Acoustic differentiation of Shiho- and Naisa-type short-finned pilot whales in the Pacific Ocean

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Divergence in acoustic signals used by different populations of marine mammals can be caused by a variety of environmental, hereditary, or social factors, and can indicate isolation between those populations. Two types of genetically and morphologically distinct short-finned pilot whales, called the Naisa- and Shiho-types when first described off Japan, have been identified in the Pacific Ocean. Acoustic differentiation between these types would support their designation as sub-species or species, and improve the understanding of their distribution in areas where genetic samples are difficult to obtain. Calls from two regions representing the two types were analyzed using 24 recordings from Hawaiʻi (Naisa-type) and 12 recordings from the eastern Pacific Ocean (Shiho-type). Calls from the two types were significantly differentiated in median start frequency, frequency range, and duration, and were significantly differentiated in the cumulative distribution of start frequency, frequency range, and duration. Gaussian mixture models were used to classify calls from the two different regions with 74% accuracy, which was significantly greater than chance. The results of these analyses indicate that the two types are acoustically distinct, which supports the hypothesis that the two types may be separate sub-species.

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I. INTRODUCTION

Divergence in animal vocalizations can be a marker of population divergence or speciation. Such acoustic divergence between geographic regions, or geographic variability (Conner, 1982), has been correlated with genetic differentiation due to reduced dispersal between regions, female-driven assortative mating, or exclusion by males (e.g., Baker and Cunningham, 1985). This type of divergence has been identified in bats [e.g., horseshoe bats (Yoshino *et al.*, 2008)], birds [e.g., rufous-collared sparrow (Tubaro *et al.*, 1993)] and cetaceans [e.g., blue whales (McDonald *et al.*, 2006), humpback whales (Winn *et al.*, 1981), and striped dolphins (Papale *et al.*, 2013)]. This variation can be caused by a variety of factors, including isolation and subsequent adaptation to a local environment (e.g., Graycar, 1976; Ding *et al.*, 1995), morphological or genetic differences between populations (Janik and Slater, 2000; Slabbekoorn and Smith, 2002), socially maintained differences between sympatric or parapatric populations, called dialects [e.g., sperm whales (Rendell and Whitehead, 2003; Rendell *et al.*, 2012; Gero *et al.*, 2016), killer whales (Ford, 1989, 1991; Filatova *et al.*, 2012)], or acoustic drift between geographically separated populations (Conner, 1982).

Vocal repertoires are often learned through vertical transmission from parent to offspring (e.g., Yurk *et al.*, 2002), or by learning when an immigrant individual adopts the vocalizations of the new group or population (Mundinger, 1980; Conner, 1982; Musser *et al.*, 2014). Geographic variability in the vocal repertoire could result in a positive feedback loop with genetic divergence, for example, when habitat-dependent selection of song characteristics promotes divergence or speciation among populations of songbirds living in different habitats (Slabbekoorn and Smith, 2002).

Pilot whales are distributed in the open ocean and along continental slopes throughout tropical and temperate oceans. In the Pacific Ocean, two morphologically and genetically distinct types of short-finned pilot whale are also

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geographically non-overlapping and may be distinct sub-species or species (Kasuya *et al.*, 1988; Oremus *et al.*, 2009; Van Cise *et al.*, 2016). These two types have been called the Naisa- and Shiho-type short-finned pilot whale, after their original description (Yamase, 1760). The Naisa-type occurs off southern Japan, southeast Asia, the Indian Ocean, and Hawai'i. The Shiho-type occurs off northern Japan and in the eastern Pacific Ocean between 45°N and 15°S latitude. Mitochondrial evidence suggests strong female fidelity to geographic regions, with little or no female-mediated genetic exchange between these two types (Van Cise *et al.*, 2016). A third genetic clade has been identified, recently diverged from the Naisa-type, and is broadly distributed throughout the Indian, Atlantic, and tropical Pacific Oceans (Hill *et al.*, 2015). The distribution of this unnamed third clade overlaps the Shiho-type in the eastern Pacific and the Naisa-type in southeast Asia and in the Mariana Islands (Hill *et al.*, 2015).

In some regions, the distribution of the Naisa- and Shiho-types remains poorly described. This is true in the eastern/central Pacific Ocean, where short-finned pilot whales are continuously distributed between the west coast of the Americas and Hawai'i (Hamilton *et al.*, 2009), but morphological and genetic samples from the pelagic ocean between the eastern Pacific region and Hawai'i are rare and difficult to collect. Where genetic samples are missing, geographic variability in acoustic signals could help to differentiate between the types and improve our understanding of their distribution.

Although little is known of the short-finned pilot whale vocal repertoire, they have been shown to exhibit distinct, repeated call types (Sayigh *et al.*, 2013). Sayigh *et al.* (2013) went on to determine that about 42% of calls produced in their study could be classified as distinct calls. Seventy percent of those were repeated more than ten times during the study and thus considered to be predominant call types. These calls, including both whistles and burst pulses, can be identified and quantified in order to examine variability in call composition, i.e., variability in which calls and components are being used, as well as variability in level of call complexity [number of components in a single call (Kershenbaum *et al.*, 2014)], between the Naisa- and Shiho-types.

Here, we examine geographic variability in short-finned pilot whale call composition, as well as acoustic features of call contours, with two main goals. The first is to determine whether Naisa- and Shiho-type short-finned pilot whales are acoustically distinct. Acoustic differentiation within a species can imply a lack of social interaction or transmission of cultural information, which may be considered an implication of sub-species or species-level differentiation. The second goal is to determine whether calls from the central Pacific can be acoustically categorized as belonging to the Naisa- or Shiho-type, in order to clarify the distributions of each type in the region where no genetic or morphological information exists to assess type.

In addition to an analysis of the composition of distinct, repeated call types, we undertake an analysis of the acoustic features (i.e., peak frequency, duration, frequency range) of all calls identified in the study (i.e., whistles and pulsed calls). Because it is difficult to know *a priori* whether call composition or acoustic features are more ecologically plastic (Slabbekoorn and Smith, 2002), a study of both aspects provides a comprehensive analysis of acoustic divergence in Pacific Ocean short-finned pilot whales.

II. METHODS

A. Data collection

In Hawai'i, recordings were obtained between 2009 and 2013 during Cascadia Research Collective surveys (Baird *et al.*, 2013) near the islands of Hawai'i and Lāna'i using two instruments: a DMON-Towfish and a Biological Underwater Recording Package [BURP 3.2, developed at Southwest Fisheries Science Center (SWFSC); see Table I for specifications of all recording instruments]. The BURP was deployed by tethering it to a buoy for periods of 15 min–1 h, while short-finned pilot whales were in the near area (<500 m). The Towfish contained a DMON acoustic recorder (e.g., Kaplan *et al.*, 2015) developed at Woods Hole Oceanographic Institution (WHOI) in a custom-built towfish body, towed ca. 15 m behind an 8.2 m Boston Whaler (Edgemont, FL) with two 150 hp outboard motors while the boat was within 30–200 m of short-finned pilot whales.

