Vol. 629: 193–206, 2019
https://doi.org/10.3354/meps13123

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published October 24

Lunar cycles influence the diving behavior and habitat use of short-finned pilot whales around the main Hawaiian Islands

Kylie Owen[1,2,*], Russel D. Andrews[1,3,4], Robin W. Baird[5], Gregory S. Schorr[4,5], Daniel L. Webster[5]

[1]Alaska SeaLife Center, Seward, Alaska 99664, USA
[2]Aquatic Megafauna Research Unit, School of Veterinary and Life Sciences, Murdoch University, Murdoch, Western Australia, 6150, Australia
[3]School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA
[4]Marine Ecology and Telemetry Research, 2468 Camp McKenzie Trail NW, Seabeck, Washington 98380, USA
[5]Cascadia Research Collective, 218½ W. 4th Avenue, Olympia, Washington 98501, USA

ABSTRACT: The availability of light, both solar and lunar, is likely to influence the behavior of vertically migrating aquatic animals and their predators. However, the influence of light level on the diving behavior and habitat use of deep-diving cetaceans is not well understood. We used data from 28 depth-transmitting satellite tags deployed on short-finned pilot whales *Globicephala macrorhynchus* around the main Hawaiian Islands to examine movements and diving behavior in relation to lunar cycles and oceanographic season. During a full moon, dives were deeper (48.1%) and longer (16.7%) than during a new moon. This change appeared to be driven primarily by an increase (25.2%) in the depth of deep dives (>200 m) completed at night and an increase in the proportion of deeper daytime and twilight dives during a full moon. Dives occurred a mean of 18.3 km farther offshore (more than twice as far from shore) during a full moon compared to a new moon. During the oceanographic season with the shortest day length (fall), dives were shallower (25.4%) and shorter (14.2%) than seasons with longer days (summer). This suggests that changes in light level, both solar and lunar, affect the depth of prey targeted by pilot whales, which in turn influences pilot whale diving behavior and distribution. Future research should determine how these changes influence the feeding success and energetics of pilot whales.

KEY WORDS: Diel migration · Foraging · *Globicephala macrorhynchus* · Lunar cycle · Oceanographic season · Solar cycle · Spatial use · Tagging · Temporal variability

1. INTRODUCTION

Understanding temporal patterns across multiple scales is a key challenge in ecological studies (Levin 1992). Animals are exposed to daily, monthly, seasonal, and inter-annual fluctuations in their environment that can influence their behavior and ability to successfully locate resources. Consequently, to fully understand how the behavior of an animal is influenced by the environment, its behavior must be examined at multiple scales (Fahrig 1992, Grémillet & Boulinier 2009, Mayor et al. 2009). However, in many systems, studying the factors influencing animal behavior over long time scales is difficult due to a lack of data. This is especially the case in marine systems, where observation of animal behavior is more challenging.

In the marine environment, zooplankton that undertake diel vertical migrations provide a valuable resource for many predators. These predators

---

*Corresponding author: kylie.owen@uqconnect.edu.au form the sound scattering layers observed to migrate closer to the surface during the nighttime (Hays 2003) and are prey for higher trophic level consumers. Consequently, the behavior and vertical movement of zooplankton has a strong influence on the behavior of a range of other marine species (Hays 2003). One of the strongest factors influencing the behavior of vertically migrating zooplankton is light (Ringelberg 1995), which influences predation risk from visual predators (Zaret & Suffern 1976). During periods of greater light availability, such as during a full moon, vertically migrating animals have been shown to spend more time in deeper water (Clarke 1973, Blaxter 1974, Hays 1995, Pinot & Jansa 2001). In some areas, the depth of sound scattering layers has been shown to change by hundreds of meters throughout the lunar cycle, likely due to animals following specific isolumes (Boden & Kampa 1967) that can also be hundreds of meters deeper during a full moon compared to a new moon (Clarke & Denton 1962). In response, many predators including sharks (Graham et al. 2006), pinnipeds (Horning & Trillmich 1999, Lea et al. 2010, Sterling et al. 2014), and seabirds (Yamamoto et al. 2008) have been shown to vary their behavior over lunar cycles.

For air-breathing predators, diving incurs a cost (Boyd 1997, Kooyman & Ponganis 1998), so changes in the depth distribution of their prey due to lunar cycles or day length are likely to influence the energetics of foraging behavior (Benoit-Bird et al. 2009). For smaller species or juveniles, there is also the possibility that the depth of their prey moves below their physiological dive capacity for longer periods, reducing the amount of time available to forage (Horning & Trillmich 1999, Lea et al. 2010). Many cetacean species have evolved to depend on prey in the sound scattering layers, and unlike other air breathing predators that rely on these layers, toothed cetaceans can use echolocation to detect prey when light levels are reduced (Au et al. 2013). Therefore, toothed cetaceans may not be as bound by changes in light level to successfully detect prey as other predators. However, an understanding of the impact that lunar illumination or seasonal light changes have on the diving behavior of cetaceans remains limited.

Pilot whales *Globicephala* sp. have evolved to exploit deep prey in the sound scattering layer (Baird et al. 2002, Heide-Jørgensen et al. 2002, Aguilar Soto et al. 2008, Alves et al. 2013, Abecassis et al. 2015). Much of what is known about pilot whale diving behavior relates to the description of daily patterns. During the day, pilot whales typically spend a greater amount of time at the surface, interspersed with deeper dives to ~800 m. During the night, they dive more frequently to depths of ~400 m to access their vertically migrating prey (Baird et al. 2002, Heide-Jørgensen et al. 2002, Aguilar Soto et al. 2008, Alves et al. 2013, Baird 2016). Around the Hawaiian Islands, short-finned pilot whales *G. macrorhynchus* are thought to target prey, primarily squid, in the mesopelagic boundary community (Abecassis et al. 2015). This is a distinct resident community of micronekton that occurs where mesopelagic waters encroach on the upper slope of the islands, typically between 400 and 1200 m during the day (Reid et al. 1991). The diving behavior of the species in this area has not been described in detail. In addition, most information on the diving behavior of the species worldwide has come from short-term archival tags, with data provided for a period of hours for each individual (e.g. Aguilar Soto et al. 2008, Alves et al. 2013, Aoki et al. 2013). This has limited the understanding of the factors that may influence longer-term diving patterns and behavior. Recent development of biotelemetry devices that transmit information on the diving behavior of individuals over longer time periods provided an opportunity to address this question.

The aim of this study was to describe the diving behavior of short-finned pilot whales around the main Hawaiian Islands and to determine whether light level, either lunar or solar (related to oceanographic season), influences diving behavior at long temporal scales. We also assessed distance from shore as a measure of habitat use because prey of pilot whales associated with the sound scattering layer may also make movements inshore and offshore associated with light levels (Reid et al. 1991). It was hypothesized that dive depth would increase during periods of greater light (lunar or solar) availability.

2. MATERIALS AND METHODS

2.1. Tagging operations

Tagging operations were conducted off the main Hawaiian Islands (Hawaiʻi, Oʻahu, and Kauaʻi) from October 2009 to February 2016 as part of a long-term study of odontocetes in Hawaiʻi (Baird 2016). A Dan-Inject pneumatic projector (Model J.M. Special 25, Dan-Inject) was used to deploy tags onto the dorsal fin or base of the dorsal fin of short-finned pilot whales *Globicephala macrorhynchus*. Tag electronics remained external to skin and were based on the SPLASH10 transmitters (MK10-A, Wildlife Computers), designed to transmit both horizontal and vertical movement of the animals via the Argos system. Tags were attached using the Low Impact Minimally Percutaneous External Electronics Transmitter (LIMPET) system (Andrews et al. 2008), attached with 2 darts designed to penetrate a maximum of 6.8 cm. Tags were programmed to transmit dive and surfacing data in the form of a Behavior Log where the start and end time of each dive and surface period was logged, as well as the maximum depth reached during the dive. To minimize gaps in dive and surface periods caused by limitations of transmissions to the satellites, tags were programmed so that dives were defined as deeper than 30 m and longer than 30 s, with periods shallower categorized as surfacing periods. In this study, we considered dives deeper than 200 m to be deep dives. For each tag, the functionality of the pressure sensor was checked by assessing sensor data reported within the status messages sent periodically by the tag.

