Spatial and temporal patterns of Risso's dolphin echolocation in the Southern California Bight

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Geographical and temporal trends in echolocation clicking activity can lead to insights into the foraging and migratory behaviors of pelagic dolphins. Using autonomous acoustic recording packages, the geographical, diel, and seasonal patterns of Risso's dolphin (*Grampus griseus*) echolocation click activity are described for six locations in the Southern California Bight between 2005 and 2007. Risso's dolphin echolocation click bouts are identified based on their unique spectral characteristics. Click bouts were identified on 739 of 1959 recording days at all 6 sites, with the majority occurring at nearshore sites. A significant diel pattern is evident in which both hourly occurrences of click bouts and click rates are higher at night than during the day. At all nearshore sites, Risso's dolphin clicks were identified year-round, with the highest daily occurrence at the southern end of Santa Catalina Island. Seasonal and interannual variabilities in occurrence were high across sites with peak occurrence in autumn of most years at most sites. These results suggest that Risso's dolphins forage at night and that the southern end of Santa Catalina Island represents an important habitat for Risso's dolphins throughout the year.
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I. INTRODUCTION

Autonomous fixed-sensor, acoustic-based surveys offer a monitoring technique that can be used for surveying dolphin activity and geographical movements over long-periods in remote locations, during adverse weather conditions and during nighttime periods. Risso's dolphins (*Grampus griseus*) produce short duration (40 us) broadband echolocation clicks with peak frequencies around 50 kHz, centroid frequencies between 60 and 90 kHz, and source levels of 202–222 dB re 1 μPa (peak to peak) (Madsen *et al.*, 2004). Recent descriptions of species-specific spectral characteristics of southern Californian Risso's dolphin echolocation clicks indicate the presence of alternating peaks and notches within individual clicks such that spectral peaks occur at 22, 25, 31, and 39 kHz and spectral notches occur at 20, 28, and 36 kHz (Soldevilla *et al.*, 2008). These characteristics allow for the use of autonomous acoustic monitoring to study the spatial and temporal patterns of these dolphins' clicking activity. However, to interpret variability in recorded click activity in terms of behavioral activity and movement patterns, it is important to first understand echolocation click usage. All odontocetes are thought to produce echolocation clicks to investigate their environment for objects, prey, predators, conspecifics, and navigational cues (Au, 1993; Akamatsu *et al.*, 2005). While no previous studies have examined Risso's dolphin click usage patterns, concurrent behavioral and acoustical studies of numerous other odontocetes indicate higher click rates and occurrence during foraging behaviors, moderate click rates during traveling and socializing behaviors, and low click rates and occurrence during resting behaviors (Norris *et al.*, 1994; Barrett-Lennard *et al.*, 1996; Van Parijs and Corkeron, 2001; Nowacek, 2005). Assuming similar patterns for Risso's dolphin behavior and click activity, the variability in recorded click rates and occurrence can be used to differentiate periods of activity and rest. Understanding click usage is also important when studying movement patterns with clicks, as Mackenzie *et al.* (2006) noted that lack of acoustic detections may result from the presence of non-vocal animals and not necessarily the absence of animals. This can be especially important when call output varies seasonally, such as for seasonal reproductive displays (e.g., Van Parijs *et al.*, 1999; Oleson *et al.*, 2007). However, given the necessity for dolphins to feed daily (Smith and Gaskin, 1974; Lockyer, 1981) and the importance of echolocation in foraging, it is unlikely that echolocation clicks could exhibit such a seasonal cycle. Therefore, echolocation clicks are an ideal call type for examining seasonal movement patterns.

Passive acoustic techniques offer a monitoring method that allows researchers to examine variability in calling activity over a range of spatial and temporal scales. The ability to monitor through the night allows analysis of diel trends in dolphin acoustic activity that is not possible with visual monitoring and offers the potential of sampling animals that might not be available to daytime visual surveys. Autonomous acoustic instruments can sample over long time periods to obtain high-resolution sampling of dolphin presence across seasons and years at a given location, which allows analysis of seasonal and interannual trends. Multiple instruments can be deployed to increase spatial coverage and allow comparisons in temporal presence across locations to exam-

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ine long-term movement patterns. This study uses long-term passive acoustic recordings to examine spatial and temporal trends in Risso's dolphin echolocation behavior and movement patterns. Autonomous acoustic recording packages were deployed at six sites throughout the Southern California Bight (SCB) over a period of 2.5 years. To examine diel variability in echolocation activity levels, click rates and hourly presence of Risso's dolphin click bouts are compared between periods of daylight and darkness. To examine seasonal and interannual movement patterns, variability in daily presence is compared among seasons, years, and sites. Diel and seasonal trends in echolocation behavior are described and the implications for foraging and movements are discussed.

II. BACKGROUND

Risso's dolphins are a tropical to temperate water species and in the Eastern North Pacific Ocean, they range from the Gulf of Alaska to the equator (Leatherwood *et al.*, 1980). Risso's dolphins off California, Oregon, and Washington comprise a single population (Carretta *et al.*, 2004). While their range extends beyond the waters of these states, most population studies focus within this region. Abundance estimates indicate approximately 11 900 dolphins throughout the region with about 3400 dolphins found off Southern California (Barlow and Forney, 2007). Risso's dolphins feed nearly exclusively on cephalopods, especially squid species (Clarke and Pascoe, 1985; Clarke, 1996), and studies off California indicate that jumbo squid (*Dosidicus gigas*) and market squid (*Loligo opalescens*) are important prey items (Orr, 1966; Kruse, 1989).

