

Diel and lunar variation in diving behavior of rough-toothed dolphins (*Steno bredanensis*) off Kauaʻi, Hawaiʻi

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Abstract

Observational studies describe rough-toothed dolphins (*Steno bredanensis*) actively foraging during the day on epipelagic species. Using data from depth-transmitting satellite tags deployed on nine individuals off Kauaʻi, we investigated diving behavior and the effects of lunar phase and solar light levels on vertical movements. Overall, tagged rough-toothed dolphins primarily used near-surface waters, spending between 83.6% and 93.7% of their time in the top 30 m of the water column. When diving, grand mean, median, and maximum dive depths were 76.9 m, 67.5 m, and 399.5 m, although individuals were in water with depths from approximately 700–1,450 m. Dive rates varied by time of day, being lowest during the day and at dawn and highest at dusk and night. Dives were deepest ($M = 133.7$ m, $SD = 52.6$ m, median = 106.5 m) and longest ($M = 4.0$ min, $SD = 0.4$ min, median = 4.0 min) at dusk, suggesting dolphins were taking advantage of prey rising to the surface in response to reduced light levels. Lunar phase indirectly affected diving, with deeper and longer dives occurring with increasing illumination. The variations in dive behavior across solar and lunar cycles indicate diving patterns shift based on the distribution of prey.

KEYWORDS

diel, diving behavior, foraging, Hawaiʻi, lunar cycle, rough-toothed dolphin, satellite tagging, *Steno bredanensis*

1 | INTRODUCTION

Understanding factors that influence species' spatial ecology, particularly movement patterns, can provide insight into habitat use and foraging patterns (Jonsen et al., 2019; Roncon et al., 2018). Predators often track their prey's behavior to maximize foraging opportunities while expending as little energy as possible. Marine predators, such as pelagic fishes, pinnipeds, and cetaceans, will follow their prey's movement through specific horizontal and vertical diving patterns to optimize this tradeoff (Furukawa et al., 2014; Gleiss et al., 2013; Owen et al., 2019; Robinson et al., 2012). These predator-prey interactions can vary across diel, lunar, and seasonal cycles, often resulting from changing light levels.

Mesopelagic micronekton and zooplankton complete vertical diel migrations, moving to the epipelagic zone at night and returning to greater depths during the day to avoid visual predators (Reid, 1994). In the open ocean off the Hawaiian Islands, a diverse group of these organisms forms a distinct layer at depths of 400–700 m during the day and above 400 m at night, referred to as the deep scattering layer as detected on an echosounder (Longhurst, 1976). Species that forage on organisms in this layer will often track this daily pattern or feed at night when the layer is easily accessible.

Changes in light levels across lunar and seasonal cycles can influence the mesopelagic layer migration, when higher light levels may cause an increase in the depth of the deep scattering layer at night (Benoit-Bird, Au, & Wisdoma, 2009). In one study off O'ahu, the timing of the movements of the scattering layer did not vary across lunar phases, but the layer was around 10 m deeper during a full moon compared to a new moon (Benoit-Bird, Dahood, & Würsig, 2009). Abundance and population dynamics can also vary across the lunar phases, along with changes in species distribution. Zooplankton abundance has been documented to increase when there is a full moon as a result of less predation risk (Hernández León et al., 2002), which can lead to an increase of food availability to fish and subsequent higher reproductive outputs (Hernández León, 2008). Although the size and species composition did not vary in the scattering layer in the O'ahu study (Benoit-Bird, Dahood, & Würsig, 2009), the abundance may change as mortality and birthing events vary with this cycle.

The abundance and distribution of prey that follows these patterns may influence marine mammal foraging. Marine mammals must also move within the scope of their physiological limits for oxygen as they maximize their food consumption while diving (Kramer, 1988). In contrast, surface movements are not constrained by this same oxygen requirement and are more likely to be influenced by prey location (Hooker & Baird, 2001). Odontocetes that feed on vertically migrating prey can either follow the diel oceanographic event, moving vertically and/or horizontally, or remain in near-shore or near-surface waters until the layer moves up at night (Au et al., 2013; Baird et al., 2001, 2002; Benoit-Bird & Au, 2003; Carlström, 2005; West et al., 2018). Studies have also found that odontocete diving and foraging behavior can vary across not only diel but also longer solar and lunar light cycles (Benoit-Bird, Dahood, & Würsig, 2009; Owen et al., 2019; Simonis et al., 2017).

Understanding both these vertical and horizontal movements can provide a background for more adaptive management strategies. We can use the relationships between marine mammals and their prey to predict movement and behavioral changes with human impacts over multiple temporal scales to better understand the long-term consequences (Rosen et al., 2017). Off the Hawaiian Islands specifically, different species of odontocetes are exposed to varying levels of anthropogenic activities (Baird, 2016), such as fisheries interactions and sonar use. The more we learn about the niche adaptations these species have to coexist in similar habitats, the better we can understand where and when species will be most vulnerable.

Out of the 18 odontocete species documented in Hawaiian waters, rough-toothed dolphins (*Steno bredanensis*) are the fourth-most frequently seen overall and the most encountered off Kaua'i and Ni'ihau during Cascadia Research Collective's (CRC) field efforts (Baird, 2016; Baird et al., 2013). Despite their relative abundance and wide distribution throughout the tropics and subtropics, information on finer-scale spatial ecology (e.g., horizontal or vertical movements) of rough-toothed dolphins remains scarce. Off Kaua'i and Ni'ihau this species was tagged to provide information on movement patterns and behavior in relation to U.S. Navy activities on

the Pacific Missile Range Facility (PMRF). Resultant movement data combined with genetic studies and long-term photo-identification revealed the existence of a resident populations of rough-toothed dolphins off Kaua'i and Ni'ihau, in addition to another off Hawai'i Island (Albertson et al. 2017; Baird, 2016; Baird, Webster, Mahaffy, et al., 2008).