Tagged and companion whales were photographed to determine sex and population identity. In Hawai‘i, there are both open-ocean (pelagic) and insular pilot whales, with the insular population divided into a number of distinct communities (Mahaffy et al. 2015, Baird 2016, Van Cise et al. 2017). Each tagged whale was assigned to a specific population (pelagic, insular), and within the insular population to 1 of 3 communities (western, central, eastern, or unknown) based on a combination of association patterns using photo-identification as well as spatial movement patterns. The gender of the whales was determined in a variety of ways: genetically for 8 individuals (involved in 9 deployments) following the methods of Morin et al. (2005); based on field assessment of relative size and the presence of secondary sexual characteristics (i.e. dorsal fin size) noted at the time of tagging or from subsequent encounters; and, in the case of females, the presence of small calves in close association at some point during the individuals' sighting history.

2.2. Data processing

Positions received via the Argos system were processed by Argos using the Kalman smoothed function (Lopez et al. 2015). We then filtered positions using the Distance, Angle and Rate filter of the Douglas Argos Filter (Douglas et al. 2012) within Movebank (Kranstauber et al. 2011). This filter uses an algorithm that identifies unlikely positions of the animal based on biologically realistic movement rates and the assumption that an animal is unlikely to move a large distance in one direction and then immediately return to a previous location. The upper limit on movement rate that an animal could sustain for a period of hours (MINRATE) was set to 15 km h^{-1}, and the maximum distance that an animal was likely to move between consecutive locations (MAXREDUN) was set to 3 km. The tolerance level for turning angles (RATECOEF) was set to 25, which is less likely to allow for acute turning angles along the track (Douglas et al. 2012). Positions with an Argos-assigned location quality class of 2 or 3 were always retained for data analysis. All filtered positions were linearly interpolated in the adehabitatLT package (Calenge 2015) in R (v.3.1.3) (R Development Core Team 2015) to provide a position every 10 min for each deployment. Each dive was assigned the closest interpolated position according to the start time of the dive.

The function 'lunar.8phases' within the lunar package (Lazaridis 2015) in R was used to determine the lunar phase for each dive. The times of the month with similar light levels were grouped (i.e. waxing and waning gibbous = gibbous, waxing and waning crescent = crescent, and first quarter and third quarter = quarter). Oceanographic seasons were defined as Fall (November to January), Winter (February to April), Spring (May to July), and Summer (August to October), following Flament et al. (1996). In addition, the period of the day (daytime, twilight, or nighttime) for each dive was determined using the 'sunriset' and 'crepuscule' functions within the maptools package (Luque et al. 2015) in R. The twilight period was defined as the times from when the sun was 18° below the horizon until sunrise and from sunset until the sun was again 18° below the horizon. The length of day was defined by calculating the number of hours between sunrise and sunset. Each dive was then annotated with data on the distance from the coast and bathymetry (NOAA ETOPO1 Global Relief Model) using the EnvData system (Dodge et al. 2013) within Movebank (Kranstauber et al. 2011).

2.3. Data analysis

The response variables (dive depth, dive duration, and distance to the coast) were plotted against a range of distribution options using the 'quantile-comparison plot (qqp)' function within the car package (Fox & Weisberg 2019) in R, in order to determine which type of distribution best described them. As the variables displayed a normal distribution (in some cases [i.e. mean dive depth] with a log transformation), a linear mixed model (LMM) was used to determine whether the response variables were influenced by social (sex, population, and community) and environmental variables (lunar phase, oceanographic season, and day length). Whale identity was added as a random effect to the model, given that multiple dives completed by a single animal are not independent. The nlme package (Pinheiro et al. 2013) in R was used with a significance level of $\alpha = 0.05$. Prior to running the model, the variables were assessed for collinearity using the 'generalized variance inflation factor' function within the car package (Fox & Weisberg 2019) in R. Day length and oceanographic season were correlated (Fig. 1), and in some oceanographic seasons, only one community was sampled (Fig. 1). As a result, day length and community were removed from the model. This left lunar phase, oceanographic season, sex and population in the final model. Given the differences in the average distance to the coast expected between pelagic and insular animals, the 2 pelagic animals were removed from the model assessing the influence of lunar cycles and oceanographic season on the distance to coast analyses. Residuals were checked for homoscedasticity and normality. The model was checked for the presence of temporal autocorrelation using the 'Auto- and Cross- Covariance and -Correlation Function Estimation (acf)' function in R (R Development Core Team 2015). The degrees of freedom were determined based on the number of tagged animals minus the number of parameters in the model. All means are calculated across individuals and presented as mean ± standard error (SE).

3. RESULTS

In total, 34 SPLASH tags were deployed onto short-finned pilot whales *Globicephala macrorhynchus*. Six of the deployments were not included in the analyses due to issues with the pressure sensor (n = 3) or a limited duration of deployment resulting in no data received via the Argos system (n = 3). For the remaining 28 deployments, the mean deployment duration was 24.8 ± 10.6 d (minimum 4.6 d, maximum 47.1 d, and median 23.7 d; Table 1). Behavior Log data were obtained for a mean of 58.6 ± 4.9% of the deployment duration (minimum 2%, maximum 97%, median 61.3%) (Table 2). The average gap in Behavior Log coverage was 4.4 ± 2.5 h (maximum 167.4 h, median 2.9 h). However, these times were largely inflated by 2 tags that had a very limited amount of Behavior Log data transmitted (GmTag079 and GmTag082; Table 2). When excluding these tags, the average gap in Behavior Log data received was 1.0 h (maximum 77.35 h, median 0.2 h).

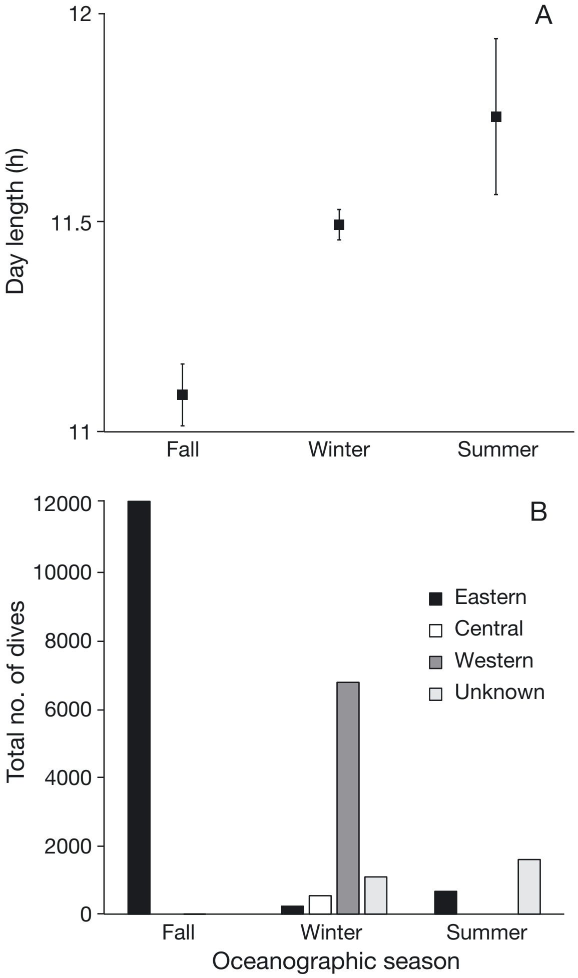

Fig. 1. The relationship between oceanographic season and (A) day length (hours) (mean ± SE) and (B) the total number of dives recorded in each oceanographic season from each community (Eastern, Central, Western, unknown) of pilot whales *Globicephala macrorhynchus* around the main Hawaiian Islands

For the 22952 dives, mean dive depth was 280.2 ± 10.8 m (maximum 1775.5 m) and mean dive duration was 9.9 ± 0.2 min (maximum 28.3 min). In contrast, mean bathymetric depth at the dive locations was 2011 ± 1284 m (minimum 871 m, maximum 5746 m). Total hours of Behavior Log data received were similar for day and night periods (43% each), whereas the remaining Behavior Log data (14%) were col-

