215-231
- Boyd I (1996) Temporal scales of foraging in a marine predator. *Ecology*:426-434
- Brodeur R, Yamamura O (2005) Micronekton of the North Pacific. *PICES Scientific Report* 30:1-115
- Choy CA, Portner E, Iwane M, Drazen JC (2013) Diets of five important predatory mesopelagic fishes of the central North Pacific. *Marine Ecology Progress Series* 492:169-184
- Choy CA, Wabnitz CCC, Weijerman M, Woodworth-Jefcoats PA, Polovina JJ (2016) Finding the way to the top: how the composition of oceanic mid-trophic micronekton groups determines apex predator biomass in the central North Pacific. *Marine Ecology Progress Series* 549:9-25
- Clarke M, Goodall N (1994) Cephalopods in the diets of three odontocete cetacean species stranded at Tierra del Fuego, *Globicephala melaena* (Traill, 1809), *Hyperoodon planifrons* Flower, 1882 and *Cephalorhynchus commersonii* (Lacepede, 1804). *Antarctic Science-Institutional Subscription* 6:149-154

- Clarke M, Young R (1998) Description and analysis of cephalopod beaks from stomachs of six species of odontocete cetaceans stranded on Hawaiian shores. *Journal of the Marine Biological Association of the United Kingdom* 78:623-641
- Clarke MR (1980) Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Reports* 37:1-324
- Clarke MR (1996a) Cephalopods as Prey. III. Cetaceans. *Philosophical Transactions: Biological Sciences* 351:1053-1065
- Clarke MR (1996b) The role of cephalopods in the world's oceans: general conclusions and the future. *Philosophical Transactions of the Royal Society-Ser B-Biological Sciences* 351:1105
- Davis RW, Ortega-Ortiz JG, Ribic CA, Evans WE, Biggs DC, Ressler PH, Cady RB, Leben RR, Mullin KD, Würsig B (2002) Cetacean habitat in the northern oceanic Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers* 49:121-142
- Delcourt HR, Delcourt PA, III TW (1983) Dynamic plant ecology: The spectrum of vegetational change in space and time. *Quaternary Science Reviews* 1:153-175
- Doty MS, Oguri M (1956) The Island Mass Effect. *J Cons* 22:33-37
- Escobar-Flores P, O'Driscoll RL, Montgomery JC (2013) Acoustic characterization of pelagic fish distribution across the South Pacific Ocean. *Marine Ecology Progress Series* 490:169-183
- Estes JA, Tinker MT, Williams TM, Doak DF (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *science* 282:473-476
- Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Marine Ecology Progress Series* 317:297-310
- Gannon DP, Ready AJ, Craddock JE, Mead JG (1997) Stomach contents of long-finned pilot whales (*Globicephala melas*) stranded on the US mid-Atlantic coast. *Marine Mammal Science* 13:405-418
- Gilmartin M, Revelante N (1974) The 'island mass' effect on the phytoplankton and primary production of the Hawaiian Islands. *Journal of Experimental Marine Biology and Ecology* 16:181-204
- Gove JM, McManus MA, Neuheimer AB, Polovina JJ, Drazen JC, Smith CR, Merrifield MA, Friedlander AM, Ehses JS, Young CW, Dillon AK, Williams GJ (2016) Near-island biological hotspots in barren ocean basins. *Nature Communications* 7:10581
- Hazen EL, Johnston DW (2010) Meridional patterns in the deep scattering layers and top predator distribution in the central equatorial Pacific. *Fisheries Oceanography* 19:427-433
- Hazen EL, Nowacek DP, St Laurent L, Halpin PN, Moretti DJ (2011) The relationship among oceanography, prey fields, and beaked whale foraging habitat in the Tongue of the Ocean. *PLoS One* 6:1-10
- Johnson M, Madsen PT, Zimmer WM, De Soto NA, Tyack PL (2004) Beaked whales echolocate on prey. *Proceedings of the Royal Society of London B: Biological Sciences* 271:S383-S386
- Johnson MP, Tyack PL (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *Oceanic Engineering, IEEE Journal of* 28:3-12
- Kenney RD, Scott GP, Thompson TJ, Winn HE (1997) Estimates of prey consumption and trophic impacts of cetaceans in the USA northeast continental shelf ecosystem. *Journal of Northwest Atlantic Fishery Science* 22:155-171

- Madsen P, Johnson M, de Soto NA, Zimmer W, Tyack P (2005) Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *Journal of Experimental Biology* 208:181-194
- Markaida U, Sosa-Nishizaki O (2003) Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Journal of the Marine Biological Association of the UK* 83:507-522
- Maynard SD, Riggs FV, Walters JF (1975) Mesopelagic micronekton in Hawaiian waters: faunal composition, standing stock, and diel vertical migration. *Fishery Bulletin* 73:726-736
- Miller PJ, Johnson MP, Tyack PL (2004) Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. *Proceedings of the Royal Society of London B: Biological Sciences* 271:2239-2247
- Møhl B, Wahlberg M, Madsen PT, Heerfordt A, Lund A (2003) The monopulsed nature of sperm whale clicks. *The Journal of the Acoustical Society of America* 114:1143-1154
- Norris KS, Prescott JH, Asa-Dorian PV, Perkins P (1961) An experimental demonstration of echo-location behavior in the porpoise, *Tursiops truncatus* (Montagu). *Biological Bulletin* 120:163-176
- Ohizumi H (2002) Dietary studies of toothed whales: A review and new topics. *Fisheries science* 68:264-267
- Ohizumi H, Kishiro T (2003) Stomach contents of a Cuvier's beaked whale (*Ziphius cavirostris*) stranded on the central Pacific coast of Japan. *Aquatic Mammals* 29:99-103
- Parry M (2006) Feeding behavior of two ommastrephid squids *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis* off Hawaii. *Marine Ecology Progress Series* 318:229-235
- Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* 55:467-481
- Phillips KL, Jackson GD, Nichols PD (2001) Predation on myctophids by the squid *Moroteuthis ingens* around Macquarie and Heard Islands: stomach contents and fatty acid analyses. *Marine Ecology Progress Series* 215:179-189
- Porter J, Arzberger P, Braun H-W, Bryant P, Gage S, Hansen T, Hanson P, Lin C-C, Lin F-P, Kratz T (2005) Wireless sensor networks for ecology. *BioScience* 55:561-572
- Roger C, Grandperrin R (1976) Pelagic food webs in the tropical Pacific. *Limnology and Oceanography* 21:731-735
- Santos MB, Pierce GJ, Herman J, López A, Guerra A, Mente E, Clarke M (2001) Feeding ecology of Cuvier's beaked whale (*Ziphius cavirostris*): a review with new information on the diet of this species. *Journal of the Marine Biological Association of the UK* 81:687-694
- Schoener TW (1971) Theory of Feeding Strategies. *Annual Review of Ecology and Systematics* 2:369-404
- Seagars DJ, Henderson JR (1985) Cephalopod remains from the stomach of a shortfinned pilot whale collected near Santa Catalina Island, California. *Journal of Mammalogy* 66:777-779
- Seki MP, Polovina JJ, Brainard RE, Bidigare RR, Leonard CL, Foley DG (2001) Biological enhancement at cyclonic eddies tracked with GOES Thermal Imagery in Hawaiian waters. *Geophysical Research Letters* 28:1583-1586
- Sinclair EH (1992) Stomach Contents of Four Short-Finned Pilot Whales (*Globicephala macrorhynchus*) from the Southern California Bight. *Marine Mammal Science* 8:76-81
- Steele JH (1978) Spatial pattern in plankton communities. Plenum Press, New York

- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press
- Thompson AR, Petty JT, Grossman GD (2001) Multi-scale effects of resource patchiness on foraging behaviour and habitat use by longnose dace, *Rhinichthys cataractae*. *Freshwater Biology* 46:145-160
- Tyack PL, Johnson M, Soto NA, Sturlese A, Madsen PT (2006) Extreme diving of beaked whales. *Journal of Experimental Biology* 209:4238-4253
- Watwood SL, Patrick JOM, Johnson M, Madsen PT, Tyack PL (2006) Deep-Diving Foraging Behaviour of Sperm Whales (*Physeter macrocephalus*). *Journal of Animal Ecology* 75:814-825
- Woodworth PA, Schorr GS, Baird RW, Webster DL, McSweeney DJ, Hanson MB, Andrews RD, Polovina JJ (2012) Eddies as offshore foraging grounds for melon-headed whales (*Peponocephala electra*). *Marine Mammal Science* 28:638-647
- Young JW, Hunt BPV, Cook TR, Llopiz JK, Hazen EL, Pethybridge HR, Ceccarelli D, Lorrain A, Olson RJ, Allain V, Menkes C, Patterson T, Nicol S, Lehodey P, Kloser RJ, Arrizabalaga H, Anela Choy C (2015) The trophodynamics of marine top predators: Current knowledge, recent advances and challenges. *Deep Sea Research Part II: Topical Studies in Oceanography* 113:170-187
- Zimmer WM, Johnson MP, Madsen PT, Tyack PL (2005) Echolocation clicks of free-ranging Cuvier's beaked whales (*Ziphius cavirostris*). *The Journal of the Acoustical Society of America* 117:3919-3927

CHAPTER II
INFLUENCES OF SPATIAL VARIABILITY OF SOUND SCATTERING ORGANISMS
IN THE NORTHWESTERN HAWAIIAN ISLANDS (NWHI) ON DEEP-DIVING
ODONTOCETE FORAGERS

Adrienne M Copeland¹, Whitlow W. L. Au¹, Amanda Bradford², Erin Oleson², and Jeffrey Polovina²

¹Hawaii Institute of Marine Biology, University of Hawaii, PO BOX 1348 Kaneohe, Hawaii 96744

²Pacific Islands Fisheries Science Center, NOAA, 1845 Wasp Blvd., Bldg. 176 Honolulu, HI 96818

Abstract

Most studies in the Northwestern Hawaiian Islands (NWHI) have focused on shallower communities in and near reefs or deep water demersal communities and did not investigate the mesopelagic organisms living in deeper waters that some apex predators rely on for food, e.g. some odontocetes forage at depths greater than 400 m. To examine the relationship between deep-diving odontocete predators and prey, a Simrad EK60 echosounder operating at 70 kHz collected micronekton backscatter throughout the NWHI from May 7 to June 4, 2013. Visual and passive acoustic surveys for marine mammal presence were conducted concurrently with the echosounder. Two broad scattering layers were found, a deep layer from 370 to 670 m and a shallow layer from 0 to 270 m. The highest densities of both deep and shallow scattering organisms were associated with deep slopes of banks and atolls. Beaked and short-finned pilot whale sightings occurred in locations of high scattering density associated with slopes of atolls and banks. It is hypothesized that the high scattering organisms associated with these features are similar to the mesopelagic boundary community found in the Main Hawaiian Islands and support a food web for the prey of the cetaceans.

Keywords: Odontocete, Echosounder, Deep Scattering Layer, Backscatter, Foraging, Mesopelagic Boundary Layer, Active Acoustics

Introduction

The Northwestern Hawaiian Islands (NWHI) are a relatively uninhabited assemblage of islands, islets, and atolls spanning over 2000 km in the Hawaiian Archipelago (Figure 1). Research in the area has focused on shallow water and reef communities (Polovina et al. 1995, Friedlander & DeMartini 2002, Williams et al. 2015) finding higher biomass and numerical densities of endemics (DeMartini & Friedlander 2006) and higher mean biomass of trophic levels (apex predators, other secondary consumers, and herbivores) than the heavily populated and fished Main Hawaiian Islands (MHI) (Friedlander & DeMartini 2002, Williams et al. 2015). There has been deep water research in the NWHI but it has focused on benthic and demersal communities (Gooding 1984, Borets 1986, Kelley et al. 2006, Yeh & Drazen 2009, Schlacher et al. 2014). As a result, studies on the distribution of deep water pelagic organisms are lacking.

The NWHI appears to have a land associated sound scattering layer (Lammers et al. 2006) similar to the mesopelagic boundary community (MBC) found in the MHI (Reid et al. 1991, Benoit-Bird et al. 2001, Au & Benoit-Bird 2008). In the MHI, the MBC has a distinct community of micronekton, mostly squid, shrimp and crustaceans 2 - 20cm in size (Reid et al. 1991), compared to the community found offshore. Both the MBC and the oceanic deep scattering layer (DSL) may be an important link in the food web connecting top predators with zooplankton (Roger & Grandperrin 1976, Choy et al. 2013, Young et al. 2015, Choy et al. 2016). Subsequently the layers may be influencing the distribution of a variety of predators, as has been observed for tuna (Dagorn et al. 2000), short-finned pilot whales (*Globicephala macrorhynchus*) (Hazen & Johnston 2010), beaked whales (Hazen et al. 2011), spinner dolphins (*Stenella longirostris*) (Benoit-Bird & Au 2003), dusky dolphins (*Lagenorhynchus obscurus*) (Benoit-Bird et al. 2004), and humpback (*Megaptera novaeangliae*) and minke (*Balaenoptera acutorstrata*)

whales (Friedlaender et al. 2006). More acoustic detections of Blainville's (*Mesoplodon densirostris*) and Cuvier's (*Ziphius cavirostris*) beaked whales in the Tongue of the Ocean, Bahamas (Hazen et al. 2011) and more sightings of short-finned pilot whales in the central equatorial Pacific (Hazen & Johnston 2010) were recorded in areas with higher backscatter of potential forage in the DSL.

Short-finned pilot whales and beaked whales are found in the NWHI leading to the hypothesis that the spatial variability of land associated and offshore scattering layers in the NWHI could influence their distribution as well as other odontocete species that utilize similar depths during foraging. In Hawaii, the mesopelagic zone is defined as the depths from 400 to 1200 meters, with the upper and lower zones being 400 to 700 meters and 700 to 1200 meters, respectively (Young 1983, Reid et al. 1991). The depths of these layers corresponds to the foraging depth of some odontocetes found in both the MHI and NWHI.

Beaked, short-finned pilot, and sperm (*Physeter macrocephalus*) whales along with Risso's dolphins have been documented to dive to depths greater than the 400 m shallow boundary of the mesopelagic layer to forage. In Hawaii, beaked whales tagged with time-depth recorders were found to dive to depths greater than 800 meters for 48 to 68 minutes, with maximum dive depths greater than 1400 meters (Baird et al. 2006). Short-finned pilot whales made regular deep dives up to 1296 meters with a mean of 359 meters (Andrews et al. 2011). The deepest dives of short-finned pilot whales in the MHI were recorded during the day with depths averaging between 600 - 800 m (Baird et al. 2003). These deep diving species feed predominately on squid (Clarke 1996a, Clarke & Young 1998) and in rare instances demersal fishes that are found at these deeper depths. Sperm whales preferentially forage on squid that have a distribution ranging from mesopelagic (200 to 1000 m) to bathypelagic (1000 to 4000 m) (Clarke 1966, 1980, Barros 2003,

Spitz et al. 2011). The colossal squid (*Mesonychoteuthis hamiltoni*), a documented prey item of sperm whales (Klumov & Yukhov 1975), forages on myctophids (Kozlov 1995) which make up from 13% (Maynard et al. 1975) to 80% (Benoit-Bird 2009, Drazen et al. 2011) of the total biomass of the micronekton in the mesopelagic layers of Hawaii. The dive depths of these odontocetes correspond to their prey range as well as the organisms their prey eat (Kozlov 1995, Clarke 1996a, Clarke 1996b, Phillips et al. 2001, Ohizumi 2002, Markaida & Sosa-Nishizaki 2003, Parry 2006). While it is known that these species dive to deep depths to forage, little is known about the distribution of the deep diving odontocetes in the NWHI and how their prey organisms might influence their distribution.

The purpose of this paper is to (1) use acoustic backscatter as a measure of relative biological biomass of scattering layer organisms, (2) determine if this backscatter is variable throughout the NWHI, (3) evaluate how environmental and geographical variables affect this variability, (4) determine the distribution patterns of the deep-diving odontocetes (sperm, short-finned pilot, and beaked whales) in the NWHI, and (5) examine the relationship between the shallow and deep scattering layer biomass and the distributions of foraging deep diving odontocetes.

Methods

Active Acoustic Data

Water column backscatter was collected continuously onboard the NOAA R/V Oscar Elton Sette in the NWHI from May 8 to June 4, 2013 (Figure 1), using a hull-mounted Simrad EK60 split beam echosounder. While backscatter was evaluated across four frequencies, 38, 70, 120, and 200 kHz, only the 70 kHz backscatter data will be discussed in this paper because the 120 and 200 kHz were unable to sample the DSL of interest and the 38 kHz was subjected to too much environmental noise for the spatial coverage desired. Due to the acoustic absorption of the 70

kHz signal, the data was only recorded down to 670 meters. To avoid skewed estimates only samples with a bottom depth greater than or equal to 670 meters were included in this study. The ocean bottom depth can be identified past the 670 meter cutoff because the backscatter from the bottom was much stronger than the background noise.

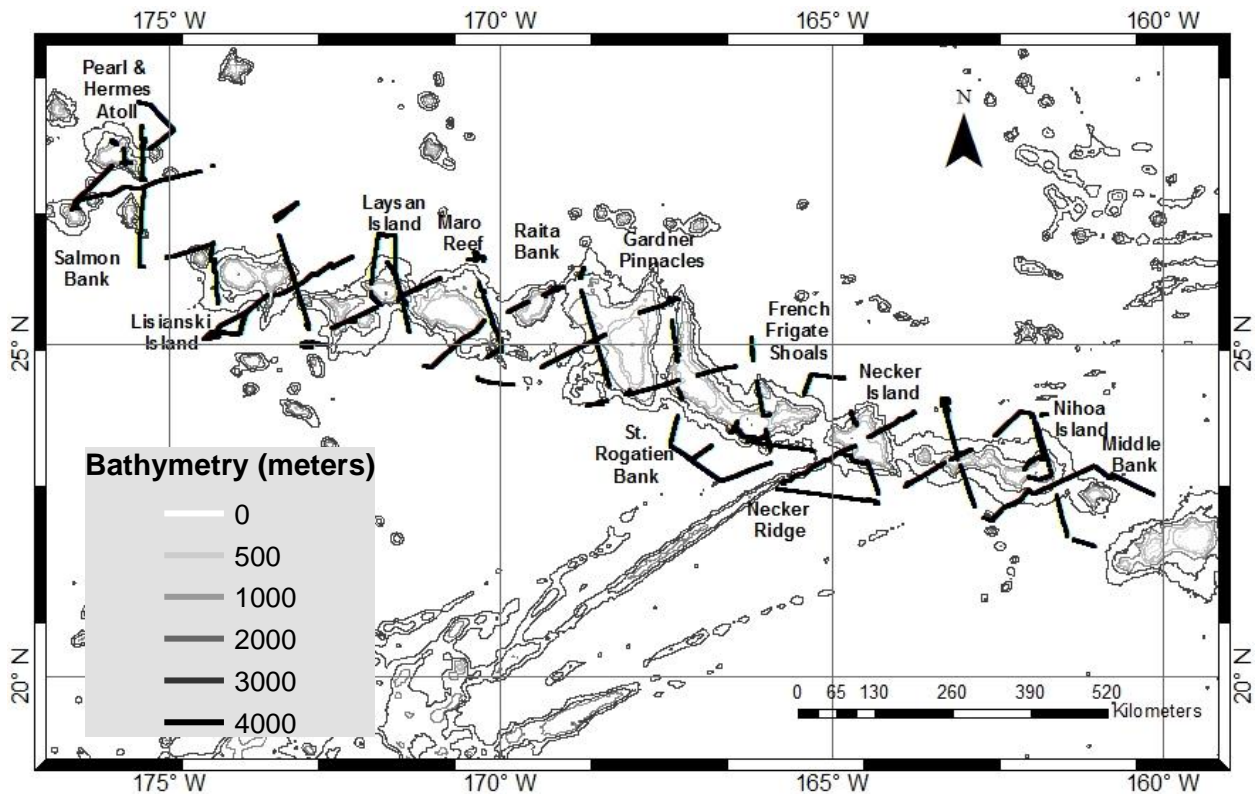


Figure 1: The sampled daytime and nighttime tracklines throughout the Northwestern Hawaiian Islands (NWHI).

The 70 kHz transducer was calibrated prior to data collection using a 38.1 mm tungsten carbide reference sphere and standard methods described in Foote et al. (1987), Demer et al. (2015). The pulse length of the 70 kHz signal was set to 1024 μ s with power at 750 W. The data were processed using Echoview 5.4 (Echoview Software Pty. Ltd. 2013) and standard cleaning techniques were employed to remove background noise and bubble dropout (De Robertis & Higginbottom 2007). A -80 dB threshold was used for the mean volume backscattering strength (Sv), a proxy for relative density (Simmonds & MacLennan 2005) to avoid sampling plankton

and other small organisms not of interest. The volume backscatter was binned into cells with 200 meter horizontal resolution and 10 meter vertical resolution. These cells were integrated to obtain the nautical area scattering coefficient (NASC; $\text{m}^2 \text{nmi}^{-2}$) and this was used as a relative measure of the acoustic biomass of scattering organisms at 10 meter vertical depth intervals. Due to restrictions in the Papahānaumokuākea Marine National Monument, scientists were unable to conduct net sampling.

Environmental and Geographical Data

For a comparison between the NASC and the environmental and geographical parameters, data in this study included the environmental data: satellite surface chlorophyll-a (mg m^{-3}) and satellite sea surface temperature (SST, $^{\circ}\text{C}$), and the geographical data: bathymetry (m) and distance from the nearest land mass (m). The monthly Moderate Resolution Imaging Spectroradiometer (MODIS) satellite surface chlorophyll-a and SRTM30+ Version 6.0 bathymetry data were extracted online from <http://coastwatch.pfeg.noaa.gov/erddap/>. The monthly MODIS surface chlorophyll-a data were reprocessed for a yearly average, prior to and including acoustic data collection, from July 2012 – July 2013 to obtain a better understanding of the chlorophyll-a and backscatter relationship, accounting for the time delay between primary producers and higher trophic levels. The monthly chlorophyll-a during the time of acoustic data collection, May 2013, was also analyzed; however, both the yearly and monthly averages provided similar results suggesting that the chlorophyll-a values are relatively stable throughout the year in the sampled area. The yearly averages provided more comprehensive temporal and spatial coverage for the analysis; thus only the results using the yearly average prior to the start and throughout acoustic data collection were reported. The monthly SST for May 2013 was

downloaded from <http://oceanwatch.pifsc.noaa.gov/> using the AVHRR Pathfinder v4.1 dataset. The distance from shore was derived using the NEAR function of Arc Map 10.1 (ESRI 2011).

Passive Acoustic Data

The presence of foraging deep diving odontocetes, specifically beaked, sperm, and short-finned pilot whales, was defined by the detection of echolocation clicks recorded using a six element hydrophone array with a 250 kHz sampling rate. The array was comprised of two inline APC hydrophones while the end array consisted of two Reson and two APC hydrophones. The APC piezoceramic elements had an approximate sensitivity of -150 ± 5 dB re 1 V/ μ Pa for 500 Hz - 400 kHz signal. The Teledyne-Reson TC4013 hydrophone elements used for recording higher frequencies had a sensitivity of approximately -211 ± 3 dB re 1 V/ μ Pa between 1 kHz - 170 kHz. The towed array data were visually monitored and the approximate location of the signal was determined using a phone-pair bearing in the digital signal-processing program ISHMAEL. The detections for each species were done during real-time operations using methods described in Rankin et al. (2008). Visual confirmation of species was done using standard line transect methods (Buckland et al. 2001, Bradford et al. 2013).

All short-finned pilot whale acoustic detections were confirmed visually due to their click frequency range being similar to clicks of false killer whales found in the MHI (Baumann-Pickering et al. 2015). The other species in this study could be clearly identified to species based solely on their click features. Most beaked whale detections were made acoustically using the known frequency range of the species as defined in Baumann-Pickering et al. (2013). Because the number of individuals detected acoustically could not be determined, and the location of detections was not always calculated, the detection of clicks was marked as whale foraging

presence and if a detection was not recorded then the species of interest was marked as absent along each 200 m of ship transect.

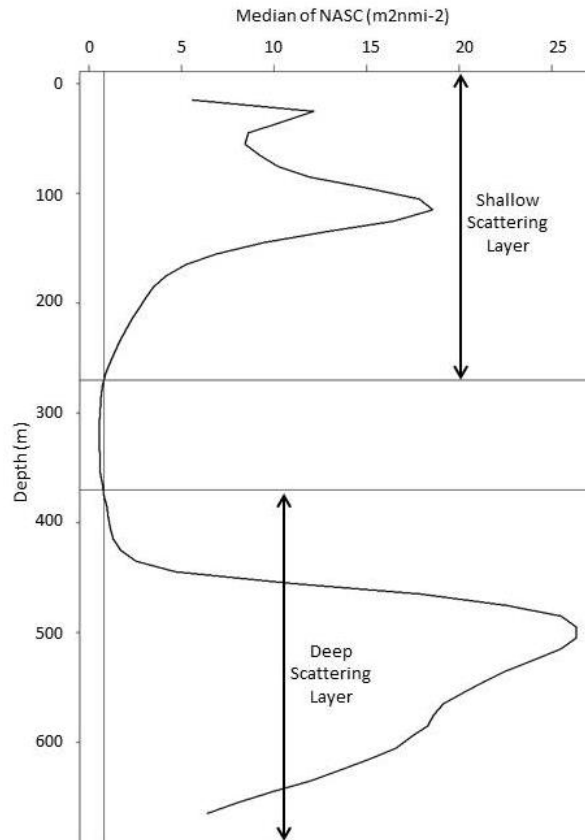


Figure 2: The median of all NASC values plotted across depth. The shallow scattering layer (SSL) and deep scattering layer (DSL) were defined by the threshold median value of 0.816 m^2/nmi^2 obtained by the top 15th percentile.

Analysis

R 3.0.1 (R Development Core Team 2014) was used for all statistical comparisons. Graphs were plotted in both Arc Map 10.1 and R 3.0.1. For further understanding of the variability of NASC throughout the NWHI, the “hotspots” of acoustic backscatter were investigated. The “hotspots” were defined as locations containing the top 1% of the NASC values. These “hotspots” were used solely for visual inspection. All statistical analysis were performed using all NASC values collected. The NASC per 10 meter depth bins were summed for two distinct depth classes: a shallow layer from 0 – 270 meters and a deep layer from 370 – 670 meters. The scattering layers

were separated by the 15th percentile threshold of the median of the data which equated to 0.816 m²/nmi². The shallow scattering layer (SSL) was defined from depth zero until the NASC value reached the threshold which occurred at 270 meters (Figure 2). The deep scattering layer (DSL) was defined as the depth deeper than the SSL that the NASC value was greater than the threshold value (Figure 2).

The comparison between Simrad EK60 acoustic backscatter and the environmental and geographical data were performed with the 10 meter vertical depth bins of backscatter collected during the daytime and nighttime summed from 0 to 670 meters to get the total water column NASC measure and to minimize temporal bias due to diel vertical migration. Daytime and nighttime samples were defined based on the migration of organisms in the DSL. A subset of the DSL performs diurnal migration and migrates to the SSL after sunset and back to DSL during sunrise so daytime was defined when the migration back to DSL ended and nighttime was defined when the migration to the SSL was complete. A generalized additive model (GAM) using the mgcv package (Wood 2006) in R 3.0.1 was used to determine the relationship between the log of NASC and the defined longitude, latitude, surface chlorophyll-a, SST, bathymetry, and distance from the nearest landmass. A smoother was fit to each of the independent variables with a two dimensional smoother (s) applied to the longitude and latitude and a single smoother (s) fitted to the remaining independent variables: chlorophyll-a, SST, bottom depth, and distance from the nearest landmass. This relationship is defined in equation 1.

$$\log(NASC) \sim s(lat, lon) + s(CHLa) + s(SST) + s(bathymetry) + s(distance) \quad (1)$$

For comparison between the passive acoustic detections of foraging whales and the backscatter values, daytime only NASC values were used because there was consistent coverage by both the passive acoustic towed array and visual marine mammal observers (MMOs). The defined DSL

corresponded to a portion of the foraging depth of the species of interest. The depth and spatial locations of the “hotspots” and whale detections were plotted to get a better understanding of the spatial agreement. A Z-score binomial test was used to determine the probability of whale foraging presence for each of the deep divers separately using the summed DSL and SSL during the daytime. A separate binomial test was used to determine the relationship between the summed water column from 0 – 670 m NASC value and whale foraging presence.

Results

In the Northwestern Hawaiian Islands, 30,532 two hundred horizontal meter of NASC samples were collected (Figure 1). The summed daytime and nighttime NASC throughout the NWHI was patchy (Figure 3) with longitude, latitude, chlorophyll-a (mg m^{-3}), depth (m), distance from the nearest land mass (m), and SST ($^{\circ}\text{C}$) significantly explaining 35.6% of this variation (Table 1). The 2-dimensional smoother of the latitude and longitude showed a significant patchiness of NASC throughout the area sampled (GAM: $F = 190.03$, $p < 0.0001$). The geographical variables of distance from the nearest land mass (GAM: $F = 86.05$, $p < 0.0001$) and bathymetry (GAM: $F = 39.10$, $p < 0.0001$), showed similar significant trends with NASC values decreasing as bottom depth and distance from the nearest land mass increased (Figure 4b & 4c). The environmental variable, chlorophyll-a (GAM: $F = 151.99$, $p < 0.0001$), had a significant positive relationship with acoustic backscatter (Figure 4a). There was a weak relationship between these values until chlorophyll-a increased from about 0.08 to 0.09 mg m^{-3} . At this threshold, there is a rapid increase in NASC values recorded. While the SST smoother was significant (GAM: $F = 29.66$, $p < 0.0001$), there did not appear to be a large effect of the changing SST on the NASC (Figure 4d).

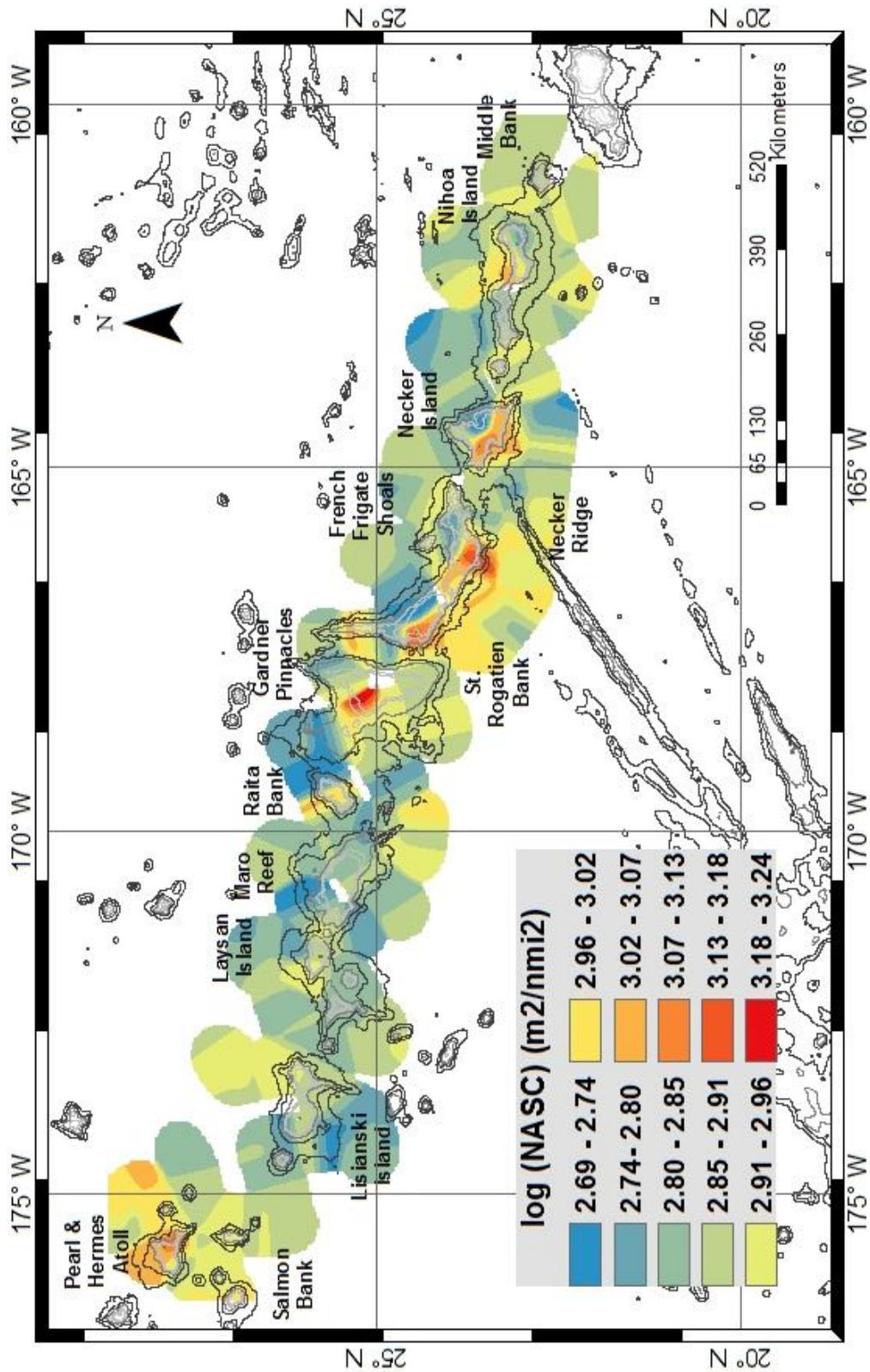


Figure 3: The patchy distribution of the log Nautical Area Scattering Coefficient ($\log(\text{NASC})$) throughout the sampled area in the Northwestern Hawaiian Islands (NWHI). Interpolated data was used solely for visual interpretation.

Table 1: Generalized Additive Model (GAM) non-linear smoothers for the log of the Nautical Area Scattering Coefficient (NASC) against latitude and longitude, surface chlorophyll-a (mg m⁻³), bottom depth (m), distance from land (m), and sea surface temperature (°C). The table includes the estimated degrees of freedom (edf) for the model terms, the F-value and associated p-value. The significant p-values are in bold with alpha defined at 0.05.

