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The behavioral context of common dolphin (*Delphinus* sp.) vocalizations

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ABSTRACT

Correlations between surface behavior and concurrent underwater vocalizations were modeled for common dolphins (*Delphinus* spp.) in the Southern California Bight (SCB) over multiple field seasons. Clicks, pulsed calls, and whistles were examined, with a total of 50 call features identified. Call features were used to classify behavior using random forest decision trees, with rates of correct classification reaching 80.6% for fast travel, 84.6% for moderate travel, 59.8% for slow travel, and 58% for foraging behavior. Common dolphins spent most of their time traveling. The highest number of clicks, pulsed calls, and complex whistles were produced during fast travel. In contrast, during foraging there were few pulsed calls and whistles produced, and the whistles were simple with narrow bandwidths and few harmonics. Behavior and vocalization patterns suggest nocturnal foraging in offshore waters as the primary feeding strategy. Group size and spacing were strongly correlated with behavior and rates of calling, with higher call rates in dispersed traveling groups and lower call rates in loosely aggregated foraging groups. These results demonstrate that surface behavior can be classified using vocalization data, which builds the framework for behavioral studies of common dolphins using passive acoustic monitoring techniques.

Key words: common dolphin, *Delphinus* spp., vocalization, echolocation, random forest decision tree, behavior.

Vocal communication plays a vital role in behavior and social interactions across a broad array of species. An examination of the behavioral context of vocalizations has been conducted for numerous taxa, ranging from crickets (Thorson *et al.* 1982); amphibians (Wells 1977, Krishna and Krishna 2005); and fish (Crawford *et al.* 1986, Bass *et al.* 1997); to birds (Roberts 2003, Mennill and Vehrencamp 2008, Naguib and Janik 2009) and mammals (Belwood and Fullard 1984, Clarke 1990, Crockford and Boesch 2003, Simeonovska-Nikolova and Bogoev 2008, Naguib and Janik 2009). Many of these studies have focused on the behavioral context of specific call types, such as distress or contact calls (Richman 1980, Clarke 1990, Vergne *et al.* 2009), calls that signal aggression (McCowan and Rommeck 2006), or calls that contain information about body size or fecundity (Charlton *et al.* 2009). For marine mammals, there has also been much research identifying the behavioral context of specific calls, particularly for foraging (Janik 2000, Leighton *et al.* 2004, Simon *et al.* 2006). In addition to examining calls with a specific function, several studies have examined acoustic behavior across broad behavioral states (Taruski 1979, Sjare and Smith 1986, Dawson 1991, Simon *et al.* 2007), demonstrating that the types and rates of calls produced vary with behavioral state.

Common dolphins (*Delphinus* spp.) are found throughout the world's oceans, in coastal and inshore warm tropical and temperate waters (Reeves *et al.* 2002). They have been shown to prefer water ranging from approximately 10°C to 28°C (Evans 1982, MacLeod *et al.* 2008) and to migrate seasonally inshore and offshore as temperatures change (Dohl *et al.* 1986, Forney and Barlow 1998, MacLeod *et al.* 2008). In addition, they appear sensitive to sea surface temperature changes related to El Niño/Southern Oscillation (ENSO) events, as evidenced by their following warmer water masses and avoiding cooler water (Tershy *et al.* 1991, Neumann 2001*b*, Benson *et al.* 2002). They are also associated with upwelled, more saline waters with weak thermoclines (Au and Perryman 1985, Reilly 1990). Prey species include epipelagic schooling fish as well as myctophids and squid (Ohizumi *et al.* 1998, Osnes-Erie 1999, Neumann and Orams 2003, Meynier *et al.* 2008), and foraging behavior appears to be dependent upon the region or prey availability (Gallo-Reynoso 1991, Neumann and Orams 2003). Some behavioral work has been conducted to examine diel behavior patterns of common dolphins off New Zealand (Neumann 2001*a*, Neumann and Orams 2003, Stockin *et al.* 2009); however behavior, particularly foraging, may be habitat specific. In addition, some limited work on vocalizations has been conducted, principally on the characterization of common dolphin whistles (Moore and Ridgway 1995, Ansmann *et al.* 2007, Petrella *et al.* in press) and attempts to classify clicks and whistles to species (Oswald *et al.* 2003, Roch *et al.* 2007). However, the present study is one of the first to examine both behavior and vocalizations of common dolphins, and to attempt to utilize vocal data to classify and predict behavior as a means to better understand habitat use.

Common dolphins produce a number of vocalizations, including whistles, clicks, and burst pulse calls (Moore and Ridgway 1995, Richardson *et al.* 1995, Soldevilla *et al.* 2008). Whistles are frequency modulated, long duration, tonal calls used for communication and often have harmonic structure as well (Richardson *et al.* 1995). Harmonics may be a result of the intensity of the call and may be received only when the calls occur on-axis; however they may also impart spacing or other information to other group members (Lammers and Au 2003) and therefore may be deliberately produced. Clicks are short duration, broadband-pulsed calls used in echolocation and navigation, and range from 23 to over 100 kHz (Richardson *et al.* 1995, Au 2004, Soldevilla *et al.* 2008). Burst pulse calls are a series of rapidly produced

clicks perceived as tonal sounds and occur both in echolocation and communication (Richardson *et al.* 1995). Common dolphins also produce buzzes (Moore and Ridgway 1995) and other nonwhistle pulsed sounds, occasionally referred to as barks, yelps, or squeals (Caldwell and Caldwell 1968, Ridgway 1983).

The western North Pacific common dolphin population, found off the coast of California, was split from the single species *Delphinus delphis* into two species, *D. delphis* and *D. capensis*, based on morphological and genetic distinctions (Heyning and Perrin 1994, Rosel *et al.* 1994). However, external features vary across a wide spectrum even within these species (*e.g.*, Farley 1995), and at-sea identifications to the species level are often difficult. Unlike Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), which have been shown to have distinctive clicks that may be population or subspecies specific (Soldevilla *et al.* 2008), preliminary analysis indicates that common dolphins do not seem to have species-specific calls (Soldevilla *et al.* 2008). Therefore, for purposes of this analysis, the genus will be considered as a whole.

The objectives of this study were to (1) create a behavioral time budget for common dolphins from the Southern California Bight (SCB), (2) create a model of surface behavior based on acoustic data, and (3) utilize that model to classify and predict behavior based on only acoustic data.