While their importance to the SCB ecosystem is recognized, little is known about Risso's dolphin diel activity patterns and descriptions of their seasonal and interannual movement patterns based on ship-board visual surveys are complex and sometimes conflicting. Diel variability in behavioral activity levels of Risso's dolphins cannot be studied completely using visual survey methods because the animals cannot be seen at night. Studies of diurnal behavioral activity off California indicate variable behavioral states during the day (Kruse, 1989) but suggest foraging/feeding at night (Shane, 1995). Seasonal and interannual variabilities have received more attention from visual survey studies. Since the late 19th century, records indicate high decadal variability in Risso's dolphin occurrence off California (Norris and Prescott, 1961; Leatherwood *et al.*, 1980; Dohl *et al.*, 1981, 1983; Shane, 1995; Kruse *et al.*, 1999), with some researchers indicating correlations between occurrence and extended periods of warm water (Leatherwood *et al.*, 1980) while others find no relationship between abundance and water temperature across years (Barlow and Forney, 2007). Studies of seasonal movements based on visual surveys indicate (1) movements between Oregon/Washington in spring/summer and California in autumn/winter (Green *et al.*, 1992; Forney and Barlow, 1998), (2) high interannual variability in seasonal patterns off central and northern California (Dohl *et al.*, 1983), and (3) year-round residency within the SCB that include inshore/northward or offshore/southward movements
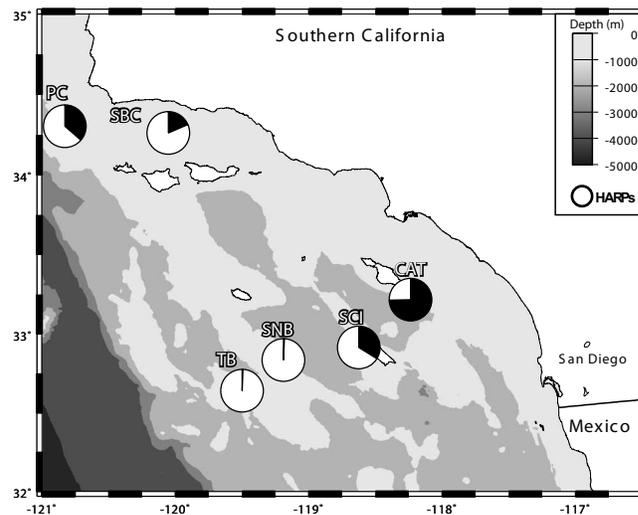

FIG. 1. Map of study area including locations of HARP deployments. Depths are indicated by colorbar. Sites: PC=Point Conception, SBC =Santa Barbara Channel, TB=Tanner Basin, SNB=San Nicholas Basin, SCI=San Clemente Island, and CAT=Santa Catalina Island. HARP locations are presented as pie charts in which the black area indicates the percentage of recording days with Risso's dolphin click bouts present. Risso's dolphins were detected most often at CAT and least often at TB and SNB.

in response to warm and cold waters, respectively (Dohl *et al.*, 1981). These results may not be mutually exclusive; discrepancies may reflect differing study areas or high interannual variability. A long-term monitoring program has the potential to clarify the temporal and spatial patterns of Risso's dolphin activity and movements.

III. METHODS

A. Instrumentation and data collection

High-frequency acoustic recording packages (HARPs) were deployed at six locations throughout the SCB between August 2005 and December 2007 at depths ranging between 300 and 1330 m (Figs. 1 and 2). A brief description of these autonomous seafloor-mounted acoustic recorders is provided here for clarity; see Wiggins and Hildebrand, 2007 for a detailed description of HARP design and capabilities. The HARP data-logging system includes a 16-bit analog to digital converter, up to 1.9 Tbytes of storage capacity, a hydrophone suspended 10 m above the seafloor, a release system, ballast weights, and flotation. The dataloggers are capable of sampling up to 200 kHz and can be set to record continuously or on a sampling schedule to accommodate variable deployment durations. This study includes data from 30 HARP deployments each lasting from 1 to 4 month durations. Temporal coverage at each of the six sites is variable due to research vessel availability and occasional instrument problems (Table I). Data from all deployments included in this study were sampled at 200 kHz, resulting in a recording bandwidth of 1 Hz–100 kHz. A variety of sampling schedules were used across deployments with 2/3 of deployments recorded on a continuous sampling schedule and the remaining 1/3 recorded on a sampling schedule of 5 min on followed by 5, 10, or 15 min off for a given deployment.
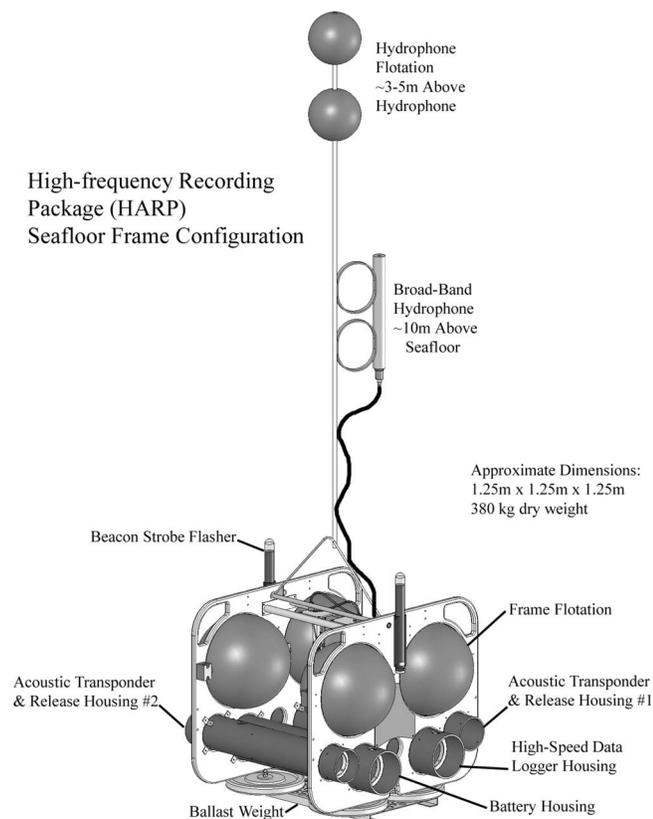
Hydrophone Flotation ~3-5m Above Hydrophone

