

Classification of behavior using vocalizations of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*)^{a)}

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Surface behavior and concurrent underwater vocalizations were recorded for Pacific white-sided dolphins in the Southern California Bight (SCB) over multiple field seasons spanning 3 years. Clicks, click trains, and pulsed calls were counted and classified based on acoustic measurements, leading to the identification of 19 key call features used for analysis. Kruskal-Wallis tests indicated that call features differ significantly across behavioral categories. Previous work had discovered two distinctive click Types (A and B), which may correspond to known subpopulations of Pacific white-side dolphins in the Southern California Bight; this study revealed that animals producing these different click types also differ in both their behavior and vocalization patterns. Click Type A groups were predominantly observed slow traveling and milling, with little daytime foraging, while click Type B groups were observed traveling and foraging. These behavioral differences may be characteristic of niche partitioning by overlapping populations; coupled with differences in vocalization patterns, they may signify that these subpopulations are cryptic species. Finally, random forest decision trees were used to classify behavior based on vocalization data, with rates of correct classification up to 86%, demonstrating the potential for the use of vocalization patterns to predict behavior. © 2011 Acoustical Society of America. [DOI: 10.1121/1.3592213]

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I. INTRODUCTION

The study of cetacean behavior can lead to insights into their social structure and habitat use (Herman, 1979; Shane *et al.*, 1986; Baird and Whitehead, 2000; Craig and Herman, 2000; Gowans *et al.*, 2001). However, cetaceans spend a limited amount of time at the surface, and long-term at-sea visual observations are limited by weather and budget considerations. Passive acoustic monitoring using autonomous instruments to record vocalizations of cetaceans can be conducted for long periods of time at relatively low cost (Wiggins, 2003; Mellinger *et al.*, 2007; Wiggins and Hildebrand, 2007), but thus far has been largely limited to ascertaining presence of animals and species identification (Sirovic *et al.*, 2004; Soldevilla *et al.*, 2008; Baumann-Pickering *et al.*, 2010). Some work has been conducted to combine visual and acoustic sampling in wild populations of a few delphinid species (Ford, 1989; Weilgart and Whitehead, 1990; Dawson, 1991; Herzing, 1996; Van Parijs and Corkeron, 2001), but few studies have attempted to model the relationship between surface activity and acoustic behavior (e.g., Cook *et al.*, 2004; Quick and Janik, 2008).

Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) are a cold temperate water species, distributed throughout the north Pacific. They are generally found between 38° and 47°N (Reeves *et al.*, 2002), although their range extends further south along the west coast of North America as far as the southern tip of Baja California, Mexico. Group size ranges from the tens to hundreds along the coast and into the thousands in the open ocean (Reeves *et al.*, 2002). There is both morphological and genetic evidence suggesting the existence of at least two distinct populations of Pacific white-sided dolphins in the eastern North Pacific (Walker *et al.*, 1986; Lux *et al.*, 1997). There appears to be a California/Oregon/Washington population found north of about 32°N, and a Baja California population distributed south of 34.5°N (Walker *et al.*, 1986). Therefore, both ranges extend into the Southern California Bight (SCB) where the two populations have overlapping distributions.

Pacific white-sided dolphins produce echolocation clicks that range in frequency from 20 to over 100 kHz (Evans, 1973; Richardson *et al.*, 1995; Soldevilla *et al.*, 2008). Echolocation clicks are primarily used in foraging and navigation, although they may be used for communication as well (Dawson, 1991). In addition to clicks, Pacific white-sided dolphins produce burst pulses and buzzes, which are series of rapid click trains with very short inter-click intervals that are used for both foraging and communication (Lammers *et al.*, 2003; Lammers *et al.*, 2006). There is some debate over whether Pacific white-sided dolphins produce

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whistles (Caldwell and Caldwell, 1971; Rankin *et al.*, 2007); in any case, whistles are at most rare and will not be considered in this analysis.

Soldevilla *et al.* (2008) determined that there are two distinct click types made by Pacific white-sided dolphins in the SCB. Type A clicks, with frequency peaks at 22, 27.5, and 39 kHz, were recorded throughout the SCB, while Type B clicks, with frequency peaks at 22, 26, and 37 kHz, were only recorded near San Clemente and Santa Catalina Islands (Soldevilla *et al.*, 2010), which were the furthest inshore sites recorded in the SCB. Soldevilla (2008) hypothesized that the two click types may be representative of the two populations, with Type A clicks produced by the northern population and Type B clicks produced by the southern population. Soldevilla determined that Type A clicks were most common at night, with peak production at dawn and dusk, whereas Type B clicks were more common during the daytime. The predominance of Type A clicks at night could indicate nighttime feeding, likely on mesopelagic fish and squid associated with the scattering layer (Norris *et al.*, 1985; Benoit-Bird and Au, 2003), while the peak in Type B clicks during daylight hours could signify foraging on pelagic fishes. We hypothesize that this may represent resource partitioning, which we examine through behavioral and acoustic comparison. If the types of calls produced and their rate of production can be associated with specific behavioral states, these vocalization patterns could then be used to predict behavior and generate a model of habitat use that could assist in parsing out whether these subpopulations are partitioning resources or otherwise utilizing the SCB differently.

This study has three principal objectives in considering surface behavioral patterns of Pacific white-sided dolphins and concurrent vocalizations: (i) to investigate the correlation of surface and acoustic behavior, (ii) to determine how those behavioral and acoustic patterns differ between click Type A and click Type B groups, and (iii) to explore the capability of using vocalizations to classify behavior.

