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Acoustic behaviour of endangered Hawaiian false killer whales

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Understanding the acoustic communication of the endangered main Hawaiian Islands insular population of false killer whales (*Pseudorca crassidens*) is essential for effective management. In this study, biologging tags were deployed on four individuals, recording 26.2 h of acoustic data. A total of 5940 high-quality possible focal pulsed calls were analysed and 52 stereotyped call types were characterized. The fundamental frequency contour ranged from a mean minimum frequency of 7.22 ± 0.78 to 9.28 ± 0.80 kHz (mean maximum frequency) with a mean duration of 0.32 ± 0.08 s. Predominant call types and call rates across dive states varied by individual. Probability of calling was higher during the descent and bottom phase compared with the surface. Four types of nonlinear phenomena (NLP) were documented including biphonation (call + clicks, 78% of all NLP), secondary sidebands, chaos and frequency jumps. Frequency jumps were commonly produced by two animals from the same group (13–19%). Most calls contained NLP (80%). The average call rate recorded by the tags on two individuals was 17.5 calls m^{-1} (hourly average) and call rates decreased as swim speed increased. Our findings suggest high repertoire diversity and high signal complexity informing future passive acoustic monitoring efforts.

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1. Introduction

Social communication in marine mammals functions in maintaining group cohesion [1,2], reproduction [3], foraging [4,5], cooperative hunting [6], parental care [7] and establishing relationships/bonds between group members [8]. The social complexity hypothesis for communicative complexity (SCHCC) asserts that groups with more complex social systems require more complex communication to manage group dynamics [9]. Prior studies have provided evidence that some toothed whale species exhibit social complexity which translates to communication complexity as exhibited by the diversity of their acoustic repertoire (Araguaian river dolphin, *Inia araguaiaensis* [10]; pantropical spotted dolphin, *Stenella attenuata* [11]), presence of dialects (killer whale, *Orcinus orca* [12–15]; sperm whale *Physeter macrocephalus* [16–18]) and signals denoting individual identity (common bottlenose dolphin, *Tursiops truncatus* [19,20]). Toothed whales generally produce three types of acoustic signals which serve different functions: clicks, whistles and burst-pulse sounds. Short-duration, directional, broadband clicks can be used for communication [21–23] but are commonly used in echolocation, and function in foraging and navigation [24,25]. Whistles are narrow-band, frequency-modulated signals that function in communication [26]. Burst-pulse signals are composed of a series of pulses produced in such rapid succession as to sound tonal and also function in communication [27]. Pulsed calls are a variant of burst-pulse signals, containing a fundamental frequency contour and harmonics, and have been described as being the predominant signal produced by killer whales and pilot whales (*Globicephala* sp.) during socialization to establish social relationships, facilitate coordination and maintain group cohesion [27–30].

Mammals commonly produce vocalizations called nonlinear phenomena that are complex and contain nonlinear irregularities due to the dynamic nature of the way airflow interacts with sound generating tissues [31]. Nonlinear phenomena can enhance communication between conspecifics and may function in individual identification, emotional expression and mating [32]. Features include subharmonics, deterministic chaos, biphonation and frequency jumps [33]. Biphonation is caused by sound emitted from two pairs of phonic lips simultaneously which has been described for multiple species including killer whales [34–36], Atlantic spotted dolphins (*Stenella frontalis* [37,38]), common bottlenose dolphins [37,39,40], pilot whales (*Globicephala macrorhynchus* (short-finned) [29,41]; *Globicephala melas* (long-finned) [42,43]), short-beaked common dolphins (*Delphinus delphis* [44]), striped dolphins (*Stenella coeruleoalba* [45]), beluga whales (*Delphinapterus leucas* [46]) and Risso's dolphins (*Grampus griseus* [47]). Studies on delphinids demonstrated that each set of phonic lips can operate independently with clicks produced by the right pair of phonic lips and whistles produced by the left pair [48,49]. The prevalence of biphonation in stereotyped whistle contours indicates it may function in a social context in contact calls/signature whistles [38,45]. Killer whale calls can include multiple, successive components exemplifying an additional layer of complexity in these signals that species can produce [28,50].

False killer whales (*Pseudorca crassidens*) are a resident toothed whale species to Hawaiian waters. Three genetically differentiated, partially sympatric populations are recognized, including a main Hawaiian Islands (MHI) insular, northwestern Hawaiian Islands (NWHI) and an open-ocean (Hawaiʻi pelagic) population. The MHI insular population numbers less than 150 individuals and is endangered under the Endangered Species Act as of 2012 [51–53]. The MHI insular population consists of four recognized social clusters that are genetically differentiated and have varying habitat use and potentially differing diet composition [54–56]. False killer whales display complex grouping behaviour where individual subgroups (spread out greater than 5 km) comprise larger groups which can be spread out over 20 km [57,58].

The social organization of false killer whales more closely resembles the matrilineal structure of killer whales and pilot whales with groups composed of multiple matrilines, rather than a fission–fusion social organization observed in some other odontocetes [56,57,59]. Strong associations between individuals from photo-identification surveys spanning over 20 years indicate strong bonds among individuals around the Hawaiian Islands [56,57]. In Hawaiʻi , false killer whales primarily feed on large pelagic game fish and have been observed engaging in prey sharing between individuals [59] which is relatively rare in animals, and in cetaceans has been reported most often in killer whales [60]. A tendency to mass strand [59,61,62] in addition to cooperative hunting [63] provides further support for the presence of stable associations and bonds.

False killer whales can be easily discriminated acoustically from other odontocetes based on production of comparatively low-frequency (mean frequency 4.7–8.3 kHz) stereotyped whistles (4–5 kHz upsweep) and high vocal production rates [64–67]. This acoustic behaviour is likely attributable to false killer whale subgroup composition and likely functions in long-range communication necessary for maintaining communication and group cohesion/coordination between spatially distant subgroups. Limited published accounts of gradient-like, pulsed call production have been documented for this species [64,68] with more accounts of whistles reported [69–71]. Nonlinearity in false killer whale signals was first described by Murray *et al.* [64].

The use of biologging tags equipped with hydrophones has enabled the collection of high-resolution data to study marine mammal communication [72], ontogeny [73], foraging ecology [74], migration [75] and effects of potential stressors [76,77]. Additionally, acoustic cue (e.g. call, click) rates of individuals recorded from tags can inform passive acoustic animal density estimation, especially for cryptic and endangered species, vital for species conservation and management [78]. Multiple blackfish species have been tagged to characterize vocal repertoires [41], identify novel signals [79], describe foraging behaviour [80,81], provide social context of foraging [82,83] and quantify behavioural response to anthropogenic noise [84–87].

The goal of this study was to use non-invasive archival tag data to describe the acoustic behaviour of false killer whales in order to provide insight into the behavioural context of social signals. Our objectives included (i) classify and characterize the pulsed call repertoire of false killer whales; (ii) describe nonlinearity observed in calls; and (iii) analyse the relationship between social sounds recorded and diving behaviour. These findings can help elucidate fine-scale social context and provide foundational information to determine potential signal functions.

2. Material and methods

2.1. Data collection and fieldwork

Two suction cup tag types were used: digital acoustic recording tags (DTAG version 3) [88] and customized animal tracking solutions (CATS) tags [89]. Both tags were equipped with acoustic sensors to record sound production, a pressure sensor to record depth and a suite of inertial sensors to measure animal orientation and allow for fine-scale movement tracking. Tags were deployed by pole during multiple boat-based field efforts in 2011 (off Hawai‘i Island) and from 2023 to 2024 (off the islands of Maui and Lānaʻi) following tagging procedures described in Friedlaender *et al.* [90] and Wiley *et al.* [91] (figure 1). HTI-96 mini hydrophones (sampling rate 96 kHz, 16 bit resolution, flat frequency response from 2 Hz to 30 kHz) were integrated in the CATS tags with a hydrophone-specific sensitivity ranging from −169.4 to −170.2 re 1V μPa^{-1}. CATS tags were equipped with multiple inertial sensors including tri-axial accelerometers (sample rate (SR) 400 Hz), magnetometers (SR 50 Hz), gyroscopes (SR 50 Hz), a light sensor (LED headlight) and a high-resolution (2K) video camera. The LED headlights were set with a low-light trigger below the photic zone. Video was only collected for two animals, thus video footage was excluded from this analysis. However, it was used to verify feeding events when applicable. The DTAG sampled at 240 kHz with a nominal tag hydrophone sensitivity of –175 dB re 1 V μPa^{-1}. All tagged individuals were photographed, and population and cluster were identified based on comparison with photo-ID catalogues (methods described in Baird *et al.* [57]). The tagged animals’ ages were estimated based on methods described in Kratofil *et al.* [92].