High-frequency Recording Package (HARP) Seafloor Frame Configuration

Broad-Band Hydrophone ~10m Above Seafloor

Approximate Dimensions: 1.25m x 1.25m x 1.25m 380 kg dry weight

Beacon Strobe Flasher

Frame Flotation

Acoustic Transponder & Release Housing #2

Acoustic Transponder & Release Housing #1

High-Speed Data Logger Housing

Ballast Weight

Battery Housing

FIG. 2. Schematic representation of autonomous seafloor recording package.

B. Acoustical analysis

Acoustic data were analyzed with a custom software program, TRITON, developed in MATLAB (The MathWorks, Inc., Natick, MA). Raw acoustic HARP data were converted to XWAV format, a format similar to WAV format that incorporates instrument meta-data in an expanded header file, including recording start and stop times. This timing information is crucial when analyzing non-continuous data. Each HARP deployment resulted in 1.6–1.9 Tbytes of data, which is impractical to analyze manually in original form. Therefore, these data were compressed for visual overview by creating long-term spectral averages (LTSAs) (Wiggins and Hildebrand, 2007) from the XWAV files. LTSAs are effectively compressed spectrograms created using the Welch algorithm (Welch, 1967) by coherently averaging 500 spectra created from 2000-point, 0%-overlapped, Hann-windowed data and displaying these averaged spectra sequentially over time. The resulting LTSAs had resolutions of 100 Hz and 5 s in frequency and time, respectively.

Using LTSAs with 100 Hz and 5 s resolution, delphinid whistling and echolocation clicking bouts, rain bouts, ship passings, and other acoustic phenomenon can easily be distinguished from background noise (e.g., Wiggins and Hildebrand, 2007). Soldevilla et al. (2008) described distinct spectral banding patterns found in individual echolocation clicks of Risso's dolphins recorded during concurrent visual and acoustic ship-based surveys. Risso's dolphin clicks exhibit spectral peaks at 22, 25, 31, and 39 kHz with spectral notches at 20, 28, and 36 kHz. These spectral banding patterns are also found in many echolocation click bouts in autonomously recorded HARP data and the banding patterns are particularly striking as visualized in LTSAs (Fig. 3). By visually examining 30 min long LTSA segments, the start and end times of click bouts exhibiting the described spectral patterns were located and logged. Numerous delphinid species occur offshore southern California. Three of the most common species produce clicks that do not have consistent spectral banding patterns, while Pacific white-sided dolphins produce two click types with spectral banding at different frequencies than Risso's dolphins (Soldevilla et al., 2008). Occasionally, click bouts without spectral banding patterns or with Pacific white-sided dolphin patterns overlapped Risso's dolphin click bouts. These bouts were labeled as Risso's dolphin mixed species groups. Click bout start and end times were used to calculate daily occurrence, hourly occurrence, and click rates for temporal analyses. Mixed species data were only included in temporal analyses of Risso's dolphin click occurrence and were removed from the remaining click rate analyses described in Sec. III C.

C. Click detection

To calculate click rates for analysis of diel patterns, an automatic call detection algorithm was developed. This algo-

TABLE I. Seasonal recording effort at each site across 3 years of study. Cells represent the number of week-long replicate samples available for statistical analysis at each site for each season of each year. Site abbreviations: PC=Point Conception, SBC=Santa Barbara Channel, TB=Tanner Basin, SNB=San Nicholas Basin, SCI=San Clemente Island, and CAT=Santa Catalina Island. TB and SNB are not included in the total samples for the seasonal analysis in this study because they were deployed during only part of the year in 2007 and did not sample across all seasons. Months included in each season are indicated by the first letter of the month.

