

Behavioral response studies of two populations of short-finned pilot whales in different paradigms: How does exposure history and social structure inform behavioral response?

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Background

In the last two decades, a substantial number of behavioral response and controlled exposure studies have been conducted on a variety of odontocete and mysticete species around the world (e.g., Dunlop et al., 2013; Miller et al., 2014; Kvadsheim et al., 2017; Wensveen et al., 2019, 2025; Southall et al., 2016, 2024, 2026) to better understand the effects of mid-frequency active sonar (MFAS) on cetaceans, after a series of strandings that occurred with multi-national training events using MFAS (e.g., D'Amico et al. 2009, Filadelfo et al. 2009). These studies have largely been conducted using vessel-based visual observations of animals affixed with acoustic recording and motion sensing tags. These tags have historically remained attached to focal individuals on the order of a day or less and are deployed on one animal at a time, leading to a focus on individual-level responses. As the studies have progressed, some longitudinal experiments have been able to aggregate data on dozens of animals of a few species (e.g., Southall et al., 2019; 2023). These studies largely relied on expert scoring of the resulting tag data to determine whether a behavioral response occurred, as well as the type and severity. This was a manually-intensive and time-consuming process, but it led to a tight coupling between the timing of the onset of a response and a specific received level of MFAS. These studies provided valuable insights into how cetaceans were responding to MFAS exposures and set the stage for all subsequent research.

In recent years, some research has moved toward complementing or replacing the use of short-term, high-resolution tags with less expensive satellite-linked tags that can be deployed on a higher number of animals and that do not need to be recovered to obtain the location and dive data. These tags yield a much longer-term (weeks to months) and broader spatial scale data set, but one that is far coarser (e.g., lower location accuracy, lower temporal resolution) than the motion-sensing tags, and does not include the associated acoustic data. Therefore, any associated MFAS exposure data must be estimated utilizing acoustic propagation modeling (Henderson et al. 2025, Schick et al. 2024, Southall et al., 2026), the efficacy of which can be evaluated with in situ calibrated acoustic recorders (e.g. Navy range hydrophones, HARPs, Sound Traps, etc.). However, statistical modeling has demonstrated that even with greater uncertainty in locations and associated received levels at the single tag level, information accrued from many satellite-linked tags is comparable to that from a few motion-sensing acoustic tags (Bouchet et al., 2021).

Two projects, one in the Atlantic Ocean and one in the Pacific Ocean, have simultaneously collected data from satellite-linked tags from a large number of short-finned pilot whales (*Globicephala*

macrorhynchus; 54 from the Atlantic and 140 from the Pacific (50 from from Kaua’i), **Tables 1 and 2**). Pilot whales were exposed to MFAS in both areas, either opportunistically during a biannual training event at the Pacific Missile Range Facility (PMRF) in Hawai’i, or during controlled exposure experiments (CEEs) associated with the Atlantic Behavioral Response (BRS) project off Cape Hatteras, North Carolina, where experimentally simulated or operational SQS-53C sonars from surface warships were used (**Figure 1**). In addition, all tagged animals have some additional data known about their social relationships and context. Off Cape Hatteras this includes at minimum the number of other animals in the group they were tagged with and some photo-identification information about the associated population; off Kaua’i this includes information known about social network-derived relationships in the island-associated population and potential individual exposure histories. These data, along with newly developed spatial movement modeling techniques (Hanks et al., 2015; Johnson et al., 2021) adapted to satellite-linked tag data, create a natural experiment to evaluate and understand possible behavioral responses of short-finned pilot whales to MFAS exposures in two different populations and environments.