2.2. Acoustic data processing

CATS tag acoustic recordings (.wav files) were segmented into 1 h files using Adobe Audition CC 2023 (Adobe Systems Inc.) for processing. Analysts identified possible focal (tagged) animal pulsed calls visually and aurally in Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics [93]) and manually identified calls from spectrograms (1024 fast Fourier transform (FFT), Hann window, 50% overlap) in a user-defined window preset. The selection tool was used in the waveform view to make two selections per call and position markers were modified as needed. The first selection only included the call and corresponding harmonics (x-axis selection borders aligned with the start and end time of the call and y-axis included the whole bandwidth). The second selection included a time buffer before the beginning of the call and after the end of the call. Selections for each call were exported from Raven as individual .wav files. Selection 1 (no buffer) was used for the signal-to-noise ratio (SNR) calculation and left box boundary considered the start time of the call. Selection 2 (with buffer) was exported as individual .wav files (16 bit) to enable extraction of the fundamental frequency

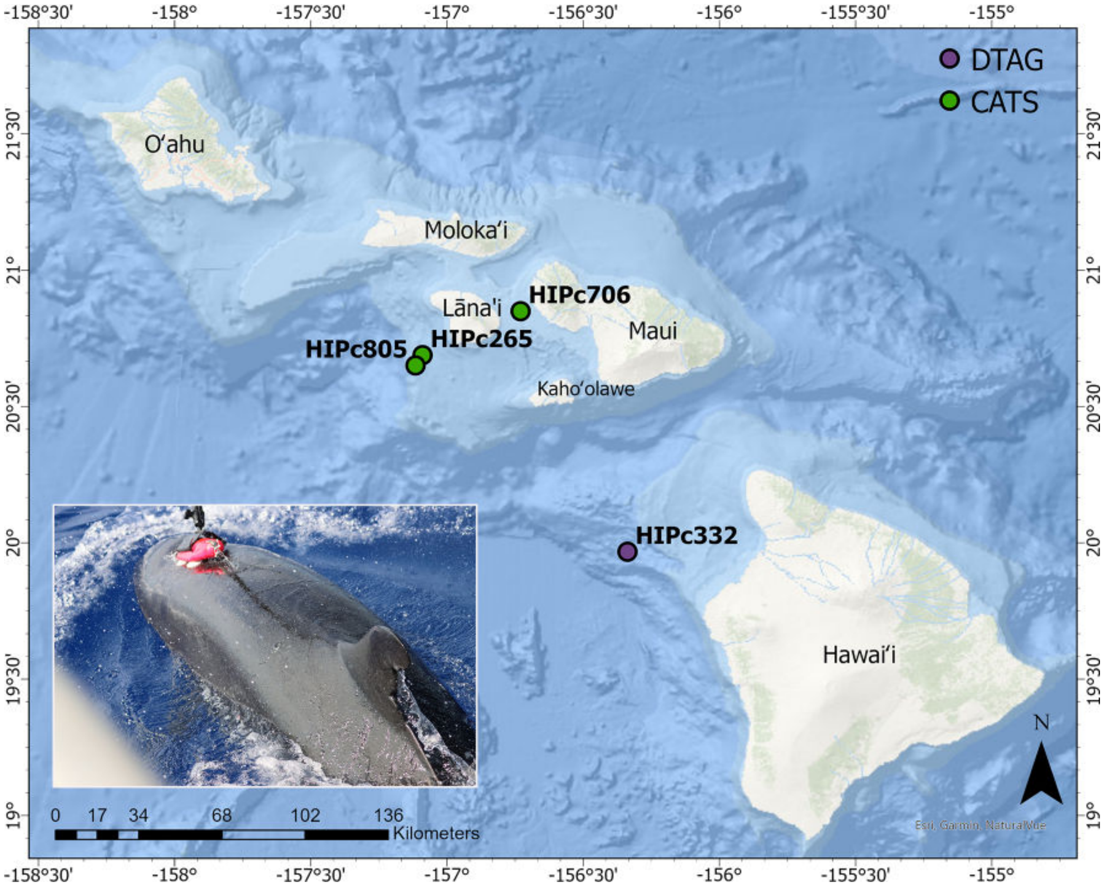

Figure 1. Map of the deployment locations for the CATS (green) and DTAG (purple) deployments off the main Hawaiian Islands, with individuals indicated by their designated catalogue ID numbers. Photo shows a suction cup custom animal tracking solutions (CATS) tag being deployed on a main Hawaiian Islands insular false killer whale off Lānaʻi island, Hawaiʻi. Photo taken under MMPA/NMFS permits nos. 27099 and 21476. Photo Credit: Grace Olson (Pacific Whale Foundation).

contour in a subsequent step. Due to lack of localization capabilities with one hydrophone, and our reliance on an SNR threshold method (detailed below) we take a conservative approach to focal animal call designation. High-quality calls recorded on the tags and likely produced by the focal animal are considered hereafter as 'possible focal calls' (PFC) since we cannot fully exclude the potential that signals may be produced by conspecifics.

Using the selection table annotation function, the following information was documented for each call based on a manual review: (i) identity of the caller (non-focal, PFC or unknown) based on the amplitude of the signal; (ii) presence of biphonation (presence/absence of clicks); (iii) presence of secondary sidebands [33]; (iv) occurrence of consecutive series of signals; (v) overlap between PFC and non-focal animal signals; (vi) presence of deterministic chaos [33]; and (vii) periods where audio cut out in the recording. All overlapping calls were omitted from further analyses as this prevented accurate calculation of the SNR. Calls containing audio cut-out periods (a by-product of the CATS tags sampling at a higher frequency) were also excluded from this analysis as this distorted the contour in the spectrogram, preventing proper classification of calls and accurate determination of the start/end times of calls. The call selection and annotation was completed by trained analysts and then reviewed and revised through the quality control process by an experienced analyst (B.C.M.).

2.3. Selection criteria for possible signals produced by the focal animal

PFC were delineated as produced by the focal animal in the manual analysis based on higher amplitude click energy in the low frequencies (15 kHz) [94,95] and the presence of high-amplitude harmonics. The SNR was calculated for each call identified as PFC or unknown in the annotation stage using custom-written scripts in MATLAB R2024b (Mathworks, Natick, MA). The signal clip was used from selection 1 (call only/no buffer). A representative noise clip was extracted for each deployment and used for all calculations as ambient noise levels were relatively consistent throughout the deployment.

Signals with unusually high ambient noise levels (e.g. after an animal surfaced) were excluded from the analysis so as to not artificially inflate SNR values. Hydrophone sensitivities of each tag varied, therefore a tag-specific SNR threshold was set to validate PFC. To calculate the SNR thresholds, a random subset of at least 100 signals was manually verified by an experienced analyst (B.C.M.) as PFC or non-focal, and the SNR was calculated with a high pass filter at 500 Hz to reduce flow noise. Plotted SNR values were visually inspected, and a threshold was defined based on a visual inspection of the graphs (Tag 1—27 dB, Tag 2—28 dB, Tag 3—29 dB, Tag 4—32 dB). PFC included in this analysis, likely representing a conservative subsample of calls produced by each animal as overlapping calls, indicative of the presence of multiple animals, were excluded, as well as calls produced right after a surfacing, due to SNR calculation limitations.

2.4. Identification of nonlinear phenomenon

Four types of nonlinear phenomena (NLP) were documented in this study. Deterministic chaos was identified as short-duration periods of non-random noise with energy surrounding the fundamental frequency and commonly reflected in the upper harmonics (figure 2a) [33,39,96]. Biphonation is considered the simultaneous production of two signal types [33,39,96]. In this study, biphonation was identified when a call and series of clicks or rasp (as defined in Pérez *et al.* [97]) were produced simultaneously and overlapped in time with the call with click onset starting milliseconds before or after the start time of the call (figure 2b). If there was uncertainty or ambiguity in the association between clicks and calls, the classification was left as 'no association' or 'unknown' and excluded from the biphonation category. Echolocation clicks were labelled as 'no association'. Frequency jumps (figure 2c) are discontinuities in the fundamental frequency call contour and the corresponding harmonics caused by abrupt shifts in frequency when the vibration rate of oscillating vocal tissues abruptly increases or decreases [33,39,96]. Secondary sidebands appear spectrally as shorter duration subharmonics that occur in evenly spaced intervals between the harmonics of the fundamental frequency contour (figure 2d). These subharmonics are fractional values (e.g. one-half, one-third) of the fundamental frequency and are caused by differences in the vibrating frequency of two oscillating sections of the sound production structures [33,39,96].

2.5. Call classification

An experienced analyst (B.C.M.) determined call classification types based on a visual review of the fundamental frequency contour. A minimum of three signals was required to be considered as a call type. Call type nomenclature was alphanumeric including the population designation (MHI), fundamental frequency contour (1–52; order arbitrary), and a numerical subscript (i) denoting a subtype which closely resembled the exemplar call but contained random energy in a portion of the call leading to a discontinuity in the overall trace [12]. A decimal value (e.g. 0.1, 0.2) indicated a call type that was composed of a successive, repetitious series of calls and the tenth decimal value denoted the specific call types comprising the overall call series. A call type with 99 appended to the end designated a variable category for that call type. Variable calls are considered non-stereotyped variants of the stereotyped call contour which enabled a conservative approach to call classification.