II. METHODS

A. Study area and survey platforms

This research was conducted in the SCB near San Clemente Island, about 60 miles offshore of San Diego (Fig. 1). Data were obtained from August 2006 through November 2008 using two research methods. The primary method was surveys conducted on the Scripps Institution of Oceanography R/P Floating Instrument Platform (FLIP), a live-aboard stationary moored platform from which visual and acoustic observations were simultaneously conducted (Fisher and Spiess, 1963). FLIP was deployed during the fall of three sequential years northeast of San Clemente Island, (Fig. 1, inset): from October 2 to November 3, 2006 in 637 m water depth, from October 30 to November 29, 2007 in 840 m water depth, and from October 17 to November 14, 2008 in 347 m water depth.

The secondary research method was small boat surveys conducted within the Southern California Offshore Range (SCORE). This work was done in conjunction with the Naval Undersea Warfare Center's Marine Mammal Monitoring

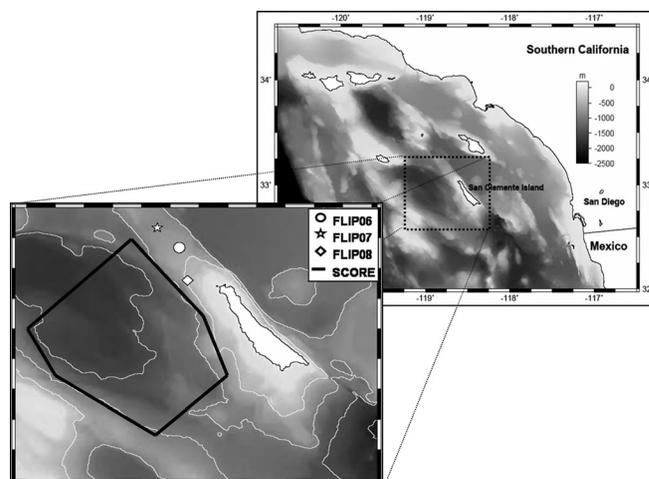


FIG. 1. Bathymetric map of Southern California Bight, with an inset of San Clemente Island. The shapes indicate the locations of FLIP moorings in 2006, 2007, and 2008. The dark line is the boundary of the SCORE range.

on Navy Ranges (M3R) program (Jarvis *et al.*, 2003; Moretti *et al.*, 2004; Falcone *et al.*, 2009). The M3R system was developed to detect and localize marine mammal sounds. Experienced observers in small boats located the animals and verified species for M3R acoustic detections. Three rigid hulled inflatable boats (5.3 m to 5.9 m in length) were used for these surveys, conducted within the SCORE range August 14–20, 2006, April 13–22 and October 22–26, 2007, and August 2–10, 2008.

B. Visual observations and behavioral sampling

Trained marine mammal visual observers conducted focal follow observations using handheld 7 × 50 Fujinon binoculars from the top deck level of FLIP, 15.24 m above the waterline. Observations were carried out on dolphin groups within 1 km to ensure that the focal observer could consistently determine the behavioral state of the majority of the group. Additionally, 1 km was chosen as a conservative distance within which the acoustics team would reliably be able to detect all vocalizations produced (Norris *et al.*, 1994; Richardson *et al.*, 1995). Focal follows were conducted using instantaneous sampling methods (Altmann, 1974; Mann, 1999), whereby behavioral states and pertinent activities (e.g., tail-slapping, high-arch dives, porpoising leaps) were recorded along with bearing, reticle, estimated group size, orientation toward FLIP, and direction of travel every 1 to 3 min. Effort was made to record behavior with a consistent interval period (e.g., 1 min) within each group focal follow; however, the interval varied slightly between groups depending on the surfacing period of the animals, the size of the group, or due to inter-observer differences. Groups were defined as animals in apparent association, moving in the same direction and generally carrying out the same activity, following Shane (1990). There were five behavioral categories used: slow, moderate, or fast travel; mill; and forage (see Henderson *et al.*, 2011, for detailed behavioral descriptions). Observers monitored the entire group to assess behavior, which was classified as what the majority of the group

was doing. Behaviors could also be combined if the group as a whole was performing multiple behaviors, or if different portions of the group were performing different behaviors. Behavioral sampling continued for the duration of the time the group was on the face side of FLIP and within 1 km. Environmental data, including Beaufort sea state, swell height, cloud cover, visibility, and overall sighting conditions, were recorded every hour or when conditions changed.

Focal follows were also conducted on delphinid groups from the small boats on the SCORE range. When a group was sighted, the vessel would attempt to approach the group without disrupting their behavior. Once the initial sighting information, including species, group size, and group envelope (the overall spread of the group) was gathered, instantaneous sampling protocol was implemented every 1 to 3 min using methods comparable to those used on FLIP. The only difference between methods was that small boat focal follow observations were made with the naked eye only, and so no bearing or reticle information was recorded. After the group appeared acclimated to the presence of the vessel, the boat would maneuver ahead of the group and deploy a drop hydrophone. Behavioral sampling would continue as the group passed the boat; once the dolphins 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 were collected hourly or when conditions changed.