Parameter	edf	F value	P(F)
<i>s</i> (Lat&Lon)	28.854	190.03	<0.0001
<i>s</i> (CHLa)	8.658	151.99	<0.0001
<i>s</i> (depth)	8.740	39.10	<0.0001
<i>s</i> (distance)	8.942	86.05	<0.0001
<i>s</i> (SST)	8.812	29.66	<0.0001

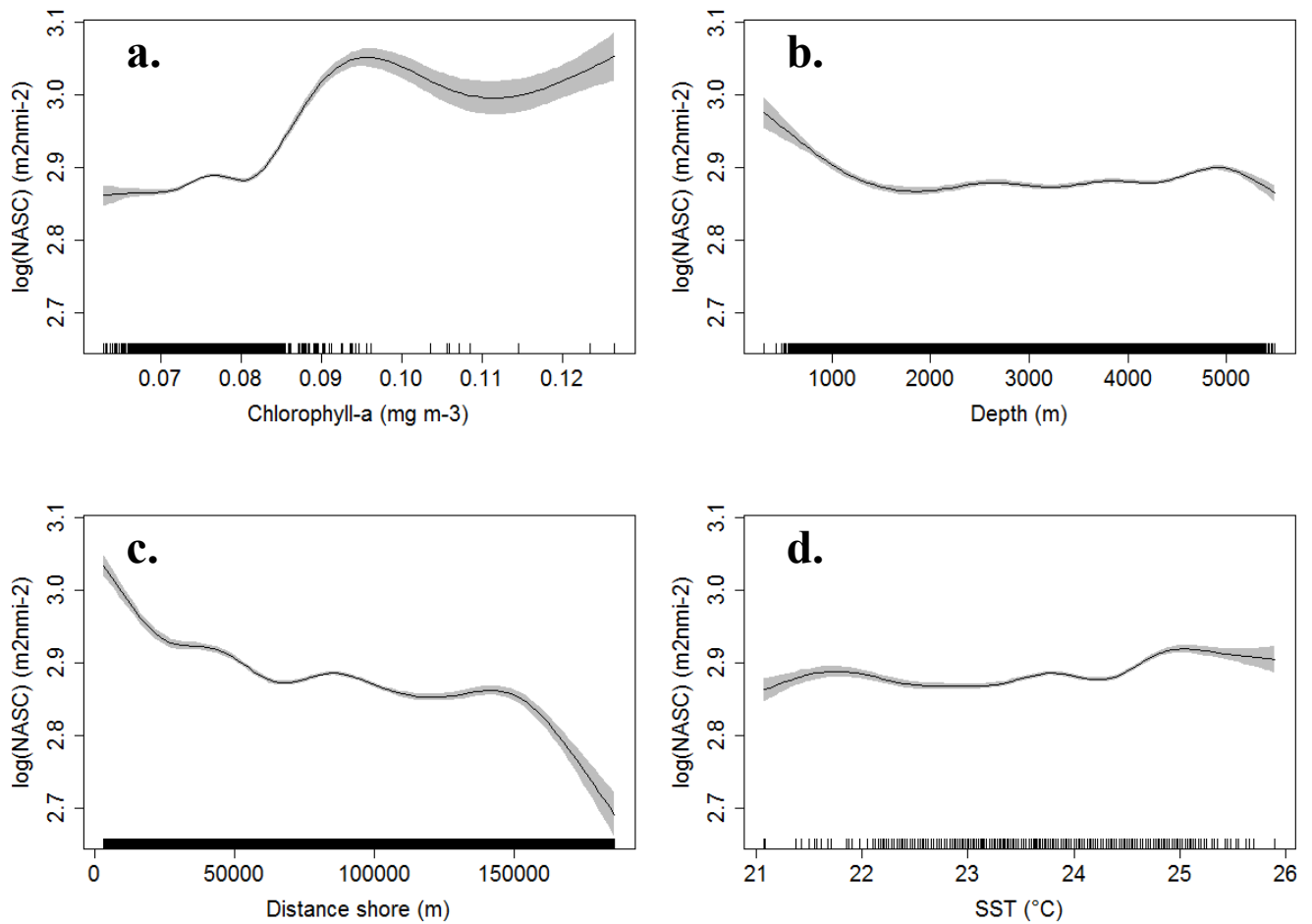


Figure 4: Plots of the generalized additive model (GAM) smoothers for the distribution of the log of Nautical Area Scattering Coefficient (NASC) relative to the environmental and geographic parameters: a) chlorophyll-a (mg m⁻³), b) depth (m), c) distance from the nearest land mass (m), and d) sea surface temperature (SST, °C). All smoothers are significant. Tick marks on the x-axis correspond to the sampling distribution. The grey shading indicates two times the standard error for each smooth function.

The acoustic backscatter throughout the northwest Hawaiian Archipelago was characterized into two distinct layers: a surface scattering layer (SSL) from 0 to 270 meters and a deep scattering layer (DSL) from 370 to 670 meters (Figure 2). To better understand the patchiness of NASC, the “hotspots” for the SSL and DSL were plotted separately for daytime and nighttime (Figure 5). The “hotspots” were defined as the top one percent of NASC values which equated to 179 daytime samples for both SSL and DSL and 118 nighttime samples. Most of the hotspots were associated with deep slopes and banks as well as emergent land masses (Figure 5). The defined emergent landmasses in the NWHI study area included Nihoa Island, Necker Island, French Frigate Shoals, Gardner Pinnacles, Laysan Island, Lisianski Island, and Pearl and Hermes, with about 30 submerged banks found throughout the NWHI, examples included St. Rogatien Bank, Raita Bank, and Salmon Bank (NOAA 2006). The daytime DSL and daytime and nighttime SSL “hotspots” had more spatial coverage throughout the sampled area than the nighttime DSL “hotspots.” The DSL “hotspots” during the night were restricted to the deep bank at St. Rogatien Bank and the emergent land masses at French Frigate Shoals and Nihoa Island (Figure 5b) with the SSL daytime and nighttime and the DSL daytime “hotspots” spanning throughout the sampled area. While spanning the NWHI archipelago, these “hotspots” were still clustered around the emergent land and deep banks as detailed in Figure 5a and 5b and were not normally found in the area outside of these boundaries.

The concentration of the “hotspots” around the bank and emergent land masses was also confirmed by the ocean depths of these locations. Both daytime and nighttime DSL “hotspots” were concentrated at shallower ocean depths (Figure 6) with the daytime samples having the shallowest bathymetry distribution (<1500 meters) than the other “hotspots” (Figure 6a). This relationship further supported the GAM bathymetry smoother demonstrating that there were

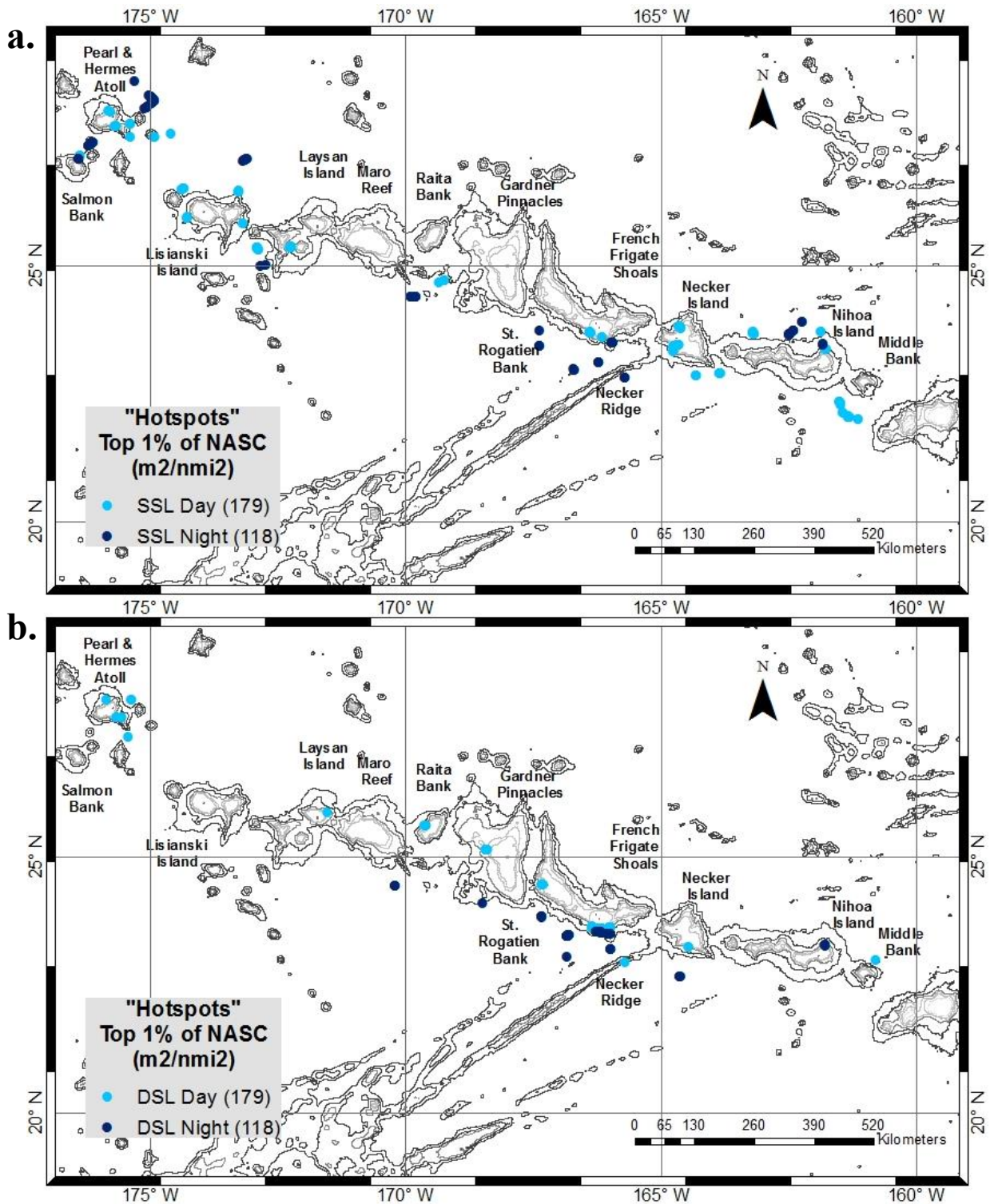


Figure 5: The top 1% NASC values (“hotspots”) plotted for a) shallow scattering layer (SSL) from 0 - 270 m and b) deep scattering layer (DSL) from 370 – 670 m during the daytime and nighttime. For both plots the daytime and nighttime points are denoted as light and dark blue, respectively. The “hotspots” were defined as the top one percent of NASC values solely for visual depiction and equated to 179 daytime samples for both SSL and DSL and 118 nighttime samples.

higher NASC values at shallow depths. Nighttime SSLs were not found predominantly shallower than 1500m suggesting lateral migration of the shallow DSL hotspot fauna such as would be found for a MBL (Reid et al 1991) (Figure 6). During the nighttime the SSL and DSL “hotspots” were concentrated at deeper depths with the greatest frequency of “hotspots” found at depths from about 2500 to 5500 meters. This depth was still shallower than most of the oceanic nighttime samples not collected near banks or emergent land.

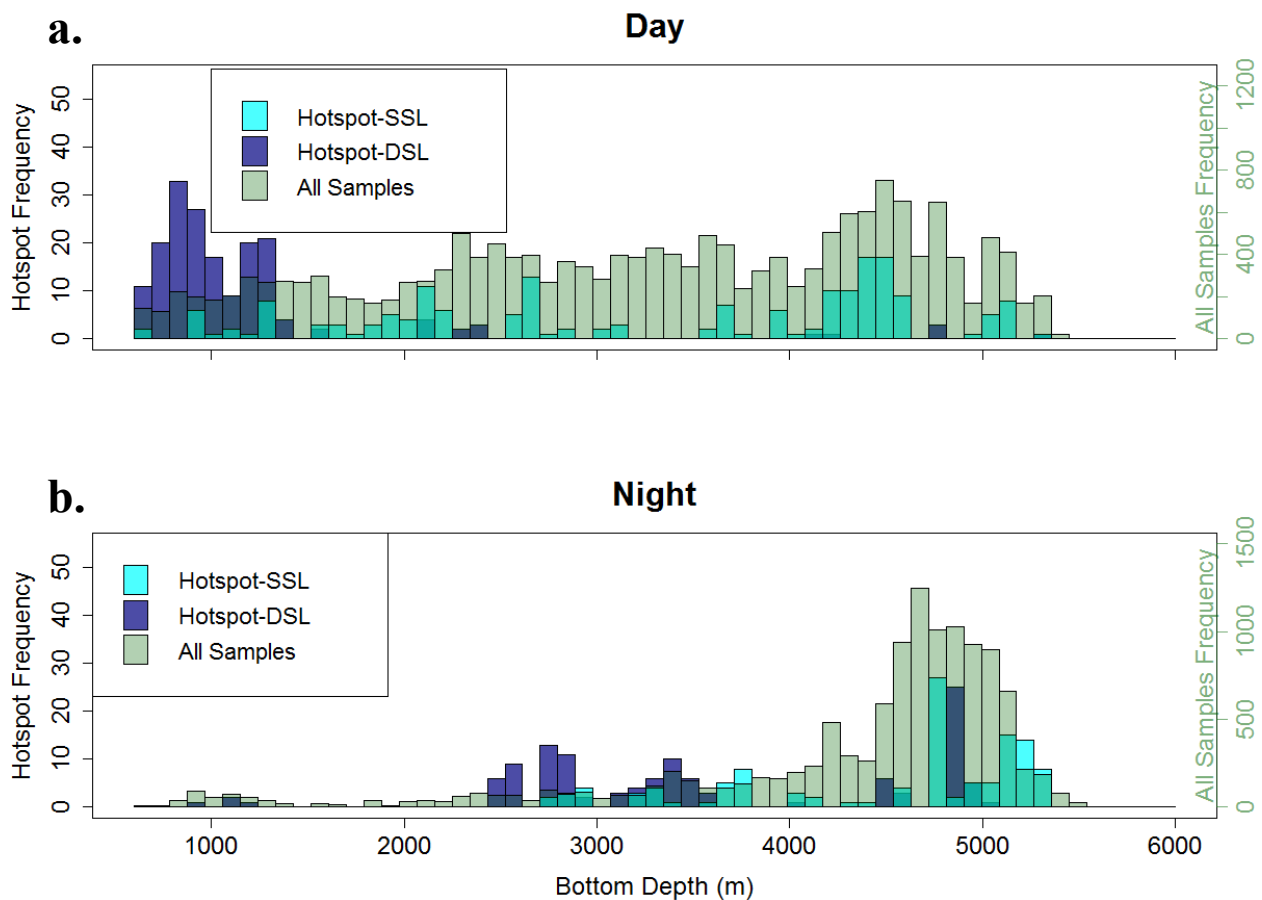


Figure 6: Frequency distribution of ocean bathymetry for the SSL and DSL “hotspots” compared against all samples collected for both a) daytime and b) nighttime. Each plot contains three histograms plotted on top of each other with light blue representing the SSL values, dark blue denoting the DSL, and green indicating all samples collected.

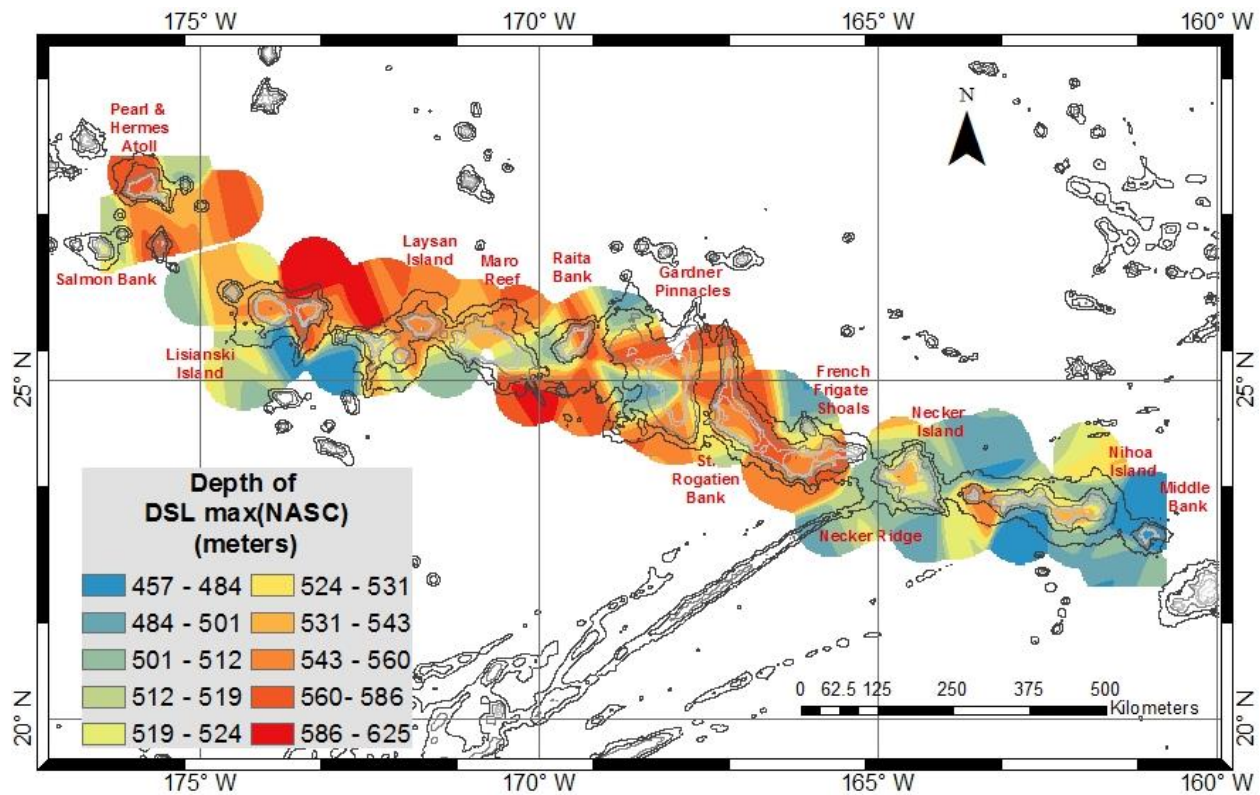


Figure 7: The spatial distribution of the daytime depth bin of the deep scattering layer (DSL) that contained the highest Nautical Area Scattering Coefficient (NASC) value.

Further investigation of the vertical structure of the daytime DSL throughout the sampled area revealed that the 10 meter vertical depth bin containing the maximum NASC values varied drastically (Figure 7). The depth of the DSL maximum NASC value was relatively shallower east of French Frigate Shoals. The deeper NASC max was highly correlated with the deep banks and emergent land masses as denoted by the red and orange colors clustering around the emergent landmass of Niihau Island, Necker Island, French Frigate Shoals, Gardner Pinnacles, Laysan Island, Lisianski Island, and Pearl and Hermes Atoll and the deep banks St. Rogatien Bank and Raita Bank (NOAA 2006) in Figure 7. This variability of the depth of the max values was not related to the vertical structure and magnitude of the “hotspots.” The vertical structure of the scattering layers of the “hotspots” for both the daytime and nighttime did not follow a latitudinal gradient but varied considerably across the sampled range (Figure 8).

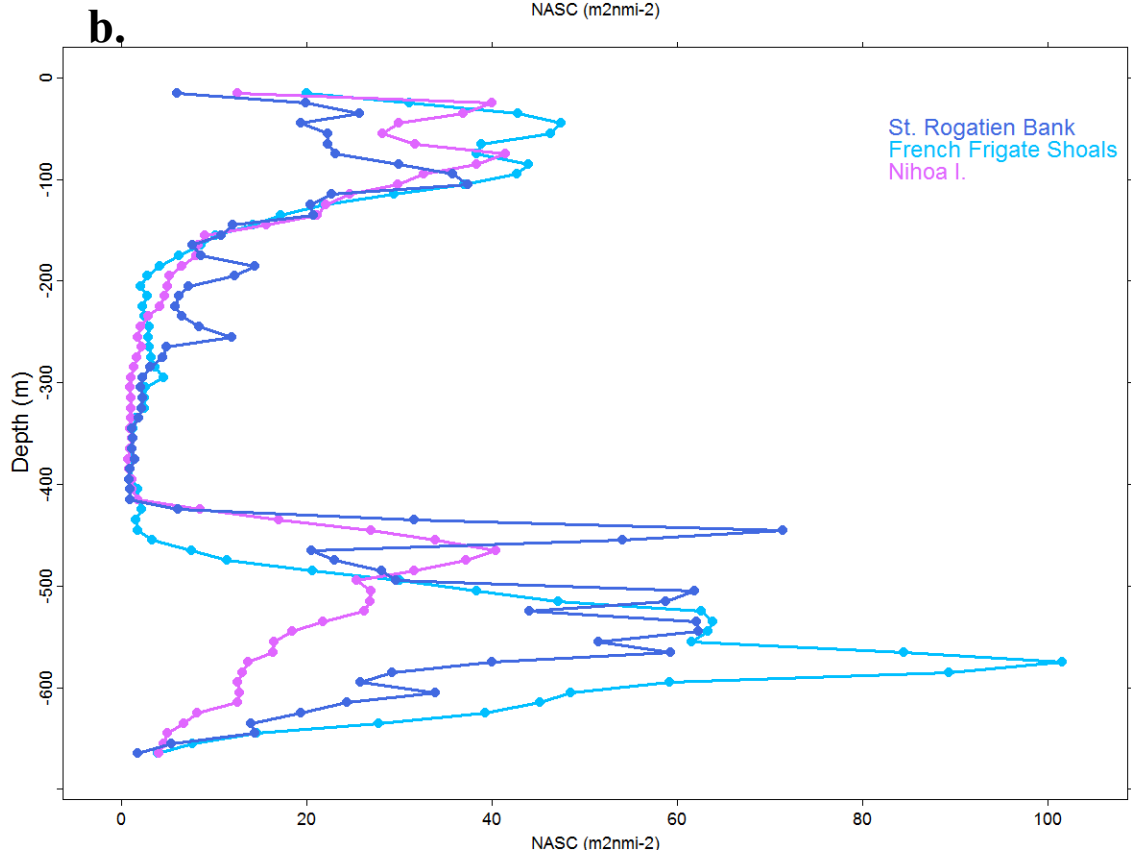
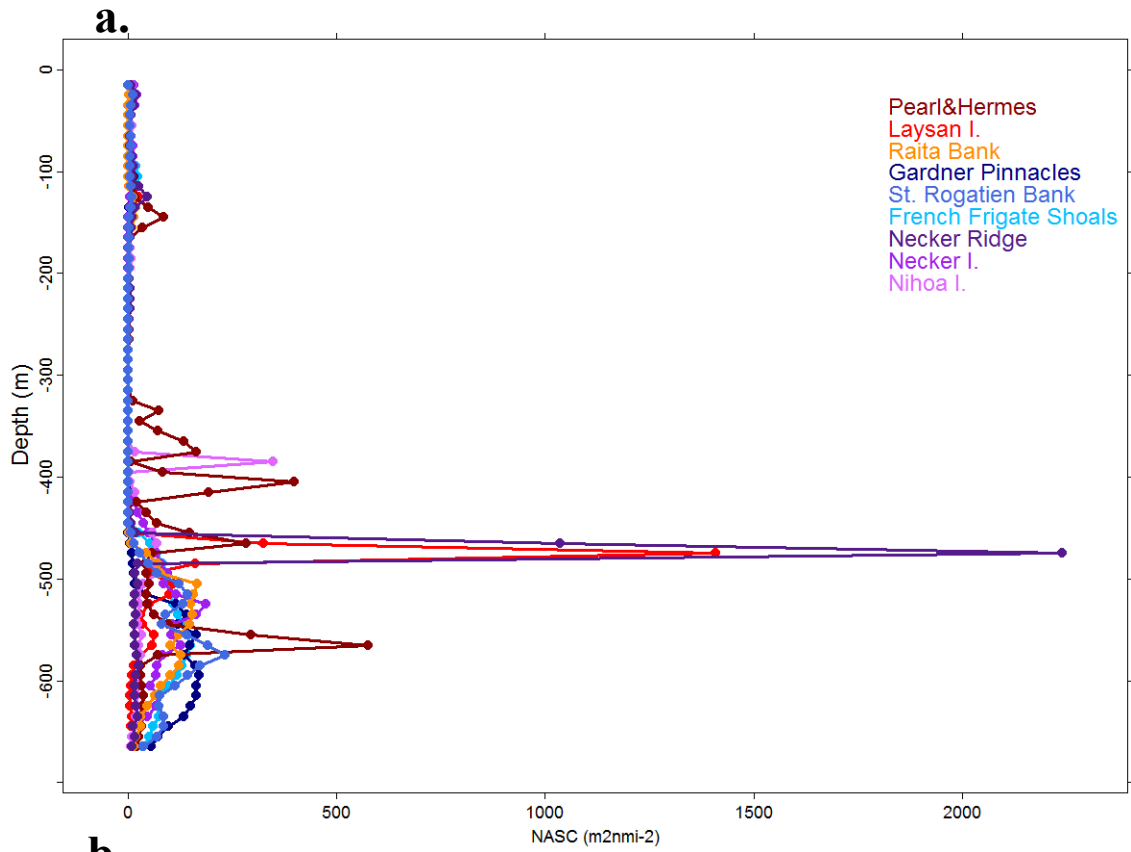


Figure 8: The mean Nautical Area Scattering Coefficient (NASC) values in the specified

“hotspot” locations were plotted against the binned 10 meter vertical depth for both the a) daytime and b) nighttime. The lines are color coded based on there geographic position.

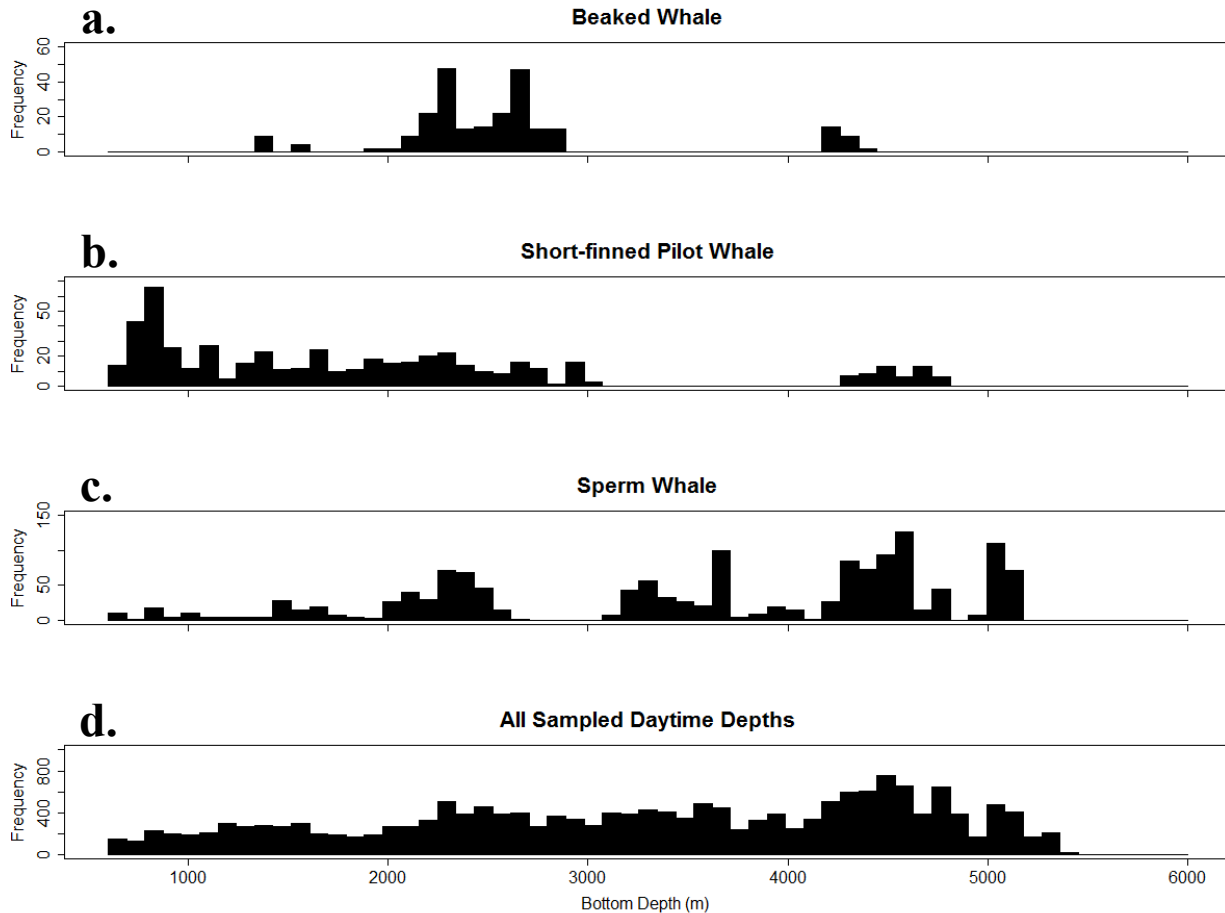


Figure 9: Histogram of the bathymetry distribution of the locations where foraging a) beaked, b) short-finned pilot, and c) sperm whales were detected compared to d) all daytime bathymetry samples. The detections of beaked, pilot, and sperm whales occurred in 243, 523, and 1425 bins of the total 17906 bins, respectively.

Of the 17906 total daytime 200 meter horizontal bins, the hydrophone array detected foraging clicks of beaked, short-finned pilot, and sperm whales in 2191 bins. The detections of beaked, pilot, and sperm whales occurred in 243, 523, and 1425 bins, respectively. The bathymetry of the daytime distribution of the foraging deep-diving odontocetes was highly variable for the different species (Figure 9). Beaked whales had the narrowest bathymetry range encompassing 1378 – 2851 m and then a second depth distribution from 4179 – 4400 m (Figure 9a). Whereas, short-

finned pilot whales had the shallowest depth range starting at the sample limit of 670 m – 3034 m and an additional depth range from 4328 – 4759 m (Figure 9b). Sperm whales had the most variable depth range preferring the deeper offshore waters down to 5150 m (Figure 9c). These trends were substantially different from the bathymetry of all daytime samples (Figure 9d) with depths being recorded from 670 to 5364 meters.

The ocean bathymetry distribution for the SSL and DSL “hotspots” had high agreement with the bottom depths of the waters with foraging short-finned pilot and beaked whale detections (Figure 10a & 10b). The sperm whale detection locations did not have high agreement (Figure 10c). A similar comparison can be made looking at the spatial distribution. The map of beaked whale detections overlapped most closely with the SSL “hotpot” locations (Figure 11a). Whereas, the spatial plot of short-finned pilot whale detections was most closely associated with the DSL “hotspots” (Figure 11b) and sperm whales detections were not associated with either the SSL or DSL “hotspots” (Figure 11c). This spatial agreement was further supported by the binomial Z-scores comparing the deep-diver foraging locations with all daytime SSL and DSL NASC values throughout the sampled area (Table 2). An increase in SSL NASC predicted a higher probability of beaked whale ($Z = 5.308$; $p < 0.0001$) and short-finned pilot whale ($Z = 4.088$; $p < 0.0001$) foragers. Additionally an increase in DSL NASC predicted a higher probability of short-finned foragers ($Z = 14.370$; $p < 0.0001$). Whereas, the DSL NASC did not have a significant relationship ($Z = 1.398$; $p = 0.162$) with beaked whale presence. For sperm whales, both a decrease in SSL ($Z = -14.207$; $p < 0.0001$) and DSL NASC ($Z = -3.543$; $p < 0.0004$) predicted an increase in foraging whale presence. Overall a higher vertically summed (from 0-670 meters) NASC predicted more foraging short-finned pilot whales ($Z = 14.84$; $p < 0.0001$) and beaked whales ($Z = 2.374$; $p = 0.0176$) suggesting that the whales were attracted to areas with more

scattering organisms. The reciprocal relationship was seen for sperm whales ($Z = -6.181$; $p < 0.0001$). It is interesting to note that the SSL and DSL NASC values were not correlated.