The fundamental frequency contour was traced from the spectrogram (SR 96 kHz, FFT size 1024, Hann window, 50% overlap, frequency resolution—93.46 Hz, time resolution—10.7 ms) of the CATS tag audio clips (selection 2 in Raven) using the real-time odontocete classification algorithm (ROCCA)[98] in the open-source software PAMGuard (version 2.02.03e; [99]). From individual traces, 50 temporal and frequency variables were measured. When more than 100 calls within a call type were present, only 100 randomly sampled calls were traced for that specific call type. A subset of the most common call types recorded on the DTAG were traced in ROCCA using the method detailed above and described (SR 240 kHz, FFT size 2048, Hann window, 50% overlap, frequency resolution—46.73 Hz, time resolution—21.40 ms). Given the difference in sampling rate, frequency and time resolution of spectrograms for each tag type, only relative comparisons between spectral and temporal features of calls were made and calls were categorized based on contour shape. PFC were categorized into one of six general contour shapes including ascending, descending, tonal, concave, sequence and frequency jumps. Ascending calls were characterized by having a lower start frequency than end frequency. Descending calls had a higher start frequency than end frequency. Tonal calls had a mean frequency range less than 50 Hz. Concave calls were characterized as having an inflection point. Sequence calls

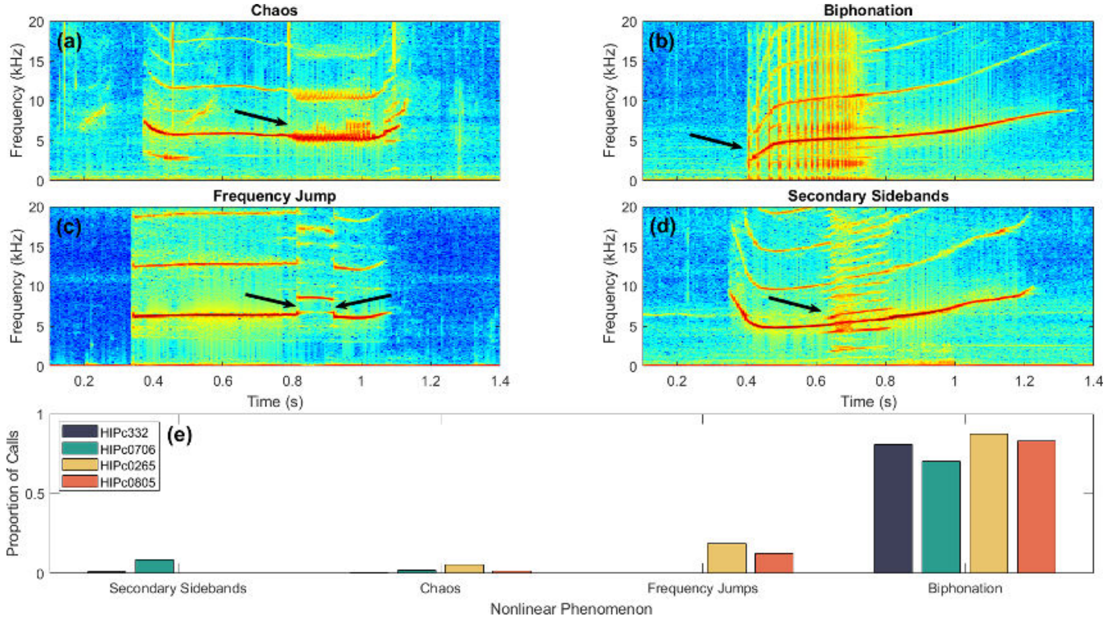

Figure 2. Nonlinear phenomena examples depicted in spectrograms (96 kHz sampling rate, FFT size 1024, Hann window, 50% overlap) including (a) chaos in a variable call, (b) biphonation in a MHI2 call, (c) frequency jumps in a MHI47 call, and (d) secondary sidebands in a MHI1 call. Arrows indicate locations of nonlinear phenomena. Panel (e) shows the occurrence of nonlinear phenomena produced by each tagged animal.

occurred in a repetitive series of multiple calls. Frequency jump calls contain the nonlinear phenomena frequency jumps detailed above. For calls with frequency jumps, alphabetical subscripts describe individual, successive components of the call. Calls in variable call types were not traced.

2.6. Inter-observer reliability test

To confirm the call categorization, a subset of 106 randomly selected PFC (two calls randomly selected from each call category) representing all call categories was given to three naive observers. Spectrograms were provided in a random order and observers were instructed to classify calls independently using the call catalogue as a reference based on (i) general call contour shape (ignoring clicks), (ii) contour modulation, (iii) relative duration, and (iv) number of components (e.g. frequency jumps). To test inter-observer reliability based on their scores, the Fleiss kappa (κ) statistic was calculated and standardized (−1 to 1 scale). Complete agreement between observers would result in a κ-statistic equal to 1, same agreement as expected by chance would result in a κ-statistic equal to 0, and less agreement than expected by chance would result in a negative κ-statistic value.

2.7. Inter-call interval

The inter-call interval (ICI) was calculated and averaged hourly for the most frequently produced PFC: MHI1 (for HIPc706) and MHI28 (HIPc805). Based on the signature identification (SIGID) method [100] that has been applied to false killer whale whistles [67], we tested if calls met the SIGID criteria with 75% of all whistles (calls in this study) in the category having an ICI of 1–10 s.

2.8. Kinematic data analysis

As part of the data processing procedure, sampling rates of all sensors (minus the acoustic recordings) were decimated to 10 Hz [101]. Five dive states were delineated: surface (0–2 m—Dive State 0), descent (Dive State 1), ascent (Dive State 2), shallow bottom phase (or dive depth less than 100 m—Dive State 3) and deep bottom phase (deeper dives greater than 100 m—Dive State 4) (methods described for pilot whales in Gough *et al.* [102]). The first and last negative-to-positive pitch changes occurring at greater than 85% of the maximal dive depth were used to delineate the boundaries between the descent, bottom and ascent phases. From inspection of depth data, 100 m was determined as the cut-off between deep dives, shallow dives and surface behaviour (based on Alves *et al.* [103]). Apart from one deep dive, all other dives recorded were shallow dives, considered the bottom phase (Dive State 3) hereafter, so the one dive in Dive State 4 was removed from the statistical analysis which excluded all calls produced at greater than 70 m depth. Synthesis of kinematic data with acoustic data was conducted using custom-written scripts in MATLAB R2024a (Mathworks, Natick, MA). Proportion of calls produced across each dive state accounted for total time spent in each dive state. Sampling rates for the tri-axial accelerometers were set at 400 Hz to assist with measurement of forward speed throughout the deployment using a regression of suction cup vibrational 'jiggle' and orientation-corrected depth rate, following methods outlined by Cade *et al.* [104]. High-quality PFC start times recorded on the tags were linked to the nearest time from the dive profile data which included dive state, speed and depth. DTAG kinematic data was unavailable so only CATS tag kinematic data was analysed in relation to the acoustic data. Due to the lack of representative 'night' tag data, a diel comparison was only conducted for the HIPc805 tag deployment which was deployed in the afternoon and spanned approximately 12.5 h.

2.9. Statistical analysis

2.9.1. Significance of call type occurrence

Chi-square analysis, conducted in MATLAB R2021a, was used to test whether the occurrence of PFC types recorded on each tag differed significantly across dive states from expected frequencies and accounted for time spent in each state. Chi-square tests were performed on specific dive states of interest compared with all other dive states. Statistical significance was based on $\propto = 0.05$.

2.9.2. Relationship between call rate and speed/depth

A negative binomial regression was performed in R (version 4.4.2) using the *glm.nb()* function in the *MASS* package (R Core Team [105]) to model the relationship between call rate (average calls per minute), average swim speed (m s^{-1}) and dive state. For dive states (0–3), the mode value was used; however, if two dive states occurred, each accounting for 40–60% of samples, the dive state was considered a transition dive state. A negative binomial distribution was selected after detecting overdispersion in the data. Call rates with zero values (minute bins with no calls) were removed as we were interested in assessing speed/dive state behaviour during calling only, which additionally prevented zero-inflation. The 'log' link was applied. Model selection was guided by the Akaike information criterion (AIC). First, to determine the appropriate functional form for the average swim speed predictor, models with increasing polynomial degrees (1–4) were fitted and compared using AIC. The polynomial form with the lowest AIC was retained. Next, full model structures were evaluated to assess the inclusion of predictor variables, including an interaction term between average swim speed and dive state, with AIC used to identify the best-fitting model. Model diagnostics were conducted to assess the adequacy of model assumptions. Deviance residuals were plotted against fitted values and visually inspected for evidence of heteroscedasticity and nonlinearity. Quantile–quantile (QQ) plots were also visually inspected. Pearson chi-square statistic including degrees of freedom and dispersion ratio was calculated to evaluate the goodness of fit. The p-value was evaluated to assess the significance of average speed and dive states. To confirm the dispersion assumption was met, the dispersion value calculated in the Pearson chi-square test was evaluated and the ratio of residual deviance to residual degrees of freedom for each model was calculated.

2.9.3. Relationship between presence/absence of calling and dive state

A generalized linear mixed model (GLMM) was fitted in R using the *glmmTMB()* function in the *glmmTMB* package to model the probability of high-quality PFC recorded on the tags as a function of dive state and time of day. GLMMs were fitted using a binomial family since the response variable was binary (0 = call absent, 1 = call present) and a 'logit' link function was applied. The original sampling rate was 10 samples per second; however, to be biologically relevant, time bins were averaged over larger time bins (greater than 1 s) since calls averaged 0.3 s in duration with the longest call being approximately 1 s in duration. A GLMM was used since both explanatory variables were categorical.