Table 1. Tags deployed onto short-finned pilot whales *Globicephala macrorhynchus* off the main Hawaiian Islands. Animals are grouped based on the tagging location. The symbols * and ^ denote both deployments that were completed on the same individual whale. N/A: not applicable as the pelagic population is not divided into communities

TagID	Community	Population	Age class	Sex	Tag deployment date	Deployment duration (d)
Hawaiʻi						
GmTag033	Eastern	Insular	Sub-adult	Male	25 Oct 2009	42.50
GmTag034	Eastern	Insular	Sub-adult	Female	25 Oct 2009	30.12
GmTag035*	Eastern	Insular	Sub-adult	Female	31 Oct 2009	39.77
GmTag036	Eastern	Insular	Adult	Unknown	15 Dec 2009	47.07
GmTag037	Eastern	Insular	Adult	Female	15 Dec 2009	19.70
GmTag038	Eastern	Insular	Sub-adult	Male	17 Dec 2009	4.55
GmTag040	Eastern	Insular	Sub-adult	Male	18 Dec 2009	16.38
GmTag048	Eastern	Insular	Sub-adult	Male	16 Dec 2010	33.91
GmTag107*	Eastern	Insular	Sub-adult	Female	23 Nov 2014	28.40
GmTag108	Eastern	Insular	Adult	Male	24 Nov 2014	15.85
GmTag111	Eastern	Insular	Sub-adult	Male	2 Dec 2014	12.40
GmTag112	Eastern	Insular	Sub-adult	Male	4 Dec 2014	31.47
Kauaʻi						
GmTag050	Western	Insular	Adult	Male	18 Feb 2011	36.80
GmTag070^	Western	Insular	Adult	Male	8 Feb 2013	19.87
GmTag078	Eastern	Insular	Adult	Male	2 Feb 2014	12.78
GmTag079^	Western	Insular	Adult	Male	2 Feb 2014	30.48
GmTag081	Western	Insular	Adult	Male	3 Feb 2014	25.84
GmTag082	Western	Insular	Adult	Female	9 Feb 2014	30.44
GmTag114	Western	Insular	Adult	Male	8 Feb 2015	7.55
GmTag132	Unknown	Insular	Adult	Male	10 Sep 2015	18.35
GmTag133	Unknown	Insular	Adult	Male	10 Sep 2015	18.93
GmTag152	N/A	Pelagic	Adult	Unknown	12 Feb 2016	16.92
GmTag153	N/A	Pelagic	Adult	Male	13 Feb 2016	39.69
GmTag154	Western	Insular	Adult	Male	14 Feb 2016	21.23
GmTag155	Western	Insular	Adult	Male	14 Feb 2016	25.01
GmTag156	Unknown	Insular	Adult	Male	14 Feb 2016	27.21
Oʻahu						
GmTag118	Western	Insular	Adult	Male	18 Feb 2015	22.44
GmTag121	Central	Insular	Adult	Male	19 Feb 2015	18.86

lected during twilight hours. The total number of dives and the proportion of dives completed across the day, twilight, and night periods for each lunar phase and oceanographic season are shown in Fig. 2. Of all the deep (>200 m) dives, 31% were completed during the day, 58% were at night, and 11% were during twilight hours. Deep dives (n = 11740) were deeper and longer during the day (666.1 ± 16.7 m; 15.6 ± 0.2 min) compared to at night (415.5 ± 14.8 m; 12.4 ± 0.2 min), with twilight dives occurring at intermediate depths and durations (470.8 ± 17.8 m; 13.0 ± 0.2 min). Although daytime dives were deeper and longer, there were more deep dives completed at nighttime compared to daytime. Deep dives occurred all around the main Hawaiian Islands, suggesting that foraging behavior occurred in most areas the whales visited (Fig. 3).

Two animals were tagged twice during the study (Table 1). One animal was an adult male that had 2 deployments (GmTag070 and GmTag079) beginning in early February separated by ~1 yr (2013 and 2014). The mean dive depth and mean dive duration were both greater during the second deployment (330.5 m vs. 448.6 m, and 10.3 min vs. 12.2 min). This difference is possibly due to the shorter length of Behavior Log data received during the second deployment, with just over 19 h of Behavior Log data received during the 30 d deployment (Table 2). The other animal was an adult female that had 2 deployments (GmTag035 and GmTag107) separated by ~5 yr (October 2009 vs. November 2014). Mean dive depth and duration (335.0 m vs. 310.9 m and 10.3 min vs. 9.8 min) did not differ substantially between these 2 deployments. For both deployments, the same individual ID was used as a random effect in all mixed models completed in this study (see below for results), lowering the sample size for the mixed models to n = 26.

Table 2. Data coverage time in terms of % total deployment time that the received Behavior Log covered for short-finned pilot whales tagged off the main Hawaiian Islands. Details of the gaps in transmission of Behavior Log data are also presented. Animals are grouped based on the tagging location. The symbols * and ^ denote both deployments that were completed on the same individual whale. Two deployments resulted in low Behavior Log coverage, with larger gaps in data reception, and these are highlighted in grey

Tag ID	Data coverage (%)	Mean break in Behavior Log data (h)	Maximum break in data (h)
Hawai'i			
GmTag033	61.2	1.6	34.7
GmTag034	80.7	0.6	45.6
GmTag035*	70.7	1.0	29.4
GmTag036	63.7	1.4	77.4
GmTag037	61.9	1.2	20.8
GmTag038	52.7	1.2	8.3
GmTag040	82.4	0.6	16.0
GmTag048	48.7	2.0	57.2
GmTag107*	59.9	0.6	14.8
GmTag108	69.4	1.3	9.1
GmTag111	82.3	0.6	9.1
GmTag112	61.3	0.1	3.2
Kaua'i			
GmTag050	60.1	2.1	46.8
GmTag070^	88.1	0.3	8.2
GmTag078	36.0	3.9	24.0
GmTag079^	2.6	37.7	116.9
GmTag081	86.3	0.0	1.5
GmTag082	2.0	60.2	167.4
GmTag114	54.3	1.8	8.6
GmTag132	97.0	0.2	4.4
GmTag133	75.0	1.0	11.9
GmTag152	52.0	0.3	6.2
GmTag153	17.1	1.0	13.1
GmTag154	38.2	0.0	0.7
GmTag155	31.6	0.1	2.5
GmTag156	28.3	0.2	5.1
O'ahu			
GmTag118	83.3	0.2	7.4
GmTag121	93.8	2.9	16.0

Lunar phase was found to influence the dive depth (Table 3), dive duration (Table 4) and the distance to the coast (Table 5) of short-finned pilot whales around the Hawaiian Islands. Dives were significantly deeper (and longer) during a full moon compared to a new moon (Fig. 4). Dives became progressively shallower and shorter as lunar illumination decreased from a full moon towards a new moon (Tables 3 & 4, Fig. 4). During the full moon, dives were on average 112.3 m (48.1 %) deeper and 1.6 min (16.7 %) longer than during a new moon. The pattern in dive depth with lunar illumination appeared to be driven by a combination of factors. Firstly, there was an increase in the mean depth of deep dives (>200 m) during the nighttime with increasing lunar illumination (on average, deep dives were 94.0 m [~25.2 %] deeper at night during a full moon compared to a new moon; Fig. 5). Secondly, there was a reduction in the proportion of nighttime dives completed during a full moon (nighttime dives represented 54.0 % of dives during a full moon and 64.1 % of dives during a new moon), which was associated with an increase in the proportion of dives that were completed during daytime and twilight periods (when dive depth is typically greater; Fig. 2). The duration of deep dives showed a similar pattern to dive depth, in that the duration of nighttime deep dives increased with increasing lunar illumination (Fig. 5). However, the duration of deep dives did not increase to the same extent as the depth, with only a 7.2 % increase between a new and full moon (mean of 0.9 min). No pattern was evident with increasing lunar illumination for either the mean depth or duration of deep daytime and deep twilight dives (Fig. 5). During a new moon, dives were closer to the coast and moved progressively farther offshore with increasing lunar illumination (on average, dives were 18.3 km farther offshore during a full moon compared to a new moon; Table 5, Fig. 4).