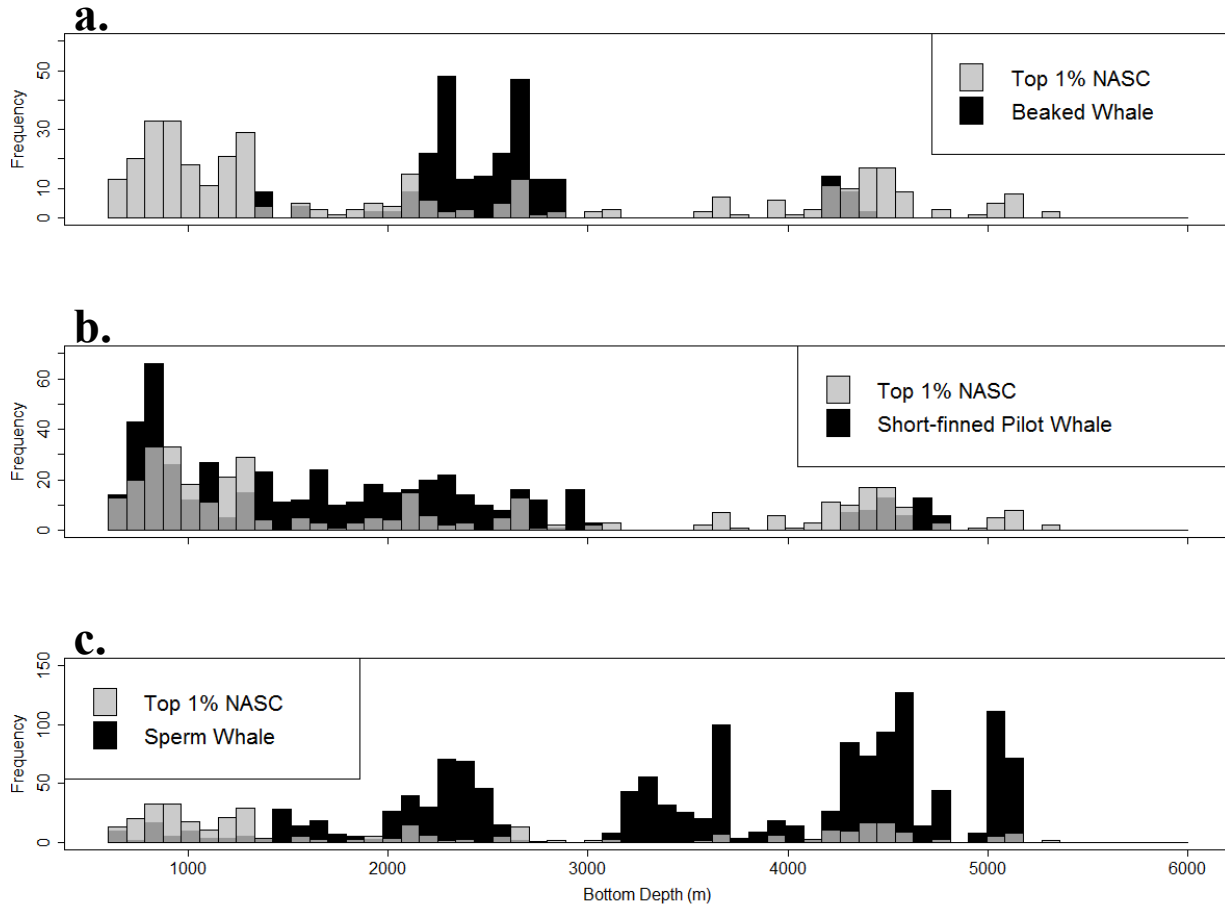
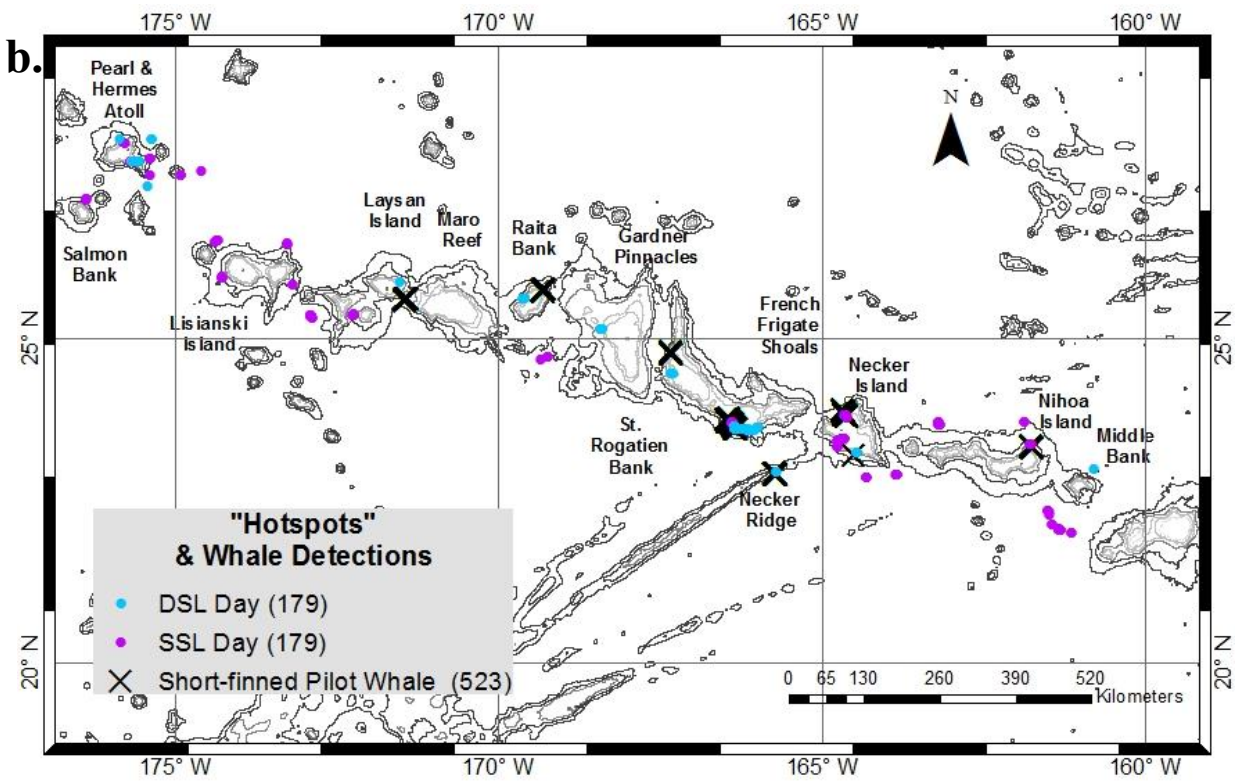
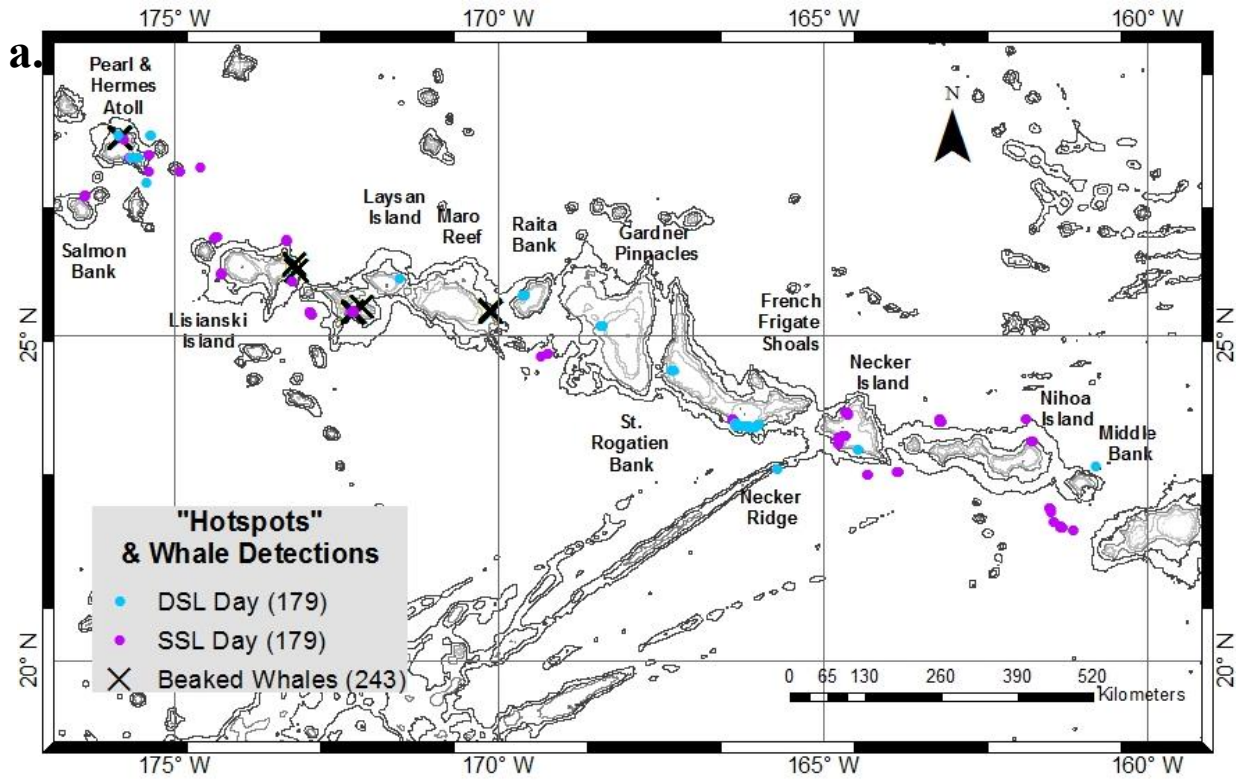


Figure 10: The frequency distribution of the “hotspots” (top 1% of the NASC) bathymetry compared with the bathymetry distribution of the foraging a) beaked, b) short-finned pilot, and c) sperm whales. The ocean depth distribution of the beaked and short-finned pilot whales was closely associated with the depth distribution of the “hotspots.” The bathymetry in areas of sperm whale detections did not match those of the “hotspots.”



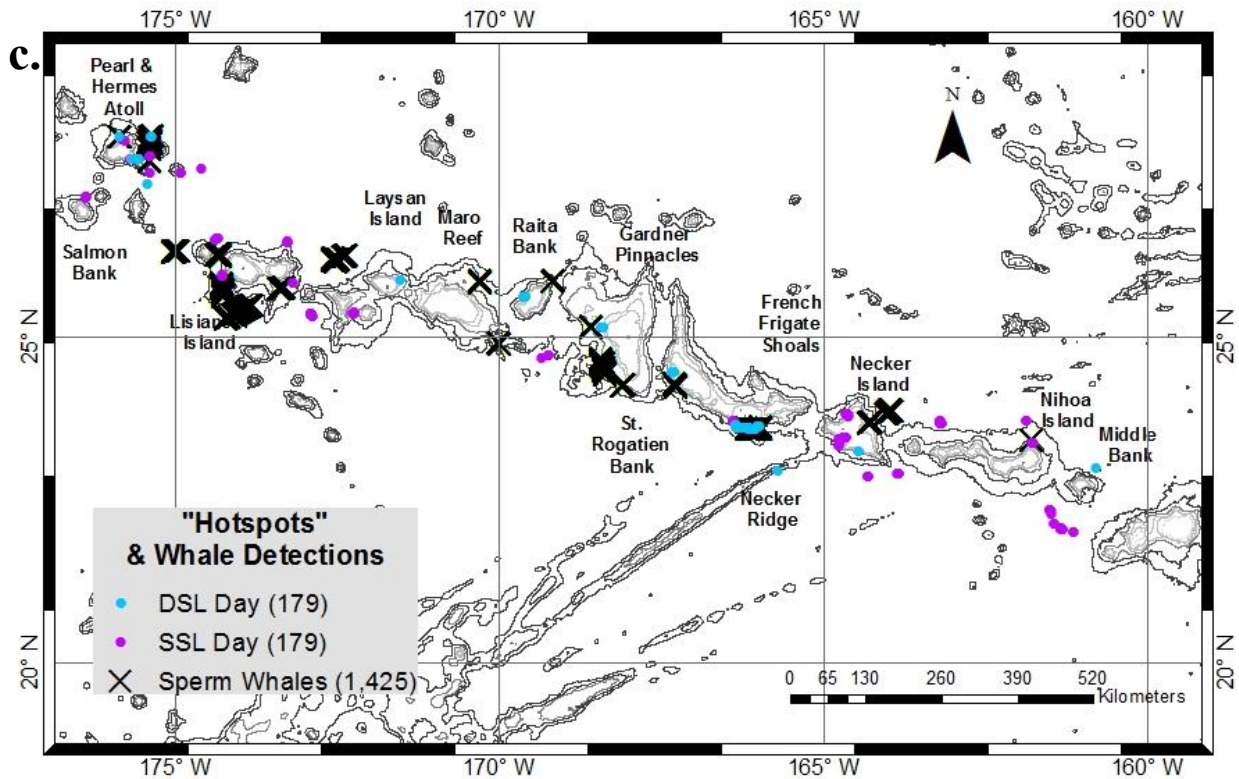


Figure 11: The spatial distribution of the shallow and deep scattering layer “hotspots” and foraging detections of a) beaked, b) short-finned pilot, and c) sperm whales. The numbers in parentheses are the corresponding sample sizes.

Table 2: Z-values and associated p-values for the predicted presence of foraging beaked, short-finned pilot, and sperm whales. The significant p-values are bolded assuming an alpha < 0.05.

	Beaked Whale		Short-finned Pilot Whale		Sperm Whale	
	Z	p-value	Z	p-value	Z	p-value
Shallow Scattering Layer (0 – 270 m)	5.308	<0.0001	4.088	<0.0001	-14.207	<0.0001
Deep Scattering Layer (370 – 670 m)	1.398	0.162	14.370	<0.0001	-3.543	0.0004
Summed Vertical (0 – 670 m)	2.374	0.0176	14.84	<0.0001	-6.181	<0.0001

Discussion

In the Northwestern Hawaiian Island Archipelago, the distribution of micronekton form discrete scattering layers that are similar to distributions found throughout the world (Hersey & Moore 1948, Tont 1976). While this study only examined the 70 kHz frequency of the Simrad EK60, not allowing for species identification in the sampled scattering layers, information can still be attained by looking at the relative distribution of acoustic backscatter relating to environmental parameters (Hazen & Johnston 2010, Escobar-Flores et al. 2013) and some top trophic level distributions (Benoit-Bird & Au 2003, Benoit-Bird et al. 2004, Friedlaender et al. 2006, Hazen & Johnston 2010, Hazen et al. 2011, Abecassis et al. 2015). The inability to characterize the scattering layer's species composition is the main drawback of this study. However the composition of these scattering layers has been well documented in the Main Hawaiian Islands and throughout the Pacific (Gjosaeter & Kawaguchi 1980). A major component of the layers in these areas are myctophids (Gjosaeter & Kawaguchi 1980, Drazen et al. 2011) sometimes comprising over 80% of the composition as seen in scattering layers off the Island of Oahu (Benoit-Bird 2009). Myctophids are a forage item of the deep-diving odontocetes' prey investigated in this study (Kozlov 1995, Clarke 1996a, Clarke 1996b, Phillips et al. 2001, Ohizumi 2002, Markaida & Sosa-Nishizaki 2003, Parry 2006) which is mostly comprised of squid and occasionally fish (Clarke 1980, Seagars & Henderson 1985, Sinclair 1992, Clarke 1996a, Clarke & Young 1998, Pauly et al. 1998) suggesting that changes in and variability of these scattering layers would affect the distribution of the whale foragers larger prey.

In this study the acoustic backscatter throughout the NWHI was highly variable with higher relative biomass found at shallower ocean depths closer to emergent land masses and deep banks. Along with distance from shore and ocean bathymetry, higher average monthly and

yearly satellite surface chlorophyll-a levels influenced the spatial variability of the backscatter. These results were further validated by the spatial orientation of the “hotspots” found predominantly around emergent land masses and deep banks. To date this is the first study investigating the variability of pelagic micronekton biomass in the NWHI. Gove et al. (2016) found that the NWHI demonstrated the Island Mass Effect (Doty & Oguri 1956) with the islands having higher amounts of chlorophyll-a or phytoplankton near shore due to more nutrients in the water. This inshore increased productivity could be leading to the higher levels of acoustic biomass that we found closer to shore and at shallower depths. This relationship is the most apparent at the French Frigate Shoals where we found much higher levels of acoustic biomass. This location also demonstrated the highest levels of chlorophyll-a (Gove et al. 2016). The influence of distance from the coastline, bathymetry, and chlorophyll-a on acoustic backscatter has been investigated in other geographic locations with similar results. Escobar-Flores et al. (2013) found that these variables similarly influenced the distribution of acoustic backscatter in the South Pacific which was composed mostly of mesopelagic fishes.

This study also found that the “hotspots” during the daytime for the DSL were strictly concentrated at much shallower depths around these deep banks and emergent land than the other “hotspots.” This relationship was less apparent for the nighttime DSL “hotspot” locations suggesting that a substantial subset of the organisms making up the increased backscatter do in fact migrate to the surface at nighttime. Additionally the lack of a strong shallow bathymetry signal in the SSL locations during nighttime suggests that the migrating organisms are dispersing at the surface by migrating horizontally as well vertically potentially migrating closer to the emergent landmasses to hypothetically increase their nighttime foraging success. This horizontal movement towards land has been documented in the MBC in the MHI (Benoit-Bird et al. 2001)

suggesting that there might be a similar community in the NWHI associated with these emergent landmasses as well as the deep banks. To truly test this hypothesis, studies would need to further characterize the dusk and dawn horizontal movement of the migrating deep scatters as well as the composition of these migrators to determine if the community structure is comparable to the MBC found in the MHI. The MBC has a very specific composition of organisms that varies from the pelagic DSL composition (Reid et al. 1991). To date there is no information on the species composition of the DSL in the NWHI because trawling, the main method for species identification, is limited in the Papahānaumokuākea Marine National Monument. Trawling as well as noninvasive techniques should be investigated to further test this hypothesis.

One potential noninvasive method could be the high frequency (>1 MHz) Dual-Frequency Identification Sonar (DIDSON). This sonar has been used in deep water off the Island of Hawaii (Giorli et al. in revision) as a noninvasive technology to survey the organisms in the DSL. This technology was able size a variety of organisms in the DSL (Giorli et al. in revision). Using this technique in the NWHI should be further investigated, as it potentially allows for identification of individual organisms in the DSL and could potentially provide information about the size of some of the scattering organisms seen in this study.

Along with the summed backscatter, the vertical structure of the scattering layers varied in relation to the emergent land and deep banks and did not vary based on a longitudinal/latitudinal gradient. It was hypothesized that there would be a shallowing of the deep scattering layer to the NW of the sample range because the depth mixed layer has been documented to decrease northward as you move from 20° to 40° N (Bathen 1972) and we hypothesize that we would see a similar trend in the deep scattering layer across the similar latitudinal range. However this was not seen for either the depth of the maximum NASC value of the deep scattering layer or the

vertical structure of the scattering layers. The depth of the maximum NASC values varied based on the location of the samples in relation to the emergent land and deep banks. The maximum NASC value was found at deeper depths around the deep banks and coastlines suggesting that scattering organisms in these locations tend to concentrate closer to the bottom during the daytime. One potential explanation for this behavior could be that the organisms cluster together near the bottom to avoid predation. As already stated, a subset of the organisms in the deep scattering layers in the NWHI do perform diurnal migration to avoid predation by migrating to the surface at night to feed and back to the DSL during the daytime. These near-shore organisms might additionally migrate closer to the bottom during the daytime to avoid predation by top trophic level predators, including the forage of the whales of interest in this study.

The foraging deep-diving whales in this study were associated with very specific bathymetry ranges with pilot whales found at the shallowest depths, beaked whale found at the narrowest depth range, and sperm whales found at the most variable and deepest depth range. While again this is the first study investigating the deep divers' distribution in the NWHI, there was high agreement between the depth ranges utilized by the species seen in this study and the depth ranges of the same species in the MHI. Of the three deep divers in this study, sperm whales in the MHI also had the highest sighting probability in waters greater than 3000 meter when compared to the other two species and did not seem to be closely associated with the islands (Baird et al. 2013) similar to this study's results. Short-finned pilot whales in the MHI had the shallowest depth range and preferred the slope waters from 500 – 2500 m (Baird et al. 2013) which is comparable to their main depth range in the NWHI from 670 – 3034 m. It is important to note that only sites with waters greater than 670 meters were sampled in this study so short-finned pilot whales might be found in waters shallower than 670 meters in the NWHI. Beaked

whales in the MHI preferred the slope waters as well as deeper depths down to 4500 meters (Baird et al. 2013) similar to the depth ranges of 1378 – 2851 m and 4179 – 4400 m found in the NWHI. This variation of bathymetry ranges for short-finned pilot and beaked whales in the MHI and NWHI can be further explained by their dive profiles from tag data in the MHI, which found that beaked whales dive to deeper depths (Baird et al. 2006) on average than short finned pilot whales (Baird et al. 2003) which is probably why short-finned pilot whales were found to be in shallow depths both in this study and the MHI. While the bathymetry distribution of this study as well as in previous studies varied between short-finned pilot and beaked whales, these species still appear to be closely associated with emergent land both in the NWHI and the Island of Hawaii, with higher numbers of sightings closer to shore throughout the MHI (Baird et al. 2013) and clustering of tagged individuals nearshore off the Island of Hawaii (Abecassis et al. 2015). The clustering of whales in leeward waters of the Island of Hawaii was linked to higher backscatter for the 70 kHz signal (Abecassis et al. 2015) similar to the results in this manuscript. Both short-finned pilot and beaked whales in the NWHI were associated with “hotspots” in the relative biomass of SSL and/or DSL along with the presence of emergent land and deep banks. Whether these species are cueing into the scattering layer or the bathymetry in the NWHI is unknown. However it is apparent that they are attracted to areas with higher backscatter suggesting that these organisms support the food web of these deep divers and their prey. It is important to note that this relationship was not demonstrated for sperm whales in the NWHI. The authors were surprised that a decrease in surface and deep scattering layer acoustic backscatter predicted an increased probability of sperm whale foragers. This was contradictory to the hypothesis that higher backscatter would attract foraging whales as seen in other studies (Hazen & Johnston 2010, Hazen et al. 2011). The authors predicted that the relationship was not

significant because the authors were unable to localize all the sperm whales detected in this study leading to a potential overestimation of sperm whales that could have been outside the 200 meter sample radius. Furthermore in other parts of the world, Sperm whales specialize on eating large highly mobile squid and the distribution of this squid can be hard to capture. Additionally the 70 kHz data only recorded down to 670 meters due to attenuation, not allowing for a complete sampling of the DSL which can extend past this depth. Other studies that saw a strong relationship between the DSL and foraging deep divers used the 38 kHz frequency and were able to sample at deeper depths than this study (Hazen & Johnston 2010, Hazen et al. 2011). We hypothesize that there might be a different relationship between sperm whales and the relative biomass if we were able to sample the entire range of foraging depths for sperm whales including collecting more offshore samples using a lower frequency (e.g. 38 kHz) to sampling the entire DSL. This might also be the reason for the lack of strong relationship between the DSL and beaked whale presence. Additionally further investigation of this area over a longer time period might help to increase understanding of the link between predators and prey allowing for the ability to study the seasonal variability of these species.

In summary this study identified that the distribution of the prey and the forage of the prey is important when understanding marine mammal foraging behavior. Future studies should include these variables when trying to fully understand the behavior of deep diving toothed whales as well as other species that might be utilizing these same “hotspots.” It is known that other species, including top predators, do congregate at these “hotspots” especially around French Frigate Shoals which had consistently high NASC values in this study and has shown high chlorophyll-a values in another study (Gove et al. 2016). Both monk seals and green sea turtles use French Frigate Shoals as their main breeding grounds in the NWHI and MHI with it being the extensive

colonial breeding area for green sea turtles in the Hawaiian Archipelago (Balazs 1976). Both species might select this area because there are potentially more prey organisms and higher productivity in the waters surrounding French Frigate Shoals than other areas in the NWHI and MHI. Previous studies have found that foraging monk seals also seem to target areas with higher bathymetric relief (e.g., submerged banks, seamounts) (Stewart et al. 2006). The “hotspot” areas in this study were also focused in areas with high bathymetry relief, supporting an argument for the inclusion of acoustic methods when trying to better understand the behaviors of predators in the NWHI.

Acknowledgements

The authors would like to thank the staff, crew, scientists, and volunteers of the R/V Oscar Elton Sette that helped with collection of this data, Ali Bayless for answering questions on the technical aspects of the hydrophone array, Yvonne Barkley for answering passive acoustics data collection questions, and Jessica Chen for reviewing the manuscript. Funding for this survey came from the National Oceanic and Atmospheric Administration (NOAA).

References

- Abecassis M, Polovina J, Baird RW, Copeland A, Drazen JC, Domokos R, Oleson E, Jia Y, Schorr GS, Webster DL, Andrews RD (2015) Characterizing a foraging hotspot for short-finned pilot whales and Blainville's beaked whales off the west side of the Island of Hawai'i with tagging and oceanographic data. *PLoS One* 10:1-22
- Andrews RD, Schorr GS, Baird RW, Webster DL, McSweeney DJ, Hanson MB (2011) New satellite-linked depth-recording LIMPET tags permit monitoring for weeks to months and reveal consistent deep nighttime feeding behavior of short-finned pilot whales in Hawai'i. Poster presentation at the Fourth International Science Symposium on Bio-logging, Hobart, Tasmania, March 2011
- Au WW, Benoit-Bird KJ (2008) Broadband backscatter from individual Hawaiian mesopelagic boundary community animals with implications for spinner dolphin foraging. *J Acoust Soc Am* 123:2884-2894
- Baird R, Webster DL, Aschettino JM, Schorr GS, McSweeney DJ (2013) Odontocete Cetaceans Around the Main Hawaiian Islands: Habitat Use and Relative Abundance from Small-Boat Sighting Surveys. *Aquatic Mammals* 39:253-269
- Baird RW, McSweeney DJ, Heithaus MR, Marshall GJ (2003) Short-finned pilot whale diving behavior: deep feeders and day-time socialities. Abstract submitted to the 15th Biennial Conference on the Biology of Marine Mammals, Greensboro, NC
- Baird RW, Webster DL, McSweeney DJ, Ligon AD, Schorr GS, Barlow J (2006) Diving behaviour of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales in Hawai'i. *Canadian Journal of Zoology* 84:1120-1128
- Balazs GH (1976) Green Turtle Migrations in the Hawaiian Archipelago. *Biological Conservation* 9:125-140
- Barros NB (2003) Diet of free-ranging and stranded sperm whales (*Physeter macrocephalus*) from the Gulf of Mexico. Mote Marine Laboratory: Mote Technical Reports:1-14
- Bathen KH (1972) On the seasonal changes in the depth of the mixed layer in the north Pacific Ocean. *Journal of Geophysical Research* 77:7138-7150
- Baumann-Pickering S, McDonald MA, Simonis AE, Solsona Berga A, Merckens KP, Oleson EM, Roch MA, Wiggins SM, Rankin S, Yack TM, Hildebrand JA (2013) Species-specific beaked whale echolocation signals. *J Acoust Soc Am* 134:2293-2301
- Baumann-Pickering S, Simonis AE, Oleson EM, Baird RW, Roch MA, Wiggins SM (2015) False killer whale and short-finned pilot whale acoustic identification. *Endangered Species Research* 28:97-108
- Benoit-Bird KJ (2009) The effects of scattering-layer composition, animal size, and numerical density on the frequency response of volume backscatter. *ICES Journal of Marine Science* 66:582-593
- Benoit-Bird KJ, Au WWL (2003) Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology* 53:364-373
- Benoit-Bird KJ, Au WWL, Brainard RE, Lammers MO (2001) Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically. *Marine Ecology Progress Series* 217:1-14

- Benoit-Bird KJ, Wursig B, Mcfadden CJ (2004) Dusky Dolphin (*Lagenorhynchus Obscurus*) Foraging in Two Different Habitats: Active Acoustic Detection of dolphins and their Prey. *Marine Mammal Science* 20:215-231
- Borets L (1986) Ichthyofauna of the Northwestern and Hawaiian submarine ranges. *Journal of Ichthyology* 26:1-13
- Bradford AL, Forney KA, Oleson EM, Barlow J (2013) Line-transect abundance estimates of cetaceans in the Hawaiian EEZ. NOAA PIFSC Working Paper WP-13-004
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford, UK
- Choy CA, Portner E, Iwane M, Drazen JC (2013) Diets of five important predatory mesopelagic fishes of the central North Pacific. *Marine Ecology Progress Series* 492:169-184
- Choy CA, Wabnitz CCC, Weijerman M, Woodworth-Jefcoats PA, Polovina JJ (2016) Finding the way to the top: how the composition of oceanic mid-trophic micronekton groups determines apex predator biomass in the central North Pacific. *Marine Ecology Progress Series* 549:9-25
- Clarke M, Young R (1998) Description and analysis of cephalopod beaks from stomachs of six species of odontocete cetaceans stranded on Hawaiian shores. *Journal of the Marine Biological Association of the United Kingdom* 78:623-641
- Clarke MR (1966) A Review of the Systematics and Ecology of Oceanic Squids. *Advances in Marine Biology* 4:91-300
- Clarke MR (1980) Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Reports* 37:1-324
- Clarke MR (1996a) Cephalopods as Prey. III. Cetaceans. *Philosophical Transactions: Biological Sciences* 351:1053-1065
- Clarke MR (1996b) The role of cephalopods in the world's oceans: general conclusions and the future. *Philosophical Transactions of the Royal Society-Ser B-Biological Sciences* 351:1105
- Dagorn L, Bach P, Josse E (2000) Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Marine Biology* 136:361-371
- De Robertis A, Higginbottom I (2007) A post-processing technique to estimate the signal-to-noise ratio and remove echosounder background noise. *ICES Journal of Marine Science* 64:1282-1291
- DeMartini EE, Friedlander AM (2006) Predation, endemism, and related processes structuring shallow-water reef fish assemblages of the NWHI. *Atoll Research Bulletin* 543:237-256
- Demer DA, Berger L, Bernasconi M, Bethke E, Boswell K, Chu D, Domokos R, Dunford A, Fassler S, Gauthier S, Hufnagle LT, Jech JM, Bouffant N, Lebourges-Dhaussy A, Lurton X, Macaulay GJ, Perrot Y, Ryan T, Parker-Stetter S, Stienessen S, Weber T, Williamson N (2015) Calibration of acoustic instruments. *ICES Cooperative Research Report* 326:1-133
- Doty MS, Oguri M (1956) The Island Mass Effect. *J Cons* 22:33-37
- Drazen JC, De Forest LG, Domokos R (2011) Micronekton abundance and biomass in Hawaiian waters as influenced by seamounts, eddies, and the moon. *Deep Sea Research Part I: Oceanographic Research Papers* 58:557-566
- Echoview Software Pty. Ltd. (2013) Echoview software, version 5.4. Echoview Software Pty. Ltd., Hobart, Australia.

- Escobar-Flores P, O'Driscoll RL, Montgomery JC (2013) Acoustic characterization of pelagic fish distribution across the South Pacific Ocean. *Marine Ecology Progress Series* 490:169-183
- ESRI (2011) ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute
- Foote KG, Vestnes G, Maclennan DN, Simmonds EJ (1987) Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Cooperative Research Report 144:1-81
- Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Marine Ecology Progress Series* 317:297–310
- Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Marine Ecology Progress Series* 230:253-264
- Giorli G, Neuheimer A, Drazen J, Copeland A, Au WWL (in revision) Deep sea animal density and size estimated using a Dual-frequency IDentification SONar (DIDSON) offshore the island of Hawaii.
- Gjosæter J, Kawaguchi K (1980) A Review of the world resources of mesopelagic fish. FAO Fisheries Technical Paper No 193:1-151
- Gooding RM (1984) Trapping Surveys for the Deepwater Caridean Shrimps, *Heferocarpus hewigatus* and *H. ensifer*, in the Northwestern Hawaiian Islands.
- Gove JM, McManus MA, Neuheimer AB, Polovina JJ, Drazen JC, Smith CR, Merrifield MA, Friedlander AM, Ehses JS, Young CW, Dillon AK, Williams GJ (2016) Near-island biological hotspots in barren ocean basins. *Nature Communications* 7:10581
- Hazen EL, Johnston DW (2010) Meridional patterns in the deep scattering layers and top predator distribution in the central equatorial Pacific. *Fisheries Oceanography* 19:427-433
- Hazen EL, Nowacek DP, St Laurent L, Halpin PN, Moretti DJ (2011) The relationship among oceanography, prey fields, and beaked whale foraging habitat in the Tongue of the Ocean. *PLoS One* 6:1-10
- Hersey JB, Moore HB (1948) Progress Report on Scattering Layer Observations in the Atlantic Ocean. *American Geophysical Union* 29:341-354
- Kelley C, Moffitt R, Smith JR (2006) Mega-to micro-scale classification and description of bottomfish essential fish habitat on four banks in the Northwestern Hawaiian Islands. *Atoll Research Bulletin* 543:319-332
- Klumov SK, Yukhov VL (1975) *Mesonychoteuthis hamiltoni* Robson 1925 (Cephalopoda, Oegopsida) and its role in feeding habits of sperm whales from the Antarctic waters Rep Antarctic Commission 14:159-189
- Kozlov AN (1995) A review of the trophic role of mesopelagic fish of the family Myctophidae in the Southern Ocean ecosystem. *CCAMLR Science* 2:71-77
- Lammers MO, Brainard RE, Au WWL (2006) Diel trends in the medopelagic biomass community of the Northwestern Hawaiian Islands observed acoustically. *Atoll Research Bulletin* 543:391-407
- Markaida U, Sosa-Nishizaki O (2003) Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Journal of the Marine Biological Association of the UK* 83:507-522

- Maynard SD, Riggs FV, Walters CF (1975) Mesopelagic micronekton faunal composition, standing stock, and diel vertical migration. *Fishery Bulletin* 73:726-736
- NOAA (2006) Northwestern Hawaiian Islands Proposed National Marine Sanctuary Draft Environmental Impact Statement and Management Plan. Draft Management Plan II
- Ohizumi H (2002) Dietary studies of toothed whales: A review and new topics. *Fisheries science* 68:264-267
- Parry M (2006) Feeding behavior of two ommastrephid squids *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis* off Hawaii. *Marine Ecology Progress Series* 318:229-235
- Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* 55:467-481
- Phillips KL, Jackson GD, Nichols PD (2001) Predation on myctophids by the squid *Moroteuthis ingens* around Macquarie and Heard Islands: stomach contents and fatty acid analyses. *Marine Ecology Progress Series* 215:179-189
- Polovina JJ, Haight WR, Moffitt RB, Parrish FA (1995) The Role of Benthic Habitat, Oceanography, and Fishing on the Population Dynamics of the Spiny Lobster, *Panulirus marginatus* (Decapoda, Palinuridae), in the Hawaiian Archipelago. *Crustaceana* 68:203-212
- R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rankin S, Barlow J, Oswald J, Ballance L (2008) Acoustics studies of marine mammals during seven years of combined visual and acoustic line-transect surveys for cetaceans in the Eastern and Central Pacific Ocean. NOAA Technical Memorandum NMFS:1-69
- Reid SB, Hirota J, Young RE, Hallacher LE (1991) Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. *Marine Biology* 109:427-440
- Roger C, Grandperrin R (1976) Pelagic food webs in the tropical Pacific. *Limnology and Oceanography* 21:731-735
- Schlacher TA, Baco AR, Rowden AA, O'Hara TD, Clark MR, Kelley C, Dower JF (2014) Seamount benthos in a cobalt-rich crust region of the central Pacific: conservation challenges for future seabed mining. *Diversity and distributions* 20:491-502
- Seagars DJ, Henderson JR (1985) Cephalopod remains from the stomach of a shortfinned pilot whale collected near Santa Catalina Island, California. *Journal of Mammalogy* 66:777-779
- Simmonds J, MacLennan DN (2005) *Fisheries Acoustics: Theory and Practice*. Blackwell Publishing
- Sinclair EH (1992) Stomach Contents of Four Short-Finned Pilot Whales (*Globicephala macrorhynchus*) from the Southern California Bight. *Marine Mammal Science* 8:76-81
- Spitz J, Cherel Y, Bertin S, Kiszka J, Dewez A, Ridoux V (2011) Prey preferences among the community of deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic. *Deep Sea Research Part I: Oceanographic Research Papers* 58:273-282
- Stewart BS, Antonelis GA, Baker JD, Yochem PK (2006) Foraging biogeography of the Hawaiian monk seal in the Northwestern Hawaiian Islands. *Atoll Research Bulletin* 543:131-145
- Tont SA (1976) Deep scattering layers: patterns in the Pacific. *California Cooperative Oceanic Fisheries Investigation* 112-117

- Williams ID, Baum JK, Heenan A, Hanson KM, Nadon MO, Brainard RE (2015) Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS One* 10:1-19
- Wood SN (2006) *Generalized Additive Models: An introduction with R*. Chapman and Hall/CRC
- Yeh J, Drazen JC (2009) Depth zonation and bathymetric trends of deep-sea megafaunal scavengers of the Hawaiian Islands. *Deep Sea Research Part I: Oceanographic Research Papers* 56:251-266
- Young JW, Hunt BPV, Cook TR, Llopiz JK, Hazen EL, Pethybridge HR, Ceccarelli D, Lorrain A, Olson RJ, Allain V, Menkes C, Patterson T, Nicol S, Lehodey P, Kloser RJ, Arrizabalaga H, Anela Choy C (2015) The trophodynamics of marine top predators: Current knowledge, recent advances and challenges. *Deep Sea Research Part II: Topical Studies in Oceanography* 113:170-187
- Young RE (1983) Oceanic bioluminescence: An overview of general functions. *Bulletin of Marine Science* 33:829-845

CHAPTER III

INFLUENCES OF TEMPORAL CHANGES IN PELAGIC SCATTERING LAYERS ON SHORT-FINNED PILOT WHALES BEHAVIOR

Adrienne M Copeland¹, Whitlow W. L. Au¹, Giacomo Giorli¹, and Jeffrey Polovina²

¹Hawaii Institute of Marine Biology, University of Hawaii, PO BOX 1348 Kaneohe, Hawaii
96744

²Pacific Islands Fisheries Science Center, NOAA, 1845 Wasp Blvd., Bldg. 176 Honolulu, HI
96818

Abstract

To understand the distribution of deep diving odontocetes, it is important to investigate the relationship between the foraging whales and their prey. Short-finned pilot whales mainly feed on squid and occasionally fish. Foraging short-finned pilot whales off the Island of Hawaii were located using trained visual observers and a passive acoustic hydrophone. A 500 meter by 500 meter survey box was set up over the foraging sites. A two-frequency split-beam echosounder collected micronekton backscatter over foraging and non-foraging control sites of the same location and similar time of day. Nautical Area Scattering Coefficient (NASC) ($\text{m}^2\text{nmi}^{-2}$) profiles were compared over the water column between foraging and non-foraging populations to analyze the relationship between micronekton density and short-finned pilot whale foraging. Using a generalized additive mixed model and a generalized linear mixed model, it was determined that short-finned pilot whales were able to exploit the daily variation of micronekton preferring to forage when the relative biomass was higher and the deep scattering layer was found at shallower depths.