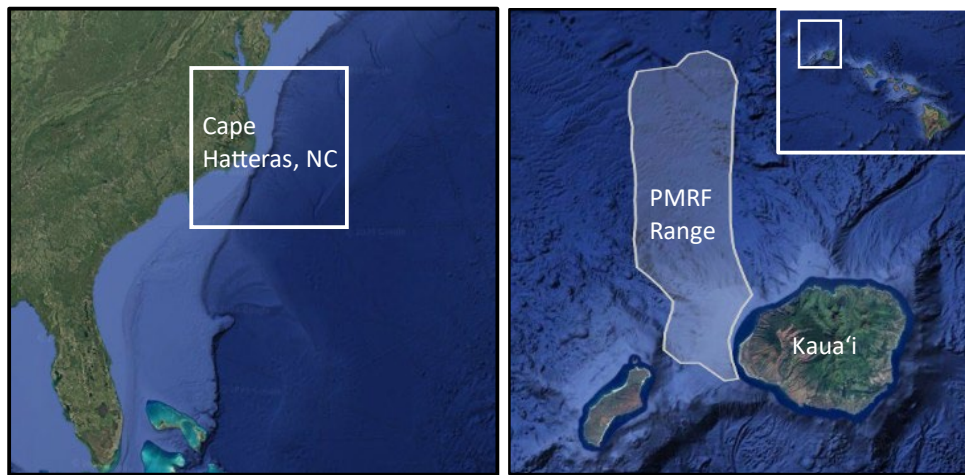


Figure 1 – Maps of study areas. Cape Hatteras, NC on the east coast of the US on the left, and the PMRF range off the island of Kaua’i in the Main Hawaiian Islands on the right.

Table 1 – Duke University and Southall Environmental Associates, Inc.’s (SEA, Inc.) summary of pilot whale data collected during the Atlantic BRS from 2017 - 2020. Tags were all SPLASH10-F tags. US Navy vessels used for real MFAS include the USS McFaul (DDG-74), the USS Nitze (DDG-94), the USS Ramage (DDG-61), the USS Cole (DDG-67), and the USS Laboon (DDG-58). R/V Barber and F/V Kahuna were used for the simulated and control studies.

Year	# Tags	CEE Type
2017	3	Real MFAS
2017	3	Simulated MFAS
2018	12	Control
2018	15	Real MFAS
2018	13	Simulated MFAS
2018	6	Simulated MFAS
2020	2	Real MFAS
Total	54	

Table 2 – Cascadia Research Collective’s short-finned pilot whale satellite tag data collected in the Main Hawaiian Islands from 2006 – 2025. The data from other islands can act as baseline data as needed. SPOT5 and SPOT6 tags

are location-only tags, while SPLASH10 tags provide location and dive data, and SPLASH10-F tags are also GPS equipped to provide additional, higher accuracy location data. SCC=Submarine Command Course.

Island	Tag Type	Year	# Tags	SCC overlap
Kaua'i	SPLASH10	2011	1	yes
Kaua'i	SPOT5	2011	2	yes
Kaua'i	SPOT5	2012	1	yes
Kaua'i	SPOT5	2012	1	no
Kaua'i	SPLASH10	2013	1	yes
Kaua'i	SPOT5	2013	1	yes
Kaua'i	SPLASH10	2014	4	yes
Kaua'i	SPLASH10	2014	1	no
Kaua'i	SPOT5	2014	2	yes
Kaua'i	SPLASH10	2015	1	yes
Kaua'i	SPOT5	2015	1	yes
Kaua'i	SPLASH10	2016	6	yes
Kaua'i	SPLASH10-F	2018	3	yes
Kaua'i	SPLASH10-F	2020	1	yes
Kaua'i	SPLASH10-F	2021	3	yes
Kaua'i	SPLASH10-F	2022	3	yes
Kaua'i	SPLASH10-F	2023	6	yes
Kaua'i	SPLASH10-F	2024	8	yes
Kaua'i	SPLASH10-F	2025	4	yes
Kaua'i Total			50	
Hawai'i	SPOT5 / 6	2006 - 2023	46	no
Hawai'i	SPLASH10-F	2009 - 2018	20	no
Ni'ihau	SPLASH10	2015	2	no
Lāna'i	SPOT5 / 6	2012 - 2017	5	no
Lāna'i	SPLASH10-F	2017	2	no
O'ahu	SPOT5 / 6	2010 - 2023	13	no
O'ahu	SPLASH10	2015	2	no
All Island Total			140	

Work completed in FY25

This project kicked off in October 2024 with a virtual meeting with all team members from Naval Postgraduate School (NPS), Naval Information Warfare Center (NIWC) Pacific, SEA Inc., Cascadia Research Collective (CRC), and Duke University. This half-day meeting allowed all the team members to meet each other, and allowed us to have an initial discussion on what data was available from each team (e.g., number of tags, tag types, tag settings, received level data, etc.), what we hoped our end results and products were going to be, and what our timeline looked like, so we were all in alignment.