Oceanographic season was found to influence the dive depth of pilot whales around the main Hawaiian Islands, but not dive duration (Tables 3 & 4). Dives were deeper in the winter (medium length days) and summer (longest days), relative to the fall (shortest days) (Fig. 6). Although dive duration followed a similar pattern (longer duration dives in winter [medium days] and summer [longest days] relative to the fall [shortest days]) (Fig. 6), this pattern was not significant. Deep (>200 m) dives were deeper and longer at all times of the day (daytime, nighttime, and twilight) in the winter and summer, relative to the fall (Fig. 7). Dives completed in the winter were also significantly farther offshore (20.3 km; 220 %) relative to dives completed in the fall (Fig. 6). However, as there was a sampling bias in communities sampled across seasons (Fig. 2), the differences in dive depth, dive duration, and distance to the coast could also be driven by differences in the movement patterns and diving behavior of the Eastern and Western communities.

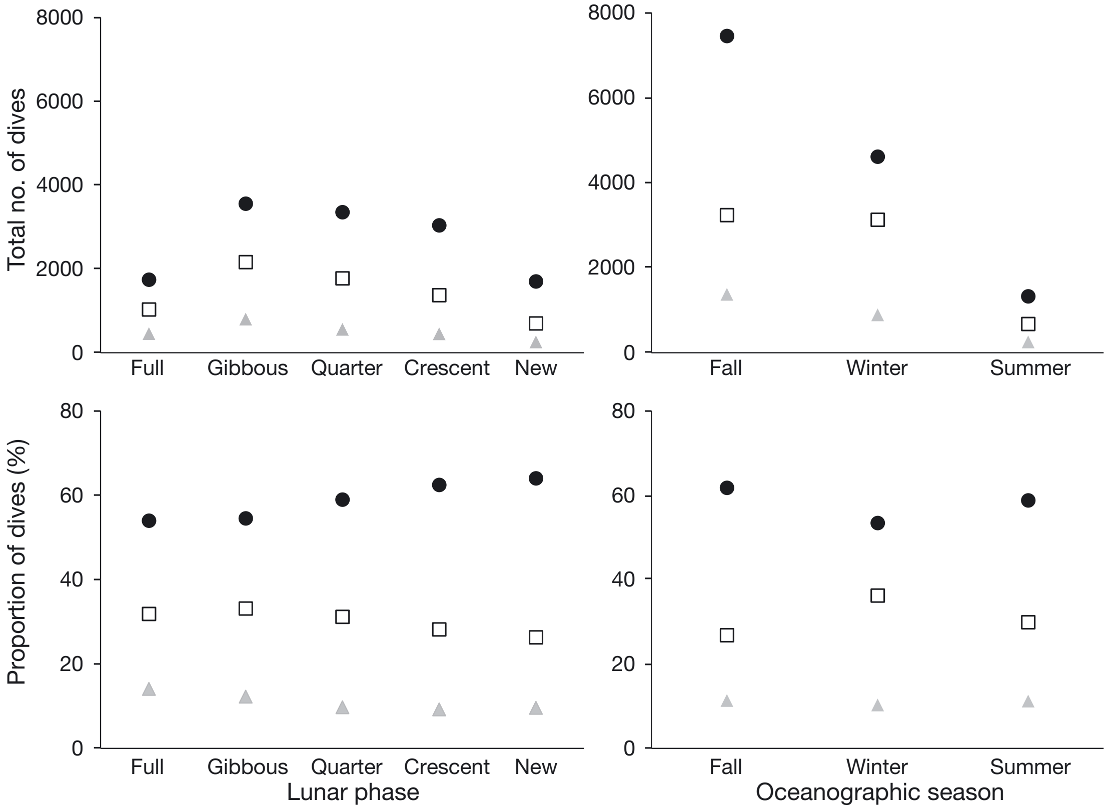

Fig. 2. Total number of dives by short-finned pilot whales around the main Hawaiian Islands across lunar phases (left) and oceanographic seasons (right) during the day (white squares), night (black circles), and twilight periods (grey triangles). The proportion of total dives (bottom) completed in each lunar phase (left) and oceanographic season (right) is a function of time of day

Mean dive depth (Table 3) and dive duration (Table 4) did not differ between the sexes or between insular and pelagic populations. Additionally, mean distance to the coast did not differ between the sexes (Table 5).

4. DISCUSSION

On a daily scale, the diving behavior of short-finned pilot whales *Globicephala macrorhynchus* around the main Hawaiian Islands was similar to what has been described for pilot whales in other parts of the world, with deeper dives during daylight hours, becoming progressively shallower through twilight into the dark hours over night (Baird et al. 2002, Heide-Jørgensen et al. 2002, Aguilar Soto et al. 2008, Alves et al. 2013). This behavior is likely to be associated with daily fluctuations in light level influencing the vertical movement of their prey, as has been previously suggested (Baird et al. 2002, Heide-Jørgensen et al. 2002, Aguilar Soto et al. 2008, Alves et al. 2013, Baird 2016). There are limited data on the diet of short-finned pilot whales worldwide, but a recent report (West et al. 2019) described the stomach contents of 5 short-finned pilot whales that stranded on Kauaʻi in 2017. Squid from 31 species made up >99% of the diet, both by number and mass, but the most prevalent squid were from the families Histioteuthidae and Onychoteuthidae. The histoteuthid *Stigmatoteuthis hoylei* was a common prey item and is a diel vertical migrator, being found in Hawaiʻi at depths between 500 and 700 m during daytime but at nighttime moving up to between 100 and 500 m, with most concentrated between 150 and 300 m (Young 1975). The Hawaiian onychotheutids are also vertical migrators (Young 1978).

In addition to day-night differences, light level also appeared to influence the diving behavior of the animals over lunar and seasonal time frames. The dives of short-finned pilot whales around the main Hawaiian Islands were deeper and longer during a full moon when lunar illumination was highest, compared to a new moon, when lunar illumination was

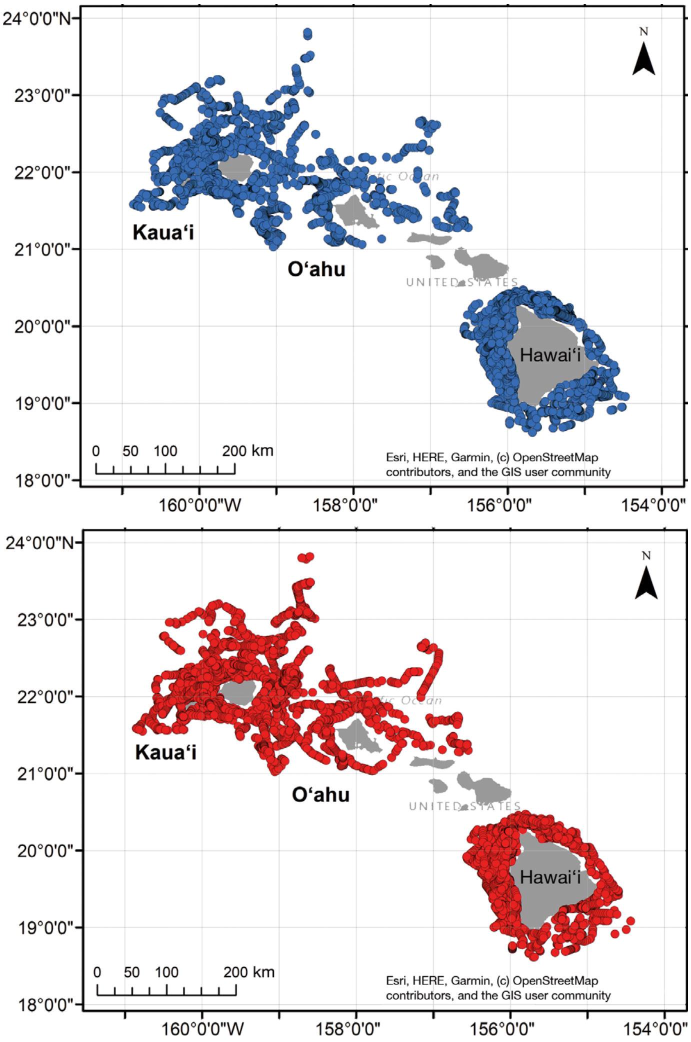

Fig. 3. Location of dives by short-finned pilot whales around the main Hawaiian Islands. There were no obvious differences in the location of shallow (<200 m) (top panel, blue dots) or deep (>200 m) (bottom panel, red dots) dives, suggesting that foraging behavior occurs all around Hawai'i

lowest (Fig. 4). Deeper dives during a full moon appeared to be driven mainly by nighttime dives becoming deeper during this time. This is expected given their vertically migrating prey are unlikely to move as shallow during the night when there is more light but may return to a similar depth during the day light hours to minimize predation. The increase in dive depth at night during a full moon also resulted in an increase in dive duration (Fig. 5). Longer dives typically require a longer recovery time at the surface (Isojunno et al. 2018), and a smaller proportion of pilot whale dives were completed at nighttime during a full moon, resulting in a greater proportion of daytime dives during a full moon.

