Geographic variation in Risso's dolphin echolocation click spectra

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Discrimination of bioacoustic signals to the species or population level is critical for using passive acoustic monitoring to study cetacean ecology. Risso's dolphins off southern California have distinctive peaks and notches in their echolocation clicks, but it was unknown whether Risso's dolphins from other geographic areas have similarly distinctive click spectra and whether populations are acoustically distinct. This study investigates using clicks for species and population identification by characterizing the spectral structure of Risso's dolphin echolocation clicks recorded over wide-ranging geographic regions including the U.S. waters of the North Atlantic Ocean, Gulf of Mexico, and North Pacific Ocean; and international waters of the Eastern Tropical Pacific. All recordings with Risso's dolphin clicks exhibited the spectral peak and notch pattern described off southern California, indicating the presence of peak banding patterns is useful for species discrimination. Geographic regions were a significant explanatory factor for variability in the frequencies of click spectral peaks, with relatively higher frequency peaks and notches found off Hawaii compared to California waters and off the southeast U.S. compared to the Gulf of Mexico. In the North Atlantic Ocean, a latitudinal cline in frequencies was evident. Potential causes of acoustic variation within and among acoustic encounters are evaluated.

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I. INTRODUCTION

Passive acoustic monitoring (PAM), which is increasingly being used by the scientific community to study cetacean ecology (e.g., Mellinger *et al.*, 2007; Van Parijs *et al.*, 2009), requires the ability to acoustically identify species to address most types of questions. All cetaceans are acoustically active, and are thought to produce species-specific signals. Within a species, acoustic differentiation in bioacoustic signal structure may also be related to population structure (Mellinger and Barlow, 2003). It is particularly challenging to determine population boundaries for cetaceans due to their wide-ranging and largely pelagic distributions, but stable bioacoustic signal differences may be a useful line of evidence for determining population structure when combined with or supported by evidence of genetic, morphological, or distributional density differences (Martien *et al.*, 2015). Population-specific differences in bioacoustic signals have been hypothesized for many mysticetes (e.g., Winn *et al.*, 1981; McDonald *et al.*, 2006; Delarue *et al.*, 2009; Castellote *et al.*, 2012) and some odontocetes (e.g., Rendell *et al.*, 2012; Barkley *et al.*, 2014; Samarra *et al.*, 2015), and in some cases, these hypotheses are supported by genetic, morphometric, or distributional lines of evidence (Branch *et al.*, 2007a; Branch *et al.*, 2007b; Torres-Florez *et al.*, 2014). As anthropogenic threats, such as pollution and fisheries interactions, increasingly impact the oceans and the cetaceans that inhabit them, it is necessary to have a solid baseline understanding of population structure to guide management decisions.

Risso's dolphins (*Grampus griseus*) have a largely pelagic distribution and limited knowledge exists on their ecology, including the extent of their global distribution (Jefferson *et al.*, 2014), population structure, and population boundaries. Given the wide range of habitats from coastal, shallow waters to deep, oceanic waters, there may be population-specific and/or ecotype-specific habitat specialization in Risso's dolphins (Jefferson *et al.*, 2014). Some

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morphological (Mizue and Yoshida, 1962; Ross, 1984; Chen *et al.*, 2011), genetic (Gaspari *et al.*, 2007), and distributional (Wade and Gerrodette, 1993; Kruse *et al.*, 1999) evidence support inter- and intra-ocean basin population divisions, but generally population delineations are not clearly defined (Baird, 2002). In U.S. waters, Risso's dolphins are divided into "stocks" for management purposes, based on distribution gaps or large-scale ecosystem breaks, with limited information available to accurately differentiate populations (Carretta *et al.*, 2013; Waring *et al.*, 2014). Additionally, stock distribution boundaries are unknown but likely extend into waters beyond the U.S. EEZ, and currently defined stocks may contain multiple demographically independent populations (Carretta *et al.*, 2013; Waring *et al.*, 2014).

Risso's dolphins produce a wide range of sounds (Caldwell *et al.*, 1969; Corkeron and Van Parijs, 2001) which can be broadly characterized as narrow-band whistles and broadband pulsed calls, used for communication, and broadband echolocation clicks, used for investigating their environment (Richardson *et al.*, 1995). Their echolocation clicks are short duration (40 μs) 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). Off southern California, Risso's dolphin echolocation clicks exhibit distinct, species-specific, spectral banding patterns in which individual echolocation clicks have spectral peaks at 22, 25, 31, and 39 kHz, with alternating spectral notches at 20, 28, and 36 kHz (Soldevilla *et al.*, 2008). These banding patterns are consistent enough across individuals within encounters in the region to identify Risso's dolphin encounters in autonomous recordings for ecological studies of spatial and temporal occurrence (Soldevilla *et al.*, 2010a) and predictive habitat modeling (Soldevilla *et al.*, 2011).

While recent research indicates some odontocete species produce echolocation clicks with consistent features which are identifiable to species (Soldevilla *et al.*, 2008; Baumann-Pickering *et al.*, 2013b; Calderan *et al.*, 2013; Baumann-Pickering *et al.*, 2015b), there has been limited investigation into geographic differences in a species' echolocation clicks that are potentially population-specific. In one example, two distinct click types produced by Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in the Southern California Bight are consistent within encounters but vary among encounters (Soldevilla *et al.*, 2008). Differences in geographic and seasonal occurrence (Soldevilla *et al.*, 2010b), habitat relationships (Soldevilla *et al.*, 2011), diel click production (Soldevilla *et al.*, 2010b), and behavioral activity budgets (Henderson *et al.*, 2011) of these click types support the hypothesis that they are indicative of two morphologically (Walker *et al.*, 1986) and genetically (Lux *et al.*, 1997) distinct populations that overlap in the Southern California Bight. However, alternative hypotheses such as changing click type with prey type have not been ruled out. Risso's dolphin echolocation clicks may also vary geographically and such variation may provide clues to population level structure. Potential population-level structure has never been explored for Risso's dolphins. It is unknown whether all populations of Risso's dolphins outside the Southern California Bight produce echolocation clicks with spectral banding patterns, and if so whether the frequency peaks in the bands vary by population or for other reasons. Visually-verified recordings of Risso's dolphins from the North Atlantic included clicks with a similar peak banding structure (Hodge, 2011), and autonomous recordings from several locations that Risso's dolphin inhabit include echolocation encounters with spectral banding (Hodge, 2011; Frasier, 2015; Baumann-Pickering *et al.*, 2016), suggesting Risso's dolphins outside the Southern California Bight may also produce clicks with spectral banding patterns. Further, it is possible the frequency peaks may vary geographically as they do for Pacific white-sided dolphins.

This study characterizes Risso's dolphin echolocation clicks from the western North Atlantic, the Gulf of Mexico, and numerous locations throughout the North Pacific Ocean. This is the first comprehensive large-scale study to describe Risso's dolphin clicks from regions beyond the Southern California Bight, and to compare spectral features of Risso's dolphin clicks among geographic regions. First, click spectra from Risso's dolphin encounters are evaluated to determine whether Risso's dolphins from all regions produce clicks with the species-specific feature of spectral peak banding. Then, k-means clustering is performed on echolocation click spectra to differentiate common click features and examine their presence and variability within and across encounters. Finally, mean spectral peak and notch frequencies are quantified for each encounter and variability in frequency values within and among regions is evaluated.

II. MATERIALS AND METHODS

A. Study area and field methods

Risso's dolphin recordings were collected during concurrent boat-based visual and acoustic surveys throughout U.S. waters including the western North Atlantic, the Gulf of Mexico, the Southern California Bight, and the Hawaiian Islands; and the international waters of the Pacific Ocean (Fig. 1). Recordings were obtained from multiple institutions over multiple studies from August 2000 through September 2013 (Table I).

All acoustic recordings were collected with concurrent visual observations using established survey protocols (e.g., Barlow, 1995). Marine mammal visual detections and species identifications were made by experienced marine mammal visual observers using either hand-held 7 × 50 binoculars on small vessels or 25 × 150 binoculars on larger platforms. Sighting information included: location of group or animal, initial distance and angle from research vessel, group size, presence of calves, and general behavior. Additionally, weather and sea state data were recorded to account for missed animals due to poor sighting conditions. For these analyses, acoustic recordings from all surveys were limited to schools determined to be single species, i.e., loud and clear signals from periods when no other odontocete species were sighted within 3 nmi and in sea states less than Beaufort 4 (Oswald *et al.*, 2003; Rankin *et al.*, 2008).

Because of the nature of this cross-organizational comparative study over large geographic and temporal scales,