Site	Winter (J F M)			Spring (A M J)			Summer (J A S)			Autumn (O N D)			Total
	2005	2006	2007	2005	2006	2007	2005	2006	2007	2005	2006	2007	
PC	0	3	10	0	0	13	7	5	13	13	4	3	71
SBC	0	4	8	0	0	3	7	0	12	13	7	5	59
TB	0	0	0	0	0	4	0	4	13	0	3	3	27
SNB	0	0	0	0	0	0	0	0	7	0	0	7	14
SCI	0	0	11	0	0	12	0	0	9	0	0	8	40
CAT	0	4	8	0	0	9	7	12	10	13	12	10	85
Total samples for seasonal analysis	0	11	37	0	0	37	21	17	44	39	23	26	255
		48			37			82			88		255

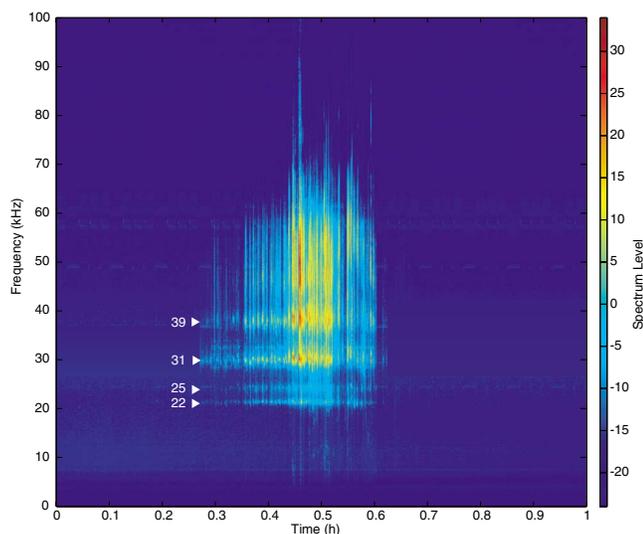Soldevilla et al.: Dolphin echolocation spatial and temporal patterns

FIG. 3. (Color online) Example LTSA illustrating echolocation click bout containing the unique spectral peak and notch structure described for Risso's dolphins by Soldevilla *et al.* (2008). LTSA spectrogram has resolutions of 100 Hz and 5 s in frequency and time, respectively, and represents coherent averages of 500 spectra created using 2000-point, 0%-overlapped, Hann-windowed HARP data. Spectral peaks occur in the Risso's dolphin clicks at approximately 22, 25, 31, and 39 kHz.

rithm simultaneously detected broadband clicks and whistles in the spectral domain, although only the click results are presented here. To obtain the best results for both whistles and clicks, spectra were calculated using a 1024-point fast Fourier transform (FFT) with 50% overlap and a Hann window. Spectral-mean-subtraction was performed on each spectrum by subtracting the mean spectral vector of the surrounding 3 s of data. Individual spectra were selected as click candidates if a minimum percentage of frequency bins exceeded a minimum threshold within the bandwidth of interest. Values for minimum percentage, threshold, and bandwidth were set as 12.5%, 11 dB, and 15–95 kHz, respectively. These values were empirically determined to detect most high quality echolocation clicks while minimizing detection of other impulsive sounds, with a trade-off of missing lower amplitude echolocation clicks. For each click candidate, start and end times of 15 ms of data surrounding the click were extracted and overlapping segments were merged.

While the click detector can automatically detect clicks, it cannot automatically classify them to species. Therefore, individual click classifications were determined from the LTSA click bout classifications described in Sec. III B. All detected clicks, which occurred within start and end times of visually classified LTSA Risso's dolphin click bouts, were classified as Risso's dolphin clicks. Detected clicks that occurred in mixed species click bouts were not included in the diel click rate portion of the analysis. Mixed species groups accounted for 35% of the hourly Risso's dolphin click bout occurrences. No diel trend in occurrence was apparent for the mixed species groups removed from the diel click rate analysis.

Several potential biases of this click detection algorithm are worth considering. As noted above, if multiple species were calling during a Risso's dolphin click bout, and it was apparent in the LTSAs, these data were classified as mixed

species and were not included in the analysis, biasing the counts to be low. However, if multiple species were present and clicking, but the click bout was classified as only Risso's dolphins, this would cause the click counts to be biased high for Risso's dolphins. This bias was minimized by making conservative decisions about species classification. Additional factors that could bias the click counts low include the following: (1) Many low amplitude clicks were present that did not exceed the thresholds, (2) during periods of intense clicking (multiple high amplitude overlapping click trains), the mean spectral intensity of the surrounding 3 s of data used for spectral-mean-subtraction would be relatively high resulting in some high amplitude clicks being missed by the detector, and (3) during periods with rapid click trains or click trains from multiple individuals in which the apparent interclick interval was greater than 15 ms, only one click was chosen per 15 ms. Overall, these biases would result in lower click rates during intense periods so that comparisons of diel click rate patterns are conservative.

D. Temporal analysis

Both click bout occurrence and click rate data were examined for diel patterns. At each site, daily sunrise, sunset, and twilight data were obtained from the U.S. Naval Observatory (2008) website to establish light and dark periods. Day and night were defined as the periods between nautical twilight, when the sun altitude was at $-12°$ from the horizon. Each click bout was assigned to either day or night. Click bouts that spanned multiple periods were segmented and each segment was assigned the appropriate dark or light period.