METHODS

Study Area and Survey Platforms

This research was conducted in the SCB near San Clemente Island, approximately 100 km offshore San Diego (Fig. 1). Data were obtained in seven sampling periods from August 2006 through November 2008 using two types of research vessel. The primary survey platform was the R/P FLIP (Floating Instrument Platform, Fig. 2), a live-aboard stationary-moored platform from which visual and acoustic observations were conducted (Fisher and Spiess 1963). FLIP was deployed northwest of San Clemente Island in the fall of 2006, 2007, and 2008 (Fig. 1, Table 2).

The secondary research method used small boats to conduct surveys within the Naval Southern California Offshore Range (SCORE). This work was done in conjunction with the Naval Undersea Warfare Center's Marine Mammal Monitoring on Navy Ranges (M3R) program (Jarvis *et al.* 2003, Moretti *et al.* 2004, Falcone *et al.* 2009). The M3R system uses seafloor hydrophones to detect and localize vocalizing marine mammals; small boats with experienced observers were utilized to verify the location and species for M3R acoustic detections. Rigid-hulled inflatable boats (RHIBs, 5.3–5.9 m in length) were used for these surveys. Four-week-long surveys were conducted in the summer and fall of 2006, 2007, and 2008 (Table 2).

Behavioral Sampling

Two observers in the crow's nest of FLIP, located 26.5 m above the waterline (Fig. 2), continuously monitored the ocean 360° around FLIP using both the naked eye and 7 × 50 Fujinon binoculars, containing a reticle scale to estimate distance and a magnetic compass to estimate bearing. These observers recorded all marine mammal and vessel sightings throughout daylight hours in Beaufort sea state 5 or less. Observers used sighting cues such as blows, splashes, leaping animals, and the presence of associated birds to initially locate marine mammals. Dolphin groups that were first identified by crow's nest observers and approached the face side of FLIP

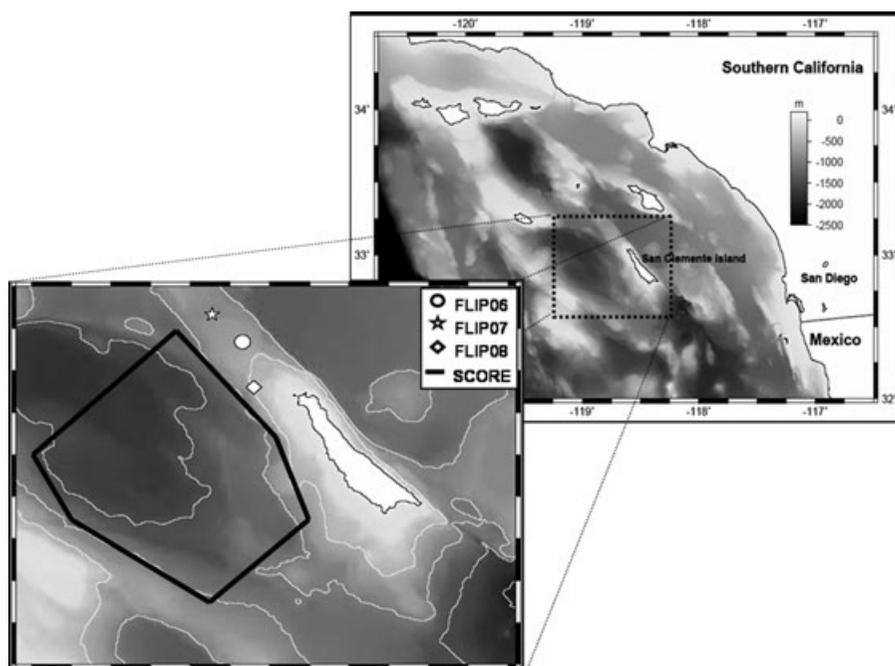


Figure 1. Bathymetric map of the study area in Southern California Bight. The shapes indicate the locations of FLIP moorings in 2006, 2007, and 2008, northwest of San Clemente Island. The dark line indicates the border of the San Clemente Offshore Range (SCORE).

within 1 km were selected for group focal follow observations, which were conducted from the top deck level, 15.24 m above the waterline. With the height this unique platform lends the observers, behavioral states and events can be confidently observed within a 1-km distance, particularly with the assistance of binoculars. Focal follow behavioral sampling continued while the group remained on the face side of FLIP and within 1 km. While a team of observers was used on FLIP, they were trained on behavioral sampling methods simultaneously to minimize interobserver bias, and each focal follow was conducted by a single individual.

Groups were defined as animals in apparent association, moving in the same direction and generally carrying out the same activity, following Shane (1990). Group focal follows were conducted using the instantaneous sampling method (Altmann 1974, Mann 1999), whereby the behavioral states and associated events (*e.g.*, high arch dives, tail slaps) of the majority (>50%) of the group were recorded every 1–3 min, or upon the next surfacing if the group was underwater (*e.g.*, Mann 1999). Behaviors were recorded within each group focal followed by a single observer at as consistent an interval period as possible (*e.g.*, 1 min); however that interval varied slightly between groups depending on the surfacing period of the animals, the size of the group, or due to interobserver differences. In addition, bearing, distance, group size, group spacing, orientation toward FLIP, and direction of travel were also recorded for each behavioral sample. Group spacing considered the overall position of animals relative to each other, defined as less than one body length apart (tight), approximately one body length apart (loose), or greater than one body length apart

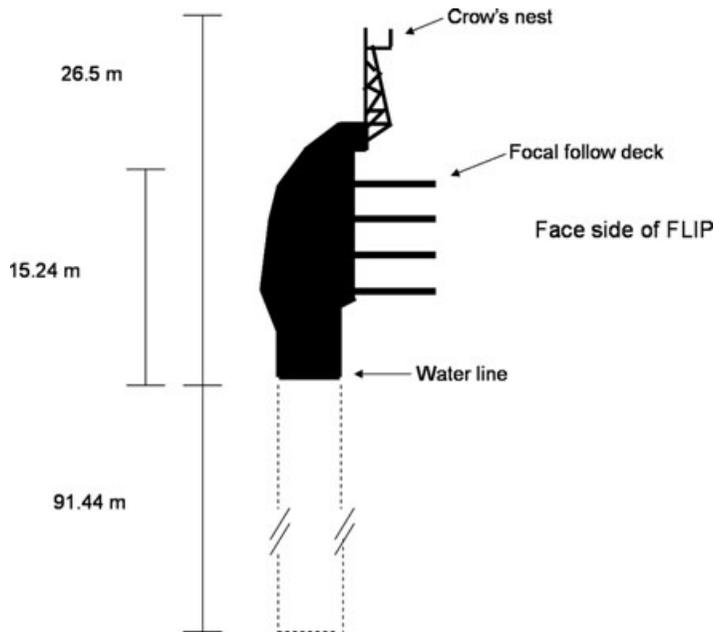


Figure 2. Schematic of FLIP. The crow's nest is 26.5 m above the water line, while the focal follow deck is 15.24 m above the water line. The entire length of FLIP is 108.2 m, with 91.44 m below the water line. In the vertical position, the deck/top side of FLIP is referred to as the face side.