Observational studies have indicated that rough-toothed dolphins frequently forage during the day, with notes of direct consumption, chasing, or herding epipelagic fish, and depredation of catch from fishing vessels (Baird, Webster, Mahaffy, et al., 2008; Gannier & West, 2005; Lodi & Hetzel, 1999; Ortega-Ortiz et al., 2014; Pitman & Stinchcomb, 2002; Ritter, 2002; Wedekin et al., 2004; Weir & Nicolson, 2014). The only other foraging information on rough-toothed dolphins comes from stomach contents from stranded animals, which contain epipelagic and coastal fish and cephalopod species (Clarke, 1986; Di Benedetto et al., 2001; Ferrero et al., 1994; Layne, 1965; Ott & Denilewicz, 1996; Perrin & Walker, 1975; Shallenberger, 1981; West et al., 2011).

Although a rough-toothed dolphin from Hawai'i was one of the first subjects of trained open-ocean diving experiments (Norris et al., 1965), most of what is known about the diving behavior of these deep-water medium-sized dolphins comes from opportunistic work that involved attaching depth-transmitting tags to individuals after stranding events in the western Atlantic (Manire & Wells, 2005; Wells et al., 1999, 2008). The results from these studies suggest that rough-toothed dolphins use near-surface waters, with most dives lasting less than three minutes and remaining shallower than 30 m (Manire & Wells, 2005; Wells et al., 1999, 2008). Although dive depths did not vary much between day and night, a higher proportion of dives were made at night (Manire & Wells, 2005; Wells et al., 2008).

Tag deployments off Kaua'i and Ni'ihau in multiple years and in multiple months provided the opportunity to examine behavior in relation to lunar and seasonal cycles, as well as to compare their diving behavior to other species that share similar habitats. Using data obtained from depth-transmitting satellite tags, we investigated the hypothesis that rough-toothed dolphins mainly forage during the day. We also examined if variability in dive behavior of rough-toothed dolphins around Kaua'i and Ni'ihau was correlated to changes in light levels with temporal (daily and seasonal) and lunar cycles.

2 | METHODS

2.1 | Field effort and tagging procedures

Field effort was undertaken from February 2000 through November 2019 as part of a long-term study on population structure and habitat use of odontocetes off the main Hawaiian Islands, with small-boat surveys occurring multiple times a year (Baird et al., 2013). When rough-toothed dolphins were encountered, basic observational information was recorded (e.g., group size and location), photographs were taken for individual identification, and foraging events were recorded on an ad hoc basis. Prey species were identified when possible in the field or from photographs taken.

From 2012 through 2016, limited satellite tagging was undertaken with this species off Kaua'i when tags were available and groups of cooperative individuals (i.e., slow-moving and easily approachable) were encountered. Tags used for this analysis were depth-transmitting satellite transmitters (SPLASH10-A; Wildlife Computers, Redmond, WA) in the Low-Impact Minimally-Percutaneous External-electronics Transmitter (LIMPET) configuration (Andrews et al., 2008). Tags were deployed using a pneumatic projector and attached to the dorsal fin or below the dorsal fin using two 4.4 cm titanium darts with backward-facing petals. Tags were programmed to transmit dive behavior information (dive start and end times, duration, and maximum depth), as well as periods of time at the "surface," in a behavior file. The depth sensor accuracy is $\pm 1\%$ of the reading and reports minimum and maximum values for each dive duration and depth. Vertical movements greater than 30 m and 30 s were set to indicate dives, whereas any movements less than these limits were considered surfacing periods. Behavior files were obtained through the Argos

system, although for deployments in 2016, a Mote (Wildlife Computers) was used to increase data throughput (Jeanniard-du-Dot et al., 2017). The amount of behavior data recorded varied because of throughput restrictions within the Argos satellite system, resulting in gaps in the behavioral record.

2.2 | Data processing

To assess the identity of tagged and companion individuals, photographs from field efforts were sorted by individual within each encounter and matched to a long-term photo-identification catalog (Baird, Webster, Mahaffy, et al., 2008). A social network analysis was undertaken to determine whether all tagged individuals were part of the island-associated social network (Baird, Webster, Mahaffy, et al., 2008). The sex of two tagged individuals was determined: one male from the presence of a postanal keel and a male genetically determined from a biopsy sample. All tagged dolphins were judged to be adults based on a combination of relative size noted at the time of tagging, length of sighting histories, and the relative size in photographs.

For each dive, we used the mean of the minimum and maximum dive depths and durations in analyses. To account for pressure transducer failures from the tags, we calculated mean descent and ascent rates for each dive, using values greater than 3 m/s as a potential indicator of transducer errors (Baird et al., 2018). We also assessed the status file associated with each deployment to see if any validated values in the “Depth” column, which correspond to depth sensor readings prior to transmission at the surface of the water, were far from zero, which may indicate an error. Location data were processed by the Argos system with a least-squares method and subsequently filtered to remove unrealistic locations using the Douglas Argos-filter v. 8.5 (Douglas et al., 2012). Argos location classes of 2 or 3 were automatically retained, maximum rate of movement was set to 20 km/hr, and minimum redundant distance was set to 3 km. This value represents the angle created from three location points that consider the farther an animal travels between locations, the less likely it will return to that original location without additional location points. The rate coefficient was set to the default for marine mammals (Ratecoef = 25). Locations that passed the Douglas Argos-Filter were associated with each dive by constructing tracks between consecutive locations and assigning locations to dives based on the assumption of constant speed of travel.

