Diving Behavior of Melon-Headed Whales around the Hawaiian Archipelago

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Antoinette Falkenstein
Marine Mammal Science
Department of Marine Biology and Ecology

UNIVERSITY OF MIAMI
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Approved by:

____
Maria Cartolano
Lecturer **|** *Department of Marine Biology and Ecology*
Committee Chair

____
Robin W. Baird
Hawaiʻi Program Director at Cascadia Research Collective
Internship Supervisor

____
Annette E. Harnish
Research Biologist at Cascadia Research Collective
Committee Member

Antoinette Falkenstein MPS, Marine Mammal Science
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Marine mammals are vital indicators of ecosystem health, but the fact that most of their lives are spent underwater poses challenges for study. Satellite tags provide a valuable tool for examining their dive behavior, offering insights into movement and habitat use. This study focuses on melon-headed whales (*Peponocephala electra*) from the Hawaiian archipelago, where two demographically independent stocks have been identified: the Hawaiian Islands Stock and the Kohala Resident Stock. Using data from 12 satellite tags deployed onto melon-headed whales, this research examines how environmental factors such as diel and lunar cycles influence dive depth, duration, and ascent/descent rates, as well as how horizontal movements are related to oceanic eddies. Generalized additive mixed-effect models (GAMMs) were used to analyze these relationships, and eddy locations identified through the Hybrid Coordinate Ocean Model were cross-referenced with horizontal whale movements. Analysis suggested distinct diel and lunar patterns in dive behavior. Most dives occurred at night, with a mean dive depth of 237 m and a mean dive duration of 7.91 min, likely reflecting prey availability driven by vertical migrations. Ascent/descent rates also varied significantly with time of day, peaking at night and decreasing during the day. Moon illumination further influenced diving behavior, with dive depth, duration, and ascent/descent rates increasing under brighter moonlight and a notable shift toward deeper dives as moonlight intensity rose, with the deepest dives recorded at illumination levels above 0.50. There were also differences in horizontal movement patterns in relation to eddies. The Kohala Resident Stock showed minimal reliance on eddy dynamics, and the Hawaiian Islands Stock appeared to actively utilize eddies for foraging, highlighting the ecological differences and habitat adaptations between these two populations. Understanding their dive behavior can be important for informing conservation strategies to mitigate anthropogenic threats and promote coexistence between human activities and marine ecosystems.

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1.0 Introduction

As many marine ecosystems and their wildlife are increasingly threatened by environmental and anthropogenic factors, it is important to understand the behaviors of species of concern to provide effective conservation efforts. Understanding factors like spatial ecology, movements in the water column, and predator-prey interactions can provide insight into habitat use and ecosystem health. However, the behavior of marine mammals can be difficult to study as some species can be elusive, and much of their lives take place beneath the surface. Marine mammals' physiological adaptations may allow for them to dive to deep depths for extended periods of time. However, most marine mammals do not push the boundaries of these physiological adaptations and are making choices in how deep and how long to dive. This study will investigate how dive behavior in marine mammals has been studied to date, with a focus on melon-headed whales (*Peponocephala electra*) in the Hawaiian Islands.

1.1 Diving Adaptations and Physiology of Marine Mammals

Marine mammals have evolved numerous physiological adaptations that aid in diving. These distinctive adaptations might have emerged as a response to the dual pressures of foraging efficiency and predator avoidance, suggesting a potential connection between these two evolutionary demands (Hooker et al., 2012; Williams et al., 1999). Some of these adaptations include the dive reflex, and respiratory and cardiovascular adaptations (Beatty et al., 2008; Hooker et al., 2012; Ponganis, 2015). The dive reflex overrides homeostatic reflexes when the animal begins to dive under water. The dive reflex triggers apnea, vasoconstriction, and bradycardia (a slowing of the heart rate) during submersion and can reduce the risk of nitrogen and decompression sickness (Beatty et al., 2008; Hooker et al., 2012; Panneton, 2013). Marine mammals also have adaptations to help them efficiently store oxygen in their muscles and blood. Some of those adaptations include high hemoglobin and myoglobin concentrations, adapted alveoli, higher density of capillaries, and lung collapse to force air away from the alveoli (Beatty et al., 2008; Hooker et al., 2012; Ponganis, 2015). These animals also have a specialized cardiovascular system that allows them to undergo bradycardia, and vasoconstriction to direct blood flow to essential organs, like the brain and the heart (Ponganis, 2015). It has been observed in blue whales *(Balaenoptera musculus*) and other marine mammal species that the compliant aortic arch helps dampen the fluctuation of blood pressure during bradycardia, a phenomenon known as the Windkessel effect (Goldbogen et al., 2019). The Windkessel effect is thought to increase the capacity of the arteries to hold more blood as an adaptation to diving, and the size of the aortic arch varies between species (Goldbogen et al., 2019; Ponganis, 2015). Thermoregulation is also achieved through complex circulatory systems that allow animals to withstand heat loss while diving (Beatty et al., 2008; Hooker et al., 2012; Ponganis, 2015). Marine mammals maintain a counter-current arrangement of blood vessels that allows for counter-current heat exchange, which controls the movement of warm blood between the body core and peripheral areas (Hooker et al., 2012; Williams et al., 1999).

Certain cetaceans and pinniped species, like beaked whales and elephant seals, are known for their ability to perform especially deep and prolonged dives. It has been suggested that marine mammals have evolved species-specific strategies to mitigate the risks of decompression sickness and deep diving (Beatty et al., 2008; Hooker et al., 2012). Toothed whales and dolphins, known collectively as odontocetes, display a wide range of such species-specific adaptations. Comparisons between shallow diving species and beaked whales have revealed that there are fewer microvessels in beaked whales' acoustic fat to counter the restraint that increased pressure at depth might have on communication (Gabler et al., 2017). It has also been found that there are differences in the microvascular structure in blubber between shallow and deep diving cetaceans. Shallow diving species have more uniform microvascular structures within the blubber whereas deep diving species have clustered arrangements of blood vessels in areas closer to the muscular interface (McClelland et al., 2012).

1.2 Influences on Dive Behavior

Daily (diel) cycles and lunar cycles influence dive patterns of multiple species across the world. Marine mammals adjust their diving patterns based on light availability, prey distribution, and predator activity (Baird et al., 2008; Scott and Cattanach, 1998; Shaff and Baird, 2021). Foraging may have a large impact on marine mammal movements (Fahlman et al., 2023; Shaff and Baird, 2021; Woodworth et al., 2011). Oceanic micronekton, which are assemblages of small shrimp, fish, and squid, can be found from the epipelagic layer to the mesopelagic layer and are known to be prey species for marine mammals and pelagic fish (Brodeur et al., 2005; Fahlman et al., 2023; Pauley, 1998; Woodworth et al., 2011). Some micronekton species perform diel vertical migrations and it has been observed that lunar illumination has a strong effect on abundance and overall biomass of micronekton (Brodeur et al., 2005; Drazen et al., 2011). Common bottlenose dolphins (*Tursiops truncatus*), spinner dolphins (*Stenella longirostris*), and other marine mammal species have been recorded to change their dive behavior based on prey (e.g., yellowfin tuna (*Thunnus albacares*), micronekton, and other pelagic species) diel patterns throughout the day (Klatsky et al., 2007; Scott and Cattanach, 1998). Many cetacean species feed on prey in the deep scattering layer at night when prey are closer to the surface to lower energy usage (Baird et al., 2008; Owen et al., 2019; Shaff and Baird, 2021). For example, bottlenose dolphins in the Bermuda area consistently engage in deep, long dives at night, suggesting a behavioral adaptation to prey availability cycling with (Fahlman et al., 2023).

Lunar cycles also influence dive patterns through changes in ambient light levels, which shift across different lunar phases (Owen et al., 2019; Shaff and Baird, 2021). Dives observed for both rough-toothed dolphins (*Steno bredanensis*) and short-finned pilot whales (*Globicephala macrorhynchus*) are deeper dives during periods of high lunar illumination, highlighting the role lunar phases can have on dive behavior (Owen et al., 2019; Shaff and Baird, 2021). A recent study showed that lunar cycles influence habitat uses in short-finned pilot whales, which also highlights that there are broader spatial considerations relating to lunar phases (Owen et al., 2019). It has been suggested that lunar illumination and seasonal time frames have shaped diving behavior for many species, but it remains unclear whether this is directly related to light exposure or associated changes in prey behavior.

An additional factor that influences diving behavior is predator evasion (Baird et al., 2004; Roncon et al., 2018; Shaff and Baird, 2021). For instance, goose-beaked whales (*Ziphius cavirostris*) exhibit a tendency to avoid the water's surface during both daytime and moonlit periods due to the surface being safer when there is reduced visibility (Baird et al., 2008; Barlow et al., 2020). Blainville's beaked whales (*Mesoplodon densirostris*) also avoid spending time in very-near surface intermediate dives during the day. Both species have been sighted with large shark bites and typically only vocalize below approximately 400m to minimize exposure to predators (Baird et al., 2008; Tyack et al., 2006).

Eddies can significantly influence marine mammal foraging behaviors and play a large role in shaping ecological dynamics. Eddies are oceanic features characterized by swirling currents and increased biological productivity, creating concentrated zones of prey aggregation that support diverse marine ecosystems and are essential for the survival and reproductive success of marine mammals (Polovina et al., 2001). Eddies are natural feeding hotspots by concentrating nutrients and prey species, such as small fish, squid, and other invertebrates, which are essential food sources for marine mammals (Polovina et al., 2001). Studies have shown that some cetaceans and certain pinnipeds exhibit unique movement patterns and foraging in correspondence to eddy dynamics, and that these are further influenced by seasonal changes and larger oceanographic processes like currents and temperature, which can impact the spatial distribution and behavior of marine mammals (Dragon et al., 2010; Fiedler et al., 2008; Qiu, 2001; Woodworth et al., 2011). For example, it has been shown that melon-headed whales around the Hawaiian Islands move offshore to dwell in the edges of cold core cyclonic eddies and the center of warm core anticyclonic eddies (Woodworth et al., 2011). It has also been observed in Southern elephant seals (*Mirounga leonina*) that cyclonic and anticyclonic eddies are heavily favored for foraging in the interfrontal zone (Bailleul et al., 2010; Dragon et al., 2010).

1.3 Methodologies for Studying Dive Behavior

The study of dive behavior has significantly evolved over time, mostly pushed forward by technological advancements in telemetry and a growing appreciation and understanding of the ecological importance of diving. Early research relied on observational methods to infer diving patterns, but the introduction of telemetry technologies marked a transformative shift (Hooker and Baird, 2001). Telemetry is a research approach that uses deployed instruments to remotely collect data, allowing for precise measurement of dive metrics, including depth, duration, and their environmental context (e.g., water temperature, salinity, etc.). Satellite-linked tags are one such instrument that has worked well to collect data from an assortment of marine mammals, including deep diving species like the goose-beaked whale (Andrews et al., 2019; Falcone et al., 2017). These tags are typically attached to animals by darts and transmit directly from the attachment location on the animal to Argos satellite systems (Falcone et al., 2017). Archival tags are another telemetry instrument that can also store data internally, but which must be retrieved from the animal to access the data (Falcone et al., 2017; Hooker and Baird, 2001).

LIMPET (low impact minimally percutaneous electronic transmitter) tags are specialized satellite-linked tags used in marine biology to track the movements and behavior of marine animals (Block et al, 2011). These tags have led to key findings in behavioral ecology (Block et al., 2011; Falcone et al., 2017). For example, studies of goose-beaked whales and Southern Ocean predators (e.g. Northern elephant seals (*Mirounga angustirostris*), sperm whales (*Physeter macrocephalus*), white sharks (*Carcharodon carcharias*), and California sea lions (*Zalophus californianus*)) have shown that dive behavior varies with factors like prey distribution, lunar cycles, and time of day (Block et al., 2011). LIMPET tags have also aided in understanding marine mammal behavior changes in response to anthropogenic disturbances (Falcone et al., 2017; Henderson et al., 2021).

Programming of tags is equally important to understanding what kind of data can be collected and analyzed. Tags are able to be programmed to collect data during limited times in order to preserve battery or to targeting the acquisition of specific data, and can be triggered to record data at predetermined depths and times of day, along with other environmental and behavioral factors (Andrews et al., 2019; Block et al, 2011; Cioffi et al., 2023; Falcone et al., 2017). A common concern is how sample size is affected by programming regimes. One study done on goose-beaked whales has suggested that a 5 min time series data stream collected for 14 days achieved a complete or nearly complete set of diving records for the majority of tags tested (Cioffi et al., 2023). However, to better address efficient data collection, it is important to understand the behavior of the targeted species (Andrews et al., 2019; Cioffi et al., 2023). For example, the programming regimes used to collect time series data or behavior data in beaked whales should not be used for common bottlenose dolphins, as they do not participate in deep, prolonged dives like beaked whales.

1.4 Using Dive Behavior for Conservation

Understanding dive behavior in marine mammals is critical to inform effective conservation strategies. Investigating patterns and changes can give us insight to their ecological needs, habitat preferences, and responses to anthropogenic disturbance. By studying dive depths, durations, and patterns, scientists have been able to determine prey availability, feeding strategies, and habitat use. For example, studies have shown that the diving behavior of sperm whales correlates with prey distribution in deep sea environments (Miller et al., 2004). The US Navy has also worked with researchers to monitor multiple marine mammal species and potential exposure to mid-frequency active sonar (MFAS) (Henderson et al., 2021). MFAS has been attributed as the cause of marine mammal strandings in areas where multinational naval training events occurred (Balcomb and Claridge, 2001; Cox et al., 2023; Henderson et al., 2021). This knowledge informs conservation planning and marine spatial management strategies aimed at protecting these vulnerable species and their habitats. For example, areas where marine mammals perform deep and prolonged dives may be designated as marine protected areas (MPAs) or subjected to regulations that limit human activities known to disrupt their behavior.

1.5 Hawaiian Islands History and Biodiversity

The Hawaiian Islands are located in the tropical Pacific Ocean and are considered the world's most isolated archipelago. The main Hawaiian Islands consist of eight major volcanic islands: Niʻihau, Kauaʻi, Oʻahu, Molokaʻi, Lānaʻi, Maui, Kahoʻolawe, Hawaiʻi. The islands have a rich diversity of wildlife and have suffered from invasive species and major environmental impacts from colonization.

Hawaiian culture and history have been deeply intertwined with the ocean and its marine life and can be traced back through centuries. The Hawaiian people developed a strong cultural heritage shaped by their relationship with the sea and land before Western interference, relying on sustainable practices to enable their long-term survival within an island ecosystem (Tabrah, 1984). Marine mammals have held a significant importance in Hawaiian culture, art, folklore, and even rituals symbolizing a connection to the ocean and ancestral spirits (Tabrah, 1984; Watson, 2011). Species like the Hawaiian monk seal (*Monachus schauinslandi*), the humpback whale (*Megaptera novaeangliae*), and the spinner dolphin are known as "ʻaumakua", which translates to "ancestral guardians" (Kalakaua, 2021). After the United States claimed sovereignty over Hawaiʻi in 1898, Native Hawaiians experienced extreme social, economic, and environmental changes, many of which have had impacts that carry forward to today. A decline in Hawaiian traditional and sustainable practices occurred, increasing overhunting, habitat degradation, and disconnect with conservation efforts (Tabrah, 1984). In 2015, The National Oceanic and Atmospheric Administration (NOAA) issued a citation against two Kānaka Maoli women for unlawfully taking and transporting a stranded melon-headed whale known as Wānanalua (Ritts et al., 2021). The women were prosecuted on the legality of traditional sea burials as they had moved Wananalua farther out to sea to help her sink, which is considered a "take" and violates the Marine Mammal Protection Act. NOAA originally had hired these women to be a part of their Marine Mammal Response Network given their background in science and Indigenous practices (Ritts et al., 2021). This event highlighted the importance biopoltics plays into finding the balance between respecting Indigenous traditions and what that means for conservation and scientific regulations. However, Native Hawaiians have made efforts to preserve and revive traditional practices including protecting marine mammals. In recent years, political ecologists have been trying to include Indigenous care practices within marine sciences.