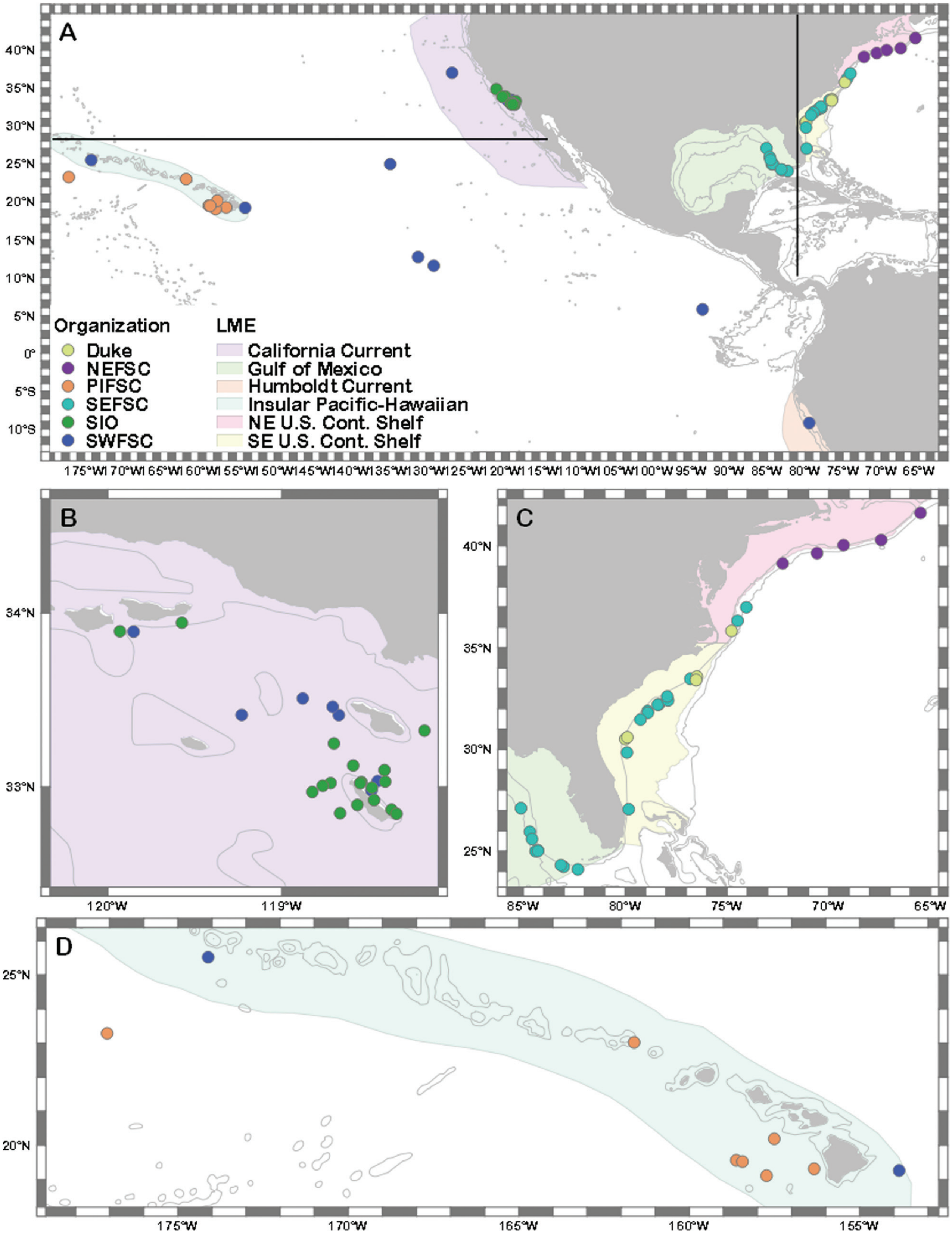

FIG. 1. Map of single-species Risso's dolphin recording locations color coded by organization that collected the data. Dotted lines in (A) indicate the breaks between California-Oregon-Washington and Hawaii Risso's dolphin stock boundaries and the Northern Gulf of Mexico and Western North Atlantic Risso's dolphin stock boundaries. Large Marine Ecosystems (LMEs) including the California Current, Gulf of Mexico, Humboldt Current, Insular Pacific-Hawaiian, Northeast U.S. Continental Shelf, and Southeast Continental Shelf LMEs are delineated as colored polygons. Remaining subplots show detail of encounter locations from the (B) Southern California Bight, (C) U.S. east coast, and (D) Hawaiian Islands. Organizations that collected the data include the Duke University Marine Lab (Duke), NMFS Northeast Fisheries Science Center (NEFSC), NMFS Pacific Islands Fisheries Science Center (PIFSC), NMFS Southeast Fisheries Science Center (SEFSC), Scripps Institution of Oceanography (SIO), and NMFS Southwest Fisheries Science Center (SWFSC).

TABLE I. Risso's dolphin encounter details by organization conducting the study and cruise ID. Total Encounters refers to single-species encounters; Stats Encounters refers to those encounters with >25 clicks included in statistical analyses of spectral features of echolocation clicks. F_s = Sample rate; WNA = Western North Atlantic; NGoMx= Northern Gulf of Mexico HI = Hawaii; and CA/OR/WA = California-Oregon-Washington stocks.

Organization (Cruise)	Region	Total Encounters	Stats Encounters	Start Date	End Date	F_s (kHz)
Duke						
Hatteras	WNA	1	1	7/25/2009	7/25/2009	192
JAX	WNA	2	2	9/17/2009	6/16/2010	192
Onslow Bay	WNA	2	2	8/9/2009	8/16/2009	192
NEFSC						
HB1303	WNA	5	5	7/12/2013	8/15/2013	192
PIFSC						
Big Island	HI	1	1	4/27/2009	4/27/2009	192
HICEAS2010	HI	4	3	9/29/2009	11/15/2010	192
HICEAS2010	HI	2	2	9/28/2010	10/1/2010	500
PICEAS2012	HI	2	1	5/16/2012	5/16/2012	192
SEFSC						
GU1102	WNA	6	6	6/21/2011	7/29/2011	192
GU1304	WNA	8	8	8/23/2013	9/11/2013	192
GU1202	NGoMx	8	6	6/14/2012	8/1/2012	192
SIO						
CalCOFI	CA/OR/WA	4	4	1/28/2007	1/18/2009	192
FLIP0610	CA/OR/WA	1	1	10/9/2006	10/9/2006	192
SCI0608	CA/OR/WA	5	5	8/13/2006	8/16/2006	192
SoCal Small Boat	CA/OR/WA	9	8	8/5/2008	7/22/2011	192
SWFSC						
BRS2012_1	CA/OR/WA	7	6	7/26/2012	8/2/2012	192
HICEAS2002	HI	3	3	10/16/2002	12/3/2002	150
ORCAWALE2001	CA/OR/WA	1	1	8/4/2001	8/4/2001	200
STAR 2000	HI	2	2	8/11/2000	9/9/2000	150
STAR 2000	HI	1	1	11/24/2000	11/24/2000	200
STAR 2003	HI	1	1	11/3/2003	11/3/2003	200
Grand Total		73	69	8/11/2000	9/11/2013	

the recording instrumentation and survey methodologies varied within and across surveys. All surveys used scientific-quality acoustic systems composed of towed hydrophone arrays including hydrophone and pre-amplifier elements, and ship-based sound digitizing and recording hardware and software systems, though specific components varied among surveys and labs. Arrays were typically towed 100–350 m behind the ship to reduce ship noise impacts and at depths of 5–20 m to reduce surface noise and improve signal detectability by towing at or below the thermocline. Hydrophone and pre-amplifier elements were all capable of measuring high-frequency signals and had appropriate filters to reduce low-frequency flow noise and prevent signal aliasing during digitization. Differences in hydrophone and preamplifier frequency response among systems were accounted for during signal processing analyses (Sec. II C). Similarly, sampling rates varied among surveys and ranged between 150 and 500 kHz, which was also accounted for during signal processing (Sec. II B). All acoustic systems recorded directly to flash memory cards or to computer hard-drives using specialized sound analysis and recording software.

Some important differences in survey methodology across studies include (1) stationary or mobile vessels, (2) passing (consistently on trackline) or closing (approaching sighted animals for further study) operation modes, and (3) visual observers' height above sea level. These may impact the sample size, recording duration, ability to confidently assess single-species group composition, and introduction of noise (e.g., from vessel operational changes and echosounders). To account for this, recordings from small boats and moored platforms were limited to periods when identified animals were within 1 km of the recording platform as determined by visual observations to reduce the likelihood that data included sounds from unsighted species due to low observer heights, and to reduce over-representation of long duration recordings. Periods with noise from vessel maneuvers and echosounder detections were removed in a later step.

B. Signal analysis

Signal analysis was performed with customized routines using MATLAB (Mathworks, Natick, MA). Click start and end times were automatically detected following the two-stage approach described by Soldevilla *et al.* (2008) and Baumann-Pickering *et al.* (2010). Briefly, during the first step, clicks were detected automatically in the spectral domain calculated from 10 ms recording segments. Individual spectra were selected as click candidates if a percentage of frequency bins exceeded a threshold within the bandwidth range of interest. The second automatic selection step determined the exact start and end point of the roughly defined clicks using a Teager energy operator in the time domain (Kaiser, 1990; Kandia and Stylianou, 2006). Detector settings [frequency range, minimum bandwidth, and signal-to-noise (SNR) threshold] were optimized for each dataset to maximize the number of good quality click detections and minimize false alarms, such as ship noise and echosounders. For each detected click, 1500 time-series signal samples and the preceding 2500 time-series noise samples were saved for further analysis. To standardize spectral characterization and comparisons of echolocation clicks across the differing sampling rates, spectra were calculated for 2.5 ms of data to yield 400 Hz spectral resolution. This value was selected as a common denominator of all sample rates that provides reasonable resolution for characterizing peaks without including excess noise. Spectra were calculated with the discrete Fourier transform (DFT) of a number of samples set by recording rate (Table II), using a Tukey window with a 0.3 taper ratio. Noise spectra were calculated as the mean spectrum of the preceding 2500 samples, using the same spectral parameters as used for calculating the click spectrum, with 0% overlap.

The use of automated click detection algorithms results in a number of false positive detections. An automated algorithm was run which removed detections with certain features, specifically, those detections in which (1) peak frequency (i.e., frequency of maximum amplitude) occurred at a standard echosounder frequency (18, 28, 38, 50, and 76 kHz), (2) peak frequency was less than 19 kHz, therefore likely to be either ship noise or sperm whales (*Physeter macrocephalus*), or (3) those in which preceding noise was greater than or equal to the click (i.e., $\text{SNR} \geq 1$), which removed closely spaced clicks ($\text{ICI} < 2.5$ ms: click rate of 400/s or higher or overlapping trains). Approximately 50% of automated detections were removed as false positives during this process. Concatenated spectrograms were created for each encounter for use in analyses of the occurrence of spectral banding (Sec. II C 1) and then a follow-up manual removal was done by visually examining the concatenated click spectrograms for groups of consecutive click detections with aberrant spectra. Specifically, groups of click detections were manually removed if artifacts were evident, including sonar signals, tonal lines or other recording artifacts, ship noise, and clicks that did not contain peak banding; this led to the removal of 4% of detections. It is possible the clicks without peak banding were made by Risso's dolphins, as Risso's dolphins produce some click types, such as buzzes, without spectral banding, or that these encounters included multi-species groups that were not identified by visual observers. Groups of nine or more consecutive non-banded clicks (range 9–6444 clicks and 0.3% to 33% of total click detections per encounter) were present in ten recordings. These groups occurred at the start or end of the encounter and were clearly separated from the banded clicks in eight of the ten encounters suggesting they likely were produced by an unsighted delphinid group. The non-banded clicks were removed from the remaining analyses (Secs. II C 2 and II C 3), because it is unlikely they were produced by Risso's dolphins and, further, is not effective to measure peaks and notches in non-banded clicks for the comparison of banding peak and notch frequencies among encounters. Concatenated spectrograms were re-created for the remaining clicks for each region. Spectral magnitudes were normalized between 0 and 1, and the mean and standard deviation of the normalized click spectra were calculated for each region.

TABLE II. Number of samples used to calculate discrete Fourier transform (DFT) for recordings at different sample rates (F_s).