Filtered location data were further processed in R (v.3.6.1; R Core Team, 2019) to determine bathymetric depth using packages *rgeos* (Bivand & Rundel, 2017) and *raster* (Hijmans & Van Etten, 2016) using the Hawaiian Island 50 Meter Bathymetry and Topography Grids (<https://www.soest.hawaii.edu/HMRG/multibeam/bathymetry.php>). Solar angles were used to determine sunrise, sunset, day, night, dawn, and dusk using the R package *maptools* (Bivand & Lewin-Koh, 2016). Angles $>6^\circ$ constituted daytime, $<-6^\circ$ constituted night, and in between -6° and 6° was either dawn or dusk. Daylength was determined by the number of hours between sunrise and sunset, ranging from approximately 11.2 to 13.5 hr. Lunar cycles were represented by lunar phase on a scale from zero to one, where zero and one represent a new moon and 0.5 represents a full moon. Individual dive rates were calculated by dividing the number of dives by hours of behavior coverage (excluding gaps in data) for each temporal period. Two individuals (SbTag017 & SbTag018) were tagged 1.4 days prior to a Submarine Command Course (SCC) at PMRF in February 2016. These individuals were exposed to mid-frequency active sonar (MFAS) at distances of 21.2 to 68.7 km over a 2.9-day period (Baird et al., 2019), representing 30.6% (SbTag017) and 17.2% (SbTag018) of the total period dive and surface data were obtained. Given the small sample size MFAS exposure was not considered in analyses.

To determine whether individuals tagged during the same field effort were acting in concert, and thus with non-independent dive data, we compared locations of pairs of individuals obtained during the same satellite overpass. We calculated the straight-line distances between the two individuals and calculated the median and maximum distances apart and the percentage of time the animals were within 1 km of each other.

2.3 | Data analysis

Preliminary data exploration took place following the protocol from Zuur et al. (2010) to determine that model assumptions were met. Univariate analyses of each covariate regarding each response variable were used to assess patterns that would be influential when running the models. Analysis of variance (ANOVA) and the post hoc Tukey–Kramer honest significant difference (HSD) test were used to determine whether mean dive rate varied among time of day, lunar phase, and daylength. Dive rates were cube-root transformed to meet assumptions of normal distribution and homogeneity of variance.

Generalized additive mixed-effect models (GAMMs) were fitted to the remaining response variables (dive depth and duration) using the packages `gamm4` (Wood et al., 2017) and `mgcv` (Wood, 2001). A gamma error distribution with log-link function was used for both models. The full models were fit with all potential explanatory variables, using a shrinkage version of the cubic regression spline (`bs = "cs"`) for daylength and cyclic cubic regression spline (`bs = "cc"`) for lunar phase. Time of day (dawn, day, dusk, night) was included as a categorical variable. Each tag ID was added as a random effect to account for individual variability that can lead to a lack of independence among dives from the same animal. When model evaluation indicated temporal autocorrelation, a nested random effect of smaller time periods within each dolphin was added to the model, choosing periods with the lowest Akaike's information criterion (AIC) in the full models as described in Falcone et al. (2017). Model selection was performed using the multimodel inference *MnMIn* package (Bartoń, 2018) based on AIC values. AIC weight was used to determine the probability that a given model was the best model when compared to all other candidates for each response variable. Models with AIC less than or equal to two were considered comparable to the top model.

3 | RESULTS

3.1 | Encounters and foraging observations

Rough-toothed dolphins were encountered 459 times between 2000 and the end of 2019, with encounter durations ranging from <1 min to 4 hr 16 min (median = 14 min). Excluding groups that were not approached, there were 436 encounters, with foraging recorded in 99 encounters (22.7%). Prey was identified to at least the family level in 26 cases, including mahi-mahi (*Coryphaena hippurus*, $n = 11$) and species in the families *Exocoetidae* (flying fish, $n = 13$) and *Belonidae* (needlefish, $n = 2$). In an additional 37 cases, rough-toothed dolphins were observed chasing or were within close proximity to unidentified small fish. Off Kaua'i and Ni'ihau specifically, foraging was observed during 41 out of 213 encounters (19.2%).

3.2 | Tagging and identity of tagged individuals

Eleven depth-transmitting satellite tags were deployed, although no dive data were obtained from one deployment, and another had less than one day of dive and surfacing data (Table 1). Based on photo-identification, the remaining nine tags were deployed on nine different individuals. Sighting histories revealed that eight of the nine individuals had been photographed off Kaua'i or Ni'ihau on one or more occasions prior to or subsequent to tagging, with seven being seen over multiple years. A social network analysis (not shown) indicated that all nine individuals linked within the main component in the island resident social network.

The three pairs of individuals tagged during the same encounter or within a day of each other were generally not together posttagging except for short periods of less than 24 hr, so each was considered independent (Table S1). Mean and median tag transmission durations were 12.9 ($SD = 2.5$) and 13.4 days, respectively. The span from first to

TABLE 1 Details on nine rough-toothed dolphin satellite tags deployed off Kaua'i between 2012–2016. Behavior coverage (days, %) represents the amount of time from the first behavior data to the last behavior data excluding gaps in behavioral data.