While the mean depth of daytime dives is likely to be well within the physiological depth limit of short-finned pilot whales (the deepest dive recorded for this species is 1775.5 m, recorded in this study), deeper dives still incur a higher cost for air-breathing predators (Isojunno et al. 2018). However, deeper daytime dives may provide access to a more energy-rich prey. For example, in the Canary Islands, pilot whales complete high-speed sprints to target high-calorie and fast-moving prey predominantly during the deeper daytime dives (Aguilar Soto et al. 2008). In addition, the increase in the duration of dives (7.2%) at night during a full moon in this study was

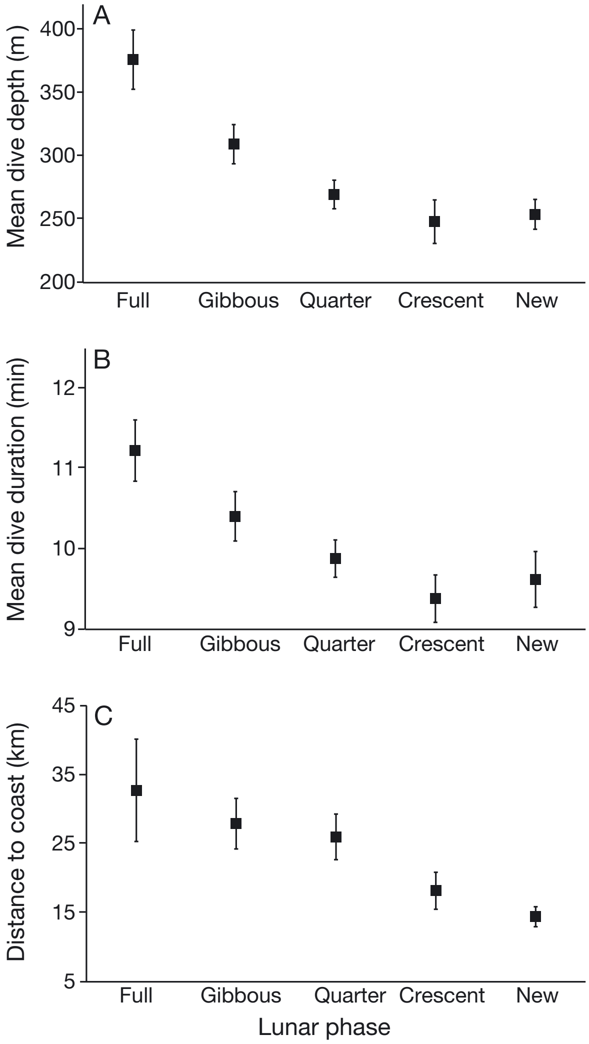

Fig. 4. Overall dive behavior (for all dives >30 m and >30 s) of short-finned pilot whales around the main Hawaiian Islands as a function of lunar phase. Diving behavior is described based on (A) mean dive depth (m), (B) mean dive duration (min), (C) and the distance to the coast (km). Lunar illumination decreases from full moon → new moon. Values are presented as mean ± SE, averaged across individuals

Table 3. Results of a linear mixed model to determine the influence of environmental and social variables on the mean dive depth (m) completed by short-finned pilot whales around the main Hawaiian Islands. Oceanographic season is defined as Fall (November to January; shortest days), Winter (February to April; medium days), and Summer (August to October; longest days)

Response variable	Estimate	SE	df	*t*	p
(Intercept)	5.43	0.14	22920	40.17	**<0.001**
Lunar phase (relative to full moon)					
Gibbous	−0.20	0.02	22920	−9.13	**<0.001**
Quarter	−0.40	0.02	22920	−17.23	**<0.001**
Crescent	−0.53	0.02	22920	−22.05	**<0.001**
New	−0.57	0.03	22920	−20.54	**<0.001**
Oceanographic season (relative to Fall)					
Winter	−0.18	0.11	22920	−1.66	0.10
Summer	−0.17	0.04	22920	−3.72	**<0.001**
Sex (relative to female)					
Male	0.14	0.15	22	0.96	0.35
Unknown	0.43	0.25	22	1.74	0.10
Population (relative to insular)					
Pelagic	−0.08	0.23	22	−0.37	0.71

Table 4. Results of a linear mixed model to determine the influence of environmental and social variables on the mean dive duration (s) completed by short-finned pilot whales around the main Hawaiian Islands. Oceanographic season as defined in Table 3

Response variable	Estimate	SE	df	*t*	p
(Intercept)	641.69	32.24	22920	19.90	**<0.001**
Lunar phase (relative to full moon)					
Gibbous	−43.04	5.49	22920	−7.84	**<0.001**
Quarter	−77.68	5.65	22920	−13.74	**<0.001**
Crescent	−107.24	5.90	22920	−18.19	**<0.001**
New	−122.21	6.85	22920	−17.84	**<0.001**
Oceanographic season (relative to Fall)					
Winter	−4.72	26.36	22920	−0.18	0.86
Summer	−18.80	11.01	22920	−1.71	0.09
Sex (relative to female)					
Male	30.01	35.54	22	0.84	0.41
Unknown	65.80	59.17	22	1.11	0.28
Population (relative to insular)					
Pelagic	−25.17	53.78	22	−0.47	0.64

not equivalent to the increase in mean dive depth observed (25.2%). This potentially indicates that the prey capture rate was greater at night during a full moon, with animals able to return to the surface sooner for a given dive depth, rather than spending more time searching for prey at depth. This response could also be due to physiological limitations preventing the pilot whales from completing longer dives. A reduction in the number of dives completed at night during a full moon could therefore be a product of greater success during each dive. It is also possible that a trade-off exists between the benefit of completing more dives to greater depth to target higher calorie prey during the day, versus completing dives to shallower depths during the night to target lower quality prey. The balance of this trade-off may be influenced by lunar illumination, with a full moon resulting in the lower-quality prey being deeper, causing a switch to pilot whales investing more time completing deeper dives during the day to target higher-quality prey. Much of this is speculative of course, and more information on the prey targeted and the success rate of each dive through daily and lunar cycles is needed to address the benefits or costs of the change in the diving behavior observed across lunar cycles.

It remains unclear whether changes in light level influences pilot whales directly, or just the behavior of their prey. It is possible that the changes we have observed are the result of pilot whales targeting prey that are themselves visual predators that are influenced by light for their own foraging success, rather than just evading predation. The histoteuthid squid preyed upon by pilot whales in Hawaiʻi are sometimes called cockeyed squids due to the asymmetry in the size, shape and positioning of their 2 eyes. Their left eye is unusually large, and in their normal body orientation, that eye is pointed upward to view objects that would be silhouetted against the dim down-welling light, while the smaller right eye is oriented downwards to view bioluminescent point sources produced by their prey (Young 1975, Thomas et al. 2017).