A 60 s time window was selected and values were averaged over those time periods. Time of day was partitioned into five categories (all times in Hawai‘i Standard Time (HST)) including night (20.00–05.59), morning (06.00–09.59), midday (10.00–13.59), afternoon (14.00–17.59), and evening (18.00–19.59). Dive state and depth variables were highly correlated since dive state was extracted based on depth so they were tested separately in models to assess performance. Time since tag on (hr) was correlated with time of day so only time of day was included in the model. Tag number (2–4) was considered the random effect because multiple data points were recorded for each tag which clustered data based on individual animal ID. GLMM residuals indicated autocorrelation, and models included an AR1 correlation structure to account for temporal dependence on an individual animal level (Time and TagNum) to reduce autocorrelation in the data. An observation-level random effect (OLRE) variable was included in the model to combat overdispersion.

The residuals of models were checked for autocorrelation with the *acf()* function from the *stats* package. A series of diagnostic tests were conducted to assess model fit. Plots were visually inspected including an autocorrelation function (ACD) plot of Pearson residuals, residuals compared with fitted values using the DHARMa package, and QQ plots. To check for overdispersion, the Kolmogorov–Smirnov test was conducted and the ratio of deviance to residual degrees of freedom was calculated. Binned residual plots were visually inspected to assess the relationship between average residuals and fitted values on the response scale as an alternative means of assessing fit given the binomial distribution of data. Plots of normalized residuals compared with fitted values were used to detect heteroscedasticity, while normality and uniformity were checked using QQ plots, and the autocorrelation function was plotted to determine if any residual autocorrelation was detected.

3. Results

3.1. General call statistics

The information reported in the subsequent results (§§3.1–3.4) and discussion (§4) sections refers to high-quality PFC that are likely produced by the focal animal but does not preclude the possibility of calls from nearby conspecifics. Therefore, the results should be interpreted as representative of the social group rather than individual-specific behaviour. All CATS tags (n = 3) were deployed on animals from social cluster 4 and the DTAG (n = 1) was deployed on one individual from cluster 3 (table 1). Tagged animals were estimated to be 11–28 years of age with 3M/1F although there is some uncertainty in the sex determination. A total of 26 hr 11 min 29 s of audio was recorded across the four tags. Cumulatively, 5940 PFC were identified in the recordings. A total of 52 call types were categorized (electronic supplementary material, figure S1). The DTAG tagged animal, HIPc332, produced 372 PFC (6% of total calls). HIPc332 produced call type MHI52 most frequently followed by call type MHI2 (figure 3a). The most PFC were recorded on two of the CATS tagged animals (HIPc706—40% of calls, n = 2372; HIPc265—2%, n = 113; HIPc805—52%, n = 3083). HIPc706 produced call type MHI1 most frequently followed by call type MHI15, MHI35, MHI7 and MHI2i (figure 3b). HIPc265 produced call type MHI28 and MHI10 most frequently followed by call type MHI48, MHI16 and MHI39 (figure 3c). HIPc805 produced call type MHI28 most frequently followed by call type MHI10, MHI39, MHI38 and MHI29 (figure 3d). The inter-observer reliability test conducted by three naive observers resulted in a Fleiss kappa statistic of 0.412 (Fleiss kappa statistic, $\kappa = 0.412$, $z = 1.61$, $p = 0.107$) reflecting a moderate level of agreement with the 52 call categories described.

Based on the tracing criteria detailed above, a subset of 2733 call segments (277–DTAG, 2456–CATS) were traced in ROCCA to extract parameters representative of all call types (electronic supplementary material, table S2). The most prevalent contour shape across call types was ascending (n = 18) in frequency followed by descending (n = 13), frequency jump (n = 12), sequence (n = 4), tonal (n = 3) and concave (n = 2) call types. Mean start and end frequency was 8.15 ± 0.77 kHz and 8.60 ± 0.86 kHz (CATS) and 5.79 ± 0.34 kHz and 7.78 ± 0.35 kHz (DTAG), respectively. Mean minimum and maximum frequency ranged from 7.22 ± 0.68 kHz to 9.28 ± 0.80 kHz (CATS) and 5.60 ± 0.24 to 7.78 ± 0.35 kHz (DTAG). The duration of call components was on average 0.32 ± 0.07 s (CATS) and 0.34 ± 0.05 s (DTAG). For call type MHI1 (produced only by HIPc706) ICI across all time bins exceeded the 10 s threshold with hourly means ranging from 14 to 257 s, progressively increasing with time from start of the deployment. For call type MHI28 (HIPc805), mean ICI of 81% of calls met the SIGID criteria and fell below the 10 s threshold for the first 3 h of the deployment (hour (Hr) 1—5.39 s; Hr 2—4.08 s; Hr 3—7.48 s) but then exceeded the 10 s threshold in subsequent hours (greater than 19.7 s ICI).

Table 1. Tag deployment information, life history details and social cluster assignment for tagged false killer whales.

tag type	deployment date	deployment latitude	deployment longitude	sampling rate (kHz)	tag #	tag on time (hh.mm.ss)	tag off time (hh.mm.ss)	recording duration (hh:mm:ss)	animal ID (PWF/CRC[b])	sex	age	social cluster
DTAG3	10/26/2011	19.96659	−156.33768	240	NA	08.20.00	unknown	04.34.06	NA/HIPc332	M[a]	11	3
CATS	2/15/2023	20.84943	−156.73	96	J1	14.26.43	03.50.00	07.51.48	150/HIPc706	M	13	4
CATS	10/01/24	20.64403	−157.11334	96	J1	14.37.29	15.33.35	01.22.52	102/HIPc265	F[a]	28	4
CATS	10/01/24	20.65028	−157.11572	96	J4	14.48.07	06.19.03	12.22.43	106/HIPc805	M	11	4

[a] Probable animal sex based on available data but assignment is still uncertain.

[b] Pacific Whale Foundation/Cascadia Research Collective

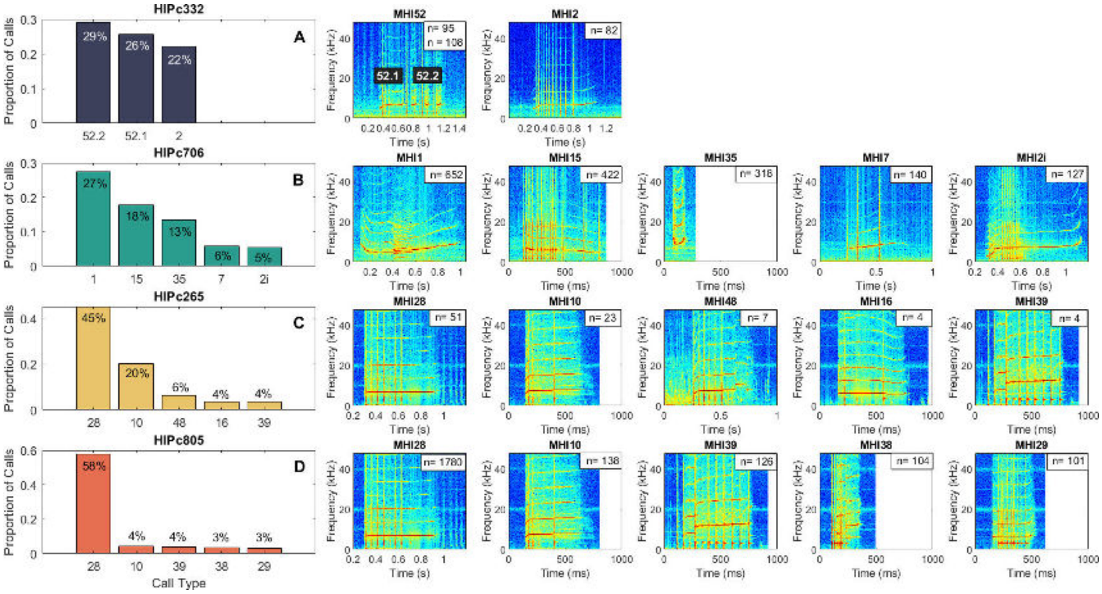

Figure 3. Predominant possible focal call (PFC) types produced by each tagged animal (DTAG–HIPc332; CATS–HIPc706, HIPc265, HIPc805). Panels (*a–d)* depict the proportion of calls for each of the most common calls. The panels on the right depict spectrograms (DTAG: 240 kHz sampling rate, FFT size 2048, Hann window, 50% overlap; CATS: 96 kHz sampling rate, FFT size 1024, Hann window, 50% overlap) for each corresponding call type. Percentage of total calls and sample size (*n*) is included for each call type.

Average PFC rates per minute were highest during the first 3 h of the deployment in the longer deployments (HIPc706 and HIPc805). Since the HIPc265 deployment was less than 1.5 h and primarily included a feeding event as observed in the video footage with higher uncertainty in PFC designation, it was excluded from this analysis. Mean PFC rate decreased with hours from start of the deployment for both HIPc706 (Hr 1—18 calls m^{-1}; Hr 2—12 calls m^{-1}; Hr 3—13 calls m^{-1}) and HIPc805 (Hr 1—28 calls m^{-1}; Hr 2—24 calls m^{-1}; Hr 3—10 calls m^{-1}). A diel call rate comparison was made for animal HIPc0805 which showed that more PFC were recorded during the day (2% of the daytime) than at night (0.03% of the night-time) proportional to the number of day/night hours recorded.