C. Acoustic sampling

Multi-channel hydrophone arrays were deployed from FLIP at depths ranging from 30 to 50 m and recorded continuously day and night. While configurations for these six-channel arrays varied from year to year, data from a single channel were used consistently across years. Single-channel hydrophones were deployed from small boats at depths ranging from 20 to 30 m and were recovered after each group encounter. HS150 (Sonar Research and Development Ltd, Beverly, UK) hydrophones were used in all arrays, with a sensitivity of -208 dB re 1 V/ μ Pa and a relatively flat response (± 2 dB) up to 100 kHz. Each hydrophone was connected to custom built preamplifiers and bandpass-filtered electronic circuit boards designed to flatten ambient noise over all frequencies (Wiggins and Hildebrand, 2007). Analog signals from all hydrophones were filtered with a 2 kHz highpass filter and were digitally sampled at 192 kHz and 24-bits. Analog data received on FLIP hydrophones were digitally converted using a MOTU 896HD firewire audio interface with an internal anti-alias filter (Mark of the Unicorn, Cambridge, MA). While potential differences in gain between recordings could bias results, in all cases only data with a high signal-to-noise ratio (at least 7 dB re 1 μ Pa) were used to minimize that bias. In the 2006 and 2007 FLIP deployments, the sound analysis and recording software Ishmael (Mellinger, 2001) was used to directly record the signal to computer hard-drive, while in 2008 the data were recorded to computer hard-drive using a custom 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).

D. Call selection

Data from Pacific white-sided dolphin focal follow groups were selected for analysis based on the following criteria: only a single group could be present both acoustically and visually so that all vocalizations could be confidently attributed to that group; and the group needed to be approaching, or at least moving parallel to, the hydrophone arrays for most of the focal follow encounter. The presence of a single group was monitored visually throughout the group encounter, and verified acoustically during post-processing by examining the signal-to-noise ratio of the calls to ensure all calls were produced at a similar level and therefore presumably by the same group. Dolphin calls, particularly clicks, are highly directional and attenuate rapidly (Au, 1993). Thus, if the dolphins are pointed away from the hydrophone or at too great a distance, calls could be missed. The exceptions to this were foraging and milling groups, since they are inherently multi-directional by definition. Finally, the peak/notch structures of clicks were examined to ensure that only one click type was produced during each focal group encounter.

All acoustic data were segmented into 30-s, non-consecutive intervals based on focal follow observation times. All segments were assigned a behavior category, identified by click group type based on peak frequencies (Soldevilla *et al.*, 2008; Soldevilla *et al.*, 2010), and associated with supplemental sighting data, including group size, group orientation relative to the hydrophone, sighting distance, and Beaufort sea state. These 30-s intervals were used as our units of analysis. While we recognize that intervals from the same group may not be independent, we did not use consecutive intervals, and so each was separated by at least 30 s and up to several minutes, depending on when the next observation time occurred. Therefore, calls in one interval may not be auto-correlated with calls in another interval.

Each 30-s file was then examined using spectrograms created in a customized MATLAB® program (Wiggins, 2003). A 1024-point Fast Fourier Transform (FFT) with a 50% overlapping Hann window was used to transform time series of the data into the frequency domain for analysis.

Clicks were detected automatically (Roch *et al.*, 2007), using bandwidth filters and conservative 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 7–8 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; as the minimum peak-to-peak value was set at 50 μ s, clicks that occurred within that interval were not counted separately. Therefore, the total number of clicks detected is a minimum estimate rather than an absolute count. Finally, inter-click interval (ICI), click duration, and number of bouts per 30-s interval were also calculated from automatic detections. Click bouts were defined as

TABLE I. Definitions of click and pulsed call types.

Call Type	Definition
Single Click	Echolocation pulse ranging in frequency from 20 to over 100 kHz
Click Bout	Period of clicking by one or more animal; clicks separated by less than 0.4 s
Click Train	Series of distinct clicks produced by a single animal as determined by the ICI
Pulsed Call	Sequence of pulses with low ICI and high repetition rate; includes burst pulses and buzzes
Pulsed Call Series	Stereotyped, repeated series of at least two pulsed calls

groups of clicks spaced less than 0.4 s apart; typical ICIs for delphinid clicks range from 10–45 ms (Au, 1993), and so a separation of 0.4 s ensures clicks in one bout are distinct from the next bout (see Table I for a description of click and call categories).

All files were also manually examined for burst pulses, buzz calls, and click trains. Burst pulses are rapid series of broadband clicks with short inter-click intervals thought to be used for communication (Lammers *et al.*, 2003). Buzzes, often referred to as “terminal buzzes,” are typically produced at the end of a click train as a dolphin is approaching its target (Johnson *et al.*, 2006; Benoit-Bird and Au, 2009; Verfuss *et al.*, 2009). However, as these calls occur on a spectrum (Murray *et al.*, 1998), the burst pulse and buzz categories were lumped together as “pulsed calls” for analysis. These typically had an ICI <3 ms (e.g., Lammers *et al.*, 2004; Au and Hastings, 2010) and were separated from click trains based on the analyst’s ability to perceive individual clicks. In addition, a number of stereotyped call series (Rankin *et al.*, 2007) were identified in the data, which were categorized separately from individual pulsed calls (e.g., Fig. 2, Table I). These pulsed call series occurred in repeated patterns of at least 2 pulsed calls, with 9 unique series identified, and many of these series were repeated throughout the data. The minimum and maximum frequencies, bandwidth, and duration of each of these call types were measured. Unlike click bouts that could be produced by multiple animals, click trains were considered series’ of distinct clicks (as opposed to burst pulses) that were obviously produced by a single animal based on the spatial characteristics of the ICIs. Click trains were also counted, with minimum and maximum fre-

quency, bandwidth, and click train length recorded (Fig. 3, Table I).

Ultimately there were 19 call features selected for this analysis, all calculated in 30-s intervals: (i) ICI, (ii) click duration, (iii) number of clicks, (iv) number of click bouts, (v) number of pulsed calls, (vi) pulsed call duration, (vii) minimum pulsed call frequency, (viii) maximum pulsed call frequency, (ix) pulsed call bandwidth, (x) number of call series, (xi) call series duration, (xii) minimum call series frequency, (xiii) maximum call series frequency, (xiv) call series bandwidth, (xv) number of click trains, (xvi) click train duration, (xvii) minimum click train frequency, (xviii) maximum click train frequency, and (xix) click train bandwidth.