TABLE I. Specifications for recording packages used in the present study.

	BURP 3.2 (buoy)	DMON Towfish (towed)	SWFSC 2000 (towed)	SWFSC 2003 (towed)	SWFSC 2006 (towed)	SWFSC (CalCurCEAS) 2014 (towed)	SoundTrap ST200 STD (buoy)
Sampling rate	192 kHz	512 kHz	48 kHz	48 kHz	48 kHz	500 kHz	188 kHz
Functional bandwidth	2–60 kHz ± 5 dB	160 kHz	2–24 kHz ± 4 dB	2–24 kHz ± 5 dB	2–24 kHz ± 5 dB	2 kHz–100 kHz ± 5 dB	20 Hz–60 kHz ± 3 dB
Recorder flat response range	2–60 kHz	5–160 kHz	1200 Hz–40 kHz	1200 Hz–40 kHz	1200 Hz–40 kHz	2 kHz-100 kHz	20 Hz–60 kHz
Pre-amplifier flat response range	>2 kHz	NA	>2 kHz	>2 kHz	>2 kHz	>2 kHz	NA
Recorder bit-depth/resolution	24-bit	16-bit	16-bit	16-bit	16-bit	16-bit	16-bit
Hydrophone manufacturer and model	HTI, Inc.	Navy type II ceramics	Sonatech, Inc. Norris	EDO E65	EDO E65	HTI, Inc.	Ocean Instruments
Number of encounters	12	11	1	1	7	2	1
Recording period	2012	2012–2013	2000	2003	2006	2014	2015
Type recorded	Naisa	Naisa	Shiho	Shiho	Shiho	Shiho	Shiho

Recordings from the eastern and central Pacific Ocean were collected and manually annotated during National Oceanic and Atmospheric Administration (NOAA) SWFSC surveys between 2000 and 2015 using either a custom-built towed array (Rankin *et al.*, 2013) or an Ocean Instruments (Aukland, New Zealand) SoundTrap 201 (Table I). Arrays were towed ~300 m behind a research vessel traveling 10 kn. The SoundTrap 201 also was tethered to a surface buoy and deployed from a recreational fishing vessel contracted by SWFSC, which then moved to a distance of ~500 m from the buoy to decrease noise levels as the animals passed the buoy. Data collected before 2006 were recorded onto digital tapes using a Tascam (Montebello, CA) recorder with a sampling rate of 48 kHz. Digital playbacks from Tascam recordings were re-digitized using a 24-bit Creative Labs (Milpitas, CA) Sound Blaster Extigy sound card with a 96 kHz sampling rate and 100 dB SNR, and recorded using Raven (Cornell Lab of Ornithology, Ithaca, NY) 4.1 software.

Recordings were used for this study if pilot whales were the only species seen in the vicinity. Trained observers identified any species that came within the horizon during encounters. Recordings were not used from conditions worse than Beaufort 5, both to minimize the impact of noise from the surface and to reduce the possibility of animals passing through the recording area undetected. Acoustic recordings were separated into three regions (Fig. 1): Hawai‘i, the eastern Pacific Ocean, and the central Pacific Ocean. Hawaiian recordings are considered to be from Naisa-type short-finned pilot whales, and eastern Pacific recordings are considered to be from Shiho-type short-finned pilot whales, based on evidence that the distribution of these two types is non-overlapping in this region (Van Cise *et al.*, 2016). Recordings from the central Pacific Ocean cannot be designated as belonging to one type or another, due to a lack of information on the distribution of these two types in that region.

B. Call extraction

Burst pulses and whistles were considered "calls" and analyzed together, based on evidence that burst pulses and whistles can be described on a continuous spectrum (Murray *et al.*, 1998), as well as evidence that pilot whales exhibit smooth transition and simultaneous use of whistles and burst pulses (Sayigh *et al.*, 2013). Spectrograms were created for each recording in Raven 1.4, using a discrete Fourier transform (DFT) with a Hamming window and 50% frame advance. DFT frame lengths were set to provide similar temporal and spectral resolution across recordings irrespective of sample rate [BURP $N_{\mathrm{DFT}} = 2048$ samples, Towfish $N_{\mathrm{DFT}} = 1280$, SWFSC towed array $N_{\mathrm{DFT}} = 512$, SWFSC (CalCurCEAS) 2015 towed array $N_{\mathrm{DFT}} = 5333$, SoundTrap $N_{\mathrm{DFT}} = 2005$]. Although recordings were collected using a variety of hydrophones, all had flat frequency response from 2 to 40 kHz. Analyses focused on frequency, range, and duration of calls to preclude any amplitude-specific influence of specific recording systems. We tested this hypothesis using an analysis of variance (ANOVA) with recorder as a random effect implemented in R (version 3.2.3).

Calls were visually characterized based on sub-units, or components, separated from each other by a short pause (>0.1 s) in sound production or a rapid change in frequency (>500 Hz in 0.25 s; Shapiro *et al.*, 2011), examples of which can be seen in Fig. 3. Call components were classified alphanumerically in the order in which they were identified; each call consisted of one or more components. Calls made by several individuals vocalizing at the same time could potentially be mistaken for a multi-component call; in order to avoid this bias, a call was labeled as multi-component only if it occurred more than three times with the same component order and timing. We use the word "non-tonal" to refer to calls without any distinct structural component, such as buzzes. Calls that occurred more than five times in the study are considered predominant call types, following the methods outlined in the study of short-finned pilot whale vocal repertoire by Sayigh *et al.* (2013); however, we modified the threshold for predominant call types from ten occurrences to five because the number of calls in our dataset is smaller.

Once calls were annotated and extracted from Raven, they were imported into PAMGUARD version 1.11.12 (Gillespie *et al.*, 2009; Gillespie *et al.*, 2013). We traced the fundamental frequency contour of each whistle, that is, the lowest frequency band associate with a whistle and its harmonics. Pulsed calls were characterized by tracing the lowest frequency band for which the entire call was visible (usually the first or second frequency band), which was determined to be the energy contour associated with the pulse repetition rate, equivalent to the fundamental frequency of whistles. This was also the frequency band with the most power in pulsed calls where one band had visibly more power than others. Up to 50 randomly selected calls were traced per encounter (Fig. 2) using ROCCA for PAMGUARD (Oswald and Oswald, 2013).

