Investigating the Diel Occurrence of Odontocetes Around the Maui Nui Region Using Passive Acoustic Techniques[1]

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Abstract: The distribution of odontocetes on a daily scale is largely driven by bottom-up processes that in turn influence foraging opportunities. Environmental variables such as bathymetry may help indicate productive foraging regions and serve as useful tools when assessing dolphin spatial and temporal patterns. To begin to understand daily spatial patterns of different odontocete species relative to heterogeneous benthic habitat, passive acoustic monitoring was conducted near an understudied basin of the Hawaiian Islands, the Maui Nui region (Maui, Lāna'i, Kaho'olawe, Moloka'i). Results showed that the acoustic activity of smaller species was stronger at night than day, particularly closer to shelf waters. In contrast, the acoustic activity of less common larger species tended not to follow a diel pattern, except at sites of a moderate proximity to shelf waters. These findings support previous research showing that smaller odontocetes, such as spinner dolphins (*Stenella longirostris*), track and feed upon the daily vertically migrating mesopelagic boundary community at night, while larger odontocetes, such as false killer whales (*Pseudorca crassidens*), may forage across most of the region during both the day and night. This information will help inform best management practices that account for interspecies variation in use of the Maui Nui basin.

Keywords: passive acoustic monitoring, spatial patterns, odontocete, Maui Nui, bathymetry

ODONTOCETE DISTRIBUTIONS ACROSS BROAD temporal scales are driven by many factors, including breeding and calving opportunities,

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predation, and anthropogenic effects, but one of the strongest influences on a daily scale may be the need to successfully forage (Acevedo-Gutiérrez et al. 1997, Davis et al. 1998, 2002, Acevedo-Gutiérrez and Parker 2000, Hastie et al. 2004, Richardson et al. 2013, Righi et al. 2013). Successful prey capture may be directly affected by prey distributions (Heithaus and Dill 2002), such as the movement patterns of dolphins tracking the location of their prey (Acevedo-Gutiérrez and Parker 2000). It may also be indirectly influenced by the distribution and densities of lower trophic levels including phytoplankton (Pardo et al. 2015) and zooplankton and micronekton (Davis et al. 2002), which undergo diel vertical migrations in the water column and horizontal migration along shelf breaks (Herman et al. 1981). In turn, many studies have documented diel trends in the occurrence of certain dolphin species, with acoustic activity frequently heightened at night, which suggests

close association between these dolphins and lower trophic levels to increase their foraging efficiency (e.g., Wang et al. 1995). Conversely, other dolphin species that track larger prey, such as tuna, may be more indirectly linked to the distribution and densities of these smaller organisms and may not exhibit as strong diel occurrence patterns.

The Maui Nui region of the Hawaiian Islands, which includes Maui, Lāna'i, Kaho'olawe, and Moloka'i, offers a unique opportunity to study diel variation in the occurrence of sympatric odontocete species across heterogeneous benthic habitat. The Maui Nui islands consist of a relatively shallow basin which slopes gradually out to around the 1000 m isobath and then drops off precipitously. Along the slope waters, a distinct land-associated community of fish, shrimp, squid, and other micronekton exists, which has been termed the mesopelagic boundary community layer (MBCL) (Reid et al. 1991, Benoit-Bird and Au 2003). This biomass-rich layer undergoes both diel vertical and horizontal migration, with micronekton rising to the surface and toward shore at night and descending to depths of 400 m to 700 m during the day, triggered by changing light levels (Forward Jr. 1988, Benoit-Bird et al. 2001). A variety of predators utilize the MBCL for food, including both open-ocean and nearshore predators (Norris and Dohl 1980, Haight et al. 1993, He et al. 1997, Skillman et al. 1998). In addition to the MBCL, larger pelagic fish are also drawn toward the islands (Itano and Holland

2000), which support predators at the highest trophic levels.

In part due to the food resources provided by the mesopelagic layer, eight species of odontocetes occur around the Maui Nui region, of which five species have resident populations: smaller-bodied pantropical spotted dolphins (*Stenella attenuata*), spinner dolphins (*S. longirostris*), medium-bodied bottlenose dolphins (*Tursiops truncatus*), larger-bodied short-finned pilot whales (*Globicephala macrorhynchus*), and false killer whales (*Pseudorca crassidens*) (Table 1) (Barlow 2006, Baird et al. 2013, Abecassis et al. 2015). Although they are not resident to the Maui Nui islands, melon-headed whales (*Peponocephala electra*) and pygmy killer whales (*Feresa attenuata*) occasionally transit through the region as well.