3.2. Nonlinear phenomena

Production of nonlinearity in PFC was persistent across all individuals and the majority of calls had at least one NLP type (80%). Percentages reported here represent the percentage of calls per deployment. Biphonation was the most common NLP present in PFC (HIPc332: 301 calls—81%, HIPC706: 1671 calls—71%, HIPc265: 99 calls—88%, HIPc805: 2558 calls—83%) (figure 2e). The onset of clicks associated with calls typically started prior to the start time of the call. The expert analyst (B.C.M.) observed overall shorter inter-click intervals for clicks associated with biphonation than inter-click interval for regular, echolocation clicks; however, these inter-click-interval values were not quantified. For HIPc332, secondary sidebands (4 calls—1%) and chaos (2 calls—0.5%) occurred in a very small percentage of PFC and no frequency jumps were documented. For HIPc706, secondary sidebands (209 calls—9%) was the second most common NLP followed by chaos (51 calls—2%) and frequency jumps (2 calls—0.01%). For HIPc265, frequency jumps (21 calls—19%) were the second most common NLP followed by chaos (6 calls—5%) and no secondary sidebands were documented. For HIPc805, frequency jumps (390 calls—13%) was the second most common NLP, followed by chaos (45 calls—1%) and secondary sidebands (13 calls—0.4%).

3.3. Acoustic behaviour related to dive state

Results are reported as (proportion of PFC/proportion of time in the respective dive state) and chi-square tests accounted for time spent in each dive state (figure 4a). The highest proportion of possible HIPc706 recorded calls were detected at the surface (33%/29%) followed by the descent (30%/21%), ascent (25%/26%) and bottom phase (11%/23%) (figure 4b). Call occurrence at the surface was significantly different from other dive states (Chi-square test: observed = 783 versus expected = 693.0;

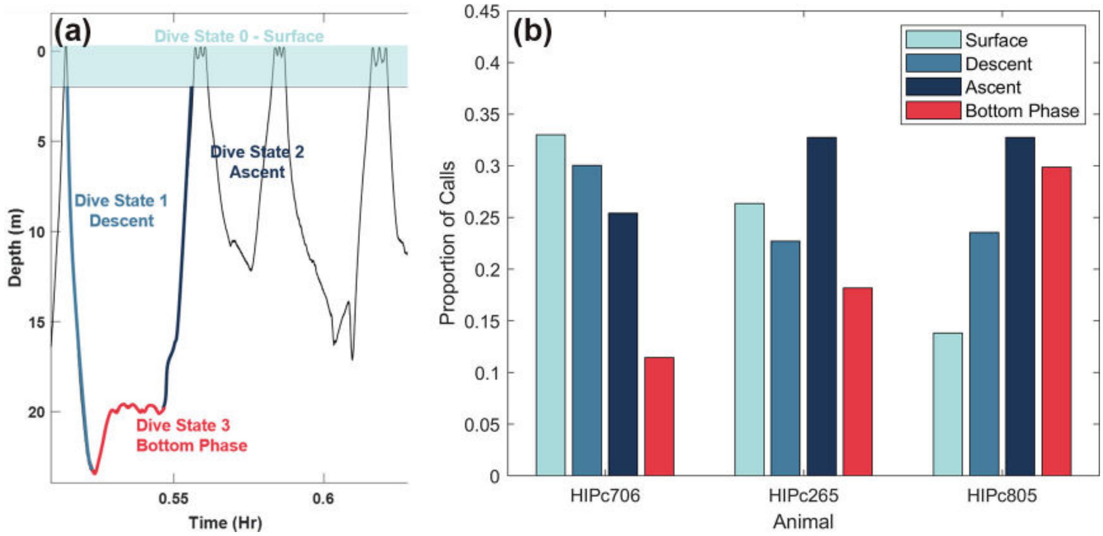

Figure 4. Possible focal call (PFC) production of each animal across the deployment. Panel (a) shows an illustration depicting the dive states including surface (dive state 0), descent (Dive State 1), ascent (Dive State 2) and bottom phase (Dive State 3). Surface includes waters from 0 to 2 m. Bottom phases were designated as dives less than 100 m. Call proportions for each CATS tagged animal are depicted in panel (b) across all dive states (0—light blue, 1—medium blue, 2—dark blue, 3—pink). Individual HIPc332 was excluded since DTAG kinematic data was unavailable.

$\chi^2(1) = 16.50$, $p < 0.001$). The highest proportion of HIPc265 PFC were detected during the ascent (32%/28%) followed by the surface (27%/30%), descent (23%/22%) and bottom phase (18%/19%) (figure 4b). Call occurrence during the ascent was higher than other dive states but did not differ significantly from other dive states (Chi-square test: observed = 36 versus expected = 31.3; $\chi^2(1) = 0.99$, $p = 0.32$). Similar to HIPc265, the highest proportion of HIPc805 PFC were detected during the ascent (33%/33%); however, the second most proportion of PFC were recorded during bottom phases (30%/26%), followed by the descent (24%/23%) and surface (14%/19%) (figure 4b). Call occurrence during the ascent was higher than other dive states but did not differ significantly from other dive states (Chi-square test: observed = 1010 versus expected = 1008.4; $\chi^2(1) = 0.00$, $p = 0.951$). The different distribution in proportion of PFC across dive states demonstrates that there is diversity in calls recorded with depth. Animals HIPc706 and HIPc805 were included in a more in-depth call type comparison across dive states since the majority of PFC (92%) were recorded by these animals. Call type MHI1 was the dominant PFC recorded by HIPc706, and occurred the highest proportion of time while at the surface (41%) and during the ascent (24%) (figure 5a). The detection of MHI1 significantly differed at the surface compared with other dive states (Chi-square test: observed = 323 versus expected = 190.5; $\chi^2(1) = 130.21$, $p < 0.001$). The second most common call type MHI15 was recorded more at the surface (21%) than the descent (17%), ascent (15%) or bottom phase (15%). Call type MHI35 was recorded in the highest proportions on the descent (21%) and ascent (18%). Across all dive states, the highest proportion of call type MHI28 recorded by HIPc805 occurred at the surface (67%), which significantly differed (Chi-square test: observed = 284 versus expected = 332.7; $\chi^2(1) = 8.77$, $p = 0.003$) from other dive states (descent—51%, ascent—60%, dive—56%) (figure 5b). In comparison, all other call types were recorded proportionally far less with less variability across dive states. There were large variable categories for each animal including PFC recorded only twice or those that did not match existing call types displaying the signal complexity and diversity of calls that are produced by false killer whales.

The mean swim speed (± s.d.) and range (min/max) for the three tagged individuals were as follows: HIPc706—1.51 ± 0.88 m s^{-1} (range: 0.66–7.18 m s^{-1}; 95% CI: 1.51–1.51 m s^{-1}), HIPc265—1.84 ± 0.79 m s^{-1} (range: 0.89–8.14 m s^{-1}; 95% CI: 1.83–1.85 m s^{-1}), and HIPc805—1.45 ± 0.76 m s^{-1} (range: 0.75–7.83 m s^{-1}; 95% CI: 1.45–1.45 m s^{-1}). The best negative binomial regression model for the relationship between calling rate (PFC min^{-1}), average speed (m s^{-1}) and dive state included both speed and dive state as predictors in the model. Residual deviance was 464.9 on 429 degrees of freedom and an AIC of 3072.9. The inclusion of an interaction term yielded a model with a higher AIC so this was excluded from the model. The model with degree 1 (AIC = 3066) for the average swim speed variable performed the best, which indicated a linear relationship. The optimal model accounted for overdispersion ($\theta = 1.412$, s.e. = 0.102) and passed all diagnostic tests of model fit. Average swim speed had a significant negative

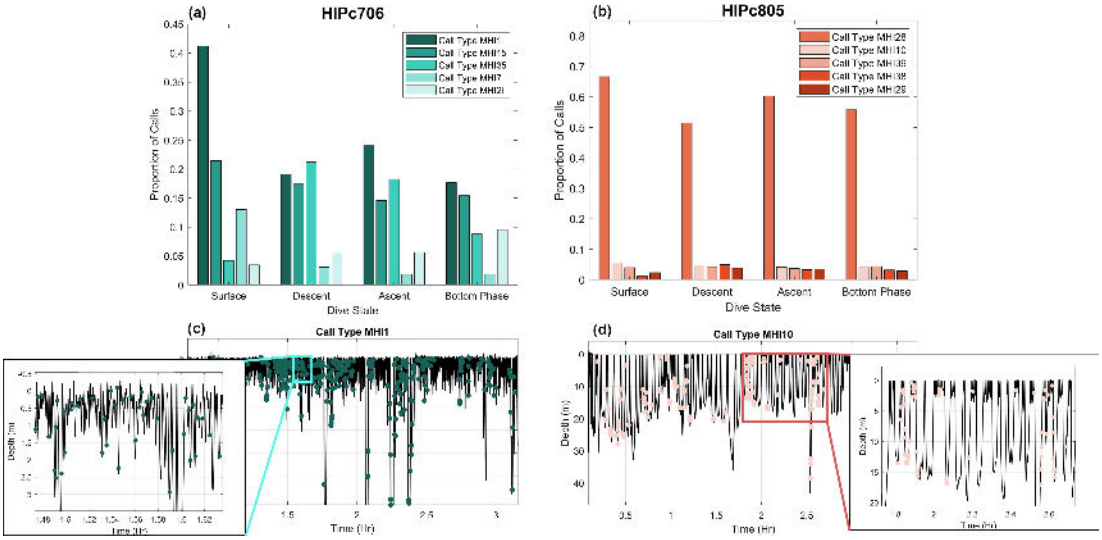

Figure 5. (a,c) Distribution of predominant possible focal call (PFC) types produced across dive states with each dot representing an individual call (0–3) for two tagged false killer whales (HIPc706 and HIPc805). Lower panels depict dive profiles for (c) call type MHI1 produced by HIPc706 and (d) call type MHI10 produced by HIPc805.

effect on call rate ($\beta = -0.209$, s.e. = 0.064, $z = -3.26$, $p < 0.001$) indicating that higher swim speeds were associated with a reduction in PFC recorded across all dive states (figure 6a; electronic supplementary material, table S3). With each one-unit (1 m s^{-1}) increase in swim speed expected, call rate decreased by 19% (Incidence Rate Ratio (IRR) = 0.81). Dive state moderately influenced call rates but was not significant ($p = 0.067$), with transition, descent and bottom phase exhibiting higher predicted call rates than other dive states (figure 6b; electronic supplementary material, table S3).