C. Data analysis

To validate the call classification system used in this study, we trained a group of five non-expert volunteers to characterize a subset of the data using a catalogue of call components developed during the initial call classification

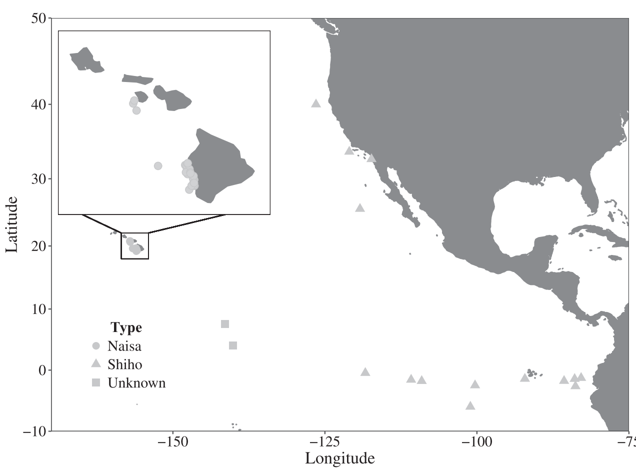

FIG. 1. Distribution of acoustic encounters throughout the Pacific Ocean. Samples were collected by the SWFSC and Cascadia Research Collective (CRC).

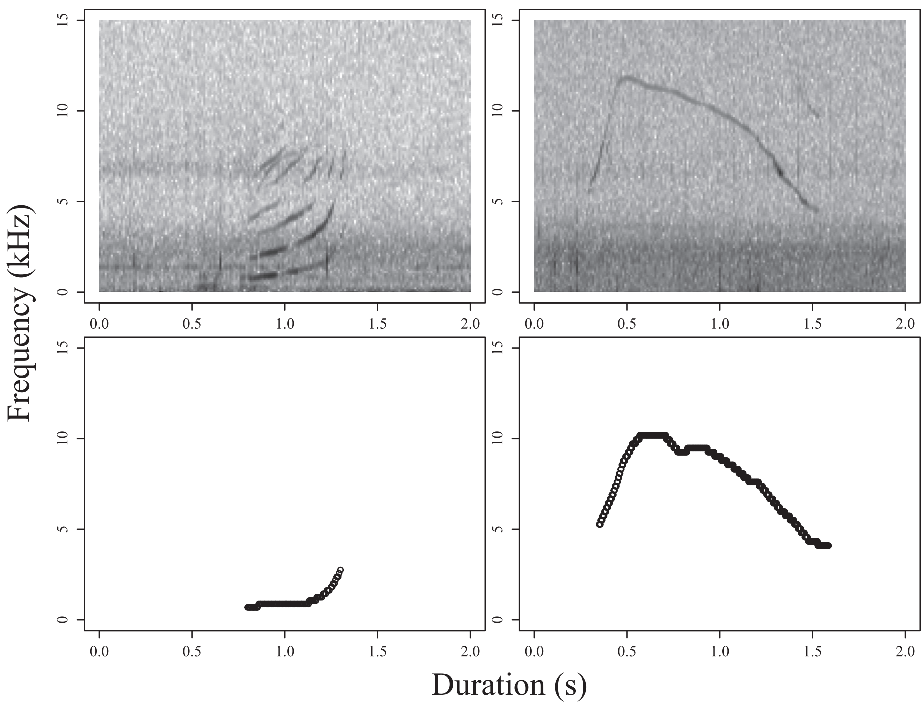

FIG. 2. Example results of manual call contour traces for a pulsed call (left) and a whistle (right). Original spectrograms are shown above; the traced contour is shown below.

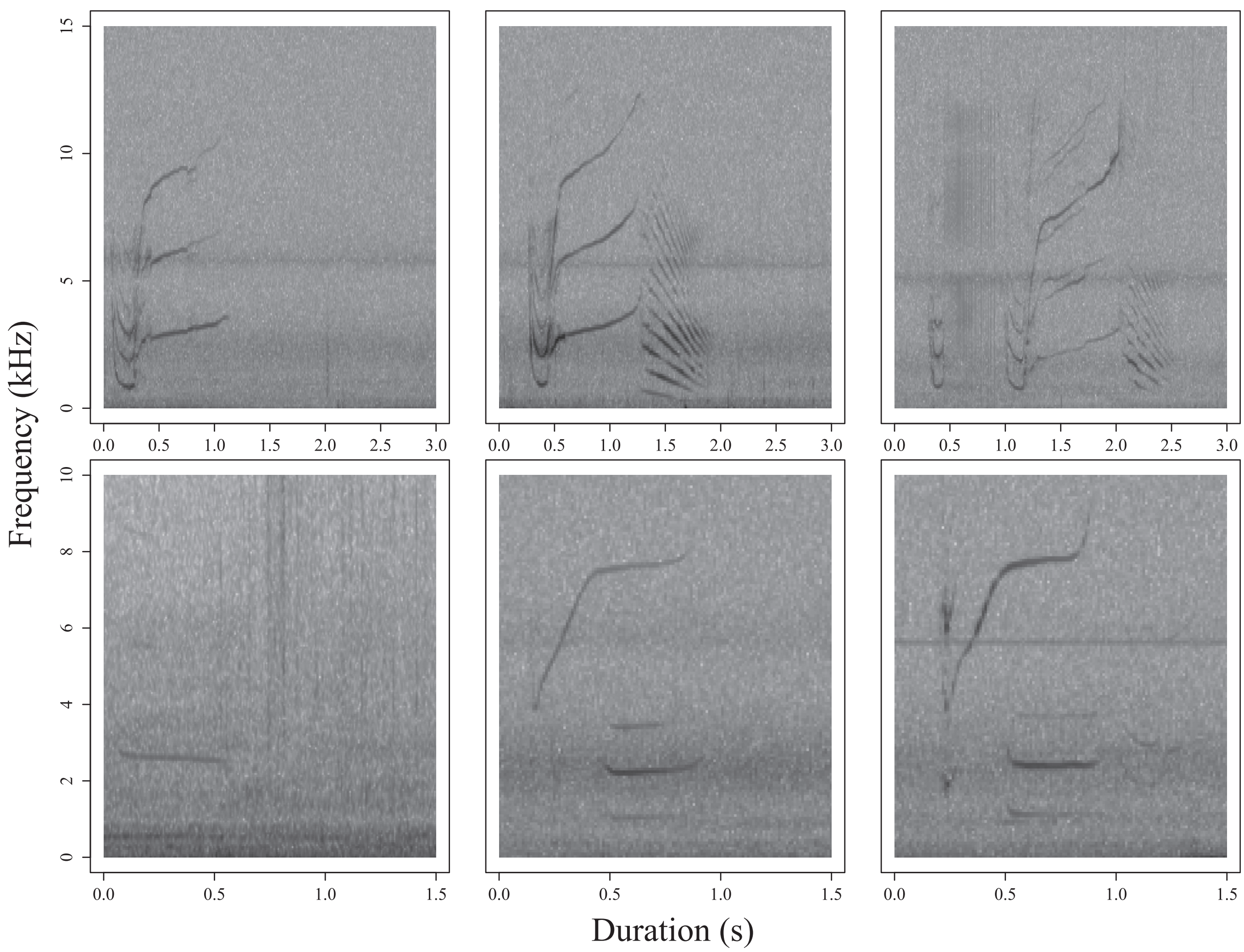

FIG. 3. Example spectrograms from vocalizations of Naisa-type short-finned pilot whales. The top and bottom rows each show a sequence of calls that increase in complexity from left to right.