The smaller *Stenella* species forage directly on fish species associated with the MBCL (Norris et al. 1994, Baird 2016). While the movement patterns of spotted dolphins have only been generally characterized around the Hawaiian Islands (Baird et al. 2001, Baird and Webster 2019), it is well documented that spinner dolphins around Oahu horizontally track the MBCL layer (Benoit-Bird and Au 2003), traveling offshore from daytime shallow resting sites to forage at night in depths of 200 m to 250 m when the MBCL is closest to the surface and to shore (Fitch and Brownell Jr. 1968, Norris and Dohl 1980, Norris et al. 1994). Of the medium-bodied insular species, the bottlenose dolphin is known to forage

TABLE 1

Odontocete Species that Occur Around the Maui Nui Islands by Increasing Body Size

Common Name	Scientific Name	Maximum Length (m)	Source	Resident to Maui Nui?
Spinner dolphin	*Stenella longirostris*	1.97	Perrin and Henderson 1984	Yes
Pantropical spotted dolphin	*Stenella attenuata*	2.23	Perrin et al. 1976, Kasuya 1976	Yes
Pygmy killer whale	*Feresa attenuata*	2.6	Baird 2016	No
Rough-toothed dolphin	*Steno bredanensis*	2.65	Jefferson 2002	No
Melon-headed whale	*Peponcephala electra*	2.78	Baird 2016	No
Common bottlenose dolphin	*Tursiops truncatus*	3.8	Wells and Scott 2018	Yes
Short-finned pilot whale	*Globicephala macrorhynchus*	5.5	Baird 2016	Yes
False killer whale	*Pseudorca crassidens*	5.96	Baird 2016	Yes

during the day on shallow reef fish as well as other schooling fish (Baird 2016). However, the species has also been documented making deep dives during night hours to likely feed upon the MBCL (Baird 2016), and thus it may not follow a consistent distribution pattern. Larger-bodied resident species, including false killer whales and short-finned pilot whales, typically inhabit waters deeper than 1500 m (Baird et al. 2013) but their resident insular populations may use nearshore waters to exploit larger prey that likewise aggregate as a result of the MBCL (Shallenberger 1981, Connor and Norris 1982, Baird et al. 2008). In fact, a recent study found that the depth of dives by short-finned pilot whales around the Hawaiian Islands correlates with lunar light levels, reflecting the influence of such factors on the prey species of pilot whales, as well as pilot whale distribution patterns (Owen et al. 2019).

As acoustic signals are considered a good proxy for the presence of dolphins in the tropics (Rankin et al. 2008, Richardson et al. 2013), this preliminary study utilized a passive acoustic monitoring approach to document the spatial occurrence of large and smaller-bodied resident dolphin species on a daily temporal scale across the Maui Nui region.

Body size can generally be differentiated by the frequency of whistles detected (Steiner 1981, Wang et al. 1995, Azzolin et al. 2014). Spatial occurrence was assessed based on proximity to the 700 m isobath, with autonomous acoustic recorders placed at varying distances to this isobath. As determined by Reid et al. (1991), the waters within the 700 m isobath contain the highest density of the MBCL, and so it was hypothesized that smaller species more closely tied to the MBCL would show stronger diel trends toward the isobath, while larger species would largely be unaffected by distance to the isobath and not exhibit diel trends in occurrence.

MATERIALS AND METHODS

Passive acoustic monitoring was carried out around Maui Nui using Ecological Acoustic Recorders (EARs), which are bottom-moored, autonomous devices programmed to record on a duty cycle (Lammers et al. 2008). No permissions or licenses were required to deploy EARs in this area. All EARs recorded on a 10% duty cycle, with 30-second file recordings made every 5 min (Table 2). EARs recorded at a sampling

TABLE 2

Summary of EAR Parameters and Deployments

Site	EAR Version	Sampling Frequency (kHz)	Distance to 700 m isobath (km)	Depth of Recorder (m)	Deployment Period(s)	Latitude	Longitude
MauiNui2	2	125	4.64	402	6/19/15–7/22/15	20.74175	−157.0346
MauiNui5	2	125	6.18	362	9/9/15–10/9/15	20.5559	−156.4682
MauiNui4	2	125	19	105	1/10/15–1/15/15	20.9905	−156.984317
MauiNui3	2	125	24.7	226	9/10/15–10/12/15	21.020133	−156.736283
MauiNui8	1	64	25.92	68	1/9/16–3/6/16	20.973783	−156.913583
MauiNui6	2	125	27.49	300	9/9/15–9/20/15	20.706667	−156.7
	1	64			1/7/16–2/19/16		
MauiNui7	1	64	36.88	56	1/9/16–3/6/16	20.913383	−156.765867
MauiNui1	2	125	42.6	76	1/18/2015–3/31/15	20.8423	−156.754266

The EAR at MauiNui4 malfunctioned and did not record any data during its deployment. The EAR was moved to site MauiNui8 for a subsequent deployment.

frequency of 125 kHz or 64 kHz. Both bandwidths are sufficiently broad to capture the whistle fundamental frequencies of all Hawaiian delphinids (Au and Herzing 2003, Oswald et al. 2004). Based on the results of a pinger test, the detection radius of an EAR in this region is approximately 2.2 km for signals ranging in frequency from 4 kHz to 7 kHz (McElligott 2018). The frequency of the pinger was similar to that of whistles produced by false killer whales and short-finned pilot whales (Oswald et al. 2007), which are known to propagate farther distances than high frequency signals. Furthermore, Richardson et al. (2013) has suggested that the maximum detection range of most delphinid signals by hydrophones is around 1 km. Thus, it can be generally assumed that the majority of odontocetes detected on the EARs were within a few kilometers of the recorder.