Hawaiʻi has unique biodiversity relating to its marine ecosystems due to both natural processes and human interactions. The archipelago chain has been formed through hotspot volcanism beneath the Pacific plate and a long series of volcanic eruptions over millions of years. This geological process has resulted in the islands having diverse sizes, topographies, and ages (Clague and Dalrymple, 1989; Spalding et al., 2019). Due to the islands' location and oceanic barriers, there has been a limited dispersal in species to and from the islands. Marine organisms, including marine mammals, exhibit notable levels of endemism in Hawaiian waters (Price and Clague, 2002). The result is that the Hawaiian archipelago is known as a biodiversity hotspot between its terrestrial and marine life. Different ecosystems like coral reefs, sea grass beds, and deep-sea habitats can contribute to the unique biodiversity of the archipelago

One of the key drivers of marine biodiversity in Hawaiʻi is the Island Mass Effect, which is a phenomenon observed in marine ecosystems that surround islands. This phenomenon describes the increase in nutrient concentrations and biological productivity around islands, compared to their surrounding open waters. This effect results in there being heightened chlorophyll concentrations surrounding the Hawaiian Islands compared to adjacent waters (Drazen et al., 2011). This then allows for diverse assemblages of mesopelagic micronekton, which in turn support biodiversity by providing a consistent food source around the islands, drawing in a multitude of species enhancing the unique biodiversity.

Another contributor to the Hawaiian archipelago's biodiversity is the presence of thin layers of plankton in coastal waters (McManus et al., 2021). These thin layers are often influenced by a complex combination of physical and biological processes. Physical factors can include tidal currents, wind, and stratification to the formation and maintenance of these areas. Biological factors can include zooplankton aggregations, phytoplankton blooms, and nutrient availability (McManus et al., 2021; Spalding et al., 2019). Hotspots of productivity can also occur within these coastal water areas. These areas can be used as indicators to study the effects of environmental variation and climate change.

The waters around the Hawaiian archipelago support a unique and diverse community of odontocetes. Some of these species include spinner dolphins, common bottlenose dolphins, various species of beaked whales, and blackfish delphinids, which include false killer whales (*Pseudorca crassidens*), killer whales (*Orcinus orca*), melon-headed whales, pygmy killer whales (*Feresa attenuata*), and short-finned pilot whales (Baird et al., 2013). Different studies showed the influence of oceanographic factors such as temperature gradients and chlorophyll concentrations on the occurrence and abundance of marine mammals (Smith et al., 1986).

1.6 Melon-Headed Whales

Melon-headed whales (hereafter shortened to "MHW") are odontocetes in the delphinid family. They are closely related to pygmy killer whales and false killer whales. They are small whales found in typically deep, tropical waters, and have a small, rounded melon with no visible beak (Perrin et al., 2009; Perryman et al., 1994). Their coloring can be different shades of dark gray, often darkest around the eyes and dorsal surface, including the dorsal fin. Their lips are often white, around the throat can be different variations of white to a lighter gray which can stretch along the ventral side (Brownell Jr. et al., 2009; Perrin et al., 2009). There are four federally recognized stocks of MHWs in the United States: the Hawaiian Islands Stock, the Kohala Resident Stock, the Northern Gulf of Mexico Stock, and the Western North Atlantic Stock (NOAA, 2021; NOAA, 2021). The population sizes for each stock differ. The Western North Atlantic Stock's abundance is unknown, while the Northern Gulf of Mexico Stock has an estimated abundance of 1,749 whales (NOAA, 2021). The Kohala Resident Stock was estimated to have 447 (95% CI = 375-519) with data collected between 2002 and 2008 (Aschettino, 2010). The Hawaiian Islands Stock is estimated to consist of 40,647 (95% CI = 11,097-148,890) whales from data collected in 2017 during the Hawaiian Islands Cetacean and Ecosystem Assessment Survey (Bradford et al., 2021). They are often found in large groups and can also be seen in mixed aggregations with Fraser's dolphin (*Lagenodelphis hosei*), spinner dolphins, and common bottlenose dolphins (Martien et al., 2017; Perrin et al., 2009). It is not uncommon for MHWs to be seen bow riding or to approach boats out of general curiosity (Perrin et al., 2009; Perryman et al., 1994).

MHWs exhibit diverse behavioral patterns across different regions of the world. While there are noticeable differences between different populations, there are similarities which reflect adaptations to local environmental conditions and social structures (Brownell Jr. et al., 2009). MHWs have a complex communication system with repeated call types for individual, subgroup, and group recognition (Kaplan et al., 2014). This system coordinates different social interactions with large groups. MHWs are also among the few species known to mass strand, with instances of several hundred whales stranding at once documented worldwide (Baird, 2016; Brownell Jr. et al., 2009; Martien et al., 2017). They also exhibit diel diving patterns that correlate with prey availability. Stomach content samples from stranded MHW have been analyzed, revealing prey items that indicate they follow diel cycles to optimize foraging efficiency based on prey movement and distribution throughout the day (West et al., 2018).

MHW population structure has not been studied extensively. Genetic analysis showed genetic differentiation among areas, suggesting limited gene flow and implying that local populations are more isolated then originally hypothesized (Martien et al., 2017). This highlights the importance of recognizing and managing these distinct populations separately. Protecting genetic diversity and maintaining connectivity between populations are crucial for ensuring the long-term survival of MHWs (Martien et al., 2017).

1.7 Melon-Headed Whales in Hawaiʻi

MHWs in Hawaiʻi exhibit distinct population structures throughout the archipelago. There are two recognized stocks in Hawaiʻi, the Hawaiian Islands Stock and the Kohala Resident Stock (Baird, 2016). Bathymetric depth influences what stock has been sighted during identification studies (Brownell Jr. et al., 2009; West et al., 2018). The Kohala Residents have a range restricted to the shallower waters of the Kohala shelf and west side of Hawaiʻi Island while the Hawaiian Islands Stock has been documented all over the archipelago (Baird, 2016; Kratofil et al., 2023). Neither stock is listed as threatened or endangered.

Females are not sexually mature until around seven years and their gestation period lasts for around a year. Females may give birth year-round, but most calves are sighted between March and June (Baird, 2016). Females have a new calf every 3-4 years. Males are not sexually mature till around their mid-teens. Average group size has been estimated to be 250 individuals and the largest at 800 (Baird, 2016). The Kohala Residents have been spotted in groups of up to 400 individuals, suggesting that at some times the whole population is together at once. MHWs in Hawaiʻi are also known to form subgroups based on sex and age and are regularly seen with other marine mammal species (Baird, 2016; Martien et al., 2017; Perrin et al., 2009). They have been sighted with rough-toothed dolphins, short-finned pilot whales, humpback whales, and bottlenose dolphins (Baird, 2016). Stomach contents of eleven stranded MHWs from the Hawaiian Islands stock were analyzed showing that their diet consists of cephalopods (77.3%) and fish (22.7%) (West et al., 2018). Diel cycles have been shown to influence the dive behavior of both stocks, although the sample size of earlier analyses was small (n=3) (West et al., 2018).

Overall, knowledge about MHW dive behavior remains limited, and more research would be beneficial to understand what factors influence their behavior.

Understanding any species' life history and threats is important to overall conservation measures. Research into diving behavior not only enhances our understanding of marine mammal ecology but also may provide some insight for their conservation. By understanding different behaviors of marine mammals, we can promote the long-term survival of these species and promote the health and resilience of marine ecosystems worldwide. Further research would be beneficial to deepen our understanding of the ecological and environmental factors influencing the population structure of melon-headed whales. This includes studying social behaviors, environmental influences, and impacts of human activities, and their effects on dive behavior across their range to inform effective conservation strategies tailored to the unique needs of each population.

1.8 Project Objective

The primary goal of this project is to gain a deeper understanding of how various environmental and temporal factors influence the dive behavior of MHWs. To explore these behavioral drivers, data was analyzed from satellite tagged MHWs from the Hawaiian Islands and Kohala Resident Stocks around the Hawaiian Archipelago. This analysis was carried out using generalized additive mixed-effect models (GAMMs), which are well-suited for handling complex and non-linear relationships between variables while accounting for nested data structures. Dive behavior metrics, including dive depth, duration, and ascent/descent rate, were analyzed in response to changes in diel and lunar cycles. The locations of MHWs derived from satellite data were also compared with the positions of known eddies to explore how these dynamic oceanographic features might affect MHW horizontal movement patterns.

Understanding the diving behavior of MHWs is critical for creating effective conservation strategies, particularly in the context of mitigating threats such as MFAS, which is used in military operations at the Pacific Missile Range Facility. By identifying the environmental and temporal factors that significantly influence MHW behavior, this research aims to provide insights that can lead to more targeted and effective conservation plans. Ultimately, this work will contribute to a better understanding of MHW habitat use and help in developing strategies to protect these species from anthropogenic impacts.

2.0 Materials & Methods

Four SPLASH10 tags and eight SPLASH10-F tags were deployed onto MHWs by Cascadia Research Collective between 2011 and 2023, with three deployed off Hawaiʻi Island and nine deployed off Kauaʻi. Tags were designed to record and transmit data on dive behavior, including dive start and end times, duration, and maximum depth, as well as periods spent at the surface (defined as periods where the animal remained above a pre-defined depth). Location data were also transmitted by tags; Argos locations were transmitted by all tags, and high-quality Fastloc®-GPS locations were transmitted by eight tags. Argos is a satellite tracking system that provides global location data for wildlife, while Fastloc® is a technology that uses GPS to enhance the accuracy of location tracking. Tags were deployed according to the methodologies in Schorr et al. (2009) using a Dan-Inject JM Special 25 pneumatic projector, with a modified arrow to hold the tag in flight at a range of 3 to 10 m. One tag (PeTag037) only recorded time series data. Six tags recorded both behavior and time series data (PeTag017, PeTag021, PeTag026, PeTag033, PeTag035, and PeTag036) and the remaining tags recorded only behavior data (PeTag014, PeTag029, PeTag031, PeTag032, and PeTag034) (Table 1). Three tags were programmed to record time series at intervals of one minute and 15 seconds (PeTag017, PeTag021, and PeTag026) while the other three recorded in intervals of five minutes (PeTag033, PeTag035, PeTag036 and PeTag037). A dive was defined as a period when the depth is greater than 50 m and time submerged is greater than 30 seconds.

Table 1. Summary of 12 LIMPET tags deployed onto Hawaiian MHWs.

Tag ID	Deployment Date (GMT)	End Date (GMT)	Stock	Data Type	Number of days Behavior data before QAQC	Number of days Behavior data after QAQC
PeTag014	2011-10-19	2011-10-31	Kohala	Behavior	8.20	7.86
PeTag017	2012-08-24	2012-09-15	Kohala	Behavior & Time Series	11.28	11.28
PeTag021	2014-07-23	2014-08-08	Hawaiian Islands	Behavior & Time Series	4.00	4.00
PeTag026	2017-08-13	2017-08-21	Hawaiian Islands	Behavior & Time Series	1.26	1.27
PeTag029	2021-08-13	2021-08-14	Hawaiian Islands	Behavior	1.24	1.24
PeTag031	2021-08-11 1	2021-09-01	Hawaiian Islands	Behavior	11.34	10.89
PeTag032	2022-08-18	2021-08-30	Hawaiian Islands	Behavior	4.42	3.96
PeTag033	2022-08-18	2022-08-29	Hawaiian Islands	Behavior & Time Series	2.45	NA
PeTag034	2022-08-24	2022-08-22	Hawaiian Islands	Behavior	0.08	NA
PeTag035	2022-08-24	2022-09-12	Hawaiian Islands	Behavior & Time Series	4.65	4.20
PeTag036	2023-08-12	2022-09-04	Hawaiian Islands	Behavior & Time Series	0.26	0.15
PeTag037	2023-08-12	2023-08-18	Hawaiian Islands	Time Series	0.00	0.00

2.1 Data Processing

Part 1: QA/QC

Quality assurance/quality control (QA/QC) tests were run on the 11 tags with dive behavior data, following the protocols in Baird et al. (2019). Briefly, CRC-checked messages were inspected for pressure transducer failure by assessing the values recorded under the 'Depth' and 'ZeroDepthOffset' columns, with potential transducer failures indicated by values exceeding +/- 10 for the Depth column and +/- 9m for the ZeroDepthOffset column. Dive data from any messages transmitted after the last CRC-checked message were discarded as a precautionary measure to ensure against undetected pressure-transducer failure. Remaining tags included PeTag014, PeTag017, PeTag021, PeTag026, PeTag029, PeTag031, PeTag032, PeTag035, PeTag036.

Once tags are assessed for pressure transducer failure, pseudotracks that link location data with individual dive and surface periods were generated for the 11 tags with behavior data using the R.utils, geosphere, lubricate, oce, lunar, suntools, raster, ncdf4, sf, dplr, and here packages in R v 4.2.3 (R Core Team, 2023). Pseudotracks assign locations to behavior dive data by interpolating closest locations from crawl (continuous time correlated random walk models) location tracklines at a 5-minute resolution. Pseudotracks also linked additional geospatial and temporal predictors such as moon phase and time of day to individual dive and surface periods. Using tag location data processed with the R package maptools (Bivand and Lewin-Koh 2016), solar angles were calculated to define the different periods of the day. Solar angles greater than 6° were categorized as day, while those less than -6° were classified as night. Periods with solar angles between -6° and +6° were considered twilight, encompassing both dawn and dusk. To determine bathymetric depth using the rgeos package (Bivand & Rundel, 2017) and the raster package (Hijmans & Van Etten, 2016), leveraging the Hawaiian Island 50 Meter Bathymetry and Topography Grids (https://www.soest.hawaii.edu/HMRG/multibeam/ bathymetry.php). Lunar cycles were represented on a scale from zero to one, with zero and one corresponding to a new moon and 0.5 representing a full moon. Individual dive rates were calculated by dividing the number of dives by the hours of behavior coverage (excluding data gaps) for each temporal period. After pseudotracks were generated, the R packages dplyr and lubricate were used to identify and split any surface periods that crossed between multiple diel periods (e.g., dawn, day) to negate any potential issues these records might cause when running summary statistics.

Part 2: Check for Pseudoreplication

Each tag that passed the QA/QC check and that was part of a temporally overlapping pair of deployments was then checked for potential pseudoreplication. The periods for each pair with overlapping dive data were identified based on the deployment and end date. Pairwise distances between simultaneous (or near simultaneous within 1-2 minutes) 5-minute crawl locations were calculated between the animals using the st_distance() function from the sf package. These distances were converted to kilometers for easier interpretation. The distances between pairs over time were visualized using line plots created with the ggplot2 package in R, as well as by plotting the crawl tracklines for each pair of tags to look for similarities in their horizontal movements during the period of overlap. The distribution of pairwise distances was summarized, and the number of instances where animals were within 1 km of each other was quantified for each animal pair. Further analysis involved comparing crawl tracklines with behavior log data from the generated pseudotracks by aligning overlapping pairs based on the date and time of the behavior logs. This allowed trimming the crawl trackline distances and visualizing the overlap in behavior data.

2.2 Data Analysis

Part 1: GAMMs

All tag data were used to produce generalized additive mixed-effect models (GAMMs). These models were constructed through three main steps: 1) determination of the distribution of the response variable, 2) specification of systematic components in context of explanatory variables, and 3) evaluation of the connection between the systematic part and the response variable, following the methods in Zuur et al. (2009). Mixed-effects models handle correlated data by integrating random effects, which can account for nested data structures. GAMMs are an ideal analysis approach for dive data as there are potentially multiple interacting predictors that influence dive behavior, including the identity of the tagged individual. R packages used to construct and evaluate GAMMs included tidyverse, ggplot2, mgcv, lubricate, nlme, geosphere, and MuMIn. Response variables included dive depth (m), dive duration (sec), and ascent/descent rate (m/sec). Random effects included in GAMMs included tag ID (to account for the non-independence of the data structure) and a specified nested time period within each tag ID as in Falcone et al., (2017). The nested time period used for each GAMM was determined by comparing the AIC values of models that incorporated different time periods, ranging from 1 hour to 1 day. Predictors that were investigated included lunar illumination (scale of 0-1, with 1 being equivalent to a full moon), dive depth, dive duration, and ascent/descent rate, with predictors examined prior to construction of each GAMM to ensure that there was no collinearity between predictors.