process. Volunteers gave all calls alphanumeric classification codes based on the components identified within each call. Classifications by these volunteers were compared to the original classification for each call (by A.M.V.C.), and match rates were calculated to determine the repeatability of this method.

Call types were quantified in each region, and call type diversity analyzed in each region using a Shannon diversity index and rarefaction curve, implemented using the *vegan* package in R (Oksanen *et al.*, 2016). The difference in number of multi-component calls and non-tonal calls such as buzzes used in each region was compared using a standard ANOVA, also implemented in R.

Call contours were characterized using two methods. First, we measured the start, minimum, maximum, and mean frequencies, as well as duration and frequency range of each call contour, and stored the results in what we will refer to as the summary statistics dataset. The second method used the intercept and four coefficients of a fourth-order Legendre polynomial fit to each call component after translating the start time to 0, a method that has been successfully used in killer whale call and sub-unit recognition (Shapiro *et al.*, 2011) and human speech processing (Bonafonte *et al.*, 1996; Dehak *et al.*, 2007). These data were stored in what we will refer to as the call contour dataset.

We used three different methods to test for acoustic differences between Naisa- and Shiho-type short-finned pilot whales in Hawai'i and the eastern Pacific Ocean. First, we tested for statistical differences between the two types. Second, we used a mixture-model-based classification algorithm. Finally, we calculated divergence between encounters and regions using Kullback-Leibler (KL) divergence (Joyce, 2011).

Using the summary statistics dataset, we first tested for statistical differences in distributions of frequency, duration, and frequency range using two tests: a Kolmogornov-Smirnoff test of differences in cumulative frequency distributions of calls from each region, and a Kruskal-Wallis test of differences in the median values for each region (assuming homogeneity of variance). Then, because short-finned pilot whales are known to form stable social groups (Mahaffy *et al.*, 2015), we used a nested, non-parametric multivariate analysis of variance (MANOVA) to test whether encounters (roughly equal to social groups) might cause statistical differences between regions, implemented in R using the *BiodiversityR* package (Kindt and Coe, 2005).

Two sets of mixture models were trained using the *mclust* package (Fraley and Raftery, 2002; Fraley *et al.*, 2012). The first set of models used the summary statistics data as call features, while the second used call contours. We used 90% of the encounters to train a mixture model for each region, using calls that were known to be from that region (i.e., Naisa- or Shiho-type animals), allowing for 1–7 components in each mixture model and choosing the best number of components using Bayesian information criterion (BIC). We then tested those models by classifying the final 10% of the data. We replicated this procedure ten times, each time using a different 10% of the data to test the model. Each call was classified individually rather than grouping calls, as is common in most acoustic classifiers, because here our goal was not to improve classification rate but to understand the magnitude of acoustic differentiation between the Naisa- and Shiho-type short-finned pilot whales in Hawai'i and the eastern Pacific. A Fisher's exact test of differentiation was used to determine whether the classification error rate was significantly different from a classification error rate achieved by chance.

Using the summary statistics mixture models only, we attempted to classify acoustic encounters from the central Pacific, where the distribution of the two types is unknown. Data from this region were available from two encounters collected during a SWFSC cruise in 2000. We performed a bootstrap analysis of the classification algorithm with 10 000 repetitions, using 90% of the calls from the summary statistics dataset, selected randomly across all encounters, to train mixture models for each region, then classifying each encounter using all calls from that encounter.

Finally, we used the summary statistics dataset to calculate the symmetric KL divergence (Joyce, 2011) between Naisa- and Shiho-type short-finned pilot whales. KL divergence is an asymmetric information theory measure of how much extra information would have to be used to represent another distribution using the first one. As such, identical distributions have KL divergence of zero and distributions that are relatively similar have low divergence. KL divergence measures only the additional information needed to describe one model using another, and is therefore non-symmetric: the symmetric KL divergence is obtained by averaging the KL divergence in each direction. We computed the symmetric KL divergence between a pair of mixture models trained to represent the Naisa- and Shio-type data (Hershey and Olsen, 2007), again using the *mclust* package in R (Fraley *et al.*, 2012). To test for within-type divergence we then constructed two datasets from the encounters within each type by generating ten random partitions of encounters from each pilot whale type. The KL divergence of within-type partitions was computed and compared with divergence between the two types.

III. RESULTS

Vocalizations were obtained from 24 encounters with Naisa-type pilot whales in Hawai'i and 12 encounters with Shiho-type pilot whales in the eastern Pacific (Fig. 1). In Hawai'i, these recordings come from at least 15 known social clusters (as defined in Mahaffy *et al.*, 2015), within at least two hypothesized island communities in the insular population of short-finned pilot whales. Social structure data are not available from the eastern Pacific Ocean; however, it is likely, due to both the spatial and temporal distance between encounters and the large population size in the region, that each encounter represents a different social group in that region. An additional two recordings, which cannot be classified as Naisa- or Shiho-type based on existing data, were collected from the central Pacific, also likely from different social groups.