F_s (kHz)	DFT size
150	375
192	480
200	500
500	1250

While a variety of metrics can be evaluated for comparing click features (e.g., Au, 1993; Baumann-Pickering *et al.*, 2013a; Buscaino *et al.*, 2015), this study focused on metrics that highlight the frequency values of spectral peaks and notches that form the spectral banding pattern, based on differences in peak and notch values found among Pacific white-sided dolphin click types (Soldevilla *et al.*, 2008). For statistical analyses, (1) the truncated, normalized spectra of echolocation clicks and (2) the frequency values of spectral peaks and notches of echolocation clicks were used as click feature metrics. The first metric relies on overall spectral shape, which is impacted by a variety of factors that are important to account for, while the second metric uses the frequency values of peaks and notches that do not depend on overall spectral shape and are less influenced by these factors. Specifically, the spectral shape of recorded signals represents the convolution of the original signal, the sound propagation pathway, and the instrumentation frequency response (Rabiner and Juang, 1993). For wild recordings of echolocation clicks, this includes effects of distance and orientation of the vocalizing animal to the recording hydrophone (e.g., Au *et al.*, 2012). To minimize the influence of high-frequency energy loss with distance and remove hydrophone-system-specific features, the click spectrum frequency range was truncated to 19 to 50 kHz and cepstral-filtering methods (described below) were applied. The low-frequency truncation removed ship noise and 18 kHz sonar artifacts while the high-frequency truncation minimized the effects of high-frequency transmission loss, all while retaining the main peak and notch features which occur between approximately 21 and 45 kHz (Soldevilla *et al.*, 2008). While spectrum truncation and cepstral-filtering methods minimize these effects on the spectra, the inclusion of many clicks from random orientations ensures the suite of variability expected in wild dolphin recordings is accounted for, leading to more robust results.

For the first click feature metric, the truncated spectra were normalized for further analyses using cepstral techniques. Cepstral techniques, in which the real cepstrum is the discrete cosine transform (DCT) of the log spectral magnitude and defines the general spectral shape, are commonly used in human speech recognition tasks to deconvolve and separate the original signal from the sound propagation pathway and the instrumentation frequency response (Picone, 1993). The low cepstral coefficients, or "quefrencies," which describe overall spectral tilt, represent transmission effects (including sound propagation channel and instrument frequency response), individual characteristics, vocal efforts and other factors. Therefore, the de-emphasis of these lower quefrencies through cepstral filtering, or "liftering" (Rabiner and Juang, 1993), is a practical method for accounting for differences in recording gear and loss of high frequencies with increasing animal distance. Each echolocation click spectrum was high-pass liftered by transforming the truncated spectrum to its cepstrum using the DCT and multiplying the cepstrum by a rectangular window function filter in which the first six quefrencies were zero and all other quefrencies were one. This removed both gain differences and the slowly fluctuating features of each spectrum while leaving the peaks and notches (Fig. 2). Then, an inverse DCT was applied to the liftered signals to return them to the spectral domain for statistical clustering analyses.

For the second click feature metric, an automated peak-picking algorithm was run in MATLAB, as described by Soldevilla *et al.* (2008), to obtain the frequency values of spectral peaks and notches for each truncated click spectrum. An automated fourth-order regression-based peak and notch selection algorithm was implemented on each click spectrum to select all major peaks and notches. To avoid selecting minor peaks or notches, the spectra were smoothed using a 5-point window and a threshold was set such that the first derivative of the peak or notch was required to deviate by 0.2 or more. Variability exists among individual clicks, such that the frequency values of the peaks and notches may shift, the peak or notch may not exist at all, and extraneous peaks and notches may exist that are not consistent across clicks. Across the recordings in this study, the number of peaks and notches selected per click spectra varied, ranging between 0 and 55 and averaging 13. For regional comparisons of spectral banding variability, the frequency values of consistent spectral peaks and notches were obtained by adapting the histogram and univariate Gaussian Mixture Modeling (GMM, Huang *et al.*, 2001) method of Soldevilla *et al.* (2008) using a random subset of clicks per encounter (e.g., Soldevilla *et al.*, 2008). For each encounter, a maximum of 250 clicks were sampled, using simple random sampling without replacement, to avoid pseudo-replication due to click trains containing multiple clicks from one individual and the potential that an individual produces multiple click trains during an encounter. The number of clicks to subsample was empirically determined as the fewest number of clicks to produce a histogram in which consistent peaks and notches could be reliably measured. Histograms were created of all selected peaks and of all selected notches between 19 and 50 kHz from the subsample of clicks, calculated such that each bin was 400 Hz wide to correspond with the FFT frequency resolution. An 11-mixture univariate GMM was fit to each histogram using an Expectation Maximization algorithm, with initial mixture means uniformly distributed across the frequency range. A semi-automated algorithm selected mixtures associated with the four strongest peaks and the three strongest notches, based on the number of consistent peaks and notches found by Soldevilla *et al.* (2008), with the option to manually change the selections to ensure the first four peaks and first three notches were selected.

C. Geographic comparisons of click features

1. Occurrence of spectral banding

To evaluate whether Risso's dolphins from all regions produce clicks with the species-specific feature of spectral banding, concatenated spectrograms were reviewed from each encounter. Each encounter was scored for the presence or absence of clicks containing spectral banding. If all clicks in an encounter were previously removed because they did not contain spectral banding, these encounters were scored as absent. Following this presence/absence evaluation, encounters with fewer than 25 clicks were removed from

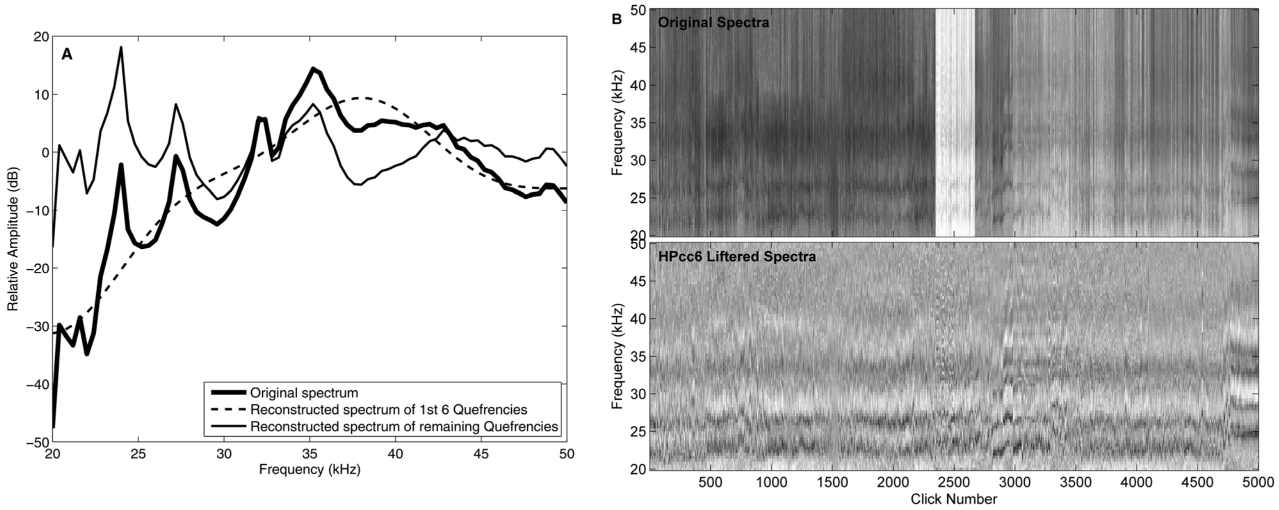

FIG. 2. Cepstral filtering (liftering) example. (A) Original Risso's dolphin echolocation click spectrum split into low-quefrency and high-quefrency content shows effect of using high-pass liftering to remove low-quefrency content. (B) Concatenated spectrograms of the original spectra and the reconstructed spectra following high-pass liftering of the first 6 quefrencies (cepstral coefficients) for a sample of 5000 clicks. By high-pass liftering the first six quefrencies, the spectra are mostly leveled, accentuating the spectral peak banding patterns.

further analyses to ensure only encounters with a representative sample were included in statistical analyses.

2. Click spectral clustering and geographic variation

To examine and characterize distinctive features of Risso's dolphin click spectra and how they vary geographically, a k-means clustering algorithm was run on all truncated and liftered click spectra and the percentage of clicks from each encounter assigned to each cluster by region were evaluated. The spectra from all clicks were partitioned by a k-means clustering analysis with nine clusters using the squared Euclidean distance. The number of clusters to use was empirically determined as the smallest number that yielded clusters with consistent spectral peak features. The centroid spectra for each of the nine clusters were sorted in order of ascending peak frequencies and plotted. Concatenated spectrograms of the original spectra and the liftered spectra of all clicks in each cluster were compared and evaluated to ensure no artifacts were introduced during the liftering process. The percentages of clicks in each cluster were evaluated by encounter to determine which click types were dominant, and these were mapped as pie charts to examine how the occurrence of click types varied geographically. Additionally, they were plotted as stacked bar charts sorted by longitude to further examine geographical variability in each ocean basin. This sorting is informative of both latitudinal and longitudinal variation as latitude and longitude are correlated in this study area, but sorting by longitude is more effective at separating the geographic regions.

3. Geographic hypothesis testing within international Pacific and U.S. waters

To evaluate hypotheses of whether Risso's dolphin peak and notch frequencies differ with geographic region, variability in these features was tested among pre-defined geographic regions. First, whether geographic variation in acoustic features is consistent with U.S. Risso's dolphin stock assignments was evaluated to determine if acoustic differentiation supports the currently defined stock boundaries. Then, whether geographic variation in these acoustic features is consistent with finer-scale geographic regions that correspond with major ecological boundaries was evaluated to investigate whether further refining of spatial structure is supported by acoustic differentiation.

The first tests evaluated acoustic variation within and between encounters grouped according to U.S. stock assignment. In U.S. waters, the National Marine Fisheries Service manages Risso's dolphins as four stocks: (1) the Hawaii (HI) stock; (2) the California-Oregon-Washington (CA/OR/WA) stock, (3) the Western North Atlantic (WNA) stock, and (4) the Northern Gulf of Mexico (NGoMx) stock (Carretta *et al.*, 2013; Waring *et al.*, 2014). These stock delineations are based on management boundaries or large scale ecosystem breaks rather than genetic or morphological evidence, and it is unknown whether distributions extend into waters beyond the U.S. Exclusive Economic Zone (EEZ) or if current stock definitions contain multiple demographically independent populations (Carretta *et al.*, 2013; Waring *et al.*, 2014). For these stock-based tests, acoustic encounters with Risso's dolphins were assigned to the WNA, NGoMx, HI, and CA/OR/WA stocks (Fig. 1) such that within-ocean-basin breaks occurred at the southern tip of Florida at 81°W in the Atlantic, and at a distribution gap at 28°N in the Pacific (e.g., Mangels and Gerrodette, 1994).

The second tests evaluated acoustic variation within and between encounters at a finer-scale by grouping encounters by Large Marine Ecosystems (LMEs; e.g., Sherman and Alexander, 1986). Acoustic encounters occurred within or near six LMEs: (1) Insular Pacific-Hawaiian (IPH), (2) California Current (CC), (3) Humboldt Current, (4) Gulf of Mexico (GoMx), (5) Southeast U.S. Continental Shelf (SEUS), and (6) Northeast U.S. Continental Shelf (NEUS). Acoustic encounters were grouped by the LME polygons (www.lme.noaa.gov) that they occurred within by mapping the encounters and polygons in QGIS 2.10.1-Pisa (www.qgis.org; Fig. 1). There were a few exceptions to this grouping because LMEs are mainly defined for shelf waters: (1) several encounters occurred just beyond the NEUS shelf boundary and these were included within the NEUS LME; (2) encounters from the offshore waters of the Pacific Ocean which are not part of an LME were assigned to a group called the Pelagic Pacific (PPac); and (3) there was only one encounter from the Humboldt Current and this was included in the PPac group.