Part 2: Eddy Movements

The eddy fields that overlap spatially and temporally with tag deployments were identified using outputs from the Hybrid Coordinate Ocean Model, like sea surface height, and current analyses to locate eddies by using horizontal gradients in both variables. Crawl tracklines were be used to visually track the location of the whales compared to the position of identified eddies. Code from a previous study on false killer whales and eddy movements was used with the R packages magick, magrittr, dplyr, tidyverse, lubridate, rerddapXtracto, plotdap, ggplot2, mgcv, progress, metR, cmocean, and RColorBrewer (Kratofil, 2020).

3.0 Results

3.1 Distance between Pairs for Overlapping Deployments

Pairs PeTag029 and PeTag031, PeTag029 and PeTag032, PeTag035 and PeTag036, and PeTag031 and PeTag032 had overlapping deployments off the same island areas and were examined for potential pseudoreplication. PeTag029 and PeTag031's deployments overlapped for 2.53 days, PeTag029 and PeTag032 for 0.52 days, PeTag031 and PeTag032 for 16.42 days, and PeTag035 and PeTag036 for 10.38 days (Figure 1). Further investigation compared each pair to behavior log data and it was found that only pairs PeTag031 and PeTag032 and PeTag035 and PeTag036 had behavior log data overlap (Figure 2). The behavior logs for PeTag031 and PeTag032 were visually inspected. The majority of PeTag032 data overlaps with PeTag031 (Figure 2a), confirming that these individuals are likely pseudoreplicates. PeTag032 was removed from the dataset for the summary statistics and GAMM analysis. Additionally, PeTag036 had little data within the behavior log compared to PeTag035 and majority of it overlapped with PeTag035 (Figure 2b), confirming that these individuals are likely pseudoreplicates. PeTag036 was excluded from analysis in summary statistics and GAMM models. More visual analysis showed the tracklines of pairs PeTag031 and PeTag032 and PeTag035 and PeTag036 to showcase how close each pair was in proximity around the islands within the overlap times (Figure 3 and Figure 4).

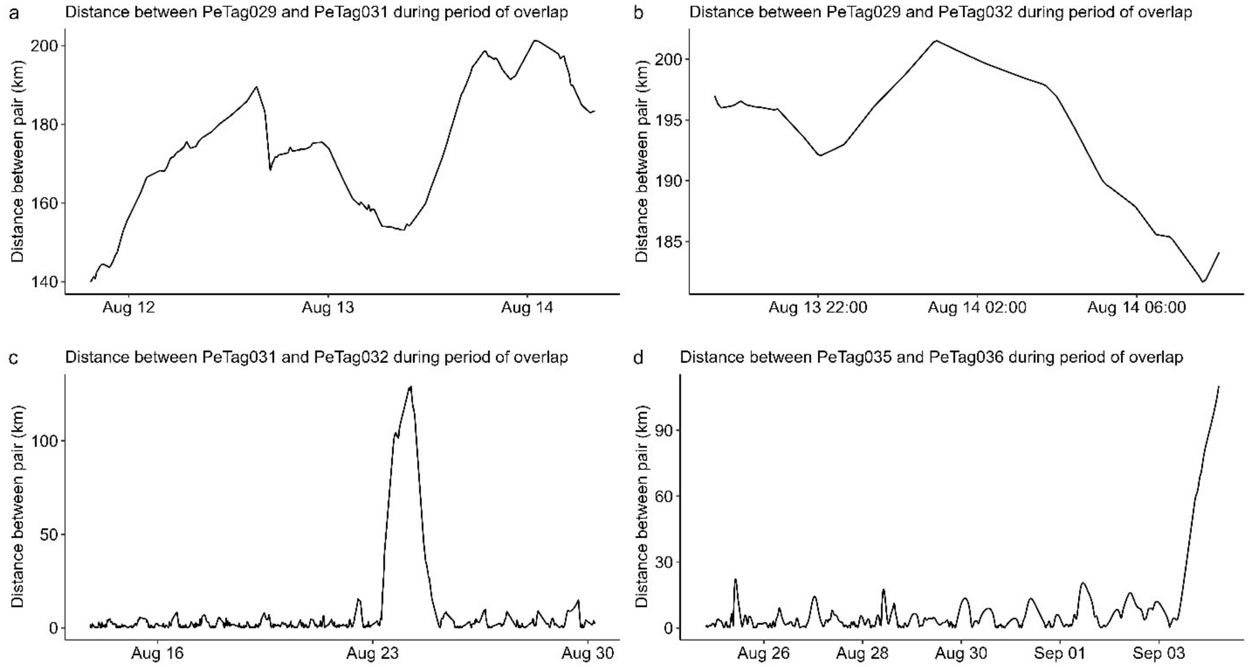

Figure 1. Distance between 5-minute predicted crawl locations for tags with overlapping deployments: (a) PeTag029 and PeTag031 and (b) PeTag029 and PeTag032 (c) PeTag031 and PeTag032 (d) PeTag035 and PeTag036.

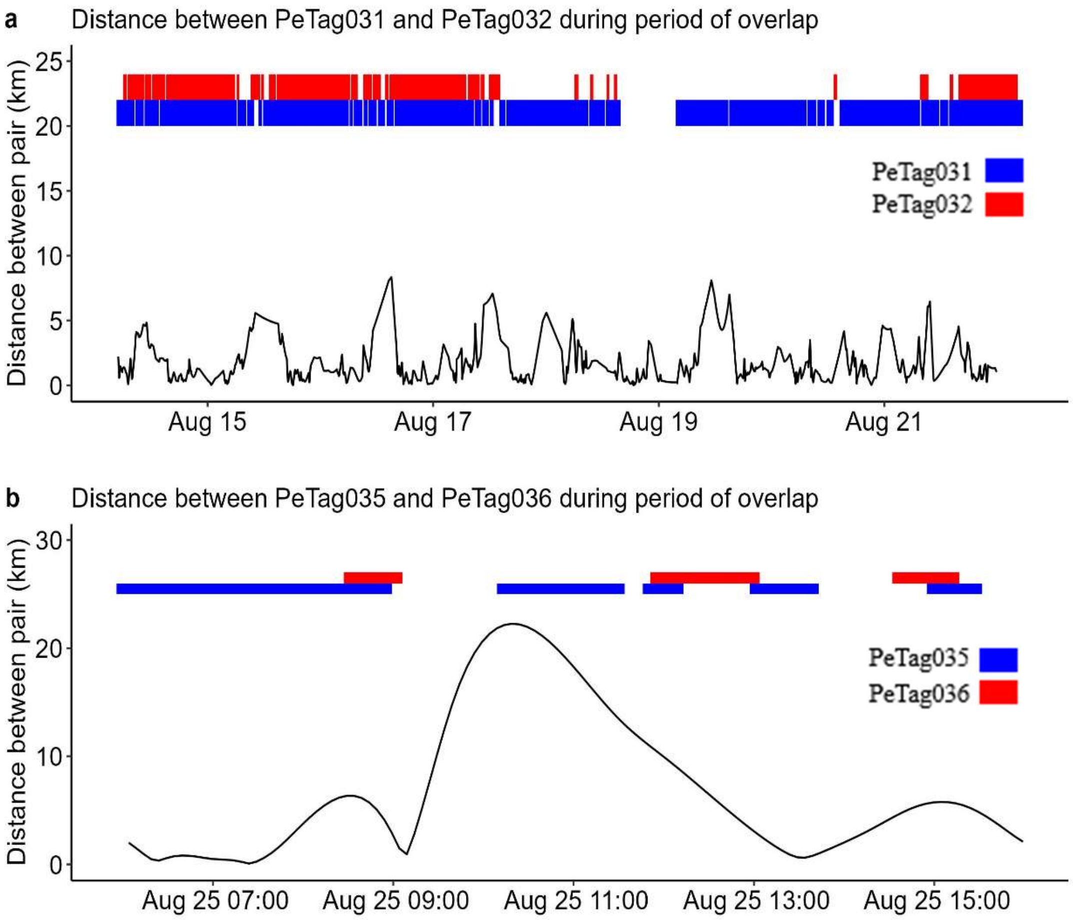

Figure 2. Distance between 5-minute predicted crawl locations and behavior log comparison for tags with overlapping deployments: (a) PeTag031 and PeTag032 and (b) PeTag035 and PeTag036.

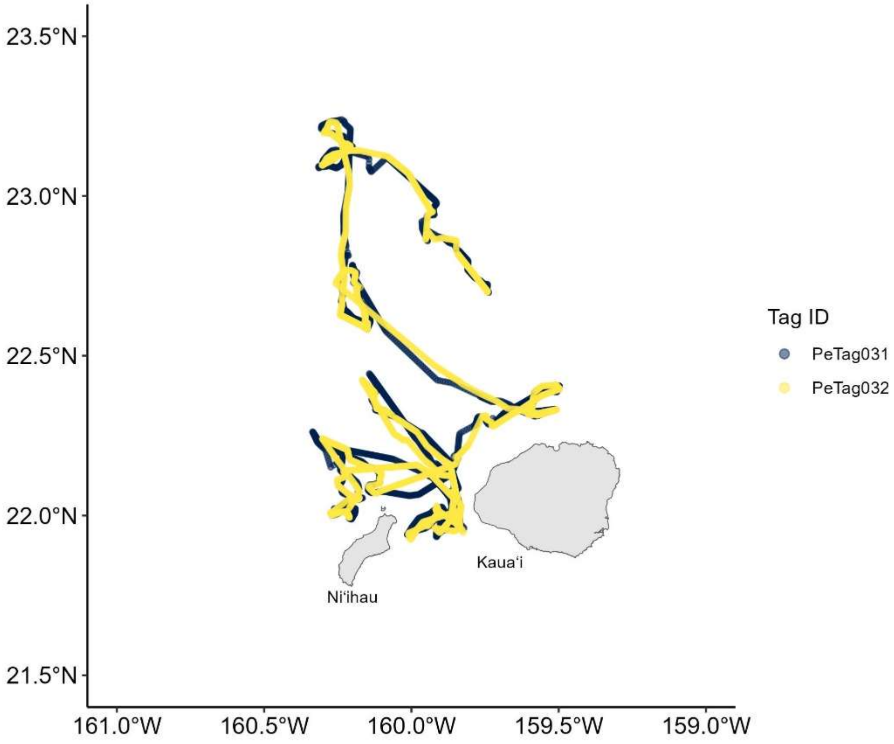

Figure 3. PeTag031 and PeTag032 crawl tracklines from August 14-22, 2021, during the period where the two deployments overlapped with behavior log data. This similarity resulted in PeTag032 being removed from data analysis due to pseudoreplication.

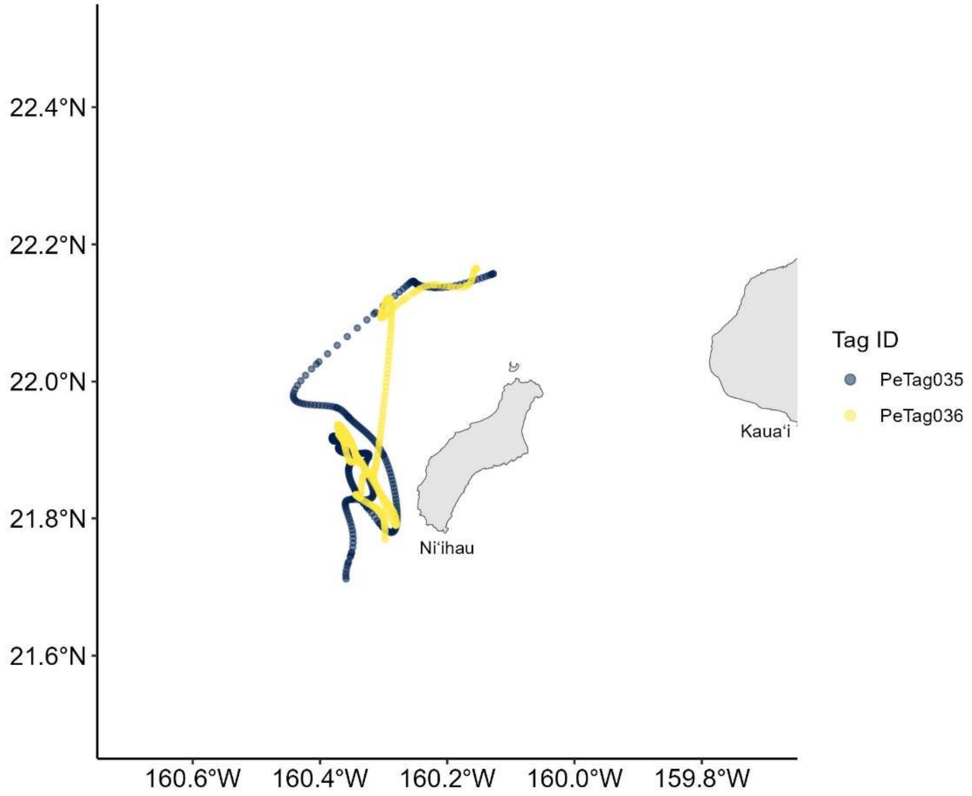

Figure 4. PeTag035 and PeTag036 crawl tracklines from August 25-26, 2022, during the period where the two deployments overlapped with behavior log data. This similarity resulted in PeTag036 being removed from data analysis due to pseudoreplication.

3.2 Summary Statistics and Data Exploration

The overall grand mean dive rate was 2.01 dives/hr, with a mean dive depth of 236 m, a mean dive duration of 7.89 min, and a mean percent surface time of 73.7%. During dawn, the mean dive rate was 0.1 dives/hr, with a mean dive depth of 344 m and a mean dive duration of 8.31 min, while the mean percent surface time was 98.7%. In contrast, during the day, the mean dive rate was 0.03 dives/hr, with a mean dive depth of 70 m and a mean dive duration of 5.21 min, with a mean percent surface time of 99.7%. At dusk, the mean dive rate was 0.24 dives/hr, with a mean dive depth of 225 m and a mean dive duration of 7.36 min, and the mean percent surface time slightly decreased to 96.9%. Notably, night exhibited the highest mean dive rate at 5.12 dives/hr, with a mean dive depth of 237 m and a mean dive duration of 7.91 min, but a significantly lower mean percent surface time of 32.8%. The variability in dive behavior is reflected in the standard deviation (mean ± SD) values across diel periods. The overall dive rate was consistent, with a mean ± SD of 0.27 dives/hr, while daytime dive rate showed low variability, with a mean ± SD of 0.04 dives/hr, indicating minimal activity. Dusk, however, had higher variability in dive depth, with a mean ± SD of 55 m. At night, the low variability in surface time, with a mean ± SD of 3.2%, indicates consistent reliance on extended dives.

Table 2. Grand means and mean ± SD values of melon-headed whales dive depth, dive rate, dive duration, and surface time for seven satellite-tagged melon-headed whales.

Time of day	**Dive rate (# dives/hr) Mean (mean ± SD)**	**Dive depth (m) Mean (mean ± SD)**	**Dive duration (min) Mean (mean ± SD)**	**Percentage surface time Mean (mean ± SD)**	**Total duration of dive/surface data (days)**
Overall	2.01 (0.27)	236 (21)	7.89 (0.46)	73.7 (3.8)	48.00
Dawn	0.1 (0.21)	344 (0)	8.31 (0.30)	98.7 (2.8)	1.79
Day	0.03 (0.04)	70 (6)	5.21 (1.94)	99.7 (0.5)	24.50
Dusk	0.24 (0.33)	225 (55)	7.36 (1.40)	96.9 (4.5)	1.83
Night	5.12 (0.34)	237 (23)	7.91 (0.47)	32.8 (3.2)	19.90

The majority of dives took place at night (Figure 5a). Day with the lowest mean dive rate exhibited 0.03 dives/hr (SD = 0.04), followed by dawn with a mean rate of 0.1 dives/hr (SD = 0.21). During dusk, the dive rate increased slightly to 0.24 dives/hr (SD = 0.33). Night showed the highest dive rate by a substantial margin, with a mean of 5.12 dives/hr (SD = 0.34) (Figure 5a). Dives were spread across the full range of moon illumination levels (Figure 5b). Visual inspection reveals a possible shift towards deeper dives with increasing moon illumination, with the deepest dives taking place at > 0.50 moon illumination (Figure 5b).