Keywords: Short-finned Pilot Whale, Foraging, Backscatter, Temporal

Introduction

The term “patch dynamics” was first quantified by Thompson (1978) describing the dynamics of a system’s heterogeneity (patches) (Pickett & White 1985). As seen in terrestrial systems, biological variability can persist on a multitude of spatial and temporal scales (Delcourt et al. 1983). This patchiness has also been documented in marine environments and can also exist on a diversity of spatial scales from meters to thousands of kilometers and time scales from hours to years (Steele 1978) with the implications affecting organisms ranging from small plankton (Steele 1978) to larger marine mammals (Benoit-Bird & Au 2003, Woodworth et al. 2012). Spatial variability in the marine environment with patchiness of primary productivity and prey abundance in pelagic waters can lead to the heterogeneous distribution and aggregations of higher trophic level predators (Benoit-Bird & Au 2003, Woodworth et al. 2012). Patchiness of productive waters can be enhanced by transient processes such as cyclonic and anticyclonic eddies due to the convergent and divergent zones of currents that upwell and downwell water increasing the local nutrients and phytoplankton (Seki et al. 2001) and zooplankton (Landry et al. 2008). Patches due to eddies have been documented to aggregate top predators including melon-headed whales, *Peponocephala electra*, off the Hawaiian Islands with whale tracks being focused toward the outer edge of the cyclonic eddies (Woodworth et al. 2012) providing further evidence of a link between primary producers and high-level consumers, with the melon headed whales foraging mostly on pelagic and mesopelagic squid and fish (Best & Shaughnessy 1981, Sekiguchi et al. 1992, Spitz et al. 2011). Spatially persistent patchiness of pelagic organisms can be enhanced by proximity to land, with surface productivity being higher closer to shore, named the island mass effect (Doty & Oguri 1956). This increased productivity has been documented throughout the Pacific Ocean with

higher biomass of phytoplankton being found closer to islands and atolls (Gilmartin & Revelante 1974, Gove et al. 2016). As seen in the previous chapter as well as Domokos (2009), the proximity to land appears to also influence the distribution of higher trophic levels with relative micronekton biomass being higher closer to land. Micronekton are organisms ranging in size from 2 cm - 20cm, including abundant small fishes (mostly myctophids), crustaceans (mostly larger euphausiids and shrimp), and cephalopods (Young 1983, Reid et al. 1991). Near island aggregations of micronekton appear to attract short-finned pilot whales in the Northwestern Hawaiian Islands (previous chapter) as well as the Kona coast of the Island of Hawaii (Abecassis et al. 2015). Short-finned pilot whales forage mostly on squid and occasionally fish (Clarke 1996a, Pauly et al. 1998) and these squid feed on micronekton (Clarke 1996b, Phillips et al. 2001, Ohizumi 2002, Markaida & Sosa-Nishizaki 2003, Parry 2006) demonstrating both a direct and indirect link between the spatial patchiness of micronekton and whale distribution, and signifies that short-finned pilot whales are able to exploit the spatial variability or patchiness of their prey as well as the forage items of their prey.

In addition to spatial variability in prey fields temporal variability is likely to exist but little is known about short-finned pilot whales' ability to exploit such variability along with the spatial variability of their prey or their prey's forage. To further understand the link between temporal variability of ocean organism biomass and short-finned pilot whale foraging activity, the authors investigated if: (1) there was a daily change in the horizontal micronekton backscatter and composition, (2) if the vertical structure of micronekton changes temporally, and (3) if these changes were correlated with short-finned pilot whale foraging. Since a relationship between the locations of foraging short-finned pilot whales and the spatial variability of micronekton has

been documented along the Kona coast of the Island of Hawaii (Abecassis et al. 2015), the connection with the temporal variability will be assessed in this paper in this area.

Methods

Data Collection

The data were collected at four sites (PW0, PW1, PW2, and PW3) in leeward waters of Hawaii Island (Figure 1), during June 2013 and February 2014. During June 2013, data were collected onboard the National Oceanic and Atmospheric Administration (NOAA) R/V Oscar Elton Sette, while the February 2014 data were collected aboard the Schmidt Ocean Institute (SOI) R/V Falkor. Short-finned pilot whales were located from both platforms using trained visual observers. Foraging individuals were confirmed by the presence of echolocation clicks using a single hydrophone or hydrophone array deployed in the vicinity of the whales. The echolocation clicks of this species were easily detectable audibly using the known frequency range of the species documented in the Hawaiian Islands with Baumann-Pickering et al. (2015) reporting an average center frequency of 25.2 kHz.

During the June 2013 cruise, a six-element hydrophone array with a 250 kHz sampling rate was used to localize the vocalizing whales and confirm foraging. The hydrophones in the array included APC piezoceramic elements with an approximate sensitivity of -150 ± 5 dB re 1 V/mPa between 500 Hz - 400 kHz, and Teledyne-Reson TC4013 hydrophone elements used for recording higher frequencies had a sensitivity of approximately -211 ± 3 dB re 1 V/ μ Pa between 1 kHz - 170 kHz. From the array, the approximate location of the signaler was further validated using a phone-pair bearing in the digital signal-processing program ISHMAEL and WhaleTrak to graphically map the location. During February 2014, the whale location was estimated by

observers, and foraging was confirmed using a single hydrophone with a sensitivity of about 160 dB re 1V/uPa and recorded on a Microtrack recorder with a sample rate of 96 kHz.

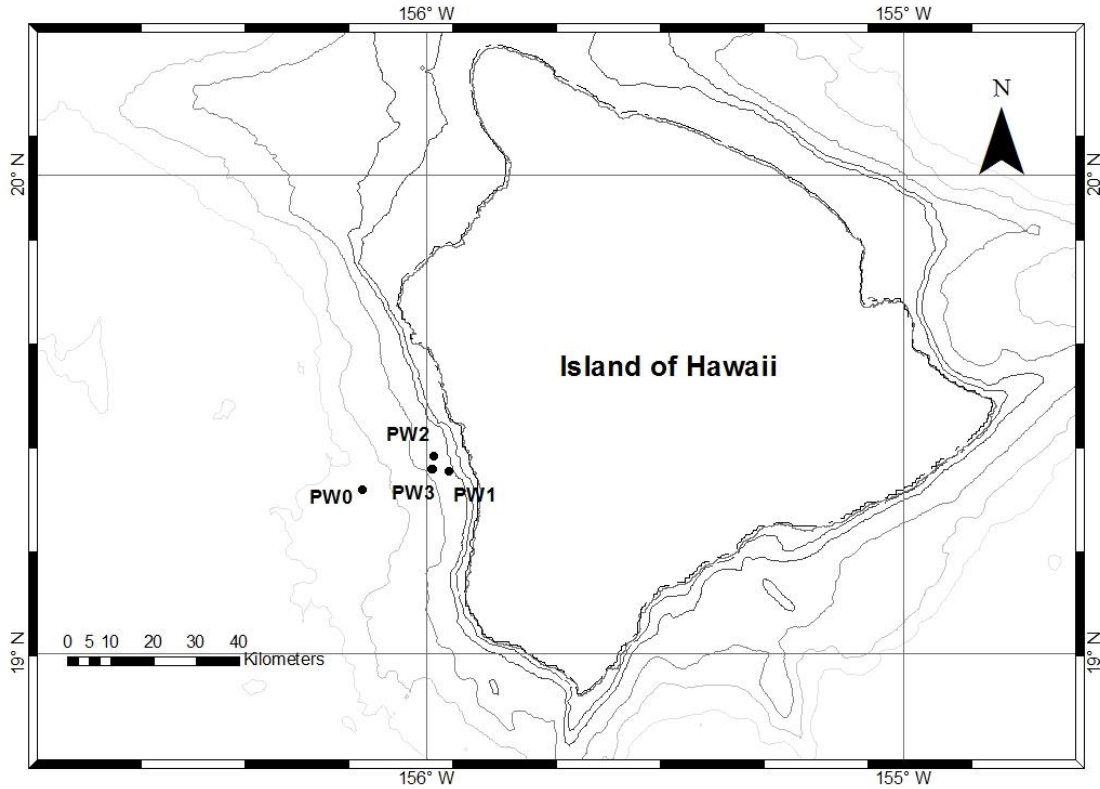


Figure 1: Sample locations in the leeward waters of the Island of Hawaii.

Once foraging was confirmed, a 500 m by 500 m sample grid was centered at four sites over the localized clicking whale (Figure 2). Relative micronekton density of the area was estimated from in situ acoustic backscatter data collected on both platforms using a calibrated hull mounted Simrad EK60 split-beam two frequency echosounder with the 38 kHz and 70 kHz frequencies operating at 2000W and 750 W, respectively. The pulse duration for both frequencies was set to 512 μ s. The frequencies were calibrated using a 38.1 mm diameter tungsten-carbide reference sphere and standard techniques described in Foote et al. (1987), Demer et al. (2015).

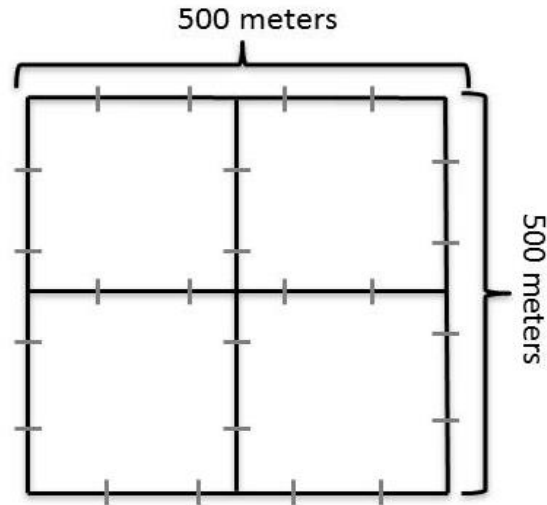


Figure 2: Pictorial representation of the 500 by 500 meters fine scale (grid) sampling design to measure the nautical area scattering coefficients (NASC) near foraging short-finned pilot whales and during control times when the foraging whales were absent. The grey dashes are the 100 meter sampling increments.

A threshold of -80 dB mean volume backscattering strengths (S_v ; units: dB re 1 m^{-1}), a proxy for relative density (Simmonds & MacLennan 2005), was used to remove backscatter from plankton and other smaller organisms. Noise and missing data were excluded in ECHOVIEW 5.4 (Echoview Software Pty. Ltd. 2013) using standard cleaning techniques (De Robertis & Higginbottom 2007). Mean volume backscattering strength was binned into cells with 100 m horizontal resolution and 10 m vertical resolution down to 1060 m and 670 m for the 38 kHz and 70 kHz frequencies. The depth of the sampling was limited by the frequency of the transducers with the 38 kHz penetrating deeper; whereas the 70 kHz signal can better resolve smaller scatterers. The cells were vertically integrated to obtain the nautical area scattering coefficients (NASC) in m^2/nmi^2 . Each 500 X 500 m grid sample (Figure 2) was averaged horizontally to obtain one value for each 10 meter vertical depth bin.

Trawling was not available for accurate sizing and species identification of the organisms within the area of interest, so the NASC represents the relative biomass of scattering organisms assuming that the daily scattering properties of the micronekton do not change significantly

(Simmonds & MacLennan 2005, Domokos 2009). The change in volume backscattering strength (δS_{V70-38}) (dB re 1 m⁻¹) calculated by subtracting the 38 kHz from the 70 kHz was used to investigate relative species composition. Frequency differencing has been used successfully in the past to determine species composition (Simmonds & MacLennan 2005, De Robertis & Higginbottom 2007) based on frequency-dependent backscatter characteristics of organisms (Fernandes et al. 2006).

Analysis

All statistical analyses were done using R 3.0.1 (R Development Core Team 2014). Micronekton formed discrete scattering layers that were defined by the 15th percentile threshold of the NASC median values of each vertical depth bin for all the data collected. Two layers were defined using this technique, a shallow scattering layer (SSL) and a deep scattering layer (DSL). A mixed-effects model from the lme4 package (Bates et al. 2015) was used to test the difference between the shallow and deep layer (“Layer” parameter) NASC values when whales were present and absent (“Whale” parameter), with the variance of the random intercept of sample location (“ α_i ”). The log (NASC+1) was tested for the different locations ($i = 1, \dots, 4$). The “Whale” parameter for equations 1 - 3 equated to 1 for whales foraging presence and 0 for the control and the β parameter for each equation was the intercept.

$$\log(\text{NASC} + 1)_i = \beta + \text{Layer}_i + \text{Whale}_i + \text{Layer}_i * \text{Whale}_i + \alpha_i \quad (1)$$

$$\alpha_i \sim N(0, \sigma^2_{\text{Location}})$$

The vertical structural differences of the scattering layers were identified using a Generalized Additive Mixed Model (GAMM) from the gamm4 package (Wood & Scheipl 2014). The GAMM equation is detailed below with a separate smoother function applied to the depth bins for the foraging and control samples.

$$\log(\text{NASC} + 1)_i = \beta + \text{Whale}_i + f_k(\text{Depth}_i) + \alpha_i \quad (2)$$

$$\alpha_i \sim N(0, \sigma^2_{\text{Location}})$$

The random factor “ α_i ” accounted for the variation between the four sites. “Depth” was the depth of the NASC value at the 10 meter vertical depth bins. The categorical variable “Whale” represents the different treatments with whale foraging presence and the control. A smoothing function was applied to both whale treatments (“k”). Again “i” denotes the different locations sampled ($i = 1, \dots, 4$).

A Generalized Additive Model (GAM) from the mgcv package (Wood 2006) was used to identify the change in species composition for the four locations separately.

$$\delta S_{V70-38 \text{ location}} = \beta + \text{Whale} + f_k(\text{Depth}) \quad (3)$$

The dB difference (δS_{V70-38}) was tested separately for each location. The δS_{V70-38} was calculated by Sv of 70 kHz minus the Sv of 38 kHz signal. The “Depth” parameter is the depth for each 10 meter vertical depth bin, while “Whale” was the foraging presence and control. A smoothing function was applied for each whale treatments (“k”).

The patchiness of the backscatter (Sv) was assessed using the index of aggregation (IA) which is high when small areas are denser than the surrounding areas. This metric was calculated from the backscatter using the EcoMetrics Python script developed by and described in (Urmy et al. 2012).

Results

The backscatter at the sampling locations formed two discrete layers varying in depth ranges for the two frequencies. The 38 kHz scattering layers were from 0 – 250 meters for the SSL and 310 – 1060 for the DSL (Figure 3); whereas, the 70 kHz scattering layers were from 0 – 290 meters for the SSL and from 320 – 670 meters for the DSL (Figure 3). These layers were defined based

on the median threshold of the NASC value at $0.3412 \text{ m}^2/\text{nmi}^2$ for the 38 kHz signal and $0.3496 \text{ m}^2/\text{nmi}^2$ for the 70 kHz signal (Figure 3: vertical line).

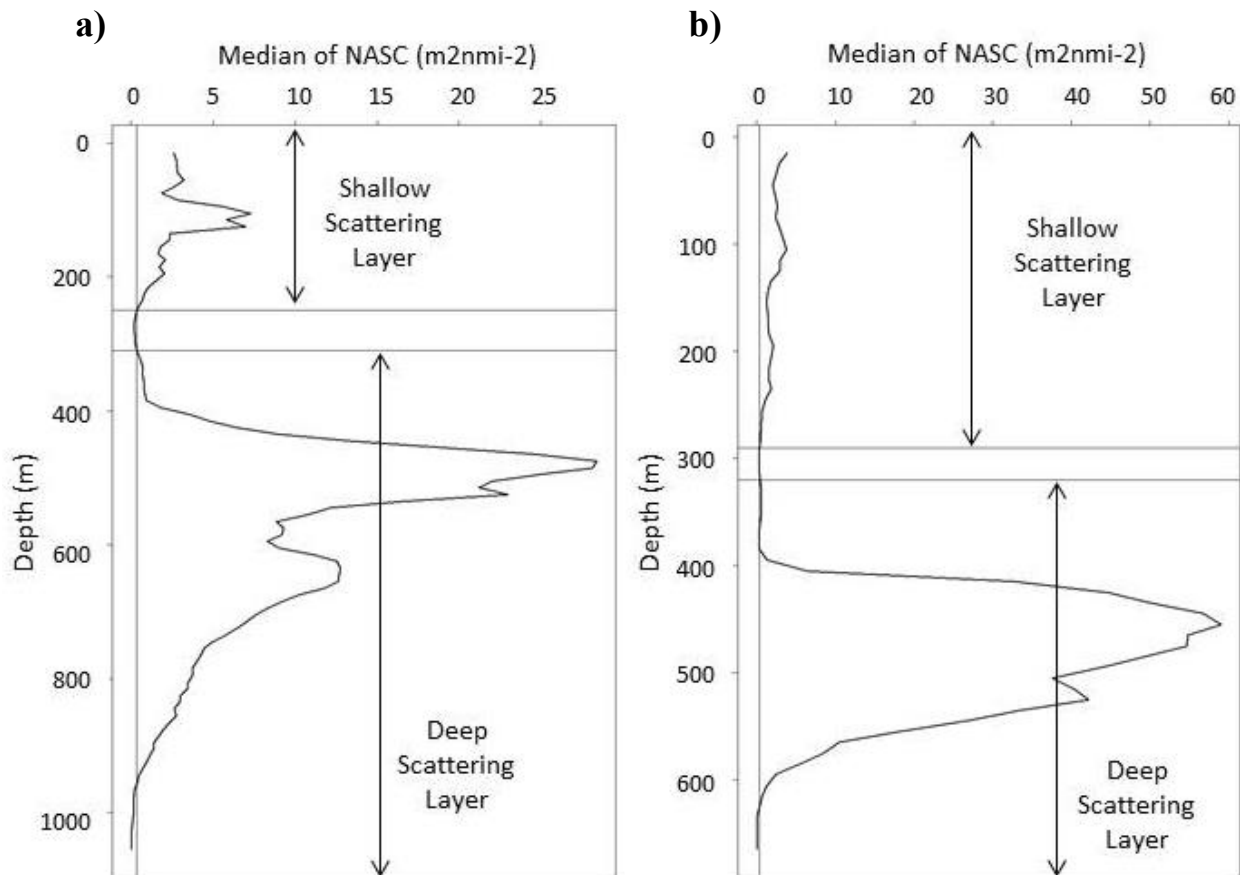
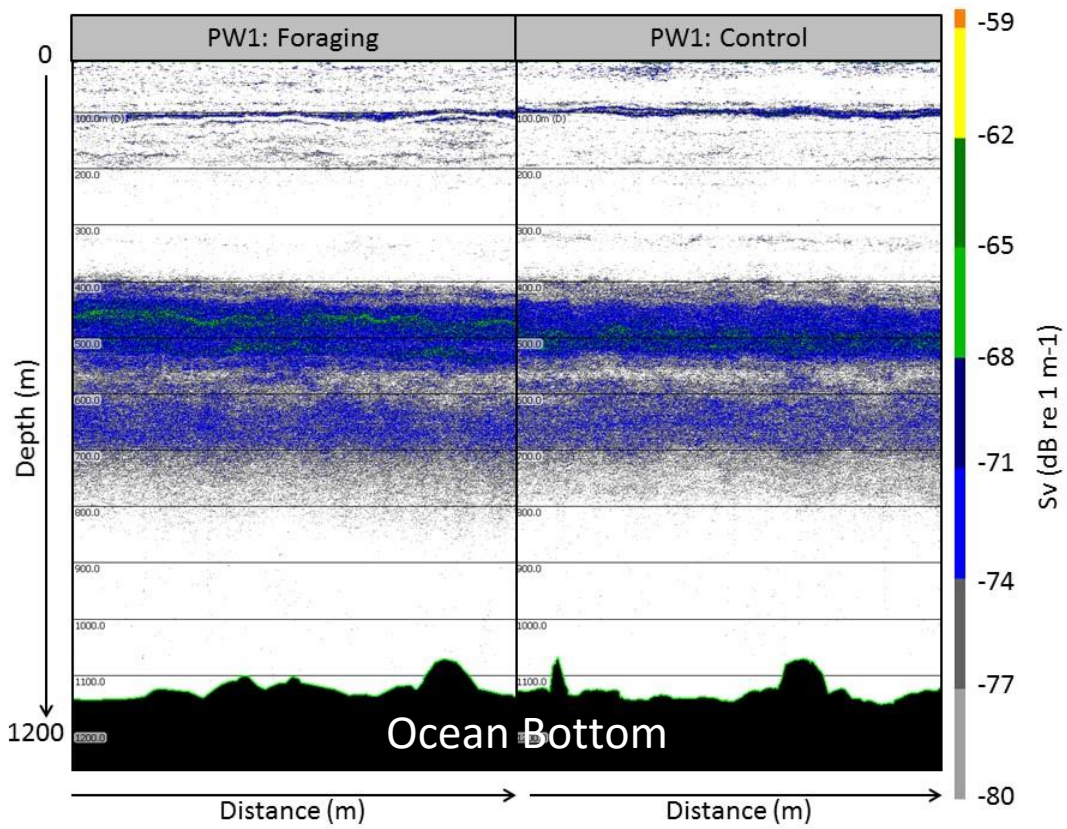
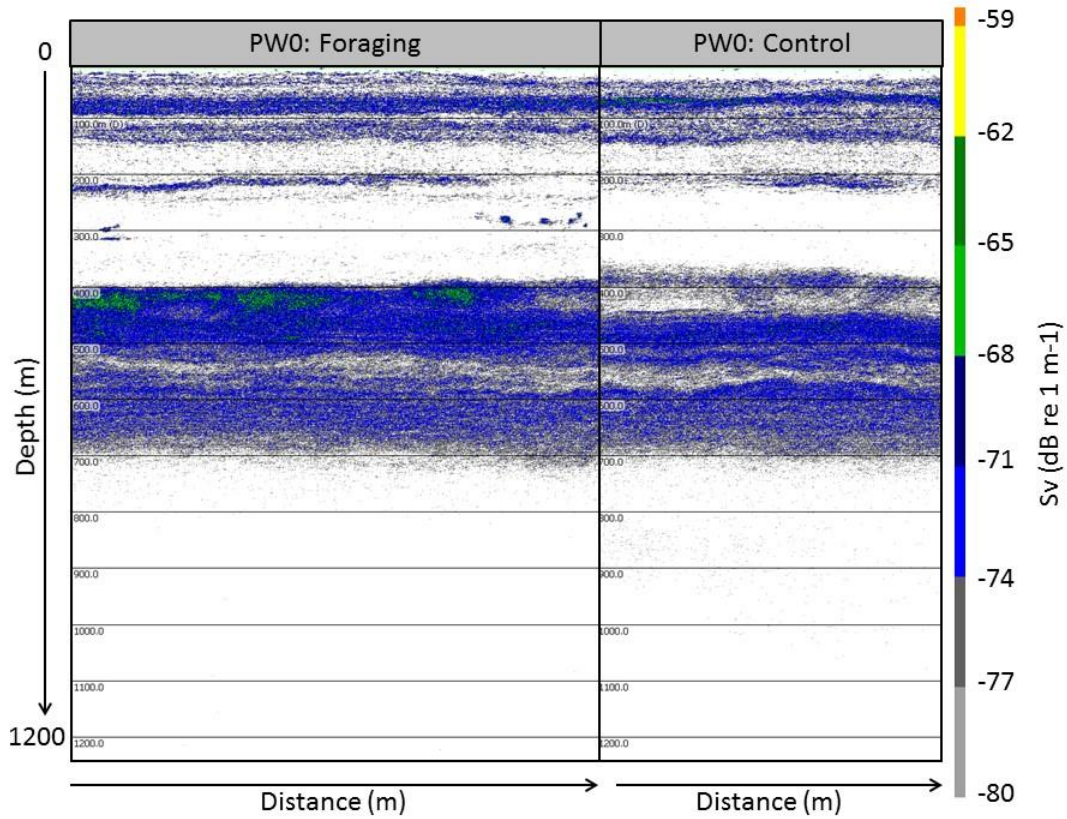


Figure 3: The separation of the shallow (SSL) and deep (DSL) scattering layer for: a) 38 kHz and b) 70 kHz frequencies. The median threshold used to define the scattering layers for the each frequency was denoted by a vertical line at $0.3412 \text{ m}^2/\text{nmi}^2$ for the 38 kHz signal and $0.3496 \text{ m}^2/\text{nmi}^2$ for the 70 kHz signal. For the 38 kHz, the SSL was defined from 0 – 250 m and the DSL was defined from 310 – 1060 m. The 70 kHz SSL and DSL were defined from 0 – 290 m and from 320 – 670 m, respectively.

NASC values were calculated for locations containing foraging short-finned pilot whales once on June 23, 2013 (PW0), twice on February 19, 2014 (PW1 and PW2), and once on February 20, 2014 (PW3) (Figure 1). Four controls were collected at each of the study sites, as close to the same time of day as the whale surveys but sometimes limited by other cruise tasks. The date and time of data collection is summarized in Table 1 and visualized in Figure 4.

Table 1: Summary of the data collected during this study.

Location	Sample	Date	Time (HST)	Platform
PW0	Foraging	6/23/2013	16:20 - 17:38	R/V Oscar Elton Sette
	Control	6/24/2013	06:14 - 07:33	R/V Oscar Elton Sette
PW1	Foraging	2/19/2014	08:15 - 08:53	R/V Falkor
	Control	2/20/2014	08:14 - 08:51	R/V Falkor
PW2	Foraging	2/19/2014	11:31 - 12:11	R/V Falkor
	Control	2/20/2014	10:30 - 11:10	R/V Falkor
PW3	Foraging	2/20/2014	14:05-14:45	R/V Falkor
	Control	2/21/2014	9:38 - 10:14	R/V Falkor



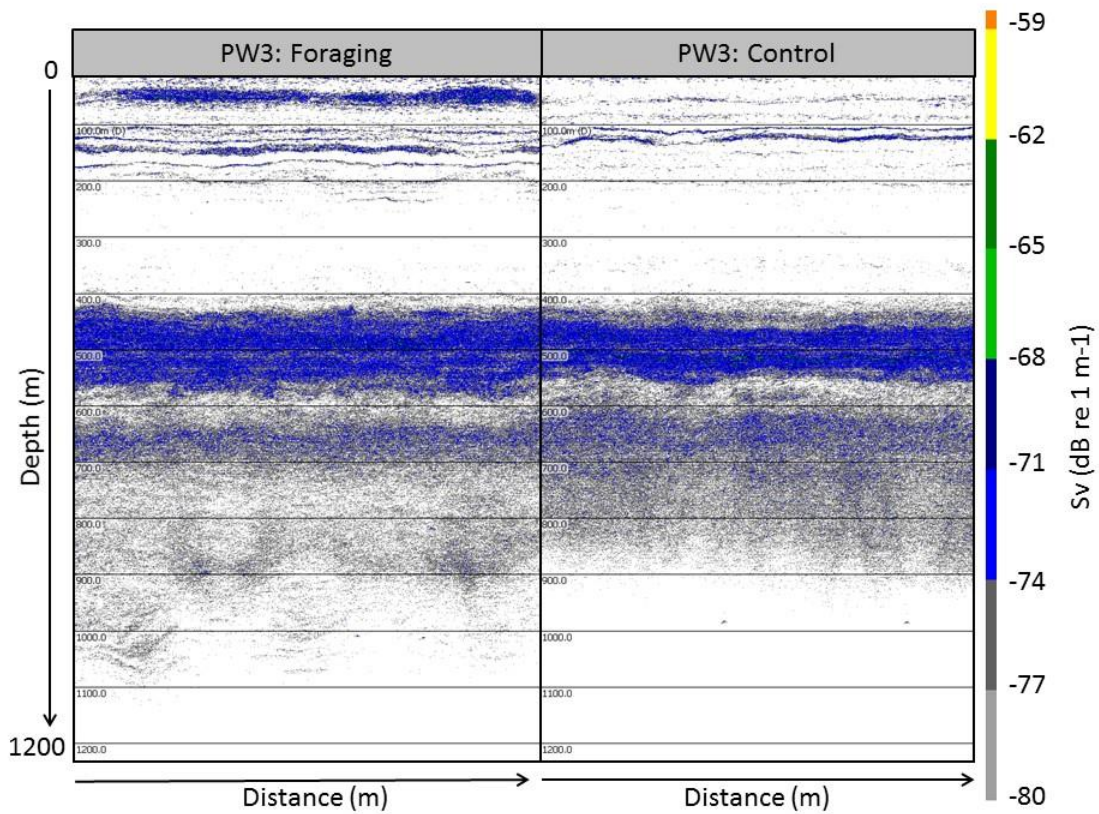
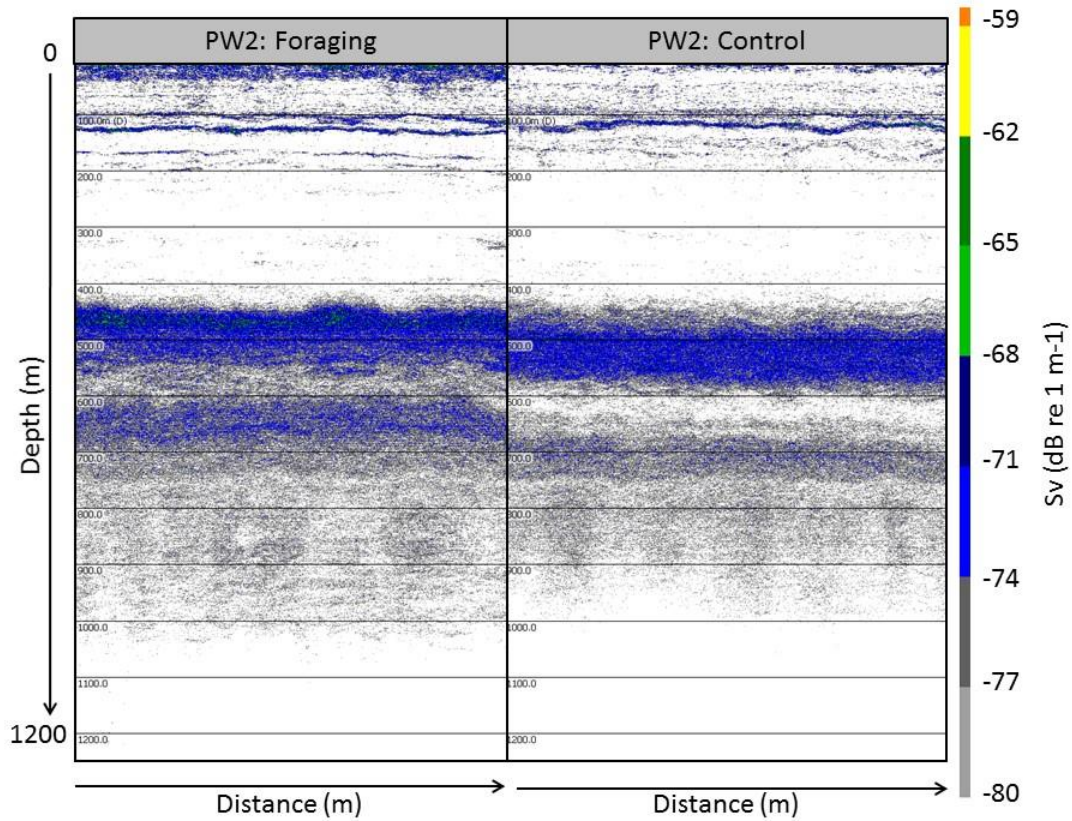


Figure 4: The 38 kHz backscatter (S_v ; units: $\text{dB re } 1 \text{ m}^{-1}$) values plotted in color as a function of depth (m) and the distance along the fine scale grid sample (m) for each location: PW0, PW1, PW2, and PW3. The S_v values are represented in the color bar to the right of each graph. The more green and yellow the color the higher the backscatter; conversely, the more grey the color the lower the backscatter.