For both the stock and LME region tests, one-way nonparametric multivariate analysis of variance (MANOVA) tests (Munzel and Brunner, 2000) were evaluated to compare the null hypothesis of no significant acoustic differences among regions, and the alternate hypotheses that (a) provisional stock regions or (b) finer-scale LME-regions have an effect on acoustic variation. These tests used four of the seven measured mean peak and notch frequencies per encounter from the peak-picking and histogram analyses. During the GMM analysis, it was found that the histograms from some encounters exhibited double peaks in which the third and fourth peaks were closely spaced while histograms from other encounters did not have this feature. Therefore, to ensure the metrics from all encounters represented comparable features, only the mean spectral frequencies of the first two peak mixtures and the first two notch mixtures per encounter were included in the MANOVA tests. In cases of significance, *post hoc* one-way analysis of variance (ANOVA) tests were run to determine which measured variables were significantly different (Zar, 1999), and multivariate *post hoc* pairwise comparison tests of least-square means, using Bonferonni's correction, were conducted to determine which regions were significantly different (Zar, 1999). Additionally, a multivariate general linear model was evaluated to test for a relationship between peak and notch frequency values and latitude, also using the mean value of the first two peaks and first two notches of each encounter. Finally, ANOVA tests using the Pillai statistic were used to determine the best model among the three multivariate models. All statistical tests were performed in the open-source statistical program R, version 2.15.0 (R Core Team, 2014).

III. RESULTS

Echolocation clicks were detected in 73 recordings from single-species Risso's dolphin sightings. Encounters were not evenly distributed among areas (Tables I and III), with

TABLE III. Summary statistics (mean ± standard deviation) for Risso's dolphin click spectral peak and notch values by U.S. Risso's dolphin stock-based regions. Stock regions include the Western North Atlantic (WNA), the Northern Gulf of Mexico (NGoMx), Hawaii (HI), and California-Oregon-Washington (CA/OR/WA).

	WNA N = 23	NGoMx N = 7	HI N = 14	CA/OR/WA N = 25
Peak 1	22.8 ± 1.1	22.4 ± 1.0	24.1 ± 0.8	21.8 ± 1.0
Peak 2	26.5 ± 0.9	25.6 ± 1.1	27.0 ± 1.1	24.8 ± 1.0
Peak 3	32.7 ± 1.6	30.4 ± 2.8	32.7 ± 1.2	31.2 ± 1.0
Peak 4	38.5 ± 3.6	36.5 ± 4.3	37.8 ± 3.2	37.9 ± 2.3
Notch 1	24.5 ± 0.9	23.8 ± 0.5	25.7 ± 0.9	23.4 ± 1.2
Notch 2	28.6 ± 1.0	27.2 ± 0.8	29.1 ± 0.9	27.0 ± 0.9
Notch 3	35.4 ± 2.1	32.5 ± 2.9	35.0 ± 1.9	34.5 ± 1.3

more encounters from the southeast U.S. Atlantic and southern California, which likely reflects the difference in number of surveys included from these regions compared to others, though it is possible Risso's dolphins are also more commonly encountered in these waters. The number of clicks detected per encounter was variable, ranging from 9 to 10 405 (mean 1260 ± 1870), and was affected by differences in ambient noise, survey methodology (e.g., passing vs closing mode), and detector parameters.

A. Occurrence of spectral banding

All 73 recordings from single-species Risso's dolphin sightings contained clicks with peak-banding structure, indicating this distinctive feature is a species-specific feature found for Risso's dolphins across ocean basins. There was within-encounter variability in both the occurrence and frequency values of this spectral peak-banding (Fig. 3). For example, the majority of clicks in regular echolocation click trains and in short click packets (brief click trains with 5–12 clicks) exhibited this structure [Figs. 3(D) and 3(E)], while the spectral structure occurred in some, but not all, rapid click trains, such as buzzes [Figs. 3(F) and 3(G)]. In 10% of recordings, there were some echolocation click trains that did not exhibit spectral peak banding features; it is unknown whether these came from Risso's dolphins or an unsighted species. Some of the within-encounter variability in frequency values of spectral peak banding appeared to be due to variability between individuals as evidenced by frequency differences between concurrent click trains [Fig. 3(E)], while on a few occasions, there was evidence of within-individual variability in peak values such that peaks shifted up or down and back again throughout a single click train [Fig. 3(H)]. It is unknown whether this within-individual variation is due to acoustic behavioral changes or is the effect of relative orientation of the animal's head to the receiver.

B. Click spectral clustering and geographic variation

There were 69 recording encounters left for click characterization after the removal of encounters with fewer than 25 click detections. The k-means clustering analysis of the liftered spectra effectively clustered echolocation clicks by the frequencies at which the spectral peaks occurred (Fig. 4). The strong and consistent peak banding seen in each cluster spectrogram shows that this method focused on the peaks and notches in each spectrum as intended, and the increasing shift in the frequency of the peaks across clusters shows that it differentiated on the change in peak frequencies in Risso's echolocation clicks. The first spectral peak shifted by as much as 6 kHz across the nine cluster centroid spectra from 20 kHz for the lowest frequency cluster to 26 kHz for the highest frequency cluster. The first two peaks typically occurred close together in the frequency-domain (~3 kHz), followed by a strong notch. An additional distinguishing feature was apparent in which the third peak either occurred as

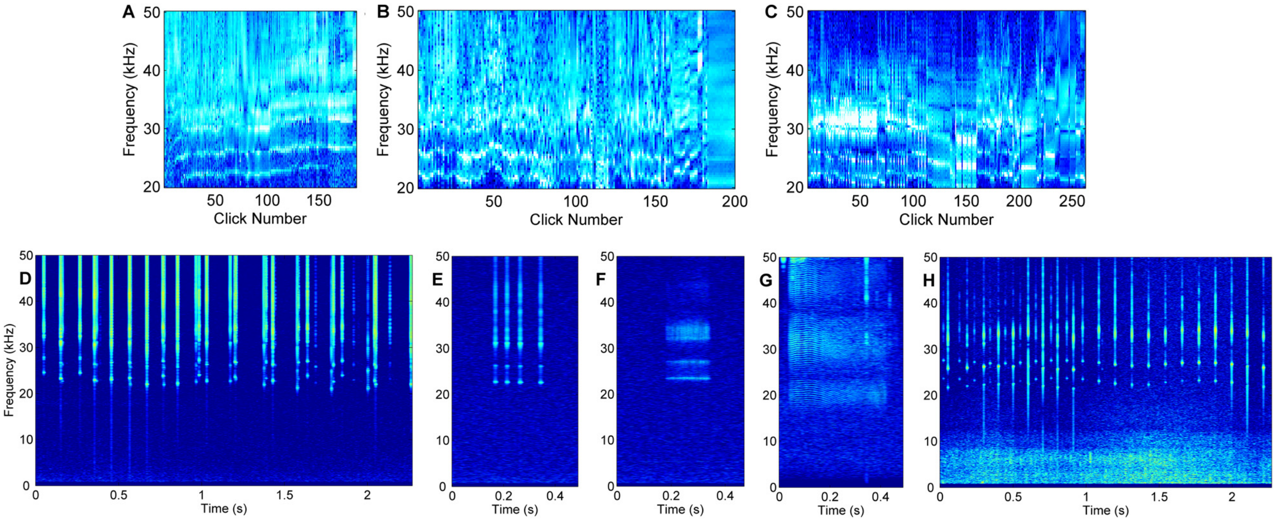

FIG. 3. (Color online) Within-encounter variability in Risso's dolphin echolocation clicks indicated in (A)-(C) concatenated spectrograms of three encounters and (D)-(H) short-time spectrograms and waveforms of individual click trains. (A) Concatenated spectrograms illustrate a consistent trend in variability across an encounter, and (B) and (C) variability within clicks trains and between click trains. Short-term spectrograms of Risso's dolphin clicks include (D) two overlapping click trains with consistent peak frequencies within trains and different peak frequencies between trains, (E) a short click packet with consistent spectral peak banding, (F) a buzz with consistent spectral peak banding, (G) a buzz without spectral peak banding, and (H) a click train with frequency shifts in spectral peak banding frequencies. Short-time spectrograms created with DFT of 6000 points and 90% overlap.

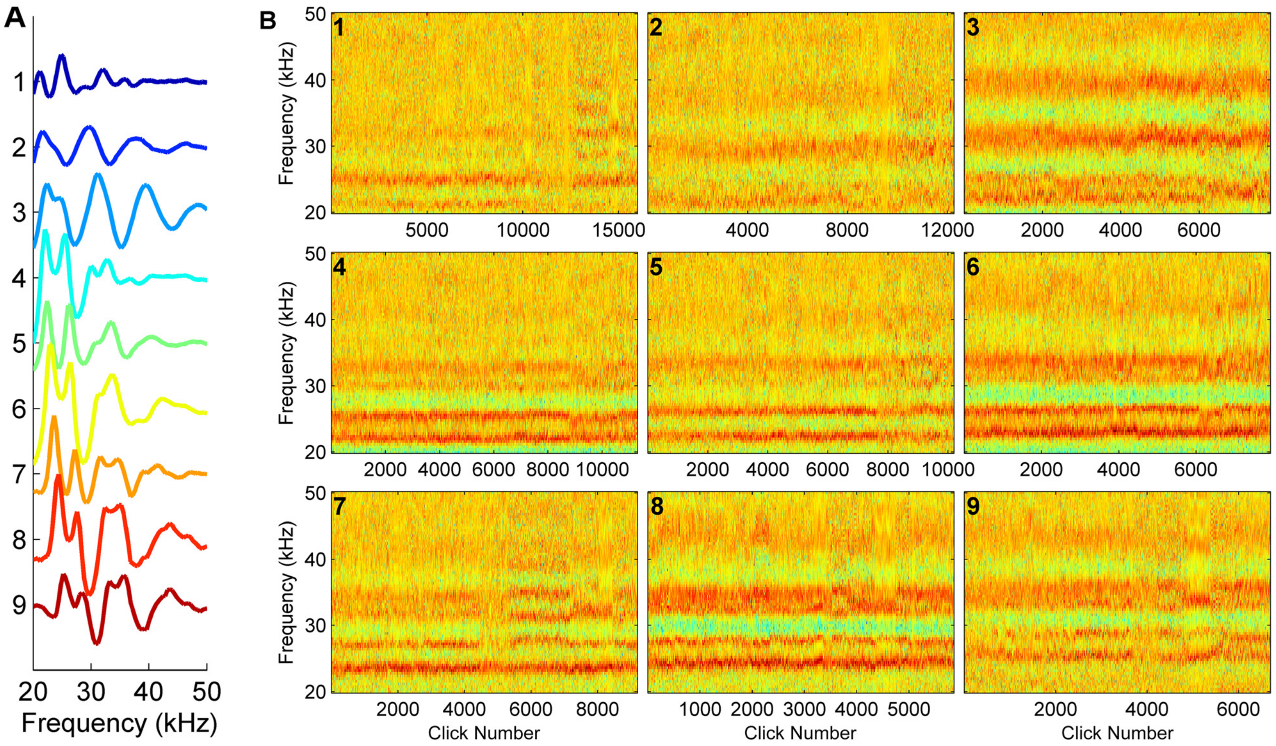

FIG. 4. (Color online) (A) Centroid cluster spectra and (B) concatenated spectrograms of Risso's dolphin echolocation clicks partitioned into each cluster. Spectrograms represent the six-frequency high-pass liftered spectra.

a single peak followed by a strong notch and more distant fourth peak or as a double peak with the third and fourth peaks occurring close together, with similar frequency-spacing to the first and second peaks. The single third peaks were most commonly associated with the lower-frequency echolocation click spectral clusters (e.g., clusters 2 and 3, Fig. 4).

