A Review of the Long-Term Study of Resident Odontocetes Off Kauaʻi and Niʻihau and the Analysis of Exposures to Mid-frequency Active Sonar

E. Elizabeth Henderson, Robin W. Baird, Stephen W. Martin,
Michaela A. Kratofil, Annette E. Harnish, Sabre D. Mahaffy,
Cameron R. Martin, and Brandon L. Southall

Contents

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E. E. Henderson (✉) · C. R. Martin
NIWC Pacific, San Diego, CA, USA
e-mail: eehenders@gmail.com; cameron.r.martin9.civ@us.navy.mil

R. W. Baird · M. A. Kratofil · A. E. Harnish · S. D. Mahaffy
Cascadia Research Collective, Olympia, WA, USA
e-mail: rwbaird@cascadiaresearch.org; mkratofil@cascadiaresearch.org;
aharnish@cascadiaresearch.org; mahaffys@cascadiaresearch.org

S. W. Martin
National Marine Mammal Foundation, San Diego, CA, USA
e-mail: stephen.w.martin26.ctr@us.navy.mil

B. L. Southall
Southall Environmental Associates, Inc., Santa Cruz, CA, USA
e-mail: brandon.southall@sea-inc.net

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Abstract

Species-typical behavior, social structure, and habitat use of multiple resident species of odontocetes have been studied off Kauaʻi and Niʻihau in the Main Hawaiian Islands since 2003. These studies have used a suite of methods, including photo-identification, passive acoustics, tagging, and biopsy sampling. Starting in 2011, these efforts were timed to precede and overlap biannual US Navy training events conducted on the Pacific Missile Range Facility in order to measure the exposure levels from mid-frequency active sonars (MFAS) and assess potential behavioral responses of tagged odontocetes to training activities. This chapter describes the early received level work, highlights improvements to analyses over the years, and summarizes some of the findings of this long-term study. Some initial quantitative attempts are also detailed to identify behavioral responses to training activity for some species, including dense-beaked whales (*Mesoplodon densirostris*) and rough-toothed dolphins (*Steno bredanensis*), which include changes in diving and horizontal avoidance of sources in some, but not all, instances, depending on species and context. These findings provide some of the first ever data on known repeated exposures of individuals and populations to MFAS for some species, which will allow investigations into long-term consequences of exposures.

Keywords

Resident odontocetes · Social structure · Received levels · Navy sonar · Behavioral response

Introduction

Sustained, systematic, long-term studies provide valuable insight into population structure, social dynamics, habitat use, interannual variability, and exposure to and potential consequences of anthropogenic impacts. As biologging, biopsy sampling, passive acoustics, physiological sampling, and associated analytical methods have become more sophisticated, the questions that can be answered in these studies have become more complex. One such study is an integrated, multimodal effort that has been conducted off the islands of Kauaʻi and Niʻihau in the Main Hawaiian Islands (MHI) since 2003 by Cascadia Research Collective (CRC; Baird et al. 2013a, 2024). Since 2011, this study has been carried out in collaboration with the Naval Undersea Warfare Center (NUWC) Newport and the Naval Information Warfare Center (NIWC) Pacific, who conduct passive acoustic monitoring of the instrumented underwater range at the Pacific Missile Range Facility (PMRF). NUWC Newport and NIWC Pacific utilize the range hydrophones to detect vocalizing odontocetes and direct the CRC vessel to a group's localized position, facilitating finding odontocete groups over a large area. Furthermore, when surveys are conducted in conjunction with US Navy (USN) training activity, such as the biannual Submarine Command Course (SCC), information on the received levels of mid-frequency active sonar (MFAS) and potential behavioral responses by tagged individuals can be obtained (Henderson et al. 2021). This chapter reviews the long-term study conducted by CRC off the islands of Kauaʻi and Niʻihau, highlighting the valuable biological and behavioral data that have been gathered from populations of several species of odontocetes, as well as the collaborative work conducted with NIWC Pacific and Southall Environmental Associates (SEA) to estimate MFAS received levels and identify behavioral responses. This chapter also describes how these efforts have developed over time from anecdotal results to quantitative analyses that inform MFAS impact assessments for environmental compliance, and outlines future work.

