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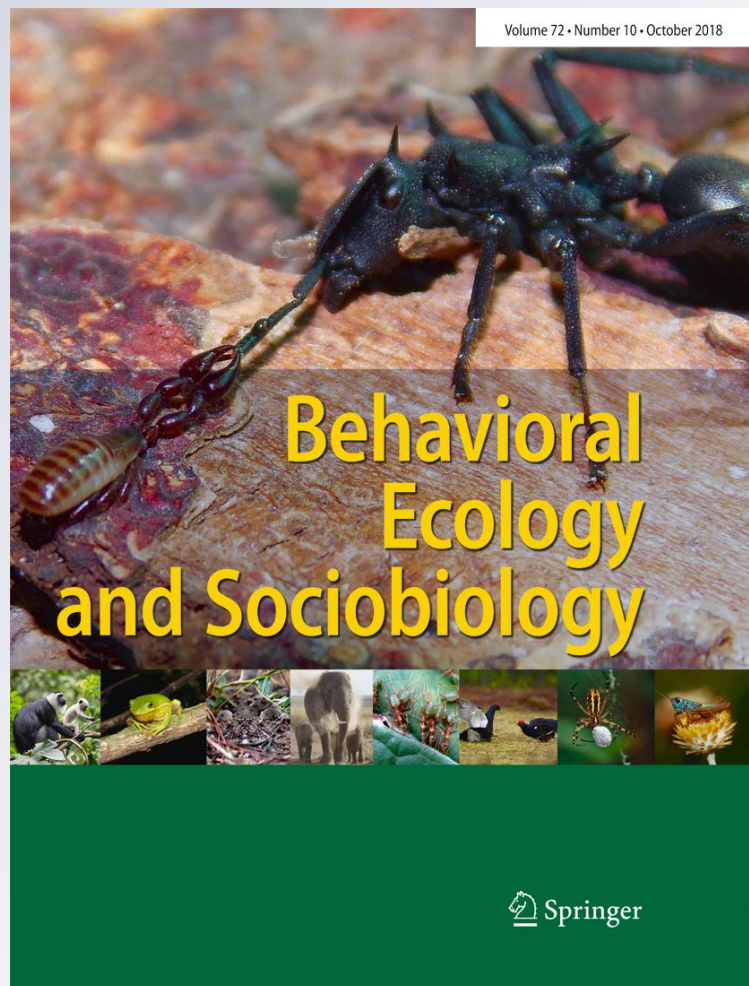
Behavioral Ecology and Sociobiology

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Song of my people: dialect differences among sympatric social groups of short-finned pilot whales in Hawai'i

Amy M. Van Cise[1,2] · Sabre D. Mahaffy[3] · Robin W. Baird[3] · T. Aran Mooney[2] · Jay Barlow[1,4]

Abstract

In many social species, acoustic dialects are used to differentiate among social groups within a local population. These acoustic dialects and their corresponding social groups are often related to distinct foraging behaviors or spatial movement patterns, and it is possible that vocal repertoire variability is one of the proximate mechanisms driving or maintaining genetic and ecological diversity at a subspecies level in social species. Short-finned pilot whales (*Globicephala macrorynchus*) inhabiting Hawaiian waters have a stable hierarchical social structure, with familial social units associating in larger social clusters within island-associated communities. In this study, we test the hypothesis that sympatric social groups of short-finned pilot whales have acoustically differentiated dialects, which may be used to maintain the social structure. We first examined call composition of social calls collected from photographically identified social clusters of short-finned pilot whales around the Main Hawaiian Islands, using a catalog of manually classified calls, and found that call composition differed among clusters. We then conducted ANOVA and support vector machine (SVM) learning analyses of the acoustic features of social calls. Social clusters were significantly differentiated in their acoustic features, and the SVM classification accuracy was 60%. These results indicate that vocal repertoire reflects social segregation in short-finned pilot whales and may be a driving mechanism of differentiation, potentially contributing to genetic diversity within populations. This suggests divergent acoustic population structure; however, the small sample size in this study decreases the ability to detect acoustic differences among groups. Additional sampling will improve our power to detect acoustic differences among social clusters of Hawaiian pilot whales and improve classification accuracy. The pattern described here highlights the importance of increasing the spatial and temporal resolution of conservation and management plans for this species, in order to conserve subpopulation genetic and social structure.

Significance statement

In some species, vocal repertoires differ among social groups or populations of a species that use the same habitat. These differences, called dialects, are thought to be important to maintaining segregation among groups of animals with overlapping distributions, and in some cases may increase intra-specific ecological or genetic variability. This study is the first to provide evidence that sympatric social clusters of short-finned pilot whales have different vocal repertoires, and that vocal repertoire within groups may change with behavioral context. In terrestrial (e.g., elephants) and marine (e.g., killer whales, sperm whales) species with similarly stable social hierarchies, where acoustic dialects, genetic diversity, and/or ecological variability are linked with social structure, anthropogenic stressors have precipitated rapid declines in abundance with slow or nonexistent recovery. Given the myriad threats faced by short-finned pilot whales in the Hawaiian Islands, including fisheries bycatch, military and commercial anthropogenic noise, and vessel strikes, understanding intra-population social structure and its links with genetic structure and ecological variability is imperative to the proper conservation and management of this species.

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Introduction

Differences in vocal repertoires, including vocal dialects, have been described among sympatric or allopatric groups at the population or subpopulation level in many vocal taxa, including birds (Baker and Cunningham 1985; Wright and Wilkinson 2001; Slabbekoorn and Smith 2002; Podos 2010), non-human primates (Green 1975; Mitani et al. 1992; Fischer et al. 1998; Lemasson et al. 2003; Crockford et al. 2004; McComb and Semple 2005; de la Torre and Snowdon 2009; Kessler et al. 2014), rock hyraxes (Kershenbaum et al. 2012), prairie dogs (Perla and Slobodchikoff 2002), bats (Esser and Schubert 1998), and cetaceans (Winn et al. 1981; Ford 1991; McDonald et al. 2006; Riesch et al. 2006; Papale et al. 2013; Balcazar et al. 2015; Cantor et al. 2015; Garland et al. 2015).