Within each encounter, the proportion of clicks assigned to each of the nine clusters was calculated and pie charts were mapped allowing a visualization of within and across encounter variation in Risso's dolphin echolocation click peak frequencies (Fig. 5). The most obvious across-region difference can be seen in the North Pacific Ocean between encounters off southern California and encounters around the main Hawaiian Islands. Off southern California, the majority of echolocation clicks from each encounter (50%–90%) were assigned to the first three, lowest frequency clusters, while around the main Hawaiian Islands, the majority of echolocation clicks from each encounter (50%–70%) were assigned to the last three, highest frequency clusters [Figs. 5(B), 5(C), and 6(A)]. While there were few samples from other regions in the North Pacific Ocean, the available examples appear different from those found off Hawaii and southern California. The two encounters off South and Central America both contain a high proportion of clicks assigned to high-frequency click types, the four encounters from the open pelagic waters between the American continents and the Hawaiian Islands contain clicks assigned to a mix of either low-frequency types or high-frequency types, with very few mid-frequency types, and the two encounters off the northern Hawaiian Islands contain a majority of clicks assigned to the mid-frequency click types. It is interesting to note that in all encounters from the North Pacific Ocean, clicks were rarely assigned to click type 5, a mid-frequency click type in which the first two peaks are more distant from each other than the first two peaks in other click types. Additionally, the second and third click types which exhibited the single third peak were common off southern California, but did not commonly occur elsewhere.

In the North Atlantic Ocean, including the Gulf of Mexico, the majority of clicks per encounter were typically assigned to the three mid-frequency click types (Fig. 5). There was not a distinct trend between regions, in contrast to southern California and the main Hawaiian Islands. However, there did appear to be a latitudinal cline [Fig. 6(B)], in which most encounters from the northeast U.S. North Atlantic waters had the majority of clicks assigned to low-frequency click types [Fig. 5(D)], those from the central U.S. North Atlantic waters had the majority of clicks assigned to the mid-frequency click types [Fig. 5(F)], and those from the southeast U.S. North Atlantic waters had the majority of clicks assigned to the high-frequency click types [Fig. 5(F)]. In contrast to the North Pacific Ocean, click type 5 was common throughout the western North Atlantic and northern Gulf of Mexico, while the second and third click types were not commonly observed. There were three encounters that appeared to be outliers, as the majority of clicks were assigned to the highest frequency click types, but they occurred at latitudes otherwise dominated by encounters with lower-frequency click types [Figs. 5 and 6(B)]. These encounters were also notable in that, similar to the Pacific they contained either high or low frequency types but few mid-frequency click types, and overall, they contained relatively few echolocation click trains compared to other encounters. Two of these apparent outliers contained fewer than 75 clicks. After removing these two, a Pearson's correlation was

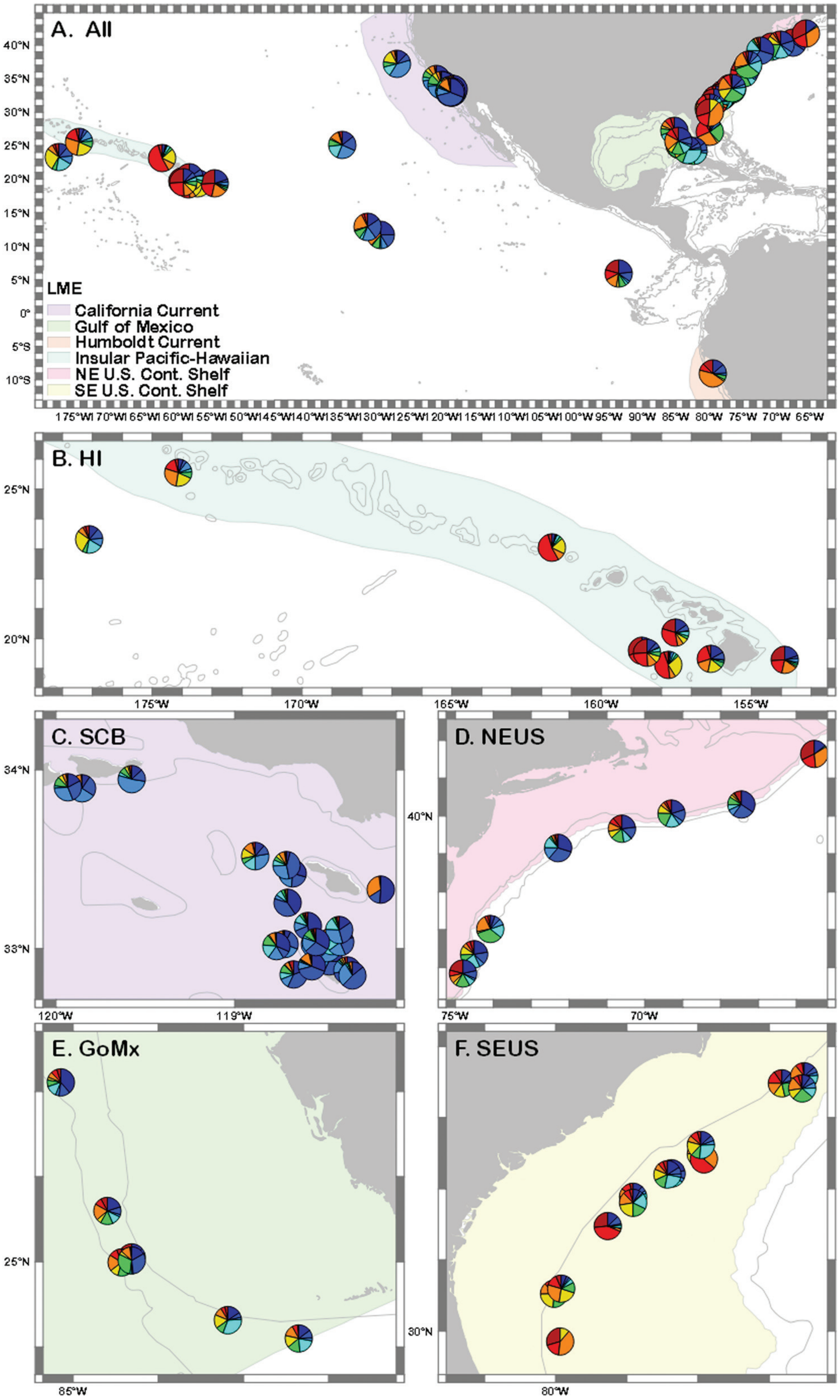

FIG. 5. Maps of proportion of Risso's dolphin echolocation click types per encounter based on clustering analysis. Encounters from (A) the entire study area, (B) Hawaii (HI), (C) Southern California Bight (SCB), (D) Northeast U.S. Atlantic, (E) eastern Gulf of Mexico, and (F) Southeast U.S. Atlantic. The nine-cluster click types are indicated by color as in Fig. 4 and increase in frequency from blue to red.

calculated for the relationship between first peak frequency and latitude for western North Atlantic encounters, and the negative linear relationship was significant ($r = 0.67$, $p = 0.002$; Fig. 7). Encounters from the Gulf of Mexico were dominated by clicks assigned to the low- and mid-frequency click types; by comparison, those from the nearby southeast U.S. North Atlantic waters were dominated by higher frequency click types. Encounters from the Gulf of Mexico tended to be more variable across click trains, with peak frequencies shifting by 3–4 kHz among different click trains.

C. Geographic hypothesis testing within international Pacific and U.S. waters

The automated peak and notch picking algorithm yielded histograms with evidence of consistent peaks and

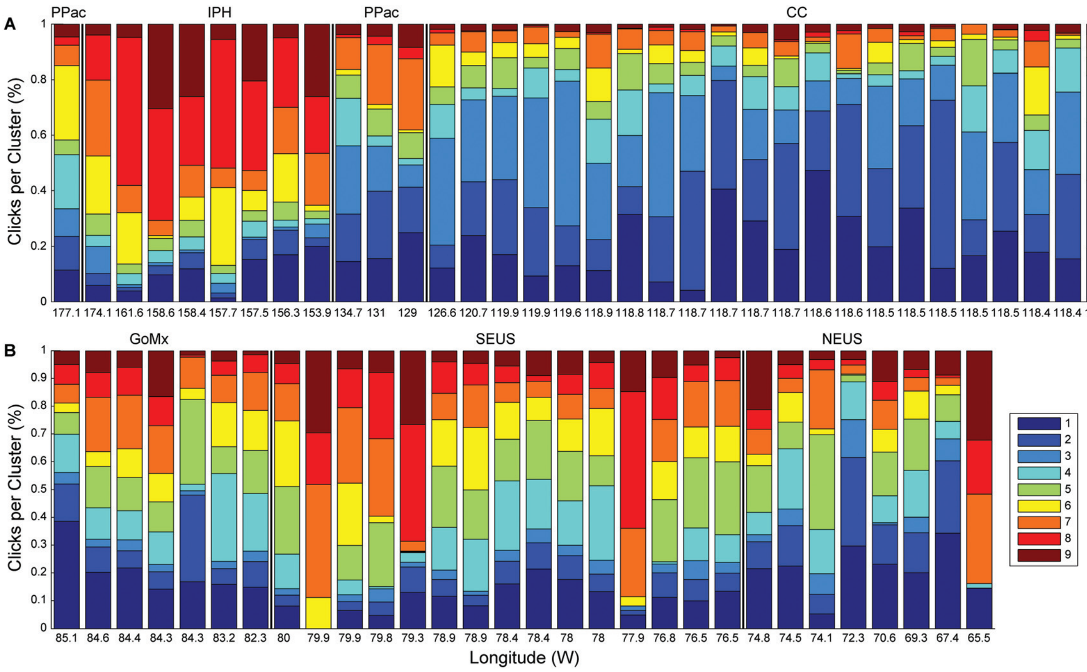

FIG. 6. Stacked bar charts of proportion of Risso's dolphin echolocation clicks from each encounter clustered in each click type, sorted by longitude, for (A) the Pacific Ocean, and (B) the Gulf of Mexico and Atlantic Ocean. The nine-cluster click types are indicated by color as described in Fig. 4. Breaks between the six LME-based regions are indicated by black vertical lines and resulting groups are labeled by region: Pelagic Pacific (PPac), Insular Pacific-Hawaiian (IPH), California Current (CC), Gulf of Mexico (GoMx), Southeast U.S. Continental Shelf (SEUS), and Northeast U.S. Continental Shelf (NEUS).

notches for most of the 69 encounters that were further characterized for statistical hypothesis testing. Summary statistics of the first four peak and first three notch frequency values, based on the univariate Gaussian mixture model fitting for each encounter, are presented by region for the four-region stock-based hypothesis (Table III) and the six-region LME-based hypothesis (Table IV). The first three peaks and two notches had low within region variability (≤ 1.5 kHz) with the exception of the third peak in the Gulf of Mexico and Southeast Atlantic regions. Conversely, the last peak and notch each had higher variability, ranging from 1 to 4.5 kHz.