EARs were deployed at eight sites around the Maui Nui region between 2015 and 2016 (Figure 1). Sites were chosen to represent a gradient of nearest distances to the 700 m isobath. Each EAR deployment spanned a period of 1 to 3 months. However, the EARs at sites MauiNui4 and MauiNui6 malfunctioned and recorded for only 6 and 12 days, respectively. The MauiNui6 EAR was deployed a second time in the same location, while the MauiNui4 EAR site was moved 8 km to the east, thus becoming site MauiNui8. The closest distance between any two EARs deployed at the same time was 17 km between MauiNui7 and Maui-Nui8, ensuring that signals recorded across EAR sites were independent of each other.

After each deployment, EAR recordings (referred to as files) were downloaded and
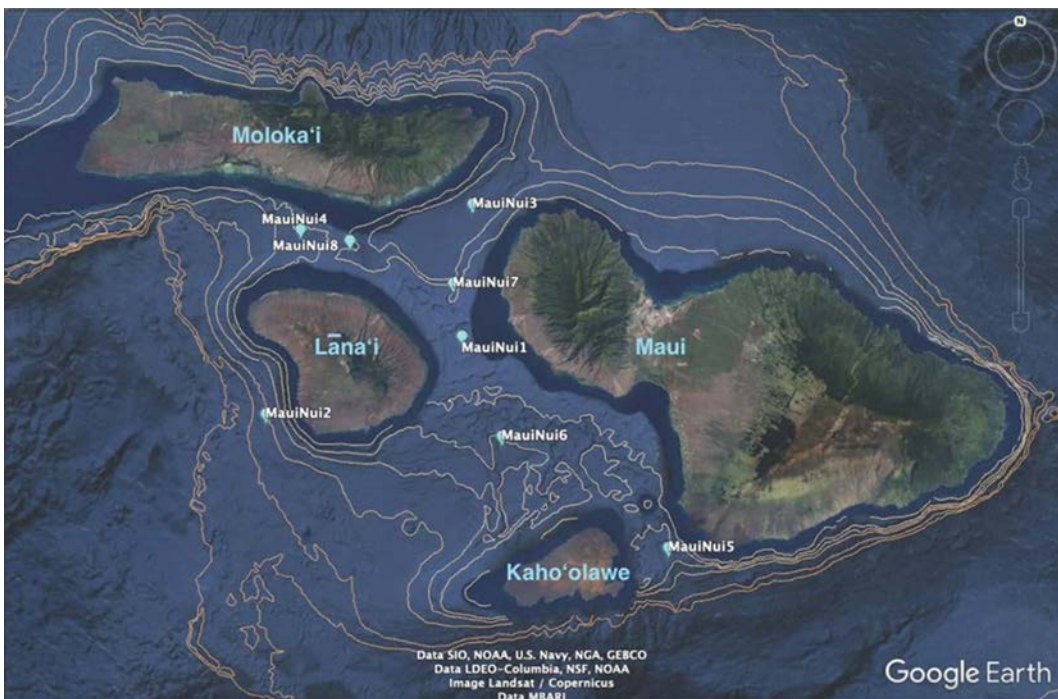

Figure 1. Eight Ecological Acoustic Recorder (EAR) sites in the Maui Nui region of Maui, Lana'i, Moloka'i, and Kaho'olawe. All EARs were deployed between 2015 and 2016 for up to 3 months per deployment. The EAR at MauiNui4 malfunctioned and did not record any data during its deployment. The EAR was moved to site MauiNui8 for a subsequent deployment. Isobaths are shown at 100 m intervals, with the deepest contour indicating the 700 m isobath.

analyzed visually as spectrograms using the Matlab-based program, *Triton* (Wiggins 2007). A trained analyst scanned spectrograms for the presence of dolphin whistles using a 10-second display window and 32 kHz bandwidth. If whistles were detected, the file was classified based on the fundamental frequency of the whistles as either low frequency (LF; all energy <10 kHz), high frequency (HF; all energy >10 kHz), or high frequency and low frequency (HFLF), a transitional ambiguous category with whistle energy both above and below 10 kHz. Low frequency whistles are indicative of the presence of larger bodied species, while high frequency whistles are indicative of the presence of one or more smaller species of odontocetes (Steiner 1981, Wang et al. 1995, Azzolin et al. 2014). Files designated "HFLF" may either indicate the presence of both large and smaller bodied species or a single species producing whistles of frequencies across the 10 kHz threshold. Each hour containing dolphin whistles was then categorized based on the classification of the individual whistle files. When an hour contained an equal number of both low and high frequency whistle files or HFLF whistles, the hour was considered ambiguous and classified as HFLF.