Baseline Hawaiian Odontocete Studies

Baird et al. (2024) began a multispecies study of cetaceans in Hawaiian waters, working off Maui in 1999. In 2002, this work expanded to include Oʻahu and Hawaiʻi Island, and in 2003, to include Kauaʻi and Niʻihau, encompassing all 18 species of odontocetes present in these waters (see Baird et al. 2013a, 2024).

These field studies utilize a variety of complementary tools, including photo-identification, passive acoustics, tagging, and biopsy sampling (which provides not only genetic data such as sex and genetic relatedness but can also be used to assess stable isotopes, toxicology, and hormones). Through CRC, individual photo-identification catalogs of 14 species of odontocetes have been developed, allowing for assessments of each species' residency and interisland movements. Eleven species are resident to one or more of the islands; for Kauaʻi, these include common bottlenose dolphins (*Tursiops truncatus*), rough-toothed dolphins (*Steno bredanensis*), spinner dolphins (*Stenella longirostris*), and short-finned pilot whales (*Globicephala macrorhynchus*) (Albertson et al. 2016; Baird et al. 2009; Kratofil et al. 2023). Two island-associated populations of false killer whales (*Pseudorca crassidens*) also overlap around Kauaʻi and Niʻihau: the Northwestern Hawaiian Islands population and the endangered MHI population (Baird et al. 2013b; Kratofil et al. 2023). Through photo-identification catalogs and genetic analyses, CRC and collaborators have been able to investigate the stock structure of many of these populations (e.g., Albertson et al. 2016; Martien et al. 2012; Van Cise et al. 2017). Additionally, photo-identification data, coupled with satellite tag data, have been used to describe the distributions and social networks for several of these populations (e.g., Corsi et al. 2025; Kratofil et al. 2023; Mahaffy et al. 2023; Van Cise et al. 2021). These data also provide information on diverse topics such as diving behavior, diurnal trends, spatial movement, and habitat utilization for ecologically and management-relevant species, which could not be done without a long-term study like this one (Baird et al. 2013a, 2024; Baird 2016).

For example, the Kauaʻi and Niʻihau island-associated population of rough-toothed dolphins has a home range of about 25,000 km^2, which extends to west

O‘ahu, where some limited interisland movements are known to occur. However, their core home range is a smaller area of 1098 km^2, located over the Kaua‘i/Ni‘ihau slope region of 500–1500 m bathymetric depth (Kratofil et al. 2023). This population, estimated to include 1665 marked individuals in 2005 (Baird et al. 2008), typically occurs in small groups (median = 5, range 1–140; Corsi et al. submitted). Rough-toothed dolphins appear to change prey and foraging behavior between day and night, feeding on epipelagic schooling fish and sometimes larger pelagic fish during the day, remaining in near-surface waters with lower dive rates (Baird et al. 2008; Shaff and Baird 2021). At night, they shift to feeding on the rising scattering layer, performing their deepest and longest dives at dusk when the scattering layer first rises (Shaff and Baird 2021).

Another well-described population in Kaua‘i waters is the common bottlenose dolphin. Genetic and photographic evidence indicates four independent island-associated populations in the MHI, with low dispersal rates between areas (Baird et al. 2009; Martien et al. 2012). The home range area for the Kaua‘i-Ni‘ihau island-associated population is approximately 2772 km^2 (Kratofil et al. 2023), with an estimated abundance in 2018 of 112 individuals (SE = 27; Van Cise et al. 2021). This population has a lower degree of social clustering than other bottlenose dolphin populations in the Hawaiian Islands (Corsi et al. 2025). Common bottlenose dolphins forage on many fish species and display considerable individual variation in diving behavior, though shallower and shorter dives are generally performed at night (Baird 2016; Harnish et al. submitted).

Baird (2016) used association patterns, photo-identification, and telemetry data to demonstrate that both island-associated and open-ocean short-finned pilot whales are found around Kaua‘i and Ni‘ihau (Baird 2016). The island-associated population appears to have a similar social structure to the well-studied population off Hawai‘i Island (Mahaffy et al. 2015), although with a larger core range (4040 km^2; Kratofil et al. 2023). Based on genetic analyses, short-finned pilot whales around the MHI are differentiated from those found in the Northwestern Hawaiian Islands (Van Cise et al. 2017). Additionally, within the MHI population, those found around Kaua‘i, Ni‘ihau, and O‘ahu (referred to as the western community) are genetically differentiated from the eastern community (around Hawai‘i Island), and both insular communities are distinct from open-ocean pilot whales (Van Cise et al. 2017).