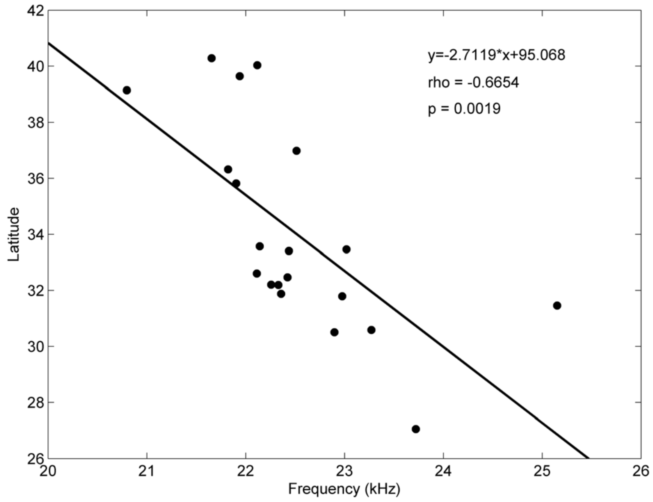

FIG. 7. The first peak value by latitude for Western North Atlantic Risso's dolphin encounters with more than 75 clicks. When small sample size encounters are excluded, a significant effect exists where the first peak frequency decreases with increasing latitude.

For the four-region stock-based model, peak and notch data were not multivariate normal, variances and covariances were heterogeneous, and the design was unbalanced, therefore a non-parametric MANOVA was conducted on the ranked data following the Munzel and Brunner (2000) method implemented in R using the mulrank() function (Wilcox, 2005). There was a significant main effect of stock-based region on peak and notch frequency values ($F = 11.72$, $p < 0.0001$). Follow-up univariate ANOVAs indicated the effect of region was significant for all four peak and notch frequency variables: peak 1 [F (3, 65) = 15.83, $p < 0.0001$], peak 2 [F (3, 65) = 19.37, $p < 0.0001$], notch 1 [F (3, 65) = 17.38, $p < 0.0001$], and notch 2 [F (3, 65) = 22.68, $p < 0.0001$]. To determine which regions were significantly different from others, multivariate *post hoc* pairwise comparison tests of least-square means, using Bonferonni's p-adjustment for six comparisons (Rice, 1989) were run, and results revealed that HI mean values were significantly higher than those for the WNA (t.ratio 3.06, $p < 0.05$), NGoMx (4.30, $p < 0.001$), and CA/OR/WA (7.81, $p < 0.0001$), and that CA/OR/WA mean values were significantly lower than HI and WNA values [–5.44, $p < 0.0001$, Fig. 8(A) and 8(C)]. The WNA and NGoMx regions effects on acoustic variation were not significant.

For the six-region LME-based model, data also were not multivariate normal, variances and covariances were heterogeneous, and the design was unbalanced, therefore a non-parametric MANOVA was conducted as above (Wilcox, 2005). There was a significant main effect of LME-based region on peak and notch frequency values ($F = 11.22$, $p < 0.0001$). Follow-up univariate ANOVAs revealed the effect of region was significant for all four peak and notch frequency variables: peak 1 [F (Df = 5, residuals Df = 63) = 12.13,

TABLE IV. Summary statistics (mean ± standard deviation) for Risso's dolphin click spectral peak and notch values by U.S. large marine ecosystem (LME) regions. The six LMEs include the Southeast U.S. Continental Shelf (SEUS), the Northeast U.S. Continental Shelf (NEUS), the Gulf of Mexico (GoMx), the Insular Pacific-Hawaiian (IPH), the Pelagic Pacifc (PPac), and the California Current (CC) ecosystems.

	SEUS N = 15	NEUS N = 8	GoMx N = 7	IPH N = 8	PPac N = 6	CC N = 25
Peak 1	23.1 ± 1.0	22.1 ± 1.0	22.4 ± 1.0	24.5 ± 0.5	23.5 ± 0.9	21.8 ± 1.0
Peak 2	26.8 ± 0.7	26.1 ± 1.0	25.6 ± 1.1	27.3 ± 0.6	26.6 ± 1.5	24.8 ± 1.0
Peak 3	33.3 ± 0.7	31.5 ± 2.1	30.4 ± 2.8	33.5 ± 0.9	31.7 ± 0.6	31.2 ± 1.0
Peak 4	39.3 ± 3.0	37.2 ± 4.5	36.5 ± 4.3	39.1 ± 3.4	36.0 ± 2.1	37.9 ± 2.3
Notch 1	24.8 ± 0.9	23.9 ± 0.8	23.8 ± 0.5	25.9 ± 0.8	25.4 ± 0.9	23.4 ± 1.2
Notch 2	28.8 ± 0.8	28.1 ± 1.2	27.2 ± 0.8	29.4 ± 0.3	28.7 ± 1.2	27.0 ± 0.9
Notch 3	36.2 ± 1.1	33.8 ± 2.7	32.5 ± 2.9	36.2 ± 1.8	33.5 ± 0.8	34.5 ± 1.3

$p < 0.0001$], peak 2 [F (5, 63) = 12.79, $p < 0.0001$], notch 1 [F (5, 63) = 11.96, $p < 0.0001$], and notch 2 [F (5, 63) = 15.63, $p < 0.0001$]. Multivariate *post hoc* pairwise comparison tests of least-square means were conducted between each of the three regions within each of the two ocean basins using Bonferroni's p-adjustment for six comparisons (Rice, 1989). Results indicated that CC mean values were significantly lower than those for IPH (–7.600, $p < 0.0001$) and PPac (–4.881, $p = 0.0003$), and that SEUS mean values were significantly higher than those from GoMx (2.91, $p = 0.03$; Fig. 8). Acoustic metrics for the NEUS were not significantly different from either the SEUS or the GoMx, nor were metrics different between the IPH and the PPac regions.

In both the North Atlantic and the Pacific Oceans, there appeared to be an effect of latitude on the peak and notch frequencies, with a shift toward lower frequencies at higher latitudes. This effect was tested as an alternative to the hypothesis of discrete regions by evaluating a multivariate linear model to examine the effect of latitude on peak and notch frequencies. The effect of latitude was significant [$F(1,67) = 11.79$, $p < 0.001$]. The three multivariate models of geographic effects were compared in R using the anova() function. While all models were significantly better than a model which only included the mean, the models including discrete regions had significantly better explanatory power than the model including latitude (Table V). The four-region and six-region models were not significantly different from each other.

IV. DISCUSSION

A. Species identification

As the uses of PAM for studying cetacean ecology continue to expand (e.g., Mellinger *et al.*, 2007; Van Parijs *et al.*, 2009), a key remaining need is the ability to identify species and populations, particularly for odontocetes. The discovery that Risso's dolphins off southern California have distinctive echolocation clicks led to ecological studies of spatio-temporal occurrence throughout the Southern California Bight and development of predictive habitat models from long-term autonomous PAM recordings (Soldevilla *et al.*, 2010a; Soldevilla *et al.*, 2011). The current study provides evidence that the distinctive spectral peak banding features of echolocation clicks are present and may be useful

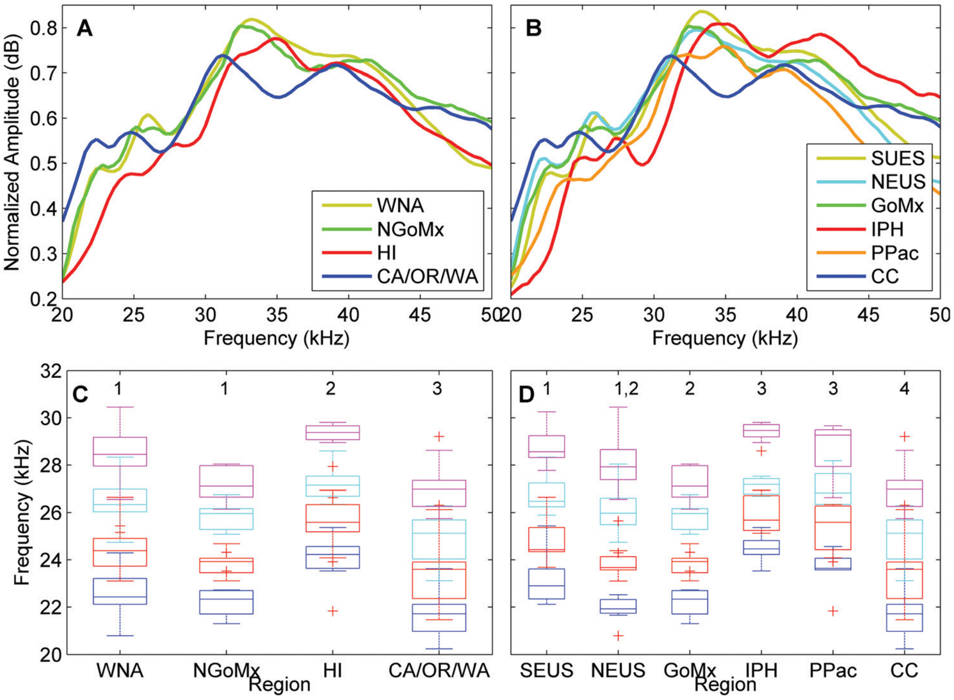

FIG. 8. Mean spectra of Risso's dolphin echolocation clicks for the (A) four-region and (B) six-region geographic hypotheses. Boxplots of the first two peaks and first two notches for the (C) four-region and (D) six-region hypotheses. Significant differences between regions are indicated in boxplots by group numbers at top of plot. Regions that share a group number are not significantly different. The four regions represent the Western North Atlantic (WNA), the Northern Gulf of Mexico (NGoMx), Hawaiian Islands (HI), and the California-Oregon-Washington (CA/OR/WA) Risso's dolphin stock regions, while the six regions represent Large Marine Ecosystems (LMEs) of Southeast U.S. Continental Shelf (SEUS), Northeast U.S. Continental Shelf (NEUS), Gulf of Mexico (GoMx), the Insular Pacific-Hawaiian (IPH), the California Current (CC), and those outside these LMEs in the pelagic waters of the Pacific Ocean (PPac).