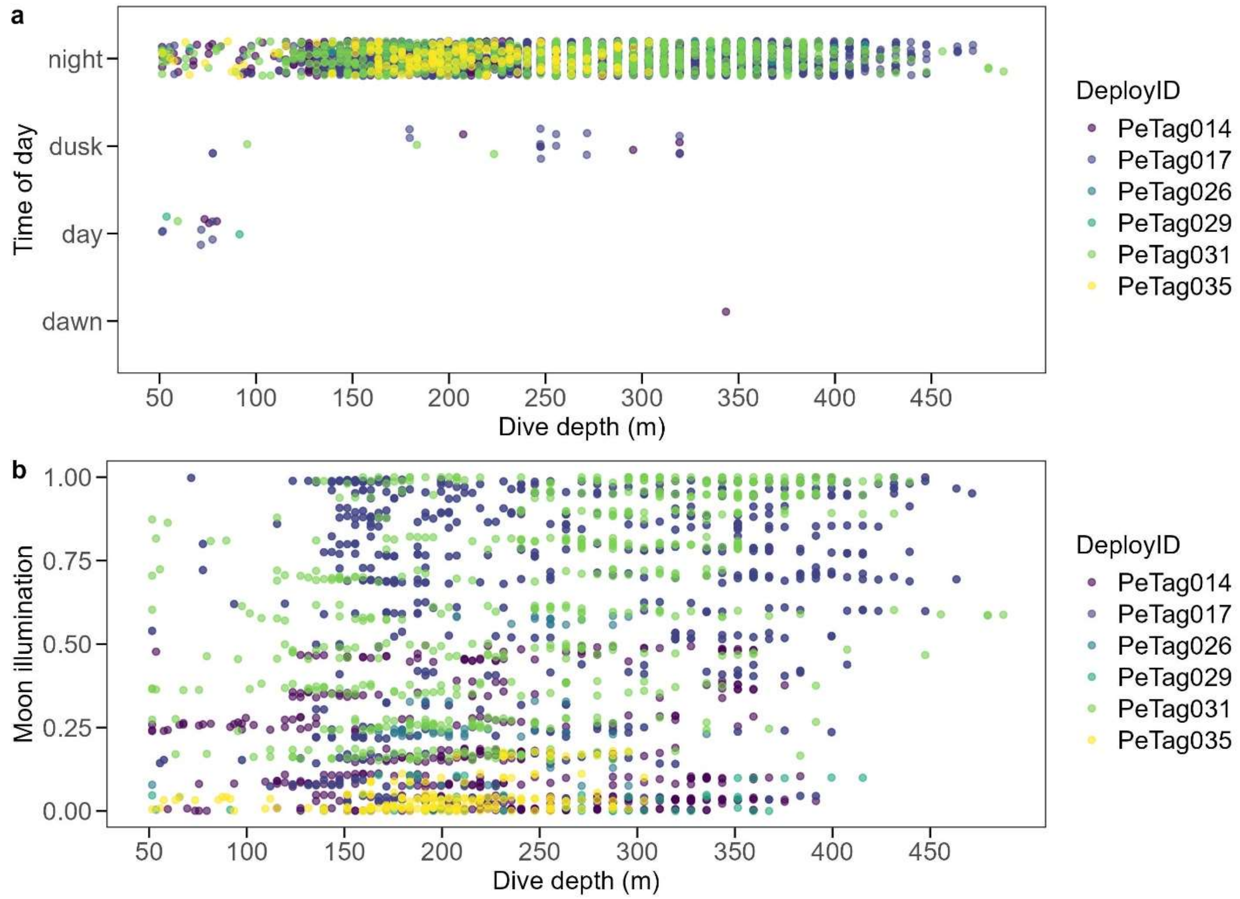

Figure 5. Relationship between (a) time of day and dive depth, and (b) moon illuminated fraction and dive depth, for seven satellite-tagged melon-headed whales (individual tags are different colors).

The longest dives took place at night, and the distribution of dive durations at night was most densely clustered between 6 and 10 min (Figure 6a). Dive durations during dusk were not as widely distributed as those for night dives, but did include durations that were longer than those recorded at dawn or during the day, which had the least variation in dive durations, as well as the shortest dive durations (Figure 6a). Upon visual inspection, there is no immediately discernable relationship between moon illumination and dive duration, with dive durations mostly clustered between 6 and 10 min across the range of moon illuminations (Figure 6b).

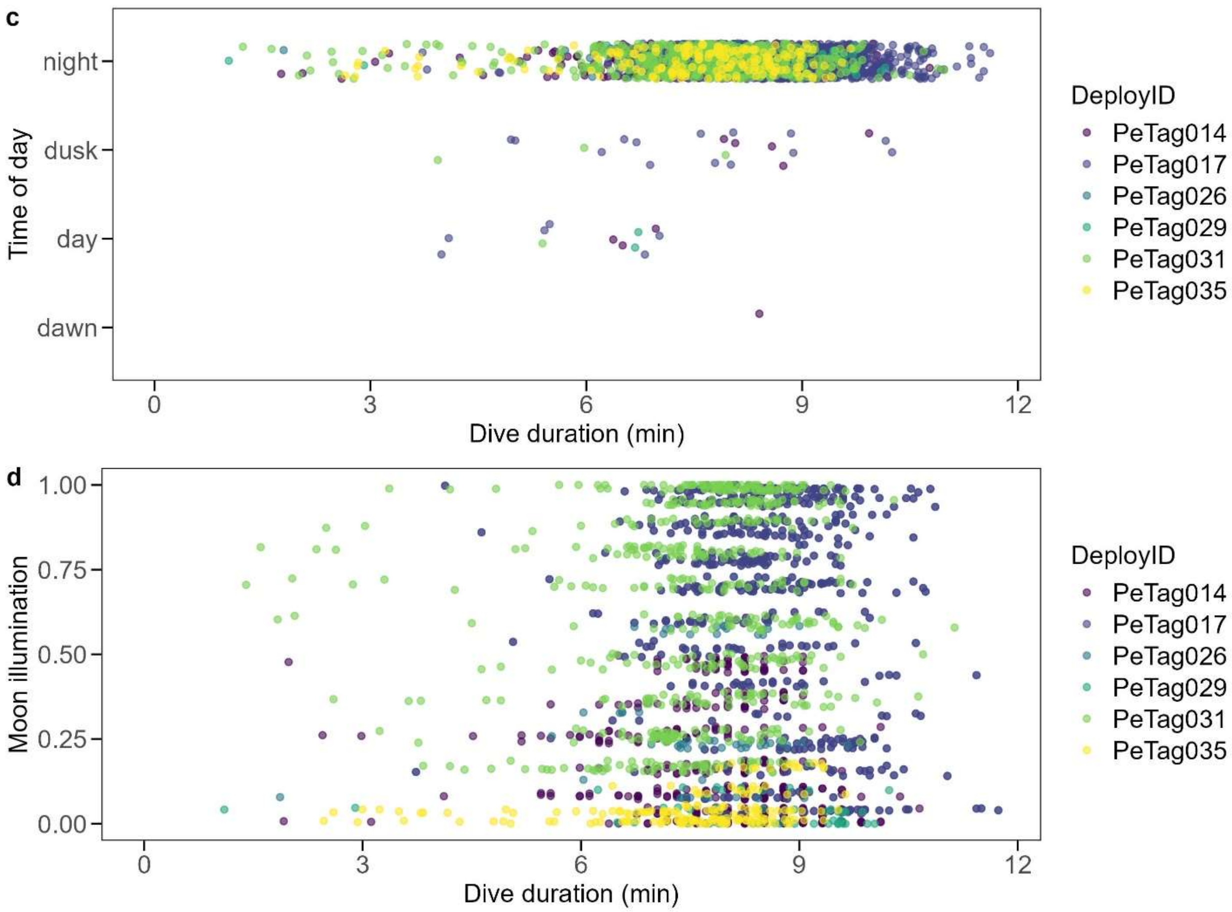

Figure 6 Relationship between (a) time of day and (b) moon illuminated fraction with dive duration for seven satellite-tagged melon-headed whales (individual tags are different colors).

Dive ascent/descent rates varied with time of day, with the highest speeds occurring at night, followed by dusk and dawn (Figure 7a). In contrast, day dives were characterized by slower ascent/descent rates, with their distribution skewed toward lower speeds compared to other periods (Figure 7a). Additionally, dive ascent/descent rates did not exhibit a noticeable trend of increasing speed as moon illumination changed (Figure 7b).

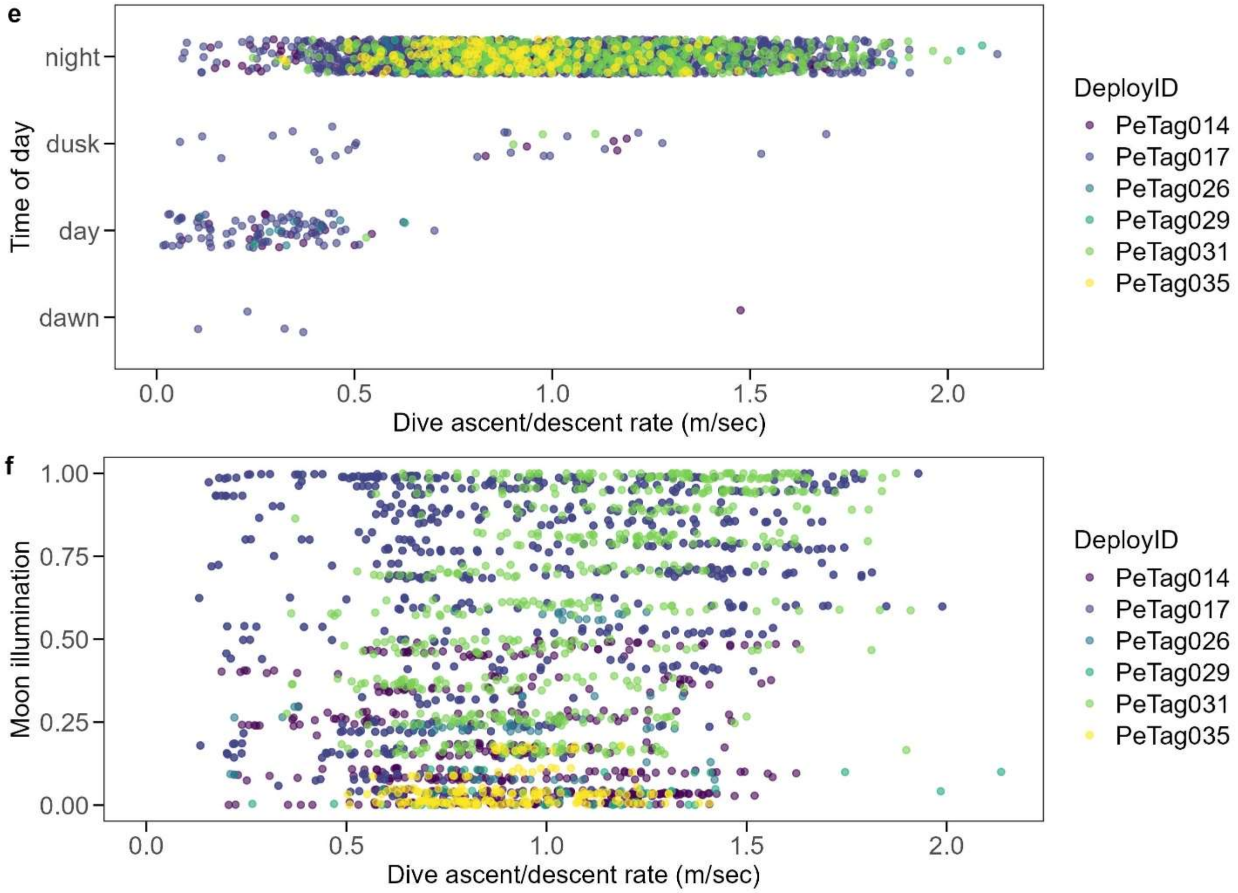

Figure 7. Relationship between (a) time of day and (b) moon illuminated fraction with dive ascent/descent rate for seven satellite-tagged melon-headed whales (individual tags are different colors).

Mean dive rates, depths, durations, and percentages of surface times were compiled for each individual by time of day, and the distributions examined. Mean dive rates (# dives/hr) vary across the times of day, with the highest rates observed at night (median = 6 dives/hr) and the lowest during dawn and day (median = 0 dives/hr) (Figure 8a). Dusk exhibits intermediate dive rates (median = 2 dives/hr) and greater variability compared to the other periods. Mean dive depths show the greatest variability at dawn, ranging from shallow to very deep dives, with a median depth of 350 m, whereas day dives are consistently shallow (median = 100 m) and show little variation (Figure 8b). Dusk dives demonstrate moderate dive depth variability (median = 200 m), and night dives are consistently deep, with a median depth of 300 m and slightly less variability than at dawn. Mean dive durations are longest at dawn (median = 7.5 min), decrease during the day (median = 5 min), are shortest at dusk (median = 4 min), and lengthen again at night (median = 6.5 min), showing relatively low variability (Figure 8c). Meanwhile, mean surface time remains consistently high during dawn and day (median = 100%) with minimal variation, but decreases significantly at dusk (median = 40%) and night (median = 30%), accompanied by greater variability at night, reflecting reduced surface activity and a shift toward sustained diving behavior during this period (Figure 8d).

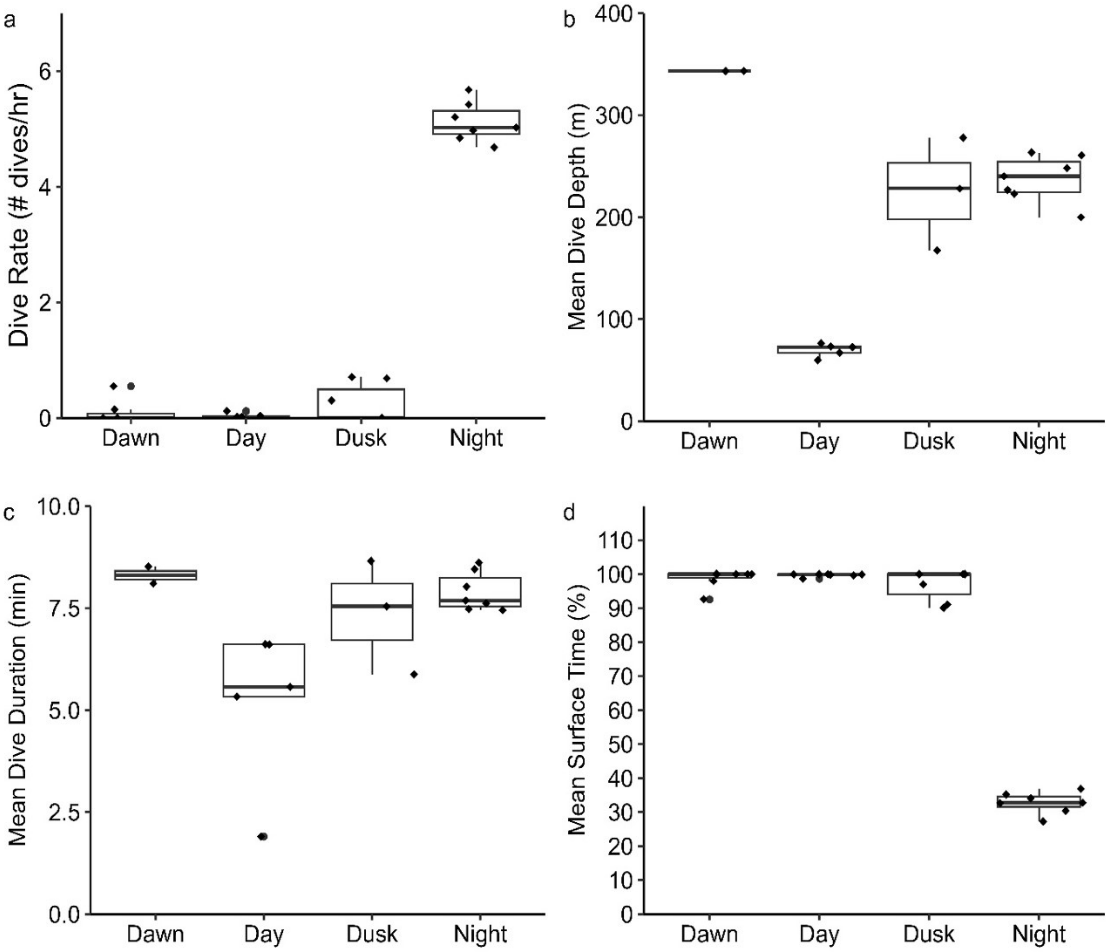

Figure 8. Boxplots of the relationship between time of day and each response variable for the mean values calculated for seven satellite-tagged melon-headed whales. Note that only one data point per individual is shown in each of these plots. (a) relationship between dive rate and time of day; (b) relationship between mean dive depth and time of day; (c) relationship between mean dive duration and time of day; (d) relationship between mean percentage surface time and time of day.