CRC efforts around Kaua‘i and Ni‘ihau have provided information both on resident populations and on apparently open-ocean odontocete populations, which appear to only occasionally move through waters around Kaua‘i and Ni‘ihau. For example, sighting rates of pygmy killer whales (*Feresa attenuata*) are less than a third of those for the same species near Hawai‘i Island, which has a resident population, and there have been limited resightings of individuals within groups that have been photo-identified there (Baird et al. 2024; CRC, unpublished data). Similarly, while there are island-associated populations of pantropical spotted dolphins (*Stenella attenuata*) off other islands, sighting rates off Kaua‘i are an order of magnitude lower than those near other islands (Baird and Webster 2020), and individuals that have been tagged near Kaua‘i have quickly left the island slopes and ranged broadly in open-ocean waters (Baird and Webster 2019).

MFAS Sonar and Hawaiian Cetaceans

Exposure and Received Level Analyses

Beginning in 2011, NIWC Pacific and NUWC Newport began supporting CRC's monitoring efforts at PMRF (Fig. 1) during the biannual SCC training event (e.g., Baird et al. 2014), while SEA, Inc. began assisting with response analyses. NIWC Pacific would also record the range hydrophone data during the tagging efforts and

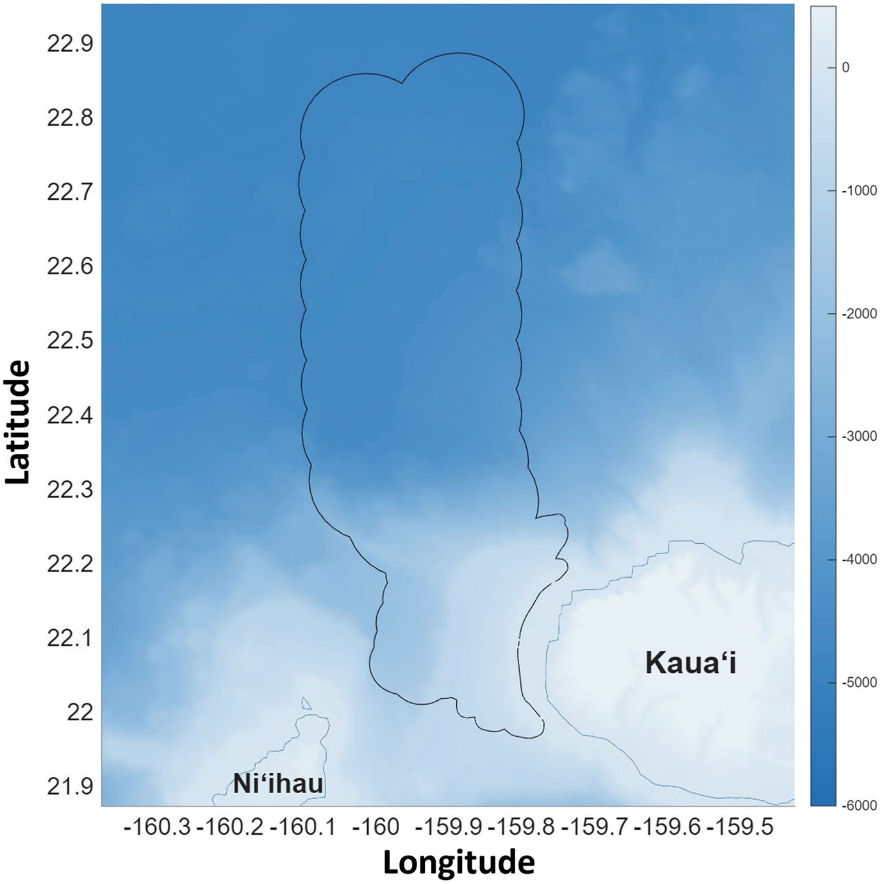

Fig. 1 Map of the Pacific Missile Range Facility's instrumented range, outlined in black, located between the islands of Kaua‘i and Ni‘ihau in the Main Hawaiian Islands. Shading reflects bathymetric depth