TABLE V. ANOVA comparison of multivariate models including (1) null model, (2) model with mean, (3) model with Latitude, (4) model with four stock-based regions, and (5) model with six LME-based regions.

	Res.Df	Df	Gen.var.	Pillai	approx F	num Df	den Df	Pr(>F)
Model 1: PeakFreqs ~ 1–1	69		2.82					
Model 2: PeakFreqs ~ 1	68	−1	0.59	1.00	18932.6	4	60	<2.2e–16[a]
Model 3: PeakFreqs ~ Latitude	67	−1	0.56	0.35	8.2	4	60	2.46E–05[a]
Model 4: PeakFreqs ~ 4Region	65	−2	0.46	0.69	8	8	122	1.39E–08[a]
Model 5: PeakFreqs ~ 6Region	63	−2	0.46	0.17	1.1	8	122	0.381

[a]Models which show significant improvement ($p < 0.0001$) over the prior model.

for species identification over a much wider geographic range, encompassing the eastern North Pacific Ocean, western North Atlantic Ocean, and Gulf of Mexico. Furthermore, Calderan *et al.* (2013) describe peaks in Risso's dolphin clicks from Scotland and peaks are evident in click spectrograms from Australia (Neves, 2013, p. 107). Therefore, this is likely a feature common to echolocation clicks of Risso's dolphins worldwide. Risso's dolphin global distribution details are generally unknown, particularly in deep oceanic zones (Jefferson *et al.*, 2014), and the ability to identify their presence in passive acoustic recordings globally can enhance understanding of their geographic ranges, seasonal and inter-annual movements (e.g., Soldevilla *et al.*, 2010b; Baumann-Pickering *et al.*, 2014), habitat preferences (e.g., Širovíc and Hildebrand, 2011; Soldevilla *et al.*, 2011), and abundance and density (e.g., Marques *et al.*, 2013).

The usefulness of this spectral peak banding feature for species identification from both real-time and autonomous PAM requires that it is distinctive from other sympatric odontocete species, and this should be carefully evaluated within each geographic region. Echolocation clicks of sperm whales (Møhl *et al.*, 2003); beaked whales (Baumann-Pickering *et al.*, 2013a); and hourglass dolphins (*L. cruciger*), Peale's dolphins (*L. australis*), Cephalorhynchiids, Phocoenids, and Kogiaiids (Morisaka and Connor, 2007) can be clearly distinguished from the broadband clicks of most delphinids. Among Delphinidae, many species produce clicks that are clearly distinguishable from Risso's dolphins as they do not contain spectral banding, including bottlenose dolphins (*Tursiops truncatus*), common dolphins (*Delphinus* spp.), melon-headed whales (*Peponocephala electra*), spinner dolphins (*Stenella longirostris*), rough-toothed dolphins (*Steno bredanensis*), Atlantic spotted dolphins (*Stenella frontalis*), and pantropical spotted dolphins (*Stenella attenuata*) from the Southern California Bight, pelagic Pacific Ocean, western North Atlantic Ocean, and the Gulf of Mexico (Soldevilla *et al.*, 2008; Baumann-Pickering *et al.*, 2010; Rankin *et al.*, 2015; Frasier, 2015). Other delphinids produce clicks that do contain spectral banding such as Pacific white-sided dolphins off southern California, white-beaked dolphins (*L. albirostris*) in UK waters, and short-finned pilot whales (*Globicephala macrorhynchus*) off Hawaii (Soldevilla *et al.*, 2008; Calderan *et al.*, 2013; Baumann-Pickering *et al.*, 2015b), and care must be taken to differentiate these species from Risso's dolphins.

To avoid misclassification, it would be helpful to know which sympatric species might produce clicks that contain spectral banding; however, the characterization of echolocation clicks from wild delphinid species remains incomplete at this time. Soldevilla *et al.* (2008) hypothesize that spectral banding is related to melon morphology. There are dramatic differences in the sound production pathway morphology of dolphins that produce clicks with spectral banding (e.g., Pacific white-sided dolphins, white-beaked dolphins, and Risso's dolphins) compared with those that do not [e.g., bottlenose dolphins, common dolphins, rough toothed dolphins, and killer whales (*Orcinus orca*)] including (1) the degree of symmetry of the monkey lip dorsal bursae complex and premaxillary bones, (2) the rostrum and beak structure, (3) presence of a vertical connective tissue column in the melon, (4) the presence of posterior melon bifurcation, and (5) the presence of an upside down pyramidal fatty basin posterior to the core melon (Cranford *et al.*, 1996; McKenna *et al.*, 2012). If melon morphology is the source of spectral banding, and this morphology is conserved within subfamilies, spectral banding is most likely to be found in the Globicephalid sub-family and in the Lagenorhynchiids that do not produce narrow-band high-frequency clicks. Therefore, extra care should be taken to characterize clicks of sympatric odontocetes in regions where members of Lagenorhynchinae and Globicephalinae subfamilies overlap. In regions where species with the spectral peak banding feature are sympatric (Hawaii, Southern California Bight, Scotland), the frequency values of the peaks are distinctive (e.g., Soldevilla *et al.*, 2008; Calderan *et al.*, 2013; Baumann-Pickering *et al.*, 2015b) and passive acoustic methodologies still can be used to distinguish between species in these regions.

B. Geographic variation

While presence of spectral banding is a useful feature for distinguishing Risso's dolphins from many delphinid species, the frequency values of the peaks vary significantly with geographic location; this may allow population discrimination and also complicate their identification in new regions. The greatest differentiation was found between dolphins recorded off southern California and those recorded around the main Hawaiian Islands, areas where within-region variability also was low. In the North Pacific Ocean, the current U.S. stock boundaries for Risso's dolphins are based on the boundaries of the U.S. EEZ. These results provide strong support for acoustic differences in the mean first and second peak and notch frequencies between these two regions, and therefore provide acoustic support for the stock delineation. The clustering analyses additionally suggest there may be finer scale acoustic differentiation among the California Current, main Hawaiian Islands, and pelagic Pacific Ocean waters (Fig. 5); however, the finer-scale LME-based MANOVA model did not differentiate the pelagic Pacific waters from the Hawaiian Islands. There were limited recordings from most of the open ocean areas, and hence low power in the unbalanced MANOVA design; it is possible that more recordings from open ocean waters would provide support for a model with greater differentiation.

The support for geographic effects on the frequency values of Risso's dolphin clicks in the western North Atlantic and the northern Gulf of Mexico was more complicated as the stock-based MANOVA model did not differentiate these two regions, yet the finer scale LME-based MANOVA supported differentiation between the southeast U.S. Atlantic waters and the Gulf of Mexico but not between the southeast and northeast U.S. Atlantic. This appears to be explained by a latitudinal cline in which a significant correlation exists between the first peak frequency value and latitude for recordings from western North Atlantic waters, with clicks shifting toward higher frequencies in southern waters. The LME-based MANOVA evidence provides acoustic support for the current stock delineations, and the results of the clustering suggest investigation into further differentiation within the western North Atlantic may be warranted to better understand the latitudinal cline. More samples should be included from the northern, southern, and pelagic waters to improve geographic resolution in future analyses.

While these results indicate that geographic regions provide significant explanatory power for the variation found in Risso's dolphin echolocation click frequencies, the underlying mechanisms driving the frequency shifts are unknown. Geographic variation in echolocation signals may result from behavioral differences related to prey type and size, behavioral differences related to ambient noise conditions, or morphological differences in the sound production pathway. If Risso's dolphins have control over the frequency of spectral banding peaks and shift them dependent on their echolocation target (e.g., captive bottlenose dolphins, Houser *et al.*, 1999), the geographic variation found in echolocation click peak frequencies may indicate prey type or size varies geographically. Research on Risso's dolphin prey types and size across regions is needed to test this hypothesis. Similarly, if Risso's shift frequencies of their echolocation signals in response to ambient noise conditions, either to shift signals out of the noise frequency range (e.g., Au *et al.*, 1985; Parks *et al.*, 2007) or as an artifact of increased signal amplitudes (e.g., Lombard response, Baumann-Pickering *et al.*, 2015a), the geographic variation found here may indicate large scale difference in ambient noise conditions among regions. The Southern California Bight and the Gulf of Mexico, where Risso's dolphin click peak frequencies were lower, have high noise levels at low frequencies due to anthropogenic activity (McKenna *et al.*, 2009; Wiggins *et al.*, 2016), while noise levels are lower around Hawaii (Širovíc *et al.*, 2013), where Risso's click peak frequencies are higher. One would expect the opposite if noise conditions were a driving mechanism for the frequency shifts, such that clicks from the Southern California Bight and Gulf of Mexico would shift higher away from low-frequency shipping and seismic survey noise; therefore, this hypothesis seems an unlikely explanation for the large-scale variation found in this study. Alternatively, if the spectral-banding peak frequencies of Risso's echolocation clicks are not plastic but dependent on sound production morphology (Cranford *et al.*, 1996; McKenna *et al.*, 2012), geographic frequency shifts of echolocation click peaks may indicate differences in the sound production pathway morphology across regions. For example, differences in the skull morphology between two sympatric populations of Pacific white-sided dolphins in the Southern California Bight led Soldevilla *et al.* (2008) to hypothesize that two distinct click types which exhibit different peak frequencies represent the two populations due to differing sizes of sound production organs. The size of sound production organs influences bioacoustic signal frequency and is often correlated with body size (May-Collado *et al.*, 2007). Body size is often correlated with latitude (Meiri and Dayan, 2003) and the latitudinal cline found in Risso's dolphin click spectral peak frequencies may reflect differences in sound production organ and body size. Risso's dolphin sound production morphology has not been well studied, particularly across regions, and this could be a promising area of study to better understand these effects.