<u>3.3 GAMMs</u>

For all GAMMs, the dataset was restricted to include only night dives because dawn, day, and dusk lacked sufficient data to enable accurate comparison across different times of day within the models.

3.3.1 Depth GAMM The predictive model used for dive depth included dive duration, moon illumination, and the interaction between dive duration and moon illumination (Table 3). The model had an R-squared value of 0.36. For the parametric coefficients, the intercept was significant, with an estimate of 5.41 ($p < 0.01$). For the smooth terms**,** dive duration had a positive significant relationship with dive depth ($p < 0.01$), meaning that dive depth increased with dive duration. Similarly, moon illumination had a positive significant relationship with dive depth ($p < 0.01$), meaning that dive depth also tended to increase with moon illumination. Additionally, the interaction between dive duration and moon illumination was significant ($p < 0.01$), meaning that dive duration and moon illumination combined have a significant positive relationship with dive depth.

Dive depth was influenced by both moon illumination and dive duration, with deeper dives observed during periods of higher moon illumination (Figure 9a) and longer dive durations (Figure 9b).

Table 3. Generalized additive mixed-effect model (GAMM) results for the effect of dive duration, moon illumination, and the interaction between dive duration and moon illumination on dive depth for seven satellite-tagged melon-headed whales.

Parametric coefficients	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
Intercept	5.41	0.02	239.74	<0.01
Smooth terms	**edf**	**Ref.df**	**F**	**p-value**
s(Dive duration)	3.95	3.95	204.10	<0.01
s(Moon illumination)	2.09	3.00	154.71	<0.01
Dive duration: moon illumination	2.40	2.40	39.02	<0.01

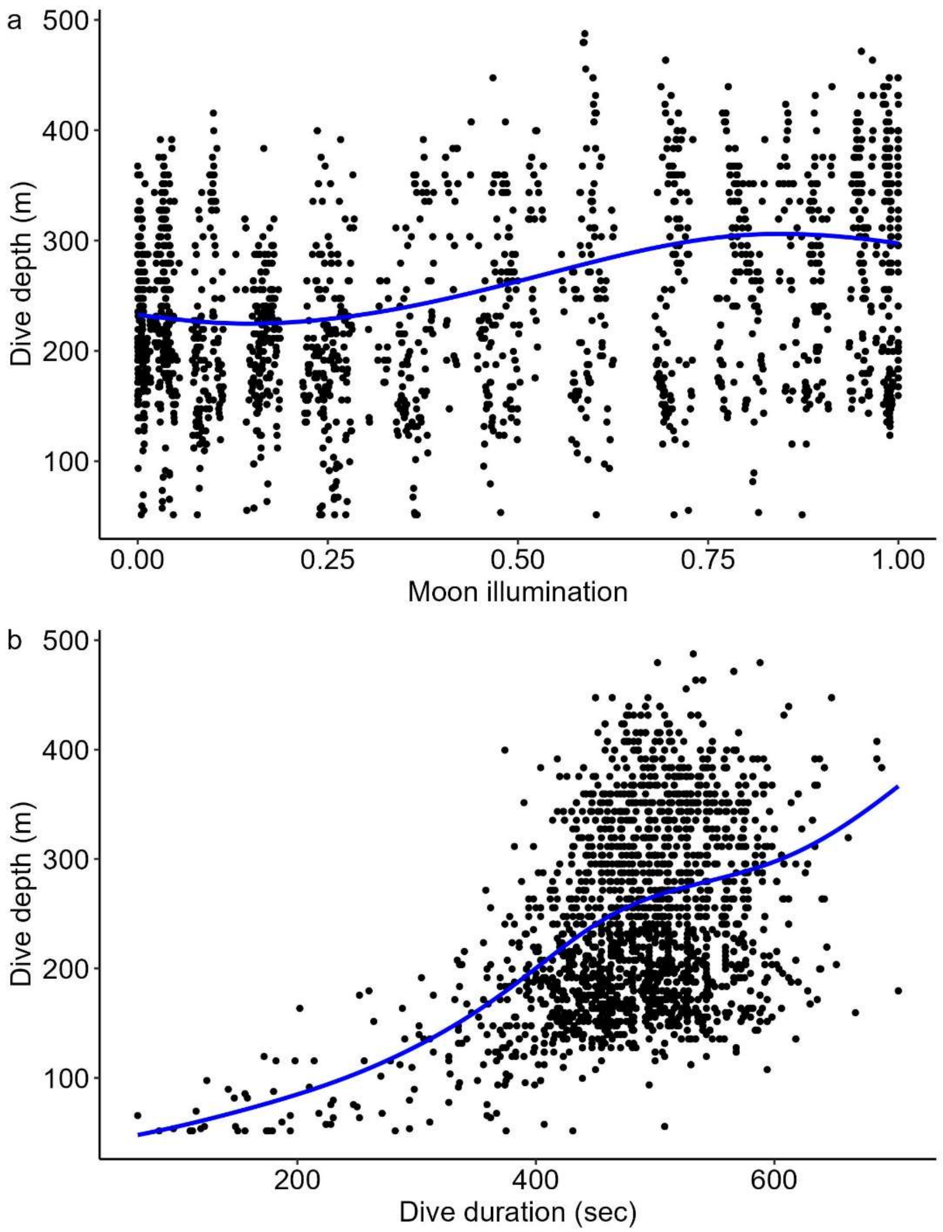

Figure 9. The relationship between dive depth and each explanatory variable in the dive depth generalized additive mixed-effect model (GAMM) for seven melon-headed whales. Fitted relationship for (a) moon illumination and (b) dive duration (min). The blue line represents the smooth term.

3.3.2 Dive Duration GAMM

The predictive model used for dive duration included dive depth, moon illumination, and the relationship between dive depth and moon illumination. The model had an R-squared value of 0.50. For parametric coefficients, the intercept was significant, with an estimate of 6.18 (p <

0.01). When examining smooth terms, the significant positive relationship between dive depth and dive duration ($p < 0.01$) indicates that dive durations tend to increase with deeper dives. Similarly, the significant positive relationship between moon illumination and dive duration ($p < 0.01$) indicates that dive durations tend to increase with greater availability of moonlight. The interaction between dive depth and moon illumination was also significant ($p < 0.01$), meaning that these two variables combined also have a significant positive relationship with dive duration.

Dive duration seemed to be influenced by both moon illumination (Figure 10a) and dive depth, with durations remaining relatively stable across varying moon illumination levels but increasing with greater dive depths (Figure 10b). Despite variability in the data, the modeled trends demonstrate a flat relationship with moon phase and a positive association with dive depth.

Table 4. Generalized additive mixed-effect model (GAMM) results for the effect of dive depth, moon illumination, and the interaction between dive depth and moon illumination on dive duration for seven satellite-tagged melon headed whales.

Parametric coefficients	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
Intercept	6.18	0.01	479.06	<0.01
Smooth terms	**edf**	**Ref.df**	**F**	**p-value**
s(Dive depth)	6.41	6.41	257.37	<0.01
s(Moon illumination)	2.18	3.00	853.64	<0.01
Dive depth: moon illumination	3.28	3.28	11.76	<0.01

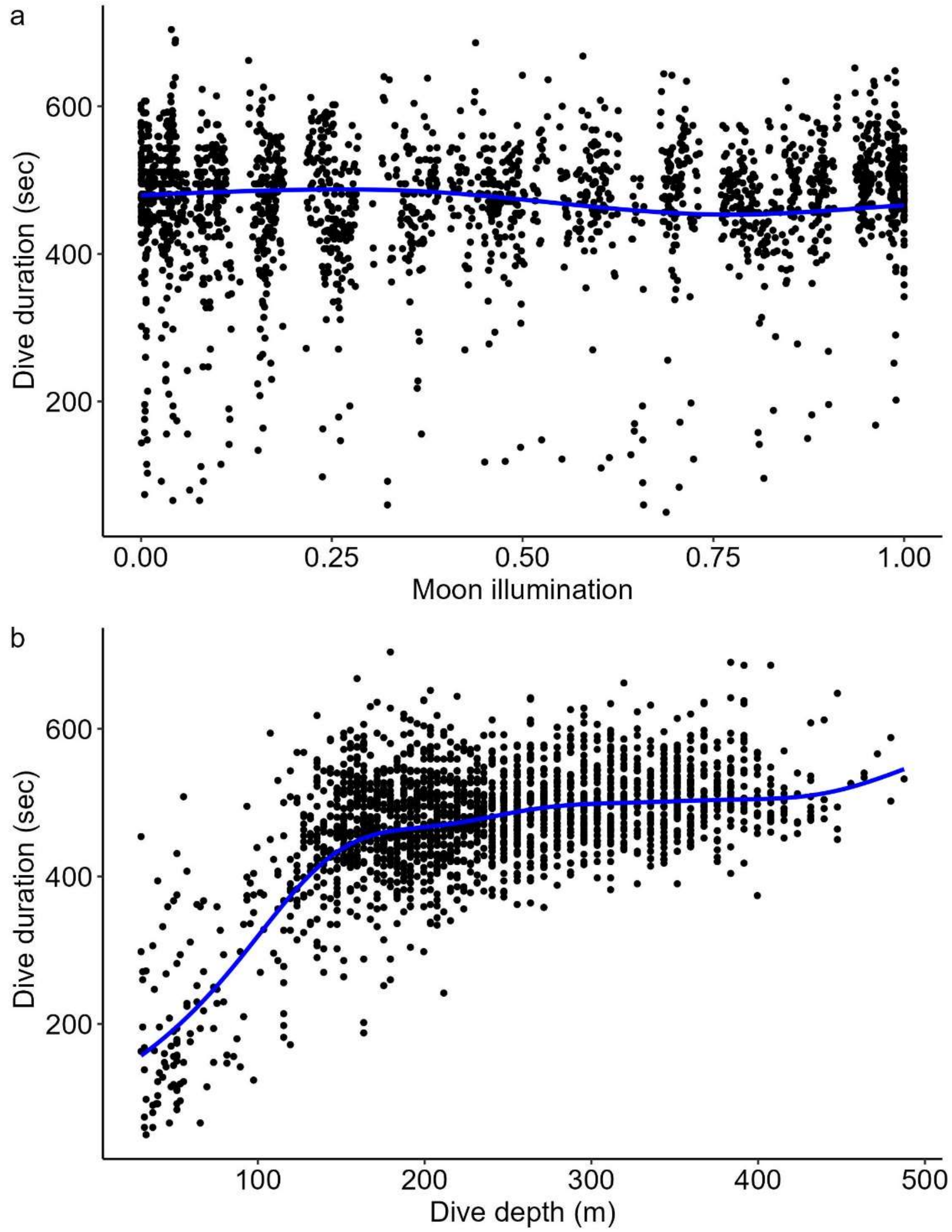

Figure 10. The relationship between dive duration and each explanatory variable in the dive duration generalized additive mixed-effect model (GAMM) for seven melon-headed whales. Fitted relationship for (a) moon illumination and (b) dive depth (m). The blue line represents the smooth term.

3.3.3 Dive Ascent/Descent Rate GAMM

The predictive model used for dive ascent/descent rate included dive depth, moon illumination, and the interaction between dive depth and moon illumination. The model had an R-squared value of 0.79. The intercept of this model was not statistically significant, with a p-value of 0.14. However, for the smooth terms, both dive depth and moon illumination had significant positive relationships with dive ascent/descent rate ($p < 0.01$), indicating that animals tended to move vertically at greater speeds with increasing dive depths and moon illumination. The interaction between dive depth and moon illumination was also significant ($p < 0.01$), indicating that these two predictors when combined also have a positive relationship with dive ascent/descent rates.

Dive ascent/descent rate showed it might be influenced by both moon illumination (Figure 11a) and dive depth (Figure 11b), with a slight increase in rates observed during periods of higher moon illumination and a stronger positive relationship with increasing dive depths. The modeled trends reveal a modest association with moon phase and a clear increase in ascent/descent rate as dives become deeper.

Table 5. Generalized additive mixed-effect model (GAMM) results for the effect of dive depth, moon illumination, and the interaction between dive depth and moon illumination on dive ascent/descent rate for seven satellite-tagged melon-headed whales

Parametric coefficients	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
Intercept	-0.02	0.01	-1.47	0.14
Smooth terms	**edf**	**Ref.df**	**F**	**p-value**
s(Dive depth)	7.44	7.44	446.03	<0.01
s(Moon illumination)	2.30	3.00	556.61	<0.01
Dive depth: moon illumination	2.39	2.39	9.16	<0.01

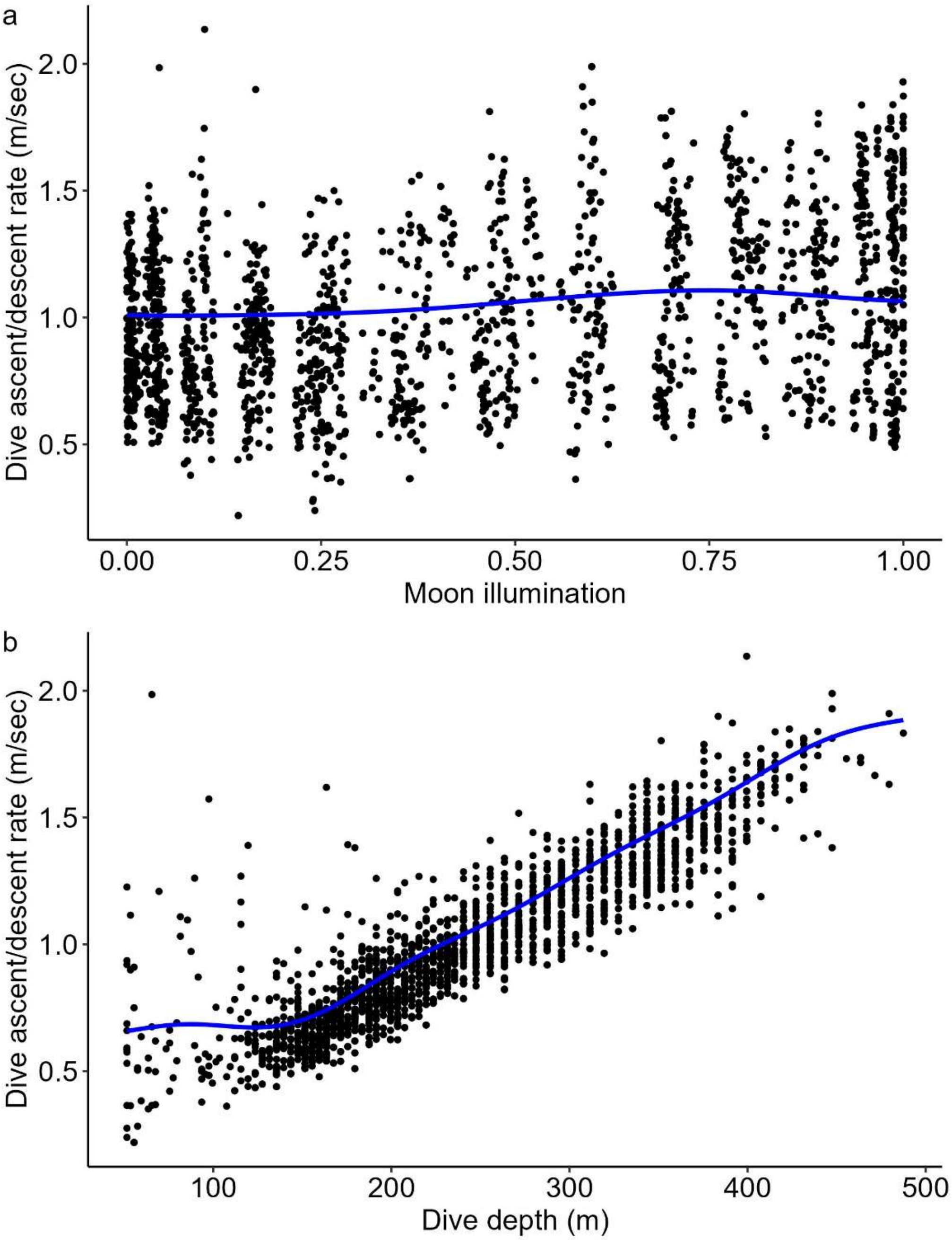

Figure 11. The relationship between dive ascent/descent rate and each explanatory variable in the dive ascent/descent generalized additive mixed-effect model (GAMM) for seven melon-headed whales. Fitted relationship for (a) moon illumination and (b) dive depth (m). The blue line represents the smooth term.