E. Analysis

Kruskal-Wallis nonparametric tests, followed by Tukey-Kramer multiple comparison tests, were used to examine whether any of the 19 call features were significantly different for each behavioral category (Kruskal and Wallis, 1952; Jaccard *et al.*, 1984). To examine the ability to predict behavior based on vocalizations, random forest decision trees were created using call features and associated behavioral data (Brieman, 2001; Siroky, 2008). Random forest models are a series of unpruned classification trees, where 5000 bootstrap samples are taken from the original dataset, then a third of the predictor variables are randomly selected at each node, and the best split is chosen among those. The behaviors are then classified based on a majority vote from the 5000 trees. An estimate of the error rate is obtained using the data not used in each bootstrap iteration, termed the “out-of-bag” (OOB) data, as a test dataset. Classifications based on the OOB data are then aggregated and used to calculate an error rate, called the OOB error estimate (Brieman, 2001; Liaw and Wiener, 2002).

Random forest models were first created using the entire dataset to look at rates of correct classification for each behavior for all groups combined, as well as for click Type A and B groups separately. Initially, this was conducted with only the 19 call features, and then estimated group size was included to evaluate the importance of group size 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 (Breiman, 2004).

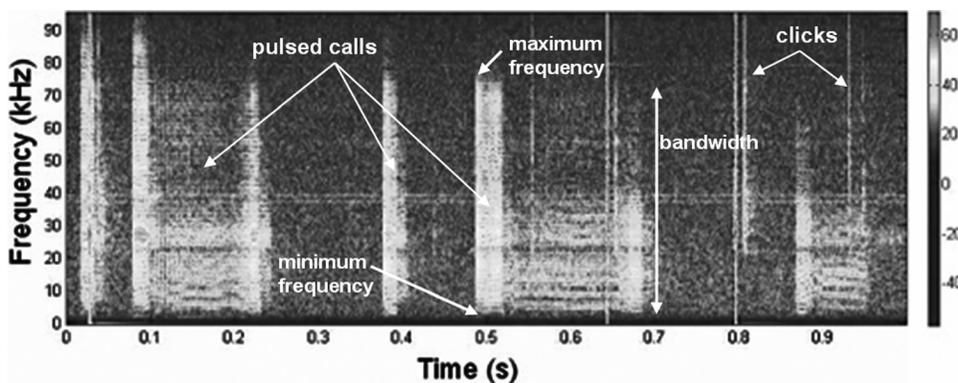


FIG. 2. Spectrogram of pulsed call series. Time in seconds is on the x axis, frequency in kHz is on the y axis, and intensity of the signal is indicated by the color bar. The minimum frequency, maximum frequency, and bandwidth of one pulsed call are indicated. Clicks are also visible in the spectrogram.

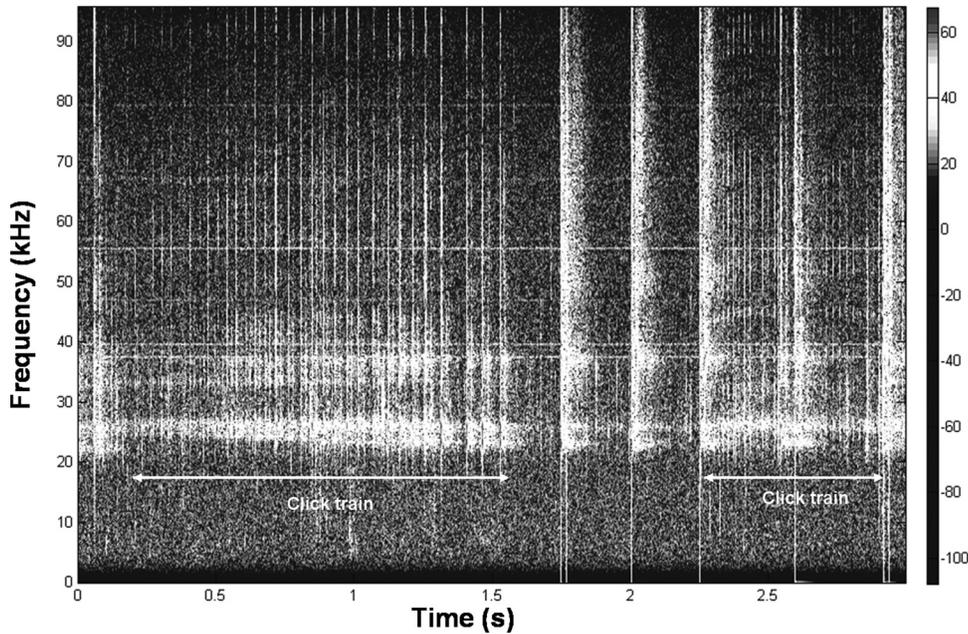


FIG. 3. Spectrogram of click trains. Time in seconds is on the x axis, frequency in kHz is on the y axis, and intensity of the signal is indicated by the color bar. Two click trains, presumed to be produced by individuals based on the spatial characteristics of the clicks and ICIs, are highlighted.

III. RESULTS

A. Survey effort

There were a total of 26 different groups selected for analysis from 97 days of effort (Table II), with 525 thirty-second intervals evaluated. Eleven of the groups were click Type A groups, while 15 were click Type B groups. All data were collected in Beaufort sea state 3 or less, with a median sea state of 1 (mean $(X) \pm SE = 1.37 \pm 0.03$, $N = 525$). Group size varied from 3 to 200, with a median size of 25 ($X \pm SE = 35.91 \pm 1.93$, $N = 525$; Fig. 4). Focal follow duration ranged from 4 to 54 min, with a mean of 19.9 min.