Tag ID	Sex (when known)	Date tagged	Group size when tagged	Tag duration (days)	Behavior coverage (days/%)	M (SD)/median/maximum gap duration (hr)
SbTag006	—	July 1, 2012	8	10.4	4.0/50.6	5.9 (7.1)/0.75/18.6
SbTag007	—	July 2, 2012	7	13.7	8.9/70.2	1.7 (4.8)/0.39/23.8
SbTag009	Male	July 29, 2013	20	9.9	8.5/93.8	0.4 (1.3)/0.35/6.6
SbTag010	—	July 31, 2013	4	13.4	8.2/71.2	2.6 (7.1)/0.03/29.8
SbTag011	—	February 4, 2014	4	12.5	9.3/80.6	1.1 (3.7)/0.02/18.8
SbTag015	—	February 11, 2015	13	14.3	4.3/33.1	4.7 (7.2)/0.55/23.2
SbTag016	Male	September 5, 2015	17	14.9	11.0/74.4	1.9 (5.1)/0.02/20.3
SbTag017 ^a	—	February 14, 2016	21	9.5	6.9/78.4	0.9 (3.1)/0.02/16.3
SbTag018 ^a	—	February 14, 2016	21	16.9	11.3/73.0	1.2 (3.8)/0.02/20.9

^aTagged within same group.

last data transmitted in the behavior file ranged from 8.0 to 15.4 days. The mean and median gaps in the behavioral data were 2.4 ($SD = 1.9$) and 1.7 hr, respectively (Table 1). When gaps were excluded, there was a total of 72.5 days (1,740 hr) of behavior data with 3,395 dives recorded. For the individuals tagged prior to the SCC (SbTag017 & SbTag018), 414 out of 1,300 dives were recorded to have sonar present.

3.3 | Diving behavior

Median dive depth was 67.5 m ($M = 76.9$, $SD = 12.8$) and median dive duration was 3.1 min ($M = 3.1$, $SD = 0.3$) (Figure S1, Figure S2, Table 2). Mean and median bathymetric depths was 1,179.9 ($SD = 319.1$) and 827.1 m across all dives. Dive rates varied significantly depending on the time of day (ANOVA, $df = 3$, $F = 26.22$, $p < .001$), with the highest dive rates during dusk and the lowest during dawn (Tukey–Kramer HSD, 95% CI of the difference = 1.2–4.0, $p < .001$; Figures 1 and 2, Table 3). There was no evidence for mean dive rates varying significantly across lunar phase and daylength (ANOVA, $df = 7$, $F = 1.232$, $p = .285$ and $df = 1$, $F = 1.402$, $p = .237$, respectively).

GAMM results suggest temporal factors on several scales influence diving behavior. The random effect of individual was relatively small compared to the significant explanatory variables (variance < 1 in all cases) but was retained to account for the variation it did contribute to and to remove the temporal autocorrelation when time periods were nested within it.

The top dive depth model received 76.1% of the model weight and included time of day, lunar phase, and daylength (Table S2, S3). Dive depth varied based on time of day, with dives occurring at dusk on average 73.4 m deeper (121.8%) than dives at dawn (Figure 3a). Dive depth also varied with lunar phase, with dives closest to a full moon (equal to 0.5) being on average 24.9 m (34.3%) deeper than those closest to a new moon (equal to zero or one) (Figure 3b). There was a negative correlation to daylength, with dives occurring during the least amount of daylength (11.2 hr) being on average 16.8 m deeper (23.4%) than those during the greatest amount of daylength (13.5 hr) (Figure 3c).

The top dive duration model included time of day and lunar phase (Tables S4 and S5), receiving 30.3% of the model weight. Similar to the dive depth model, dives were longest at dusk (Figure 4a). Dusk dives were, on average, 1.7 min longer (73.0%) than dives at dawn. Dive duration also varied with lunar phase, with dives closest to a full

TABLE 2 Dive summary statistics from nine rough-toothed dolphin satellite tags deployed off Kaua'i between 2012 and 2016. The percentage (%) of time at surface represents periods when the animal did not dive below 30 m out of the total amount of behavior coverage.

Tag ID	Total dives	Time at surface (%)	Dive depth (m) M (SD)/median/ maximum	Dive duration (min) M (SD)/median/ maximum	Bathymetric depth (m) M (SD)/median/ maximum
SbTag006	149	91.6	78.5 (44.6)/67.5/235.5	3.4 (1.7)/3.2/15.3	897.8 (413.9)/798.9/1832.2
SbTag007	432	90.2	64.2 (39.1)/51.5/311.5	3.0 (1.0)/3.0/7.2	809.0 (376.2)/699.5/1971.0
SbTag009	307	93.5	64.3 (39.2)/51.5/287.5	2.7 (1.0)/2.6/6.3	1,424.6 (730.4)/1166.3/3932.9
SbTag010	245	93.7	62.2 (34.6)/51.5/203.5	3.2 (0.9)/3.2/5.9	1,069.7 (411.1)/872.0/2053.2
SbTag011	367	91.2	98.2 (55.0)/91.5/311.5	3.4 (1.1)/3.4/6.8	1,390.1 (812.4)/1163.3/4062.3
SbTag015	227	90.0	74.0 (57.2)/57.5/351.5	3.0 (1.0)/2.9/7.4	1,556.5 (703.3)/1449.4/3776.9
SbTag016	368	93.7	72.8 (51.7)/56.5/399.5	2.9 (1.0)/2.9/6.2	1,620.9 (1059.2)/1419.8/4192.2
SbTag017	510	85.1	90.1 (38.1)/89.5/247.5	3.0 (0.9)/3.0/5.6	1,012.8 (566.0)/837.7/3059.0
SbTag018	790	83.6	88.0 (40.1)/85.5/295.5	3.5 (0.9)/3.6/6.0	837.5 (546.5)/695.9/3807.9

moon (equal to 0.5) being on average 26 s (14.7%) longer than those closest to a new moon (equal to zero or one) (Figure 4b). Other highly ranked models within two AIC (Table S4) included time of day and daylength (AIC model weight = 27.6%) and just time of day (AIC model weight = 26.2%). In both cases, the same time of day pattern was observed, and dive duration increased with daylength, similar to the pattern observed for dive depth.