during and after the SCC to obtain acoustic data associated with training activities. The types of tags deployed changed over time, gradually improving the location data quality. Satellite-linked tags deployed in 2011 and 2012 were primarily location-only Argos tags (Wildlife Computers SPOT5 LIMPET tags). From 2013 through 2017, most tags deployed were SPLASH10 tags, which provided information on diving behavior (e.g., dive depth and duration) in addition to Argos location data. Beginning in 2013, land-based receiving stations were installed on Kaua‘i to increase behavior data acquisition (Baird et al. 2014). In 2016, this Kaua‘i-based system was upgraded to a MOTE receiver (Jeanniard-du-Dot et al. 2017), and an additional MOTE was installed on Ni‘ihau in 2017.

Received levels of MFAS that occurred during training events could be estimated based on tag location information. However, tag data were sparse, with long gaps in Argos coverage and tagged animal positions limited by animal diving behavior. Bouts of MFAS were also intermittent, occurring periodically for approximately 3 days during training events. As finding tag locations of animals that overlapped with periods of MFAS was difficult, the exposure window broadly included an hour before and after the time of the tag Argos location to augment the positional data. This methodology, although the best available approach at the time, led to a high level of uncertainty in MFAS exposure levels received for tagged individuals (e.g., Fig. 2; Baird et al. 2014).

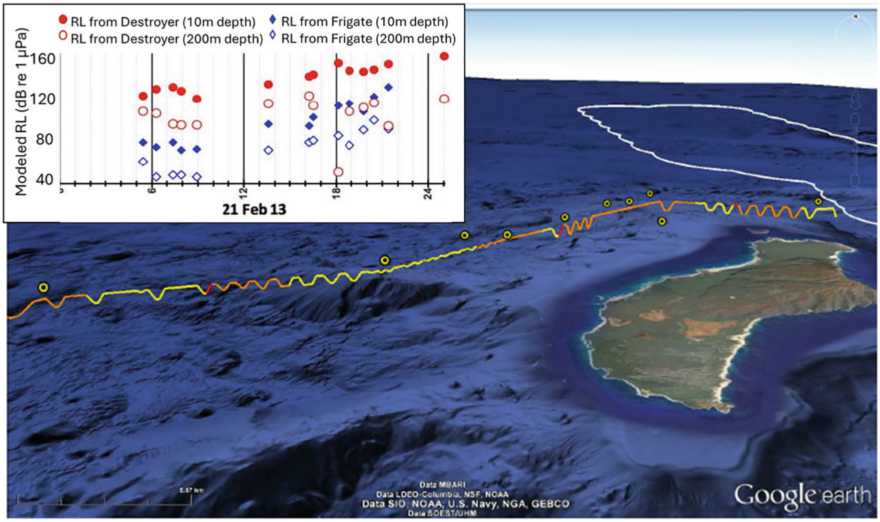

Fig. 2 Interpolated trackline of a SPLASH10 tagged pilot whale (GmTag070) moving away from the PMRF range (outlined in white) off the island of Ni‘ihau. Dives are shown in yellow during periods without MFAS, in red at the onset of MFAS, and in orange during periods of MFAS. Argos location updates are shown as yellow circles. The inset figure shows modeled received levels from a USN Destroyer (red) and Frigate (blue) over 1 day of training in February 2013 that aligned with Argos satellite generated locations for GmTag070 at depths of 10 m (filled symbols) and 200 m (open symbols). (Both figures adapted with permission from Baird et al. 2014)

Extrapolating behavioral responses from Argos-only tag data was also difficult and limited to observations of large-scale movements during the 3 days of intermittent MFAS use (e.g., Fig. 2). Given sparse location data, the interpolated trackline between positions was by default a straight line, and any nuanced movement behavior in response to the MFAS activity was lost (Fig. 2).

Technological and Analytical Improvements

Beginning in 2018, tags that obtained Fastloc®-GPS locations in addition to Argos locations and behavior data (Wildlife Computers SPLASH10-F tags) were used in most deployments, reducing temporal gaps and improving location accuracy (Table 1). The land-based MOTE receivers increased the number of GPS locations and behavior data received from these tags. In 2020, analytical methods were developed to account for these expanded positional data, improve track processing, and more accurately estimate received levels (detailed in Henderson et al. 2021). Other behavioral response analyses were developed and applied to optimize the information gained from these large, aggregated, and long-term datasets (e.g., Henderson et al. 2025b).