In contrast to geographic variation in vocal repertoire, which can be defined as "differences in song over long distances and between populations which normally do not come together," dialects are "song differences between neighboring populations of potentially interbreeding individuals" (Nottebohm 1969; Conner 1982). A similar working definition distinguishes between microgeographic variation, between groups with shared boundaries, and macrogeographic variation, between groups that do not normally mix (Krebs and Kroodsma 1980). In both of these definitions, geographic variation in vocal repertoire is considered to be the natural product of variability in evolutionary and environmental influences found among non-interacting populations (Krebs and Kroodsma 1980; Nottebohm 1969; Conner 1982). Dialects, on the other hand, occur between allopatric or sympatric groups with no geographic or environmental barriers to gene flow. Differences in dialects among sympatric groups may be behaviorally driven; understanding the proximate and ultimate mechanisms for vocal dialects may increase our understanding of the ecological and evolutionary role of acoustic communication in vocalizing species.

In the marine environment, there are relatively few boundaries to individual or group dispersal. However, localized genetic structure occurs within many populations, indicating restricted mating and gene flow within those populations (e.g., Foote et al. 2009; Pilot et al. 2010; Ansmann et al. 2012; Martien et al. 2014). In the absence of barriers, observed genetic structure within species or populations may be caused by social structure and behavior (e.g., Rendell et al. 2012; Whitehead 2017).

In some social species, differences in vocal dialects may be a proximate mechanism driving or maintaining genetic differentiation among sympatric social groups. Correlations between genetic and acoustic structure have been identified in several taxa, including some birds (e.g., white-crowned sparrows (*Zonotrichia leucophrys oriantha*) (MacDougall-Shackleton and MacDougall-Shackleton 2001; Soha et al. 2004)), bats (e.g., least horseshoe bat (*Rhinolophus cornutus pumilus*) (Yoshino et al. 2008)), and frogs (e.g., Túngara frogs (*Engystomops pustulosus*) (Prohl et al. 2006), Amazonian frogs (*Allobates femoralis*) (Amézquita et al. 2009)). Social odontocetes, such as sperm whales (*Physeter microcephalus*) and killer whales (*Orcinus orca*), have been shown to use acoustic features to distinguish among social groups in an environment with few barriers to dispersal (e.g., Ivkovich et al. 2010; Filatova et al. 2012; Rendell et al. 2012). Sperm whale clans, for example, remain vocally and genetically segregated, although they are geographically and temporally sympatric in distribution (Rendell and Whitehead 2003). Killer whales also form distinct vocal clans among genetically distinct sympatric social groups (e.g., Yurk et al. 2002).

Vocal dialects are culturally inherited in some species, vertically or horizontally transmitted through learning (Mundinger 1980). Vocal learning has been demonstrated in birds (Baker and Cunningham 1985) as well as social cetaceans (Janik and Slater 1997; Deecke et al. 2000; Crance et al. 2014), and may be maintained by gene-culture coevolution (Lachlan and Slater 1999; Whitehead 2017). Via the same coevolutionary process, some social cetaceans culturally inherit certain behaviors through learning, such as hunting strategies or habitat preferences (Whitehead 2007; Cantor et al. 2015). In these species, an understanding of acoustic dialects may help scientists differentiate between social groups with different culturally learned behaviors, such as differences in habitat use. However, well-studied examples of this pattern are rare. Perhaps the most well-known example is within the killer whale species, where ecologically and acoustically divergent groups of sympatric killer whales have been identified in several of the world's oceans, such as the North Pacific Ocean (e.g., Ford and Fisher 1982; Baird et al. 1992; Yurk et al. 2002; Deecke et al. 2010; Riesch et al. 2012; Foote and Morin 2016), and these groups may be undergoing a process of culturally-driven speciation.

Short-finned pilot whales are a highly social species, known to form stable social groups averaging about 12 individuals for periods of a decade or more (Alves et al. 2013; Mahaffy et al. 2015). They produce discrete, repeated social calls, which make up approximately 40% of their vocal repertoire and may be shared by members of the same group (Sayigh et al. 2013; Van Cise et al. 2017a). Within repeated call sequences, calls may be modified, as has been exhibited by closely-related long-finned pilot whales (Zwamborn and Whitehead 2017). Individuals have been shown to make

social calls while diving, a behavior that is thought to help them maintain group cohesion with group members at the surface (Jensen et al. 2011). Social calls are thought to be produced along a continuum, from burst pulses to tonal whistles, similar to other odontocetes (Murray et al. 1998; Madsen et al. 2012; Sayigh et al. 2013).

In the Pacific Ocean, two types of short-finned pilot whales have been described morphologically and genetically (Kasuya et al. 1988; Oremus et al. 2009) and have discrete distributions, one found mainly in the eastern Pacific Ocean and the other extending from Hawai'i to the western Pacific Ocean (Van Cise et al. 2016). These two types exhibit geographic variability in their vocal repertoire: encounters from the eastern Pacific Ocean and Hawai'i can be differentiated based on the presence and frequency of stereotyped calls, as well as differences in acoustic features such as frequency, duration, and frequency range of calls (Van Cise et al. 2017a).

In the Main Hawaiian Islands (MHI), stable groups of short-finned pilot whales, called social units, will only associate with specific other social units. These associations form larger groups called clusters, with an average of 23 individuals from 1 to 3 social units (Mahaffy et al. 2015). Social units are predominantly composed of immediate family members, while clusters likely represent extended family groupings (Van Cise et al. 2017b). Longitudinal observations and photo identification data collected since 2000 have revealed that individuals within social units spend an average of 76% of their time together, indicating a strong affinity for association (Mahaffy et al. 2015). Clusters, the next hierarchical level, comprise one or more social units that are observed together an average of 50% (range 30–90%) of the time. Communities, the highest level of social organization, comprise multiple clusters that are generally resident to either Hawai'i Island (eastern MHI community), O'ahu/ Kaua'i Islands (western MHI community), or O'ahu/Lāna'i Islands (central MHI community) (Baird 2016). Thirty-seven clusters have been identified in the eastern MHI community and 57 in the rest of the MHI, although additional data from outside the eastern MHI community will likely reveal a larger number of clusters.

