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# Biogeographic patterns of Pacific white-sided dolphins based on long-term passive acoustic records

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## Abstract

**Aim:** This study investigates the biogeographic patterns of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in the Eastern North Pacific based on long-term passive acoustic records. We aim to elucidate the ecological and behavioural significance of distinct echolocation click types and their implications for population delineation, geographic distribution, environmental adaptation and management.

**Location:** Eastern North Pacific Ocean.

**Time Period:** 2005–2021.

**Major Taxa Studied:** Pacific white-sided dolphin.

**Methods:** Over 50 cumulative years of passive acoustic monitoring (PAM) data from 14 locations were analyzed using a deep neural network to classify two distinct Pacific white-sided dolphin echolocation click types. The study assessed spatial, diel, seasonal and interannual patterns of the two click types, correlating them with major environmental drivers such as the El Niño Southern Oscillation and the North Pacific Gyre Oscillation, and modeling long-term spatial-seasonal patterns.

**Results:** Distinct spatial, diel and seasonal patterns were observed for each click type. Significant biogeographical shifts in presence were observed following the 2014–2016 marine heatwave event.

**Main Conclusions:** Distinct spatial distributions of the two click types support the hypothesis that Pacific white-sided dolphins produce population-specific echolocation clicks. Seasonal and diel patterns suggest spatiotemporal niche partitioning between the populations in Southern California. Interannual changes, notably initiated during the 2014–2016 marine heatwave, indicate climate-driven range expansions and contractions related to gradual tropicalization of the Southern California Bight.

KEYWORDS
acoustics, biogeography, echolocation, machine learning, niche partitioning, Pacific white-sided dolphin, population dynamics, range expansion

## 1 | INTRODUCTION

Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) are small pelagic delphinids endemic to the eastern and western North Pacific Ocean (Walker et al., 1986). From east to west their distribution ranges as far south as the Gulf of California, up to the Gulf of Alaska, across to the Sea of Okhotsk and down into the East China Sea (Hayano et al., 2004; Leatherwood et al., 1984; Walker et al., 1986). Multiple genetically and morphologically distinct populations exist throughout the Pacific white-sided dolphins' geographic range (Hayano et al., 2004; Lux et al., 1997; Walker et al., 1986). However, as is true for many cetacean populations, understanding of gene flow, population dynamics and geographic overlap has been limited by survey effort and data processing capacity and technology.

In the Eastern North Pacific, at least two Pacific white-sided dolphin populations occur along the west coast of North America (Walker et al., 1986). Walker et al. (1986) observed that animal crania recovered off the coast of Baja California (below 32° N) were markedly different in shape and size than those recovered north of 37° N. In the Southern California Bight, between 32°3′ N and 34°3′ N, they observed significant variability in cranial morphometrics. Taken together, Walker et al. (1986) interpreted these results as evidence of two morphometrically distinct populations: with a southern form occupying Southern California and Baja, and a northern form occupying central and northern California, Oregon and Washington (CA/OR/WA population), with the Southern California Bight being a region of overlap between the two. Additionally, Lux et al. (1997) examined genetic samples from four regions including Baja California, the U.S. West Coast, British Columbia and Alaska and offshore waters of the North Pacific. Their findings revealed genotypic distinctions between each region, suggesting that four populations may exist across the eastern North Pacific (Lux et al., 1997). Lastly, Soldevilla et al. (2008) hypothesized that the Southern California/Baja form and California/Oregon/Washington form described by Walker et al. (1986) could be distinguished acoustically.