Morphology, prey, and large-scale ambient noise are all potential drivers of acoustic signal frequency shifts, but the interrelationships between them and their relationships to population differentiation are less clear. Over evolutionary time-scales, behaviorally-induced frequency shifts caused by differences in prey or ambient noise conditions may become stable and lead to morphologic differences due to genetic selection or morphologic differences may occur as a result of genetic drift (e.g., May-Collado *et al.*, 2007; Morisaka and Connor, 2007). If the differences in spectral banding frequencies are related to stable morphological differences, they can serve as a proxy for morphological-based population differences. Concurrent genetic and acoustic sampling is needed to evaluate whether these acoustic features are useful for population identification or whether they are more plastic behavioral differences that could lead one to misidentify a population if noise or prey conditions changed. During large vessel surveys, obtaining remote-biopsy genetic samples is most efficient when dolphins bow-ride. However, Risso's dolphins do not commonly approach large vessels to bow-ride, so a concerted effort would be needed to obtain concurrent biopsy and acoustic samples during the large vessel surveys commonly used in the deeper pelagic waters that Risso's dolphins inhabit.

C. Within-encounter variability

There is evidence for geographic-scale differences in Risso's dolphin echolocation click frequencies, however lower levels of variability were also evident within encounters (Fig. 3). Click features are influenced by morphological, behavioral, and sound propagation factors including individual variation in size, relationship of beam axis with respect to recorder, diving depth, and individual ability to shift frequencies likely affect the variability in frequency of peaks within a given encounter. Captive odontocetes, including bottlenose dolphins, false killer whales (*Pseudorca crassidens*), and beluga whales (*Delphinapterus leucas*), exhibit a degree of control over their echolocation signal production, including frequency content, duration, inter-click intervals, source levels, directionality, and field of view (Au, 1993; Finneran *et al*., 2014). Additionally, received spectral and temporal features vary as a function of beam angle and distance (Finneran *et al*., 2014), and these factors make it particularly important to include many echolocation clicks recorded over a range of conditions when obtaining field recordings for passive acoustic monitoring and species or population identification to encompass the full suite of variability present (e.g., Baumann-Pickering *et al*., 2015b). Intra- and inter-individual variability in spectral features of clicks appears to account for some of the variability found within encounters.

In some recordings from the western North Atlantic and northern Gulf of Mexico, where within encounter variability was greater, shifts in the frequency values of spectral peaks and notches were evident over the course of an encounter (Fig. 4). This may indicate (1) changes due to axis orientation as the animals or ship approach or travel away from each other; (2) effects of dive depth on spectra if animals are moving from deep diving to the surface over the encounter; (3) formation structure within a group, e.g., smaller younger dolphins at the front and larger or male dolphins at the back; or (4) a change in acoustic focus from long-range detection to short-range detection or small object focus, e.g., change frequency to investigate hydrophone as they pass it (Jensen *et al*., 2015). Controlled experimental studies of Risso's dolphin echolocation abilities which investigate the effects of animal depth, axis of orientation, and ability to shift frequency based on focus object size and composition would help clarify which additional factors need to be considered.

D. Geographical variation and seasonal movements

Numerous studies indicate Risso's dolphins make seasonal movements, generally toward polar waters in warm seasons and equatorward in cool seasons (Green *et al*., 1992; Forney and Barlow, 1998; de Boer *et al*., 2013). Such movements could impact a geographic comparison of acoustic characters if acoustic variations reflect population structure and those populations are moving. In this study, all Atlantic and Gulf of Mexico recordings were obtained during summer which should minimize this effect. While recordings in the Pacific were collected over a wider seasonal range, low variability within regions in the Pacific indicates this was not a problem.

If acoustic variation represents population structure, fixed PAM can be used to help distinguish stocks, to determine the extent of their geographic ranges, and to determine seasonal changes in population distribution (McDonald *et al*., 2006; Delarue *et al*., 2009; Baumann-Pickering *et al*., 2014). Differential use of regions by populations over time might be clarified through use of fixed instruments deployed throughout the region and through concurrent visual and acoustic ship surveys that provide an ability to acoustically assign visually-sighted Risso's dolphins in line-transect surveys to the population level. By assigning acoustic encounters to click types and associated hypothesized populations, one can evaluate if there is diel, seasonal, and spatial coherence in acoustic types that support the population ID hypothesis (e.g., Soldevilla *et al*., 2010b). Further, if population hypotheses are supported, the boundaries and seasonal occurrence of these groups can be refined with recordings from autonomous long-term fixed instruments and mobile gliders.

E. Automated feature extraction and classification

Automated classifiers make it possible to efficiently process the large quantities of data that can be collected from autonomous passive acoustics instruments. The finding of geographic-based shifts in the frequency of peaks in Risso's echolocation clicks indicate automated classifiers need to be robust to these frequency shifts, or be developed as region-specific classifiers. This could be done by ensuring automated classifiers are developed with recordings of animals from the same region as the intended study area, or by including sufficient examples from a wide range of regions to encompass the full variability of the species.

The selection of features to include in an automated classifier is important as these metrics need to both differentiate the species from others and be reliably measured using automated methods. In this study, two feature sets were used: (1) the frequency values of the first 4 peaks and notches in each click, and (2) the liftered spectrum. The automated peak picking algorithm for the first metric was not reliable for individual clicks as it often missed important peaks or notches and additionally picked many insignificant ones. This effect was moderated by producing encounter-level histograms including peaks and notches from many clicks, but to obtain smooth histograms, around 200 or more clicks are needed and this results in a single metric per encounter rather than per click. It is possible that with sufficient clicks per encounter, consecutive sets of clicks could be used to obtain multiple histograms and GMM metrics per encounter. However, even once each histogram is created, the process is only semi-automated as automatically selecting the correct Gaussian distributions to ensure peaks and notches are aligned across encounters can be difficult. In some cases, the two most significant peaks are the first and second peaks, but not always. Further, the frequency shift presented an additional challenge as the first peak of some encounters (e.g., Hawaii) occurs at the frequency of the second peak of other encounters (e.g., California Current). Manual supervision of the process was necessary to ensure the first and second peaks were selected correctly so the following statistical procedures were comparing the same consecutive peaks in the correct order. The additional inclusion of the third and fourth peaks may add useful information, particularly given the single vs double peak that was found to vary regionally in the clustering analysis. However, it proved particularly unreliable to select these peaks and have any meaningful data for comparison across encounters. Future studies should consider better metrics which are easier to automate. Obtaining averaged spectra and fitting Gaussian mixture models to them may result in reasonable metrics (Baumann-Pickering *et al.*, 2010). Alternatively, Gaussian mixture model classifiers built using the entire cepstrum may be an acceptable method for regional classification (e.g., Roch *et al.*, 2011). This method was not used in this study as the goal was to characterize the frequency values to guide future studies.

For the second metric, the spectral normalization achieved by incorporating cepstral techniques, i.e., high-pass liftering, was essential for the k-means clustering to be an effective method for exploring variation in the spectral peak banding patterns of Risso's dolphin echolocation clicks. In preliminary analyses without liftering methods, exploration showed that cluster formation focused on overall amplitude of clicks, or once normalized for amplitude, focused on large scale spectral features such as overall peak frequency or hydrophone characteristics, rather than on the finer scale spectral banding features of interest. Once liftering methods were incorporated, however, the clusters clearly focused on the peaks and notches as desired. While liftering was especially effective for this particular feature, where the peaks and notches were of interest rather than amplitude features, it is unknown how well it will work for echolocation clicks of other species. Clustering algorithms have been effectively used for delphinid echolocation clicks to discover consistent patterns that may be related to species (Frasier, 2015), but these typically were used on long-term recordings from the same instruments. Roch *et al.* (2015) found that GMM classification was improved when different noise conditions (site-specific) and differences in recording equipment were accounted for. In particular, high frequencies are lost due to longer propagation distances, and hydrophone frequency response and ambient noise conditions may have affected the spectra. Liftering removes hydrophone and propagation effects (Juang *et al.*, 1987; Rabiner and Juang, 1993) and therefore may be useful for improving classification rates in other species as well if species-specific features are represented in higher-order cepstral coefficients.

V. CONCLUSIONS

This study is the first large-scale comparison of the spectral properties of Risso's dolphin echolocation clicks. Findings indicate that Risso's dolphins from a wide range of regions produce echolocation clicks that exhibit spectral banding patterns of peaks and notches, which are a distinguishing feature for use in species identification in near-real time and autonomous passive acoustic surveys. Findings also indicate significant geographical variation in the frequency values at which peaks occur, highlighting the need to develop and verify accuracy of region-specific species classification methods. These findings also highlight the need to acoustically characterize echolocation clicks of sympatric species on a region-by-region basis to ensure either the peak banding pattern or the frequencies at which peaks occur are unique to Risso's dolphins in the region. Thus far, in the main Hawaiian Islands, the California Current ecosystem, the Gulf of Mexico, and the southeast U.S. Atlantic, the frequency values of Risso's clicks appear to be distinct from those of sympatric delphinid and beaked whale species which also have peak banding. In the northeast U.S. Atlantic and pelagic Pacific waters, more species need to be characterized to safeguard against misclassifications. In the described locations where Risso's clicks are clearly distinct, PAM can be used to understand spatio-temporal patterns of occurrence and distribution over large scales, to hypothesize population identity (e.g., species ID of Baumann-Pickering *et al.*, 2013a; Baumann-Pickering *et al.*, 2014), to refine spatio-temporal boundaries of click types (e.g., Baumann-Pickering *et al.*, 2014), and to delineate population boundaries (Sveegaard *et al.*, 2015). In addition to improving the ability to use fixed PAM as an independent survey method, the ability to acoustically identify species and populations can improve the collection and interpretation of concurrent acoustic and visual survey data (e.g., for assistance in finding animals to improve abundance estimation, Peel *et al.*, 2014; Miller *et al.*, 2015).

Geographic regions are a significant factor explaining acoustic variation in Risso's dolphins, but the cause of the geographic variation is unknown. In the Pacific, within-encounter variability was low and clicks were distinct between the Hawaiian Islands and the California Current ecosystem; in the Atlantic, within-encounter variability was higher and clicks were not strongly distinguishable among geographic regions, though a latitudinal cline was evident. The two most plausible explanations for the large-spatial-scale differences found in Risso's dolphin acoustic signals are differences either in animal size or morphology or in behavior due to prey size or type. These two explanations can also explain the lower levels of within-encounter variability that were found if Atlantic dolphins exhibit a greater degree of morphological variability across ages and sexes or individuals target a wider variety of prey size classes compared to those around the Hawaiian Islands and the California Current ecosystem. However, this is complicated by behavioral and sound propagation effects. To better evaluate these effects and the biological significance of the acoustic types, concurrent recordings and genetic sampling should be conducted from vessel-based surveys, and concurrent visual observations should record details with regular updates about group composition, formation, location, heading, and behavioral state. Obtaining information to understand acoustic changes with prey type would be useful, but may be more challenging since Risso's dolphins mainly forage at night. Finally, the capability of animals to adjust spectral features by echolocation task and the potential impacts of orientation axis, animal depth, and distance can be evaluated with controlled experiments. Further investigation into the causes of geographic variability and its potential relationship with population structure may improve the ability to manage these stocks.

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