4 | DISCUSSION

Combining observational work with tagging efforts provided insight into rough-toothed dolphin diving behavior over different temporal periods. Our study and others (e.g., Lodi & Hetzel, 1999; Ortega-Ortiz et al., 2014; Pitman & Stinchcomb, 2002; Ritter, 2002; Wedekin et al., 2004; Weir & Nicolson, 2014) have frequently documented rough-toothed dolphins feeding on epipelagic prey species during the day. This is also consistent with prey identified from stomach content analyses of stranded animals (e.g., Di Benedetto et al., 2001; Ferrero et al., 1994; Layne, 1965; Ott & Denilewicz, 1996; Perrin & Walker, 1975; Shallenberger, 1981). Our dive data obtained using depth-transmitting satellite tags show that individuals of this species in Hawai'i spend the vast majority of their time diving to depths <30 m (Table 2). When diving >30 m during the day, they are generally still within the range of epipelagic species identified from gut content analyses (Table 3). However, dive rates are highest at dusk and night (Figures 1 and 2), suggesting that rough-toothed dolphins may switch to mesopelagic prey that rise towards the surface in response to reduced light levels. Dives were deepest at dusk (Figure 3a), similar to other delphinid species that feed on mesopelagic prey in Hawaiian waters, such as melon-headed whales (*Peponocephala electra*), and pantropical spotted dolphins (*Stenella attenuata*) (Baird et al., 2001; West et al., 2018). Deeper dives at dusk suggest the use of "exploratory" dives (Baird et al., 2001) to meet the deep scattering layer as organisms migrate towards the surface with decreasing sunlight (Reid et al., 1991).

The diel variation documented is relatively consistent with the tagged rehabilitated individual rough-toothed dolphins in the Atlantic that showed more dives occurring at night with little difference between day and night dive depths (Manire & Wells, 2005; Wells et al., 2008). The greater frequency of night dives is also similar to diel diving behavior found in other pelagic dolphin species, including spinner dolphins (*Stenella longirostris*), Risso's dolphins (*Grampus griseus*), melon-headed whales, and pantropical spotted dolphins (Baird et al., 2001; Benoit-Bird & Au, 2003; Norris et al., 1994; Scott & Chivers, 2009; Soldevilla et al., 2010; West et al., 2018). Many cetacean