The arithmetic means of positive whistle hours per day for each whistle type by EAR site were first calculated and plotted by distance to the 700 m isobath. Then, to examine overall diel trends in the occurrence of high and low frequency whistles, HF, LF, and HFLF whistle hours were pooled across EAR sites, which was considered appropriate given the assumed independence of the signals, as described previously in the methods. In addition, data was pooled across different time periods, as seasonality was likely not a significant factor influencing dolphin presence due to the fact that sea surface temperatures undergo minimal fluctuations throughout the year around the Hawaiian Islands (Flament et al. 1996). In addition, little seasonal variation in the occurrence of odontocetes around the Islands has been documented (Baird et al. 2013), with only false killer whales exhibiting some seasonal variability in their spatial movements (Baird et al. 2019).

Histograms were created and visually assessed for the percentage of positive whistle hours for each whistle type for each hour of the day (0000–2300). To account for proximity to the 700 m isobath in diel variation, EAR sites were also binned into one of the following proximity groups: "Near" (0–15 km from the 700 m isobath), "Mid" (16–31 km), and "Far" (32+ km). The ranges of each group allow for maximum replication within each group and a high probability that detected whistles originated from dolphins within those proximity areas. The percentage of positive whistle hours for HF, LF, and HFLF whistles from each group by hour of the day were again visually examined using histograms. To examine the statistical relationship between the count of night versus day dolphin detections, only three hours in the middle of the night (2300–0159) were compared with three hours in the middle of the day (1100–1359). This was to ensure that the potential transition periods of dawn and dusk when spinner dolphins are transiting to and from resting bays did not confound the diel analysis. The observed hours with whistle detections for both the night and day periods were compared to an expected 1:1 ratio by whistle type and by proximity group using a two-tailed G-test using Yates' continuity correction. Significance was set at 0.05.

To validate the assumption that low frequency whistles were indicative of the presence of larger species and that high frequency whistles were indicative of smaller species, a subset of whistles were classified using the Real-Time Odontocete Call Classification Algorithm (ROCCA) (Oswald et al. 2007). ROCCA is used to extract time-frequency contours of delphinid whistles and measure their features, which function as inputs for a random forest-based classifier used to identify each whistle to a species (Oswald and Oswald 2013). Whistle classifications are then grouped by a user-defined "encounter" of dolphins, and the overall species encounter classification is determined based on the summed results of all whistle classifications within that encounter.

Two EAR deployments with low ambient noise levels and a high rate of whistle

detections per encounter were selected to subsample using ROCCA. For this analysis, an encounter was defined as an hour of the day during which dolphins were present and whistling. Encounters were excluded from the analysis if fewer than 20 whistles were present within the encounter. In addition, if fewer than 20 whistles were present between gaps of 30 or more minutes within the encounter, the encounter was also excluded. If more than 40 whistles occurred within an encounter, whistle files were randomly chosen for analysis without replacement until the 40-whistle threshold was crossed. All low frequency whistle encounters in these two data sets were analyzed using ROCCA. Ten high frequency and four ambiguous (HFLF) encounters were also randomly selected for classification.