In January 2025, we had a follow-on highly successful 3-day in-person workshop at NPS. While this workshop was largely focused on the propagation modeling efforts by NPS and NIWC Pacific, additional topics included further details on tag and data processing methods as

well as post-processing workflows, an introduction to the social network data in Hawai'i, and how the data needed to be formatted and aligned for the continuous time discrete-space (*ctds*) behavioral response model (Hanks et al., 2015; Johnson et al., 2021).

The full team met every quarter to check in and report on progress being made by each team. Most of the focused effort in the first year has been on aligning the propagation modeling methods as closely as possible between the Atlantic and Pacific datasets, and determining the optimal grid size for the gridded wind noise data and received level data that provides the best resolution in noise data while optimizing the grid size for pilot whale swim speeds. Specific tasks are described in more detail below.

CRC and NIWC Pacific – Pilot whale tracks at PMRF

One benefit of the PMRF dataset was that most of the propagation modeling from the hull-mounted surface ship MFAS sources for the tags from 2011 - 2024 had previously been completed, along with the modeling for the active sonobuoys and helicopter-dipping sonar from the most recent years (see Henderson et al., 2021, 2025, 2026). This is a benefit because this is a very time-consuming process; the tag tracks are interpolated every 5-minutes by CRC using the *crawl* package in R (Johnson et al., 2008; Johnson & London, 2018), and NIWC Pacific models the closest sound source to the tag's model-estimated error ellipse (95% confidence interval) location for every 5-minute period of active MFAS (see below for more detail). During the first year of this project, NIWC Pacific completed the remainder of the propagation modeling for the sonobuoy and helicopter-dipping MFAS.

In previous years of collaboration, CRC provided NIWC Pacific a single interpolated 5-min track with associated error ellipses at each position for each tagged individual for our joint received level and behavioral response analyses (Henderson et al., 2021, 2023, 2025, 2026). However, for the new *ctds* model, 32 imputed tracks are required for each individual (Scharf et al., 2017). This posed a complication, as imputed tracks are always slightly different from each other; specifically, the spatial extent of each imputation differs and does not always spatially align with the propagation model output that had been previously modeled using the error ellipses from the mean track. Thus to ensure all imputed tracks fell within the same error ellipses for the locations with MFAS exposures, CRC developed an R-script that iterated through *crawl*-imputations and checked that the exposure locations fell within the existing error ellipses; if a track had locations outside those ellipses it was discarded and a new imputation was generated. This was computationally time consuming but successful, and ultimately all the 28 pilot whale tracks with MFAS exposure ended up with 32 imputed tracks with locations that fell within the existing error ellipses at times of MFAS exposures. This allowed us to use the existing propagation modeling results moving forward.

NIWC Pacific and Duke University – Pilot whale dive modeling

Satellite-linked tags calculate dive parameters based on a pressure sensor that records a pressure time-series archive from which a behavior log is created if the animal dives below a pre-determined depth threshold. Once this depth threshold is crossed and a pre-determined time (in seconds) has also lapsed at or beyond that depth then a "dive" has begun. Once those conditions have been triggered, the behavior log records the start and end time of the dive, and the minimum and maximum bounds of the deepest dive depth. It also categorizes the shape of each dive, again based on pre-defined conditions from the tag manufacturer. Using data from suction-cup attached time-depth recorder tags deployed on short-finned pilot whales in Hawai'i in the 2000s by CRC, NIWC Pacific had

developed a dive modeling method that used derived or published ascent and descent rates for pilot whales, plus bottom time information based on the dive shape, to create models of dive behavior from satellite tag data. These were coarse models that had never been ground-truthed. However, Duke University had DTag data from pilot whales in which the fine-scale dive profiles were actually measured, and so they were able to apply the coarse dive modeling code to the DTag data and then refine the reconstruction of the satellite tag dive profile(s) to make them more realistic and match measured dive profiles. NIWC Pacific and Duke University then applied this shared dive model to our respective datasets to extrapolate dive profiles for all SPLASH10 tagged pilot whales. This is a critical step as it will allow us to use the more finely resolved depth estimates to more precisely extract the modeled RL at the times of exposure (Henderson et al., 2021; Schick et al., 2024).