In Hawaiian waters, short-finned pilot whales face a number of anthropogenic threats, including vessel strikes, interactions with fisheries that can cause injury or death, and anthropogenic noise, including noise from private or industrial fishing vessels, tourist whale watching ships, and high-intensity Navy sonar (Baird 2016). Their stable social structure may increase specialization and adaptive fitness in the short term (Whitehead and Ford 2018). However, if social structure is linked with cultural and ecological diversity in this species, it may also increase their vulnerability to loss of genetic or ecological diversity from anthropogenic stressors through the extirpation of social groups (Wade et al. 2012).

Clusters are genetically distinct, indicating that they remain socially segregated over multiple generations (Van Cise et al. 2017b), yet the proximate mechanism for social segregation is unknown. It is possible that acoustic dialects among social groups are used to identify group membership and may act as a driver maintaining social and genetic structure. In this study, we examine acoustic variability in Hawaiian pilot whales, specifically testing whether clusters within the eastern community are acoustically distinct. Correlation between acoustic dialects and social cluster organization would indicate a link between cultural and acoustic diversity within the population and that acoustic dialects are one mechanism used to maintain social segregation among groups of short-finned pilot whales. This correlation would have important implications for the vulnerability of this population to current anthropogenic threats, as well as its conservation.

Methods

Data collection

Data for this study were collected as in Van Cise et al. (2017a). Recordings were collected from around Hawai'i and Kaua'i Islands during Cascadia Research Collective field projects (Baird et al. 2013) from 2012 to 2015. It was not possible to record data blind because our study involved focal animals in the field. Three recording instruments were used: a Biological Underwater Recording Package (BURP 3.2, developed at SWFSC), a DMON Towfish (developed at WHOI, e.g., Kaplan et al. (2014)), and an Ocean Instruments SoundTrap ST200. Table 1 displays specifications for each of the recorders used in this project.

Recording packages were deployed during encounters with short-finned pilot whale clusters, if no other species were identified by trained observers within the horizon (approximately 2 km) during the encounter. To minimize the impact of noise and decrease the likelihood that other species pass through the recording area undetected, recordings were collected when conditions ranged from 0 to 4 on the Beaufort scale. The BURP and the SoundTrap were attached to a surface buoy and deployed from an 8.2 m Boston Whaler, which then left the area for periods of 15 min to 1 h to minimize engine noise. The Towfish was towed approximately 15 m behind the Boston Whaler with two 150 hp outboard motors.

Photographs were taken during each encounter and used to identify the social unit(s) and cluster(s) present during each encounter using notches and marks on the dorsal fins, based on the hierarchical social structure described by Mahaffy et al. (2015). Recordings were only used for this study if the social unit or cluster could be identified using photographs from the encounter. Encounters were assigned one or more clusters based on group membership of individuals

Table 1 Technical specifications for recording packages used in this study

	BURP 3.2	DMON towfish	SoundTrap ST200
Sampling rate	192 kHz	512 kHz	188 kHz
Functional bandwidth	2–60 kHz ± 5 dB	5–160 kHz	20 Hz − 60 kHz
Recorder flat response range	2–60 kHz	5–160 kHz	20 Hz − 60 kHz
Pre-amplifier flat response range	> 2 kHz	NA	NA
Recorder bit-depth/resolution	24-bit	16-bit	16-bit
Hydrophone manufacturer and model	HTI, Inc.	Navy type II ceramics	Ocean Instruments
Number of encounters	12	10	4
Recording period	2012	2012–2013	2014–2015

photographed during the encounter (Mahaffy et al. 2015). Encounters for which multiple clusters were identified were removed from all analyses of acoustic variability among social clusters and were later used to quantify variability in group vocal behavior when clusters are alone versus when clusters interact with other clusters.

Call extraction

All calls were manually extracted using Raven 1.4. Recordings made using the DMON Towfish had higher noise levels than other recording packages, due to the proximity of the recorder to the research vessel; therefore, some calls were obscured. Calls were only extracted if the entire contour was clearly visible. Spectrograms were created using a DFT with a Hamming window (50% frame advance), and frame lengths were set to provide similar temporal and spectral resolution across recordings with different sampling rates (BURP N_{DFT} = 2048, Towfish N_{DFT} = 1280, SoundTrap N_{DFT} = 2005). Since pilot whales exhibit smooth transitions between pulsed calls and whistles (Sayigh et al. 2013), and some evidence indicates that these vocalizations may exist on the same continuous spectrum (Murray et al. 1998), both pulsed calls and whistles are considered together in this study, and referred to as "calls."

Calls were visually classified and annotated as part of a previous study (Van Cise et al. 2017a). Once extracted, calls were imported into PAMGUARD version 1.11.12 (Gillespie et al. 2009, 2013). The fundamental frequency of each whistle was traced using ROCCA for PAMGUARD (Oswald and Oswald 2013). For pulsed calls, the lowest band for which the entire call was visible was traced (i.e., the frequency band with the most power), representing the pulse repetition rate (Watkins 1968). Fundamental frequency and pulse repetition rate values were both analyzed as call frequency values. Up to 50 randomly selected calls were traced per encounter. Summary parameters were calculated for each call using the call trace exported from ROCCA (start frequency, min and max frequencies, mean frequency, frequency range, duration). Because the frequency parameters were all highly correlated (R^2 = 0.80–0.92), to avoid including redundant information,

we chose start frequency to represent this group of measurements.

Data analysis

We first described the composition of calls produced by each cluster and examined differences among clusters in call composition. To avoid psuedoreplication due to repeated measurements of, for example, the same behavioral state, recordings were used from no more than one encounter with each social group per day. Using a call catalog of manually classified calls that was previously validated by a group of experts and volunteers (Van Cise et al. 2017a), we tested for differences in the distributions of call types produced by each cluster using Pearson's χ^2 statistic, implemented in the R computing environment (R Core Team 2016). Each cluster is represented by n encounters (n = 1–4), with variability in call type distribution among encounters, causing extra-multinomial dispersion that we expect to inflate the cluster χ^2 statistic if not accounted for. We therefore correct for extra-multinomial dispersion by estimating an over-dispersion parameter using a method adapted from McCullagh and Nelder (1989). To do this, we calculate the χ^2 statistic among encounters within social clusters for each of the three social clusters with multiple encounters. Summing these statistics and dividing by the summed degrees of freedom gives an inflation factor, which we used to divide the original χ^2 statistic, resulting in a final "nested" χ^2 statistic that measures the effect of social cluster membership on variability in call composition, after accounting for variability among encounters within social clusters.