Around the Hawaiian Islands, animals found in the mesopelagic boundary community migrate between depths of 400 to 700 m during the day to between the surface and 400 m at night (Reid 1994). These depth ranges suggest pilot whales around Hawaiʻi are likely targeting the bottom of this layer, potentially in search of higher-calorie prey that make diving to those depths worth the energetic investment. In other parts of the world, the depths of vertical migrants vary by hundreds

Table 5. Results of a linear mixed model to determine the influence of environmental and social variables on the distance to the coast (km) of dives completed by short-finned pilot whales around the main Hawaiian Islands. Oceanographic season as defined in Table 3

Response variable	Estimate	SE	df	*t*	p
(Intercept)	2.61	0.18	21835	14.55	**<0.001**
Lunar phase (relative to full moon)					
Gibbous	−0.03	0.01	21835	−2.01	**0.04**
Quarter	−0.01	0.01	21835	−0.44	0.66
Crescent	−0.10	0.01	21835	−7.29	**<0.001**
New	−0.26	0.02	21835	−16.62	**<0.001**
Oceanographic season (relative to Fall)					
Winter	0.49	0.14	21835	3.40	**<0.001**
Summer	−0.30	0.03	21835	−11.93	**<0.001**
Sex (relative to female)					
Male	0.16	0.20	21	0.83	0.42
Unknown	−0.05	0.39	21	−0.12	0.90

of meters across lunar cycles (Clarke & Denton 1962, Boden & Kampa 1967), which is similar to the change in the depth ranges of pilot whales over the lunar cycle observed during this study. The lunar cycle has been shown to have an impact on the mesopelagic scattering layer in the upper 150 m around Hawaiʻi (Benoit-Bird et al. 2009). However, the impact of the lunar cycle on the deeper parts of the mesopelagic layer has not been well studied. It is possible that when there is more light, the whales dive deeper than normal as they are able to rely on both echolocation and vision to detect prey when light penetrates further. The light level at 150 m during a full moon has been shown to be similar to the light level at 500 m during the day (Clarke & Denton 1962). The importance of vision for prey detection and capture coupled with echolocation during periods of higher illumination has previously been discussed for several species of odontocetes (Baird 2000, Benoit-Bird et al. 2009). In addition, Blainville's beaked whales *Mesoplodon densirostris* in Hawaiʻi have also exhibited changes in diving behavior in response to lunar cycles (Henderson et al. 2016, Baird 2019), suggesting that changes in the vertical migrations of prey with the lunar cycle may influence many predators around the Hawaiian Islands. However, more needs to be understood about the changes in the depth distribution of the

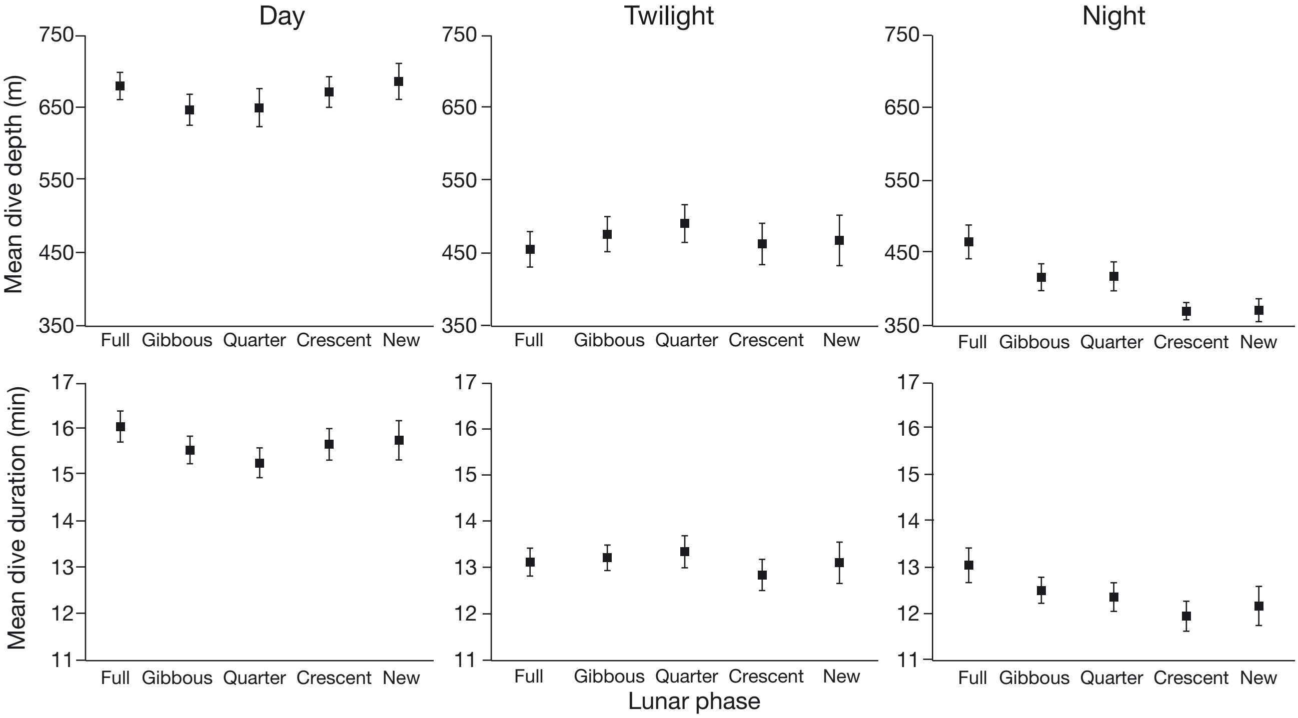

Fig. 5. Dive depth (top) and dive duration (bottom) for deep dives (>200 m) completed by short-finned pilot whales around the main Hawaiian Islands during the day (left), twilight (center), and night (right) as a function of lunar phase. Values are presented as mean ± SE, averaged across individuals

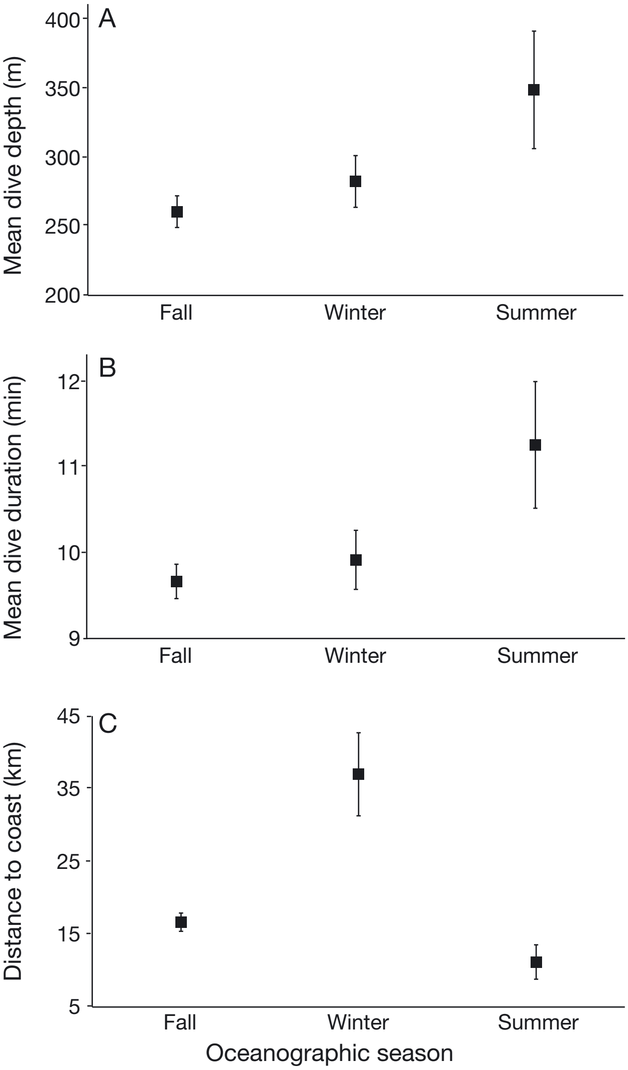

Fig. 6. Overall dive behavior (for all dives >30 m and >30 s) of short-finned pilot whales around the main Hawaiian Islands as a function of oceanographic season (Oceanographic seasons: Fall [November to January; shortest days], Winter [February to April; medium days], and Summer [August to October; longest days]). Diving behavior is described based on (A) mean dive depth (m), (B) mean dive duration (min), (C) and the distance to the coast (km). Values are presented as mean ± SE, averaged across individuals

mesopelagic layer across lunar cycles before any conclusions about the reason for deeper dives during a full moon by pilot whales can be determined.