With the SPLASH10-F tags, positional data were obtained more frequently, often with several locations per hour, particularly when tagged individuals remained near one of the islands with a MOTE receiver. This, coupled with improved software to filter, smooth, and interpolate the data (see Henderson et al. 2021 for details), allowed tracks to be almost continuous across their deployment with improved estimates of accuracy at each position. Specifically, each position has an associated

Table 1 List of species tagged off the island of Kaua‘i from 2003 to 2025, including the number of tags deployed, the number of tags with Fastloc®-GPS, and the number of years with data per species

Species	Number of tags deployed total	Number of tags with Fastloc®-GPS	Number of years with tag data
Short-finned pilot whale	50	28	11
Rough-toothed dolphin	18	3	9
Common bottlenose dolphin	20	5	7
Melon-headed whale	11	9	5
False killer whale	7	3	5
Dense-beaked whale	6	5	5
Pantropical spotted dolphin	5	1	4
Sperm whale	1	0	1
Humpback whale	3	2	1

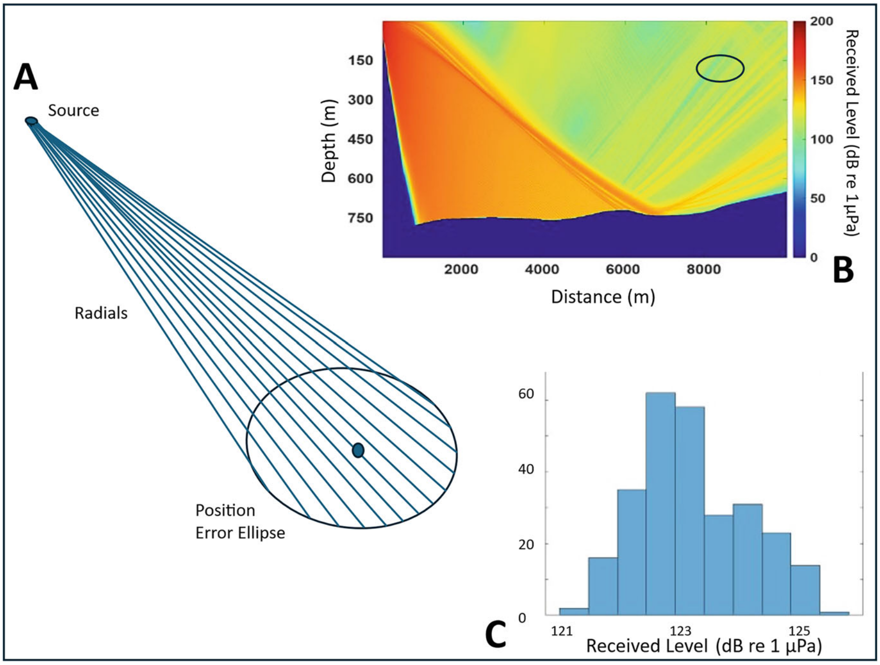

Fig. 3 A hypothetical example of a three-dimensional estimate of received level. (**a**) Multiple propagation radials are taken from the source to each positional error ellipse such that the area of the ellipse that is occupied by the focal animal is fully sampled. (**b**) One radial slice with the position in depth of a mock animal. (**c**) Histogram representing modeled maximum median levels ± 2*SD within the three-dimensional area of an ellipse, reported for each location along a track

error ellipse to provide a spatial estimate of accuracy. The tracks are typically interpolated every 5 min using movement models, and during periods of MFAS, a received level can be estimated for transmissions from hull-mounted ship sonars, helicopter-dipping sonar, and active sonobuoys, down-sampled to one ping per source per 5-min period. Furthermore, rather than reporting one value of estimated transmission loss between the source and animal at each position, the full error ellipse is utilized and transmission loss is estimated using a sound propagation model along multiple radials across the width and extent of the ellipse (Fig. 3a). Finally, when available, dive profile models can be built using each species' known diving behavior (e.g., ascent and descent rates, maximum dive depths) as well as behavior log data. This allows the three-dimensional position to be further refined by calculating animal depth at the ping arrival time with some area above and below to account for uncertainty (Fig. 3b). Resulting received levels are aggregated per 5-min bin from the 3D area of the ellipse for each source type, reported as the maximum median received level per 5-min bin with two times the standard deviation as a metric of variance (Figs. 3c and 4). The improved temporal scale for this type of