To examine diel variation in hourly click bout occurrence, ones and zeros were assigned to 1 h interval bins indicating presence or absence, respectively. Seasonal variation in duration of day and night periods was normalized by dividing the number of 1 h bins with clicks present per period per day by the total number of 1 h bins per period per day. Bins that crossed boundaries between periods were assigned to the period that contained the greater portion of the hour. Analysis of variance (ANOVA) was used to test whether variability in percentage of hours with clicks was significantly different between day and night periods (Zar, 1999).

To examine diel variation in Risso's dolphin click rates, click rates were calculated as the number of clicks detected divided by the total recording duration in minutes for each light and dark period of each day. To account for shorter recording durations caused by the sampling schedule in noncontinuous data, total recording duration was calculated from recording start times and durations stored in the XWAV header files. Variability between days was accounted for by calculating a mean-adjusted calling rate in which the daily click rate was subtracted from the click rate for each light and dark period for each day. ANOVA was used to test whether variability in click rates was significantly different between day and night periods (Zar, 1999).

To examine seasonal variation in click bout occurrence, the metric total number of days with click detections present

TABLE II. Summary of number of days and hours with recording effort, number of days and hours with Risso's dolphin click bouts present, percentage of days and hours with Risso's click bouts present, and mean instrument depth for each of the six HARP sites. Site abbreviations: PC=Point Conception, SBC=Santa Barbara Channel, TB=Tanner Basin, SNB=San Nicholas Basin, SCI=San Clemente Island, and CAT=Santa Catalina Island.

	PC	SBC	TB	SNB	SCI	CAT	Total
No. of recording days	457	377	199	110	266	550	1 959
Days with Risso's click bouts	166	70	1	1	90	411	739
Days with Risso's click bouts (%)	36	19	1	1	34	75	38
No. of recording hours	10 499	8753	4647	2469	6277	12 862	45 507
Hours with Risso's click bouts	561	173	1	2	252	2 117	3 106
Hours with Risso's click bouts (%)	5	2	0	0	4	17	7
Instrument depth (m)	787	585	1013	1316	435	351	

per week was calculated and compared across seasons, sites, and years. Seasons were defined by quarters of the year and data were included only from sites with complete seasonal coverage. The two northern nearshore sites (Point Conception and Santa Barbara Channel) and the two southern nearshore sites (Santa Catalina Island and San Clemente Island) met the criteria for inclusion as they sampled all four seasons while data from the two southern offshore sites (Tanner Basin and San Nicholas Basin) did not (Table I). The metric total number of days with click detections present per week was chosen to minimize bias caused by differences in sampling effort across sites and seasons. Presence at 1-day resolution was chosen to minimize the bias due to sampling schedule as the mean probabilities of detecting Risso's dolphin click presence on a given day are 99%, 98%, and 97% for sampling schedules of 5 min on and 5, 10, and 15 min off, respectively (Soldevilla, 2008). Weeks were chosen for the sample duration to provide a reasonable number of replicates per season, site, and year, and because 83% of 255 week-long samples contained 7 complete days of recording effort. The remaining samples were normalized by the number of recording days to account for reduced effort. While this metric ensured that effort was comparable across samples, the number of replicate samples per season, site, and year varied (Table I), requiring the use of a statistical test that accounts for the unbalanced design. Therefore, the null hypotheses of equal means across seasons, years, and sites were tested using the generalized linear model (GLM) ANOVA function in SPSS 11.5 (SPSS Inc., Chicago, IL) with three-way full factorial design and type IV sum of squares to account for the unbalanced design. An ANOVA can only test if all means are equal or not; Tamhane's T2 *post hoc* test was used to determine which seasons, sites, or years were different (Zar, 1999; Garson, 2008).

IV. RESULTS

About 2000 recording days including over 45 500 h of data were analyzed from instruments at the six locations in the SCB, with the majority of sampling effort at the Santa Catalina Island, Santa Barbara Channel, Point Conception, and San Clemente Island sites (Table II). Risso's dolphin click bouts were identified at all six locations on a total of 739 recording days (38% of all recording days) and 3106 recording hours (7% of all recording hours). They were identified most often at the nearshore sites, in particular, at Santa Catalina Island where click bouts were identified on 75% of days and 17% of hours (Fig. 1, Table II). At the remaining three nearshore sites, Point Conception, Santa Barbara Channel, and San Clemente Island, Risso's dolphin click bouts were identified on 19%–36% of days and 2%–5% of hours. Risso's dolphin click bouts were rarely identified at the two southern offshore sites at Tanner Basin and San Clemente Basin ($<1\%$ of days and hours) (Fig. 1, Table II).