CRC and Duke University – Social Network Analysis

While most of the early years of the Kaua'i pilot whale photographs had been matched to the CRC photo-identification catalog, photographs from the most recent years had yet to be matched. During FY25, photographs available through 2023 were completely matched and photographs from 2024 and 2025 were partially matched. Upon completion, the next step will be undertaking social-network analyses to determine social cluster and assess sighting history (see Mahaffy et al., 2023, **Figure 2**). Similarly, a photo-identification catalog exists for the Atlantic coast pilot whales and photographs have been matched through 2022, which encompasses all tagged focal pilot whales from the CEE effort. A comparable social-network analysis will be performed to investigate possible social clustering in the Hatteras population.

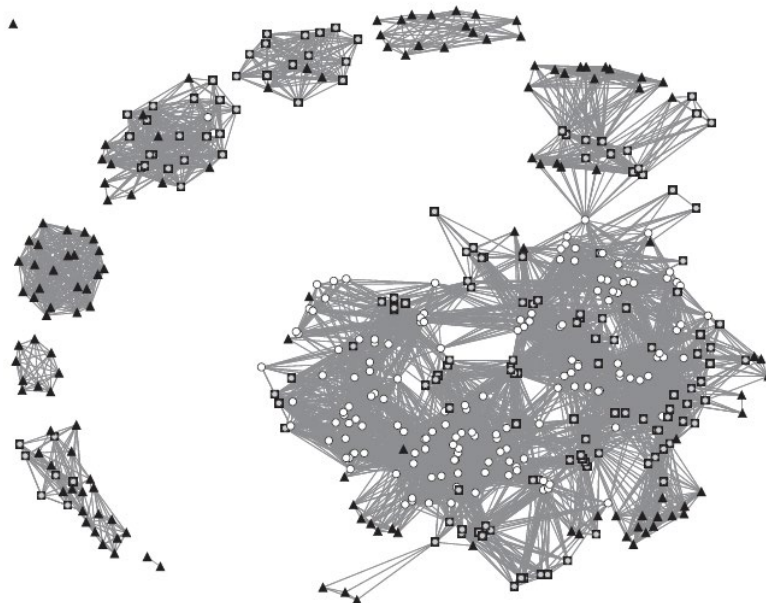


Figure 2 – Example of a social network diagram, taken from Mahaffy et al., 2015. This example shows social clusters of short-finned pilot whales off the island of Hawai'i based on photographs from 2003 - 2007. A similar analysis will be conducted on the resident Kaua'i-island associated population of pilot whales.

NIWC Pacific, NPS, Sea INC., and CRC – Grid size

Some time needed to be spent with the team determining the appropriate grid size needed for the wind noise and received level covariate layers that are fed into the *ctds* model. The *ctds* model estimates the likelihood of an animal remaining in the same grid cell or moving to a new grid cell based on covariates that include the MFAS received level (or ambient noise level); thus, the grid size variable is very important. If the grid size is too small, less than a typical travel speed for a pilot whale in 5 minutes, then it doesn't make sense biologically as they would be skipping over one grid cell and arriving in the next within 5 minutes. In contrast, if the cell size is too large, and there is no way a pilot whale could reach the next cell in 5 minutes, even at a burst speed, then that is not a logical size either. After an examination of past tag and focal follow data and a literature review, we determined that 250 m was a reasonable grid size, both in terms of realistic animal movement but also computational feasibility. This size balanced pilot whale movement behavior and swim speeds while retaining salient features in the smoothed wind noise and MFAS received level data.