B. Behavior and group size

Ultimately, there were five behavioral categories used for analysis: moderate/fast travel, slow travel, mill, forage, and mixed forage. Fast and moderate travel behavior categories were combined into “moderate/fast travel” due to smaller sample sizes. In addition, observers recorded the dolphins foraging while simultaneously milling or traveling in nine of the groups; therefore, a “mixed forage” category was created. A summary of behavioral data is shown in Fig. 5 and sample sizes (based on focal follow instantaneous sam-

TABLE II. Summary of effort and number of Pacific white-sided dolphin groups sighted for all surveys.

Survey	Effort (days)	Total Number of Groups	Number of Click Type A Groups	Number of Click Type B Groups
FLIP 2006	17	14	4	10
FLIP 2007	27	4	1	1
FLIP 2008	25	5	1	4
SCI 2006	9	1	1	–
SCI 2007a	4	1	1	–
SCI 2007b	5	1	1	–
SCI 2008	10	2	2	–
TOTAL	97	26	11	15

ples) are given in Table III. Slow travel was the predominant behavior (30.0%), followed by moderate/fast travel (21.5%), and then mixed forage (18.8%) and forage (15.4%). Behavior was also stratified by click type and compared using a Mann-Whitney U/Wilcoxon rank sum test, which indicated that differences in behavioral patterns between click type groups approached significance at an α value of 0.05 ($U = 36.5$, $p = 0.064$). Click Type B groups had high rates of slow travel (25.0%) and moderate/fast travel (25.0%), followed closely by foraging (20.4%), with minimal milling (9.8%). In contrast, click Type A groups were primarily observed to slow travel (39.9%) and mill (23.0%), with a very low rate of forage (5.6%).

Group size statistics were skewed for forage behavior with the inclusion of a single 200-animal group; this led to a median group size of 30 and a mean of 76.48 ± 9.54 . However, this group was observed foraging in small subgroups and then coming together to travel, thus the inclusion as a single large group during forage behavior inflates the apparent group size. Excluding this group led to a median group size of 10 with a mean group size of 18.09 ± 1.31 , falling closer to the expected since foraging groups are often, although not always, smaller (e.g., Würsig, 1986; Baird and Dill, 1996). The next smallest group size was observed during milling [$X \pm SE = 21.31 \pm 1.55$, median (M) = 25], while larger group sizes occurred during mixed forage ($X \pm SE = 36.21 \pm 3.16$, M = 20). Overall group sizes were also significantly smaller for click Type A groups than for click Type B groups during all behaviors except mill (Mann-Whitney U/Wilcoxon rank sum = 18, $p = 0.0556$) (Fig. 4; median values given in Table IV).

C. Correlation of surface and acoustic behavior

Kruskal-Wallis nonparametric tests and Tukey-Kramer multiple comparison tests showed that differences across each behavioral category for the 19 call features were significant (e.g., Figure 6; samples sizes given in Table III).

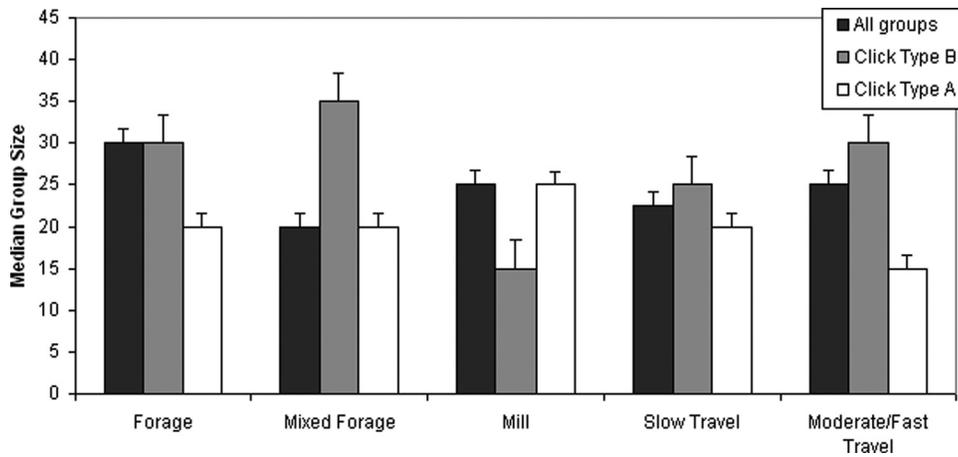


FIG. 4. Median group size for each behavior. Bars show median group size for all groups in black, click Type A groups in dark gray, and click Type B groups in white, with error bars of standard error.

For every call parameter there was at least one behavior with a 95% confidence interval that did not overlap with the confidence intervals of the other behaviors, indicating a significant difference from the other behaviors (X^2_4 ranges from 12.41 to 317.42, $P < 0.0001$). Median call rates for each behavior are presented in Table IV. Median click rates were lowest for forage, moderate/fast travel, and slow travel, and were highest during mixed forage (Fig. 6). Meanwhile, the median bout rates were highest for moderate/fast travel, slow travel, and forage. The median ICI was also highest for moderate/fast travel, forage, and slow travel. There were few pulsed calls during forage behavior and no call series; in contrast, there were high numbers of both individual pulsed calls and call series during mixed forage behavior.