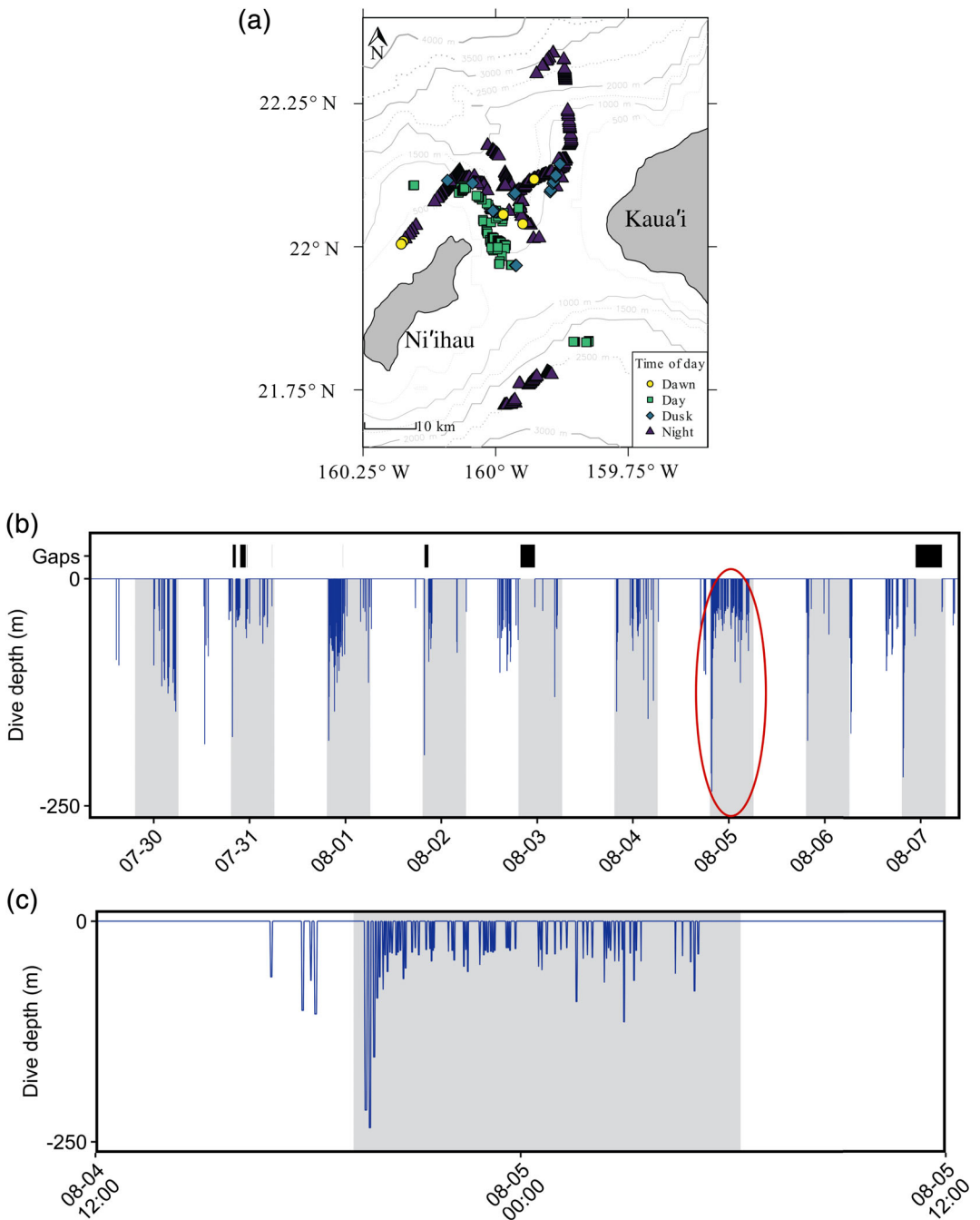


FIGURE 1 Dive data by time of day from rough-toothed dolphin SbTag009 over entire tag deployment from July 29 to August 7, 2013. Bathymetric depth was greater than 500 m for the entire record. Dives are represented by vertical blue lines. Night periods are indicated by gray shading, and gaps in data are shown in the solid black bars at the top of the plot. Times are in HST, and dives less than 30 m are considered surfacing bouts, shown as solid blue line at 0 m. (a) Map of locations of each dive. (b) Dive data over entire tag deployment. (c) Dive data for 24 hr period from August 4 at 12:00 HST through August 5 12:00 HST.

FIGURE 2 Box plot of dive rates (number of dives/hr of behavior coverage) of rough-toothed dolphins tagged off Kaua'i by time of day. A single value for each individual was used. Middle line shows the median, while lower and upper lines of the boxes show 25th and 75th percentiles, respectively. The ends of the vertical line indicate minimum and maximum values.

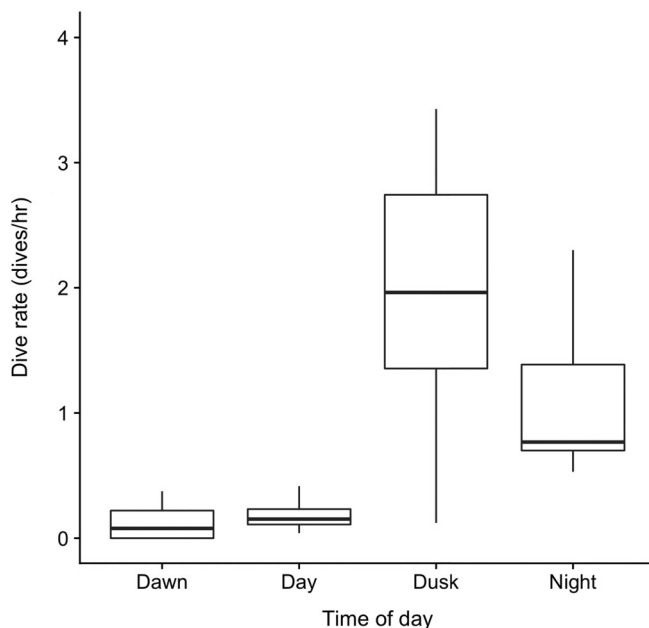


TABLE 3 Grand mean and standard deviations (SD) and medians for dive depth, dive duration, and percentage (%) of time at surface (periods when the animal did not dive below 30 m out of the total amount of behavior coverage) for nine rough-toothed dolphin satellite tags deployed off Kaua'i between 2012 and 2016.

Time of day	Dive rate (# dives/hr of behavior coverage) M (SD)/median	Dive depth (m) M (SD)/median	Dive duration (min) M (SD)/median	Time at surface (%) M (SD)/median
Dawn	0.6 (1.4)/0.1	60.3 (19.2)/55.5	2.3 (0.6)/2.2	93.1 (17.5)/99.4
Day	0.2 (0.1)/0.2	84.0 (42.7)/57.5	2.8 (0.8)/3.2	97.7 (2.1)/98.6
Dusk	1.9 (1.1)/2.0	133.7 (52.6)/106.5	4.0 (0.4)/4.0	70.2 (17.5)/69.4
Night	1.1 (0.7)/0.8	75.5 (13.7)/69.5	3.1 (0.3)/3.1	85.6 (9.2)/89.7

species that feed on organisms in the deep scattering layer likely feed primarily at night when prey is closer to the surface, to expend less energy on diving or because they have physiological constraints that prevent them from diving deeper (e.g., Aoki et al., 2007; Baird, Webster, Schorr, et al., 2008; Benoit-Bird & Au, 2003; Norris et al., 1994). Ascent and descent rates for deep dives of rough-toothed dolphins have not been reported, but the similar pantropical spotted dolphin has ascent and descent rates of approximately 1.5 m/s (Baird et al., 2001). With a maximum dive duration of 15.3 min (Table 2), assuming ascent and descent rates of 1.5 m/s, rough-toothed dolphins could, in theory, dive to over 600 m, reaching the deep scattering layer during the day, if there are no physiological limitations at play. However, the maximum dive depth recorded was 399.5 m (recorded at night), and median dive durations for all individuals ranged from 2.6 to 3.6 min (Table 2), with only one individual's dives exceeding 8 min. While the deep scattering layer during the day may still be within the physiological limits for this species, it is likely not energetically worth reaching during the day because of the tradeoff between transit time and the time available to forage at such depths. However, at night, the layer ascends to between the surface and 400 m (Reid, 1994), which would allow the dolphins to reach the top half of the layer for foraging. Two mesopelagic squid species, *Thysanoteuthis rhombus* and *Sthenoteuthis oualaniensis*, identified from a regurgitation sample from a rough-toothed dolphin off Hawai'i Island (William Walker, personal communication, September 2020) have previously been found at depths greater than