Because we do not know a priori whether call composition or acoustic features (e.g., frequency, duration) are more likely to vary among clusters, we additionally used acoustic features to examine differences in vocal behavior among clusters. We used a nested, non-parametric, multivariate analysis of variance (MANOVA), implemented using the BiodiversityR package (Kindt and Coe 2005), with encounters nested as random effect within cluster. We then used a post hoc Tukey's honestly significant difference (HSD) test to determine whether significant results were driven by a single

encounter or cluster. ANOVA and Tukey's test analyses were performed in R.

We additionally used a support vector machine (SVM) learning classification algorithm to test whether differences in acoustic features among clusters could be used to classify calls to the appropriate cluster. SVM learning is a supervised classification method that uses a training dataset to choose multivariate separating boundaries between two clusters. The preferred boundary maximizes the correct classification of training data while also maximizing the distance between the boundary and the points closest to it (Bennett and Campbell 2000). We used the package e1071 (Meyer et al. 2018), implemented in R, to expand this concept to allow for classification of multiple groups using the same algorithm.

Finally, we tested for differences in acoustic behavior between multi-cluster and single-cluster encounters. For this test, we used the multi-cluster encounters that were previously removed from analyses of social structure and compared those encounters with the single-cluster encounters used in previous analyses in this paper. We examined differences in the true distributions of multi- and single-cluster encounters using Kolmogorov-Smirnov and Kruskal-Wallis tests of differentiation in the cumulative distribution and median values, respectively, of frequency, range, and duration of calls. Kolmogorov-Smirnov and Kruskal-Wallis tests were both implemented in R.

Data availability

The datasets collected and/or analyzed during the current study are available from the corresponding author on reasonable request.

Results

Between 2012 and 2015, acoustic recordings were collected during 36 encounters with short-finned pilot whales. Of these encounters, cluster membership was identified for 33 encounters. Multiple clusters were present during 11 encounters. The remaining 22 encounters were of a single cluster, with 11 total clusters recorded. Short-finned pilot whales did not vocalize during all encounters; calls were only extracted from the subset of encounters during which animals vocalized. Vocalizations were successfully extracted from 15 encounters representing nine clusters. Number of encounters per cluster as well as number of extracted calls can be found in Table 2. Three clusters (H27, W32, and W16) had sample sizes that were too small to be included in analyses of acoustic variability among clusters and were therefore removed.

A total of 34 call types were identified, of which 14 represented at least 1% of the dataset. Collectively, these 14 calls comprised 95% of stereotyped calls in the dataset. Calls were

Table 2 Number of encounters and sample size for social clusters included in this study. Cluster labels beginning with H indicate clusters from the eastern MHI (Hawai'i Island) community, while cluster labels beginning with W indicate clusters from the western MHI (Kaua'i /O'ahu Islands) community

Cluster	Number of encounters	Number of calls
H22	4	148
H35	1	291
H7	3	76
H20	2	160
H19	1	131
H31	1	246
H27	1	4
W32	1	6
W16	1	10

produced by combining one or more basic components, examples of which can be seen in Fig. 1. While most calls comprised only one or two call components, some calls were observed to have five or more components in a sequence, which could be repeated by one or more individuals in the group. Some repeated call types were similar in overall shape but varied enough in structure to be considered distinct calls (see examples in Fig. 2). Of the 14 call types that made up at least 1% of the dataset, six were unique to a single cluster, while eight were shared among two or more clusters (Fig. 3). Call composition differed significantly among clusters, after accounting for within-cluster variability among encounters (Pearson's χ^2 p value < 0.0001, df = 65).