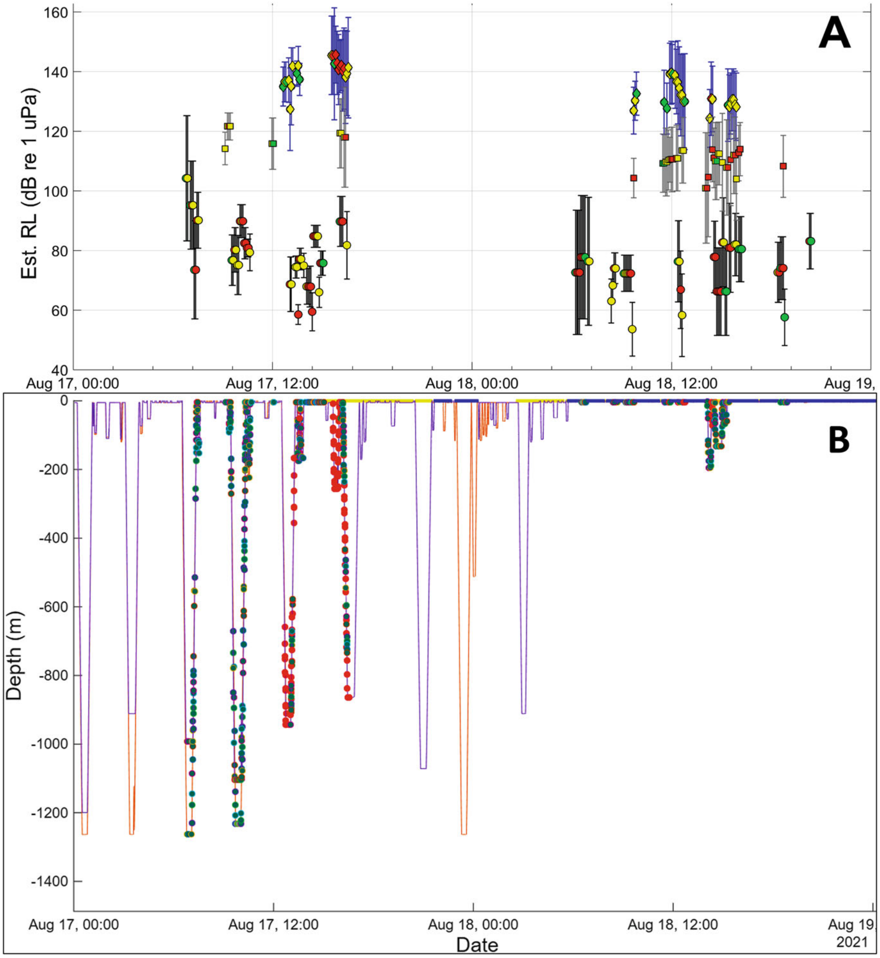

Fig. 4 (**a**) Maximum median received levels estimated for a SPLASH10-F tagged dense-beaked whale (MdTag020) over a 2-day period. MFAS from hull-mounted ship sonar shown in diamonds with blue error bars, from helicopter-dipping sonar in squares with gray error bars, and from active sonobuoys in circles with black error bars (error bars indicate ± 2*SD around the median). Symbol colors provide the relative number of pings per 5-min bin, with green being low, yellow moderate, and red high. (**b**) Dive records for the same tagged dense-beaked whales (MdTag020, a female (orange), and MdTag021, a male (purple)). The green dots indicate arrival times of helicopter-dipping or sonobuoy MFAS pings, while the red dots indicate arrival times of ship MFAS pings; the arrival times are aligned with the ping times in (**a**). The yellow bar at the top indicates periods of missing dive data for MdTag020, while the blue bar indicates periods of missing dive data for MdTag021. (Taken with permission from Henderson et al. 2025a)

received level analysis is a major improvement over the original received level estimates and provides greater insight into the acoustic scene that cetaceans experience at PMRF during USN training activities.