Accounting for sampling location variability, there were higher NASC values in the deep scattering layer than the shallow layer for both the 38 kHz (GLMM: $\chi^2 = 339.685$, $p < 0.0001$) and the 70 kHz (GLMM: $\chi^2 = 2143.797$, $p < 0.0001$) frequencies (Figure 5). This relationship was expected because fewer scattering organisms are located in the SSL during the daytime. The inverse is seen at nighttime after a subset of the DSL organisms migrate to the surface (Maynard et al. 1975). In past trawl samples off the Island of Oahu, approximately 90% of the mean total micronekton standing stock biomass was found deeper than 400 m during the daytime (Maynard et al. 1975, Drazen et al. 2011). The NASC values for scattering organisms was higher during foraging surveys than during control surveys for both frequencies: 38 kHz (GLMM: $\chi^2 = 113.720$, $p < 0.0001$) and 70 kHz (GLMM: $\chi^2 = 6.884$, $p = 0.009$) (Figure 5). However the difference in scatterers for the 70 kHz was less pronounced most likely due to the depth limit of 670 meters. The interaction between the scattering layer and whale presence for both frequencies, 38 kHz (GLMM: $\chi^2 = 17.817$, $p < 0.0001$) and 70 kHz (GLMM: $\chi^2 = 26.747$, $p < 0.0001$), was highly significant suggesting a mixed pattern of effects. The 38 kHz shallow and deep scattering layers had higher NASC values during foraging than control (Figure 5). The backscatter was visually higher in the SSL and DSL for all locations during foraging compared to the control (Figure 4). However, for the 70 kHz signal only the shallow scattering layer had significantly higher NASC values during foraging (Figure 5). There was no difference in NASC values in the defined deep scattering layer at 70 kHz.

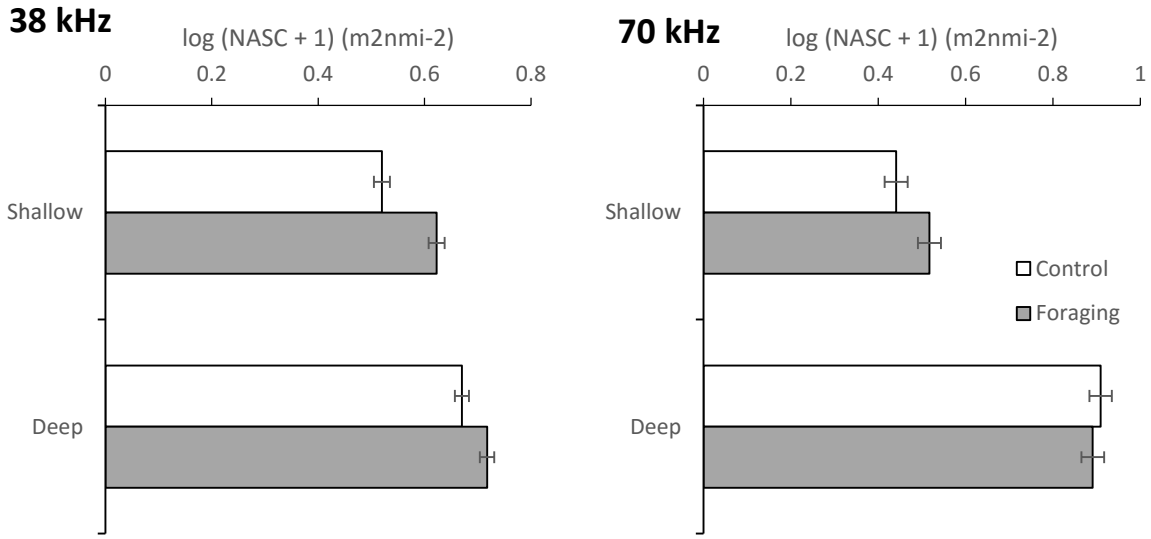
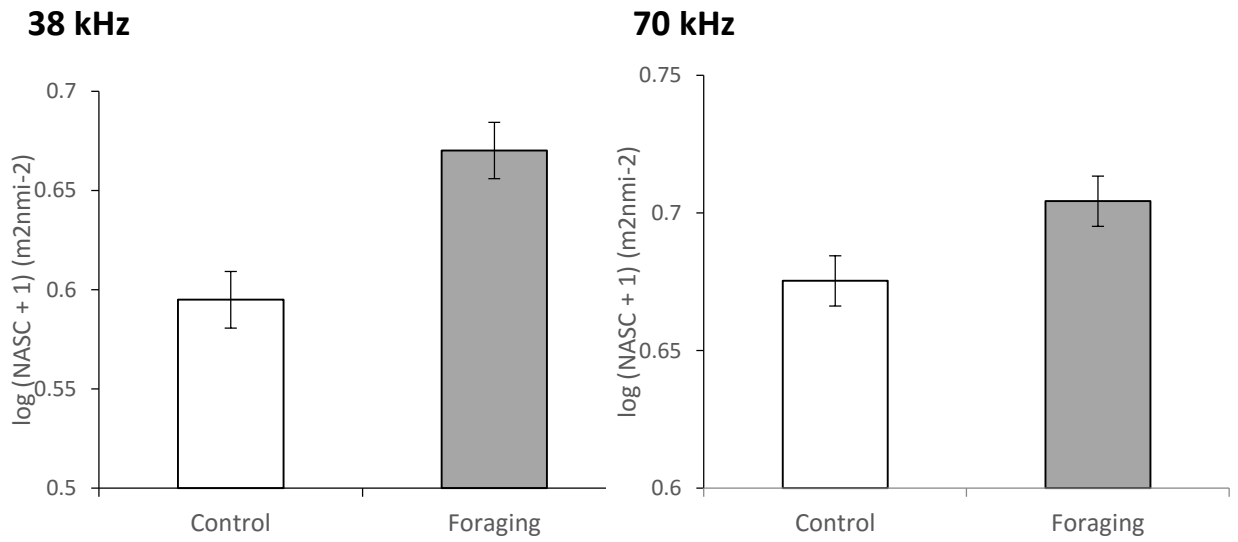
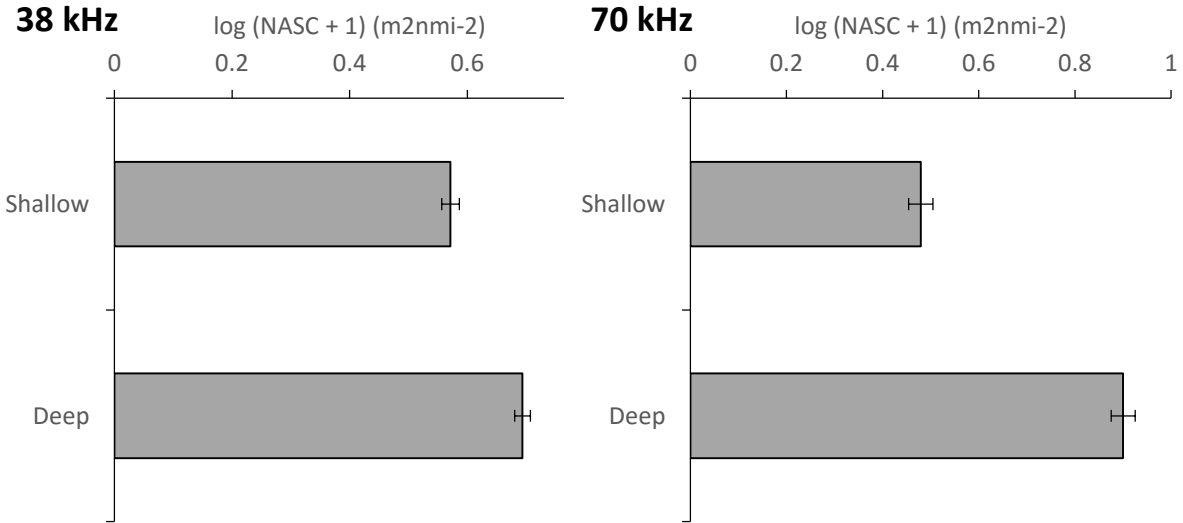


Figure 5: Results of the mixed effects model. The left column contains the graphs of the 38 kHz

signal and the right column is the 70 kHz. The top graphs are the shallow scattering layer versus deep scattering layer test. The middle graphs are the test of the control versus foraging for the log of NASC. The bottom graph is the interaction test of control and foraging for each scattering layer. For this plot, the control is colored white and the foraging samples are in grey.

A significantly higher NASC during foraging (38 kHz: GAMM: $t = 5.225$, $p < 0.0001$; 70 kHz: GAMM: $t = 18.73$, $p < 0.0001$) was found when not separating the data into their respective layers but by investigating the water column's vertical distribution of the scattering organisms while still accounting for sampling location variability for both frequencies. The smoother of the 38 kHz data identified an increase in NASC from about 900 – 1060 meters during foraging as denoted by the black line in Figure 6. This is further demonstrated by the histograms of the NASC values for this depth range (Figure 7) where mean and maximum NASC values are greater for the foraging samples than the control. Further in Figure 4, locations PW2 and PW3 clearly show an extension of the DSL past 900 m only during foraging and location PW1 shows an extension past 800 m only during foraging. The depth of the bottom of the DSL is shallower for the control at PW0, PW1, and PW3 locations. This relationship was not seen in the 70 kHz results due to depth limitation. The vertical structure smoothers for both frequencies identified a shallowing of the deep scattering layer for the foraging samples with a peak at about 515 meters shifting to about 495 meters for the 38 kHz and 495 m shifting to 475 m for the 70 kHz signal (Figure 6). Additionally there was a greater maximum NASC value for the foraging samples at about 500 meters for both frequencies when compared to the control samples (Figure 6).

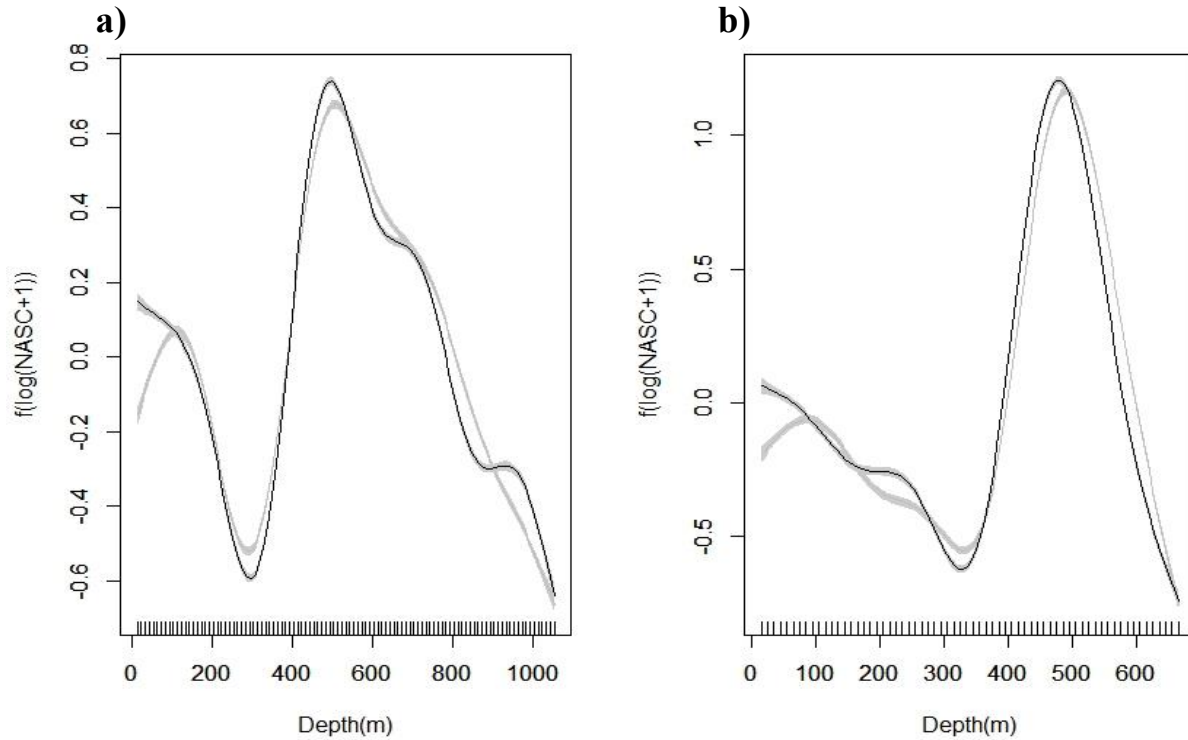


Figure 6: Generalized additive model with a smoother of depth as a function of the log (NASC +1) for a) 38 kHz and b) 70 kHz signal. The foraging smoother is denoted by the black line and the grey is the control. Tick marks on the x-axis correspond to the sampling distribution. The grey shading indicates two times the standard error for each smooth function.

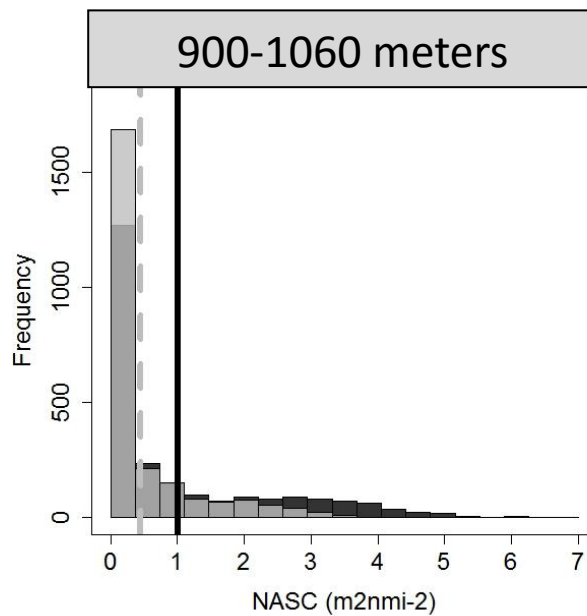


Figure 7: Histogram of the NASC values for the depth range from 900 – 1060 meters. The control histogram in grey is plotted on top of the foraging samples in black. The mean for the foraging samples is indicated by a vertical black line.

control samples is represented by the grey dashed line and the foraging mean is denoted by a black solid line.

The composition of the scattering layers was investigated using the Sv (dB re 1 m⁻¹), “dB difference,” of the 70 kHz frequency minus the 38 kHz. The mean of the dB difference across depth varied for the four locations (Figure 8). There did not appear to be a clear pattern other than a strong positive peak from about 400 – 500 meters at the four locations. There was a strong daily variation of the mean for the four locations with the offshore location, PW0, having what appears to be the least daily variation even with one of the larger time differences between the control and foraging samples for this location (Figure 8). Modeling the data for the four locations, when comparing the whale foraging to the control, there was a significant daily variation for all four locations: PW0: GAM: $t = -17.25$, $p \leq 0.0001$; PW1: GAM: $t = 3.933$, $p \leq 0.0001$; PW2: GAM: $t = -41.76$, $p \leq 0.0001$; PW3: GAM: $t = 17.63$, $p \leq 0.0001$ (Figure 9). While the modeled smoothers of the dB difference for all four locations were significantly different from the control, the trend of the offshore location (PW0) seemed to vary less than the three near-shore locations (PW1, PW2, and PW3) (Figure 9).

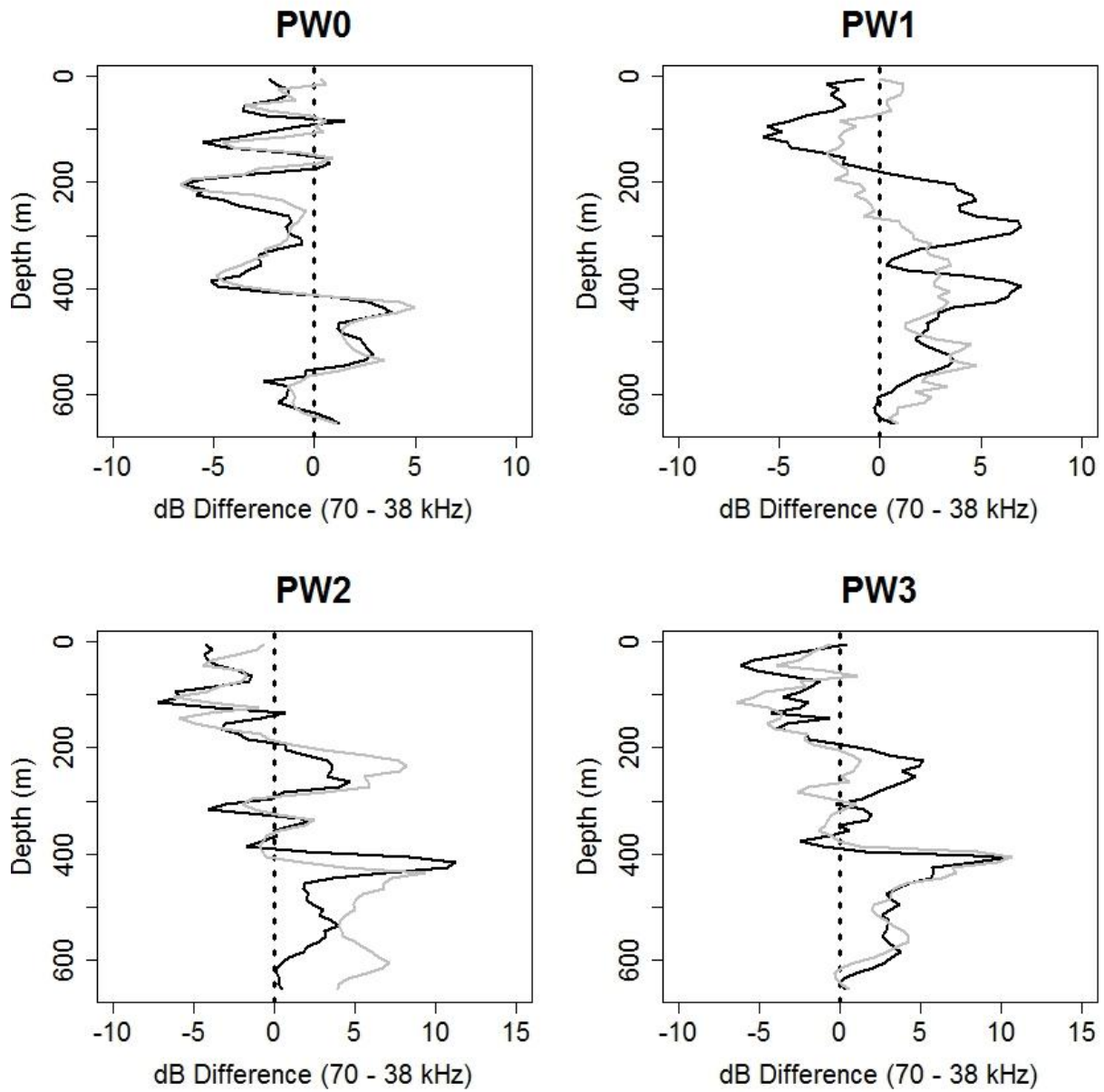


Figure 8: The mean of the volume backscattering strengths (dB) difference between the 70 and 38 kHz frequency across depth. The black lines indicate the foraging samples and the grey is the control for the four locations: PW0, PW1, PW2, and PW3.

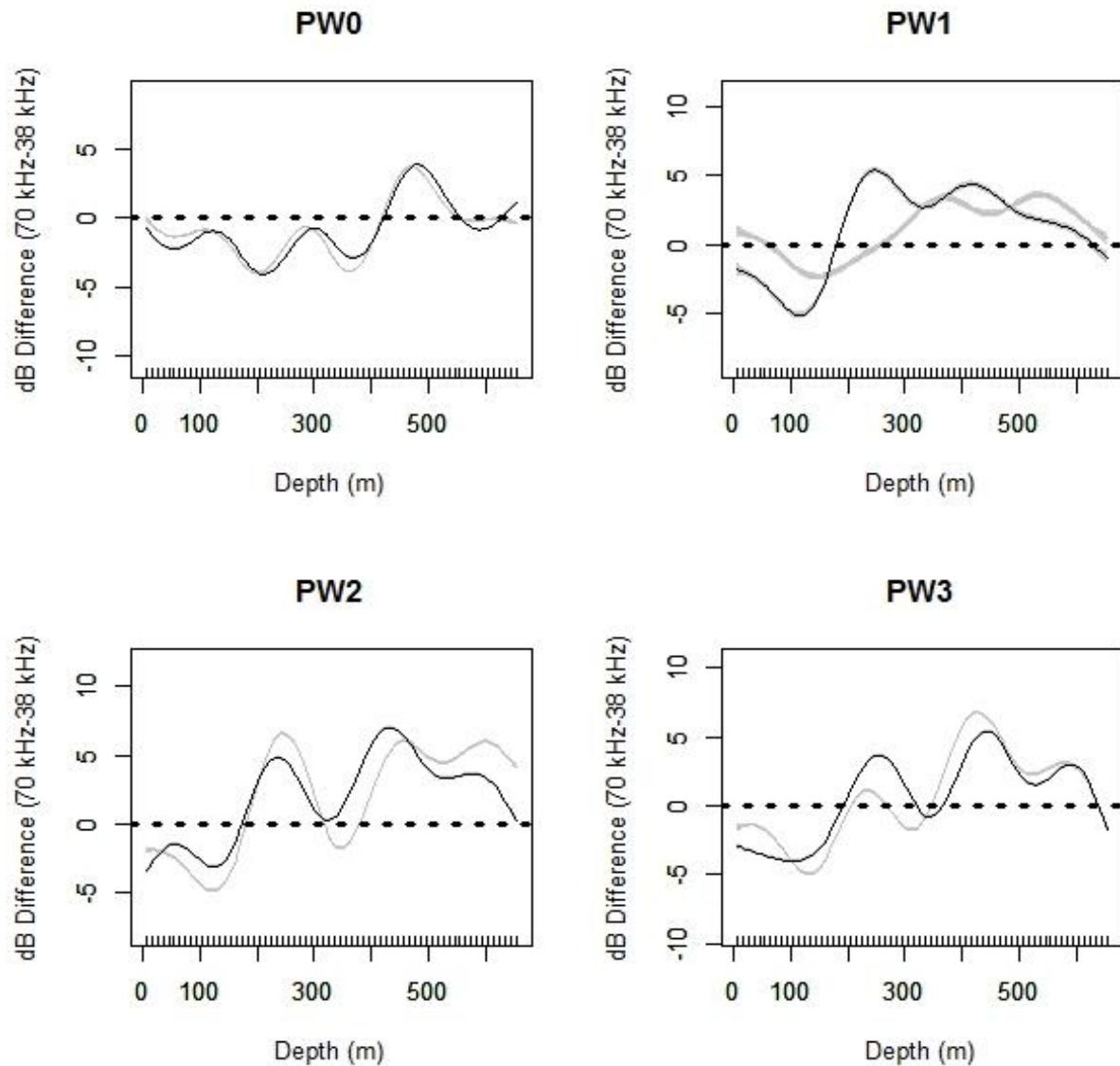


Figure 9: Generalized additive model (GAM) smooth functions of the mean of the volume backscattering strengths (dB) difference of the 70 and 38 kHz frequency across depth. The black lines indicate the foraging samples and the grey is the control for the four locations: PW0, PW1, PW2, and PW3. Tick marks on the x-axis correspond to the sampling distribution. The grey shading indicates two times the standard error for each smooth function.

The patchiness of the backscatter was assessed using the index of aggregation (IA). Higher IA values indicated more vertical patchiness with backscatter densities being higher over a smaller area when compared to other areas. For the 38 kHz and 70 kHz frequencies, the water column and DSL IA values for each location varied drastically. The highest level of patchiness from

surface to 1060 m for the 38 kHz frequency was found at location PW1 when whales were absent (Figure 10; PC1) with a value of 0.0359 m^{-1} . The lowest value of 0.0193 m^{-1} was recorded at PW3 when whales were present (Figure 10; PW3). The 70 kHz frequency showed a different relationship with location PW2 when whales were present having the highest IA value of 0.0694 m^{-1} calculated from 0 – 670 m (Figure 10; PW2) and PW0 when whales were absent having the lowest value of 0.0371 m^{-1} (Figure 10; PC0). For the DSL only, the highest level of patchiness for the 38 kHz occurred at PW0 site when whales were present (Figure 11; PW0) with a value of 0.0515 m^{-1} and the lowest value was recorded at PW3 when whales were present with a value of 0.0242 m^{-1} (Figure 10; PW3). For the 70 kHz, the highest level of DSL patchiness was at PW2 location when whales were present (Figure 11; PW2) and the lowest value was 0.0578 m^{-1} at PW3 when whales were absent (Figure 11; PC3). For all calculations except the 38 kHz from surface to 1060 m, the highest IA occurred when whales were present in the area.

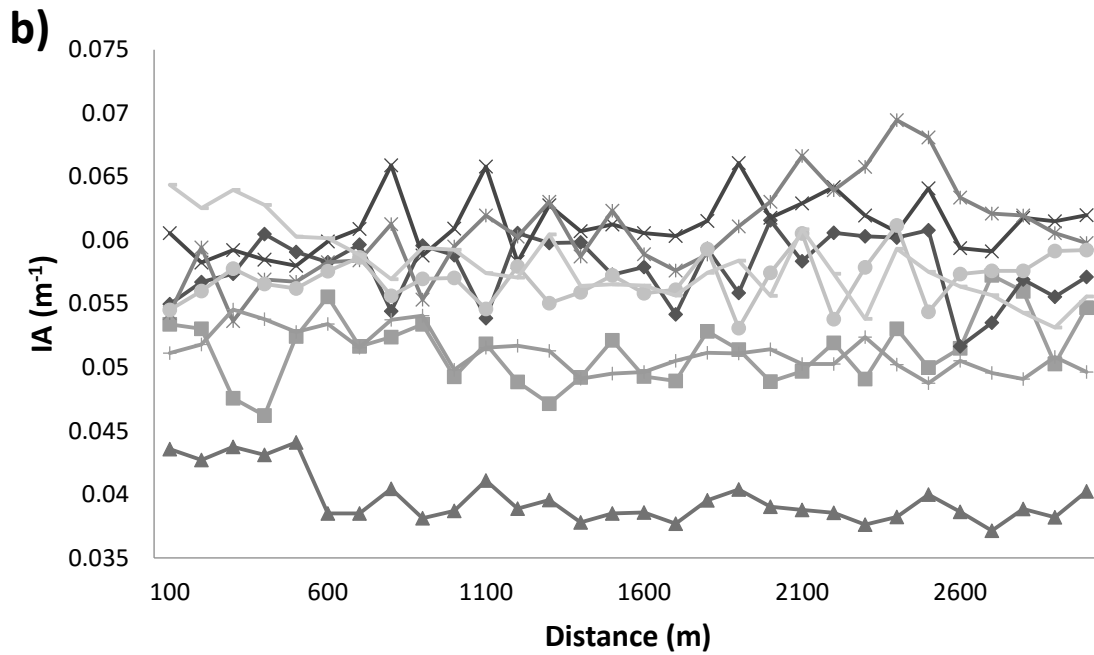
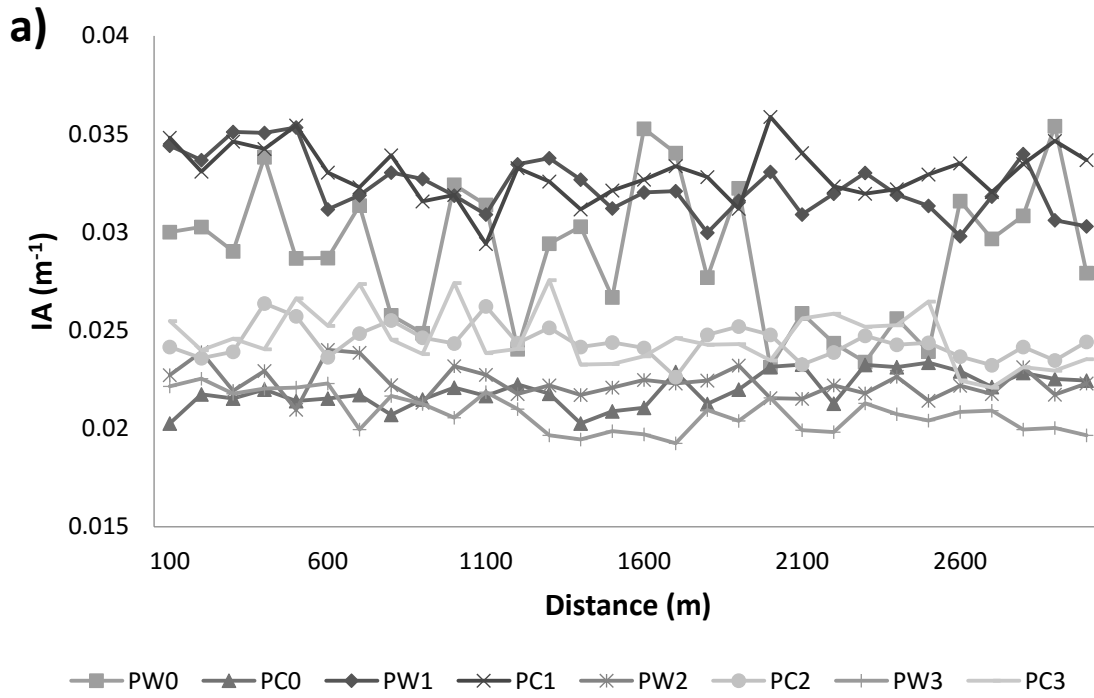


Figure 10: The index of aggregation from surface to depth for the a) 38 kHz and b) 70 kHz frequencies for the four locations 0 - 1. PW indicates a sample when whales were present and PC is a sample when whales were absent. The IA was calculated from 0 – 1060 m for the 38 kHz and from 0 – 670 m for the 70 kHz.

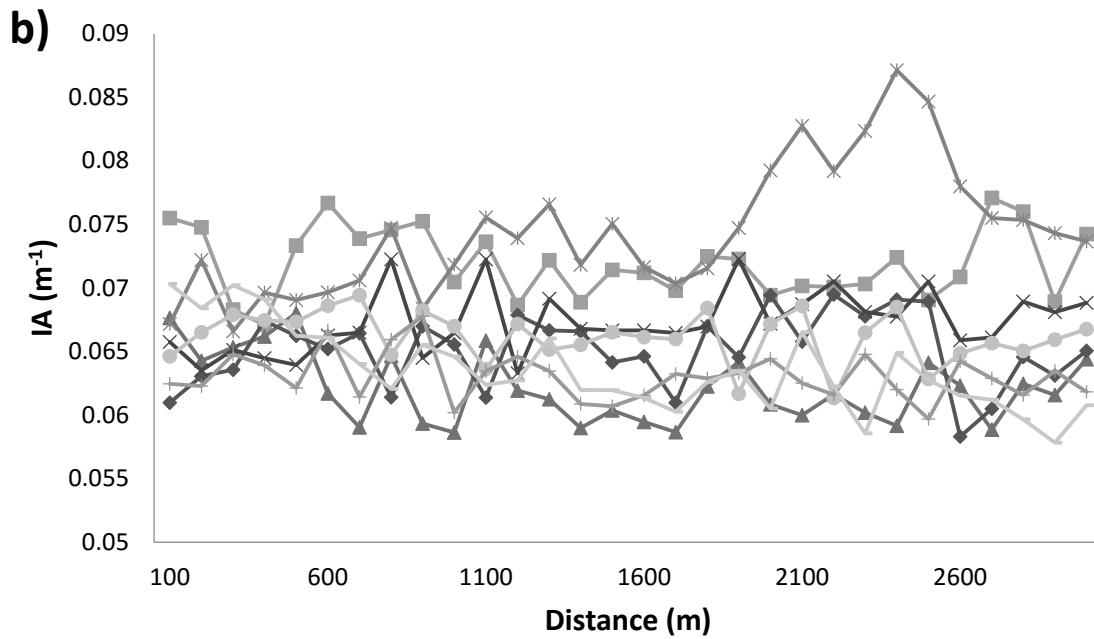
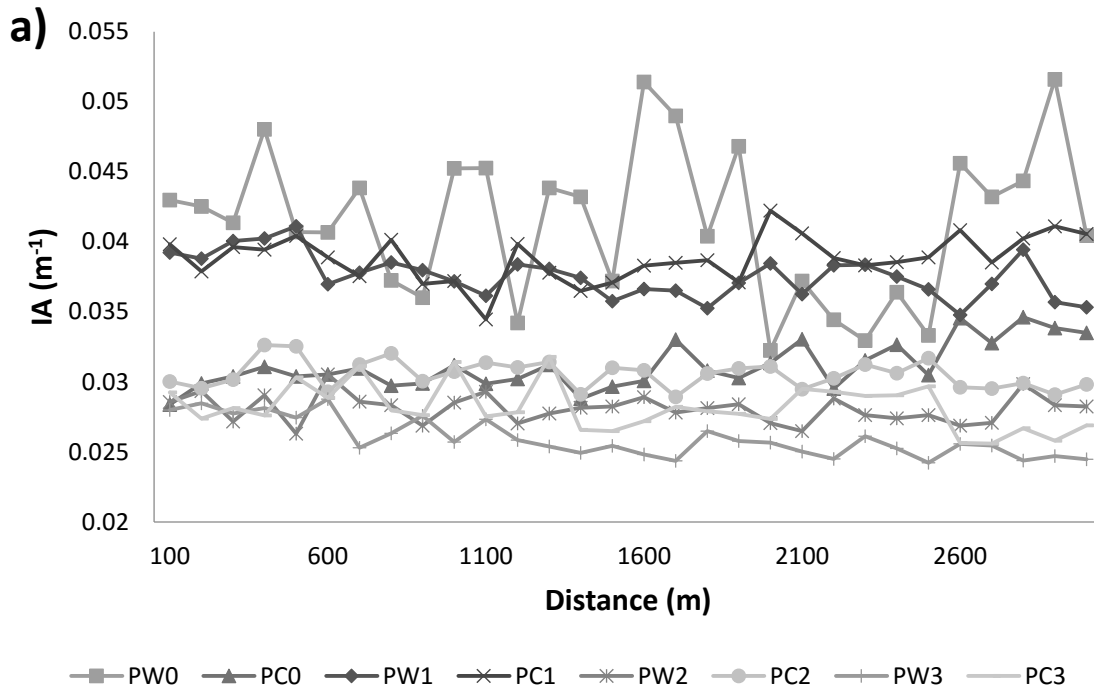


Figure 11: The index of aggregation of the DSL for the a) 38 kHz and b) 70 kHz frequencies for the four locations 0 - 1. PW indicates a sample when whales were present and PC is a sample when whales were absent. The IA was calculated from 310 – 1060 m for the 38 kHz and from 320 – 670 m for the 70 kHz.