(dispersed), as well as the formation of the group as a whole (clustered, in a line, or spread out). Group size was determined using minimum, maximum, and best size estimates; the best estimate was used in subsequent analyses.

There were six behavioral states recorded: slow, moderate, or fast travel, mill/rest, forage, and social/surface active (see Table 1 for behavior descriptions); these could also be recorded simultaneously if the group as a whole was doing more than one behavior at a time, or if portions of the group were doing different behaviors (Shane 1990, Hanson and Defran 1993, Henderson and Würsig 2007). The primary behavior was defined as the ongoing behavior or the most prevalent behavior of the group. For example, if the ongoing behavior of the group was travel and then surface activity commenced while still traveling, the primary activity was considered travel and the secondary behavior surface active. If the dominant behavior was travel and some individuals engaged in brief milling, travel was the primary behavior with mill secondary. However, if a portion of the group broke off and distinctly changed behavior or direction of travel, they were then counted as a separate group and the focal follow continued on the original group. Likewise, if additional animals joined a group, the new configuration was counted as a separate group.

Focal follows were also conducted on delphinid groups from the small boats on the SCORE range. Many of these dolphin groups were first encountered based on M3R acoustic detections, and were therefore biased toward larger, more active groups easily sighted from the RHIBs. Groups were located after positioning the small boats at the location of the acoustic detection and then scanning the area until they

Table 1. Descriptions of the group behavioral categories used for analysis.

Behavior	Description
Travel	<ul style="list-style-type: none"> • Categorized by speed <ul style="list-style-type: none"> ○ Slow: low to the water, little leaping, slow moving, no white water. ○ Moderate: increased directional leaping, faster swim speeds, some white water. ○ Fast: rapid movement, mostly directional leaping, lots of white water. • Move in same direction. • Move steadily and/or rapidly. • Often synchronous and/or frequent surfacings.
Forage	<ul style="list-style-type: none"> • Variable direction of movement by individuals within the group. • Generally remain in same area but can be spread out. • May have high arching dives/leaps. • Visible fish chasing/tossing or bursts of rapid directed swimming.
Mill/rest	<ul style="list-style-type: none"> • Variable direction of movement by individuals within the group. • Remain in one area in close proximity. • Slow swimming speeds. • No surface active behavior, contact, or long dives; stay near surface.
Social/surface active	<ul style="list-style-type: none"> • Possible variable direction of movement by individuals within the group. • Individuals in close proximity/touching. • Frequent surface active behaviors, including leaps, tail slaps, and body slaps.

were sighted; occasionally, dolphin groups were also encountered by chance. When groups were sighted, the small boat would attempt to approach the group without disrupting their behavior. This was accomplished by remaining far enough from the group to minimize individuals approaching to bowride or otherwise changing their direction of travel, and maintaining a slow, steady vessel speed behind and to the side of the group. Once the initial sighting data were gathered, including species, group size, group spacing, group composition, and associated species, the instantaneous sampling protocol was implemented every 3–5 min using methods comparable to those used on FLIP, except without the use of binoculars and only conducted by a single observer. After the group appeared acclimated to the presence of the boat, it would maneuver ahead of the group, turn off the engine, and deploy a drop hydrophone. Behavioral sampling would continue as the group passed the boat; once they had passed, the hydrophone was retrieved and the process repeated until several recordings had been obtained or until the group was out of sight. Finally, environmental data (Beaufort sea state, swell height, cloud cover, and visibility) were collected hourly, or when conditions changed.

Acoustic Sampling

FLIP hydrophones were deployed at depths ranging from 30 to 50 m and recorded continuously. Small boat hydrophones were deployed at depths ranging from 20 to

30 m, and were deployed and recovered for each group encounter. Both AQ-1 (Teledyne Benthos, North Falmouth, MA) and HS150 (Sonar Research and Development Ltd., Beverly, U.K.) hydrophones were used. These were connected to custom built preamplifiers and bandpass filtered electronic circuit boards designed to flatten ambient noise over all frequencies (Wiggins and Hildebrand 2007). All hydrophones had a 2 kHz high pass filter and were sampled to 192 kHz with 24 bits. Analog data received on FLIP hydrophones were digitally converted using a MOTU 896HD IEEE 1394 audio interface (Mark of the Unicorn, Cambridge, MA) with gain on all channels set to maximize signal input while avoiding clipping. Since potential differences in gain between recordings could bias results, in all cases only data with a high signal-to-noise ratio (at least 6 dB SNR) were used to minimize bias. In the 2006 and 2007 FLIP deployments, the sound analysis and recording software program Ishmael (Mellinger 2001) was used to record the signal to a computer hard drive. In 2008, the data were recorded to computer hard drive using a program written in MATLAB (Mathworks, Natick, MA). The analog-to-digital converter used on board the small boats was the two-channel Fostex FR2 field memory recorder (Fostex America, Foster Electric, USA, Inc., Gardena, CA).

Call Selection

To ensure that vocalizations could be attributed to a single group, common dolphin focal follow groups selected for analysis were the only group present both acoustically and visually. In addition, each group was located within 1 km of FLIP, or generally within 500 m for the small boats, so behavior could be consistently observed, and the acoustics team could reliably detect all vocalizations produced (Richardson *et al.* 1995). All acoustic data were cut into 30 s intervals based on focal follow time stamps. Each of these 30 s files was tagged with a behavioral category and was associated with supplemental sighting data, including group size, group orientation (toward the vessel), group spacing, and sighting distance. Each 30 s file was examined using spectrograms created in a customized MATLAB program (Wiggins 2003). A 1,024 point Fast Fourier Transform (FFT) with a 50% overlapping Hann window was used to transform time series of the data into the frequency domain.