Soldevilla et al. (2008) identified two distinct echolocation click types produced by Pacific white-sided dolphins off Southern California: Type A with spectral peaks at 22, 27 and 39.5 kHz, and Type B at 22, 26 and 36 kHz. Further investigation (Soldevilla et al., 2010) revealed that these types had unique spatial and diel patterns in the Southern California Bight, with Type A present at six passive acoustic monitoring (PAM) stations, mainly at night, and Type B at two southern inshore stations, mainly during the day. The diel activity patterns, combined with differences in spatial presence, lead to multiple hypotheses regarding the biological significance of each click type: the two click types might represent different behaviours within a single dolphin population or distinct populations with unique acoustic signatures. Combining these findings with morphometric and genetic data (Lux et al., 1997; Walker et al., 1986) suggests two overlapping, morphologically and acoustically distinct Pacific white-sided dolphin populations occupying the region. Furthermore, Henderson et al. (2011) conducted visual and acoustic observations in Southern California and demonstrated that Pacific white-sided dolphin groups producing Type A clicks were travelling slowly, milling and exhibited little daytime foraging activity, whereas groups producing Type B clicks were travelling and actively foraging (Henderson et al., 2011). The coupled spatial, temporal and behavioural differences between the two Pacific white-sided dolphin click types support the hypothesis that Type A and Type B clicks represent two distinct populations overlapping in the Southern California Bight (Henderson et al., 2011; Soldevilla et al., 2008, 2010). Here, we build upon these seminal studies to investigate Type A (LoA) and Type B (LoB) click usage patterns across the Eastern North Pacific. We use an automated classification method combined with expert review to compare the distribution of LoA and LoB click presence in 57 cumulative years of PAM data from 14 long-term monitoring stations distributed between the Gulf of California and the Gulf of Alaska.

Our study aimed to assess whether the spatiotemporal distribution of the two click types aligns with proposed population geographic ranges in the Eastern North Pacific (Lux et al., 1997; Walker et al., 1986), therefore illuminating possible population-specific biogeographic patterns. Conflicting hypotheses regarding the migration patterns of Pacific white-sided dolphins (Brown & Norris, 1956; Forney & Barlow, 1998; Leatherwood et al., 1984) prompted our investigation of spatial-seasonal trends to identify the potential influence of latitude and season on Pacific white-sided dolphin acoustic presence.

Multiple hypotheses suggesting that Pacific white-sided dolphin presence is influenced by fluctuations in sea surface temperature (SST) guided our examination of long-term changes in acoustic presence in the Southern California Bight. Henderson et al. (2014) linked Pacific white-sided dolphin visual presence in Southern California to positive phases of the Pacific Decadal Oscillation (PDO), hypothesizing that warmer, less productive conditions may push animals closer to shore, resulting in more apparent presence during warmer periods (Henderson et al., 2014). Additionally, Salvadeo et al. (2010) hypothesized that a poleward range shift was occurring for Pacific white-sided dolphins out of the Gulf of California, potentially linked to warming SSTs as they moved poleward to remain within their preferred thermal gradients (Salvadeo et al., 2010). The decade from 2010 to 2020 witnessed extreme climatic events in the North Pacific Ocean, including a coupled marine heatwave and El Niño between 2014 and 2016 leading to persistent positive temperature anomalies (Leising et al., 2015; Wells et al., 2017), biogeographic range shifts (Cavole et al., 2016) and widespread die-offs of marine mammals and seabirds (McClatchie et al., 2016; Piatt et al., 2020; Savage, 2017). Our study period, spanning 2008–2021, coincides with these events at three long-term monitoring sites in Southern California. Nearly continuous recording effort and frequent Pacific white-sided dolphin detections at each site allowed us to examine the relationship between click type presence and environmental drivers including the

North Pacific Gyre Oscillation (NPGO) index (Di Lorenzo et al., 2008) and Ocean Niño index (ONI), and to compare relative presence before, during and after the marine heatwave of 2014–2016.

As our rapidly changing climate continues to affect the distribution of marine foraging habitats, it is important that researchers can predict the shifting movement patterns (MacLeod, 2009) of protected species such as Pacific white-sided dolphins who are known to interact with fisheries (Carretta et al., 2022). The two cryptic populations are currently managed as a single stock by the National Marine Fisheries Service (NMFS) as they are visually indistinguishable (Carretta et al., 2022). By investigating potential acoustic delineation, we aim to address the knowledge gap regarding population-specific biogeographic patterns of Pacific white-sided dolphins with the goal that this information can be used to support future policy and management directives (Martien et al., 2019).