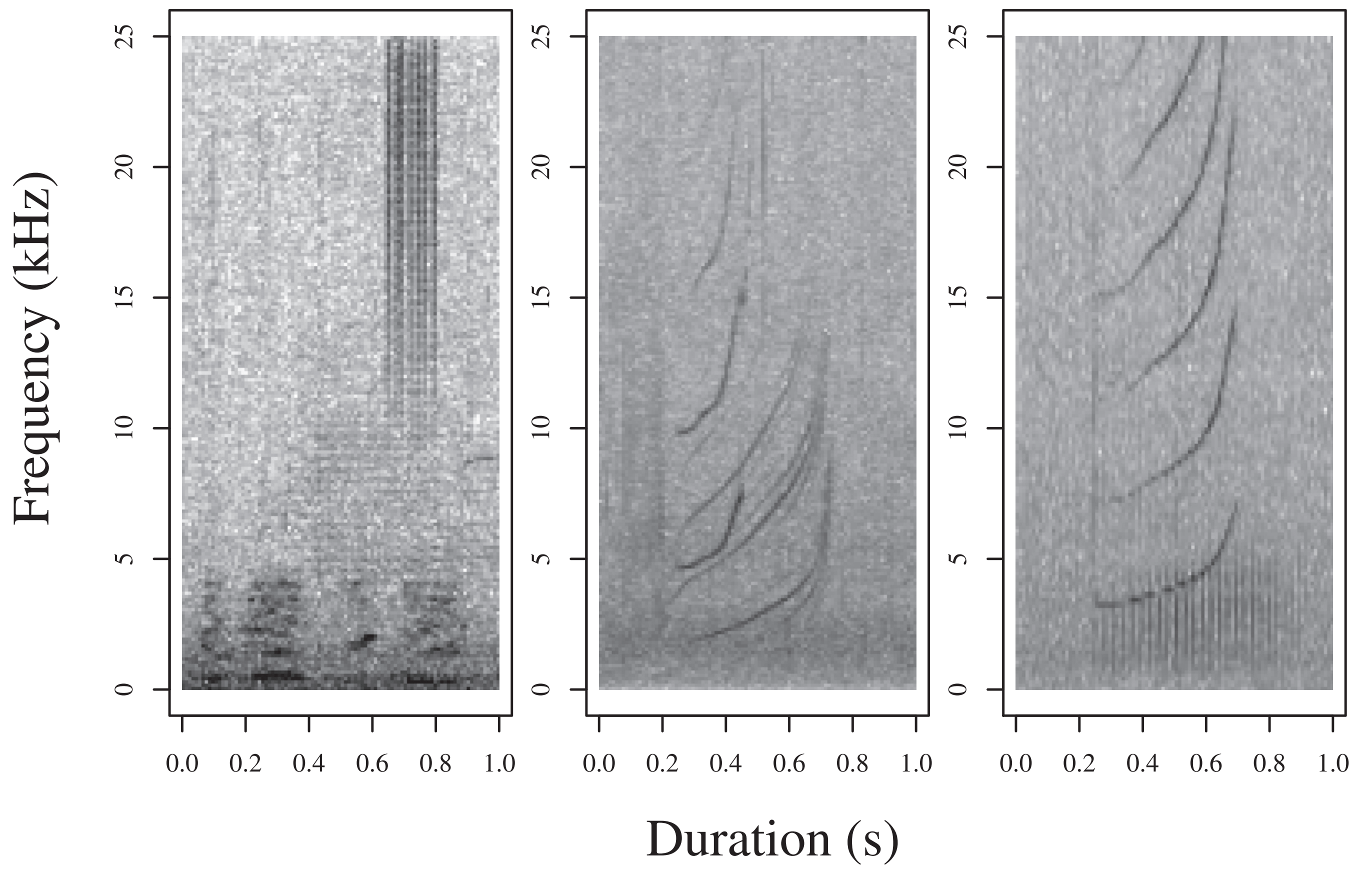

FIG. 4. Example spectrograms from vocalizations of Shiho-type short-finned pilot whales. Non-tonal calls were more common in this type (left), as well as repeated simultaneous calls (center). A low frequency, staccato, pulsed sound, not seen in the recordings of Naisa-type short-finned pilot whales, was found in several encounters in combination with an upsweep call (right, supplementary wav file S1; footnote 1).

A. Call composition

A total of 1745 calls were classified from Naisa-type pilot whale recordings in Hawai'i, and 1178 Shiho-type pilot whale calls were classified from eastern Pacific recordings. Manual call classification resulted in 31 discrete, repeated call types from the Naisa-type pilot whales, representing 1508 of the classified calls from that type, and 16 discrete, repeated call types from the Shiho-type pilot whales, representing 736 of the classified calls from that type (Figs. 3 and 4). The Naisa-type vocal repertoire had a Shannon diversity index value of 3.39, while the Shiho-type vocal repertoire had a value of 2.25. A rarefaction curve indicates that call diversity is divergent between the two regions (Fig. 5). Volunteer analyst classification of a subset of the data (1948 observations) had a 79% match rate with their original classification by AMVC, using example call types in a component-based call catalogue.

Naisa-type vocalizations had more multi-component calls, which made up 27% of the total vocalizations recorded in Hawai'i (Fig. 3) and only 6% of the total Shiho-type vocalizations recorded in the eastern Pacific Ocean. A nested ANOVA showed that both region and encounter were significant predictors of whether or not a call had multiple components ($p < 0.000001$ for both variables). Additionally, there were more non-tonal calls observed in recordings from the Shiho-type (27%) than from the Naisa-type (2%); again, region and encounter were both significant predictors of whether or not a call was non-tonal ($p < 0.000001$ for both variables). A unique vocalization, characterized by rapid, staccato, low-frequency pulses, was found only in the Naisa-type short-finned pilot whales, and always simultaneously expressed with an upsweep pulsed call (Fig. 4 supplementary wav file S1).[1]

Of the discrete, repeated call types identified in each region, 12 were shared between regions. Those 12 calls comprise 74% of all calls in the Hawai'i dataset, even though a total

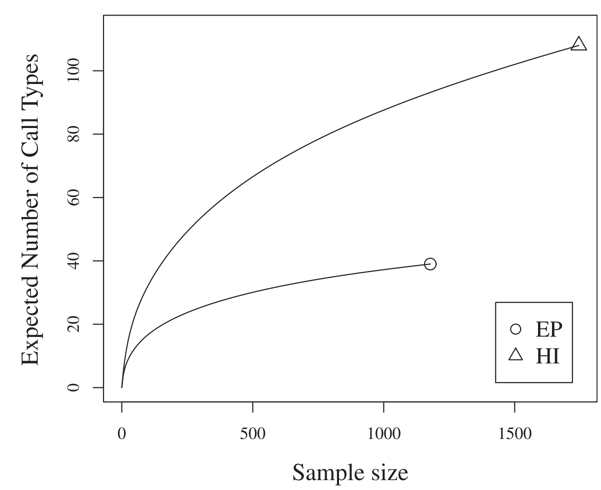

FIG. 5. Rarefaction curve depicting richness of the vocal repertoire in each type. Sub-sample was taken from the entire call repertoire, including calls that were considered repeated call types and calls that were not.