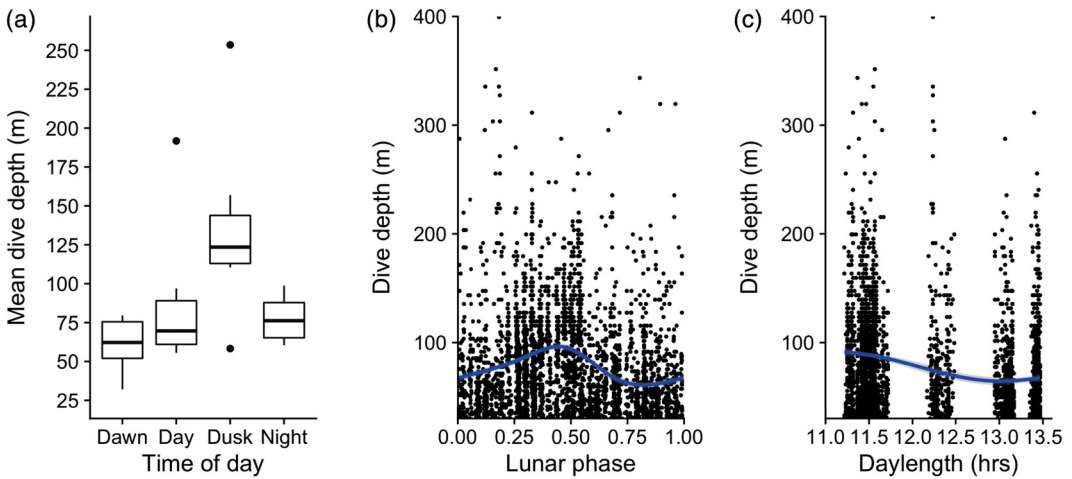


FIGURE 3 The relationship between dive depth and each explanatory variable in the top fitted GAMM model for rough-toothed dolphins tagged off Kaua'i. Lowest dive depth values begin at 30 m. (a) Boxplots of the time of day as a factor variable. A single mean value for each individual was used. Middle line shows the median, lower, and upper lines of the boxes show 25th and 75th percentiles, respectively. The ends of the vertical line indicate most extreme values within 1.5 interquartile range of the 25th and 75th percentile, and black points represent outliers. (b) Fitted relationship for lunar phase and (c) daylength. Gray shading represents the 95% CI for the smooth terms and black points represent raw data of dives ($n = 3,395$).

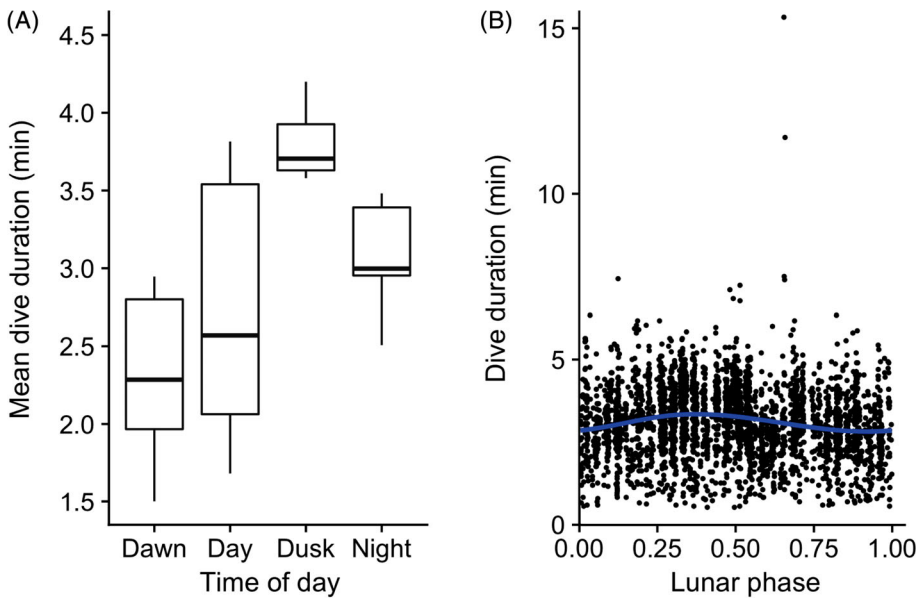


FIGURE 4 The relationship between dive duration and each explanatory variable in the top fitted GAMM model for rough-toothed dolphins tagged off Kaua'i. (a) Boxplots of the time of day as a factor variable. A single mean value for each individual was used. Middle line shows the median, lower, and upper lines of the boxes show 25th and 75th percentiles, respectively. The ends of the vertical line indicate most extreme values within 1.5 interquartile range of the 25th and 75th percentile. (b) Fitted relationship for lunar phase. Gray shading represents the 95% CI for the smooth terms and black points represent raw data of dives ($n = 3,395$).

400 m during the day, but are known to ascend towards the surface at night, where they become accessible to dolphins (Jereb & Roper, 2010; Parry, 2003; Young & Hirota, 1990). A third epipelagic species (*Pholidoteuthis massyae*) from the same sample (William Walker, personal communication, September 2020) also completes diel vertical movements towards surface waters at night but is epipelagic and remains within the range of rough-toothed dolphins during the day (Miyahara et al., 2006, 2008). Alternatively, rough-toothed dolphins may continue to feed primarily on epipelagic species at night. As the mesopelagic boundary layer ascends towards the surface at night, it might compress the available habitat of epipelagic species and cause greater densities of prey that rough-toothed dolphins can target.