A total of six vocalization types were counted using both automated and manual techniques: clicks, click trains, pulsed calls, single whistles, whistles with harmonics, and whistle bouts. Each vocalization type had a suite of 7–9 call features that were calculated, including minimum and maximum frequencies, bandwidth, length, and total duration of each type for each 30 s interval. For whistles, the start and end frequencies, the number of steps or turns, and, if applicable, the number of harmonics were counted. This resulted in a total of 50 call features available for analysis.

Clicks were detected automatically (Roch *et al.* 2007), using bandwidth filters and threshold levels appropriate for each recording session such that the majority of clicks were detected while false positives were minimized. In most cases, this method was sufficient to count all high-quality clicks (*e.g.*, above a 6–7 dB signal-to-noise threshold); however, in some cases there were high numbers of clicks present that could not all be counted due to click envelope length constraints. Therefore, the total number of clicks detected should be viewed as a minimum estimate rather than an absolute count. Interclick interval (ICI), click length, and number of bouts (defined as a sequence of clicks spaced less than 0.4 s apart) were also calculated from automatic detections.

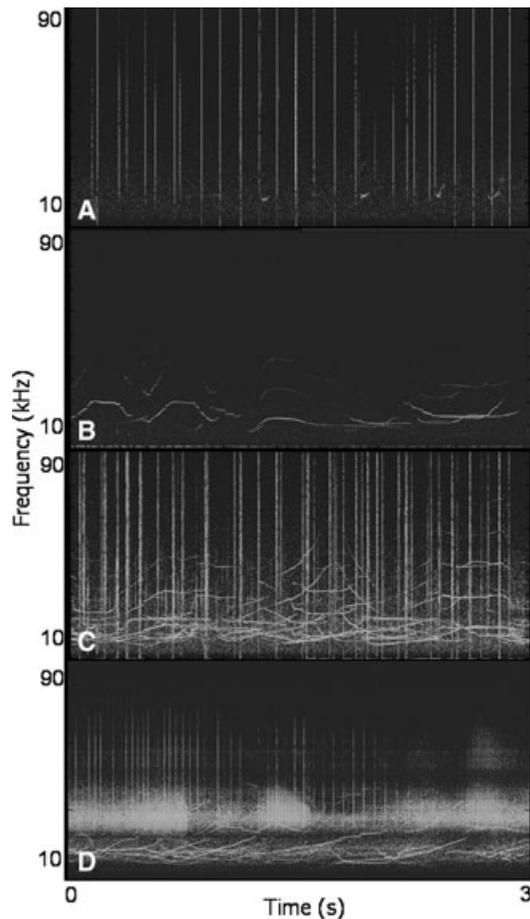


Figure 3. Spectrograms of common dolphin whistle categories: (A) distinct individual whistles with no harmonics; (B) whistles with harmonics that are still individually distinct from each other; (C and D) overlapped whistle bouts, with whistles that cannot be uniquely identified. Clicks are also visible as vertical lines in (A), (C), and (D), and pulsed calls are visible in (D).

All files were also manually examined for burst pulses, whistles, and click trains. All burst pulse and buzz-type calls were pooled for analysis as pulsed calls (Fig. 3). The start and end frequencies, bandwidth, call length, and total call duration for each 30 s interval were calculated for all pulsed calls. Click trains that were still distinct as clicks, but were obviously produced by a single animal based on their ICI, were also counted, with minimum and maximum frequency, bandwidth, and click train length recorded. Due to a high degree of variation among whistles, these were broken down into three categories for analysis. The first category was single whistles with no harmonics and with distinct start, end, minimum, and maximum frequencies (Fig. 3a). The numbers of steps or turns per whistle were also calculated, along with bandwidth, individual whistle length, and total duration

for each 30 s interval. The second category of whistles included those that were still distinct, but contained harmonics (Fig. 3b). As with single whistles, the start, end, minimum, and maximum frequencies were recorded, along with bandwidth, whistle length, total whistle duration for each 30 s interval, number of steps or turns, and, finally, the number of harmonics present. The last whistle category was that of overlapped whistles, where the start and end frequencies of individual whistles were no longer distinguishable (Fig. 3c). In this case, the start and end times, minimum and maximum frequencies, and bandwidth of each whistle bout were documented, along with the duration of the bout for each 30 s interval.

Analysis

Chi-square analyses were conducted on behavioral data to examine differences across time-of-day categories, group size, and group spacing. Acoustic detection results (including median call counts, start, end, minimum and maximum frequencies, bandwidth, call length, and durations per 30 s interval) were bootstrapped 1,000 times for a Kruskal–Wallis nonparametric analysis. This was followed by Tukey–Kramer multiple comparison tests, to examine whether any of the 50 call features were significantly different for each behavioral category (Kruskal and Wallis 1952, Jaccard *et al.* 1984).

To examine the ability to classify behavior based on vocalizations, random forest decision trees were created using call feature and associated behavioral data (Brieman 2001, Siroky 2009). Random forest models are a series of unpruned classification trees, with 5,000 bootstrap samples taken from the original data set. Two-thirds of the predictor variables were then randomly selected at each node and the best split was chosen among those. Behaviors were then classified based on a majority vote from the 5,000 trees. An estimate of the error rate was obtained using the data not used in each bootstrap iteration, termed the “out-of-bag” (OOB) data, as a test data set. Classifications based on the OOB data were then aggregated and used to calculate an error rate, called the OOB error estimate (Brieman 2001, Liaw and Wiener 2002). Random forest models were created using the entire data set to look at rates of correct classification for each behavior. Initially, this was conducted with only the 50 call features, and then group size and spacing data were included to determine their contribution to the model. Next, the Gini variable importance measure was implemented to reduce the number of call features included in the model. This metric is based on a weighted mean of the improvement of individual trees based on the inclusion of each variable as a predictor. Finally, a five-fold cross validation procedure was conducted, with the data set randomly divided without replacement such that 80% of the data were used for training and 20% were used for testing five times. Since individual 30 s segments were not independent of each other when they came from the same group, the division of data was based on number of groups rather than segments. Thus, 30 s files from one group were always included in the training or testing data sets together. Group size and spacing information were excluded from this procedure as they would not be known from acoustic data alone.

RESULTS

A total of 61 common dolphin groups were selected for analysis from 97 d of effort (Table 2), with 669 30 s intervals evaluated. Only one long-beaked common dolphin group was selected, while 43 short-beaked common dolphin groups and 17 common

Table 2. Summary of effort and the number of common dolphin groups used for analysis for all surveys, conducted from the Floating Instrument Platform (FLIP) and small boat work conducted off San Clemente Island (SCI).