As well as migrating vertically, the mesopelagic boundary community around the Hawaiian Islands also migrates horizontally towards shore during the night (Benoit-Bird et al. 2001). Pilot whales (Abecassis et al. 2015) and spinner dolphins *Stenella longirostris* (Benoit-Bird & Au 2003) have been shown to follow prey in the mesopelagic layer horizontally during the day/night cycle. However, the horizontal migration of the mesopelagic boundary community is thought to be consistent across seasonal and lunar cycles, although the effect of lunar phase on the horizontal movement of the layer has not been directly tested (Benoit-Bird et al. 2001). Differences of ~18 km between the diving location of pilot whales during a full moon and a new moon (Fig. 4) suggest the horizontal distribution of the prey layer does change across the lunar cycle. Further research on the movement and composition of the mesopelagic boundary community around the Hawaiian Islands over lunar cycles is needed to determine what factors might be driving the observed horizontal shift in distribution of pilot whales over the lunar cycle.

Similar to changes in lunar light levels, changes in the oceanographic season (correlated to the changes in day length) also appeared to influence the diving behavior of the pilot whales (Fig. 6). In summer (correlated with longer day length in this study), vertically migrating prey have less time to migrate during the night and may not make it to shallow depths before needing to head back to greater depths for predator protection during daylight hours (Hays 1995). This pattern should result in both the nighttime and twilight dives of the pilot whales becoming deeper as day length increases. However, this pattern was not observed, suggesting that other seasonal factors may play a role or that there may be differences in the diving behavior of the pilot whale communities around Hawaiʻi (due to the sampling bias, the Eastern community was sampled more in the Fall, and the Western community sampled more in the Winter). The role of seasonal factors or community bias is also supported by the observation that the depth of daytime dives varied across seasons/day length (Fig. 7). Deep dives completed during the day should not change with day length because the depth (light level) that prey reaches to seek shelter from predators during the day should be constant, regardless of day length. Sampling the communities over all seasons will help confirm whether the observed changes in diving behavior are primarily the result of light levels or whether other community differences or other seasonal factors, such as changes in sea temperature and seasonal prey availability, are important.

Acknowledgements. Funding for tags and field efforts was provided by the U.S. Navy (Pacific Fleet, Living Marine Resources and Office of Naval Research) and the National Marine Fisheries Service (Pacific Island Fisheries Science Center and Southwest Fisheries Science Center). We thank

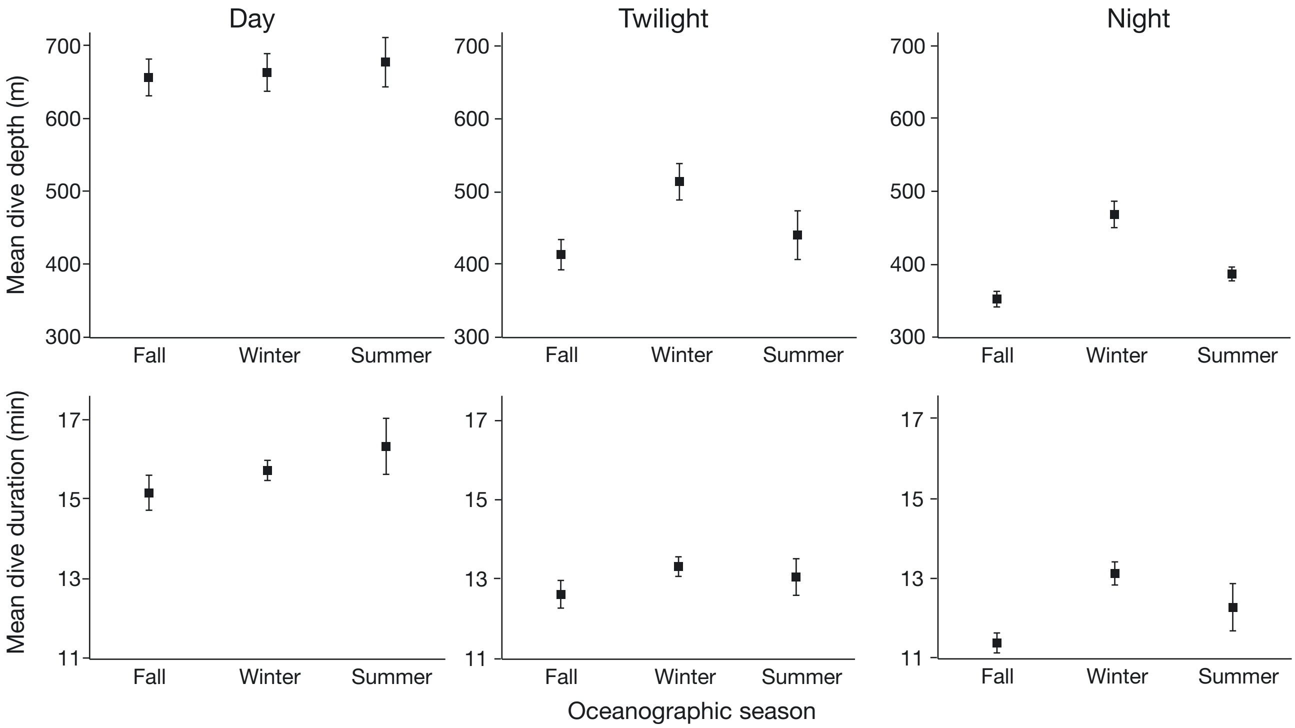

Fig. 7. Dive depth (top) and dive duration (bottom) for deep dives (>200 m) completed by short-finned pilot whales around the main Hawaiian Islands during the day (left), twilight (center), and night (right) as a function of oceanographic season (Fall [November to January; shortest days], Winter [February to April; medium days], and Summer [August to October; longest days]). Values are presented as mean ± SE, averaged across individuals

several individuals for assisting in the field, Sabre Mahaffy for identifying tagged individuals, the Southwest Fisheries Science Center for providing sex determinations from biopsied individuals, and 2 anonymous reviewers for helpful comments on the manuscript. Tagging operations were completed under permit number 731-1774 and 15330 with ethical approval from the IACUCs of the Alaska SeaLife Center and Cascadia Research Collective.

LITERATURE CITED

Abecassis M, Polovina J, Baird RW, Copeland A and others (2015) Characterizing a foraging hotspot for short-finned pilot whales and Blainville's beaked whales located off the west side of Hawai'i by using tagging and oceanographic data. PLOS ONE 10:e0142628

Aguilar Soto N, Johnson MP, Madsen PT, Diaz F, Dominguez I, Brito A, Tyack P (2008) Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). J Anim Ecol 77:936–947

Alves F, Dinis A, Ribeiro C, Nicolau C, Kaufmann M, Fortuna CM, Freitas L (2013) Daytime dive characteristics from six short-finned pilot whales *Globicephala macrorhychus* off Madeira Island. Arquipelago Life Mar Sci 31:1–8

Andrews RD, Pitman RL, Ballance LT (2008) Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. Polar Biol 31:1461–1468

Aoki K, Sakai M, Miller PJO, Visser F, Sato K (2013) Body contact and synchronous diving in long-finned pilot whales. Behav Processes 99:12–20

Au WWL, Giorli G, Chen J, Copeland A and others (2013) Nighttime foraging by deep diving echolocating odontocetes off the Hawaiian Islands of Kauai and Ni'ihau as determined by passive acoustic monitors. J Acoust Soc Am 133:3119–3127

Baird RW (2000) The killer whale: foraging specializations and group hunting. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies. University of Chicago Press, Chicago, IL, p 127–153

Baird RW (2016) The lives of Hawai'i's dolphins and whales: natural history and conservation. University of Hawai'i Press, Honolulu, HI

Baird RW (2019) Behavior and ecology of not-so-social Odontocetes: Cuvier's and Blainville's beaked whales. In: Würsig B (ed) Ethology and behavioral ecology of toothed whales and dolphins, the Odontocetes, ethology and behavioral ecology of marine mammals. Springer, Cham, p 305–329

Baird RW, Borsani JF, Hanson MB, Tyack PL (2002) Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. Mar Ecol Prog Ser 237:301–305

Benoit-Bird KJ, Au WWL (2003) Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behav Ecol Sociobiol 53:364–373