The best fit binomial GLMM model included the dive state and time of day explanatory variables, with the response evaluated in 60 s time bins, which helped reduce pseudoreplication and autocorrelation. At this resolution, a total of 1727 observations were included from CATS tag deployments. Swim speed did not significantly influence R^2 and the models with swim speed included produced a lower marginal R^2, so this variable was also excluded from the model. Dive state and time of day were ultimately the two explanatory terms included in the most parsimonious model (AIC: 823.2). Fixed effects explained 70% (marginal $R^2 = 0.698$) of the variation in the probability of calling. Conditional R^2 was unable to be calculated due to the incorporation of the autocorrelation structure. Tag number was considered a random effect and these results indicated moderate between-individual variability (variance = 0.151, s.d. = 0.39). Time and tag number were added in the autocorrelation structure. All diagnostic tests supported the best fit model and met all assumptions with no overdispersion, residual autocorrelation (electronic supplementary material, table S4) or patterns in residuals.

Results showed that most dive states were strong predictors of the probability of recording PFC and descent ($\beta = 0.81$, s.e. = 0.29, $p = 0.006$), ascent ($\beta = 0.78$, s.e. = 0.26, $p = 0.003$), bottom phase ($\beta = 1.46$, s.e. = 0.34, $p < 0.001$) and transition ($\beta = 1.14$, s.e. = 0.35, $p = 0.001$) dive states were associated with a statistically significant higher probability of calling compared with the reference (surface) (figure 7; electronic supplementary material, table S5). The highest effect was during the bottom phase and descent suggesting animals were more likely to call during these phases (figure 7). The odds of calling were approximately 2.18 higher in the descent phase and 4.29 times higher in the bottom phase state compared with the surface. Calling probability (logit scale) was significantly reduced in the evening and night periods compared with the reference (afternoon) (figure 7). The caveat is that most data were collected in the afternoon period which likely influenced the temporal results. Additionally, the deployment duration for animal HIPc805 was the longest and this animal produced a high percentage of total PFC so the behaviour of this animal likely influenced model predictions.

3.4. Recordings during prey sharing activity

During 2024, the crew observed false killer whales engaged in prey sharing during a feeding event. We captured recordings from two of the tagged animals (HIPc265 and HIPc805) participating in the prey sharing at the time they were tagged, as confirmed during a focal follow of the tagged individuals.

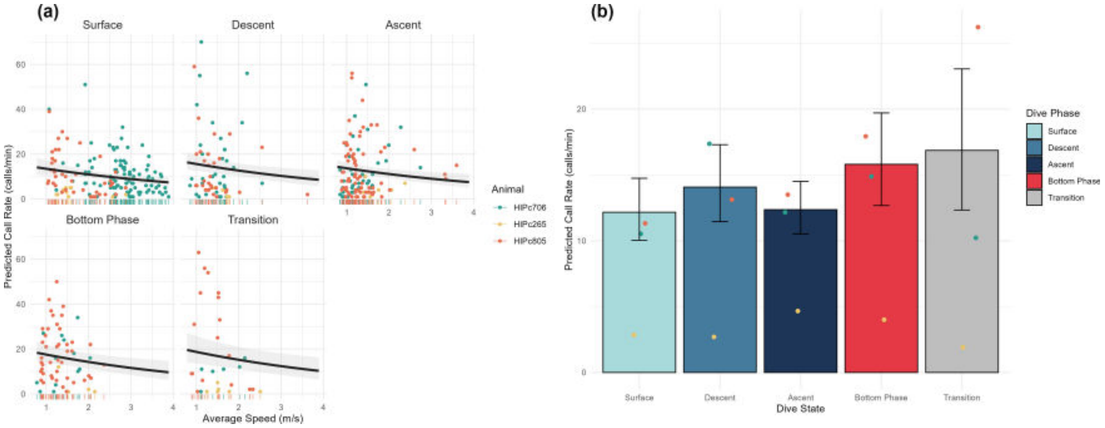

Figure 6. Relationship between (a) predicted mean possible focal call (PFC) rate (calls min^{-1}) and average speed (m s^{-1}) for each dive state including rug plots representing the distribution of data points and (b) predicted mean call rate across dive state (surface—light blue; descent—medium blue, ascent—dark blue; bottom phase—pink) based on the negative binomial regression. Colour indicates animal (green—HIPc706; yellow—HIPc265; HIPc805—orange).

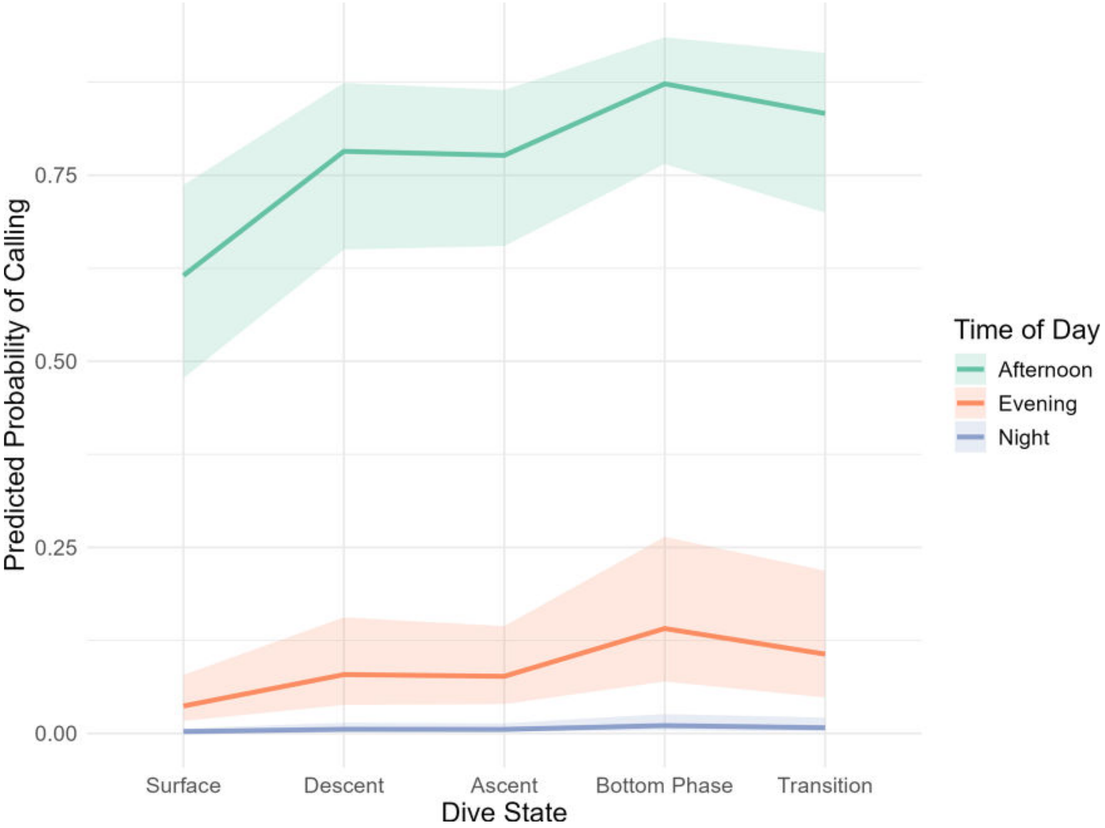

Figure 7. Predicted probability of possible focal calls (PFC) recorded by dive state based on the GLMM best fit model. Explanatory variables include dive state, time of day (green—afternoon, orange—evening, purple—night) and individual animal as a random effect. Shaded regions indicate confidence intervals.

Animals were feeding on wahoo (ono *Acanthocybium solandri*) with an approximate size of 0.6–0.9 m. (J.J.C., personal observations, 2025). Due to signal overlap and the close proximity of conspecifics, these periods in the recording were often too acoustically chaotic to distinguish the PFC from non-focal calls. Therefore, many of these periods of active feeding were omitted from the analysis. However, on a broad scale, during a prey sharing event, a unique acoustic behaviour was observed where animals produced longer duration, higher frequency, modulated signals (figure 8) than typical calls produced by these animals (electronic supplementary material, figure S1 for reference). These signals were produced multiple times and were dissimilar to most stereotypical calls produced by animals in this study.