Survey (year)	Survey dates	Effort (d)	Total number of groups
FLIP (2006)	2 October to 3 November	17	14
FLIP (2007)	30 October to 29 November	27	4
FLIP (2008)	17 October to 14 November	25	14
SCI (2006)	14–20 August	9	13
SCI (2007a)	13–22 April	4	1
SCI (2007b)	22–26 October	5	4
SCI (2008)	2–10 August	10	15
Total		97	61

dolphin groups not identified to species were used. To avoid pseudo-replication by counting the same group twice in 1 d, groups were chosen that were considered to be independent groups either spatially or temporally (*e.g.*, identified as independent groups by crew's nest observers on FLIP, or encountered in different parts of the SCORE range for small boats). Group size varied from 2 to 1,000, with a median size of 120 (mean = 207 ± 9). Overall focal follow duration ranged from 2 to 70 min, with a mean of 23.1 ± 2.3 min. Since FLIP was stationary, focal follow periods were constrained by the proximity of the animals and so were much shorter (mean = 12.9 ± 1.7 min); in contrast, the small boats were able to stay with focal groups and consequently had longer observation periods (mean = 31.6 ± 3.3 min). Although observations were made in Beaufort sea state of 5 or less, the majority of focal follows (49 groups) were conducted in a sea state of 3 or less, and the median Beaufort sea state was 2 (mean = 2.1 ± 0.2). While overall median focal follow group distance was 550 m (mean = 611.8 ± 31.3 m), this varied by observation platform. The median distance from FLIP for focal follow groups was 692.4 m (mean = 752.6 ± 35.6 m), while the median distance from the small boats was 150 m (mean = 210.2 ± 25.3 m). However, observations from FLIP were conducted 15 m above the water line and were carried out with both binoculars and the naked eye, whereas small boat observations were conducted just above the waterline and only with the naked eye, therefore the ability of the observer to evaluate behavior was comparable.

While multiple behaviors were counted simultaneously, the primary behavior of common dolphins was almost always traveling, with other behaviors (*e.g.*, social/surface activity or milling) counted as secondary. In addition, there were too few instances of travel/mill or travel/surface active to be considered as separate categories. Therefore, a "mixed travel" category was created for observations of travel as the primary behavior when a secondary behavior was also occurring. Additionally, surface active/social behavior always occurred with travel, and was never observed as the primary behavior. Therefore, no separate social behavior category was used for analysis, and all social behavior was included in the mixed travel category. Ultimately six behavioral categories were utilized: forage, mill, slow travel, moderate travel, fast travel, and mixed travel (summarized in Fig. 4).

Moderate travel was the dominant behavior (28.0%), with foraging the least frequent (7.5%). When the data were divided into four time-of-day categories (early morning, mid-morning, mid-afternoon, and late afternoon), the observed rates

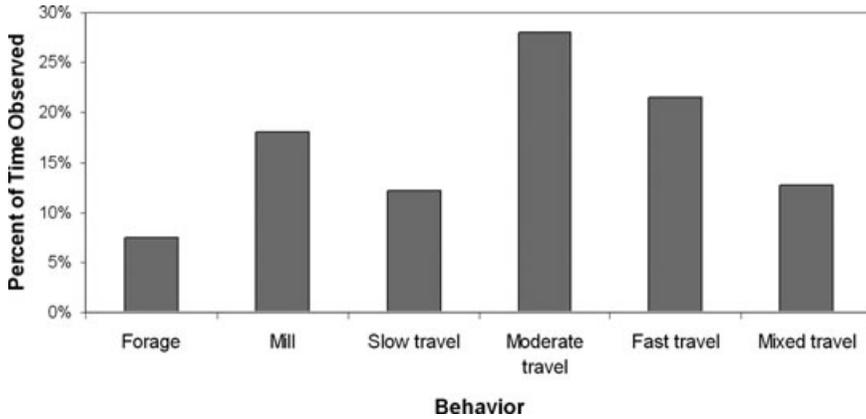


Figure 4. Behavioral categories for common dolphins. The bars show the percent time animals were observed in each behavioral state.

of each behavior in each time period were highly significantly different ($\chi^2_{15} = 9.76 \times 10^{-18}$, $P < 0.001$; Fig. 5). The little foraging that was observed largely occurred in the morning, with a peak at mid-morning. Slow travel also peaked at mid-morning and decreased throughout the day, while moderate and fast travel increased throughout the day, indicating an increase in activity and travel speed throughout the day. Finally, milling and mixed travel peaked during the mid-afternoon period.

Group size varied significantly across behavioral categories ($\chi^2_{20} = 2.47 \times 10^{-47}$, $P < 0.001$; Fig. 6). Fast traveling occurred in larger groups (66% of groups had 101–500 animals) while slow travel mainly occurred in midsize groups (47.6% of groups had 51–100 animals). Foraging groups were mostly comprised of both smaller and larger groups; 40% of groups had 11–50 animals and 56% of groups had

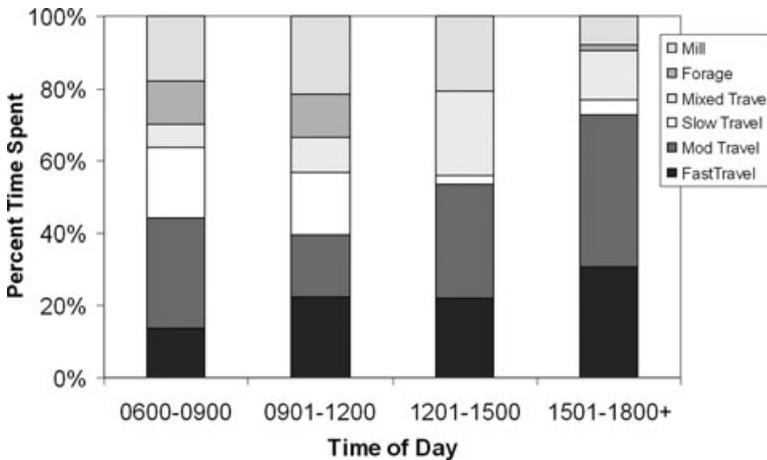


Figure 5. Daily behavioral patterns of common dolphins. Observed rates of all behaviors in each time period were significantly different from expected using chi-square analyses.