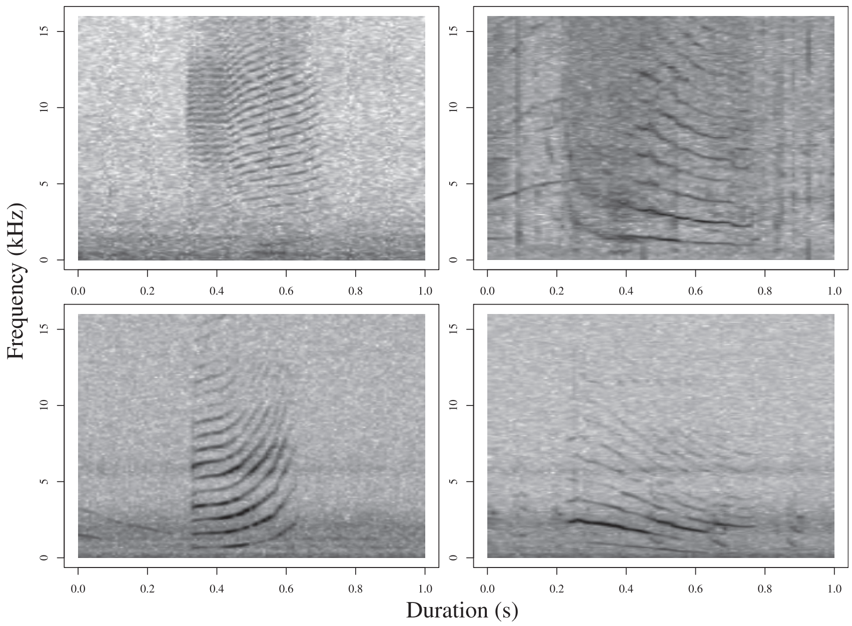

FIG. 6. Example spectrograms of components that were shared between Shiho- (top) and Naisa- (bottom) types, showing the variability within a component type. Call type 10, a pulsed upsweep call, is on the left, and call type 6, a pulsed downsweep, is on the right.

of 31 call types were identified, indicating a high rate of repetition of those 12 call types. Similarly, in the eastern Pacific these 12 call types represent 92% of all discrete, repeated calls in the eastern Pacific dataset, although a total of 16 call types were identified. The 12 discrete call types, although identified in recordings from both regions, were variable both between recordings and between regions (i.e., between the Naisa- and Shiho-type short-finned pilot whales, Fig. 6).

B. Differentiation using acoustic features

Our call traces resulted in measurements of start frequency, mean frequency, minimum and maximum frequencies, frequency range, and duration for each call. A pairwise correlation test showed that all of the measured frequency variables were highly correlated with each other ($R^2 = 0.80–0.92$); therefore, we included only start frequency as a representative of the suite of frequency variables that were measured. Start frequency, frequency range, and duration of vocalizations from Naisa- and Shiho-type pilot whales were significantly different in both their medians and cumulative distributions (Fig. 7, Table II). However, when the encounter effect was nested within each region using a nested, non-parametric MANOVA, the encounter effect was found to be significant ($p < 0.01$), while the region effect was not ($p = 0.67$). The recorder used did not to have a significant effect on differentiation in acoustic features.

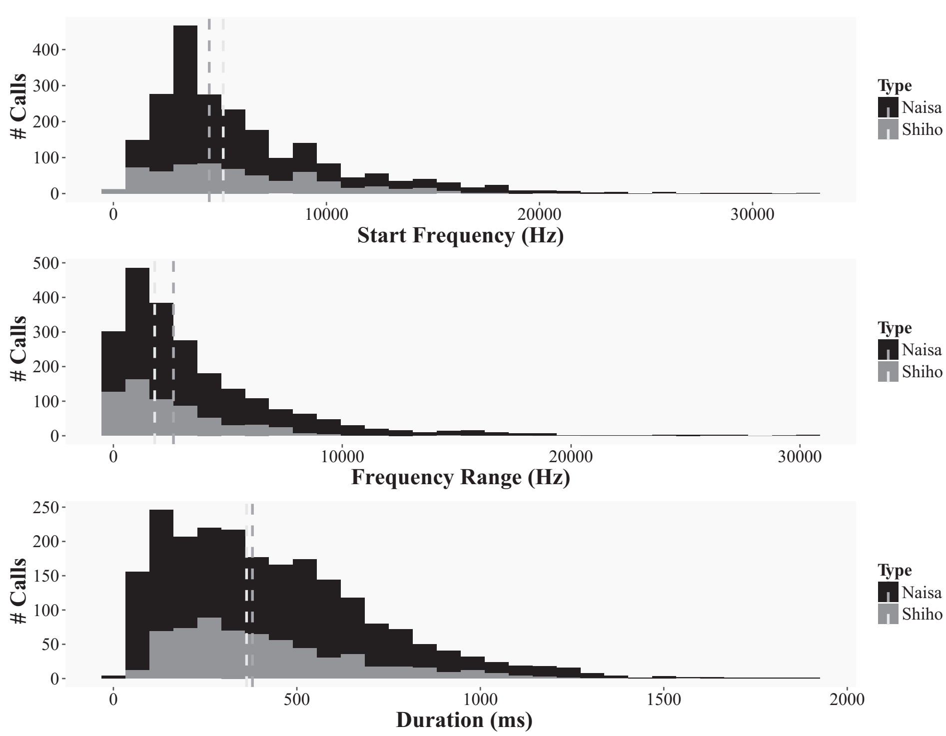

FIG. 7. Histograms of start frequency, frequency range, and duration of calls from Naisa- and Shiho-type short-finned pilot whales. Dashed lines represent median values for both types.

TABLE II. Kruskal-Wallis and Kolmogorov-Smirnoff tests of differentiation between Naisa- and Shiho-type short-finned pilot whales, using start frequency, frequency range, and call duration as input parameters for each test.

	Start Frequency	Frequency range	Duration
Kolmogornov-Smirnoff test			
p-value	0.0004	<0.0001	0.0002
Kruskal-Wallis test			
p-value	0.008	0.0001	0.0002

Two mixture-model based classification algorithms were built, the first using the call contour dataset and the second using the summary statistics dataset. No difference in vocalizations was found between the two types using the call contour dataset, while the models using the summary statistics were able to classify individual calls with a mean error rate of 26% (95% CI = 15%–37%, Fig. 8). Using the summary statistics dataset, mixture models for Hawai'i (Naisa-type) had seven components for nine out of ten models, while mixture models for the eastern Pacific (Shiho-type) had six components for nine out of ten models. A Fisher's exact test indicated that this classification rate was significantly different from chance ($p = 0.0013$).

Using the classification algorithm developed for the summary statistics dataset, two encounters from the central Pacific Ocean were classified using a tenfold cross-validation model. One was classified as Naisa-type in 97% of the classification attempts, while the other was classified as Shiho-type in 60% of the classification attempts.

Intra-type KL divergence within the Shiho-type made up 15% of the divergence between the two types, while KL divergence within the Naisa-type made up 11% of the divergence between types.