RESULTS

In total, 77,760 files (6,480 hours) were recorded from six of the eight sites. Data from EAR site MauiNui4 were excluded from statistical analyses, as a data set of 6 days was considered too small to properly represent dolphin occurrence at that site. Considered hourly, 1,491 hours of recordings (23%) contained whistle detections. When examined by whistle type, 1,007 hours (68%) of total positive whistle hours contained HF whistles, 263 hours (18%) contained LF whistles, and 221 hours (15%) contained HFLF whistles. Average daily HF whistle hours were higher than average daily LF and HFLF positive whistle hours across all EAR sites, although there was considerable overlap in the standard deviations of each whistle type (Figure 2). Given that HFLF whistle hours made up the
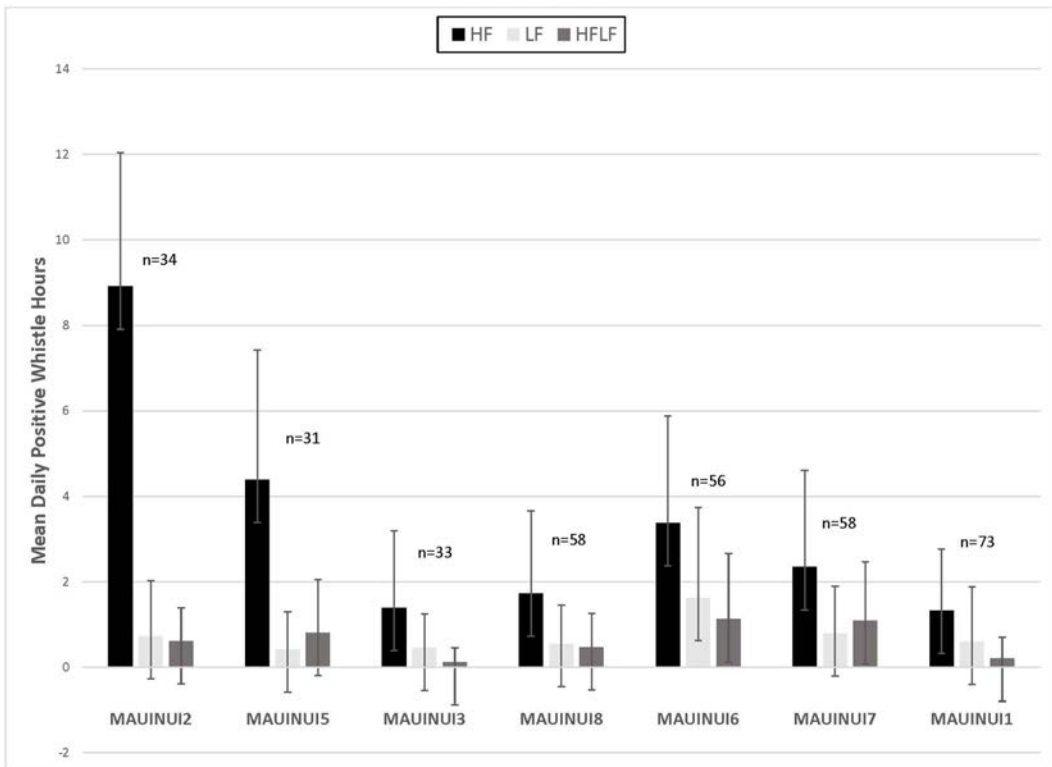

FIGURE 2. Mean number of hours per day with HF, LF, and HFLF whistles for each EAR site, excluding MauiNui4. Standard deviation bars are included. Sample sizes indicate the number of days that an EAR recorded at each site. Sites are arranged from left to right by increasing distance to the 700 m isobath.

smallest proportion of total whistle hours and could not be clearly attributed to either a large or smaller odontocete species, this whistle category was excluded from any statistical analyses.

When percentage of hours with each whistle type were examined relative to hour of day (Figure 3), analysis of HF whistle hours pooled across all EAR sites revealed strong differences in nighttime versus daytime detections, with fewer detections made during the day. Gradual changes in detections of HF whistles occurred during the dawn and dusk transition hours, with minimum detections at hour 1300 HST. The same pattern was also observed for HFLF hours, which perhaps suggests that a large proportion of these inconclusive whistle detections were in fact produced by smaller-bodied, HF-whistling species. In contrast, there was little diel

pattern for LF detections across all EAR sites. A slight dip in detections occurred during the midday hours but substantial variability exists during both daytime and nighttime hours.

When diel trends at Maui Nui EAR sites were further examined based on proximity to the 700 m isobath, patterns of HF whistle hours recorded at the "Near" (Figure 4A, $n = 434$) and "Mid" (Figure 4B, $n = 338$) sites were generally similar to those for the pooled HF whistle hours. However, the trend became less apparent for sites "Far" from the 700 m isobath (Figure 4C, $n = 338$), with little apparent difference in detection counts between night and day hours. When tested statistically against the expectation of a 1:1 ratio of night to day whistle hours, there was a significantly greater proportion of nighttime HF hours for the "Near" and "Mid"
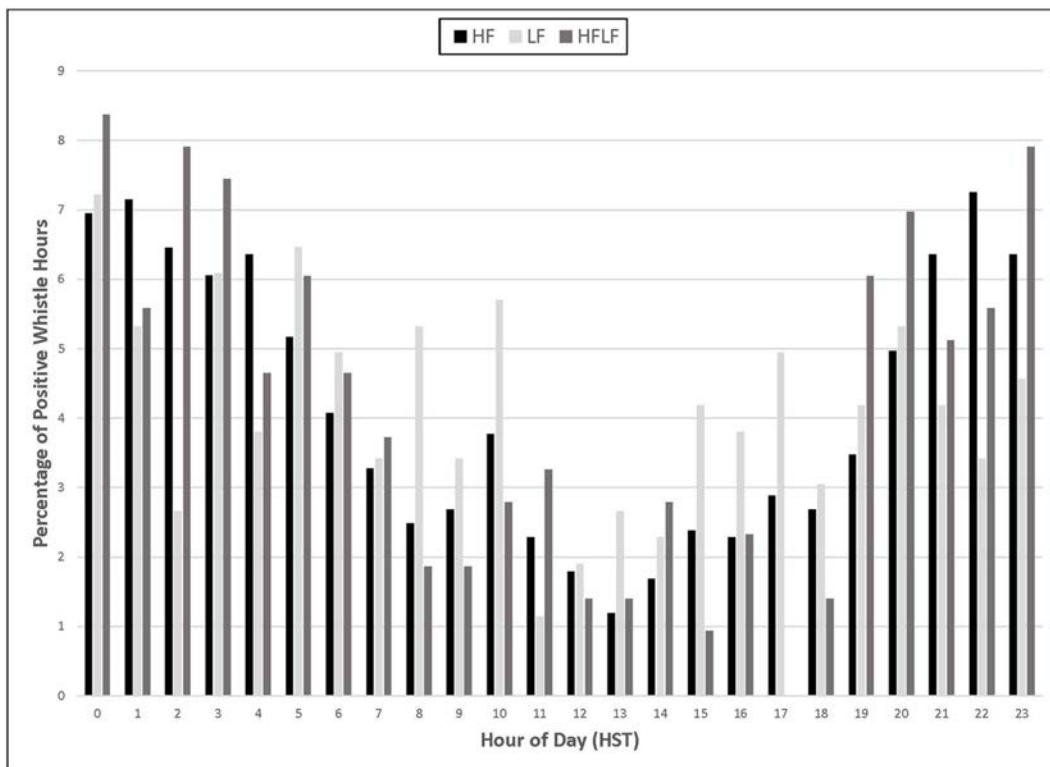