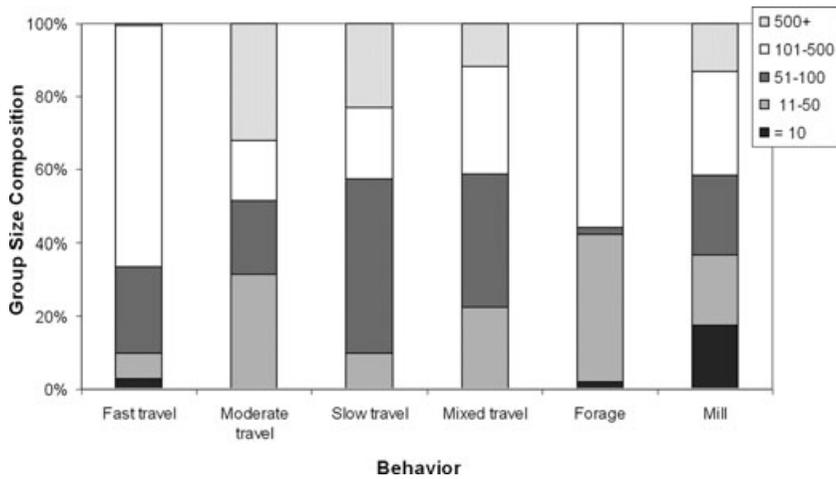


Figure 6. Group size composition for each behavior category. The best group size estimates were lumped as <10 animals per group, 11–50, 51–100, 101–500, or >500 animals per group.

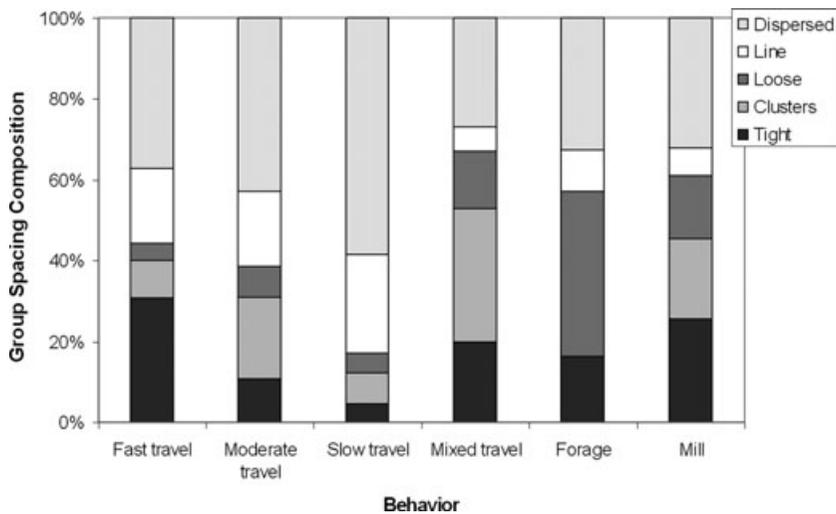


Figure 7. Group spacing composition for each behavior category. Group spacing was defined as all animals less than one body length apart (tight), approximately one body length apart (loose), or greater than one body length apart (dispersed), clustered in small groups tightly spaced (clustered) or in a chorus line or parade line formation (line).

101–500 animals. Finally, while milling occurred in groups of all sizes, it dominated the smallest size class (≤ 10 animals). Overall, fast travel involved the largest groups (median = 140) and milling involved the smallest groups (median = 70). Group spacing also varied significantly across behavioral categories ($\chi^2_{20} = 1.38 \times 10^{-19}$, $P < 0.001$; Fig. 7). While traveling groups tended to be spread out, particularly at slower swimming speeds (fast travel = 37.1%; moderate travel = 42.9%; slow

travel = 58.5%), the animals appeared to come closer together as travel speed increased, with 30.1% of fast travel groups tightly spaced, compared to 10.7% of moderate travel and only 4.6% of slow travel groups. In contrast, foraging groups were predominately loosely spaced (40.8%); mixed travel groups were most often observed in clusters (32.9%); and milling groups were observed in all formations.

Kruskal–Wallis nonparametric tests and Tukey–Kramer multiple comparison tests indicated that differences across each behavioral category for all 50 call features were significant; for each call feature there was at least one behavior that ranked outside the confidence intervals of the other behaviors. The highest number of clicks and pulsed calls were recorded during fast travel behavior, with median values of 388 clicks and 3 pulsed calls per 30 s interval (mean = 464 ± 35.3 and 5.5 ± 0.6 , respectively), whereas the fewest clicks were recorded during moderate travel (median = 203.5, mean = 421 ± 40.7) and slow travel (median = 210, mean = 293 ± 26.4). The fewest pulsed calls were recorded during foraging (median = 0, mean = 1.2 ± 0.2) and slow travel (median = 0, mean = 1.7 ± 0.2).

The highest number of single whistles were recorded during fast travel (median = 5.5, mean = 6.8 ± 0.6) and moderate travel (median = 7, mean = 7.9 ± 0.6); the highest number of whistles with harmonics also occurred during fast travel (median = 4, mean = 5.0 ± 0.4). In addition, both single whistles and whistles with harmonics were more complex and had the most harmonics during fast travel (single whistles: median = 0.5, mean = 0.7 ± 0.1 number of steps; whistles with harmonics: median = 2, mean = 2.1 ± 0.2 number of steps, and median = 1, mean = 1.1 ± 0.1 number of harmonics). The fewest number of both types of whistles occurred during slow travel (single whistles: median = 1, mean = 4.6 ± 0.6 ; whistles with harmonics: median = 0, mean = 2.0 ± 0.3). Additionally, fast travel, moderate travel, and mixed travel exhibited the longest duration and bandwidth of whistle bouts. Mean whistle bout duration was 11.3 ± 0.9 s for fast travel, 10.4 ± 0.9 s for moderate travel, and 9.7 ± 1.0 s for mixed travel, while mean whistle bout bandwidth was 20.6 ± 1.5 kHz for fast travel, 15.2 ± 1.2 kHz for moderate travel, and 19.5 ± 19.7 kHz for mixed travel. In contrast, during foraging mean whistle bout duration was only 3.8 ± 0.6 s, and mean whistle bout bandwidth was only 9.4 ± 1.1 kHz, less than half the bandwidth recorded during fast travel. Individual whistles were shortest during foraging (median = 0.2 s, mean = 0.2 ± 0.02 s), and were almost the least complex, only above slow travel in the fewest number of steps (forage: mean = 0.4 ± 0.1 ; slow travel: mean = 0.3 ± 0.1) and fewest number of harmonics (forage: mean = 0.8 ± 0.1 ; slow travel: mean = 0.8 ± 0.1).