A distinct diel pattern was evident in the occurrence of Risso's dolphin echolocation click bouts across hours of the day. Across all sites, there was a sharp increase in click detections during the early part of the night, with a slight decrease in the middle of the night followed by another increase before sunrise (Fig. 4). This was followed by a sharp decrease after sunrise, though an additional moderate peak was evident in the late morning. Click bouts were detected least often in the afternoon (Fig. 4). Comparisons of the variability in click bout occurrence and click rate between day and night reveal that click bouts occurred significantly more often and that click rates are significantly higher at night than during the day (ANOVA: $F_{1,1472}=236$, $P<0.0005$, and $F_{1,1164}=93$, $P<0.0005$, respectively) (Fig. 5).

Risso's dolphin click bouts were identified throughout all four seasons at the four sites included in the seasonal analysis (Fig. 6). Variability in occurrence per week is high
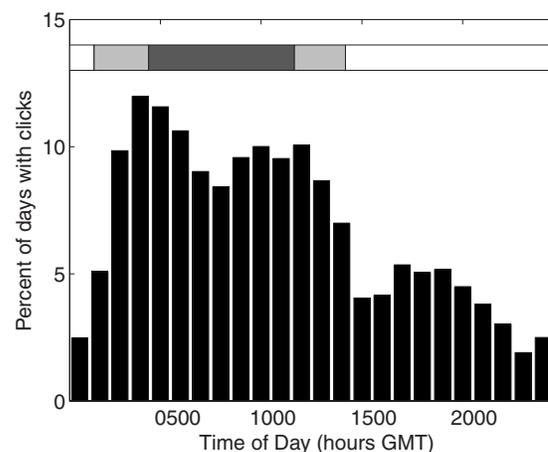

FIG. 4. Diel pattern of Risso's dolphin echolocation click bouts combined across the six HARP locations. Vertical bars represent the percentage of days that have clicks present in each 1 h time bin. Horizontal bar indicates periods of light (white) or darkness (dark gray). Light gray areas represent periods that may be light or dark depending on time of year.
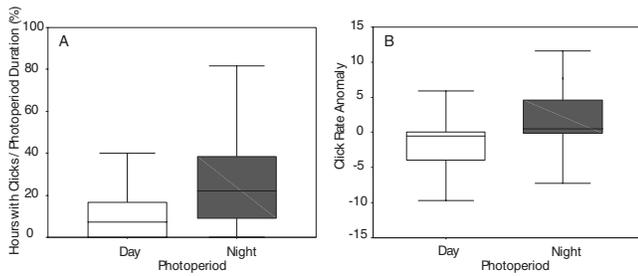
FIG. 5. Variation in Risso's dolphin click bout occurrence (a) and daily mean-adjusted click rate (b) between day and night periods. Central lines represent median value, boxes contain 25th to 75th percentiles, and whiskers contain 5th to 95th percentiles of data. Click bout occurrence and daily click rate anomaly are both significantly higher during the night than during the day.

between seasons, sites, and years. ANOVA results indicate that the main factors of season and site, as well as the interaction effects of season*site, season*year, and season*site*year, were significant sources of variation in mean occurrence of Risso's dolphin click bouts (Table III). Tamhane's T2 *post hoc* test demonstrates that mean occurrence was significantly higher in autumn than in winter, and that Risso's click bouts occurred significantly more often at Santa Catalina Island and significantly less often in the Santa Barbara Channel than at the other three sites, respectively. At
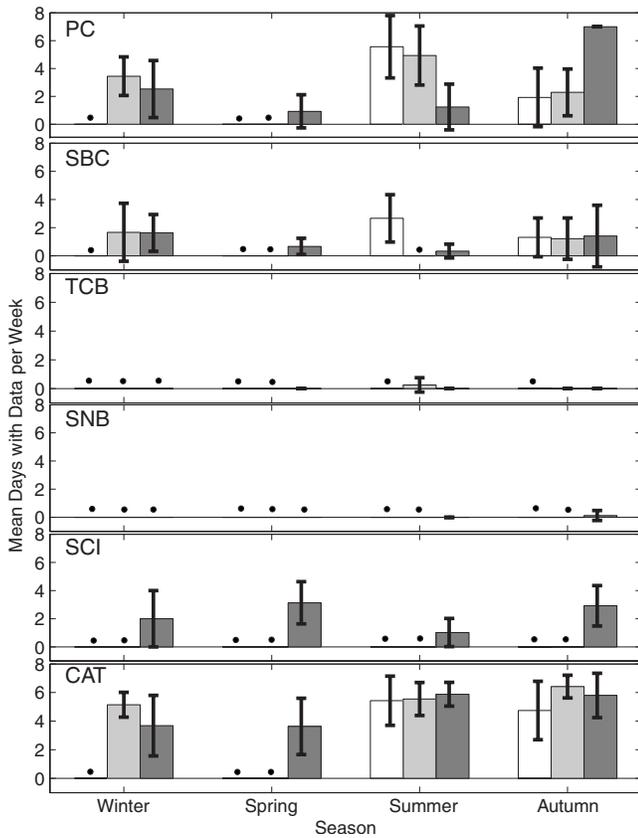

FIG. 6. Seasonal and annual variation in mean days per week with Risso's dolphin click bouts at the six HARP sites. Bar colors indicate year: white =2005, light gray=2006, and dark gray=2007. Error bars indicate standard deviation. Black dots indicate no data available in that season and year. Sites: PC=Point Conception, SBC=Santa Barbara Channel, TB=Tanner Basin, SNB=San Nicholas Basin, SCI=San Clemente Island, and CAT =Santa Catalina Island.