FIGURE 3. Percentage of positive whistle hours with HF, LF, and HFLF whistle spooled across all EAR sites, excluding MauiNui4, by hour of day. (Total HF whistle hours = 1,007; total LF whistle hours = 263; total HFLF whistle hours = 215)
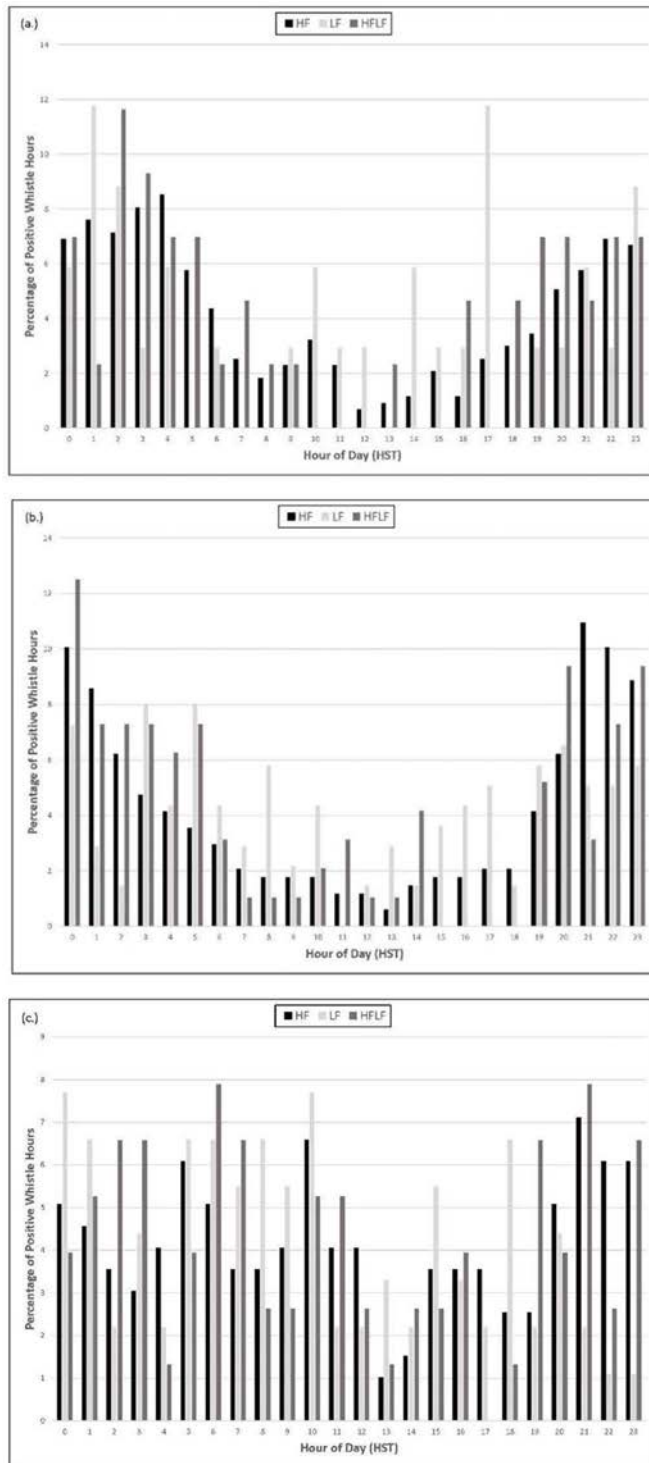
FIGURE 4. Percentage of positive whistle hours with HF, LF, and HFLF whistles by hour of day at (*A*) "Near" sites, 0–15 km from 700 m isobath (MauiNui2, MauiNui5, Total HF whistle hours = 434; total LF whistle hours = 34; total HFLF whistle hours = 43), (*B*) "Mid" sites, 16–31 km from isobath (MauiNui3, MauiNui6, MauiNui8, Total HF whistle hours = 338; total LF whistle hours = 138; total HFLF whistle hours = 96), and (*C*) "Far" sites, greater than 32 km from isobath (MauiNui1, MauiNui7, Total HF whistle hours = 197; total LF whistle hours = 91; total HFLF whistle hours = 76).