Discussion

Foraging short-finned pilot whales in the leeward waters off the Island of Hawaii appear to temporally select areas when there is higher backscatter of organisms detected for both the 38 kHz and 70 kHz frequency data. Increase of backscatter along a wide spectrum of frequencies indicates higher relative biomass. Due to thresholding, backscatter at both frequencies is mostly due to micronekton. Based on past studies, myctophids are the major component of the micronekton (Maynard et al. 1975, Drazen et al. 2011) that make up the diet of the prey of pilot whales (Clarke 1996b, Phillips et al. 2001, Ohizumi 2002, Markaida & Sosa-Nishizaki 2003, Parry 2006) which consists mostly of cephalopods (Seagars & Henderson 1985, Sinclair 1992, Clarke & Goodall 1994, Clarke 1996a, Gannon et al. 1997, Pauly et al. 1998). During whale foraging there was an increase of micronekton in the water column for both frequencies. These results were similar to other results documented in and around the Hawaiian Islands. Both the previous chapter and Abecassis et al. (2015) found that short-finned pilot whales were attracted to areas with increased biomass of organisms that scatter sound at 70 kHz. Abecassis et al. (2015) additionally found the whales were attracted to areas with increased biomass of scattering organism in the 38 kHz, and Hazen and Johnston (2010) found that they were attracted to areas with higher 38 kHz scatterers south of the Main Hawaiian Island (MHI) chain probably because their prey were attracted to this increased backscatter.

The results of this study show that micronektonic organisms formed discrete scattering layers similar to the distribution found in the Northwestern Hawaiian Islands (NWHI) in the previous chapter and other areas around the Island of Hawaii (Abecassis et al. 2015). For this study, the scatterers were grouped into a SSL and a DSL based on the detections in the 38 and 70 kHz frequencies. The depth of the layers varied based on the recording frequency with the 38 kHz

SSL defined from 0 – 250 m and the DSL from 310 – 1060 m; whereas, the 70 kHz scattering layer was from 0 – 290 m and a DSL from 320 – 670 m. These depths were comparable to the depths defined for the SSL and DSL in the previous chapter in the NWHI. These layer depths were also comparable to those of another study in the leeward waters of Hawaii Island reported in Abecassis et al. (2015): SSL was 0 – 250 m and DSL was 375 – 665 m (70 kHz) or 375 – 725 m (38 kHz). The DSL was slightly shallower in this study, which might be due to the limited spatial range of the data. The intent of this study was to have a limited spatial range to focus on temporal changes instead of the spatial differences.

While the increase in 38 kHz and 70 kHz SSL and the 38kHz DSL organism backscatter indicated foraging whales preference, it is interesting that the 70 kHz DSL organism backscatter did not seem to indicate foraging preference. We believe this is due to the depth limitation of the 70 kHz frequency to 670 meters. This depth is shallower than the average depth range of the foraging whales during the daytime. Based on tagged whales in the Hawaiian Islands, short-finned pilot whales make regular deep dives up to 1296 meters (Andrews et al. 2011) with deepest dives recorded during the day with depths averaging between 600 - 800 m (Baird et al. 2003). Additionally the higher frequency, 70 kHz, resolves organisms smaller than the 38 kHz due to the physical limitation of the 38 kHz frequency and these smaller organisms might not be as biologically relevant to the short-finned pilot whales and their prey.

While past studies including the previous chapter of this dissertation have identified potential “hotspots” in the NWHI and the MHI that might attract foraging short-finned pilot whales (Abecassis et al. 2015), they did not assess daily variation in prey distribution and abundance or the ability of the whales to exploit this potential temporal variability, or the response of these layers to foraging whales. Our analysis shows that there was a significant daily variation in

micronekton at the same location, both abundance and composition. Further the whales foraged when micronekton abundance was greater, an expected pattern based on previous studies (Hazen & Johnston 2010, Abecassis et al. 2015). The variation of behavior in response to temporal patchiness of prey has been documented in pinnipeds, specifically the Antarctic fur seals (*Arctocephalus gazelle*), whose prey (krill) form patches (Boyd 1996). It has also been documented in dolphins, specifically spinner dolphins (*Stenella longirostris*), whose prey (small fishes, shrimps, and squid) (Norris & Dohl 1979), also form discrete patches (Benoit-Bird & Au 2003). Fur seals are able to change the temporal variability of their dives in relationship to the spatial pattern of their prey (Boyd 1996) and spinner dolphins are able to vary their behavior based on the diurnal vertical and horizontal migration of their prey (Benoit-Bird & Au 2003). In addition to high temporal variation in backscatter of the layers, the vertical structure of the layers varied daily. To the authors' knowledge, this study was the first attempt to directly measure the structure of the scatterers during short-finned pilot whale foraging. Other studies have analyzed the relationship between deep divers and overall biomass (previous chapter), DSL biomass (previous chapter, Hazen et al. 2011, Abecassis et al. 2015), or surface layer biomass (previous chapter, Abecassis et al. 2015).

While results of this study suggest that overall relative biomass of micronekton is highly variable and their specific composition might attract foraging whales, there may be characteristics of the vertical structure that also influence the distribution of short-finned pilot whales in Hawaiian waters. The highest levels of patchiness in the DSL were recorded during whale foraging suggesting that high patchiness of micronekton might be attracting more prey of the odontocetes. Additionally, the shallower distribution of the DSL could make the potential prey more accessible, thus attracting whales. Another reason for this vertical structure change could be due

to the scatterers avoiding the foraging whale which typically dive to depths deeper than this shallowing DSL depth of about 495 meters for the 38 kHz signal and 475 m for the 70 kHz signal seen in this study (Baird et al. 2003, Andrews et al. 2011).

The authors saw an increase in the DSL backscatter during foraging for the depth from about 900 to 1060 meters. The average dive depth during the day of tagged pilot whales is from 600 to 800 m (Baird et al. 2003) which is right above the depth of increased DSL backscatter. While the recorded dive depths are shallower than the depth of higher backscatter, the whales have been recorded to dive deeper (Aguilar Soto et al. 2008, Andrews et al. 2011), suggesting they can target the higher biomass in this depth during foraging. Additionally the increase of backscatter below the dive depth might be due to micronekton avoidance or being chased by the echolocating whales. Micronekton have been observed to dive deeper when startled by submarines (Drazen, pers. comm.); therefore, it wouldn't be farfetched to assume that these micronekton might be swimming deeper to avoid the foraging whales resulting in higher backscatter below the foraging depth when whales are present.

The composition of the scattering layers showed high daily variability. Myctophids, a documented prey item of large cephalopods (Clarke 1996b, Phillips et al. 2001, Ohizumi 2002, Markaida & Sosa-Nishizaki 2003, Parry 2006) eaten by pilot whales (Seagars & Henderson 1985, Sinclair 1992, Clarke & Goodall 1994, Clarke 1996a, Gannon et al. 1997, Pauly et al. 1998), make up a large component of the deep scattering layer off the Island of Hawaii (Drazen et al. 2011) and have been documented to have a different δS_v than other organisms (Au & Benoit-Bird 2008, Benoit-Bird 2009, De Robertis et al. 2010). Since we found a change in positive and negative values between the samples collected during whale foraging and the control, we can conclude that the composition varied between the samples. However it hard to

generalize what species were present because the micronekton is comprised of a diverse array of species and the only study in Hawaiian waters comparing the δS_{V70-38} were of micronekton in very shallow or surface waters and not at depth (Au & Benoit-Bird 2008, Benoit-Bird 2009). The depth and orientation of the different species can affect the backscatter values. It will be important for future studies to compare the δS_{V70-38} and trawl composition to have a better understanding of how differing concentrations of the different species will affect the δS_{V70-38} values recorded. There was some concern that the changes in composition might be due to changes in the current structure at our sampling locations. However reviewing the currents in the sampling area during the dates of sampling (Figure 12) showed a consistent pattern which did not vary temporal leading to the assumption that ocean currents are not driving this relationship.

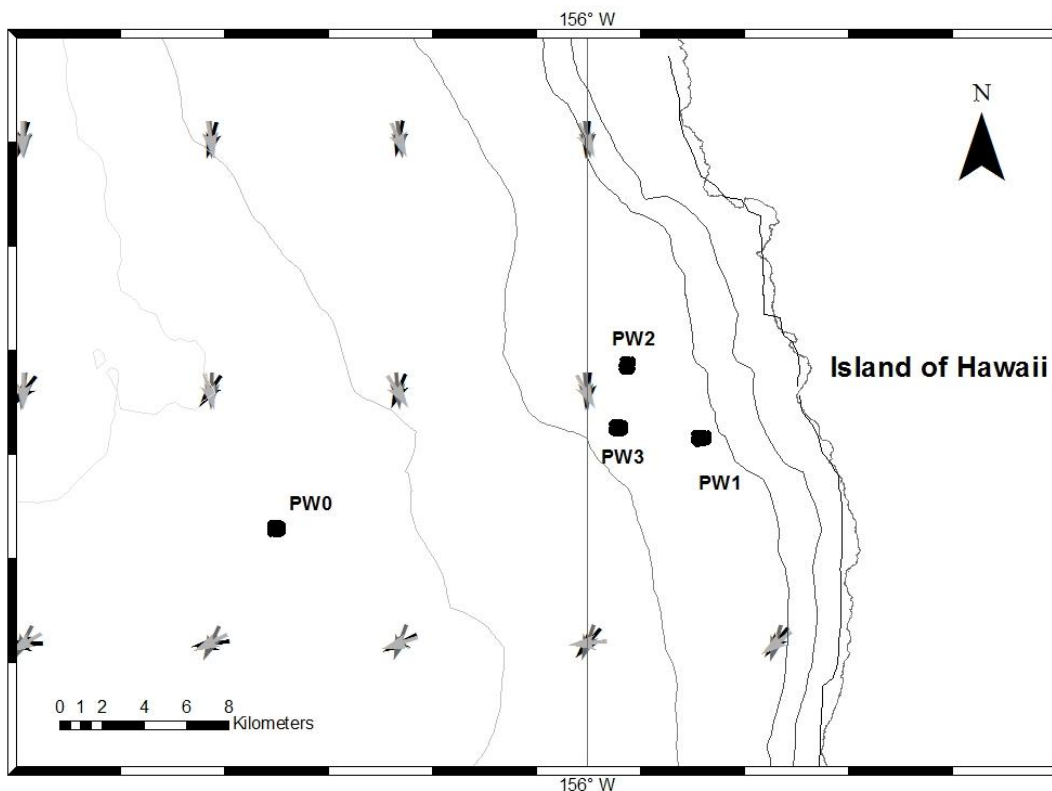


Figure 12: The ocean surface currents in the sample area with the dates sampled overlaid on top of one another, February 19th is in black, February 20th in dark grey, and February 21st is in light grey. There was minimal variability in direction and magnitude over the sampling dates.

The currents were obtained from the daily NRL HYCOM + NCODA Global 1/12 degree model from <http://coastwatch.pfeg.noaa.gov/>.

There was not a clear pattern of scattering layer composition relative to the presence of foraging whales. Another deep diving odontocete, Cuvier's beaked whales off southern California, appear to have the ability to detect and exploit the different composition in the deep scattering layers by preferring habitats with a higher amount of larger squid clustered together (Benoit-Bird et al. 2016). A similar pattern might arise for short-finned pilot whales if the sample size is increased or if there is better sampling of the composition of the scattering layer at the foraging depth either through trawling or with high frequency in situ acoustic methods (Giorli et al. in revision). The daily variation of organism composition was less apparent at the offshore site (PW0) even with the larger time delay between samplings with the near shore sites having higher variability (PW1, PW2, and PW3). The authors speculate that this variation between sites might be due to the proximity of the coast of Hawaii Island. The Island of Hawaii has a mesopelagic boundary community (MBC) near shore that is different in composition to the offshore locations (Reid et al. 1991). The MBC is comprised of a distinct composition of fish, shrimp, and squid (Reid et al. 1991) that is different from the pelagic deep scattering layer (Young 1983). Potentially this nearshore MBC organism composition could be more variable than the offshore DSL. To have a better understanding of this, it would be important to conduct daily trawl sampling at depth for these locations offshore and near shore to see if the MBC composition is truly more variable than the oceanic DSL.

This paper suggests that specific changes in amount of backscatter and vertical distribution of micronektonic organisms in the scattering layers influence foraging short-finned pilot whales behavior. This study also indicates that the short-finned pilot whales are able to exploit the temporal variability along with the spatial patchiness of their prey and their prey's forage as

documented in (Abecassis et al. 2015) along Hawaii Island's Kona coast. Future research should examine the vertical structure as well as species composition of scattering layers when trying to understand the appeal of the area to foraging deep diving odontocetes.

Acknowledgements

The authors thank the officers, crew, scientists, and volunteers of the R/V Oscar Elton Sette and the R/V Falkor for their assistance with data collection. Specifically the authors thank Jessica Chen for training the marine mammal observers that assisted with spotting the short-finned pilot whales, Ali Bayless for helping with the passive acoustic system deployment, and Reka Domokos for providing acoustic input. The funding for this project was provided by Office of Naval Research, National Oceanic and Atmospheric Administration, and the funding for ship time on the R/V Falkor was provided by Schmidt Ocean Institute.

References

- Abecassis M, Polovina J, Baird RW, Copeland A, Drazen JC, Domokos R, Oleson E, Jia Y, Schorr GS, Webster DL, Andrews RD (2015) Characterizing a foraging hotspot for short-finned pilot whales and Blainville's beaked whales off the west side of the Island of Hawai'i with tagging and oceanographic data. *PLoS One* 10:1-22
- Aguilar Soto N, Johnson MP, Madsen PT, Diaz F, Dominguez I, Brito A, Tyack P (2008) Cheetahs of the Deep Sea: Deep Foraging Sprints in Short-Finned Pilot Whales off Tenerife (Canary Islands). *Journal of Animal Ecology* 77:936-947
- Andrews RD, Schorr GS, Baird RW, Webster DL, McSweeney DJ, Hanson MB (2011) New satellite-linked depth-recording LIMPET tags permit monitoring for weeks to months and reveal consistent deep nighttime feeding behavior of short-finned pilot whales in Hawai'i. Poster presentation at the Fourth International Science Symposium on Bio-logging, Hobart, Tasmania, March 2011
- Au WW, Benoit-Bird KJ (2008) Broadband backscatter from individual Hawaiian mesopelagic boundary community animals with implications for spinner dolphin foraging. *J Acoust Soc Am* 123:2884-2894
- Baird RW, McSweeney DJ, Heithaus MR, Marshall GJ (2003) Short-finned pilot whale diving behavior: deep feeders and day-time socialities. Abstract submitted to the 15th Biennial Conference on the Biology of Marine Mammals, Greensboro, NC
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1-48
- Baumann-Pickering S, Simonis AE, Oleson EM, Baird RW, Roch MA, Wiggins SM (2015) False killer whale and short-finned pilot whale acoustic identification. *Endangered Species Research* 28:97-108
- Benoit-Bird KJ (2009) The effects of scattering-layer composition, animal size, and numerical density on the frequency response of volume backscatter. *ICES Journal of Marine Science* 66:582-593
- Benoit-Bird KJ, Au WWL (2003) Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology* 53:364-373
- Benoit-Bird KJ, Southall BL, Moline MA (2016) Predator-guided sampling reveals biotic structure in the bathypelagic. *Proc Biol Sci* 283
- Best PB, Shaughnessy PD (1981) First record of the melon-headed whale, *Peponocephala electra*, from South Africa. *Annals of the South African Museum* 83:33-47
- Clarke M, Goodall N (1994) Cephalopods in the diets of three odontocete cetacean species stranded at Tierra del Fuego, *Globicephala melaena* (Traill, 1809), *Hyperoodon planifrons* Flower, 1882 and *Cephalorhynchus commersonii* (Lacepede, 1804). *Antarctic Science-Institutional Subscription* 6:149-154
- Clarke MR (1996a) Cephalopods as Prey. III. Cetaceans. *Philosophical Transactions: Biological Sciences* 351:1053-1065
- Clarke MR (1996b) The role of cephalopods in the world's oceans: general conclusions and the future. *Philosophical Transactions of the Royal Society-Ser B-Biological Sciences* 351:1105

- De Robertis A, Higginbottom I (2007) A post-processing technique to estimate the signal-to-noise ratio and remove echosounder background noise. *ICES Journal of Marine Science* 64:1282-1291
- De Robertis A, McKelvey DR, Ressler PH (2010) Development and application of an empirical multifrequency method for backscatter classification. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1459-1474
- Delcourt HR, Delcourt PA, III TW (1983) Dynamic plant ecology: The spectrum of vegetational change in space and time. *Quaternary Science Reviews* 1:153-175
- Demer DA, Berger L, Bernasconi M, Bethke E, Boswell K, Chu D, Domokos R, Dunford A, Fassler S, Gauthier S, Hufnagle LT, Jech JM, Bouffant N, Lebourges-Dhaussy A, Lurton X, Macaulay GJ, Perrot Y, Ryan T, Parker-Stetter S, Stienessen S, Weber T, Williamson N (2015) Calibration of acoustic instruments. *ICES Cooperative Research Report* 326:1-133
- Domokos R (2009) Environmental effects on forage and longline fishery performance for albacore (*Thunnus alalunga*) in the American Samoa Exclusive Economic Zone. *Fisheries Oceanography* 18:419-438
- Doty MS, Oguri M (1956) The Island Mass Effect. *J Cons* 22:33-37
- Drazen JC, De Forest LG, Domokos R (2011) Micronekton abundance and biomass in Hawaiian waters as influenced by seamounts, eddies, and the moon. *Deep Sea Research Part I: Oceanographic Research Papers* 58:557-566
- Echoview Software Pty. Ltd. (2013) Echoview software, version 5.4. Echoview Software Pty. Ltd., Hobart, Australia.
- Fernandes PG, Korneliussen RJ, Lebourges-Dhaussy A, Massé J, Iglesias M, Diner N, Ona E (2006) The SIMFAMI project: Species identification methods from acoustic multifrequency information. Final report to the EC:i-486
- Foote KG, Vestnes G, Maclennan DN, Simmonds EJ (1987) Calibration of acoustic instruments for fish density estimation: a practical guide. *ICES Cooperative Research Report* 144:1-81
- Gannon DP, Ready AJ, Craddock JE, Mead JG (1997) Stomach contents of long-finned pilot whales (*Globicephala melas*) stranded on the US mid-Atlantic coast. *Marine Mammal Science* 13:405-418
- Gilmartin M, Revelante N (1974) The 'island mass' effect on the phytoplankton and primary production of the Hawaiian Islands. *Journal of Experimental Marine Biology and Ecology* 16:181-204
- Giorli G, Neuheimer A, Drazen J, Copeland A, Au WWL (in revision) Deep sea animal density and size estimated using a Dual-frequency IDentification SONar (DIDSON) offshore the island of Hawaii.
- Gove JM, McManus MA, Neuheimer AB, Polovina JJ, Drazen JC, Smith CR, Merrifield MA, Friedlander AM, Ehses JS, Young CW, Dillon AK, Williams GJ (2016) Near-island biological hotspots in barren ocean basins. *Nature Communications* 7:10581
- Hazen EL, Johnston DW (2010) Meridional patterns in the deep scattering layers and top predator distribution in the central equatorial Pacific. *Fisheries Oceanography* 19:427-433
- Hazen EL, Nowacek DP, St Laurent L, Halpin PN, Moretti DJ (2011) The relationship among oceanography, prey fields, and beaked whale foraging habitat in the Tongue of the Ocean. *PLoS One* 6:1-10

- Landry MR, Decima M, Simmons MP, Hannides CC, Daniels E (2008) Mesozooplankton biomass and grazing responses to Cyclone Opal, a subtropical mesoscale eddy. *Deep Sea Research Part II: Topical Studies in Oceanography* 55:1378-1388
- Markaida U, Sosa-Nishizaki O (2003) Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Journal of the Marine Biological Association of the UK* 83:507-522
- Maynard SD, Riggs FV, Walters JF (1975) Mesopelagic micronekton in Hawaiian waters: faunal composition, standing stock, and diel vertical migration. *Fishery Bulletin* 73:726-736
- Norris KS, Dohl TP (1979) Behavior of the Hawaiian Spinner Dolphin *Stenella longirostris* (Schlegel, 1841). DTIC Document
- Ohizumi H (2002) Dietary studies of toothed whales: A review and new topics. *Fisheries science* 68:264-267
- Parry M (2006) Feeding behavior of two ommastrephid squids *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis* off Hawaii. *Marine Ecology Progress Series* 318:229-235
- Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* 55:467-481
- Phillips KL, Jackson GD, Nichols PD (2001) Predation on myctophids by the squid *Moroteuthis ingens* around Macquarie and Heard Islands: stomach contents and fatty acid analyses. *Marine Ecology Progress Series* 215:179-189
- Pickett STA, White PS (1985) *The ecology of natural disturbance and patch dynamics*. Academic Press, New York
- R Development Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria
- Reid SB, Hirota J, Young RE, Hallacher LE (1991) Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. *Marine Biology* 109:427-440
- Seagars DJ, Henderson JR (1985) Cephalopod remains from the stomach of a shortfinned pilot whale collected near Santa Catalina Island, California. *Journal of Mammalogy* 66:777-779
- Seki MP, Polovina JJ, Brainard RE, Bidigare RR, Leonard CL, Foley DG (2001) Biological enhancement at cyclonic eddies tracked with GOES thermal imagery in Hawaiian waters. *Geophysical Research Letters* 28:1583-1586
- Sekiguchi K, Klages NTW, Best PB (1992) Comparative analysis of the diets of smaller odontocete cetaceans along the coast of southern Africa. *South African Journal of Marine Science* 12:843-861
- Simmonds J, MacLennan DN (2005) *Fisheries Acoustics: Theory and Practice*. Blackwell Publishing
- Sinclair EH (1992) Stomach Contents of Four Short-Finned Pilot Whales (*Globicephala macrorhynchus*) from the Southern California Bight. *Marine Mammal Science* 8:76-81
- Spitz J, Chérel Y, Bertin S, Kiszka J, Dewez A, Ridoux V (2011) Prey preferences among the community of deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic. *Deep Sea Research Part I: Oceanographic Research Papers* 58:273-282
- Steele JH (1978) *Spatial pattern in plankton communities*. Plenum Press, New York
- Thompson JN (1978) Within-patch structure and dynamics in *Pastinaca sativa* and resource availability to a specialized herbivore. *Ecology* 59:443-448

- Urmy SS, Horne JK, Barbee DH (2012) Measuring the vertical distributional variability of pelagic fauna in Monterey Bay. *ICES Journal of Marine Science: Journal du Conseil* 69:184-196
- Wood S, Scheipl F (2014) gamm4: Generalized additive mixed models using mgcv and lme4. R package version 02-3
- Wood SN (2006) *Generalized Additive Models: An introduction with R*. Chapman and Hall/CRC
- Woodworth PA, Schorr GS, Baird RW, Webster DL, McSweeney DJ, Hanson MB, Andrews RD, Polovina JJ (2012) Eddies as offshore foraging grounds for melon-headed whales (*Peponocephala electra*). *Marine Mammal Science* 28:638-647
- Young RE (1983) Oceanic bioluminescence: An overview of general functions. *Bulletin of Marine Science* 33:829-845

CHAPTER IV
INFLUENCES OF SPATIAL VARIABILITY IN PELAGIC SCATTERING LAYERS ON
SPERM WHALES BEHAVIOR

Adrienne M Copeland¹, Ladd Irvine², Bruce Mate² and Whitlow W. L. Au¹

¹Hawaii Institute of Marine Biology, University of Hawaii, PO BOX 1348 Kaneohe, Hawaii
96744

²Marine Mammal Institute, Department of Fisheries and Wildlife, and Coastal Oregon Marine
Experiment Station, Oregon State University, Hatfield Marine Science Center, 2030 SE Marine
Science Drive, Newport, Oregon 97365

Abstract

The central slope of the Gulf of Mexico is home to over 20 different species of marine mammals. Previous to the Deep Horizon Oil Spill in 2010, sperm whales were the predominately sighted large whale in the area. Post Deep Horizon Oil Spill there appeared to be a decrease in detections of sperm whales. This study aimed to investigate and understand the distribution and utilization of this area by sperm whales two years after the oil spill. The backscatter of micronekton (organisms from 2 – 20 cm) was highly variable in this area and driven mostly by proximity to the Mississippi Delta. Sperm whales were sighted by trained visual observers and foraging was detected using a hydrophone array in the north central Gulf of Mexico. The sperm whales appeared to prefer the shallow slope waters less than 900 meters in areas with higher backscatter of micronekton, suggesting that the waters above sloping bottoms with dense patches of mesopelagic micronekton support the prey of sperm whales.

Keywords: Micronekton, Backscatter, Active Acoustics, Sperm Whales

Introduction

The Gulf of Mexico is a large ocean basin supporting a diverse array of marine life including over 25 species of cetaceans (Jefferson & Schiro 1997). Many of these cetaceans are regularly sighted along the northern continental slope in waters less than 3000 meters in depth (Mullin et al. 1994, Jefferson 1996, Davis et al. 1998, Mullin & Fulling 2004). The waters above these slopes can be influenced by anticyclonic eddies that originate from the Loop current, a prominent feature in the Gulf of Mexico (Nowlin & McLellan 1967). The Loop current is created by warm water that travels up from the Caribbean, past the Yucatan Peninsula, and into the Gulf of Mexico. This current is highly variable and seasonally unpredictable, and can sometimes extend as far north as the Mississippi River Delta or the Florida continental shelf (Wiseman Jr & Dinnel 1988, Müller-Karger et al. 1991, Nowlin Jr. et al. 2001). As the loop current and/or the eddies that originate from the current flow onto the shallower continental slope it causes nutrient-rich upwellings (Paluszkiwicz et al. 1983, He & Weisberg 2003, Jochens & DiMarco 2008) increasing the area's productivity.

This increased productivity due to the Gulf's oceanographic features or anticyclonic mesoscale eddies may influence the distribution of the cetaceans sighted in this area (Mullin et al. 1994, Baumgartner 1997), in particular the regularly sighted vulnerable sperm whale (Davis et al. 2002). Based on stomach contents of stranded sperm whales in the Gulf of Mexico, they feed solely on cephalopods with a strong preference for the *Histioteuthis* species (Barros 2003). Most of their forage species have a mesopelagic or bathypelagic distribution (Barros 2003) which corresponds to the foraging dive depths recorded from tagged whales (Watkins et al. 1993, Miller et al. 2004, Watwood et al. 2006). These cephalopods forage on some of the micronekton, organisms ranging in size from 2 - 20 cm, species found in the scattering layers suggesting that a

comprehensive analysis of these layers might further the understanding of sperm whale distribution (Benoit-Bird et al. 2008, Benoit-Bird & Gilly 2012).

On April 10, 2010, the Deep Horizon Oil Spill occurred in the north central Gulf of Mexico where whales were regularly sighted. Immediately following the spill in 2010 there was a significant decrease in the passive acoustic detections of sperm whales (Ackleh et al. 2012) signifying a decrease of sperm whales foraging in this area. Subsequent studies in the Gulf of Mexico have tried to determine the long range effects of the oil spill on the health and distribution of cetaceans (Ackleh et al. 2012, Schwacke et al. 2013). Two years following the oil spill this study aims to understand the utilization of the north central Gulf of Mexico by sperm whales and the spatial relationship between the micronekton biomass and foraging whales. Specifically we wanted to identify a) if sperm whales still utilize the north central Gulf of Mexico and what factors appear to affect their distribution, b) if there is spatial variation in relative acoustic biomass of micronektonic organisms, c) if this variability is due to specific geographic or environmental parameters and d) how does variability of micronekton relate to sperm whale presence.

Methods

Data Collection

Data were collected from the M/V Sarah Bordelon in the Gulf of Mexico (GOM) cruise on August 9 – 18, 2012 (OSU 12) (Figure 1). Sampling areas were selected based on sperm whale utilization of the GOM determined from previous years' satellite tagging tracks of whales (Bruce Mate, pers. comm.). Sampling dates were limited due to Hurricane Isaac from August 26 – 30, 2012. Acoustic backscatter data were collected using a two-frequency, split-beam, pole-mounted echosounder (Simrad EK60) placed approximately 5.62 m below the water's surface. The 38 and

70 kHz signals had an operating power of 2000 W and 700 W, respectively, with a pulse length of 512 μ s. The pulse length and power were defined based on previous years sampling. The frequencies were calibrated using a 38.1 mm diameter, tungsten-carbide reference sphere positioned about 15 m below the transducer depth and standard techniques described by Foote et al. (1987) and Demer et al. (2015). Pings with missing data or large noise values were removed from the analysis using Echoview 6.1 (Echoview Software Pty. Ltd. 2014) and standard methods (De Robertis & Higginbottom 2007). Additionally data within 3.5 m from the transducers were removed to avoid analyzing surface noise. Backscatter from plankton and other smaller organisms was removed using a threshold of -80 dB re 1 m^{-1} mean volume backscattering strengths (S_v ; units: dB re 1 m^{-1}), a proxy for relative density (Simmonds & MacLennan 2005). The data were binned with a horizontal resolution of 200 m and a vertical resolution of 10 m. The bins were vertically integrated to obtain the nautical area scattering coefficients (NASC) in m^2/nmi^2 . The vertically integrated backscatter values (NASC) were summed from surface to 800 m, the signal depth limit, and log transformed for each 200 meter horizontal sample. Trawling was not available for accurate sizing and species identification of the organisms within the area of interest, so the NASC represents the relative biomass of scattering organisms assuming that the daily scattering properties of the micronekton do not change significantly (Simmonds & MacLennan 2005). The backscatter data were collected continuously and contained daytime to nighttime biomass variation. Daytime and nighttime distinctions were classified using the time of sunrise and sunset.

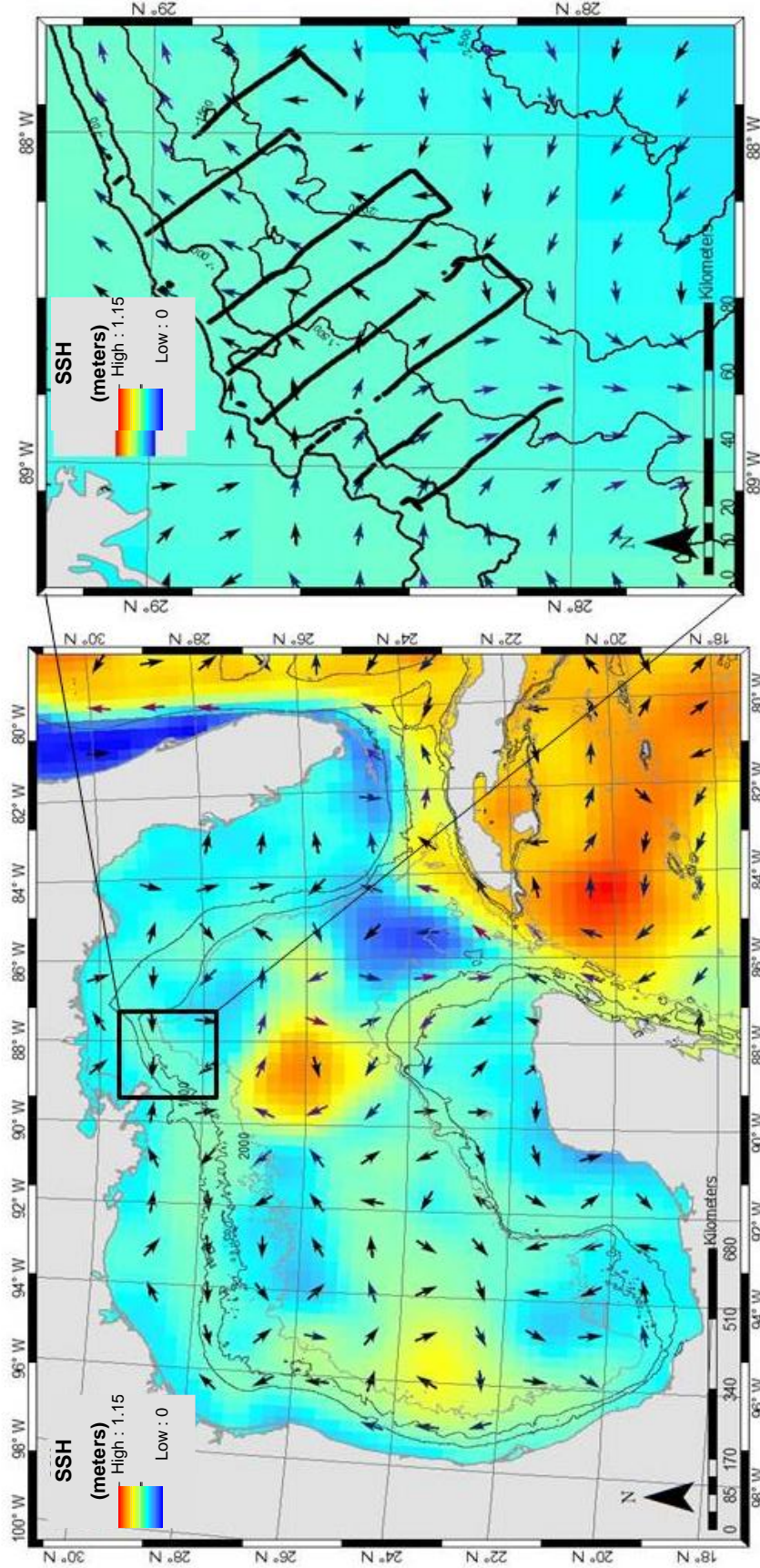


Figure 1: The sea surface height (SSH) in meters and surface current vectors plotted for the a) Gulf of Mexico and the b) sample location for August 12, 2016 during the middle of the sample period. The SSH is denoted in color ranging from 0 meters in blue to 1.15 meters in red.