Random forest models were initially created using all 50 call features. Additional models were then created using the top 30 ranked call features (Gini > 10) and top 10 ranked call features (Gini > 20). This was done to remove potentially spurious or autocorrelated data, improving model performance. Ultimately included in the model were all click variables (click length, ICI, click count per 30 s interval, and number of click bouts per 30 s interval), pulsed call bandwidth, single whistle length and duration, the count of single whistles per 30 s interval, the count of whistles with harmonics per 30 s interval, and the duration and bandwidth of whistles with harmonics.

Rates of correct classification of behavioral state by random forest models changed notably with the inclusion of group size and group spacing. In Table 3, results are presented both with and without the inclusion of group size and group spacing. When group size and spacing were excluded from the model with all 50 call features, the OOB error rate was 56.9%. With group size and spacing data included, the

Table 3. Correct classification rates of surface behavior using random forest decision trees based on call features, with group size and group spacing included as a predictor variable in all but the first column.

Behavior	All 50 call features (excluding group size and spacing) (%)	All 50 call features (%)	Top 30 call features (%)	Top 10 call features (%)
Fast travel	52.1	69.4	75.7	80.6
Moderate travel	73.0	81.9	83.5	84.6
Slow travel	24.1	42.7	47.6	59.8
Mixed travel	19.8	24.7	24.7	41.2
Forage	26.0	46.0	46.0	58.0
Mill	22.2	39.7	42.1	52.1

OOB error decreased to 43.1%. When only the top 30 call features were included, as well as group size and spacing data, the OOB error rate declined further to 40.3%. Finally, when only the top 10 call features, group size, and group spacing data were included, the OOB error rate was only 32.7%. Classification rates increased for all behaviors across each of the four model iterations, with improvement more than double in some cases. The best classified behaviors were fast travel at 80.6% and moderate travel at 84.6% correct classification rates.

The cross-validated predictive random forest models were created using both the top 30 call feature data set and the top 10 call feature data set; both excluded group size and group spacing data, as these would not be known from an acoustic recording. Results were better than expected by chance for both data sets for all behaviors except mill (Table 4), although no behaviors were predicted as successfully as they had been classified in the original random forest models. The OOB error rate for the top 30 call feature data set was 39.9%, and 35.8% for the top 10 call feature data set.

DISCUSSION

Common dolphins encountered in the region off San Clemente Island in the SCB were most often observed to be traveling. A distinct diurnal movement pattern has been observed, with common dolphins moving offshore into deeper waters in the late

Table 4. Correct prediction rates of surface behavior using random forest decision trees based on the five-fold cross validation technique, with group size and spacing data excluded.

Behavior	Top 30 call features (%)	Top 10 call features (%)
Fast travel	55.9	60.1
Moderate travel	32.0	42.0
Slow travel	19.2	39.2
Mixed travel	65.6	64.6
Forage	26.8	30.5
Mill	7.1	11.8

afternoon and evening, and returning inshore at dawn.¹ This movement, coupled with the low rate of observed daytime foraging, suggests that this population is foraging at night, likely on the rising deep scattering layer (DSL) present in deeper waters, which supports the findings of Ohizumi *et al.* (1998). In addition, daytime foraging was primarily observed in the morning, and may represent opportunistic feeding on epipelagic schooling fish. Morning foraging was followed by a period of increased milling and mixed travel/social behavior. This pattern is similar to those observed for other dolphin species. In dusky dolphins (*Lagenorhynchus obscurus*) in Argentina that feed on schools of anchovy (*Engraulis anchoita*), morning foraging bouts are followed by a period of rest and then an increase in social behavior. Dusky dolphins in New Zealand, on the other hand, feed on the rising DSL at night, and tend to remain near land in the morning, then move offshore into deeper water in the afternoon and evening (Würsig *et al.* 1991). Hawaiian spinner dolphins (*Stenella longirostris*) also feed on the DSL, and follow an inshore–offshore diurnal pattern. Alternating rest and social behavior, they remain in shallow bays during the day, and then move offshore in the late afternoon to begin foraging (Norris and Dohl 1980, Norris *et al.* 1994, Benoit-Bird and Au 2003).

Common dolphin nighttime vocalization data had numerous call periods with patterns similar to daytime foraging vocalization patterns: discrete click bouts and few whistles or pulsed calls, with whistles frequently occurring at the start and end of click bouts. Further analysis of these nocturnal call patterns is needed, but the qualitative pattern supports the idea that this population of common dolphins is feeding at night on the DSL. This is similar to the pattern found by Goold (2000), who recorded common dolphin vocalizations off the British Isles and found peaks in “acoustic contact” (the number of call bouts) in early morning and late evening that were presumed to correspond with feeding behavior. In addition, Goold found a call rate minimum in the early afternoon period, corresponding in this study to the peak in mill and slow travel behaviors, both of which had fewer calls. Osnes-Eire (1999) found that the stomach contents of short-beaked common dolphins bycaught in fisheries off California were dominated by myctophid and squid species, and the stomach contents of long-beaked common dolphins had myctophid, epipelagic fish, and squid remains. These findings also lend support to the hypothesis that common dolphins in this region are primarily engaged in nighttime feeding.

Vocalization patterns during travel are markedly different than during foraging, with rates of clicks, whistles, and pulsed calls increasing as travel speed increases. In addition to a higher overall call rate during fast travel, whistle bouts were longer and more broadband (indicating the presence of harmonics), and individually distinguishable whistles were more complex and had more harmonics. Ansmann *et al.* (2007) described common dolphin whistles from the Celtic Sea and examined whistle parameters against behavior and group size. While harmonics were not recorded in this case, the authors did find whistles to be more complex when dolphins were traveling. Petrella *et al.* (in press) also found longer, more broadband whistles during travel behavior than during foraging behavior for common dolphins, although whistle density (number of whistles per second) was higher during foraging. Weilgart and Whitehead (1990) recorded North Atlantic pilot whale (*Globicephala melaena*) calls and examined comparable behavioral categories. They also found an increase

¹Personal communication from Kait Frasier, Scripps Institution of Oceanography, University of California San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0205, April 2009.

in whistling with increased travel speed, and recorded less complex whistles during milling. More whistles and pulsed calls were also recorded during “directive swimming” in beluga whales (*Delphinapterus leucas*) than most other behavioral states except social interactions (Sjare and Smith 1986).