Santa Catalina Island, click bout occurrence was higher during summer and autumn in years 2006 and 2007 but decreased during autumn in 2005. At San Clemente Island, data were only available for 2007, in which there were peaks in click bout occurrence in spring and autumn. At Point Conception and in the Santa Barbara Channel, click bout occurrence was higher in winter and autumn during 2007 while occurrence was higher summer than autumn during 2005.

V. DISCUSSION

Recent discoveries that enable Risso's dolphin echolocation clicks to be identified to species have opened the door to using passive acoustic monitoring to examine temporal and spatial trends in Risso's dolphin echolocation click bouts. The ability of acoustic techniques to survey through the night has allowed the examination of diel patterns of click activity. Statistical comparisons of both click bout occurrence and click rates between day and night reveal a diel pattern in which both click activity metrics are higher at night than during the day. On a finer scale, hourly variability in Risso's dolphin click bout occurrence indicates high levels through the night, moderate levels during the morning, and low levels during the afternoon. In light of relationships found in prior studies of acoustic output and behavioral state (Norris *et al.*, 1994; Barrett-Lennard *et al.*, 1996; Van Parijs and Corkeron, 2001; Nowacek, 2005), the authors hypothesize that Risso's dolphins are generally foraging at night, traveling and/or socializing during the morning, and resting during the afternoon. This diel vocal and behavioral activity pattern is similar to that found for Hawaiian spinner dolphins at Kealakekua Bay, which echolocate at high rates while foraging at night, exhibit low vocal activity while resting during the morning, and exhibit moderate vocal activity while socializing in the afternoon (Norris *et al.*, 1994). Foraging at night is similar between the species and is consistent with Shane's (1995) hypothesis based on daytime visual surveys. However, these results indicate inverse behavior patterns between Risso's and Hawaiian spinner dolphins for morning and afternoon. A comparative visual and acoustic study of Risso's dolphin behavior could test these hypotheses about relationships between clicking and behavioral activities.

Additional support for the hypothesis that Risso's dolphins forage at night can be found in similarities between diel click occurrence and squid dive patterns. Nocturnal click bout occurrence is high throughout the night, in particular, during the early and late parts of the night with a dip in occurrence in the middle of the night (Fig. 4). Dive profiles of jumbo squid, a known Risso's dolphin prey item off California (Orr, 1966), indicate that they are found in deep waters during the daytime, rise to shallow waters at night, where they are readily available to Risso's dolphins, and often return to depth for a short-period in the middle of the night (Gilly, 2006). While detailed dive patterns of other squid prey species have not been described, many squid species found in the SCB are known to follow diel vertical migrations (Roper and Young, 1975) thereby increasing their availability to Risso's dolphins at night. Spinner and dusky dolphins have both been shown to follow the vertical move-

TABLE III. Results of three-way ANOVA for seasonal, annual, and site effects on Risso's dolphin occurrence. The main effects of season and site, and the interaction effects of season*site, season*year, and season*site*year all significantly influenced the occurrence of Risso's dolphin click bouts.

Source	Type IV sum of squares	df	Mean square	F	Sig.	
Corrected model	955.6	29	33.0	13.0	0.000	
Intercept	2083.1	1	2083.1	823.2	0.000	
Season	69.1	3	23.0	9.1	0.000	*
Site	218.5	3	72.8	28.8	0.000	*
Year	1.0	2	0.5	0.2	0.822	
Season*site	126.5	9	14.1	5.6	0.000	*
Season*year	106.2	3	35.4	14.0	0.000	*
Site*year	20.5	4	5.1	2.0	0.092	
Season*site*year	100.2	5	20.0	7.9	0.000	*
Error	569.32	225	2.5			
Total	3996.7	255				
Corrected total	1525.0	254				

ments of their diel-vertically migrating prey while in near-surface waters (Benoit-Bird and Au, 2003; Benoit-Bird et al., 2004). Results for Risso's dolphins suggest a similar pattern in which Risso's dolphins are actively feeding and echolocating when squid are within a preferred shallow depth range.

Diel patterns of vocal activity have been described for several other odontocete species. A study of harbor porpoise click rates off Scotland revealed greater echolocation activity at dawn and night (Carlstrom, 2005), while off Ireland, bottlenose dolphin clicks exhibited no distinct diel pattern (Philpott et al., 2007). Goold (2000) found that common dolphins (Delphinus delphis) off New Zealand produced significantly more whistle and click vocalizations during dusk and night, which he suggested may be related to greater foraging activity as common dolphins forage on diel-vertically migrating prey.

Geographically, Risso's dolphin click bouts were mostly confined to the four nearest-shore sites with rare detections occurring at the two offshore sites. This distribution is similar to that found by Forney and Barlow (1998) during visual line-transect surveys off California. Okutani and McGowan (1969) provided distributions for paralarvae of a variety of squid species found in the SCB. Market squid, a known prey item of Risso's dolphins off Monterey (Kruse, 1989), is the only squid with neritic spawning grounds and these grounds closely match the distribution of Risso's dolphin detections. Stomach content analyses off California are rare (e.g., Orr, 1966) so preferred prey in this area is unknown. These distribution results suggest that market squid is likely a preferred prey item. However, this study only includes six sites so it is possible that Risso's dolphins inhabit other regions outside of market squid spawning grounds. Additionally, sampling at the two offshore sites did not cover the entire year, so it is possible that they inhabit offshore regions during winter or spring.