We tested for a general pattern of acoustic differentiation among clusters using a non-parametric nested MANOVA, with encounters nested within clusters, and tested significant results with a post hoc Tukey's HSD. Because all frequency variables measured (start frequency, min and max frequencies, mean frequency) were highly correlated ($R^2 = 0.80$–0.92, $n = 1072$), we selected one variable, start frequency, to represent all frequency variables in the MANOVA. Before testing for variability among clusters, we estimated variability among encounters and found significant differentiation at the encounter level (encounter p value < 0.0001, $F = 19.27$, df = 11). Then, using only clusters with multiple encounters, we nested encounter within cluster to account for variability among encounters. Start frequency, frequency range, and duration were found to differ significantly among clusters (cluster p value < 0.0001, $F = 9.3$, df = 8). Tukey's HSD indicated that the MANOVA p value was not overly biased by a few samples, but rather was representative of the overall sample set (Fig. 4). The HSD also showed that differentiation in start frequency and frequency range of calls was significant for a greater number of clusters than differentiation in duration of calls.
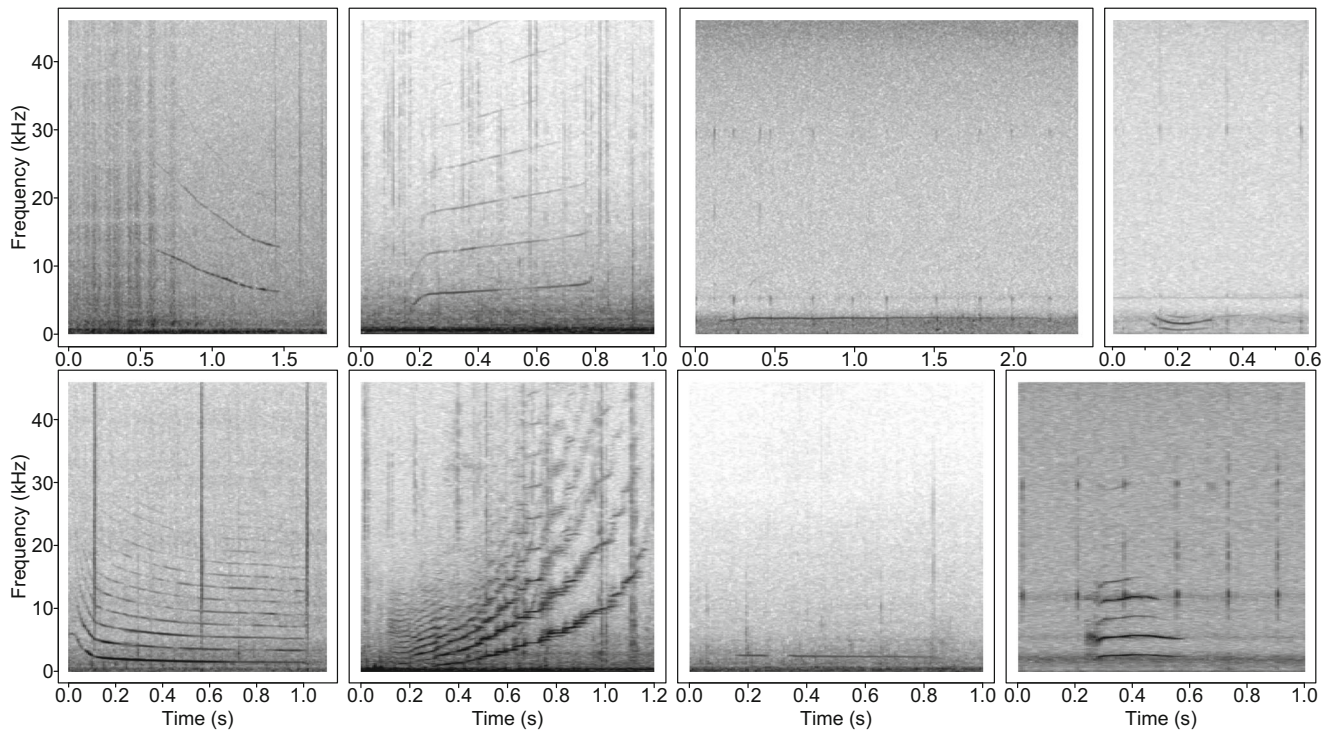
Fig. 1 Example spectrograms of stereotyped calls produced by clusters in the eastern community. Each call displayed in this figure could occur as a standalone call or in combination with others as a component of longer stereotyped calls. Dark vertical lines represent echolocation clicks that are likely from other members of the group and are assumed to be independent of the calls with tonal characteristics
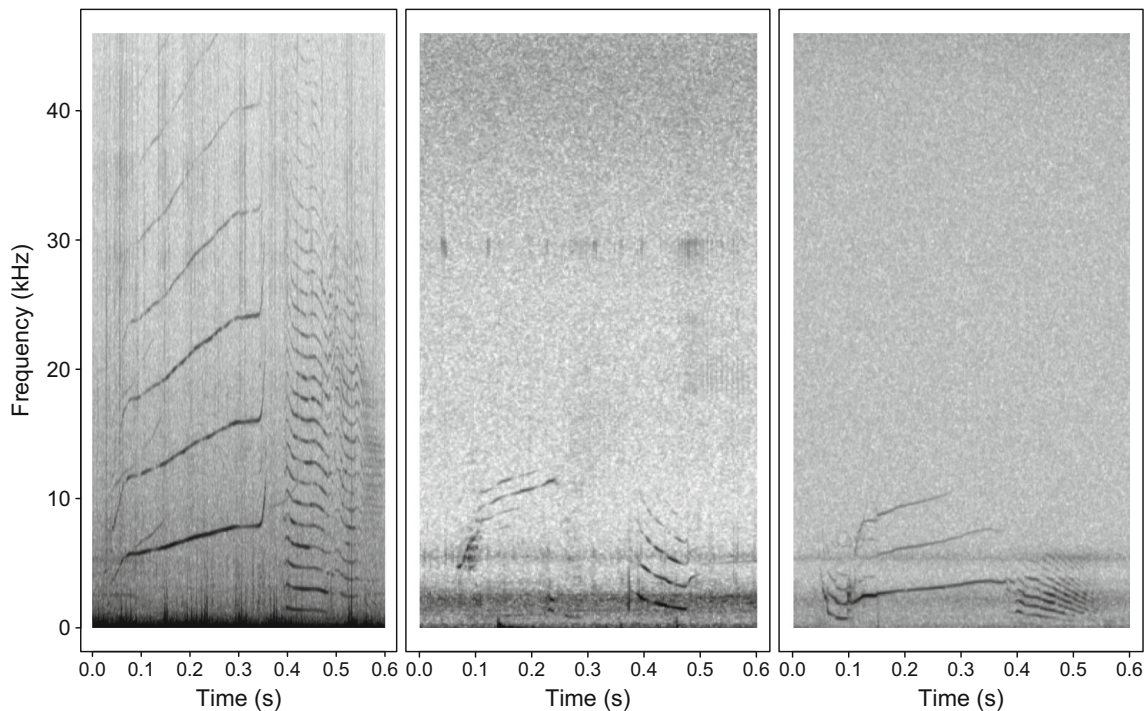

Fig. 2 Spectrograms from three ascending-descending call types with similar overall shape and sound but structural variability in the way they are produced. The first and last calls were produced by multiple social clusters, while the middle call was produced in only a single group. Similar variations were found to be unique to several of the social clusters in this study

Fig. 3 For each of six clusters in the eastern community, the proportion of each stereotyped call produced during recorded encounters. The 14 stereotyped calls included each represent at least 1% of all stereotyped calls recorded and which collectively comprise 95% of all stereotyped calls
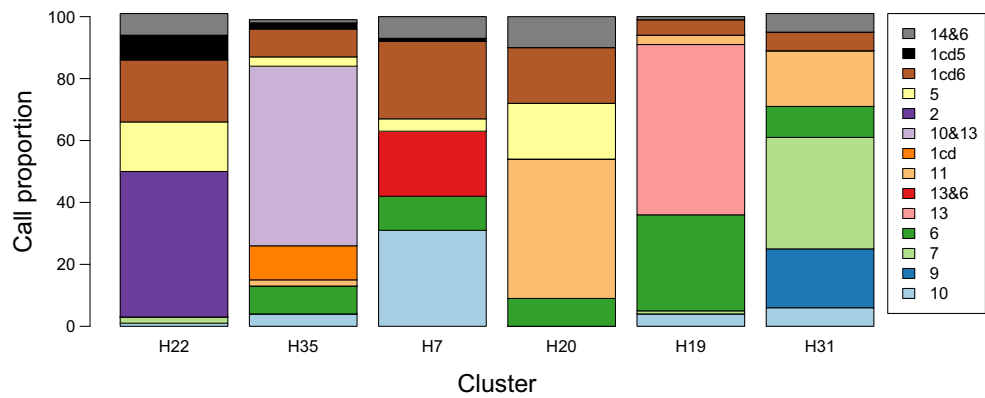
Using an SVM learning algorithm, we were able to successfully assign calls to their cluster with an accuracy of 60%, using a random 10% cross-validation method. Classification accuracy varied among clusters, with higher classification accuracy for clusters with larger sample sizes (Table 3). For five out of six of the clusters, classification accuracy was substantially higher than expected by chance (17%). When whistles were grouped by encounter for cross-validation rather than randomly, the classification accuracy was highly variable, with a mean classification accuracy of 36% and a range of 0–91% accuracy. Classes and support vectors are shown in Fig. 5.