3.4 Eddy Movements

A preliminary analysis including a visual exploration of individual MHW movement and eddy movements was conducted. The horizontal movements were visually explored for PeTag014 (Figure 12) and PeTag017 (Figure 13) in relation to eddy movements. These tags were on MHWs that are members of the Kohala Resident Stock, which are known to inhabit the coastal waters off Hawaiʻi Island, specifically around the Kohala coast on the island's northwest side. While both animals' paths cross some areas with mild variations in sea surface height (SSH), neither appears to stay within these regions or consistently align with the swirling velocity patterns that indicate eddies. In most 24-hour frames, the animals' paths either move across eddies or skirt around them rather than showing a consistent pattern of staying within or tracking the eddy boundaries.

The movement patterns for PeTag021 (Figure 14) and PeTag026 (Figures 15) suggest interaction with areas of varying SSH, aligning strongly with eddy dynamics. In most observed instances, the animals either remained within the boundaries of eddies or closely tracked their edges, suggesting that they were actively utilizing these oceanic features. These animals belong to the Hawaiian Islands Stock, which are known to spend more of their time offshore and are not as limited in their horizontal movements as the Kohala Resident Stock.

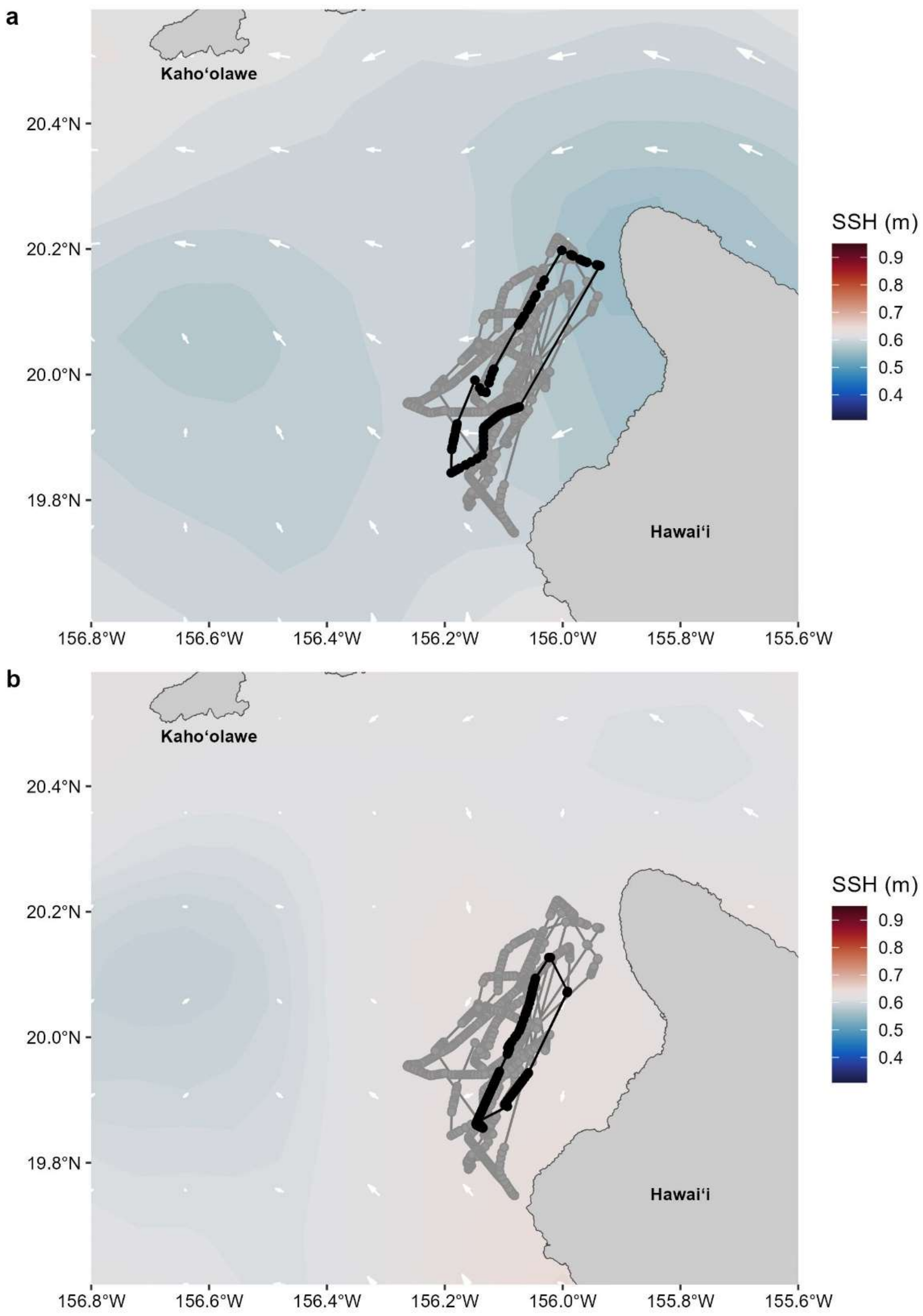

Figure 12. Maps of movement in relation to eddy fields for PeTag014 on (a) 21 October 2011, and (b) 22 October 2011. White arrows indicate the direction and relative velocity (represented by the magnitude of the arrow) of eddies (2 m/sec). Black dots indicate the locations that correspond with each 24-hour frame, while gray dots provide context for the animal's locations during other 24-hour frames.

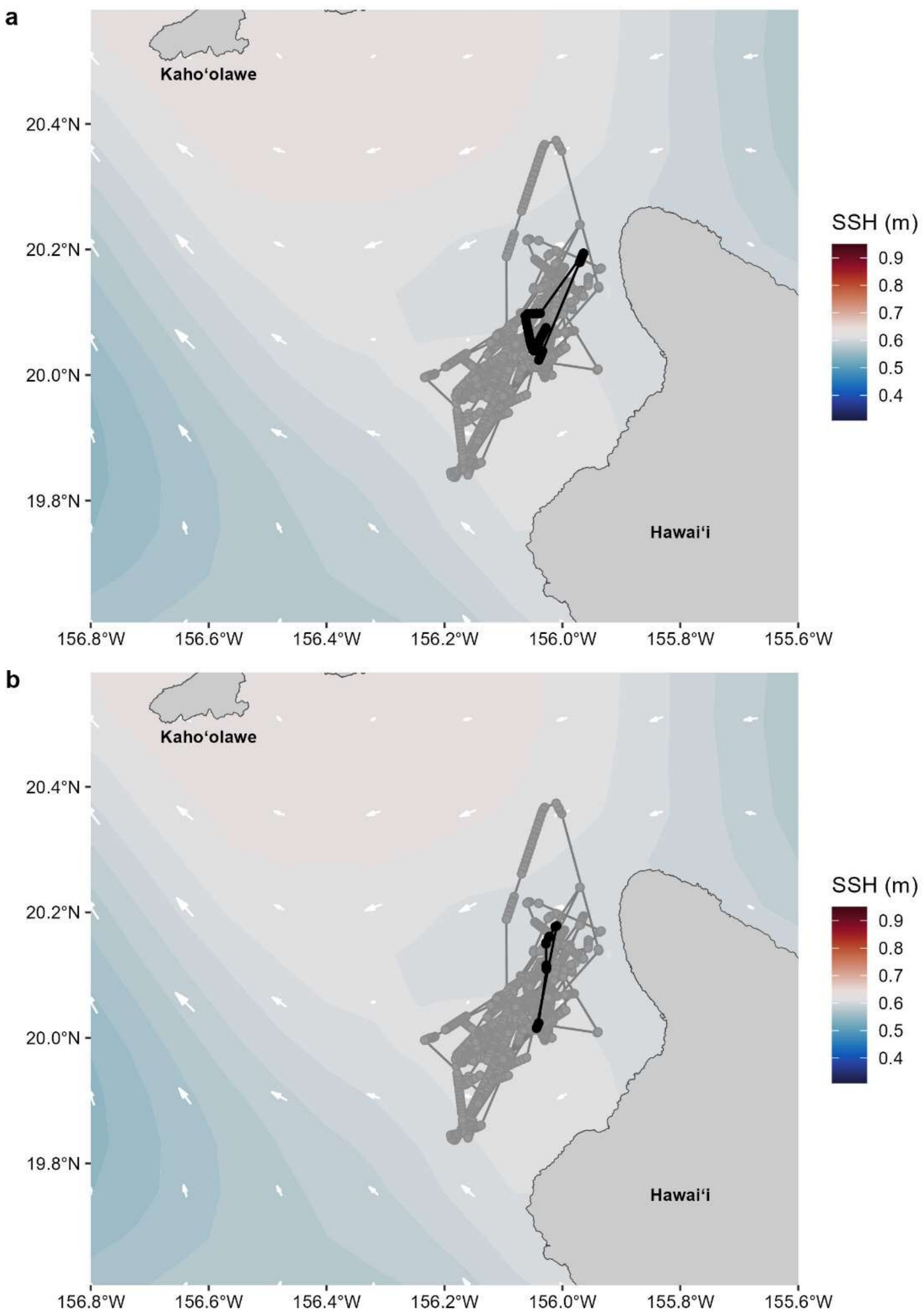

Figure 13. Maps of movement in relation to eddy fields for PeTag017 on (a) 30 August 2012, and (b) 31 August 2012. White arrows indicate the direction and relative velocity (represented by the magnitude of the arrow) of eddies (2 m/sec). Black dots indicate the locations that correspond with each 24-hour frame, while gray dots provide context for the animal’s locations during other 24-hour frames.

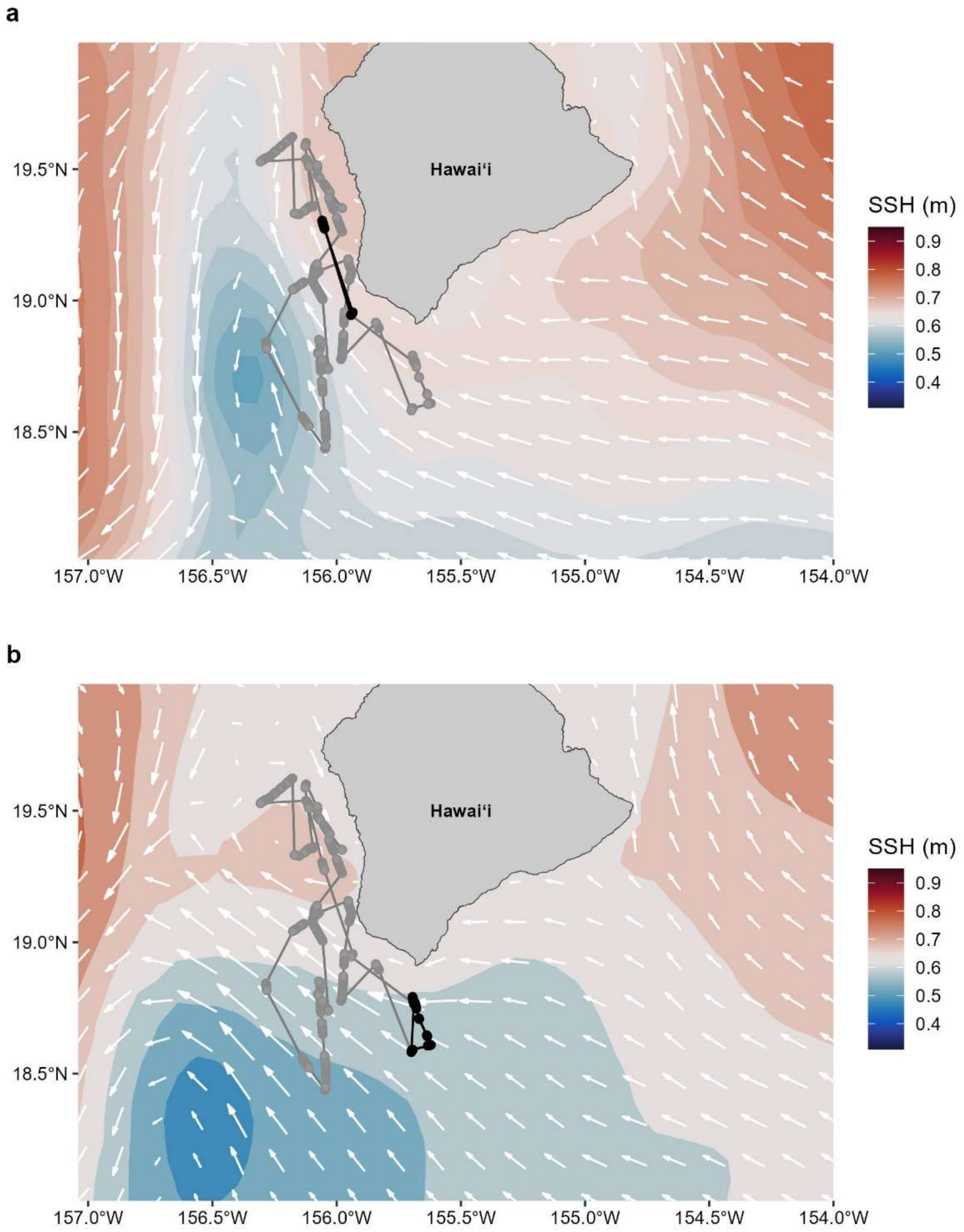

Figure 14. Maps of movement in relation to eddy fields for PeTag021 on (a) 25 July 2014, and (b) 28 July 2014. White arrows indicate the direction and relative velocity (represented by the magnitude of the arrow) of eddies (2 m/sec). Black dots indicate the locations that correspond with each 24-hour frame, while gray dots provide context for the animal’s locations during other 24-hour frames.