While Risso's dolphin click bouts were identified throughout the year at all inshore sites, the temporal changes in Risso's dolphin distribution for the SCB show high seasonal and interannual variabilities at all sites. Acoustic occurrence was generally higher during autumn across all four inshore sites, particularly during 2007, although the peak occurred during summer in some years at the northern sites. Dohl et al. (1981) reported similar results from visual surveys of the entire SCB in which dolphins are present year-round with a peak in sightings occurring during September. Based on ship-board and aerial visual survey results, Green et al. (1992) and Forney and Barlow (1998) indicated that dolphins move from Oregon/Washington during spring/summer to California in autumn/winter. In this study, acoustic occurrence remained high during spring 2007 at San Clemente Island. Several possible explanations for this high occurrence include the following: The year 2007 was an anomalously cold year to the north of the SCB, only a portion of the population moves out of the region during spring and summer, or a distinct resident population remains in the region year-round. Risso's dolphin click bouts were identified on 75% of days at the Santa Catalina Island site. This is clearly an important habitat for these animals, but it remains unknown whether this represents a habitat of a resident population or if it is just a common feeding ground for animals moving over a larger area. Photo-identification studies, such as those conducted by Shane (1994) and Kruse (1989), or use of satellite tags could help answer this question.

A. Limitations

When considering the diel behavior of highly mobile species such as dolphins, it is unclear whether a lack of acoustic detections represents absence of the dolphins from the study site or presence of non-vocalizing animals. Dolphins are capable of moving into and out of a study site within 1 day, as shown by visual surveys of spinner dolphins off Hawaii that exhibit diel movements between inshore resting areas during the day to offshore feeding zones at night (Norris et al., 1994; Benoit-Bird and Au, 2003). Dolphins may also produce more than one echolocation click type, as has been found in Pacific white-sided dolphins (Soldevilla et al., 2008). Therefore, the diel variation in occurrence of Risso's dolphin clicks could either represent movements out of the area during the day and movements into the area during the night, or it could represent variability in echolocation

activity as a function of varying behavior state. Since Risso's dolphins exhibited greater echolocation activity at night at all sites it seems likely that this variation represents a changing behavioral state, for example, increased foraging, particularly when one considers the correspondence of increased click activity with squid diving behavior. Risso's dolphins have only been recorded producing one click type off southern California, but the sample size is small (Soldevilla *et al.*, 2008). Whether they produce other click types and, if so, whether click type production varies with behavior state deserve further study. The development of compact acoustic tags, similar to those used on larger whales, may provide more definitive answers to these questions.

Factors that may affect acoustic detection area and therefore the probability of detecting calling animals include directionality of the sound source, distance from hydrophone, sound propagation conditions, and acoustic masking. Echolocation clicks are highly directional (Au, 1993). Given a highly directional sound source combined with distance from the hydrophone, variability between light periods or sites could be caused by variability in probability of detection due to diel variability in dive depth of the animals or site variability in the depth of the HARPs if the dolphins' beams are rarely directed downward. Studies that examine how click detectability varies with depth on a vertical hydrophone array could answer this question. Sound propagation conditions may vary across sites and seasons. However, at the frequencies used for echolocation, attenuation severely limits detection range, and therefore the potential for significant variation owing to seasonal variations is reduced. Vessels, sonars, other animals, rain, wind, and waves may produce sounds that mask echolocation clicks so it is important to consider seasonality in these sources. Preliminary analyses indicate that vessel noise is consistent throughout the year at all sites except Santa Catalina Island where there is an increase in occurrence during the summer (May–September), while wind and rain noise within the frequency band of clicks occur minimally throughout the year. A more thorough investigation of seasonal variation related to these noise sources is the topic of another study.

VI. CONCLUSIONS

Temporal and spatial patterns are evident for Risso's dolphin click bout occurrence and click rates in the SCB. Diel patterns exist in which Risso's dolphins click more frequently and at higher rates during the night than day at all sites. These diel patterns provide insight into the behavioral ecology of these animals and add support to suggestions that Risso's dolphins are nighttime foragers. This type of data is important when designing passive acoustic monitoring surveys. Oftentimes, data sampling schedules are necessary so it is imperative that survey designs should either sample different periods of the day equally or at least sample at the same time each day. Seasonal and interannual variations among sites in the SCB were high as has been found during studies using visual survey methods. The year-round occurrence of Risso's dolphins in the SCB and high occurrence rates at Santa Catalina Island suggest the possibility of a resident population in addition to a population that moves seasonally between California and Oregon/Washington waters. This should be investigated further with photo-identification and satellite-tagging techniques. While the time series described in this study is not long enough to examine interannual and interdecadal changes such as those described in previous studies (e.g., Shane, 1995; Kruse *et al.*, 1999), this study is on-going and has the potential to answer such questions in the future especially when coupled with detailed environmental observations.

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