categories than day hours (Table 3). However, for the "Far" category, there was no significant difference between the proportion of daytime to nighttime whistle hours to a 1:1 ratio, which supports the apparent lack of a diel trend observed in the "Far" histogram. Once again, the same patterns were generally observed for HFLF hours, providing further evidence that this ambiguous category may have been comprised largely of HF whistles.

In contrast, counts of LF whistle hours at each binned distance showed fairly consistent variability throughout the daytime and nighttime. The counts of nighttime and daytime LF whistle detections (averaged hourly) were also not significantly different from a 1:1 ratio for any of the distance categories with the exception of the "Mid" bin, which had significantly more night than day detections. The lack of significance for the "Near" and "Far" bins for LF whistles further corroborates the variable diel pattern of detections observed in each LF histogram.

Based on ROCCA analyses of encounters from MauiNui2 and MauiNui5, those manually and visually classified as "LF" ($n = 30$) resulted in a definitive species classification of false killer whale for all encounters except for one from MauiNui2, which was classified as

short-finned pilot whale. Thus, encounters containing whistles with the majority of their energy below 10 kHz indicate the presence of these two larger species. For the "HF" encounters ($n = 20$), nine were classified as spinner dolphin, 10 as bottlenose dolphin, and one as pantropical spotted dolphin. All encounters containing whistles of a frequency mostly above 10 kHz were thus classified as these three smaller-bodied odontocetes. Finally, not surprisingly, analysis of the ambiguous HFLF encounters produced species classifications of both large and smaller odontocetes. Of the eight HFLF encounters analyzed, four were classified as false killer whale and four were categorized as bottlenose dolphin. The equal classification of small and large odontocete species for HFLF whistles reaffirms the transition and somewhat ambiguous nature of this whistle category.

DISCUSSION

The acoustic evidence presented in this preliminary study indicates that diel patterns of HF and LF whistle detections differ by whistle type and vary spatially in proximity to the 700 m isobath around the Maui Nui islands. HF whistling dolphins exhibited clear

TABLE 3

Summary of G-Test with Yates Continuity Correction Results for Counts of HF and LF Whistle Hours During the Night (2300–0159) and Day (1100–1359) by Proximity to 700 m Isobath Bin

Whistle Type	EAR Site	Total Combined Hours Recorded	Proximity to 700 m Isobath Bin	Night (2300–0159)	Day (1100–1359)	G-Score	*P*-Value (Two-Tailed)
HF	MauiNui2, MauiNui5	1560	Near	92	17	55.059	<<0.05*
	MauiNui3, MauiNui6, MauiNui8	3528	Mid	93	10	74.947	<<0.05*
	MauiNui1, MauiNui7	3144	Far	31	18	2.969	0.085
LF	MauiNui2, MauiNui5	1560	Near	9	6	0.267	0.303
	MauiNui3, MauiNui6, MauiNui8	3528	Mid	22	6	8.472	<<0.05*
	MauiNui1, MauiNui7	3144	Far	14	7	1.783	0.187

Observed counts were compared to an expected 1:1 ratio of day to night counts. Significant results are indicated with a *.

diel trends, with greater detections at night than day, particularly near the deeper waters. In contrast, LF whistling dolphins showed little diel pattern, regardless of location. The two whistling cohorts generally matched with the body size cohorts, as ROCCA analyses showed that HF dolphin whistles belonged to bottlenose dolphins and *Stenella* species, while all LF dolphins were classified as large odontocetes, with false killer whales representing the majority of detections.

Given that prey availability is one of the strongest factors driving odontocete spatial patterns (e.g., Acevedo-Gutiérrez et al. 1997, 1997, Richardson et al. 2013), the results from this passive acoustic study likely reflect differences in prey distributions and/or prey capture strategies among the two cohorts around Maui Nui. Along the steep slopes of the Hawaiian Islands, the 700 m contour is closely associated with the MBCL, which ranges from depths of 400 to 700 m and extends horizontally many kilometers during daytime hours (Reid et al. 1991, Benoit-Bird and Au 2003). Cyclical differences in habitat use by smaller dolphins on a daily scale coincides with the diel migration of micronekton in the MBCL, as spinner dolphins time their foraging with the rise of organisms in the evening (Norris and Dohl 1980, Benoit-Bird 2004). This diel trend was strong at EAR sites closest to the 700 m isobath, but was also clearly apparent at EAR sites up to 30 km inshore from the isobath, reflecting that *Stenella* species may be foraging on the MBCL across a 20 to 30 km area at night around Maui Nui. For sites farthest away from the 700 m isobath, little diel variation existed in the detection of smaller odontocetes, and so these sites may be used for transiting to and from daytime resting bays (Lammers 2004, Thorne et al. 2012, Stack et al. 2020) or perhaps opportunistic foraging.