Finally, calls from single-cluster encounters ($n = 1072$ calls) versus multi-cluster encounters ($n = 646$ calls) were significantly different in both the median and cumulative distribution of all three acoustic features analyzed (Kruskal-Wallis and Kolmogorov-Smirnov non-parametric differentiation test p values all < 0.0001). The distributions and median values of the start frequency, frequency range, and duration of calls were all shifted toward higher values during single-cluster encounters compared with multi-cluster encounters, with broader distributions (greater variability) during

single encounters compared with multi-cluster encounters (Fig. 6).

Discussion

Complex hierarchical social structure is known to increase complexity in vocal repertoires and dialects (Freeberg et al. 2012). In social cetaceans, this can be seen as an increase in the number and variability of the types of calls produced, as well as the variability in the acoustic features of those calls. For example, killer whales have complex vocal repertoires, in which individuals share most of their calls with their acoustic subclan, a few calls with other subclans within the same clan, and no calls with different clans (Ford 1991; Riesch et al. 2006). Sperm whales have also been shown to have complex communication systems, with variable codas that encode individual, unit, and clan identity (Gero et al. 2016). Studies in birds have shown that this vocal repertoire complexity may play an important role in acoustic communication within and between groups, in that animals respond differently to familiar song types than unfamiliar song types or song types produced
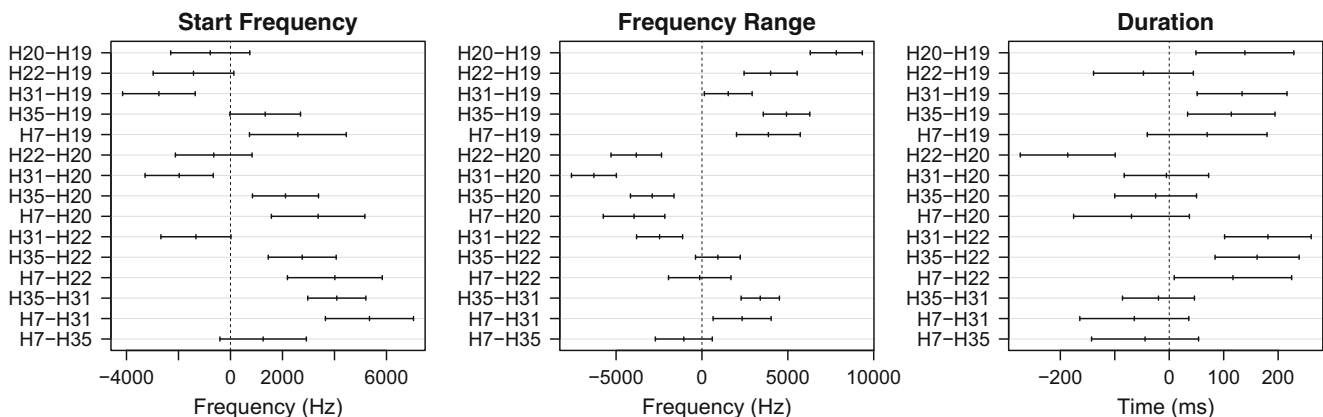

Fig. 4 Tukey's honest significant difference test results for each of the three acoustic parameters included in this study. Mean and 95% confidence intervals of the difference between two clusters shown on each row; differences without a zero crossing are considered significant

Table 3 Contingency table showing true (columns) vs. SVM (rows) cluster assignment for each call. Correct assignments are found along the diagonal (in bold). Total calls per cluster and SVM assignment accuracy are shown at the bottom. Expected assignment accuracy at random is approximately 17%

	H19	H20	H22	H31	H35	H7
H19	**94**	6	13	9	9	21
H20	0	**76**	5	0	14	4
H22	1	6	**51**	17	15	13
H31	21	32	45	**190**	19	4
H35	15	40	33	30	**234**	29
H7	0	0	0	0	0	**5**
Total	131	160	148	246	291	76
Accuracy	71%	48%	34%	77%	80%	7%

by neighboring groups (e.g., Stoddard 1996; Beecher and Campbell 2005; Lovell and Ross 2005).

Short-finned pilot whale social clusters show evidence of having distinct vocal dialects, differing both in the composition of stereotyped calls (Fig. 3) as well as the acoustic features of calls produced (Fig. 4). It is important to note here that within-cluster sample sizes were small, which likely decreased our power to detect differences in cluster means. Increased data collection from these social clusters, as well as additional clusters throughout the Hawaiian Islands, would improve our ability to differentiate among individual social clusters.

In the Hawaiian Islands, stable social structure over multiple generations has restricted mating and gene flow among clusters and led to genetic differentiation among them (Van Cise et al. 2017b). The dialect variation described here may play a role in facilitating group identity, maintaining group cohesion, and preserving social structure, as in other social cetaceans (e.g., Yurk et al. 2002; Gero et al. 2016). Alternatively, vocal repertoire differences among clusters could be the result of passive drift among socially-isolated clusters that interact with each other relatively infrequently (Mahaffy et al. 2015), with limited information transfer between them.