As noted above, the model from Hanks et al. (2015) and Johnson et al. (2021) assume a discrete space representation of the environment over which animals move. Since the sound propagation has been done differently in each site, we conducted several experiments to find the best gridding approach to ensure common approaches to the construction of this gridded space across the two sites. For example, at PMRF most of our modeling is done at a very fine resolution, in steps or bins of 10s of meters of water depth, but this is limited to the error ellipses of each animal's position. In contrast, in the Atlantic the propagation modeling was traditionally done to cover a broader spatial area that encompasses all tagged animals during an experiment. The sound propagation model is run along each of 360 one degree radials around a source. Because of this radial structure in the data, when they are gridded there are far more points near the source than far from the source. Therefore, there is a tradeoff in cell size to capture the spatial signal without over or undersmoothing the data. We needed to assess these tradeoffs when determining an optimal grid size, as one dataset was losing resolution moving from a finer gridding to 250 m, while the other dataset was losing resolution by trying to smooth a very coarse dataset to a finer resolution of 250 m and thus losing some of the highest received levels closest to the source.

NPS, NIWC Pacific, and SEA, Inc. – Propagation Modeling

NPS and NIWC Pacific use different underlying propagation models (Navy Standard Parabolic Equation and BELLHOP vs a range dependent parabolic equation, respectively), as well as different modeling approaches. NPS runs 360 radials with 1° spacing around the source and out to ~130 km. Tagged animal locations are then either snapped to the closest two radials to estimate an MFAS received level, or the area between the radials is interpolated to obtain a received level at the location of the animal. Depth data are used to refine these estimates, i.e., they are used to extract the depth-specific RLs experienced by the animal. The received levels are only modeled once at a temporal resolution of 5 minutes for the duration of the CEE. If the source was a DDG, then it was steaming at approximately 8 knots for an hour; whereas if it was a simulated exposure, the vessel with the sound source was typically drifting. In the Atlantic, the source is positioned with reference to a single focal animal, however RLs can be estimated for all tagged animals within ~130 km of the source (Southall et al., 2026). NPS reports a single received level at a time and location, i.e., uncertainty in the propagation is not included. We account for the spatial uncertainty in the satellite tag data by imputing 100 tracks and extracting 100 received levels for each location at each 5-minute period in the CEE. NPS also only models to 1,500 m depth rather than to the seafloor.

In contrast, for training activities at PMRF, NIWC Pacific has access to the classified ship and source locations and can determine the closest source to the tagged animal for each 5-minute track position. NIWC uses the 95% Confidence Interval (CI) error ellipse associated with each track position and models a number of radials from the source through the error ellipse to the far edge and from one edge of the ellipse to the other, and from the surface to the seafloor (**Figure 3**; See Henderson et al., 2021 for more details). NIWC also uses the modeled dive information (as described above) and the estimated time of arrival of the MFAS ping to determine the approximate location of the animal in the water column and uses a three-dimensional area around that location in depth and the cross sections of each of the radials in the error ellipse to estimate received levels throughout that volume of water (Figure 3). Finally, NIWC reports the maximum median received level from that three-dimensional volume of water around the animal's position, plus 2 standard deviations, for each of the 5-minute positions along the whale's track during the entire period of exposure. This creates a series of wedge-shaped areas with modeled received levels that follow the movements of both the source and the whale and therefore are classified.