It is important to note that HF whistles were also classified by ROCCA as bottlenose dolphins, a mid-sized odontocete which consumes both shallow reef fish during the day and species likely associated with the MBCL at night (Baird 2016). Given that bottlenose dolphins are one of the most commonly sighted dolphin species in shallow Hawaiian waters (Baird 2016) and thus likely frequently detected on EARs, they may be following similar daily distribution patterns to those of the *Stenella* species. The other mid-size odontocete that occasionally passes through Maui Nui, the melon-headed whale, produces tonal signals with fundamental frequencies that range from 890 Hz to 23.5 kHz (Frankel and Yin 2010) but is not currently included in the ROCCA classifier algorithm (Oswald et al. 2003). Melon-headed whales are not commonly sighted in the region (Baird 2016), as the individuals that do transit through are likely of the resident Big Island stock, and so it is unlikely that any signals detected during this study were produced by melon-headed whales. Additionally, any melon-headed whale signals detected during visual spectrogram scans would likely have been classified as ambiguous HFLF whistles.

In contrast with the HF-whistling species, the larger, LF-whistling false killer whales and short-finned pilot whales exhibited little diel variation in their spatial occurrence around Maui Nui. This held true when LF whistle hours were assessed across all EAR sites as well as at those EAR sites closest and furthest from the 700 m isobath. Both large species are known to pursue prey during daytime and nighttime hours, with pilot whales possibly representing most of the LF detections near shelf waters as they pursue cephalopods known to feed on the MBCL (Pauly 1998, Aguilar Soto et al. 2008, Abecassis et al. 2015, Owen et al. 2019). Conversely, LF whistle hours at EAR sites furthest from the 700 m isobath may represent false killer whales, which prefer mahi mahi (*Coryphaena hippurus*) as prey and are more frequently sighted in depths up to 500 m in insular Hawaiian waters (Baird et al. 2013). However, at "Mid" EAR sites between 16 and 31 km from the isobath, there were significantly more LF detections at night than during the day. The larger species may therefore be tracking prey associated with the MBCL as it moves in toward shore at night, or perhaps be driven by an extrinsic factor such as vessel avoidance. With such a small sample size of LF detections, confounded by potential greater propagation distances of these low frequency signals, it

is difficult to definitively assess large odontocete spatial occurrence throughout the day in insular Maui Nui waters. As such, a more concerted effort to understand habitat use by insular short-finned pilot and false killer whales in the region is needed, perhaps with a dual PAM and satellite-tagging approach.

This study provides the first step in utilizing PAM methods to reveal insular odontocete distributions around the Maui Nui islands. This information will help inform best management practices that account for interspecies variation in use of the shallow basin. It also may serve as a model to understanding variation in the distribution of insular populations of odontocetes around other tropical Pacific islands. While other intrinsic factors such as reproductive opportunities may influence occurrence across a broader temporal scale, it is likely that around Maui Nui, cyclical, diel spatial patterns of dolphin occurrence are predominately linked with foraging needs. For spinner dolphins, diel patterns are also driven by the need to rest during the day in shallow resting bays (Lammers 2004, Thorne et al. 2012, Tyne et al. 2015), which reflects the importance of considering interspecies differences in resource needs when examining differences in spatial patterns.

With these relatively low-cost, low-effort PAM approaches, some caveats do exist when analyzing acoustic data from a biological perspective. These include the fact that, even though signals are considered an appropriate proxy for dolphin presence (Rankin et al. 2008, Richardson et al. 2013), dolphins do not constantly produce whistles. Echolocation signals are in fact likely a better direct proxy for foraging behavior, yet with no existing species classifier for clicks, assessing the presence of echolocation in the acoustic files did not align with the purposes of this study. Whistle rates of dolphins may also be influenced by behavioral state or group size (Quick et al. 2017). In addition, the transmission distance of whistles varies with numerous factors, including water depth, benthic habitat, frequency, and source level (Nowacek et al. 2001), and so it is nearly impossible to determine the exact distance of a signaling dolphin to the recorder. In particular for this study, acoustic detections were only analyzed on a daily temporal scale to assess odontocete occurrence. Thus, many other factors, such as lunar, seasonality, and annual variation, should be modeled with respect to the detection of different whistle types to provide a comprehensive understanding of the distribution of Maui Nui insular odontocete populations, particularly as it relates to spatial patterns of intense human activity in the region, such as recreational fishing and dolphin-watching tour operations.

ETHICS

No ethical approval was required to conduct the fieldwork for this study. No animal subjects or tissues were used.

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