The proximate cause of acoustic cluster differentiation may be some combination of vertical transmission along matrilines (e.g., Yurk et al. 2002) and horizontal transmission (social learning) within social clusters (e.g., Filatova et al. 2013), a phenomenon that has also been described in killer whales (e.g., Deecke et al. 2000). Several stereotyped calls described in this study appeared similar in structure, but with modifications that may have been produced through a combination of random drift and social learning, which has been described in killer whales (Deecke et al. 2000) and their sister species, long-finned pilot whales (Zwamborn and Whitehead 2017). Figure 2 is an example of this, where all of the calls are similar

in overall shape, having an upsweep component and a downsweep component, but with structural variability in each call. One was shared by all six clusters examined, one was produced by three clusters, and one by only a single cluster. This pattern of modifications on calls of similar structure is indicative of social learning both within and among clusters; future research could target call types such as these to improve our understanding of the direction and rate of information flow both within and among clusters.

In other social cetaceans, such as killer whales and sperm whales, acoustically and genetically distinct social groups also exhibit differences in ecological behaviors, such as prey preference, foraging techniques, and temporal movements (e.g., Whitehead 1998, 2017; Rendell and Whitehead 2003; Foote et al. 2009, 2016; Foote 2012; Cantor et al. 2015). These socially driven differences in behaviors, as well as the increase in genetic diversity caused by social structure (Parreira and Chikhi 2015), may increase a species' resilience to local environmental perturbations (Whitehead and Ford 2018). However, individual social groups may be more vulnerable to anthropogenic stressors due to the group's reliance on a few key individuals for cultural knowledge (Wade et al. 2012).

In short-finned pilot whales, we know that social clusters are genetically distinct (Van Cise et al. 2017b), and the results of this study indicate they have acoustically distinct dialects indicating cultural segregation, although we do not yet know whether clusters also differ in their ecological behaviors. These results highlight the vulnerability of this species to anthropogenic threats, such as fisheries interactions, vessel strikes, and Navy sonar in the Hawaiian population (Baird 2016). Conservation-minded management of this species should account for vulnerability to the loss of genetic and cultural diversity if social groups are lost, to prevent a precipitous decline similar to that observed in killer whales, sperm whales, and other highly social species. Understanding socially driven structure within populations and how that structure is maintained is key to conserving this species. Using an acoustic classifier, such as the SVM algorithm tested in this study, passive monitoring of specific social clusters could be used to examine cultural and ecological differences among clusters and may be an efficient way to manage and mitigate risk among clusters in order to conserve genetic diversity within the population. Additional data collection and refinement of the classification methods presented in this study would allow passive acoustic monitoring of short-finned pilot whale social groups and their behaviors throughout the Hawaiian Islands.

Behavioral and environmental context are also likely to have an effect on which calls an individual may produce, as well as the acoustic features of those calls. In killer whales, frequency and duration have both been shown to vary with environmental context (Foote et al. 2004; Foote and Nystuen 2008), such as shifts to avoid masking from wind

Fig. 5 Two-dimensional parameter space occupied by each social cluster in this study, delimited using a support vector machine (SVM) learning algorithm. Start frequency, frequency range, and duration are shown on the *x* and *y* axes
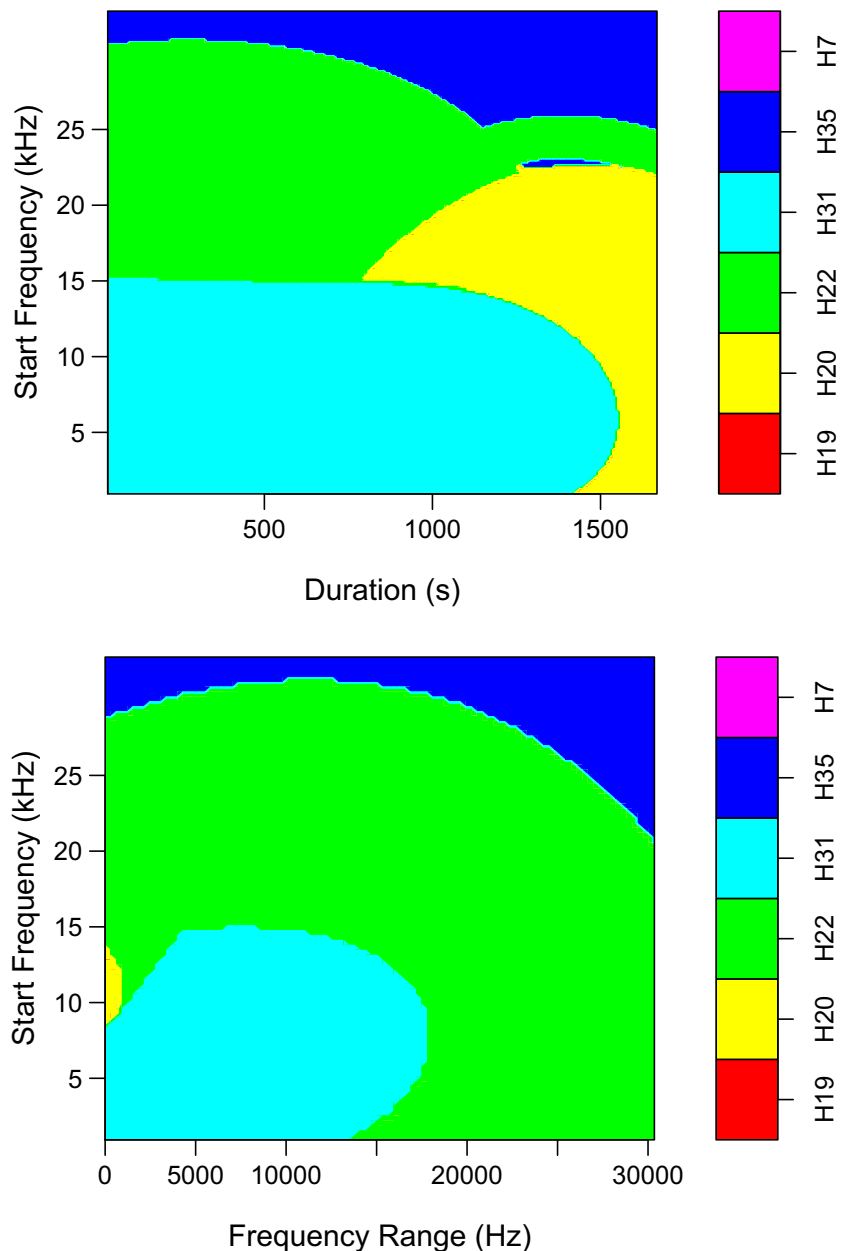
or ship noise, or to avoid detection by their prey (Deecke et al. 2005). We therefore expect that pilot whales may have vocal repertoires that differ in certain behavioral contexts, such as foraging versus socializing or environmental contexts such as ambient noise level. This variability is captured in this study as differences between encounters, as evidenced by the significant χ^2 test of independence of call types produced among encounters, as well as significant differentiation in acoustic features among encounters in the hierarchical ANOVA. Although these were treated as a random effect in this study, future work could focus on the behavioral and environmental context of recordings in order to better understand the effect of these on vocal communication in short-finned pilot whales.