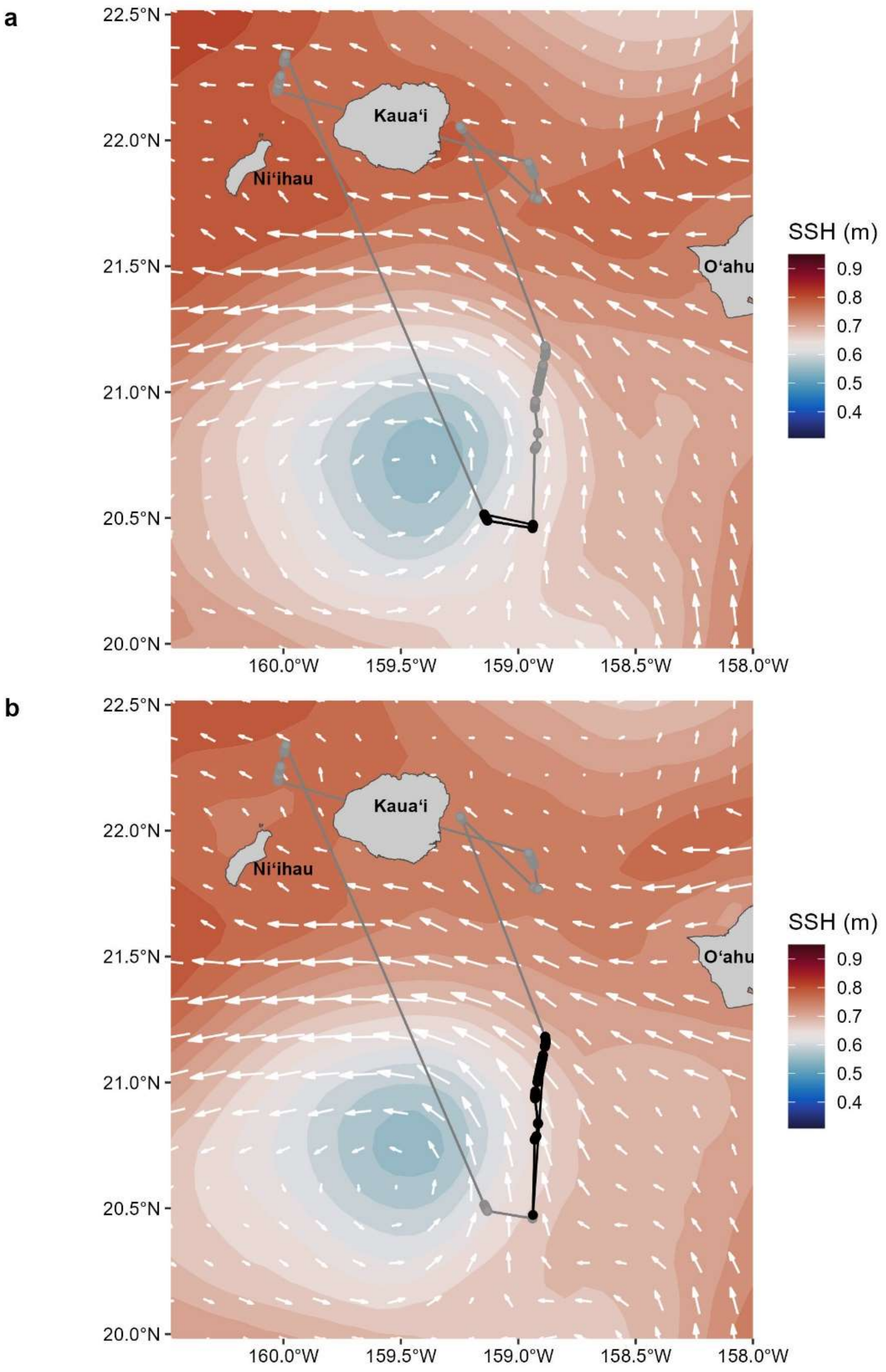

Figure 15. Maps of movement in relation to eddy fields for PeTag026 on (a) 16 August 2017, and (b) 17 August 2017. White arrows indicate the direction and relative velocity (represented by the magnitude of the arrow) of eddies (2 m/sec). Black dots indicate the locations that correspond with each 24-hour frame, while gray dots provide context for the animal's locations during other 24-hour frames.

5.0 Discussion

Environmental factors have been previously shown to influence the dive behavior of species like rough-toothed dolphins and short-finned pilot whales (Owen et al., 2019, Shaff and Baird, 2021). Both the summary statistics and GAMM modeling presented as part of this study support that the dive behavior of melon-headed whales is also influenced by diel and lunar cycles. The overwhelming majority of dives took place at night, and night dives were, on average, the deepest and longest. Lunar illumination was also significantly correlated with dive depth, duration, and ascent/descent rates across all GAMM models, although these relationships were weak. Additionally, preliminary analysis reveals potential differences in the influence of oceanic eddies on movement patterns between the Kohala Resident Stock and the Hawaiian Islands Stock. While the Kohala Resident Stock showed no notable changes in movement relative to eddies, the Hawaiian Islands Stock may adjust their movements in response to these features, as had been previously demonstrated by Woodworth et al. (2011). These findings underscore the complex interplay between environmental factors and melon-headed whale dive behavior, highlighting the significant roles of diel and lunar cycles, as well as the potential influence of oceanic eddies on movement patterns

The satellite-tagged melon-headed whales examined in this study exhibited distinct diel patterns in their diving, likely linked to foraging behaviors, prey distribution, and energy conservation. Night dives were characterized by mean dive depths ranging between 220–250 m, the longest grand mean dive durations around 8 min on average, and the highest grand mean dive rates with around 5 dives per hour. These patterns align closely with the diel vertical migration of prey such as mesopelagic fish and squid (Brodeur et al., 2005; Drazen et al., 2011). The presence of cephalopods in the diet of melon-headed whales suggests they target deep-water prey during nocturnal foraging (West et al., 2018). The consistent dive depth range at night likely reflects targeting prey that migrate vertically into accessible parts of the water column under low-light conditions. Dawn dives were rare in the dataset, with only a small number recorded despite 1.79 days of combined dawn data. These dives showed the greatest depth but the lowest dive rate. The narrow ranges in dawn dive depth might reflect opportunistic foraging, as prey behavior changes during transitional light conditions (Brodeur et al., 2005; Drazen et al., 2011). Dawn also displayed a lot of time, around 98.7%, on the surface suggesting it may function as a resting period following the frequent, energy-intensive dives observed at night. Dusk exhibited dive depths that were intermediate compared to those of day, night, and dawn, with a grand mean dive depth of 225 m. This pattern suggests a shift in foraging strategies as light levels decrease, with whales likely engaging in exploratory dives to locate prey as it begins its nightly ascent. Dusk dive durations and dive rates also indicate intermediate activity levels, reflecting a transition between daytime energy conservation strategies and the intense foraging activity seen at night. Day dives were shallow at around 70m and with a shorter dive duration around 5 min, likely reflecting a strategy to minimize energetic costs during periods when prey are less accessible. Shallow dives are less energy-demanding, and the high percentage of surface time observed during the day (grand mean = 99.7%) may be linked to thermoregulation, as whales remain in warmer surface layers, as well as opportunities for social interactions (Beatty et al., 2008). Unlike some species, such as Blainville's beaked whales, which avoid surface waters during the day to reduce predator interactions (Baird et al., 2008; Barlow et al., 2020), melon-headed whales spend extensive time at the surface during daylight hours, suggesting they employ different strategies for avoiding predation. These findings highlight the reliance of melon-headed whales on diel cycles to optimize foraging efficiency, conserve energy, and adapt to dynamic environmental conditions. The interplay of prey distribution, light-driven environmental transitions, and physiological strategies appears to shape their behavior, underscoring the complex ecological relationships that govern their diving and surface activity patterns (Hooker et al., 2012; Ponganis, 2015; Scott and Cattanach, 1998).

Melon-headed whales exhibit changes in their diving behavior in response to lunar illumination, with statistically significant relationships between lunar illumination and dive depth, duration, and ascent/descent rates revealed by the GAMM models. Dive depth was significantly deeper during periods of higher moon illumination, with dives often exceeding 250 m when the lunar illumination fraction was ≥ 0.50, likely reflecting increased prey visibility for the whales or shifts in prey availability at depth due to increased lunar light (Brodeur et al., 2005; Drazen et al., 2011). Longer dive durations were initially reported to be significantly associated with increased lunar illumination; however, upon closer inspection, there's a slight decrease from the dive duration GAMM smooth term output, suggesting this relationship may not be as straightforward as previously interpreted. Alternatively, this could suggest that high prey densities at depth during periods of increased lunar illumination (Owen et al., 2019). However, the weak relationships observed limit the strength of this interpretation. Similarly, while ascent/descent rates increased with lunar illumination ($p < 0.01$), indicating potential adjustments in vertical movement speed (Figure 11), these findings should be interrupted within context. Overall, the data hint at a possible influence of lunar illumination on dive behavior, but the relationships appear subtle and warrant further investigation to better understand their ecological significance.

Based on the preliminary analysis, movements in relation to oceanic eddies were observed only within three whales from the Hawaiian Resident Stock, but not for members of the Kohala Resident Stock. Eddy dynamics can play a critical role in shaping marine mammal foraging behaviors by creating nutrient-rich zones that attract prey species (Polovina et al., 2001). These swirling oceanic features, characterized by variations in SSH and swirling velocity, act as natural feeding hotspots for various marine predators, including cetaceans and pinnipeds (Polovina et al., 2001; Qiu, 2001). A 2011 study showed that melon-headed whales in Hawaiian waters exhibit preferences for the edges of cold-core cyclonic eddies and the centers of warm-core anticyclonic eddies, however the sample size of this study was very limited (n= 3; Woodworth et al., 2011). Using a larger sample size to visually explore the movement patterns of melon-headed whales, distinct differences emerge between members of the Kohala Resident Stock (PeTag014 and PeTag017), and those of the Hawaiian Islands Stock (PeTag021 and PeTag0265). PeTag014 and PeTag017, which inhabit the coastal waters around the Kohala coast of Hawaiʻi Island, show minimal alignment in their movements with eddy boundaries or swirling velocity patterns. These animals often crossed or skirted eddies rather than staying within them, suggesting a limited reliance on eddy-associated prey aggregations. This behavior likely reflects their localized, nearshore habitat preferences, where prey resources may be more stable and less influenced by dynamic offshore processes. In contrast, PeTag021 and PeTag026 (Hawaiian Islands Stock) demonstrate stronger interactions with eddy dynamics, frequently remaining within eddy boundaries or closely tracking their edges. This behavior suggests an active utilization of these oceanic features, likely driven by their offshore movements and greater exposure to variable SSH zones. As members of the Hawaiian Islands Stock, these animals exhibit greater ecological flexibility, which might make them rely more heavily on the dynamic productivity of eddies for foraging. These contrasting movement patterns underscore the ecological differences between the two stocks and their adaptations to distinct habitats. While the Kohala Resident Stock may depend more on stable coastal prey, the Hawaiian Islands Stock appears to exploit the dynamic and productive nature of offshore eddy habitats.

Overall, while this study of melon-headed whale dive behavior and movement in relation to eddies provides valuable insights, several limitations must be considered. The small sample size, with only seven satellite-tagged individuals, reduces the generalizability of the findings and may not fully capture the variability in dive and movement patterns. Specifically, for the Kohala Resident Stock, only two individuals (PeTag014 and PeTag017) were analyzed in this study. Another limitation was the presence of two pseudoreplicates (PeTag032 and PeTag036), where data from individual whales were not independent and were removed from analysis to not skew the results. However, there was virtually no data for PeTag036, so while this is true, it represents a trivial loss. Additionally, this study primarily focuses on dive depth, duration, ascent/descent rates, and eddy interactions, without considering other environmental factors like ocean temperature or salinity, which could influence behavior. Furthermore, unanalyzed data from tags deployed in 2021-2022, focusing on whale movements in relation to eddies, could provide additional insights but remains untapped. The study also does not address the impact of eddies across varying temporal scales. Future research should involve a larger sample size, extended tracking periods, and consideration of additional environmental variables to provide a more comprehensive understanding of how melon-headed whales adapt their dive behavior and movement in response to dynamic ocean conditions.

5.0 Conclusion

By revealing how diel and lunar cycles shape diving behavior, this study highlights aspects of habitat use and foraging strategies. For example, the strong association with nighttime dives underscores the importance of protecting habitats that support diverse prey availability during this time of day. Additionally, the association with eddy dynamics, such as cold-core cyclonic and warm-core anticyclonic eddies, identifies key feeding hotspots and gives a better understanding of melon-headed whale behavior. Moreover, the insights into individual and stock-level behavioral differences, such as the ecological flexibility of the Hawaiian Islands Stock, can guide tailored management strategies. Together, these findings emphasize how temporal, spatial, and ecological dynamics can influence marine animals' behavior.

Future work will expand on this analysis by continuing to track eddy movements using satellite tags deployed between 2021 and 2022. This will involve a more comprehensive assessment of how eddy dynamics, including variations in sea surface height and velocity, affect melon-headed whale foraging and movement patterns. Additionally, continued exploration of stock-level differences will provide further insights into the behavioral plasticity of melon-headed whales and how they adapt to varying oceanographic conditions, ultimately supporting more effective, targeted conservation strategies.

6.0 References

Andrews, R. D., Baird, R. W., Calambokidis, J., Goertz, C. E. C., Gulland, F. M. D., Heide-Jørgensen, M. P., Hooker, S. K., Johnson, M., Mate, B., Mitani, Y., Nowacek, D. P., Owen, K., Quakenbush, L. T., Raverty, S., Robbins, J., Schorr, G. S., Shpak, O. V., Townsend Jr., F. I., Uhart, M., & Wells, R. S. (2019). Best practice guidelines for cetacean tagging. *IWC Journal of Cetacean Research and Management, 20*(1), 27–66. https://doi.org/10.47536/jcrm.v20i1.237

Aschettino, J. M. (2010). Population size and structure of melon-headed whales *(Peponocephala electra*) around the main Hawaiian Islands: evidence of multiple populations based on photographic data [Master's thesis]. Hawai‘i Pacific University.

Aschettino, J. M., Baird, R. W., McSweeney, D. J., Webster, D. L., Schorr, G. S., Huggins, J. L. Martien, K. K., Mahaffy, S. D., & West, K. L. (2012). Population structure of melon headed whales (*Peponocephala electra*) in the Hawaiian Archipelago: evidence of multiple populations based on photo identification. *Marine Mammal Science*, *28*(4), 666-689. https://doi.org/10.1111/j.1748-7692.2011.00517.x

Bailleul, F., Cotté, C., & Guinet, C. (2010). Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. *Marine Ecology Progress Series*, *408*, 251–264. https://doi.org/10.3354/meps08560

Baird, R. W. (2016). *The lives of Hawai'i's dolphins and whales: natural history and conservation*. University of Hawai‘i Press.

Baird, R.W., Henderson E. E., Martin S. W., and Southall B. L. (2019). *Assessing odontocete exposure and response to mid-frequency active sonar during Submarine Command*

Courses at the Pacific Missile Range Facility: 2016-2018. Prepared for Commander, Pacific Fleet, under Contract No. N62470-15-D-8006 Task Order KB16 issued to HDR Inc., Honolulu, HI

Baird, R. W., Ligon, A. D., Hooker, S. K., & Gorgone, A. M. (2001). Subsurface and nighttime behaviour of pantropical spotted dolphins in Hawaiʻi. *Canadian Journal of Zoology, 79*, 988–996. https://doi.org/10.1139/z01-070

Baird, R. W., McSweeney, D. J., Ligon, A. D., & Webster, D. L. (2004). *Tagging feasibility and diving of Cuvier's beaked whales (Ziphius cavirostris) and Blainville's beaked whales (Mesoplodon densirostris) in Hawai'i*. Report prepared under Order No. AB133F-03-SE 0986 to the Southwest Fisheries Science Center, National Marine Fisheries Service.

Baird, R. W., Webster, D. L., Aschettino, J. M., Schorr, G. S., & McSweeney, D. J. (2013). Odontocete cetaceans around the main Hawaiian Islands: habitat use and relative abundance from small-boat sighting surveys. *Aquatic Mammals*, *39*(3), 253–269. https://doi.org/10.1578/am.39.3.2013.253

Baird, R. W., Webster D. L., Schorr, G. S., McSweeney, D. J., & Barlow, J. (2008). Diel variation in beaked whale diving behavior. *Marine Mammal Science, 24*(3), 630-642. https://doi.org/10.1111/j.1748-7692.2008.00211.x

Balcomb, K. C. & Claridge, D. E. (2001). A mass stranding of cetaceans caused by naval sonar in the Bahamas. *Bahamas Journal of Science*, *5*, 2-12.