Dives were deeper closer to a full moon, suggesting the lunar cycle indirectly influences rough-toothed dolphin vertical movement patterns as they follow their prey and providing additional support for feeding on mesopelagic prey that are responding to lunar illumination. Benoit-Bird, Au, and Wisdoma (2009) found that the lunar cycle influences the vertical migration of the mesopelagic boundary layer above 150 m, in the range of depths the tagged rough-toothed dolphins were spending the majority of their time. We would expect greater lunar illumination to cause vertically migrating organisms to remain deeper in the water column at night to avoid the visually-hunting predators taking advantage of increased light levels (Owen et al., 2019). To reach those organisms during a full moon, rough-toothed dolphins would need to dive deeper and subsequently longer at night, which is consistent with our findings. Without accounting for cloud cover, we cannot say for sure that absolute lunar light levels caused the change in diving behavior. Although the size and composition of species that complete diel vertical migrations were not found to change, the distribution of organisms (i.e., patchiness of the scattering layer) and maximum depth ascended have been known to vary across lunar phases off O'ahu (Benoit-Bird, Dahood, & Würsig, 2009). The change in diving depth and duration over this cycle could be in response to this pattern.

When daylength increases, the scattering layer is hypothesized to be found deeper at night because the organisms have less time to migrate close to the surface before needing to return to depth (Hays, 1995). If longer-term solar light cycles were influencing rough-toothed dolphin behavior, we would expect to see them diving deeper when daylength was the greatest. However, we found the opposite to be true. With less than 2.5 hr differences in daylength throughout the year around the main Hawaiian Islands, Benoit-Bird, Dahood, and Würsig (2009) noted that the duration of the scattering layer migration towards the surface varied only slightly. In this case, the driver of diving behavior changes may not directly be in response to changes in solar and lunar light levels.

Our study describes the variation in rough-toothed dolphin diving behavior across different temporal cycles, but we cannot conclude if light levels directly influence rough-toothed dolphins or do so indirectly through the behavior, abundance, or distribution of their prey. Without adequate gut content analyses, we cannot confidently say whether rough-toothed dolphins are switching prey across temporal cycles and what the drivers for this would be if they were. Since the species of the mesopelagic boundary community are fairly well documented (Clark, 1980; Reid et al., 1991), assessing their presence in future rough-toothed dolphin diet studies, possibly through genetic analyses of fecal samples (e.g., Ford et al., 2016), may provide further data on whether they are feeding on mesopelagic prey in the deep scattering layer at dusk and night (Reid et al., 1991; Roncon et al., 2018). Identifying prey could also help determine if the abundance, caloric differences, or catchability of different prey may make the investment in diving deeper worthwhile.

Because tag deployments were rarely greater than 2 weeks, a sampling bias for both lunar phase and daylength is present. As Owen et al. (2019) describes, this potentially means that there are other seasonal drivers for the dive depth and duration results. For example, during different times of year, prey availability likely varies due to other abiotic factors, such as water temperature. Biotic factors, such as competition with other top predators or predation risks to rough-toothed dolphins, could also influence the patterns we found. The predator-prey dynamics likely influence general foraging patterns, but finer scale foraging techniques when feeding in habitats and similar depths with other top predators likely result in niche adaptations (Soto et al., 2008). The maximum dive depth recorded for rough-toothed dolphins anywhere is the 399.5 m depth found in this study, which is less than maximum dives recorded for other deep-diving odontocetes in Hawaiian waters, such as short-finned pilot whales or beaked whales

that frequently dive to depths of 1,000 m or greater (Baird, Webster, Schorr, et al., 2008; Owen et al., 2019). Killer whales (*Orcinus orca*) have been observed chasing a rough-toothed dolphin off Kaua'i (Baird, 2016), and changes in rough-toothed dolphin acoustic behavior has been recorded when killer whales were acoustically detected in the area (Jarvis et al., 2019). Presumably, large sharks also at least occasionally prey on rough-toothed dolphins, although they are likely regularly in the area where our tagged animals were found, and thus their influence on diving behavior is likely to be continuously felt. Tagged individuals were consistently in water with depths far beyond what they were diving to, so bathymetric depth was not a limiting factor (Table 2).

Another factor potentially influencing the diving behavior of rough-toothed dolphins includes MFAS used on PMRF. Two of our nine tagged dolphins were known to have been exposed to MFAS for part of their dive records. An assessment of diving behavior of these two individuals for periods before, during and after MFAS exposure did reveal significant differences in both dive depth and duration, but the trends were not consistent between the two individuals (Baird et al., 2019), suggesting that if there is an influence of MFAS on diving patterns, it may not affect all individuals similarly. Further tagging efforts prior to sonar exposure would allow for a more robust analysis of the potential effects of MFAS on rough-toothed dolphin diving behavior. Additionally, tagging individuals from the Hawai'i Island population for comparison to individuals off Kaua'i may offer insight into differing diving and foraging patterns between the populations, given that they are already known to vary in several other ways (Baird, Webster, Mahaffy, et al., 2008). With the Kaua'i population's overlap with PMRF, a comparison between the two may offer insight into the effects regular exposure to MFAS may have on diving patterns.

Observational data on rough-toothed dolphins alone provided an incomplete picture of their foraging behavior and daily cycles. As remote tagging technologically advances, combining study methods can help us get a better idea of overall movement ecology to provide more insight into habitat use and foraging behavior. For species like rough-toothed dolphins that live in an area with a diversity of other species of odontocetes, getting a fuller picture can help us understand niche partitioning and have implications for management of anthropogenic threats.

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AUTHOR CONTRIBUTIONS

Jacquelyn Shaff: Conceptualization; formal analysis; visualization; writing-original draft. **Robin Baird:** Conceptualization; data curation; investigation; project administration; resources; supervision; writing-review & editing.

ETHICAL APPROVAL

Tagging was undertaken under permit number 15330 from the National Marine Fisheries Service and following protocols approved by the Cascadia Research Collective Institutional Animal Care and Use Committee.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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