4. Discussion

This study provides high-resolution insight into the acoustic behaviour of the endangered false killer whale population in Hawaiian waters by describing previously unreported pulsed call repertoires, call diversity, acoustic complexity and calling in relation to dive behaviour. False killer whale social signals have most commonly been described in the literature as whistles [67,69,70]. Murray *et al.* [64] was the first to describe false killer whale signals as pulsed in nature. MacIver [68] reported whistles included click to burst-pulse gradient components with the 'burst-pulse whistle' referenced most closely resembling the calls recorded in our study. Our study shows that pulsed calls were the predominant sound type produced. The term 'pulsed calls' has been used to reference discrete, repetitious vocalizations produced by killer whales [28,106,107] and pilot whales [108,109]. Pulsed calls are the most common vocal type produced by killer whales and typically occur during foraging and activities when pod members are widely dispersed, so are likely used to maintain group cohesion [12]. This is likely also true for false killer whales that travel in spatially distant subgroups that may rely on pulsed calls to maintain group cohesion and contact [57,58]. The lack of accounts of pulsed calls described in the literature is likely attributed to the distances animals typically are from the recorders during passive acoustic monitoring (PAM). The low-frequency fundamental frequency contour, which propagates farthest, may appear whistle-like spectrally if lacking higher frequency sidebands to provide more context. In addition, both previous studies that recorded pulsed components of calls produced by this species had hydrophones in close proximity to the animals (via tag or captive environment) [64,68]. Tag data record very high-quality signals which capture both the full fundamental frequency contour as well as corresponding harmonics and biphonation to capture the pulsed nature and complexity of these signals. However, tag placement posterior to the sound production site may influence the number of harmonics recorded [110] and/or affect higher frequency components of certain calls [76].

This study highlights the diversity in call types produced by MHI insular false killer whales. Previous studies have described false killer whale whistles as stereotyped, tonal, low-frequency signals relative to other odontocetes with less frequency modulation (containing few inflection points) and a narrow frequency range [66]. These temporally and spectrally distinct signals allow false killer whales to be detected and classified to species with higher certainty in Hawai'i [70]. However, despite their previously described repetitious, stereotypic nature, this study demonstrates that diversity in repertoire composition is much more extensive than previously reported. Although two animals in this study predominantly produced tonal signals (call type MHI28) that minimally varied in frequency (mean frequency range less than 50 Hz), the classification of over 50 call types exemplifies the complexity of sound production possible for this species despite the low sample size (n = 4 animals). Previous work by Rio & Rosales-Nanduca [67], provided evidence of eight possible stereotyped whistle types produced by false killer whales in the Gulf of California from a dipping hydrophone close to the animals. Acoustic tags provide high-quality signals compared with other passive acoustic recording systems—mainly due to the close proximity of the hydrophone to the sound generating structures in the head—with the caveat that signal quality may fluctuate if recorded off-axis. MacIver [68] used DTAGs to classify 40 predominant whistle categories and 29 shared whistle categories between individuals from false killer whales in the Bahamas. In this study, multiple call types were recorded on different tags, indicating potentially shared call types among individuals. Notably, call type MHI28 and MHI10 were both the most common call types produced by HIPc265 and HIPc805, which were tagged from the same group on the same day. Due to the small sample size of possible HIPc265 calls (n = 113), it is difficult to make an in-depth repertoire comparison to potentially suggest confirmed shared call types. In the CATs tag data, for a subset of call categories (e.g. call MHI1), there was a short-duration signal (mean less than 0.03 ± 0.08 s) that commonly occurred before and/or after the primary fundamental frequency contour. Due to the variability in production rate of these components, they did not influence call classification. Although the function of these short-duration segments is unknown, these components add an additional level of signal complexity that should be explored in the future. Conversely, there may be no function to these signals as they may be an artefact of sound production or the recording due to the location of the tag and directionality of calls.

We compared our call parameter results with whistles recorded from several false killer whale populations in the eastern tropical Pacific (Costa Rica [65]; Mexico [67], ETP [66]), western Atlantic (Grenada [65]) and the main Hawaiian Islands [69]. Due to the limited availability of pulsed call accounts in the literature, we compared our signals with published whistle descriptions as a point of acoustic reference. Overall, the mean minimum (7.22 ± 0.68 kHz) and maximum (9.28 ± 0.79 kHz)

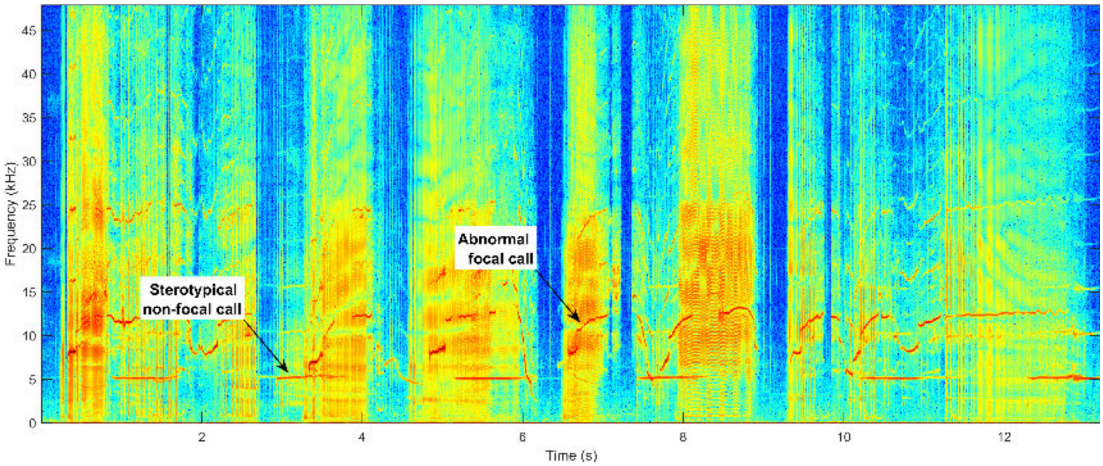

Figure 8. Example of unique signals recorded during a prey sharing event from a spectrogram (96 kHz sampling rate, FFT size 1024, Hann window, 50% overlap).

frequency range of calls recorded from CATS tags in this study was higher than other locations. However, it is difficult to compare across studies due to variation in sampling rates and equipment used. Therefore, we compared our calls with whistles recorded from a towed array and traced using the same method in ROCCA on the same population of MHI insular false killer whales from Barkley *et al.* [69]. Overall, our average CATS tag values for min/max frequency and frequency range were still higher by 2.48 kHz (max frequency), 1.56 kHz (min frequency) and 1.07 kHz (frequency range). DTAG max frequency and frequency range were also higher by 0.98 kHz and 1.18 kHz, respectively. However, the mean duration for both CATS (0.32 ± 0.08 s) and DTAG (0.34 ± 0.05 s) signals was comparable to those reported by Barkley *et al.* [69] (0.39 ± 0.17 s) as opposed to other studies which reported durations from 0.4 to 0.77 s [65–67]. The higher frequencies recorded in this study may be due to various factors related to differences in data collection between towed arrays and tags. The energy in the higher frequencies of pulsed calls recorded from towed arrays changes based on the animal's movement towards or away from the array [111]. Additionally, the depth range of the towed array remained relatively consistent (4–10 m) in comparison with the variable depth of the tagged animals, adding an additional confounding factor of depth that could affect signal characteristics.

We observed a significant decrease in PFC rate as tag deployments progressed, a result that was also reported by MacIver [68] for two false killer whales tagged with DTAGs in the Bahamas. Given that the tags used in this study are only attached with suction cups, slippage down the length of the body and away from the head may explain the progressive decrease in call rates and difficulty in identifying PFC based on SNR. Alternatively, the reduction in calls recorded may also be a by-product of animals being sighted and therefore tagged in high-activity states corresponding with high calling rates and then as animals transition out of a high-activity state to a low-activity state they call less. This call rate pattern may also be a by-product of the tagging event or time of day. A diel comparison was conducted for one animal (HIPc805) which found that calls were more likely to be produced during the day than at night. Similarly, Kratofil *et al.* [112] reported much higher rates of deep (greater than 50 m), long-duration dives during the day than at night for satellite-tagged individuals from the same population, suggesting reduced diving activity at night. Call rates reported here are conservative given that we excluded all overlapping calls and calls with high ambient noise levels so as not to bias SNR values. We were also unable to use localization to confirm PFC when conspecifics were in close proximity to the tagged animal since the CATS tags only contained one hydrophone. Therefore, these reported rates should be considered a lower limit and not an absolute value. PFC rates derived from this work may help inform studies aiming to improve acoustic density estimation and examining false killer whale behaviour as related to fishing activity and other human interactions.