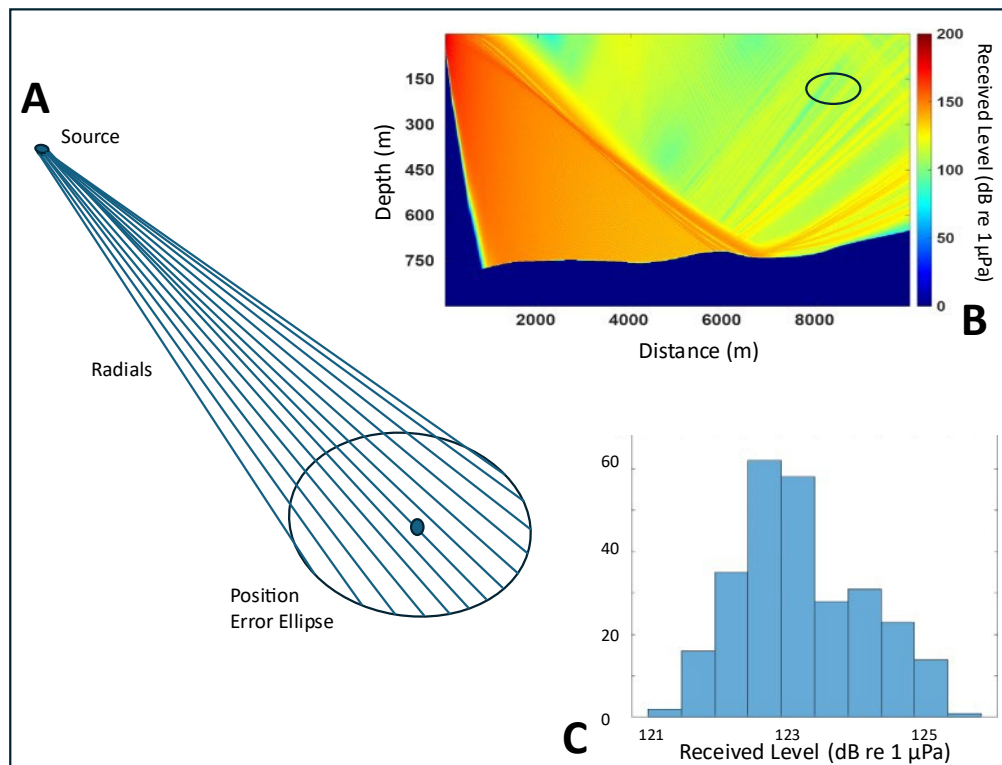


Figure 3 – A hypothetical example of a three-dimensional estimate of received level at PMRF. (A) Multiple radials are taken from the source to each positional error ellipse such that the area of the ellipse is fully sampled. (B) The animal's position relative to source and dive behavior are also modeled against the depth in the water column when the MFAS arrives (top right image of one radial slice with the position in depth of an animal). (C) The received levels of that three-dimensional area are modeled, and the maximum median level ± 2 *SD is reported for each location along the track. Figure taken from Henderson et al. (2026).

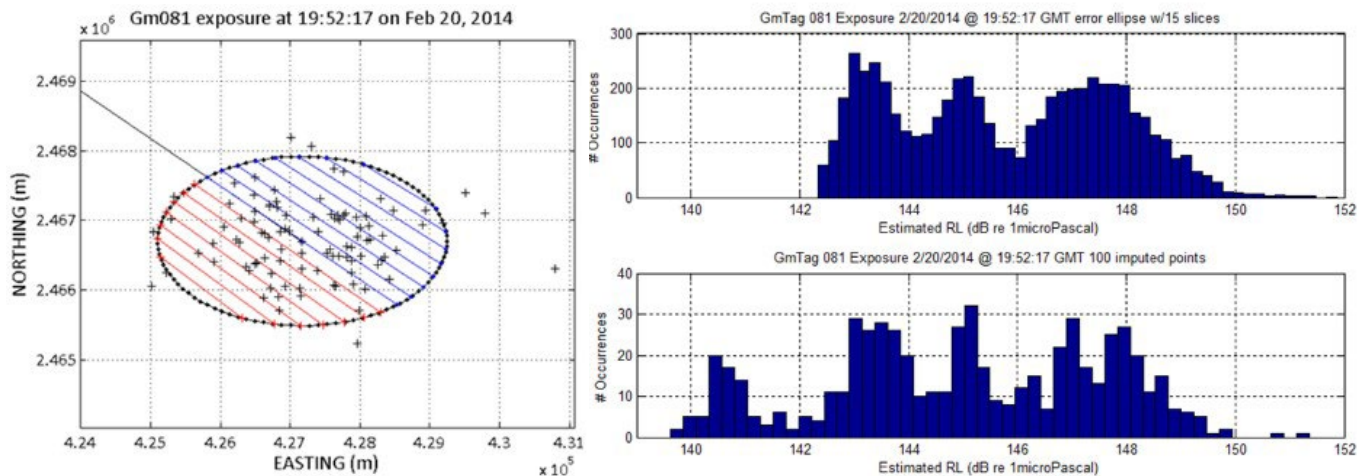


Figure 4 – A comparison of obtaining received levels using radial slices through an error ellipse versus 100 imputed points per track location was conducted at specified water depths; the imputed points overlapped the single error ellipse well (left), and the resulting histograms of received levels (right) matched closely. This example is from GmTag081, tagged off Kaua’i in 2014.