Barlow, J., Schorr, G., Falcone, E., & Moretti, D. (2020). Variation in dive behavior of Cuvier's beaked whales with seafloor depth, time of day, and lunar illumination. *Marine Ecology Progress Series*, *644*, 199–214. https://doi.org/10.3354/meps13350

Beatty, B. L., & Rothschild, B. M. (2008). Decompression syndrome and the evolution of deep diving physiology in the cetacea. *Naturwissenschaften*, *95*(9), 793–801. https://doi.org/10.1007/s00114-008-0385-9

Bivand, R., and N. Lewin-Koh. 2016. maptools: Tools for reading and handling spatial objects. Rpackage version 0.8-39. Available at https://CRAN.R-project.org/package=maptools.

Bivand, R., & Rundel, C. (2017). rgeos: interface to geometry engine-open source (GEOS) [Computer software]. R package version 0.3–23. https://cran.r-project.org/package=rgeos

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E. L., Foley, D. G., Breed, G. A., Harrison, A.-L., Ganong, J. E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B. R., Shillinger, G. L., Schaefer, K. M., Benson, S. R., Weise, M. J., & Henry, R. W. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, *475*(7354), 86–90. https://doi.org/10.1038/nature10082

Bradford, A. L., Oleson, E. M., Forney, K. A., Moore, J. E., & Barlow, J. (2021). *Line-transect abundance estimates of cetaceans in U.S. waters around the Hawaiian Islands in 2002, 2010, and 2017. (NOAA Technical Memorandum NMFS-PIFSC-115)*. U.S. Department of Commerce. https://doi.org/10.25923/daz4-kw84

Brodeur, R. D., Seki, M. P., Pakhomov, E. A., & Suntsov, A. V. (2005). Micronekton - what are they and why are they important? *PICES Press, 13,* 7-11.

Brownell Jr., R. L., Ralls, K., Baumann-Pickering, S., & Poole, M. M. (2009). Behavior of melon-headed whales, *Peponocephala electra,* near oceanic islands. *Marine Mammal Science*, *25*(3), 639–658. https://doi.org/10.1111/j.1748-7692.2009.00281.x

Cioffi, W.R., Quick N.J, Swaim, Z.T., Foley H.J., Waples, D.M., Webster, D.L., Baird, R.W., Southall, B.L., Nowacek, D.P., and Read, A.J. (2023). Trade-offs in telemetry tag programming for deep-diving cetaceans: data longevity, resolution, and continuity. *Animal Biotelemetry, 11,* 223. https://doi.org/10.1186/s40317-023-00334-1
Clague, D. A., & Dalrymple, G. B. (1989). Tectonics, geochronology, and origin of the Hawaii Emperor volcanic chain. In Winterer, E. L., Hussong, D. M., & Decker, R. W. (Eds.), *The eastern Pacific Ocean and Hawaii.* 188–217. The Geological Society of America.

Cox, T., Ragen, T. J., Read, A. J., Vos, E., Baird, R. W., Balcomb, K. C., Barlow, J., Caldwell, J., Cranford, T. W., Crum, L. A., D'Amico, A., D'Spain, G. L., Fernández, A., Finneran, J. J., Gentry, R. L., Gerth, W., Frances, Hildebrand, J. A., Houser, D. S., & T. Hullar. (2023). Understanding the impacts of anthropogenic sound on beaked whales. *The Journal of Cetacean Research and Management*, *7*(3), 177–187. https://doi.org/10.47536/jcrm.v7i3.729

Dragon, A., Monestiez, P., Bar-Hen, A., & Guinet, C. (2010). Linking foraging behaviour to physical oceanographic structures: southern elephant seals and mesoscale eddies east of Kerguelen Islands. *Progress in Oceanography/Progress in Oceanography*, *87*(1–4), 61-71. https://doi.org/10.1016/j.pocean.2010.09.025

Drazen, J. C., De Forest, L. G., & 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*(5), 557–566. https://doi.org/10.1016/j.dsr.2011.03.002

Fahlman, A., Tyson, R. B., Stone, R., Sweeney, J., Trainor, R. F., Barleycorn, A. A., McHugh, K., Allen, J. B., & Wells, R. S. (2023). Deep diving by offshore bottlenose dolphins (*Tursiops spp*.). *Marine Mammal Science*, *39*(4), 1251-1266. https://doi.org/10.1111/mms.13045

Falcone, E. A., Schorr, G. S., Watwood, S. L., DeRuiter, S. L., Zerbini, A. N., Andrews, R. D., Morrissey, R. P., & Moretti, D. J. (2017). Diving behaviour of Cuvier's beaked whales exposed to two types of military sonar. *Royal Society Open Science, 4*(8), 170-629. https://doi.org/10.1098/rsos.170629

Fiedler, P. C., Reilly, S. B., Hewitt, R. P., Demer, D. A., Philbrick, V. A., Smith, S., Armstrong, W., Croll, D. A., Tershy, B. R., Mate, B. R., & Ballance, L. T. (2008). Blue whale habitat and prey in the California Channel Islands. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *55*(1-2), 160-186. https://doi.org/10.1016/j.dsr2.2007.11.004

Gabler, M. K., Gay, D. M., Westgate, A. J., & Koopman, H. N. (2017). Microvascular characteristics of the acoustic fats: novel data suggesting taxonomic differences between deep and shallow-diving odontocetes. *Journal of Morphology*, *279*(4), 458-471. https://doi.org/10.1002/jmor.20782

Goldbogen, J. A., Cade, D. E., Calambokidis, J., Czapanskiy, M. F., Fahlbusch, J., Friedlaender, A. S., Gough, W. T., Kahane-Rapport, S. R., Savoca, M. S., Ponganis, K. V., & Ponganis, P. J. (2019). Extreme bradycardia and tachycardia in the world's largest animal. *Proceedings of the National Academy of Sciences*, *116*(5), 25329–25332. https://doi.org/10.1073/pnas.1914273116

Henderson, E. E., Martin, C. R., Baird, R. W., Kratofil, M. A., Martin, S. W., & Southall, B. L. (2021). *FY20 summary report on the received level analysis of satellite tagged odontocetes at the Pacific Missile Range Facility*. Naval Information Warfare Center Pacific.

Hijmans, R. J., & Van Etten, J. (2016). raster: Geographic data analysis and modeling [Computer software]. R package version 2. 5–8. https://cran.r-project.org/package=raster

Hooker, S. K., & Baird, R. W. (2001). Diving and ranging behaviour of odontocetes: a methodological review and critique. *Mammal Review*, *31*(1), 81–105. https://doi.org/10.1046/j.1365-2907.2001.00080.x

Hooker, S. K., Fahlman, A., Moore, M. J., Aguilar de Soto, N., Bernaldo de Quirós, Y., Brubakk, A. O., Costa, D. P., Costidis, A. M., Dennison, S., Falke, K. J., Fernandez, A., Ferrigno, M., Fitz-Clarke, J. R., Garner, M. M., Houser, D. S., Jepson, P. D., Ketten, D. R., Kvadsheim, P. H., Madsen, P. T., & Pollock, N. W. (2012). Deadly diving? Physiological and behavioural management of decompression stress in diving mammals. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1731), 1041- 1050. https://doi.org/10.1098/rspb.2011.2088

Kalakaua, D. (2021). *The legends and myths of Hawaii*. Mint Editions.

Kaplan, M. B., Mooney, T. A., Sayigh, L. S., & Baird, R. W. (2014). Repeated call types in Hawaiian melon-headed whales (*Peponocephala electra*). *The Journal of the Acoustical Society of America*, *136*(3), 1394–1401. https://doi.org/10.1121/1.4892759

Klatsky, L. J., Wells, R. S., & Sweeney, J. C. (2007). Offshore bottlenose dolphins (*Tursiops truncatus*): movement and dive behavior near the Bermuda Pedestal. *Journal of Mammalogy*, *88*(1), 59–66. https://doi.org/10.1644/05-mamm-a-365r1.1

Kratofil, M. (2020). Eddy vector track plots [R script]. GitHub. https://github.com/makratofil/crc-hawaii-tags/blob/master/EddyVectorTrackPlots.R

Kratofil, M. A., Harnish A. E., Mahaffy S. D., Henderson E. E., Bradford A. L., Martin S. W., Lagerquist B. A., Palacios D. M., Oleson E. M., and Baird R. W. (2023). Biologically important areas II for cetaceans within U.S. and adjacent waters – Hawai‘i region. *Frontiers in Marine Science, 10,* 1053581. https://doi.org/10.3389/fmars.2023.1053581.

Martien, K. K., Hancock-Hanser, B. L., Baird, R. W., Kiszka, J. J., Aschettino, J. M., Oremus, M., & Hill, M. C. (2017). Unexpected patterns of global population structure in melon headed whales (*Peponocephala electra*). *Marine Ecology Progress Series, 577,* 205-220. https://doi.org/10.3354/meps12203

McClelland, S. J., Gay, M., Pabst, D. A., Dillaman, R., Westgate, A. J., & Koopman, H. N. (2012). Microvascular patterns in the blubber of shallow and deep diving odontocetes. *Journal of Morphology*, *273*(8), 932–942. https://doi.org/10.1002/jmor.20032

McManus, M. A., Greer, A. T., Timmerman, A. H. V., Sevadjian, J. C., Woodson, C. B., Cowen, R., Fong, D. A., Monismith, S., & Cheriton, O. M. (2021). Characterization of the biological, physical, and chemical properties of a toxic thin layer in a temperate marine system. *Marine Ecology Progress Series*, *678*, 17–35. https://doi.org/10.3354/meps13879

Miller, P. J. O., Johnson, M., Tyack, P. L., & Madsen, P. T. (2004). Diving behaviour and fine scale kinematics of free-ranging Risso's dolphins foraging in shallow and deep-water Habitats. *Journal of Experimental Biology, 207*(24), 4211–4221. https://doi.org/10.1242/jeb.01338

NOAA. (2021). Melon-headed Whale *(Peponocephala electra):* Northern Gulf of Mexico stock. https://media.fisheries.noaa.gov/202107/f2020_AtlGmexSARs_GmexMelonHeaded.pdf?null

NOAA. (2020). Melon-headed whale *(Peponocephala electra):* Western North Atlantic stock. https://media.fisheries.noaa.gov/dam-migration/2019_sars_atlantic_melonheaded.pdf

Owen, K., Andrews, R. D., Baird, R. W., Schorr, G. S., & Webster, D. L. (2019). Lunar cycles influence the diving behavior and habitat use of short-finned pilot whales around the main Hawaiian Islands. *Marine Ecology Progress Series*, *629*, 193–206. https://doi.org/10.3354/meps13123

Panneton, W. M. (2013). The mammalian diving response: an enigmatic reflex to preserve life? *Physiology*, *28*(5), 284–297. https://doi.org/10.1152/physiol.00020.2013

Perrin, W. F., Würsig, B. G., & Thewissen, J. G. M. (2009). *Encyclopedia of marine mammals*. Elsevier/Academic Press.

Perryman, W. L., Au, D. W. K., Leatherwood, S., & Jefferson, T. A. (1994). Melon-headed whale *Peponocephala electra* Gray, 1846. *Handbook of marine mammals*, *5*, 363-386.

Polovina, J. J., Balazs, G. H., Howell, E. A., Parker, D. M., Seki, M. P., & Dutton, P. H. (2001). Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the Central North Pacific Ocean. *Fisheries Oceanography*, *10*(2), 269-282. https://doi.org/10.1046/j.1365-2419.2003.00270.x

Ponganis, P. J. (2015). *Diving physiology of marine mammals and seabirds*. Cambridge

University Press. Diving physiology of marine mammals and seabirds - Paul J. Ponganis - Google Books

Price, J. P., & Clague, D. A. (2002). How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1508), 2429–2435. https://doi.org/10.1098/rspb.2002.2175

Qiu, B. (2001). Kuroshio and Oyashio currents. *In Encyclopedia of Ocean Sciences* (Vol. 3, pp. 1448-1458*). Academic Press.* Ocean Currents - Google Books

R Core Team. (2023). R: *A language and environment for statistical computing* [Computer software]. R Foundation for Statistical Computing

Ritts, M., & Wiebe, S. M. (2021). The story of Wānanalua: stranded whales and contested marine sovereignties in Hawai‘i. *Environment and Planning E: Nature and Space, 4*(2), 317-336. https://doi-org.access.library.miami.edu/10.1177/2514848620901438

Roncon, G., Bestley, S., McMahon, C. R., Wienecke, B., & Hindell, M. A. (2018). View from below: inferring behavior and physiology of Southern Ocean marine predators from dive telemetry. *Frontiers in Marine Science, 5*, 464. https://doi.org/10.3389/fmars.2018.00464

Schorr, G., Baird, R. W., Hanson, M. B., Webster, D., McSweeney, D. & Andrews, R. (2009). Movements of satellite-tagged Blainville's beaked whales off the island of Hawai'i. *Endangered Species Research, 10*, 203–213. https://doi.org/10.3354/esr00229

Scott, M. D., & Cattanach, K. L. (1998). Diel patterns in aggregations of pelagic dolphins and tunas in the Eastern Pacific. *Marine Mammal Science, 14*(3), 401–422. https://doi.org/10.1111/j.1748-7692.1998.tb00735.x

Shaff, J. F., & Baird, R. W. (2021). Diel and lunar variation in diving behavior of rough-toothed dolphins (*Steno bredanensis*) off Kaua‘i, Hawai‘i. *Marine Mammal Science, 37*(4), 12611276. https://doi.org/10.1111/mms.12811

Smith, R. C., Dustan, P., Au, D., Baker, K. S., & Dunlap, E. A. (1986). Distribution of cetaceans and sea-surface chlorophyll concentrations in the California current. *Marine Biology*, *91*(3), 385–402. https://doi.org/10.1007/bf00428633

Spalding, H. L., Copus, J. M., Bowen, B. W., Kosaki, R. K., Longenecker, K., Montgomery, A. D., Padilla-Gamiño, J. L., Parrish, F. A., Roth, M. S., Rowley, S. J., & Toonen, R. J. (2019). The Hawaiian Archipelago. *Mesophotic coral ecosystems*, 445-464.

Tabrah, R. M. (1984). *Hawaii: a history*. WW Norton & Company.

Tyack, P. L., Johnson, M., Soto, N. A., Sturlese, A., & Madsen, P. T. (2006). Extreme diving of beaked whales. *Journal of Experimental Biology*, *209*(21), 4238–4253. https://doi.org/10.1242/jeb.02505

Watson, T. (2011). Culture, conservation, and conflict: assessing the human dimensions of Hawaiian monk seal recovery. *Aquatic Mammals, 37*(3), 386–396. https://doi.org/10.1578/am.37.3.2011.386

West, K. L., Walker, W. A., Baird, R. W., Webster, D. L., & Schorr, G. S. (2018). Stomach contents and diel diving behavior of melon-headed whales (*Peponocephala electra*) in Hawaiian waters. *Marine Mammal Science, 34*(4), 1082–1096. https://doi.org/10.1111/mms.12507

Williams, T. M., Noren, D., Berry, P., Estes, J. A., Allison, C., & Kirtland, J. (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*). III. Thermoregulation at depth. *Journal of Experimental Biology*, *202*(20), 2763–2769. https://doi.org/10.1242/jeb.202.20.2763

Woodworth, P. A., Schorr, G. S., Baird, R. W., Webster, D. L., McSweeney, D., Hanson, M. B., Andrews, R. D., & Polovina, J. J. (2011). Eddies as offshore foraging grounds for melon headed whales (*Peponocephala electra*). Marine Mammal Science, 28(3), 638-647. https://doi.org/10.1111/j.1748-7692.2011.00509.x

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., Smith, G. M., Ieno, E. N., Luque, P. L., Pierce, G. J., Zuur, A. F., Santos, M. B. and Walker, N. J. & Smith, G. M. (2009). Three way nested data for age determination techniques applied to cetaceans. *Mixed effects models and extensions in ecology with R*, 459-468.