While we recognize that the low sample size limits our ability to identify the presence of group-specific dialects, due to the occurrence of repetitious, dominant call types produced by individuals, we were interested in exploring whether these calls may be signature-whistle-like in nature and serve as an individual identifier. For example, call types MHI1 and MHI28 were predominantly produced by HIPc706 and HIPc805, respectively. Many blackfish species produce repeated call types (melon-headed whales *Peponocephala electra* [113]; pilot whales [29,43]), which possibly function in individual or group identification, maintaining contact when spatially distant and enabling the receiver to localize calling conspecifics [43]. Signature whistles are produced in fusion–fission societies (e.g. bottlenose dolphins) where individuals use unique identifiers to be distinguishable especially when separated from conspecifics [19,20]. By contrast to the fluid fusion–fission societies, stable matrilineal societies, like killer whales and sperm whales, produce group-specific identification calls that can comprise dialects [13,17,28]. Both signature whistles and dialects develop through vocal learning [14,20,114]. Prior studies have shown through photo identification and genetic analyses that false killer whales appear to have a stable, matrilineal society [56,63]. Rio & Rosales-Nanduca [67] identified possible signature whistles produced by false killer whales that constituted 31% of whistles recorded, a lower rate than the 38–70% signature whistle rate for bottlenose dolphins [115]. The data from this study indicate that none of the predominant calls produced met the criteria of SIGID [100] to be defined as signature-like calls except for in the first 3 h of the deployment for one animal (HIPc805). Therefore, it remains unclear if false killer whales produce calls that function as an individual identifier or if call types are indicative of cluster specific repertoires.

This study provided a comprehensive report on acoustic nonlinearities in false killer whale calls. Murray *et al.* [64] and MacIver [68] reported biphonic calls produced by captive and wild false killer whales in the Bahamas, respectively. Biphonation is the most widespread NLP in mammalian vocalizations and has been documented to occur in terrestrial (dhole *Cuon alpinus* [116]; Asian elephant *Elephas maximus* [117]; chimpanzee *Pan troglodytes* [96]) and marine species (common bottlenose dolphin [39], killer whale [33,118], short-beaked common dolphin [44], humpback whale *Megaptera novaeangliae* [119], bowhead whale *Balaena mysticetus* [120], humpback dolphin *Sousa plumbea* [121]). Similarly to the biphonation rates in this study (78% of calls), killer whales have been also documented to have high biphonation rates comprising up to 89% of calls [33,118]. Biphonation in killer whales was found to be more prevalent when multiple groups were present [118]. Previous studies have shown that biphonation likely functions in individual discrimination by increasing signal complexity and decreasing sound attenuation, further supporting the potential function of biphonation for individual recognition when spatially distant [122]. It remains unclear whether biphonation produced by these animals functions in short- or long-distance communication between conspecifics. Clicks are directional and although they do not typically function in long-distance communication, Sportelli *et al.* [39] postulated that highly directional clicks produced simultaneously to whistles potentially amplify the energy of omnidirectional whistles towards the intended receiver(s), which may help propagate energy further. This type of biphonation may facilitate long-distance communication. Alternatively, the use of clicks in these biphonic calls may also function in short-distance communication among conspecifics as clicks are directional and higher frequencies attenuate more across greater ranges. Future studies with multiple tagged animals in a group or an experimental design including a hydrophone array configuration for localization, may enable calculation of the response latency between caller/receiver and prevalence of NLP to derive the potential function of these signals.

Frequency jumps were overall the second most common NLP produced by the individuals in this study. Species like the short-beaked common dolphin [44] have been reported to produce frequent frequency jumps. Although there is little literature on the occurrence of frequency jumps in blackfish, sonar mimicry [87] was reported for three blackfish species (pilot whales, melon-headed whales and false killer whales) which described these shifts in frequency as a response to mid-frequency active (MFA) sonar produced in the area. Although no anthropogenic sonar was recorded on our tags, the two animals tagged in 2024 both produced calls with frequency jumps resembling the MFA-like sonar mimicry described in DeRuiter *et al.* [87]. This feature should be explored in the future to assess the functionality and social context of these signals. The occurrence of relatively abnormal vocalizations during a prey sharing event suggests the unique calls may be shared by individuals in the group and disseminate important information during feeding/prey sharing. Future work may benefit from leveraging new tools to focus on calling behaviour during feeding events and associated occurrences of prey sharing in these data. These subsequent findings may provide more evidence in support of calls associated with prey sharing with important implications for PAM efforts and bioenergetic modelling.

Our understanding of diving behaviour in respect to social call production is limited for blackfish species, and it can be difficult to make comparisons across studies given differences in dive state definitions and behaviour for species that occupy different ecological niches. Calls recorded in this study decreased with an increase in speed. This could be due to energy limitations of calling while swimming faster, or could be a by-product of the recording where higher speeds induce more flow noise at the tag hydrophones, which may decrease the SNR of signals, reducing the likelihood they are classified as PFC [97]. Alternatively, when animals are swimming faster, they may decrease calling rates in order to listen for calling conspecifics in the area as they are commonly observed increasing high speed travel before joining another distant individual or subgroup (R.W.B., personal observations, 2025). In this study, an overall increase in PFC with progressive dive states was observed. Dive state results may have been largely influenced by one animal (HIPc805), which produced the most overall PFC given that inter-tag variability was significant and explained the majority of the variance. Studies on tagged pilot whales have shown that call production generally decreases with depth [82,97]. However, an increase in pilot whale calling was observed in the descent [123] and ascent phases [82,123], with call types (non-inflection versus inflection) varying by dive state [123], similar to what was observed in this study, where predicted call rates were higher in the descent but differed since predicted call rates were higher in the bottom phase. However, considering that pilot whales behave very differently from false killer whales and the difference in dive scales in our study (0–30 m for false killer whales; 0–900 m for pilot whales), limited comparisons can be made. Additionally, the probability of recording PFC in this study was low across most dive states and, given the significant inter-tag variability, the influence of PFC recorded on individual tags likely strongly influenced our results. Due to the small number of individuals and inability to localize or leverage accelerometer data to confirm sound production, it is difficult to reveal larger patterns, therefore future work may provide valuable information for the context of false killer whale social calling in respect to diving behaviour. False killer whales are known to dive much deeper than recorded in our study, occasionally over 1000 m [112], and their calling behaviour on deeper dives remains unknown.

Given the challenges of tagging MHI insular false killer whales (e.g. low abundance, unique subgroup composition/distribution, high-speed travel behaviour, occasional boat avoidance) our sample size is small. This limits our ability to make social cluster comparisons, especially with only one representative animal from cluster 3 (HIPc332). Due to the uncertainty in sex, we were similarly unable to make comparisons between males and females. Future data collection may support diel patterns in calling rates along with evidence for potential differences in sex, social cluster and time of day. While clicks were not the focus of this study, we acknowledge that a more in-depth click analysis would be interesting to assess the potential functionality of these clicks for communication and in the context of NLP. Due to a lack of usable video, behavioural observations were limited and therefore unable to inform behavioural states and foraging behaviour. Improvement in tag design will provide more opportunities for further in-depth analysis. Given our ability to calculate the relative amplitude of signals, future work could include deriving source levels of signals from calibrated hydrophones if the distance between the recorder and blowhole is known for focal animals. For signals produced by non-focal animals, video footage may be able to indicate animal range opportunistically for a subset of calls from vocalizing animals in camera view. In order to better understand the behaviour of false killer whales, future work deriving source levels may provide insight into animal perception of signals they are hearing in their environment and information transmitted to intended receivers.

5. Conclusion

This study provides important acoustic and behavioural data obtained from archival tags on an endangered population of false killer whales in the MHI. Significant data gaps exist for false killer whale vocal repertoire characterization in Hawai‘i. This study highlights the acoustic complexity of MHI insular false killer whales as evidenced by the diversity in call types and presence of nonlinear phenomena. Although some call types were shared across individuals, the occurrence of calling and predominance of different call types across dive states shows the individual-level variability in acoustic behaviour over short temporal scales. Given the multitude of anthropogenic stressors faced by endangered MHI insular false killer whales, it is important to better understand their communication and acoustic behaviour during their dive cycle to improve PAM of this rare population. This study contributes valuable information to PAM efforts in this region which have sought to use PAM to improve towed array monitoring efforts for abundance estimation. These tagged individuals provide important foundational information which contributes to our future understanding of social structure, vocal learning and the individual recognition mechanism of this species.

Ethics. Animal research was conducted under the authorization of the National Oceanic and Atmospheric Administration National Marine Fisheries Service/ Marine Mammal Protection Act permit nos. 21476, 15330, and 27099 and the Institutional Animal Care and Use Committees of the University of Hawai‘i at Mānoa (approved protocol no. 18-2971-5) and Cascadia Research Collective.

Data accessibility. Data and relevant code for this research work have been archived within a Dryad repository [124].

Supplementary material is available online [125].

Declaration of AI use. AI was used to assist in writing code for the analysis.

Authors' contributions. B.C.M.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; W.T.G.: conceptualization, data curation, formal analysis, investigation, methodology, writing—review and editing; J.J.C.: data curation, formal analysis funding acquisition, investigation, methodology, project administration, resources, writing—review and editing; L.B.: funding acquisition, project administration, resources, supervision, writing—review and editing; A.H.: data curation, investigation, writing—review and editing; R.W.B.: data curation, investigation, writing—review and editing; T.A.M.: data curation, investigation, writing—review and editing; A.P.: funding acquisition, investigation, methodology, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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