Behavioral Response Analyses

The refined received level estimates from three MFAS sources, coupled with the rich life history data from the long-term studies of the Kaua‘i-Ni‘ihau island-associated resident odontocete populations, provide an opportunity for unprecedented insight into the exposure and potential behavioral responses to and long-term consequences of repeated MFAS exposure.

For example, using these more robust methods, a recent study was conducted on MFAS exposures and possible behavioral responses of dense-beaked whales (*Mesoplodon densirostris*; Henderson et al. 2025a). Beaked whales are of great concern to the USN due to their apparent heightened sensitivity to MFAS and the potential for a strong response to lead to a stranding in certain conditions (Henderson 2023). In Henderson et al. (2025a), three tagged dense-beaked whales were documented to move off the range and away from the area of MFAS activity. Two whales continued to forage on the range at the initial onset of helicopter-dipping and sonobuoy MFAS (Fig. 4b) and appeared to continue to forage once they moved away from the area of activity after the onset of surface ship MFAS, based on the similarity in the bathymetry and their movement and dive behavior; no hydrophones were present off the range and so no foraging dives could be acoustically confirmed. However, the pair of whales, whose dive and movement behavior had been highly synchronized for 6 days, appeared to separate at the onset of ship MFAS (Fig. 4b); this was also the only time the maximum dive depth during an inter-deep dive interval exceeded the 95th percentile of their typical dive behavior, indicating a likely response (Henderson et al. 2025a). These beaked whales were 20–34 km from training activity, much farther than the distances in most controlled exposure studies of MFAS where most of the strong avoidance behavioral responses have been observed, which could explain the more moderate responses (e.g., Henderson 2023, but see Southall et al. 2026).

A similar exposure and movement behavior analysis was also conducted for rough-toothed dolphins (Henderson et al. 2025b); movement behavior was compared before, during, and after the SCCs. While movement behavior varied considerably between individuals and significantly across training phases, there were no obvious responses when examined broadly across the SCC phases. However, when examined over shorter intervals and factoring in the amount of MFAS activity and number of sources, there were evident changes in some individual dolphins’ behavior that may have indicated a response. These resident animals may be habituated to, or at least tolerant of, MFAS activity occurring on the range, with behavior influenced by the movement of their prey over longer time and spatial scales. On the other hand, they may respond on shorter time scales when more sound is produced over a broader bandwidth and from multiple directions (e.g., more sources are active simultaneously) due to the increased potential for masking of conspecifics or reduced detection of predators. Rough-toothed dolphins have been observed previously to demonstrate a strong acoustic response to the presence of killer whales (*Orcinus orca*) at PMRF (Jarvis et al. 2019). Thus, they are likely constantly listening for predator vocalizations and may be more cautious when more MFAS is occurring. Alternatively, it has been proposed that MFAS could sound like killer whale pulsed calls to beaked whales, and perhaps other odontocetes could also be reacting to MFAS as they would a predator (e.g., Henderson 2023). It should be noted that there is no true baseline behavior data for this or any odontocete species off Kauaʻi, as testing and training activity have occurred on and off the range (e.g., the biannual Rim of the Pacific exercise, https://www.cpf.navy.mil/About-Us/Exercises-Missions/RIMPAC/) in Hawaiian waters before these focal studies began in 2003.

Future Directions

As additional data continue to be acquired and new analytical methods are developed, more insight into odontocete behavioral responses to MFAS will be gained. For example, a new horizontal movement model that was developed for goose-beaked whales (*Ziphius cavirostris*; Southall et al. 2026) is being applied to short-finned pilot whales. This satellite tag dataset is incredibly robust, with 50 tags from Kauaʻi between 2006 and 2025 and almost 100 tags from the other Main Hawaiian Islands. These animals also have extensive photographic data and sighting histories that will provide unprecedented knowledge about individual and group exposure histories, allowing for the first time not just a quantitative snapshot of individual responses to single exposures, but also population-level responses given their historical context. This type of longitudinal study allows for an unprecedented level of insight, and it is hoped that such studies will continue to advance this edge of research into the future. As additional data are gathered on other well-studied resident species, such as common bottlenose dolphins or rough-toothed dolphins, these quantitative models could also be applied to them in the future.

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