D. Classification of behavior using vocalizations

Random forest models were created first using all 19 call features as well as group size. Then, the Gini variable importance measure was implemented to estimate the importance of each variable. If applicable, additional models were then created using only the top ranked call features ($Gini > 10$) until the OOB error estimate could no longer be reduced. Random forest models were run using the sample sizes given in Table III; while unequal sample sizes could

possibly inflate the correct classification results for the behaviors with larger sample sizes, there was no way to run the models with equal sample sizes without losing much of the data. Ultimately, all click and pulsed call variables were used for the all-group model. For the click Type A model, all click variables plus the duration, maximum frequency, and bandwidth of click trains and the minimum frequency, maximum frequency, and bandwidth of pulsed calls were included. For the click Type B data, the lowest OOB error rate occurred for the model that included all 19 call features, while the Gini importance variable ranked all click and pulsed call features as important ($Gini > 20$). No features of pulsed call series were included as an important predictor variable for any of the models. Furthermore, rates of correct classification of behavioral state by random forest models changed notably with the inclusion of group size; therefore, results are presented both with group size included (Table V) and without (Table VI).

When group size was excluded, the OOB error rates were higher for all three group categories: the OOB error estimate for all groups was 44.19%, for click Type A groups it was 49.15%, and for click Type B groups it was 40.52%. When group size was included, the overall OOB error estimate decreased to 35.24%, 45.76%, and 30.17%, respectively, for all groups, click Type A groups, and click Type B

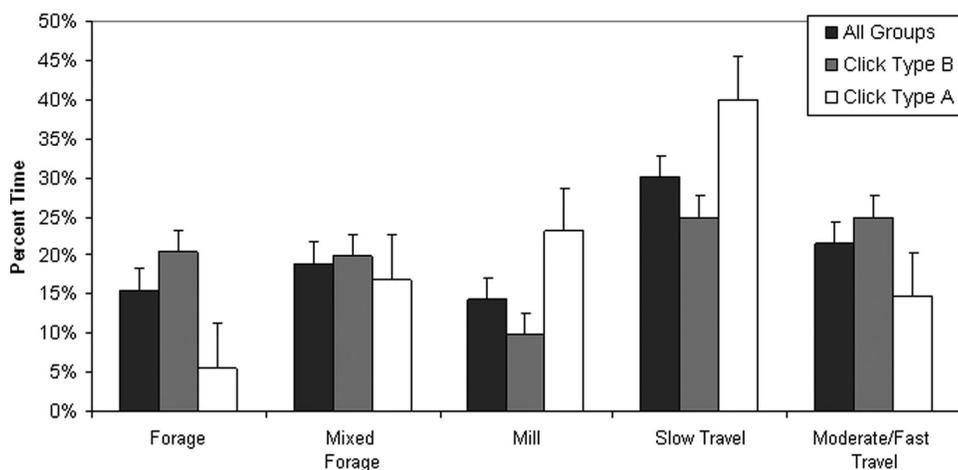


FIG. 5. Summary of behavioral data. Bars show the percent of time animals were observed at each behavior, with all groups in black, click Type B groups in gray, and click Type A groups in white, with error bars of standard error.

TABLE III. Sample size for behavioral and acoustic analyses. Values are the number of 30-second segments, based on focal follow observation samples, for each behavior and for each click type group.

Behavior	Total	Click Type A	Click Type B
Forage	81	10	71
Mixed Forage	99	30	69
Mill	74	40	34
Slow Travel	158	71	87
Moderate/Fast Travel	113	26	87
Total Sample Size	525	177	348

groups. However, the inclusion of group size had a greater impact on some behaviors. For example, for click Type A groups, there is no change in the rate of correct classification of slow travel or forage when group size is included, but a 10% increase from 36.7% to 46.7% was observed for the mixed forage category. The behaviors with the highest classification rates for all groups were slow travel (74.1%), forage (74.1%), and mixed forage (70.%); for click Type B groups they were forage (85.9%), mixed forage (75.4%), and moderate/fast travel (75.4%); and for click Type A groups the highest classification rate was for slow travel (84.5%; Table III).

IV. DISCUSSION

Pacific white-sided dolphin vocalizations differ between click Type A and click Type B groups and between behavioral states both within and across the click type groups, with characteristic differences between vocalizations for most behavioral states. Forage, slow travel, and mixed forage seem to have the most distinct call patterns; however, there were some differences found for all behavior categories. These differences in call features between the behaviors allowed statistical models to be built that classified surface behaviors based on call rates and specific call features, particularly click rates, ICIs, and pulsed call rates. The resulting high correct classification rates for most behaviors indicate the potential to predict behavior based on vocalizations without the need for concurrent visual observations.

A. Correlation of behavior and vocalizations

When correlating vocal and surface behavior, the fewest number of both clicks and pulsed calls were recorded during

TABLE IV. Median values for group size, call counts, and inter-click intervals during 30-second periods for each behavioral category.