Finally, multi-group vs. single-group encounters were significantly different in frequency, range, and duration of the calls produced (Fig. 6), which likely indicates a difference in acoustic behavior with different social contexts. In killer whales, the presence of other matrilines has been associated with an increase in the production of family-specific call types, as well as an increase in variable (non-stereotyped) calls (Weiß et al. 2007). Killer whales have also been shown to produce biphonic calls more frequently in the presence of other groups (Filatova et al. 2009, 2013), which are therefore thought to serve as group identifiers and help maintain group cohesion. Our data indicate that short-finned pilot whales use a parred-down subset of their vocal repertoire while in the presence of other groups, with decreased variability in both

Fig. 6 Frequency distribution (solid and dotted lines) and median values (vertical dashed lines) for start frequency, frequency range, and duration of calls recorded during single-group and multi-group encounters
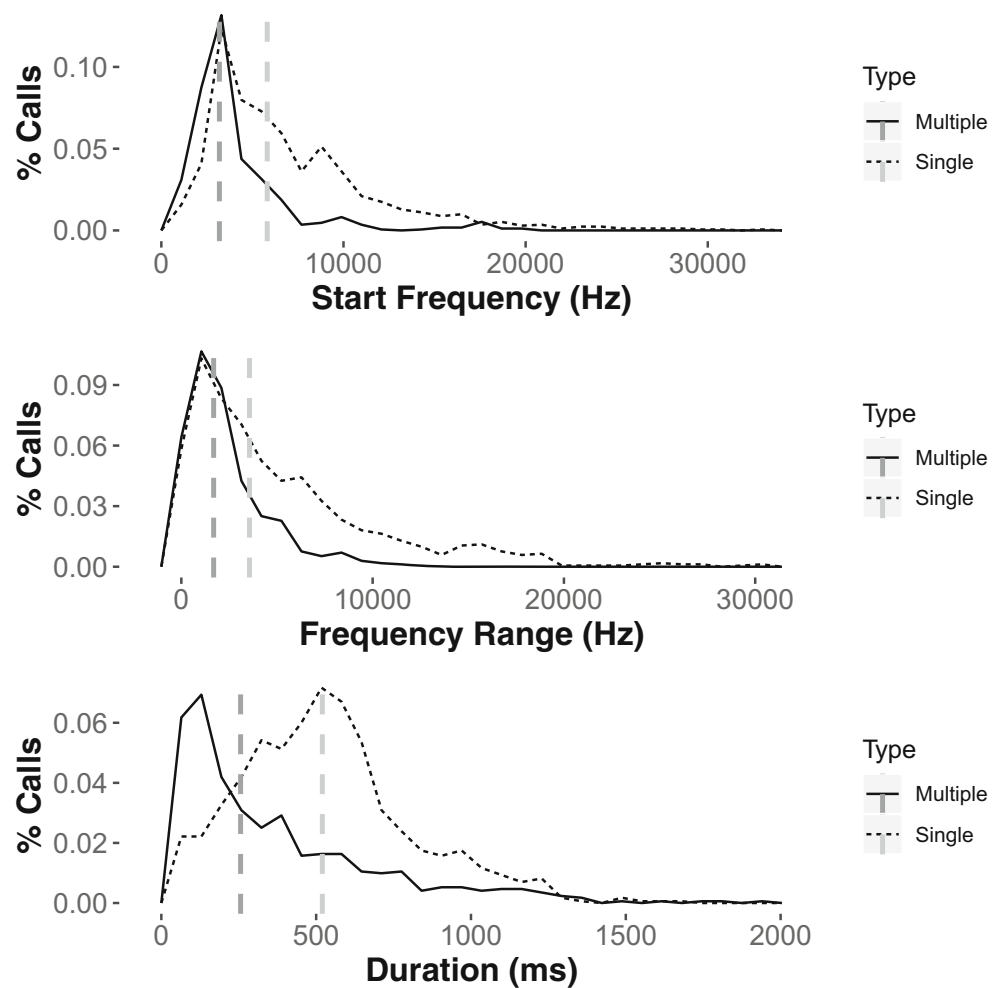
frequency and range of calls produced. This further indicates that Hawaiian short-finned pilot whales may use specific calls to communicate information, such as group identity in the presence of multiple groups. We found the greatest magnitude of differentiation in call duration, with shorter calls favored in multi-group encounters. It is possible that social clusters use shorter, simpler calls to maintain group cohesion when with other groups, as they may be easier to hear in acoustically complex settings. Social cohesion may also be important in other behavioral contexts, such as foraging, when short-finned pilot whales are known make social calls while diving (Jensen et al. 2011). Comparing calls in these contexts may improve our understanding of the types of calls and acoustic features that are used to maintain cohesion among social clusters.

Understanding acoustic population structure within a species, and its relationship with aspects such as social structure, genetic structure, and ecological variability, allows a more nuanced approach to species conservation and management – one that conserves the diversity and ecological resilience of a species, rather than simply its abundance. If acoustic dialects are a proxy for genetic diversity and ecological resilience, acoustic research could be used as a non-invasive tool for

the conservation and management of a species. Passive monitoring of social groups and their behaviorally dependent vocalizations would improve our understanding of local habitat use, providing a spatially and temporally explicit understanding of socially driven spatial ecology at a subspecies level.

Compliance with ethical standards

Conflict of interest   The authors declare that they have no conflict of interest.

Ethical approval   All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in this study were in accordance with the ethical standards of the institution or practice at which the studies were conducted. These data were collected under NMFS permit #15530 to RWB and WHOI Institutional Animal Care and Use Committee approval (BI15245.00).

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