During the daytime sperm whales were localized visually in reference to the ship track exclusively by trained marine mammal observers (MMO). The sighted whales' latitude and longitude were corrected in ArcMap 10.3 (ESRI 2011) based on the bearing and distance relative to the ship's bearing and location. During the nighttime whales were localized by real-time monitoring of the passive acoustic hydrophone array with a sampling rate sufficient to detect sperm whale biosonar clicks. Sperm whale clicks can be clearly identified by visually examining real-time spectrograms in a passive listening system and by listening to the sounds. These clicks are distinct from other echolocators in the Gulf of Mexico being the only species whose impulsive sounds have a lower frequency range less than 15 kHz (Goold & Jones 1995) and heard easily with past studies reporting source levels as high as 236 dB re: 1 μ Pa (rms) for on axis clicks (Møhl et al. 2003). The actual location of the signaler was determined using the time of arrival difference for each element of the array which provided a distance and bearing relative to the array. The location of the whale was corrected using ArcMap 10.3. Due to technical issues with the array, acoustic data were only available for the first day of sampling on August 9 – 10 not allowing for nighttime localizing of sperm whales after August 10.

Environmental and geographic data were obtained from the National Oceanic and Atmospheric Administration (NOAA) Coastwatch and OceanWatch satellite data servers. The daily averaged Archiving, Validation and Interpretation of Satellite Oceanographic data (AVISO) sea surface height (SSH) during the sampling period (August 8 -18, 2012), monthly averaged Moderate Resolution Imaging Spectroradiometer (MODIS) surface chlorophyll-a one month prior to data collection (July 2012), SRTM 30+ topography Version 6.0, and Hybrid Coordinate Ocean Model (HYCOM) 1/25 degree high resolution current vectors for the sampling area datasets were obtained from the NOAA Coastwatch ERRDAP server

(<http://coastwatch.pfeg.noaa.gov/erddap/griddap/>). The weekly averaged Pathfinder sea surface temperature (SST) for the sampling period (August 8 -18, 2012) was downloaded from the NOAA OceanWatch server (<http://oceanwatch.pifsc.noaa.gov/thredds/catalog.html>). Distance from the nearest land mass in meters was calculated using the NEAR function in ArcMap 10.3 (ESRI 2011) and the slope percentage of the bathymetry was calculated using the Slope tool from ArcMap 10.3 which is calculated by tangent of the degree of the slope angle multiplied by 100.

Data Analysis

The NASC values were summed from the surface to the depth limit of the signal. Empirical Bayesian Kriging in ArcMap 10.3 was used to interpolate the NASC values over the sampled region. Kriging is a powerful technique and is regularly used to interpolate fisheries acoustic data (e.g. Petitgas 1993, Maravelias et al. 1996, Georgakarakos & Kitsiou 2008) because it does not require the samples to be statistically independent. In this study, the interpolation was restricted to ocean bottom depths greater than 700 meters and the outermost edge of the tracklines.

Comparison between the NASC values and satellite and geographic datasets as well as sperm whale sightings and detections were done using R 3.0.1 (R Development Core Team 2014). The ocean bathymetry and the NASC value distribution of the sperm whale location was statistically compared to the ship sampled ocean topography and NASC values for the daytime and nighttime separately using a Kolmogorov–Smirnov (KS) test, which calculates the maximum vertical distance between two cumulative frequency distributions (D_{max}) (Zar 1984). An ANOVA from the ‘car’ package (Fox & Weisberg 2011) and a Generalized Linear Mixed Model (GLMM) from the ‘lme4’ package (Bates et al. 2015) were used to test difference between the daytime and nighttime NASC values. A Generalized Additive Model (GAM) from the ‘mgcv’ package

(Wood 2006) was used to determine the relationship between NASC and the environmental and geographic parameters using the equation detailed below:

$$\log(NASC) \sim s(CHLa) + s(distance) + s(SST) + s(SSH) + s(slope) \quad (1)$$

where NASC is the integrated backscatter and a smoother function (s) is applied to each of the independent variables. A single dimensional smooth function was fitted to the parameters CHLa, the surface satellite chlorophyll-a values (units: mgm-3), the distance (from the nearest landmass in meters), SST or satellite sea surface temperature ($^{\circ}$ C), SSH or satellite sea surface height (m), and slope of the bathymetry (%).

Results

A total of 623 km or about 336 nautical miles of acoustic backscatter data were collected in the Gulf of Mexico (Figure 1). While the loop current can extend as far north as the Mississippi River Delta, this was not the case during the sampling time from August 9 – 17, 2012. While the loop current was not prominent during the sampling time, an anticyclonic eddy was present south of the sampling location (Figure 1). There was relatively even sampling of backscatter during daytime and nighttime (Figure 2). During the daytime, 1258 points along the trackline were sampled; whereas at nighttime 1249 points were sampled. While the nighttime samples had significantly higher NASC mean and variation than the daytime samples (ANOVA: $F(1, 2505) = 263.8$; $p \leq 0.0001$), the authors are fairly confident that the NASC spatial variability was not due to time of day but rather the location of the sampling because there was representation of both high and low NASC values both during the daytime and the nighttime (Figure 3).

Additionally when accounting for the variation of NASC values due to ocean bathymetry (location) as a random factor, the difference between daytime and nighttime NASC values was no longer significant (GLMM: $\chi^2 = 0.3016$, $p = 0.5829$) demonstrating that the location

contributes to the variability in NASC values not the time of day. In the area sampled, sperm whales were visually sighted during the daytime at 20 different locations (Table 1). Nighttime acoustic detections of sperm whales were documented only on August 9 in 7 locations (Table 1). The ocean depth at the sighted whales during the daytime was compared against all samples collected during the daytime. The whales significantly preferred the shallower slope depths from 448 m to 846 m during the daytime; whereas the ship sampling extended to deeper depths down to 2387 m (KS: $D = 0.9475$; $p \leq 0.0001$; Figure 4a). The distribution of depths for the sperm whales during the nighttime did not show significant depth preferences likely due to the limited sampling of the array data (KS: $D = 0.4059$, $p = 0.2015$; Figure 4b). While the daytime sighted whales preferred shallower bathymetry, there was no preference for the area with steeper bathymetric slope when the daytime and nighttime samples were combined and compared to the percent slope throughout the interpolated area (KS: $D = 0.2256$, $p\text{-value} = 0.1283$; Figure 5). The sighted whales during the daytime additionally preferred locations with a higher distribution of NASC values than the overall sampled distribution (KS: $D = 0.6823$, $p \leq 0.0001$; Figure 6a). The nighttime distribution of whales acoustically detected was significantly different having a narrower distribution than the overall sampled nighttime NASC values (KS: $D = 0.6429$, $p = 0.0064$; Figure 6b). The daytime depth of the sperm whales had high agreement with the bathymetry that had the highest NASC values. The NASC values decreased as the bathymetry increased (GAM: $F = 8895$; $p < 0.0001$) and the whales were concentrated at the shallowest depths with the highest backscatter values (Figure 7). In modeling the spatial variability of NASC values throughout the sampled area, the distance from the closest land mass and the bathymetry were highly correlated and the distance term explained more of the variation so depth was not included in the model. The geographic and environmental parameters, chlorophyll-a

(mgm⁻³), distance from land (m), SST (°C), SSH (m), and slope (%), explained 55.9% of the NASC spatial variation. Table 2 details the significance of each parameter smooth function. While all smooth functions of the environmental and geographic parameters were significant (Table 2), only the distance and chlorophyll-a showed a clear pattern. As the distance from land increased (GAM: $F = 1712.3$; $p < 0.0001$, Figure 8) and chlorophyll-a increased (GAM: $F = 841.5$; $p < 0.0001$, Figure 8) the NASC values decreased. Due to high variation, all other parameters did not show a clear relationship to the log of NASC (Figure 8).

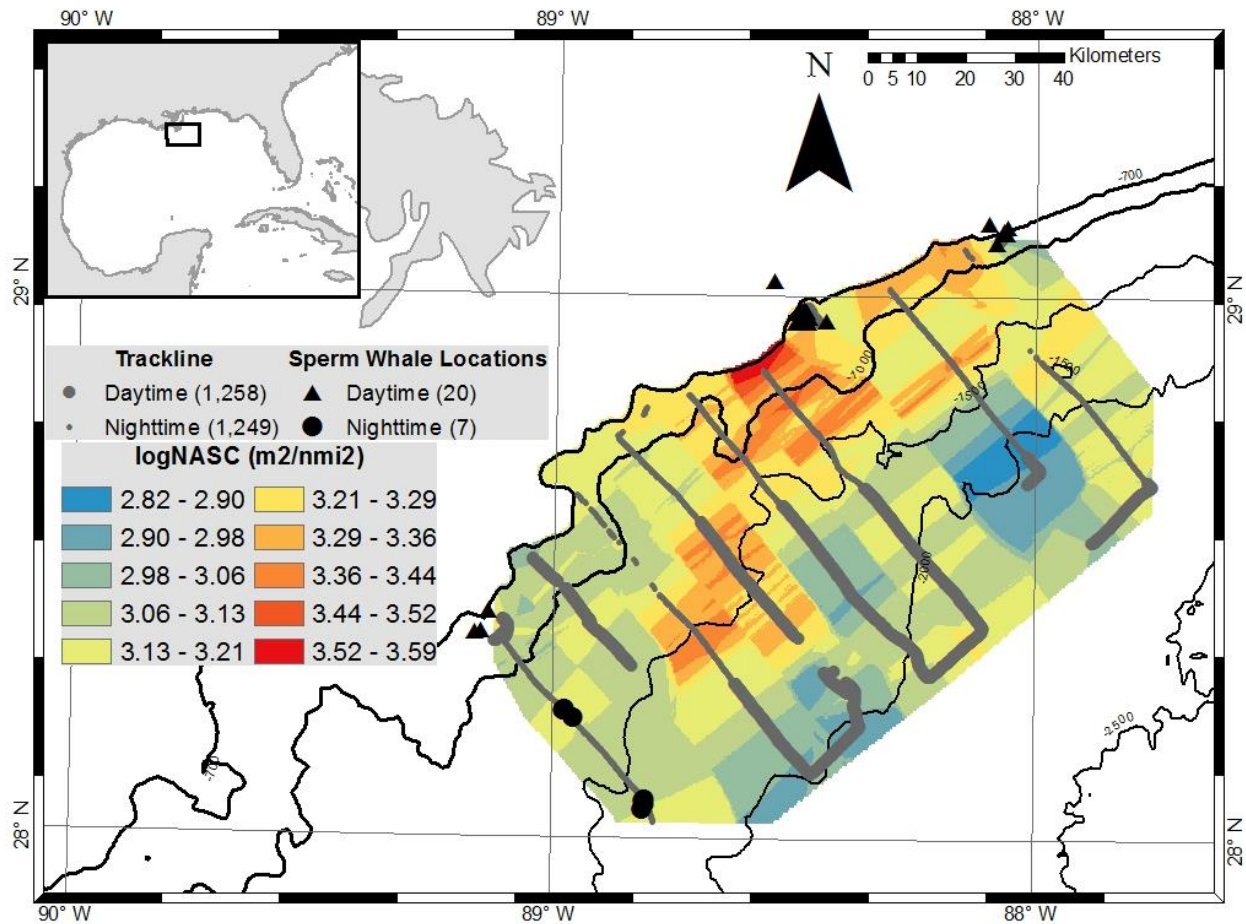


Figure 2: The sightings during the daytime (▲) and acoustic detections at nighttime (●) of sperm whales and interpolated log NASC values for the 38 kHz signal from 0 – 800 m in color from 2.82 m²nmi⁻² in blue to 3.59 m²nmi⁻² in red are spatially plotted. The ship track lines are separated by daytime (thicker grey line) and nighttime (thinner grey line). The high and low log NASC values and bathymetry were represented in both daytime and nighttime samples.

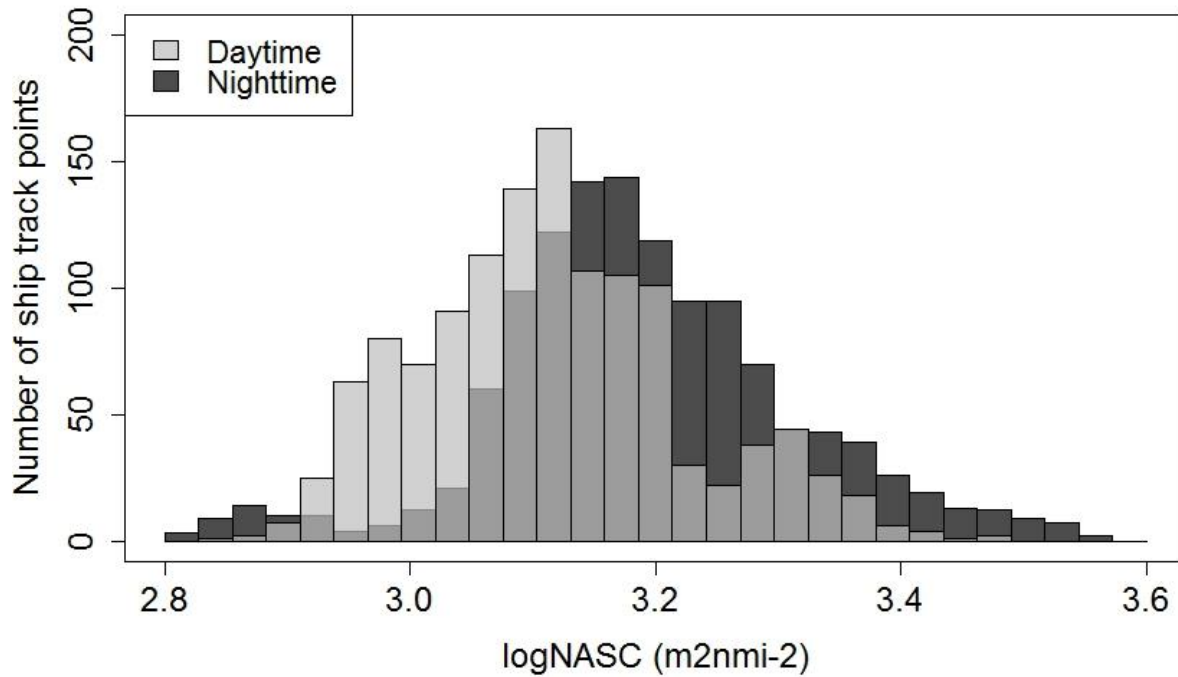
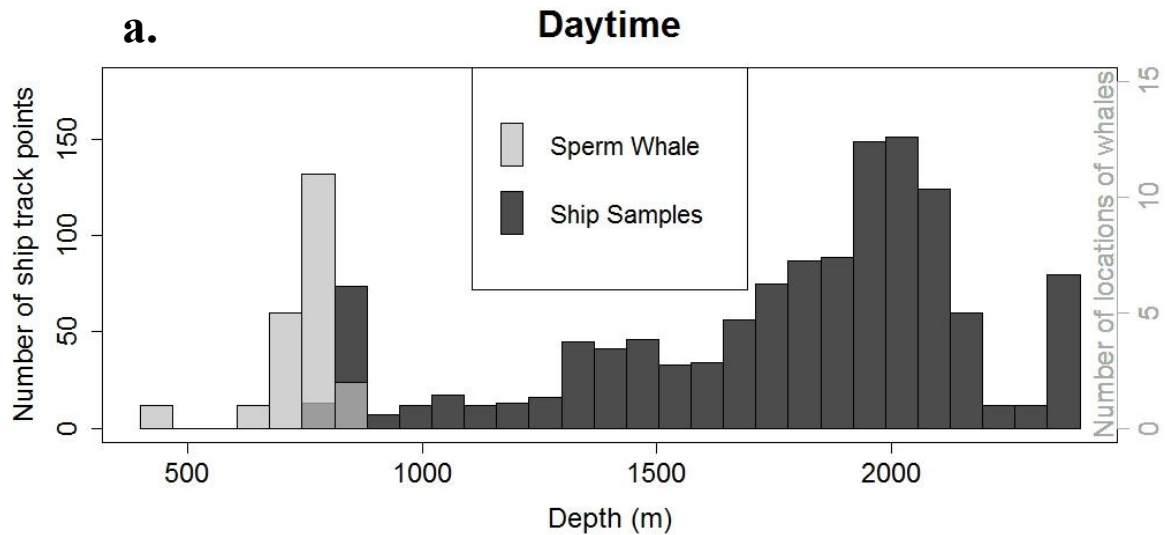


Figure 3: A comparison between the distributions of logNASC (m^2nmi^{-2}) collected during the daytime in light grey and nighttime in dark grey with the medium grey representing the overlap between the two distributions.

Table 1: Summary of the sperm whale visual sightings and acoustic detection locations for daytime and nighttime.

Date	Time (UTC)	Latitude	Longitude	Acoustic	Visual	Day/Night
8/9/2012	20:52	28.4172	-89.152	Yes	Yes	Daytime
8/9/2012	21:19	28.3923	-89.129	Yes	Yes	Daytime
8/9/2012	21:42	28.3727	-89.138	No	Yes	Daytime
8/10/2012	4:26	28.2371	-88.973	Yes	No	Nighttime
8/10/2012	4:30	28.2355	-88.971	Yes	No	Nighttime
8/10/2012	4:56	28.2181	-88.955	Yes	No	Nighttime
8/10/2012	9:01	28.0653	-88.802	Yes	No	Nighttime
8/10/2012	9:01	28.0653	-88.802	Yes	No	Nighttime
8/10/2012	9:01	28.0653	-88.802	Yes	No	Nighttime
8/10/2012	10:57	28.0609	-88.806	Yes	No	Nighttime
8/15/2012	16:48	28.9468	-88.452	No	Yes	Daytime
8/15/2012	17:42	28.9896	-88.488	No	Yes	Daytime

8/15/2012	18:03	28.9914	-88.505	No	Yes	Daytime
8/15/2012	20:33	28.9621	-88.531	No	Yes	Daytime
8/15/2012	21:00	28.9594	-88.495	No	Yes	Daytime
8/15/2012	21:27	28.9562	-88.481	No	Yes	Daytime
8/15/2012	21:42	28.9717	-88.486	No	Yes	Daytime
8/15/2012	21:52	28.9824	-88.489	No	Yes	Daytime
8/15/2012	22:25	28.9532	-88.51	No	Yes	Daytime
8/15/2012	23:30	28.9656	-88.51	No	Yes	Daytime
8/15/2012	23:48	28.9569	-88.491	No	Yes	Daytime
8/15/2012	23:55	28.9549	-88.482	No	Yes	Daytime
8/17/2012	15:27	29.1207	-88.063	No	Yes	Daytime
8/17/2012	15:29	29.1207	-88.063	No	Yes	Daytime
8/17/2012	15:53	29.1221	-88.056	No	Yes	Daytime
8/17/2012	16:25	29.1054	-88.071	No	Yes	Daytime
8/17/2012	16:45	29.1138	-88.075	No	Yes	Daytime



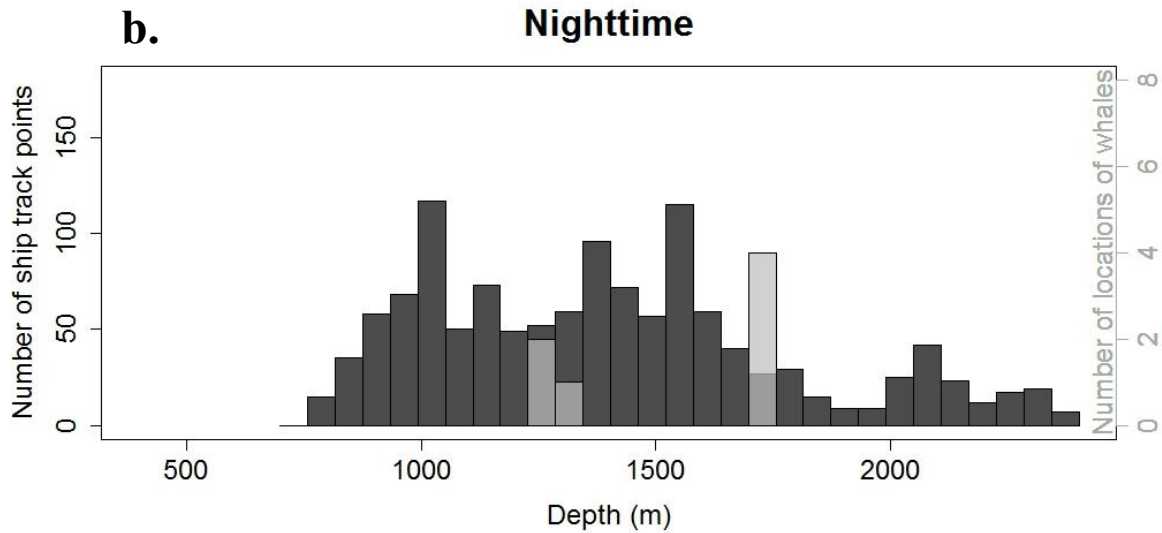


Figure 4: A comparison between the distributions of ocean bottom depth (m) collected along the ship track in dark grey and the depth of the sperm whale locations in light grey and medium grey representing the overlap between the two distributions for both the a) daytime and b) nighttime.

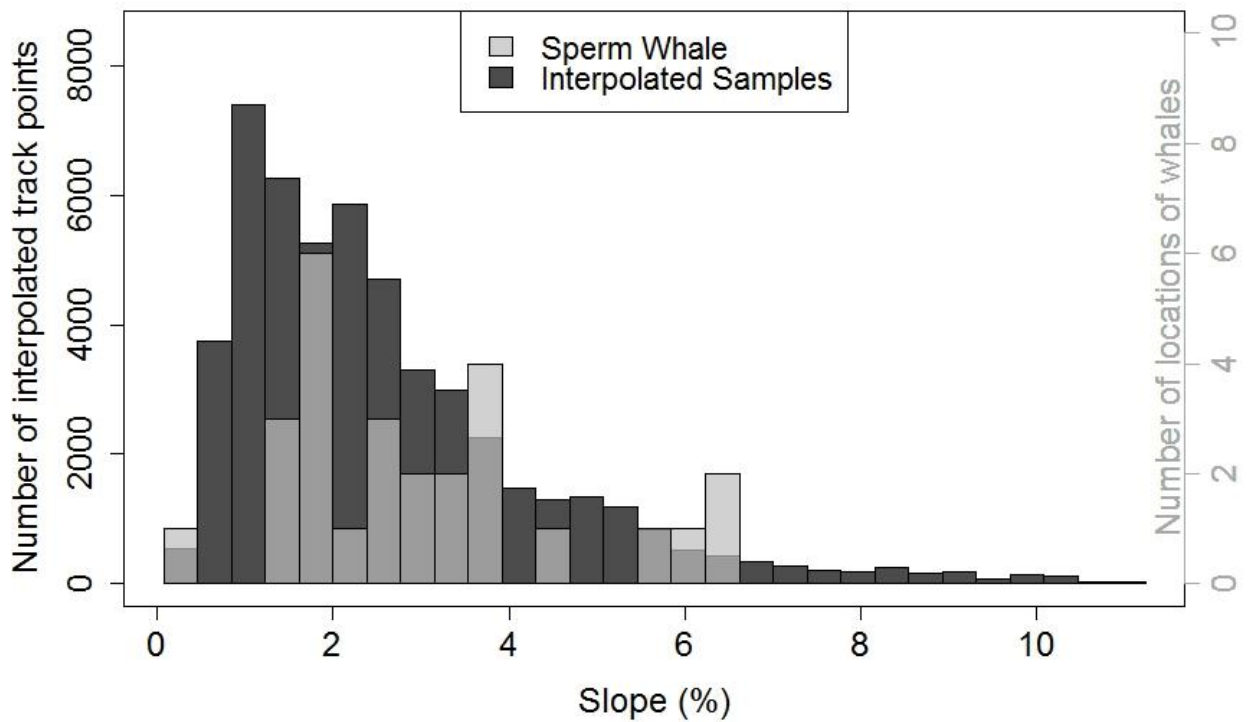


Figure 5: A comparison between the percent slope of the bathymetry over the interpolated range in dark grey and the percent slope for the sperm whale locations in light grey and medium grey representing the overlap between the two distributions for both daytime and nighttime.

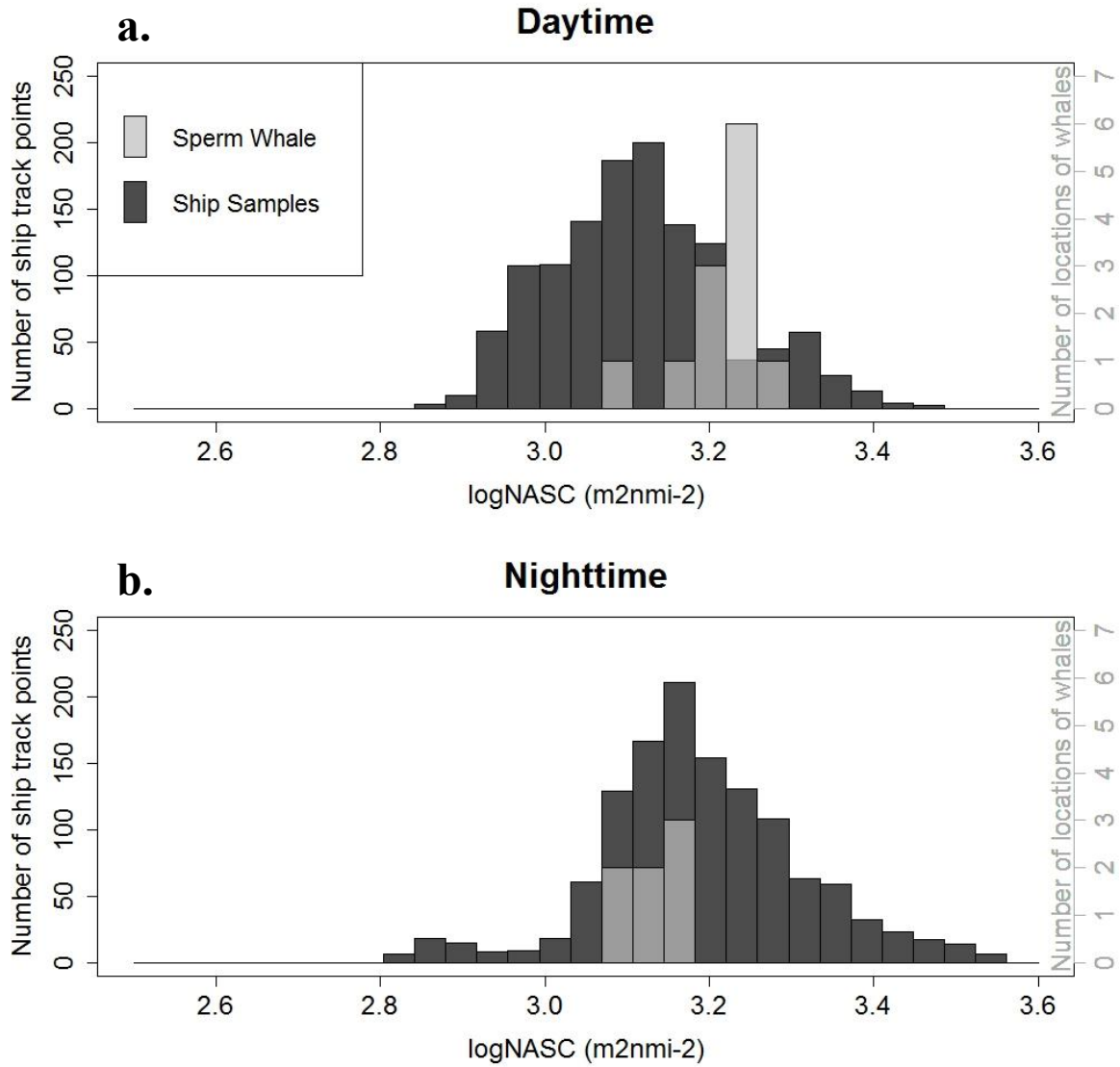


Figure 6: A comparison between the distribution of log NASC ($m2nmi-2$) values collected along the ship track in dark grey and the NASC values collected for the sperm whale location in light grey and medium grey representing the overlap between the two distributions for both the a) daytime and b) nighttime.

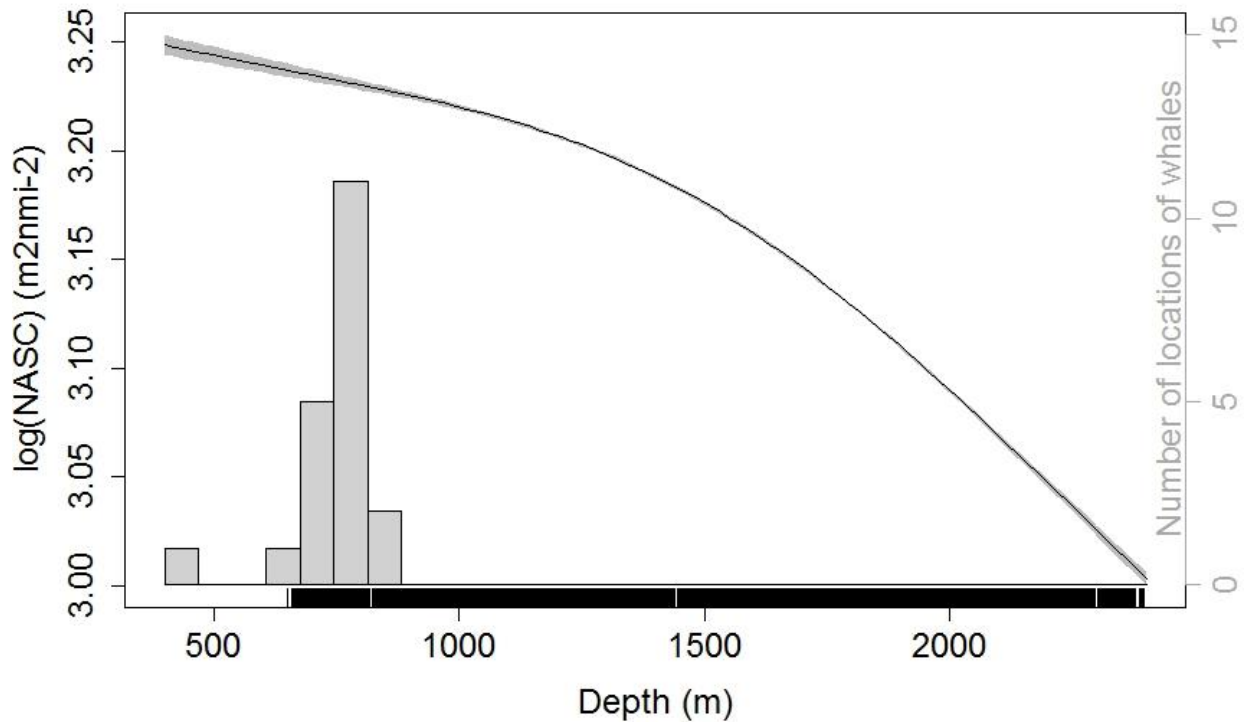


Figure 7: Plots of the generalized additive model (GAM) smoother for the distribution of the log of Nautical Area Scattering Coefficient (NASC) relative to the bathymetry and a histogram of the number of locations of sperm whales. The sperm whales are concentrated in depths with higher modeled log NASC value. Tick marks on the x-axis correspond to the sampling distribution. The grey shading of the smooth function indicates two times the standard error.

Table 2: Generalized Additive Model (GAM) non-linear smoothers for the log of the Nautical Area Scattering Coefficient (NASC) against latitude and longitude, satellite surface chlorophyll-a (mg m^{-3}), distance from land (m), satellite sea surface temperature ($^{\circ}\text{C}$), satellite sea surface height (m), and slope percentage from the bathymetry. The table includes the estimated degrees of freedom (edf) for the model terms, the F-value and associated p-value. The significant p-values are in bold with alpha defined at 0.05.