Behavior	Group Size	Number of Clicks	Number of Bouts	ICI (in s)	Number of Pulsed Calls	Number of Pulsed Call Series
Forage	30	112	10	0.09	0	0
Mixed Forage	20	788	3	0.03	2	2
Mill	25	446.5	6	0.05	2	0
Slow Travel	22.5	216.5	10	0.07	0	0
Moderate/ Fast Travel	25	107	12	0.09	1	0

moderate/fast travel and forage behavior. In this study, forage behavior also had a high number of discrete click bouts, likely indicating search or scan behavior. Van Parijs and Corkeron (2001) also found the fewest vocalizations during travel in Pacific humpback dolphins (*Sousa chinensis*). Simon *et al.* (2007) found fewer clicks and calls in killer whales (*Orcinus orca*) during travel than during other activity, while Dudzinski (1996) found the fewest of all call types, including clicks, in foraging than in any other behavior for Atlantic spotted dolphins (*Stenella frontalis*). However, increased clicking and whistling were recorded for Hawaiian spinner dolphins (*Stenella longirostris*) during travel (Brownlee, 1983), and spotted dolphins demonstrated more click trains but fewer whistles or chirps than expected during travel behavior (Dudzinski, 1996). Additionally, several studies have detected the highest number of clicks during presumed feeding activity (Weilgart and Whitehead, 1990; Van Parijs and Corkeron, 2001; Simon *et al.*, 2007). These mixed results across studies may indicate site-specific differences, as found for bottlenose dolphins in four regions of the southeast Atlantic Ocean (e.g., Jones and Sayigh, 2002), or species-specific differences, as found in vocalization patterns of Hawaiian spinner and spotted dolphins (Lammers *et al.*, 2003). The differences across studies could also be due to methodological differences, including definitions of behaviors and the acoustic sampling methods used (e.g., Quick and Janik, 2008).

In contrast to the low rate of vocalization during foraging, the highest rates of clicks, pulsed calls, and pulsed call series occurred during mixed foraging behavior. While mixed foraging groups had a higher median group size than foraging groups, they were smaller than slow or moderate/fast traveling groups. Therefore, the increase in click and pulsed call rates may only be partially explained by group size. In addition, the dolphins would be equally variable in their direction of movement during foraging as during mixed foraging; therefore, it is unlikely that calls would be missed during one behavior but not the other due to directionality. Benoit-Bird and Au (2009) also recorded higher click rates for spinner dolphins during periods of transition between foraging stages. We hypothesize that this behavior of Pacific white-sided dolphins represents search behavior and/or a transition between behaviors; high rates of communication might be expected when dolphins are looking for prey, coordinating movement, or beginning or ending a foraging bout.

B. Classification of behavior using vocalizations

Classification results varied widely across behaviors; generally, those with multiple distinct call features and/or larger sample sizes were better classified. For example, the highest number of clicks, click trains, and the longest pulsed calls occurred during mixed forage behavior, while the fewest clicks, pulsed calls, pulsed call series, and the longest click durations occurred with forage behavior. Those distinct features resulted in mixed forage and forage behaviors being well-classified by the random forest decision trees. However, mill behavior had the highest maximum pulsed call frequencies and bandwidth; yet, due to overlapping characteristics

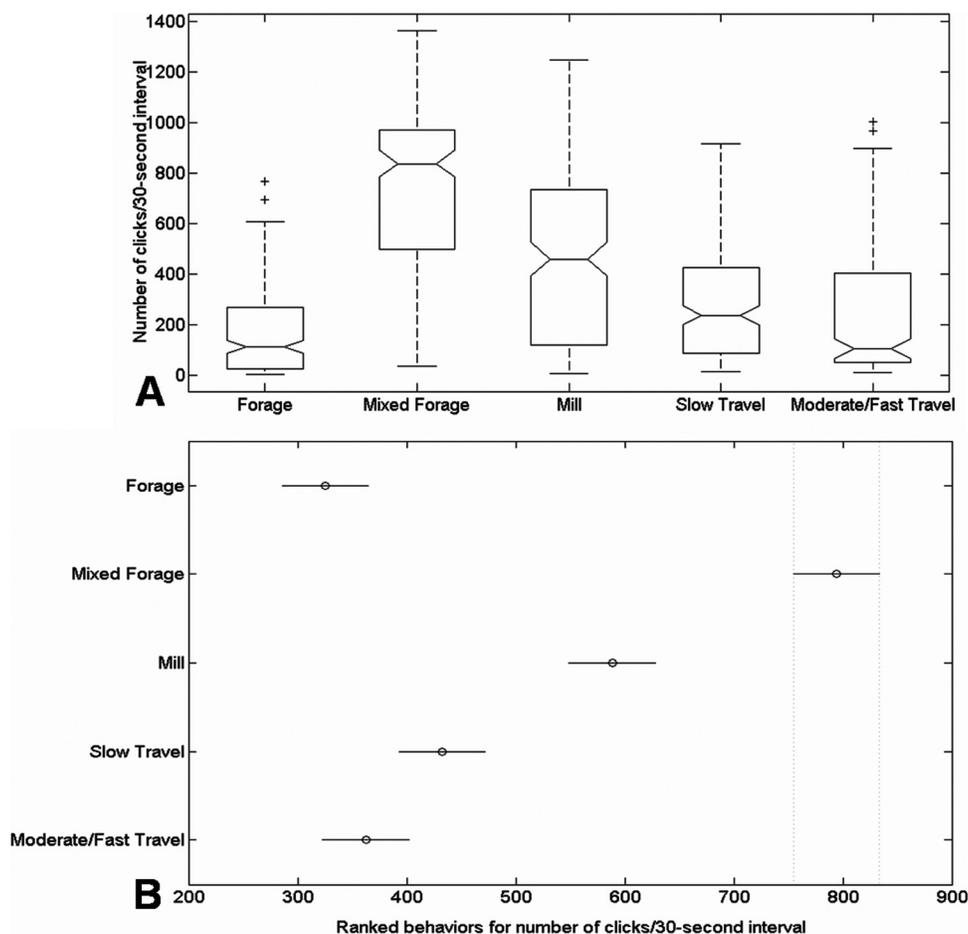


FIG. 6. Boxplots and rank confidence intervals for the median number of clicks per 30-s interval. (a) The boxplots of the median number of clicks per 30-s interval for each behavioral category. (b) The rank calculated in the Kruskal-Wallis analysis and confidence interval (the line around the point) of each behavior for the median number of clicks per 30-s interval. The rank is determined by ordering the data from smallest to largest, then taking the numerical index of the resulting order.

with other call features, was more difficult to distinguish. On the other hand, slow and moderate/fast travel behaviors had fewer distinctive call features, but were readily classifiable due to larger sample sizes. As classification rates could be inflated in behaviors with higher sample sizes, additional data for all behaviors should be gathered and included in the models. This increase in sample size of vocalizations for all behaviors would likely lead to higher rates of classification overall.