IV. DISCUSSION

The call composition and acoustic features of Naisa- and Shiho-type vocal repertoires were found to be differentiated in all analyses. We found statistically significant differences in the type and number of call components per call used by each type, as well as the start frequency, frequency

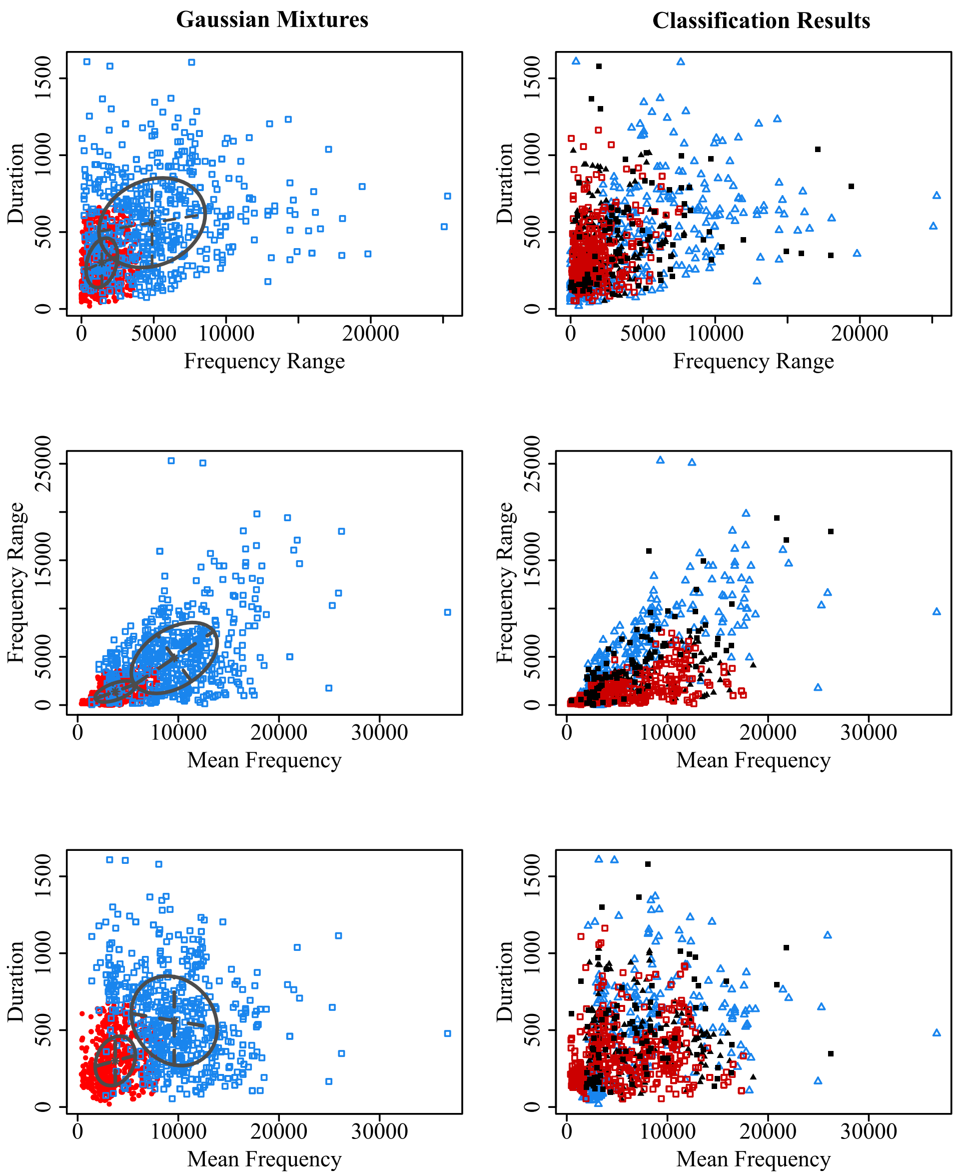

FIG. 8. (Color online) Mixture-model based classification of acoustic vocalizations as either Naisa- or Shiho-type vocalizations using the *summary statistics* data set. Two-dimensional plots of model-based classifications based on mean peak frequency (Hz), frequency range (Hz), and duration (s). (Left) Gaussian mixtures created using training data, labeled as Naisa (blue) or Shiho (red). Ellipses are centered on the mean of the most important mixture (mean number of mixtures for Naisa-type = 7 and Shiho-type = 6). (Right) Results of classifying the training data. Calls that were correctly classified are labeled as Naisa (blue) or Shiho (red). Misclassified calls are labeled in black.

range, and duration of calls. We were further able to use the differences in acoustic features to build a classification algorithm using mixture models, and quantify divergence within and between types using KL divergence.

A. Call composition

The vocal repertoires of the Naisa- and Shiho-types were distinct both in call diversity and number of call components (e.g., Fig. 5). The social complexity hypothesis suggests that more complex communication systems are needed as social structure becomes more complex (Freeberg *et al.*, 2012). The larger number of multi-component calls observed in the Hawaiian vocal repertoire may indicate a more complex social structure, as communication signals tend to be more complex in contexts that require greater information transfer, such as social interactions (Bradbury and Vehrencamp, 1998). There is evidence of both pelagic and insular populations of pilot whales around the main Hawaiian Islands, and multiple communities within the insular population (Baird, 2016), and the greater number of multi-component calls may reflect this complexity in social structure. However, it is also possible that this difference is due to sampling bias, if we simply encountered groups during periods of foraging or social interaction more often in the Hawaiian Islands than we did in the eastern Pacific Ocean, as differences in the number of multi-component calls we identified may reflect behavioral state or social context during an encounter.

Untrained analysts used the call catalogue we developed to correctly classify 79% of the calls they were provided, which is similar to results from a similar study on short-finned pilot whale vocalizations in the Bahamas (Sayigh *et al.*, 2013). That study identified calls as a single unit, unlike the present study, which identified calls as combinations of different sub-units or components. The similar success rate between the two methods suggests convergence and could support a component-based classification system of discrete, repeated call types for short-finned pilot whales, similar to a component-based classification system developed for killer whales (Shapiro *et al.*, 2011). The identification of components within each call may prove useful in future studies of vocal behavior or social structure. For example, killer whales' repertoire of monophonic calls is more diverse in larger populations, while biphonic calls are less diverse, suggesting that they are driven by different evolutionary factors (Filatova *et al.*, 2012).

B. Differentiation using acoustic features

Significant statistical differentiation in start frequency, duration, and frequency range of Naisa- and Shiho-type vocalizations indicates that these two types have distinct acoustic features in their vocal repertoires (Table II, Fig. 8). Inter-type KL divergence was also greater than intra-type KL divergence, confirming divergence of acoustic features between the two types. Similar results have been reported for short-finned pilot whales in the Atlantic Ocean, where Caribbean and Canary Island populations have been shown to exhibit divergence in the acoustic features of their tonal calls (Rendell *et al.*, 1999), although it is unknown whether there are morphological differences between these populations.