Benoit-Bird KJ, Au WWL, Brainard RE, Lammers MO (2001) Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically. Mar Ecol Prog Ser 217:1–14

Benoit-Bird KJ, Dahood AD, Würsig B (2009) Using active acoustics to compare lunar effects on predator–prey behavior in two marine mammal species. Mar Ecol Prog Ser 395:119–135

Blaxter JHS (1974) The role of light in the vertical migration of fish — a review. In: Evans GC, Bainbridge R, Rackhan O (eds) Light as an ecological factor II: 16th Symp British Ecol Soc. Blackwell Scientific Publications, Oxford, p 189–210

Boden BP, Kampa EM (1967) The influence of natural light on the vertical migrations of an animal community in the seas. Symp Zool Soc Lond 19:15–26

Boyd IL (1997) The behavioural and physiological ecology of diving. Trends Ecol Evol 12:213–217

Calenge C (2015) Analysis of animal movements in R: the adehabitatLT package. R Package version 0.3.20. https://cran.R-project.org/package=adehabitatLT

Clarke T (1973) Some aspects of the ecology of lanternfishes in the Pacific Ocean near Hawaii. Fish Bull 71:401–434

Clarke GW, Denton EJ (1962) Light and animal life. In: Hill MN (ed) The sea, Vol 1. Interscience, New York, NY, p 456–468

Dodge S, Bohrer G, Weinzierl R, Davidson SC and others (2013) The environmental-data automated track annotation (*Env-DATA*) system: linking animal tracks with environmental data. Mov Ecol 1:3

Douglas DC, Weinzierl R, Davidson SC, Kays R, Wikelski M, Bohrer G (2012) Moderating Argos location errors in animal tracking data. Methods Ecol Evol 3:999–1007

Fahrig L (1992) Relative importance of spatial and temporal scales in a patchy environment. Theor Popul Biol 41:300–314

Flament P, Kennan S, Lumpkin R, Sawyer M, Stroup ED (1996) Ocean atlas of Hawai'i. www.pacioos.hawaii.edu/education/ocean-atlas/

Fox J, Weisberg S (2019) An R companion to applied regression, v 3.0-3. Sage, Thousand Oaks, CA

Graham RT, Roberts CM, Smart JCR (2006) Diving behaviour of whale sharks in relation to a predictable food pulse. J R Soc Interface 3:109–116

Grémillet D, Boulinier T (2009) Spatial ecology and conservation of seabirds facing global climate change: a review. Mar Ecol Prog Ser 391:121–137

Hays GC (1995) Ontogenetic and seasonal variation in the diel vertical migration of the copepods *Metridia lucens* and *Metridia longa.* Limnol Oceanogr 40:1461–1465

Hays GC (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Hydrobiologia 503:163–170

Heide-Jørgensen MP, Bloch D, Stefansson E, Mikkelsen B, Ofstad LH, Dietz R (2002) Diving behaviour of long-finned pilot whales *Globimelas* around the Faroe Islands. Wildl Biol 8:307–311

Henderson EE, Martin SW, Manzano-Roth R, Matsuyama BM (2016) Occurrence and habitat use of foraging Blainville's beaked whales (*Mesoplodon densirostris*) on a U.S. Navy range in Hawaii. Aquat Mamm 42:549–562

Horning M, Trillmich F (1999) Lunar cycles in diel prey migrations exert a stronger effect on the diving of juveniles than adult Galapagos fur seals. Proc Biol Sci 266:1127–1132

Isojunno S, Aoki K, Cure C, Kvadsheim PH, Miller PJO (2018) Breathing patterns indicate cost of exercise during diving and response to experimental sound exposures in long-finned pilot whales. Front Physiol 9:1462

Kooyman GL, Ponganis PJ (1998) The physiological basis of diving to depth: birds and mammal*s.* Annu Rev Physiol 60:19–32

Kranstauber B, Cameron A, Weinzerl R, Fountain T, Tilak S, Wikelski M, Kays R (2011) The Movebank data model for animal tracking. Environ Model Softw 26:834–835

Lazaridis E (2015) Package 'lunar'. R Package version 0.1-04. https://cran.R-project.org/package=lunar

Lea MA, Johnson D, Melin S, Ream R, Gelatt T (2010) Diving ontogeny and lunar responses in a highly migratory mammal, the northern fur seal *Callorhinus ursinus.* Mar Ecol Prog Ser 419:233–247

Levin SA (1992) The problem of pattern and scale in ecology. The Robert H. MacArthur Award Lecture. Ecology 73:1943–1967

Lopez R, Malardé JP, Danès P, Gaspar P (2015) Improving Argos Doppler location using multiple-model smoothing. Anim Biotelem 3:32

Luque SP, Pelletier G, Bivand R (2015) Methods for sun ephemerides calculations. R Package version 0.8-36. https://cran.R-project.org/package=maptools

Mahaffy SD, Baird RW, McSweeney DJ, Webster DL, Schorr GS (2015) High site fidelity, strong associations, and long-term bonds: Short-finned pilot whales off the island of Hawai'i. Mar Mamm Sci 31:1427–1451

Mayor SJ, Schneider DC, Schaefer JA, Mahoney SP (2009) Habitat selection at multiple scales. Ecoscience 16:238–247

Morin PA, Nestler A, Rubio-Cisneros NT, Robertson KM, Mesnick SL (2005) Interfamilial characterization of a region of the ZFX and ZFY genes facilitates sex determination in cetaceans and other mammals. Mol Ecol 14:3275–3286

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2019) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-141. https://CRAN.R-project.org/package=nlme

Pinot JM, Jansá J (2001) Time variability of acoustic backscatter from zooplankton in the Ibiza Channel (western Mediterranean). Deep Sea Res I 48:1651–1670

R Development Core Team (2015) R: a language and environment for statistical computing, reference index version 3.1.3. R Foundation for Statistical Computing, Vienna, www.r-project.org

Reid SB (1994) Spatial structure of the mesopelagic fish community in the Hawaiian boundary region. PhD dissertation, University of Hawaii, Honolulu, HI

Reid SB, Hirota J, Young RE, Hallacher LE (1991) Mesopelagic-boundary community in Hawaii: micronecton at the interface between neritic and oceanic ecosystems. Mar Biol 109:427–440

Ringelberg J (1995) Changes in light intensity and diel vertical migration: a comparison of marine and freshwater environments. J Mar Biol Assoc UK 75:15–25

Sterling JT, Springer AM, Iverson SJ, Johnson SP and others (2014) The sun, moon, wind, and biological imperative–shaping contrasting wintertime migration and foraging strategies of adult male and female northern fur seals (*Callorhinus ursinus*). PLOS ONE 9:e93068

Thomas KN, Robison BH, Johnsen S (2017) Two eyes for two purposes: *in situ* evidence for asymmetric vision in the cockeyed squids *Histioteuthis heteropsis* and *Stigmatoteuthis dofleini.* Philos Trans R Soc Lond B Biol Sci 372:20160069

Van Cise AM, Martien KK, Mahaffy SD, Baird RW and others (2017) Familial social structure and socially driven genetic differentiation in Hawaiian short-finned pilot whales. Mol Ecol 26:6730–6741

West KL, Walker WA, Baird RW (2019) The diet composition of short-finned pilot whales, dwarf sperm whales and pygmy sperm whales in the North Pacific. In: ONR marine mammal & biology program review abstract book. Alexandria, VA, p 17−18

Yamamoto T, Takahashi A, Yoda K, Katsumata N, Watanabe H, Sato KT, Trathan PN (2008) The lunar cycle affects at sea behaviour in a pelagic seabird, the streaked shearwater, *Calonectris leucomelas.* Anim Behav 76:1647−1652

Young RE (1975) Function of the dimorphic eyes in the midwater squid *Histioteuthis dofleini.* Pac Sci 29:211−218

Young RE (1978) Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. Fish Bull 76:583−615

Zaret TM, Suffern JS (1976) Vertical migration in zooplankton as a predator avoidance mechanism. Limnol Oceanogr 21:804−813

Editorial responsibility: Peter Corkeron,
Woods Hole, Massachusetts, USA

Submitted: May 3, 2019; Accepted: August 29, 2019
Proofs received from author(s): October 15, 2019