There are no studies correlating common dolphin clicks or pulsed calls with behavior; however a comparison with other species shows mixed results. In a study similar to this one, few whistles and pulsed calls, and fewer than expected echolocation clicks were recorded during foraging bouts of Hawaiian spinner dolphins (Benoit-Bird and Au 2009). Also similar to this study, Brownlee (1983) recorded the most clicks and whistles during travel for Hawaiian spinner dolphins, and the fewest clicks, whistles, or burst pulses during milling behavior. However, Brownlee (1983) found a high rate of clicks during foraging. Furthermore, high click rates were recorded during foraging for Pacific humpback dolphins (*Sousa chinensis*); during “surface activity” (which was attributed to foraging in this study) for pilot whales; and during feeding bouts of killer whales (Weilgart and Whitehead 1990, Van Parijs and Corkeron 2001, Simon *et al.* 2007). Burst pulses were also associated with foraging and social behavior in Pacific humpback dolphins (Van Parijs and Corkeron 2001) and with foraging in killer whales (Simon *et al.* 2007).

An increase in echolocation clicks may be expected during foraging as the dolphins detect and localize prey targets, and an increase in communicative calls anticipated as dolphins forage cooperatively. Therefore, it may be that the multi-directional nature of foraging behavior, coupled with the strong directionality and rapid attenuation rates of clicks (Au 1993) are leading to clicks and pulsed calls being missed as the dolphins turn away from the hydrophone. However, Benoit-Bird and Au (2009) recorded more clicks during the transitions between foraging stages than during discrete foraging bouts. While they attributed some of that difference to missed clicks, they also theorized that clicks may be used to coordinate the group or even as a form of communication, and therefore fewer clicks may be produced during discrete feeding bouts. In addition, whistles or pulsed calls may be used to signal the start and end of foraging bouts, but may not be produced during discrete periods of foraging (Henderson, unpublished data). To investigate this further, research is being conducted in the SCB using a suite of widely spaced (~1 km) hydrophones to determine if calls are being produced but missed on a single hydrophone, or if call rate estimation by a single hydrophone is accurate.

Group size and spacing data were strongly correlated with behavior and seemed additionally to influence call rates. While call rates of common dolphins generally increase with group size it is not a linear relationship; in addition, call rates were highest in dispersed groups followed by tightly clustered groups, with the fewest calls in loosely aggregated groups. Weilgart and Whitehead (1990) also did not find a correlation between the numbers of whistles produced and group size for pilot whales. Rather, they recorded more whistles when more subgroups were present. These relationships are likely tied to behavior; fast traveling groups had the highest call rates of all types of calls and were predominantly spread out in large groups or were tightly clustered. In contrast, foraging groups produced fewer calls and were most often loosely aggregated in both small and large groups. Therefore, the role of behavior is important to call production rates, and an increase in group size alone cannot predict an increase in calls without additional information.

There were very positive results in the use of vocalization data to classify behavioral states, and classification rates improved as only the most important call features were included in the random forest model. While some behaviors such as fast and moderate

travel were classified very well, other behaviors were not as well classified. Still, all behaviors were classified far better than by chance. When the five-fold cross validation was performed, correct prediction rates were lower than the original classification rates; however, all behaviors except for mill were still predicted better than by chance.

The classification model results may reflect the limitations of this data set, since the behaviors that were classified most successfully were also those that dominated the behavioral budget of this population. It may be that as additional focal follow data are collected with a broader range of behaviors, the classification models will improve. It could also be that behavioral states may not have been correctly identified and therefore calls were incorrectly categorized and the models were corrupted. This caveat is particularly salient for observations made from the small boats, where behavior may still be impacted by the presence of the boat even after a period of acclimation, and where perspective of the whole group may be limited in rough conditions or for very large groups. Misclassifications of behavior could have occurred on FLIP as well, since there were multiple observers used across the three years of sampling. However, there was consistency in the primary observers and training methods in order to reduce interobserver differences and specifically to minimize the possibility of misclassification. There could also be too much overlap in the types and rates of vocalizations produced in certain behaviors to discretely classify them. Finally, the inclusion of multiple common dolphin groups not identified to species could have affected the results; while preliminary analyses comparing long- and short-beaked common dolphin vocalizations found no differences (Soldevilla 2008), there could in fact be behavioral and vocalization differences between the species. However, long-beaked common dolphins are found predominantly inshore in the SCB (Heyning and Perrin 1994, Reeves *et al.* 2002), and short-beaked common dolphins dominated the sighting data. Thus, it is more likely that most of the unidentified groups were in fact short-beaked common dolphins and a species-difference effect did not influence the model results. Despite these possible limitations, this modeling technique was also applied to Pacific white-sided dolphin vocalization and behavioral data, with comparable classification success (Henderson, unpublished data). In that case, forage and moderate/fast travel were the top predicted behaviors at 85.9% and 77% correct classification, respectively. Therefore, these results support the idea that this technique is limited by lack of data, not by poorly categorized behavior or overlap in call types with behavior.

Further work with more species and additional data will help to strengthen these models and reduce uncertainty. These more robust models can eventually be used to predict the behavior of animals from vocalizations recorded at night or from autonomous instruments. This will permit greater insight into dolphin habitat use across longer spatial and temporal scales than can be learned from visual observations alone. These models can also be used as a baseline of vocal and surface behavior to compare against observations from impacted areas, allowing for a greater understanding of the effect of vessel traffic and other anthropogenic noise, and prey reduction through overfishing.

Conclusions

Daily behavioral patterns of common dolphins in the SCB are dominated by inshore/offshore travel. A small amount of foraging was observed during the morning, but most foraging is occurring at night, likely on the DSL, after the dolphins

have moved further offshore into deeper waters. Surface behavior, group size, and group spatial configurations were all correlated, with the largest groups engaged in traveling, while milling and foraging occurred in smaller groups; foraging groups were also spaced more loosely, while traveling groups were either very spread out or tightly clustered. Analyses of vocalizations indicate an increase in the number of clicks, pulsed calls, and whistles, as well as an increase in the complexity of whistles with travel speed; most vocalizations were recorded during fast travel, while the fewest clicks, pulsed calls, and simplest whistles were recorded during slow travel and forage. Models of call features have proven to be capable of classifying and predicting surface behavior, and could be used to classify behavior when visual data are not available, allowing passive acoustic monitoring techniques to be integrated into future behavioral research.

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