A significant effect of encounter (a proxy for social group) in the nested MANOVA indicates that divergence between the two regions may be affected by differences between social groups. Cultural factors, such as vertical transmission, may be working in combination with acoustic drift to drive differentiation between the vocal repertoires of these two types.

The classification algorithm was able to correctly classify Naisa- and Shiho-type vocalizations with an accuracy of 74% (Fig. 8). Acoustic differentiation, therefore, may be an important tool in rapidly identifying Naisa- and Shiho-type short-finned pilot whales in the field, especially in areas where the distribution of the two types is unknown and possibly overlapping (e.g., the central Pacific Ocean). As additional data are collected from areas where genetic samples are not available, this classification algorithm will be useful in further delineating boundaries between the two types, as well as identifying areas of possible overlap or temporal variability in distribution.

While the classification algorithm based on summary statistics was able to distinguish between Naisa- and Shiho-type calls ∼74% of the time, the algorithm based on call contours did not show a difference between the two types. This may indicate that the call contours did not capture the information necessary to differentiate between the two types; adding variables such as duration may improve this method. It is also possible that any signal in this data set was masked by the large amount of variability in call contours within each type, which may be caused by a combination of social structure within each type and variability in behavior, both of which have been shown to occur in social cetaceans such as killer whales (Deecke *et al.*, 2010; Holt *et al.*, 2013). Therefore, when analyzing groups of animals with suspected acoustic variability due to structure within the group, basic summary statistics may perform better than call contours. Call contours may be better used as a higher-resolution test for acoustic structure within a group, for example, due to social structure or acoustic behavior (e.g., Deecke *et al.*, 2010), or in classifying call types (e.g., Shapiro *et al.*, 2011).

C. Classification of unknown encounters

Two encounters with pilot whales of unknown type from the central Pacific Ocean were classified, one as Naisa-type and the other as Shiho-type. Acoustic data from additional encounters could aide in the determination of distributional boundaries between the two types in this area, or other areas where genetic and morphological data are scarce and difficult to collect (e.g., Van Cise *et al.*, 2016). Acoustic data have been used to describe population boundaries of several other cetaceans, for example, blue whales (McDonald *et al.*, 2006; Balcazar *et al.*, 2015) and humpback whales (Garland *et al.*, 2015). Here, acoustic data correlate with the two morphologically and genetically distinct types; if they are determined to be sub-species or species, acoustic data may be important to their management and conservation.

In the central Pacific, the distribution of the two types may be parapatric or temporally distinct, as is the case off Japan where both types are found separated by the Kuroshio-Oyashio Extension Current and move north-south throughout the year following the boundary set by this current (Kasuya, 1986; Kasuya *et al.*, 1988). However, if the two types are sympatric in their distributions in the central Pacific Ocean, then it could be a region of acoustic mixing between the two types, which will decrease the effect of acoustic drift between them through horizontal learning, a phenomenon that has been described in several taxa, including birds and marine mammals (e.g., Slabbekoorn and Smith, 2002; Crance *et al.*, 2014).

Alternatively, acoustic structure may be important to the maintenance of genetic structure in this area, i.e., individuals prefer mates that sound similar to themselves over potential mates with different vocal repertoires. This acoustic sorting could cause a positive feedback loop in which animals only mate with similar sounding animals, thus increasing the differentiation between the two types. This has been demonstrated to occur in several bird species using playback experiments (Slabbekoorn and Smith, 2002), and could be similarly tested in pilot whales.

D. Future work

The results of this study suggest that short-finned pilot whale vocal repertoires are variable at a local level within each region, possibly driving the differentiation we see between the two types; this was illustrated by a significant effect of encounter in the nested, non-parametric MANOVA. Evidence suggests that, for other social cetaceans, variability in the vocal repertoire can be both socially driven [e.g., killer whales (Yurk *et al.*, 2002; Riesch *et al.*, 2006; Deecke *et al.*, 2010; Filatova *et al.*, 2012; Crance *et al.*, 2014; Musser *et al.*, 2014) and sperm whales (e.g., Rendell *et al.*, 2012; Cantor *et al.*, 2015)] and behaviorally driven [e.g., killer whales (Filatova *et al.*, 2013; Holt *et al.*, 2013)]. Short-finned pilot whales are a highly social cetacean, known to form stable social groups for a decade or more (Heimlich-Boran and Hall, 1993; Mahaffy *et al.*, 2015). In the Hawaiian Islands, these social groups form island-associated communities within a Main Hawaiian Island insular population (Baird, 2016). Acoustic differences among these communities, or the social groups within these communities, may be important to driving the acoustic variability we see within the Hawaiian region (Janik and Slater, 2000). This could be tested by conducting a higher resolution comparison of acoustic and photo ID data within the region to differentiate acoustically among identified social groups.

Differences in behavioral state may also be a driver of the acoustic divergence within regions, as has been documented in a number of cetaceans, including killer whales (e.g., Holt *et al.*, 2013). Differences in group behavior during the recording (e.g., foraging, socializing, or resting), which may be, in turn, affected by environmental factors (e.g., seasonality, time of day, productivity) will introduce variability into low resolution studies of vocal repertoire such as this one. Similar to the variability introduced by acoustic differences among social groups within a region, this pattern could be tested with a high resolution study of vocal activity recorded during distinct behavioral states.

Additionally, the present study does not cover the entire range of either of the two types. Continued sampling from their entire Pacific (or global) range is needed to determine whether this pattern of acoustic divergence between the two types is consistent throughout their range, especially in areas of possible overlap between the two types. Further study of acoustic divergence between social groups would provide insight into the role vocal repertoire may have in maintaining divergence between groups.

E. Conclusion

Geographic variability in acoustic structure between Naisa- and Shiho-type short-finned pilot whales suggests that these two groups are acoustically differentiated. A nested MANOVA indicates that the difference between regions is largely driven by differences between encounters within regions, possibly due to sub-population structure or social structure. This evidence can be added to previous studies of their genetics, morphology, and geographic distribution (Kasuya and Marsh, 1984; Wada, 1988; Oremus *et al.*, 2009; Van Cise *et al.*, 2016) to suggest that the two types may be separate sub-species or species. The classification algorithm developed here shows that acoustic divergence between the two types can be used to improve our understanding of their spatial and temporal distribution in areas where genetic or morphological samples are difficult to acquire, such as the central Pacific Ocean.

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[1]See supplementary material at http://dx.doi.org/10.1121/1.4974858 to hear an audio recording of the unique vocalization described herein.

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