While the inclusion of group size increased the correct classification rates in the random forest models, this improvement seemed to be behaviorally specific. This may indicate that over longer observation periods there could be changes in group composition or size related to behavior, similar to the fission-fusion effect as groups transition between behaviors as has been observed for spinner and dusky (*Lagenorhynchus obscurus*) dolphins (Norris and

Dohl, 1980; Würsig and Würsig, 1980). Alternately, call rates for some behaviors may be influenced by group size while in other cases the behavior alone may determine call rates.

C. Comparison of click type groups

Click Type B groups had higher correct classification rates than click Type A groups, which again is likely due to a larger sample size. In particular, foraging behavior was highly classifiable for the click Type B groups and was the second most frequently observed behavior, while very little foraging was observed for click Type A groups, which made those vocalizations difficult to characterize. Additionally, the top ranked call features differed between the two click Type groups. For click Type A groups, click, click train, and pulsed call features received top Gini rank scores, while for

TABLE V. Percent correct classification of surface behavior based on call features for random forest models with group size *included* as a predictor variable.

Behavior	All Groups	Click Type A Groups	Click Type B Groups
Forage	74.1%	0.0%	85.9%
Mixed Forage	70.7%	46.7%	75.4%
Mill	33.8%	45.0%	20.6%
Slow Travel	74.1%	84.5%	64.3%
Mod/Fast Travel	60.2%	15.4%	77.0%

TABLE VI. Percent correct classification of surface behavior based on call features for random forest models with group size *excluded* as a predictor variable.

Behavior	All Groups	Click Type A Groups	Click Type B Groups
Forage	59.3%	0.0%	70.4%
Mixed Forage	62.6%	36.7%	75.4%
Mill	33.8%	40.0%	14.7%
Slow Travel	63.3%	84.5%	55.2%
Mod/Fast Travel	51.3%	11.5%	59.8%

click Type B groups, only click and pulsed call features received top Gini rank scores. These results indicate that the click type groups are producing and utilizing vocalizations differently.

In addition to being vocally distinct, the two click groups also differed with respect to their behavioral time budgets. Click Type B groups were observed foraging throughout daylight hours, while click Type A groups were generally observed slow traveling and/or milling. This seems to indicate resource partitioning, or at least niche separation, by the two populations and supports Soldevilla's (2008) hypothesis that click Type A dolphins may be foraging at night on squid and myctophids rising in the scattering layer, while click Type B dolphins are foraging during the day on epipelagic schooling fish.

The strong behavioral and vocal distinctions between the two groups may in fact demonstrate that these groups are in the process of speciation, if not fully genetically distinct. Vocal differences have been used to distinguish cryptic species that are genetically different but morphologically similar (Smith and Friesen, 2007; Braune *et al.*, 2008; Foerschler and Kalko, 2009) and may develop as a precursor to genotypic divergence. To fully verify this hypothesis, concurrent acoustic and genetic sampling needs to be conducted on these animals to determine if the click types represent the genetically distinct populations that have already been shown to overlap in the SCB (Lux *et al.*, 1997). Additionally, genetic sampling and stomach content analysis of stranded animals could be conducted to determine if populations are consuming different prey as predicted. Finally, nighttime feeding behavior by click Type A dolphins needs to be substantiated, perhaps through the use of acoustic tags or active high-frequency sonar (e.g., Benoit-Bird and Au, 2001), in addition to comparing daytime acoustic data supported by visual observations with nighttime acoustic recordings.

V. CONCLUSIONS

Pacific white-sided dolphin vocalizations differed across behavioral states, with strong correlations between surface and acoustic behavior for forage, moderate/fast travel, slow travel, and mixed forage behaviors. These correlations will make it possible in the future to examine diel and seasonal behavior patterns of Pacific white-sided dolphins across a wider spatial and temporal range throughout the SCB than is possible with visual surveys. Furthermore, the distinct differences in calls and behaviors provide further support for the hypotheses that click Type A and click Type B groups represent unique populations that overlap in the SCB and have developed distinct click types. This may be an indication that these populations are cryptic species or subspecies, and potentially have partitioned their prey resources to reduce overlap. Finally, the observed mixed foraging behavior may represent a search or transition phase of foraging behavior, previously unrecorded for Pacific white-sided dolphins.

These results can be used to begin to build a model of habitat use for Pacific white-sided dolphins in the SCB region. Recordings with Pacific white-sided dolphin acoustic data could be analyzed to examine behavior patterns over

time and space, and, with additional oceanographic data, used to detect patterns in sea surface temperature, salinity, chlorophyll, or other parameters that may also correlate with feeding. Travel behavior could be monitored to follow seasonal migrations or illuminate frequent routes to feeding hot-spots. There already appear to be some reliable differences in diel behavior, and, with further work, seasonal behavior patterns could be identified and compared between click Type A and B groups. Finally, a baseline of "normal" acoustic behavior for Pacific white-sided could be established to evaluate levels of anthropogenic stressors such as heavy shipping traffic, sonar, and other acoustic signals that increase ambient noise and may affect behavior.

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