Because these methods and the resulting received level mapped “products” are so different, even though the resulting received level values are similar (**Figure 4**), a good deal of time was spent in the first year of this project discussing the best way to align these methods if possible, as well as to determine how the different received level maps could be integrated into the *ctds* movement model.

Due to the classification issue for NIWC Pacific’s propagation modeling results, the teams decided that CRC would generate 33 imputed tracks for one of the pilot whales tagged off Kaua’i during a time that did not coincide with a training event, and NIWC Pacific would generate a dummy training event with pseudo-ship tracks and MFAS. Then NIWC could run their propagation modeling for this, and give the results to SEA, Inc. for testing in the *ctds* model. This will be completed in FY26. Once the data is working in the model, most likely NIWC Pacific will be running the *ctds* model in-house using classified data.

NPS, SEA Inc., and NIWC Pacific – Wind Noise

The *ctds* also utilize maps of ambient wind noise to provide baseline received levels for the whales before and after the exposure periods. Finding the right source for wind data in Hawai’i proved challenging, and even once good wind data was identified it took time to determine the right way to both fill in missing data gaps as well as create an effective land mask such that the remaining wind data was usable for the *ctds* model. NPS and SEA, Inc. worked closely with NIWC Pacific during this process, and ultimately the teams were successful, and good wind noise data were generated for both the Atlantic and Pacific Ocean areas of interest and were gridded to 250 m.

SEA Inc. – Movement model preparation

One of the challenges in data preparation is the spatial and temporal integration of the different gridded data sources to create a temporally contiguous noise covariate. Whereas, when testing for response to sonar in the Atlantic BRS we first used a static distance to ship raster construction (Southall et al., 2026), in the extension of the Hanks et al. (2015) model by Johnson et al. (2021), a time series of rasters is needed whose temporal extent covers the duration of the tag deployment. As noted above, the wind data and the sound propagation data are at both different spatial and temporal resolutions and extents. Thus, we have spent time in Q4 2025 and Q1 2026 developing the code to build and assemble these covariates. Specifically, we are constructing space-time raster stacks on a common 250 m grid that are combinations of wind-driven ambient noise in the Third-octave band centered on 3.4 kHz, and the sound propagation model output. The wind-driven ambient is at a 3-hour resolution over the duration of the tag, whereas the RL data are at a 5-minute resolution for up to an hour. Despite the data being at different temporal resolution, the model from Johnson et al. (2021) tracks the explicit time of changes in the covariate layer(s).

Figure 5 – A raster covariate showing the merged wind-driven ambient and the modeled RL footprint at full extent of the ambient data (left), and zoomed to show the detail of the gridded RL data (right). This is for one time period of one CEE, and for a given tag deployment we have built stacks that cover the duration and are comprised of the wind driven ambient noise and the RL data.

Summary and Year Two Tasking

From our proposed plan, we have successfully completed Task 1 (complete modeling received levels at PMRF), Task 2 (complete modeling received levels at Hatteras), and are in progress on Task 3 (conduct social network analyses) and Task 4 (apply *ctds* model to track data). We started the year well ahead of schedule, but ended up behind schedule slightly due to the unexpected time spent on the questions of grid size, alignment of received level “products”, and preparing the Hawai‘i wind noise “products”. The government shutdown also closed NPS which cost us 6 weeks of work time as well. However, we now have all of the pieces in place to begin testing the *ctds* model in Q1 of FY26. Furthermore, the photo-identification matching and social network analysis work has been conducted in parallel with the work on preparing the track and noise data for the model, and so that work will be completed in FY26 and can dovetail with the modeling results to provide the bigger picture of behavioral responses in both populations. Finally, Task 5 (apply HMMs to the dive data) will be conducted in Year 2.

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