Parameter	edf	F value	P(F)
s (CHLa)	8.947	841.5	<0.0001
s (Distance)	8.890	1712.3	<0.0001
s (SST)	8.987	395.3	<0.0001
s (SSH)	8.999	747.3	<0.0001
s (Slope)	8.882	133.0	<0.0001

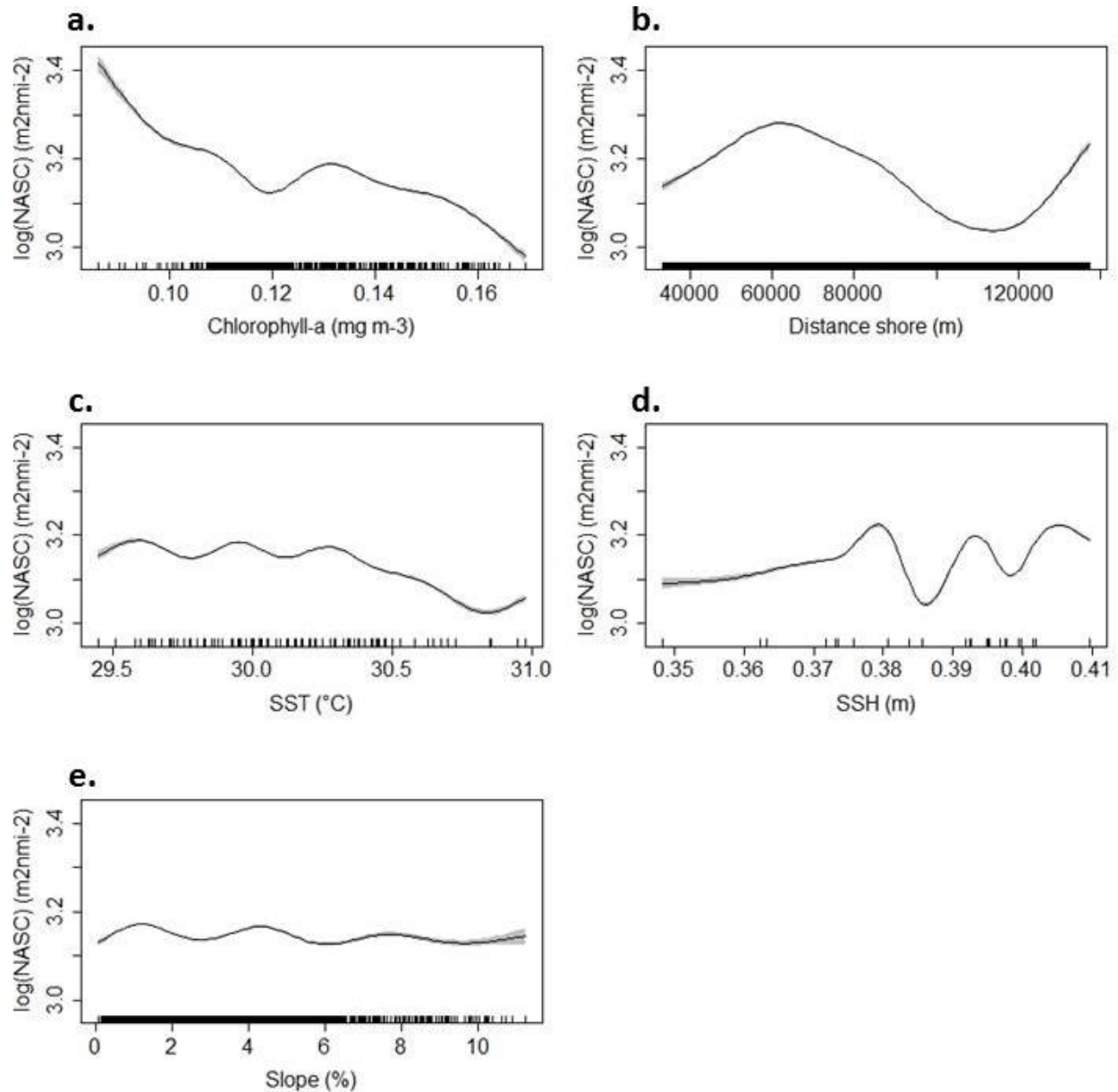


Figure 8: Plots of the generalized additive model (GAM) smoothers for the distribution of the log of Nautical Area Scattering Coefficient (NASC) relative to the environmental and geographic parameters: a) chlorophyll-a (mg m⁻³), b) distance from land (m), c) satellite sea surface temperature (SST, °C), d) satellite sea surface height (SSH, m), and e) bathymetry slope percentage. All smoothers are significant. Tick marks on the x-axis correspond to the sampling distribution. The grey shading indicates two times the standard error for each smooth function.

Discussion

In 2010 the Deep Horizon Oil spill occurred in the north central Gulf of Mexico with the oil dispersing throughout this area. See the ‘*’ in figure 9 for the start location of the spill. There

were concerns about the long term effects of the oil spill on the behavior and health of mobile animals in the Gulf. After the oil spill the health of dolphins declined with the dolphins showing signs of hypoadrenocorticism and having higher probability of moderate to severe lung disease (Schwacke et al. 2013) and there was a decrease in the vocalizations of sperm whales suggesting that less individuals were present in this area (Ackleh et al. 2012). The purpose of this project was to understand the post-spill utilization of this area by sperm whales, one of the predominantly sighted large whales in the central Gulf of Mexico (Mullin et al. 1994, Jefferson 1996, Davis et al. 1998, Mullin & Fulling 2004) as well as the distribution and relationship to micronekton backscatter. This study demonstrated that two years post spill in 2012 the whales were still sighted in the area of the spill and echolocation clicks were also recorded in this area indicating foraging activity (Figure 2).

For this study, the bathymetry of the ocean seemed to be the major factor influencing the daytime locations of whale sightings in the central Gulf of Mexico. The whales appeared to prefer the shallower slope depths from 448 m to 846 m and were not sighted in the deeper waters. This agrees well with the recorded dive depths of tagged sperm whales in the Gulf of Mexico with the whales diving shallower with a maximum dive depth of 644 meters when compared to other locations (Watwood et al. 2006). For example, max dive depths in the Atlantic Ocean and the Ligurian Sea have been documented for depths greater than 800 meters (Watwood et al. 2006).

Comparison between the sighting locations in this study and a study from 1997 (Davis et al. (2002) showed some overlap area pre- and post- Deep Horizon Oil Spill (Figure 9). Davis et al. (2002) found that sperm whales were sighted in the central slope waters less than 3000 meters with slope instead of depth being the major factor for the sighting locations of the whales. While

depth was a significant factor determining sperm whale distribution in our study and slope was not (Figure 5), the authors of the Davis et al. (2002) paper speculate that the significant slope relationship was skewed by a clustering of sightings along the Florida escarpment. This area was not sampled during our study which might explain the differing results.

The sperm whales in our study also preferred locations with higher micronekton density as reflected in the backscatter values. This relationship agreed quite well with two studies prior to the Deep Horizon Oil Spill that found that sperm whales in this area were sighted in areas with higher acoustic volume backscatter intensity (ABI) (Sindlinger et al. 2005) and higher acoustically estimated mean biomass (EMB) of zooplankton (Davis et al. 2002) from an Acoustic Doppler Current Profiler (ADCP). The backscatter from the Sindlinger et al. (2005) paper along with our study can record the relative micronekton biomass. Stranded whales in the Gulf of Mexico as well as other parts of the world show a preference for foraging on cephalopods (Clarke 1980, 1996, Barros 2003). These cephalopods feed on micronekton (Passarella & Hopkins 1991, Markaida & Sosa-Nishizaki 2003) and past trawls in the Gulf of Mexico found that the cephalopod paralarvae per m^2 was significantly correlated with zooplankton biomass (Davis et al. 2002). It would be logical to assume that higher backscatter values from micronekton in the water column would indicate more organisms available for the whales' prey to feed on; therefore, attracting more of the whale's prey and subsequently more sperm whales to the area.

The other objective of this study was to understand the spatial variability of the micronekton community in the sampled area based on the geographic and environmental variability. The spatial variability in this study was explained by distance from the coast with points closer to shore having the highest log NASC values. The closest coastline to the study sight was the

Mississippi River Delta. The Mississippi River is the largest river chain in North America and its delta has been documented to increase nutrient influx into the Gulf (Turner & Rabalais 1994, Rabalais et al. 1996). This increased nutrient flux has led to increased phytoplankton levels (Riley 1937, Thomas & Simmons 1960, Rabalais et al. 1996) that could lead to increased levels of micronekton as seen in this study location. This relationship has additionally been documented with higher densities of zooplankton and micronekton closer to the river delta (Sindlinger et al. 2005).

For this study the environmental variables, specifically SST and SSH did not influence the distribution of NASC values. We speculate that the main reason for this was the low variation of these values during the sampling time. Additionally while chlorophyll-a did have an inverse relationship with NASC this was at a relatively narrow range of chlorophyll-a values from 0.086 to 0.169 mg m⁻³ and was driven by only a couple data points at the high and low end and therefore probably doesn't give a true indication of the relationship between chlorophyll-a and NASC. During parts of the year the loop current can penetrate as far north as the sampling area (Wiseman Jr & Dinnel 1988, Müller-Karger et al. 1991, Nowlin Jr. et al. 2001) causing higher variability of these environmental parameters in this location. The penetration of this current can lead to changes in the SSH as well as an increase in chlorophyll-a values due to the upwelling along the slope increasing the nutrients in the water (Paluszkiwicz et al. 1983, He & Weisberg 2003, Jochens & DiMarco 2008). Additionally the movement of the current can create an influx of the warmer waters in the central Gulf of Mexico altering the SST. However during the study time the loop current and anticyclonic eddies that separate from the current were farther south of the sampling location (Figure 1) leading to a rather homogenous area with low variability in the

environmental variables leading to the lack of relationship between the micronekton backscatter and these variables.

This paper displays the importance of studying the bathymetry and micronekton backscatter when trying to understand the distribution of sperm whales in the central Gulf of Mexico and other parts of the world. Even after the Deep Horizon Oil spill the sperm whales still utilize this area preferring the slope water with higher forage available for their prey similar to their behavior documented prior to the oil spill in 2010.

Acknowledgements

The authors would like to thank the crew of the M/V Sara Bordelon as well as the volunteers and scientists from Oregon State University. The authors would like to specifically thank Justin Miyano for his assistance with removing noise from the echosounder data. The funding for this project was provided by Oregon State University.

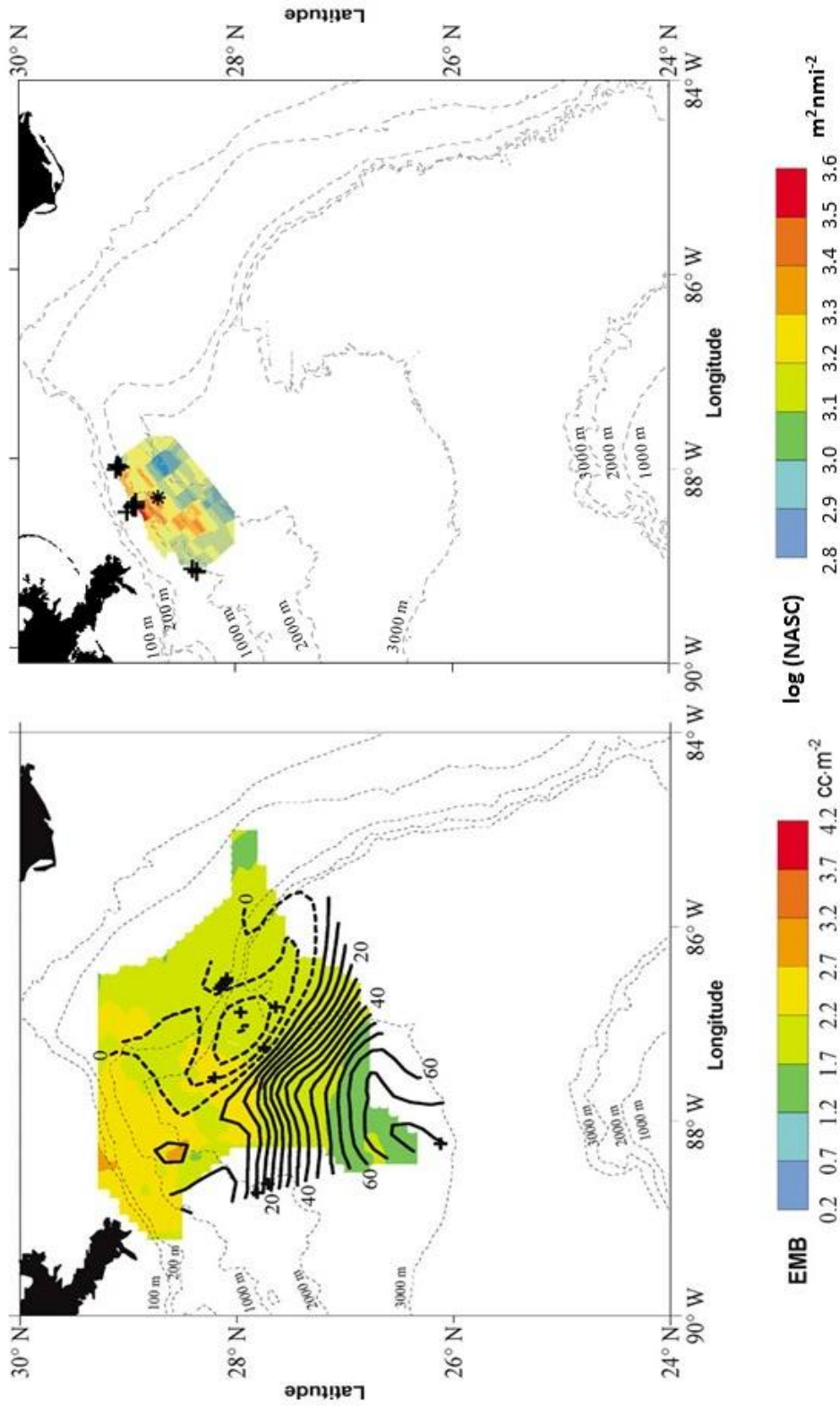


Figure 9: a) Adapted from (Stephens & Krebs 1986) from a mid-summer 1997 cruise with the color contours indicating nighttime estimated mean biomass (EMB, $\text{cm}^3 \text{m}^{-2}$) b) is this study with the color contours indicating the log Nautical Area Scattering Coefficient (NASC, $\text{m}^2 \text{nmi}^{-2}$). For both figures the sperm whale sightings (+) are plotted with the thin dashed lines representing isobaths. The * is the site of the Deep Horizon Oil Spill.

References

- Ackleh AS, Ioup GE, Ioup JW, Ma B, Newcomb JJ, Pal N, Sidorovskaia NA, Tiemann C (2012) Assessing the Deepwater Horizon oil spill impact on marine mammal population through acoustics: Endangered sperm whales. *The Journal of the Acoustical Society of America* 131:2306-2314
- Barros NB (2003) Diet of free-ranging and stranded sperm whales (*Physeter macrocephalus*) from the Gulf of Mexico. Mote Marine Laboratory Technical Report Number 895:1-14
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1-48
- Baumgartner MF (1997) The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. *Marine Mammal Science* 13:614-638
- Benoit-Bird KJ, Gilly WF (2012) Coordinated nocturnal behavior of foraging jumbo squid *Dosidicus gigas*.
- Benoit-Bird KJ, Gilly WF, Au WWL, Mate B (2008) Controlled and in situ target strengths of the jumbo squid *Dosidicus gigas* and identification of potential acoustic scattering sources. *The Journal of the Acoustical Society of America* 123:1318-1328
- Clarke MR (1980) Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Reports* 37:1-324
- Clarke MR (1996) Cephalopods as Prey. III. Cetaceans. *Philosophical Transactions: Biological Sciences* 351:1053-1065
- Davis R, Fargion G, May N, Leming T, Baumgartner M, Evans W, Hansen L, Mullin K (1998) Physical habitat of cetaceans along the continental slope in the northcentral and western Gulf of Mexico. *Marine Mammal Science* 14:490-507
- Davis RW, Ortega-Ortiz JG, Ribic CA, Evans WE, Biggs DC, Ressler PH, Cady RB, Leben RR, Mullin KD, Würsig B (2002) Cetacean habitat in the northern oceanic Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers* 49:121-142
- De Robertis A, Higginbottom I (2007) A post-processing technique to estimate the signal-to-noise ratio and remove echosounder background noise. *ICES Journal of Marine Science* 64:1282-1291
- Demer DA, Berger L, Bernasconi M, Bethke E, Boswell K, Chu D, Domokos R, Dunford A, Fassler S, Gauthier S, Hufnagle LT, Jech JM, Bouffant N, Lebourges-Dhaussy A, Lurton X, Macaulay GJ, Perrot Y, Ryan T, Parker-Stetter S, Stienessen S, Weber T, Williamson N (2015) Calibration of acoustic instruments. *ICES Cooperative Research Report* 326:1-133
- Echoview Software Pty. Ltd. (2014) Echoview software, version 6.1. Echoview Software Pty. Ltd., Hobart, Australia.
- ESRI (2011) ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute
- Foote KG, Vestnes G, Maclennan DN, Simmonds EJ (1987) Calibration of acoustic instruments for fish density estimation: a practical guide. *ICES Cooperative Research Report* 144:1-81
- Fox J, Weisberg S (2011) An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage.
- Georgakarakos S, Kitsiou D (2008) Mapping abundance distribution of small pelagic species applying hydroacoustics and Co-Kriging techniques. *Hydrobiologia* 612:155-169

- Goold JC, Jones SE (1995) Time and frequency domain characteristics of sperm whale clicks. *The Journal of the Acoustical Society of America* 98:1279-1291
- He R, Weisberg RH (2003) A Loop Current Intrusion Case Study on the West Florida Shelf. *Journal of Physical Oceanography* 33:465-477
- Jefferson T, Schiro A (1997) Distribution of cetaceans in the offshore Gulf of Mexico. *Mammal Review* 27:27-50
- Jefferson TA (1996) Estimates of Abundance of Cetaceans in Offshore Waters of the Northwestern Gulf of Mexico, 1992-1993. *The Southwestern Naturalist* 41:279-287
- Jochens AE, DiMarco SF (2008) Physical oceanographic conditions in the deepwater Gulf of Mexico in summer 2000–2002. *Deep Sea Research Part II: Topical Studies in Oceanography* 55:2541-2554
- Maravelias CD, Reid DG, Simmonds EJ, Haralabous J (1996) Spatial analysis and mapping of acoustic survey data in the presence of high local variability: geostatistical application to North Sea herring (*Clupea harengus*). *Canadian Journal of Fisheries and Aquatic Sciences* 53:1497-1505
- Markaida U, Sosa-Nishizaki O (2003) Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Journal of the Marine Biological Association of the UK* 83:507-522
- Miller PJ, Johnson MP, Tyack PL (2004) Sperm whale behaviour indicates the use of echolocation click buzzes ‘creaks’ in prey capture. *Proceedings of the Royal Society of London B: Biological Sciences* 271:2239-2247
- Møhl B, Wahlberg M, Madsen PT, Heerfordt A, Lund A (2003) The monopulsed nature of sperm whale clicks. *The Journal of the Acoustical Society of America* 114:1143-1154
- Müller-Karger FE, Walsh JJ, Evans RH, Meyers MB (1991) On the seasonal phytoplankton concentration and sea surface temperature cycles of the Gulf of Mexico as determined by satellites. *Journal of Geophysical Research: Oceans* 96:12645-12665
- Mullin K, Hoggard W, Roden C, Lohofener R, Rogers C, Taggart B (1994) Cetaceans on the upper continental slope in the north-central Gulf of Mexico. *Fishery Bulletin* 92:773-786
- Mullin KD, Fulling GL (2004) Abundance of cetaceans in the oceanic northern Gulf of Mexico, 1996–2001. *Marine Mammal Science* 20:787-807
- Nowlin Jr. WD, Jochens AE, DiMarco SF, Reid RO, Howard MK (2001) Deepwater physical oceanography reanalysis and synthesis of historical data: Synthesis Report. OCS Study MMS 2001-064. In: U.S. Dept. of the Interior MMS, Gulf of México OCS Region (ed), New Orleans, LA
- Nowlin WDJ, McLellan HJ (1967) A Characterization of the Gulf of Mexico Waters in Winter. *Journal of Marine Research* 25:29-59
- Paluszkiwicz T, Atkinson LP, Posmentier ES, McClain CR (1983) Observations of a loop current frontal eddy intrusion onto the West Florida Shelf. *Journal of Geophysical Research: Oceans* 88:9639-9651
- Passarella KC, Hopkins TL (1991) Species composition and food habits of the micronektonic cephalopod assemblage in the eastern Gulf of Mexico. *Bulletin of Marine Science* 49:638-659
- Petitgas P (1993) Use of a disjunctive kriging to model areas of high pelagic fish density in acoustic fisheries surveys. *Aquatic Living Resources* 6:201-209
- R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

- Rabalais NN, Turner RE, Justic D, Dortch Q, Wiseman WJ, Barun KSG (1996) Nutrient Changes in the Mississippi River and System Responses on the Adjacent Continental Shelf. *Estuaries* 19:386-407
- Riley GA (1937) The significance of the Mississippi River drainage for biological conditions in the Northern Gulf of Mexico. *Journal of Marine Research* 1:60-74
- Schwacke LH, Smith CR, Townsend FI, Wells RS, Hart LB, Balmer BC, Collier TK, De Guise S, Fry MM, Guillette Jr LJ (2013) Health of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana, following the Deepwater Horizon oil spill. *Environmental science & technology* 48:93-103
- Simmonds J, MacLennan DN (2005) *Fisheries Acoustics: Theory and Practice*. Blackwell Publishing
- Sindlinger LR, Biggs DC, DiMarco SF (2005) Temporal and spatial variability of ADCP backscatter on a continental slope. *Continental Shelf Research* 25:259-275
- Thomas WH, Simmons EG (1960) Phytoplankton production in the Mississippi Delta.
- Turner RE, Rabalais NN (1994) Coastal eutrophication near the Mississippi river delta. *Nature* 368:619-621
- Watkins WA, Daher MA, Fristrup KM, Howald TJ, Sciara D, Notarbartolo G (1993) Sperm whales tagged with transponders and tracked underwater by sonar. *Marine mammal science* 9:55-67
- Watwood SL, Patrick JOM, Johnson M, Madsen PT, Tyack PL (2006) Deep-Diving Foraging Behaviour of Sperm Whales (*Physeter macrocephalus*). *Journal of Animal Ecology* 75:814-825
- Wiseman Jr WJ, Dinnel S (1988) Shelf currents near the mouth of the Mississippi River. *Journal of physical oceanography* 18:1287-1291
- Wood SN (2006) *Generalized Additive Models: An introduction with R*. Chapman and Hall/CRC
- Zar J (1984) *Biostatistical analysis*. Prentice-Hall, New Jersey

CHAPTER V

DISCUSSION AND CONCLUSIONS

Micronekton, organisms 2 – 20 cm, including small fishes, crustaceans, and cephalopods (Brodeur & Yamamura 2005) are an important component linking primary producers to higher trophic levels (Roger & Grandperrin 1976, Choy et al. 2013, Young et al. 2015, Choy et al. 2016) influencing the behavior and distribution of higher trophic levels including tuna, sharks, and marine mammals. Demonstrating the importance in understanding the composition and distribution of micronekton and what components of the environment can affect these factors. This dissertation demonstrated that throughout three geographic locations the micronekton, formed discrete layers, a low density surface layer and a more robust deep scattering layer (Chapter II, III & IV). These layers appeared to form patchy aggregations with locations closer to shore and at shallower bathymetry having higher backscatter (Chapter II & IV) similar to aggregations in the South Pacific (Escobar-Flores et al. 2013). These areas of higher backscatter were linked to the presence of echolocating short-finned pilot and beaked whales in the Northwestern Hawaiian Islands (NWHI) and locations of sperm whales in the Gulf of Mexico (GOM) suggesting that these micronekton are part of the food web supporting deep-diving odontocetes and their prey.

Past research has demonstrated a link between shallow water foragers and micronekton distributions (Benoit-Bird & Au 2003, Benoit-Bird et al. 2004) with limited studies on marine mammal species that dive deeper than 200 meters to feed (Hazen & Johnston 2010, Hazen et al. 2011, Abecassis et al. 2015). This dissertation demonstrated that deep-diving cetaceans in the NWHI, the Main Hawaiian Island's (MHI) Island of Hawaii, and the Gulf of Mexico (Chapter II, III & IV) echolocate, indicating that they are searching for prey, in areas of higher micronekton

backscatter similar to the behavior seen in shallow water cetacean foragers. The main forage of these cetaceans are larger cephalopods and fish (Clarke 1980, Sekiguchi et al. 1992, Clarke & Goodall 1994, Clarke 1996, Gannon et al. 1997, Clarke & Young 1998, Pauly et al. 1998, Barros 2003, MacLeod et al. 2003) that can be hard to sample using standard techniques, i.e. trawling. Understanding micronekton distribution, a trophic intermediate, might be an alternative method to understand what is driving the behavior of these deep diving foragers.

To further expand on what was learned it is important to determine the species composition of the micronekton comprising the acoustic backscatter. To do this trawling data is needed in the NWHI to describe the species composition within the mesopelagic layers. We found that similar to the Island of Hawaii (Abecassis et al. 2015) the backscatter levels closer to shore and at shallower depths in the NWHI was higher than the off shore samples (Chapter II). The inshore waters of the main Hawaiian islands have a distinct assemblage of micronekton termed the Mesopelagic Boundary Community (MBC) different from the offshore composition (Reid et al. 1991). Our work suggests that there might be a similar community in the NWHI and trawling and/or other optical sampling of the deep scattering layer will better inform if there is this distinct community similar to the MBC in the MHI.

It is also important to further the understanding of the relationship between the micronekton distribution in the NWHI and the MHI. Past research has found higher biomass and numerical densities of endemics (DeMartini & Friedlander 2006) and higher mean biomass of trophic levels (apex predators, other secondary consumers, and herbivores) in the NWHI compared to the heavily populated and fished MHI (Friedlander & DeMartini 2002, Williams et al. 2015). These studies have been focused on shallow waters and have not investigated pelagic species leaving a gap in our understanding of the density of mesopelagic animals in the NWHI compared

to the MHI. While fishing pressure in the MHI versus the NWHI appears to be the culprit for the reduction in biomass of these shallow water species, geography and higher levels of near shore productivity (Gove et al. 2016) might be influencing the micronekton at depth. Cursory analysis of the Island of Hawaii compared to the NWHI found that the NWHI had significantly higher backscatter than the Island of Hawaii across both inshore and off shore samples suggesting that there are higher densities of pelagic micronekton in the NWHI similar to the relationship seen in shallow water reef communities. It will be important to collect more backscatter throughout the MHI as well as trawling throughout both the NWHI and MHI to better understand the difference between the MHI and the NWHI.

Finally Chapter III of this dissertation highlighted the variability of the scattering layers with the composition and distribution varying significantly over a 24 hour period. Future work should take this temporal variation into account when trying to understand foraging behavior of the deep diving odontocetes as well as other oceanic predators. Past work has mostly focused on spatial variability (Hazen & Johnston 2010, Hazen et al. 2011) with the temporal variability being ignored or assumed to be negligible which can lead to assumptions that these micronekton layers are stagnant and not changing in time. If the composition and distribution of these layers can change significantly over a 24 hour period then it can be hypothesized that the highly mobile marine mammals will change their behavior in response to this variability. To better address and understand this variability we are planning to do nightly paired trawling and acoustics studies along the leeward side of the Island of Hawaii both inshore and off shore to better explain this temporal variability in composition and structure.

This dissertation really underscores the limited knowledge in the field of pelagic acoustic ecology and the importance to better understand the distribution of mesopelagic organisms

because they are a key component in the food web and thus subsequently influence the behavior of mobile predators. There are still many questions that can and should be addressed when studying mesopelagic micronekton including but not limited to how micronekton distribution changes over long time periods, seasonally, under climate change conditions; how geography might influence this distribution because it appears that the NWHI has higher backscatter than the MHI; how distance to land might influence the composition of the micronekton; and how these differences relate to mobile predators including but not limited to deep diving tooth whales. Acoustics is just one tool to address these questions. It will be important for future work to develop and use other tools concurrent with acoustics to better address these questions. Development and use of imaging, high frequency sonar (ex. DIDSON (Giorli et al. in revision)), and more mobile (ex. Remote or Autonomous Ocean Vehicles) technology that can be used at depth with acoustics will be able to provide near real time comparisons between the backscatter and the composition allowing for a better understanding of how backscatter values can change as a function of composition. Additionally the use of tags on the mobile predators in coincidence with acoustic techniques could allow for better targeted sampling of the mobile predator's depth allowing for the determination of where in the layers these animals are spending most of their time. Are they feeding below or within these layers and how is the distribution patterned at these depths? Are the micronekton more patchy or homogenous in these areas the tagged animal is spending most of its time and is it this patchiness that the animals are cuing in on? Additionally this might increase the rare chances of documenting the mobile predator in the active acoustics. Getting the mobile predator in the acoustics while sampling could give us a better understanding of how the micronekton respond to the presence of these animals. Do they avoid the predators by

swimming shallower or deeper than the predators' depth and how does this influence the behavior of the predators?

Micronekton are found throughout every ocean and might be the keystone species affecting the distribution of these predators so furthering the understanding of how the environment can influence these organisms might give us a better understanding on how environmental changes, whether it is increases in oceanic water temperature or sea level rise or another factor, might affect large mobile predator populations. Linking the distribution of micronekton to marine mammals' distribution will help managers better protect hotspots of whale activity by mapping locations that could be more biologically productive.

References

- Abecassis M, Polovina J, Baird RW, Copeland A, Drazen JC, Domokos R, Oleson E, Jia Y, Schorr GS, Webster DL, Andrews RD (2015) Characterizing a foraging hotspot for short-finned pilot whales and Blainville's beaked whales off the west side of the Island of Hawai'i with tagging and oceanographic data. *PLoS One* 10:1-22
- Barros NB (2003) Diet of free-ranging and stranded sperm whales (*Physeter macrocephalus*) from the Gulf of Mexico. Mote Marine Laboratory: Mote Technical Reports:1-14
- Benoit-Bird KJ, Au WWL (2003) Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology* 53:364-373
- Benoit-Bird KJ, Wursig B, Mcfadden CJ (2004) Dusky Dolphin (*Lagenorhynchus Obscurus*) Foraging in Two Different Habitats: Active Acoustic Detection of dolphins and their Prey. *Marine Mammal Science* 20:215-231
- Brodeur R, Yamamura O (2005) Micronekton of the North Pacific. *PICES Scientific Report* 30:1-115
- Choy CA, Portner E, Iwane M, Drazen JC (2013) Diets of five important predatory mesopelagic fishes of the central North Pacific. *Marine Ecology Progress Series* 492:169-184
- Choy CA, Wabnitz CCC, Weijerman M, Woodworth-Jefcoats PA, Polovina JJ (2016) Finding the way to the top: how the composition of oceanic mid-trophic micronekton groups determines apex predator biomass in the central North Pacific. *Marine Ecology Progress Series* 549:9-25
- Clarke M, Goodall N (1994) Cephalopods in the diets of three odontocete cetacean species stranded at Tierra del Fuego, *Globicephala melaena* (Traill, 1809), *Hyperoodon planifrons* Flower, 1882 and *Cephalorhynchus commersonii* (Lacepede, 1804). *Antarctic Science-Institutional Subscription* 6:149-154
- Clarke M, Young R (1998) Description and analysis of cephalopod beaks from stomachs of six species of odontocete cetaceans stranded on Hawaiian shores. *Journal of the Marine Biological Association of the United Kingdom* 78:623-641
- Clarke MR (1980) Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Reports* 37:1-324
- Clarke MR (1996) Cephalopods as Prey. III. Cetaceans. *Philosophical Transactions: Biological Sciences* 351:1053-1065
- DeMartini EE, Friedlander AM (2006) Predation, endemism, and related processes structuring shallow-water reef fish assemblages of the NWHI. *Atoll Research Bulletin* 543:237-256
- Escobar-Flores P, O'Driscoll RL, Montgomery JC (2013) Acoustic characterization of pelagic fish distribution across the South Pacific Ocean. *Marine Ecology Progress Series* 490:169-183
- Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Marine Ecology Progress Series* 230:253-264
- Gannon DP, Ready AJ, Craddock JE, Mead JG (1997) Stomach contents of long-finned pilot whales (*Globicephala melas*) stranded on the US mid-Atlantic coast. *Marine Mammal Science* 13:405-418

- Giorli G, Neuheimer A, Drazen J, Copeland A, Au WWL (in revision) Deep sea animal density and size estimated using a Dual-frequency IDentification SONar (DIDSON) offshore the island of Hawaii.
- Gove JM, McManus MA, Neuheimer AB, Polovina JJ, Drazen JC, Smith CR, Merrifield MA, Friedlander AM, Ehses JS, Young CW, Dillon AK, Williams GJ (2016) Near-island biological hotspots in barren ocean basins. *Nature Communications* 7:10581
- Hazen EL, Johnston DW (2010) Meridional patterns in the deep scattering layers and top predator distribution in the central equatorial Pacific. *Fisheries Oceanography* 19:427-433
- Hazen EL, Nowacek DP, St Laurent L, Halpin PN, Moretti DJ (2011) The relationship among oceanography, prey fields, and beaked whale foraging habitat in the Tongue of the Ocean. *PLoS One* 6:1-10
- MacLeod CD, Santos MB, Pierce GJ (2003) Review of data on diets of beaked whales: evidence of niche separation and geographic segregation. *Journal of the Marine Biological Association of the UK* 83:651-665
- Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* 55:467-481
- Reid SB, Hirota J, Young RE, Hallacher LE (1991) Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. *Marine Biology* 109:427-440
- Roger C, Grandperrin R (1976) Pelagic food webs in the tropical Pacific. *Limnology and Oceanography* 21:731-735
- Sekiguchi K, Klages NTW, Best PB (1992) Comparative analysis of the diets of smaller odontocete cetaceans along the coast of southern Africa. *South African Journal of Marine Science* 12:843-861
- Williams ID, Baum JK, Heenan A, Hanson KM, Nadon MO, Brainard RE (2015) Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS One* 10:1-19
- Young JW, Hunt BPV, Cook TR, Llopiz JK, Hazen EL, Pethybridge HR, Ceccarelli D, Lorrain A, Olson RJ, Allain V, Menkes C, Patterson T, Nicol S, Lehodey P, Kloser RJ, Arrizabalaga H, Anela Choy C (2015) The trophodynamics of marine top predators: Current knowledge, recent advances and challenges. *Deep Sea Research Part II: Topical Studies in Oceanography* 113:170-187