## 2 | METHODS

### 2.1 | Data collection

We selected 14 long-term passive acoustic monitoring (PAM) stations across the Eastern North Pacific (Table 1, Table S1, Figure 1). These included a southernmost station at the mouth of the Gulf of California (GofCA_P1), two further north in the Gulf (GofCA_P2, GofCA_P3), a station west of Guadalupe Island (Baja_GI), six in the Southern California Bight (SCB: H, M, N, P, T, U), one off Point Conception near the Channel Islands National Marine Sanctuary (CINMS) and three northern stations at Point Sur (PS), in the Olympic Coast National Marine Sanctuary (OCNMS), and in the Gulf of Alaska (GofAK). The temporal coverage varied from 2005 to 2021, with nearly continuous recording at two Southern California Bight stations (H and N) and the CINMS station. However, temporal coverage at high (GofAK, OCNMS)

**TABLE 1** Summary of recording locations, depths, recording effort and number of days with Pacific white-sided dolphin LoA and LoB click presence at each site.

| Site | Coordinates | Instrument depth (m) | Recording effort (# days) | Recording period | LoA present (# days)<br>(% days) | LoB present (# days)<br>(% days) |
|---|---|---|---|---|---|---|
| GofAK | 56.243′ N<br>−142.757′ W | 990 | 679 | 9/9/2012–9/10/2014 | 39<br>5.70% | 0<br>0% |
| OCNMS | 47.501′ N<br>−125.353′ W | 650 | 1056 | 1/27/2011–5/2/2014 | 310<br>29.30% | 0<br>0% |
| PS | 36.299′ N<br>−122.393′ W | 1220 | 1645 | 1/25/2007–1/25/2020 | 486<br>29.50% | 0<br>0% |
| CINMS | 34.316′ N<br>−120.805′ W | 770 | 2794 | 11/4/2009–1/3/2020 | 689<br>24.70% | 2<br>0.00% |
| SCB_M | 33.509′ N<br>−119.254′ W | 940 | 2008 | 1/13/2009–2/5/2015 | 107<br>5.30% | 35<br>1.70% |
| SCB_H | 32.847′ N<br>−119.176′ W | 1100 | 3800 | 6/5/2008–4/24/2021 | 627<br>16.50% | 191<br>5.10% |
| SCB_T | 32.886′ N<br>−117.556′ W | 850 | 397 | 9/29/2016–1/18/2018 | 6<br>1.50% | 37<br>9.30% |
| SCB_P | 32.523′ N<br>−117.163′ W | 520 | 1645 | 2/12/2013–11/8/2018 | 14<br>0.85% | 50<br>3.00% |
| SCB_N | 32.369′ N<br>−118.565′ W | 1230 | 3756 | 1/14/2009–4/15/2021 | 436<br>11.60% | 57<br>1.50% |
| SCB_U | 31.851′ N<br>−118.484′ W | 1200 | 466 | 11/17/2018–11/2/2020 | 8<br>1.70% | 1<br>0.21% |
| Baja_GI | 29.085′ N<br>−118.155′ W | 1180 | 706 | 11/19/2018–9/13/2022 | 1<br>0.14% | 0<br>0% |
| GofCA_P1 | 23.498′ N<br>−109.378′ W | 660 | 743 | 3/10/2004–6/5/2007 | 0<br>0% | 2<br>0.26% |
| GofCA_P2 | 28.364′ N<br>−112.303′ W | 400 | 430 | 6/20/2007–3/17/2008 | 0<br>0% | 0<br>0% |
| GofCA_P3 | 29.016′ N<br>−113.225′ W | 600 | 433 | 8/8/2008–5/18/2010 | 0<br>0% | 0<br>0% |

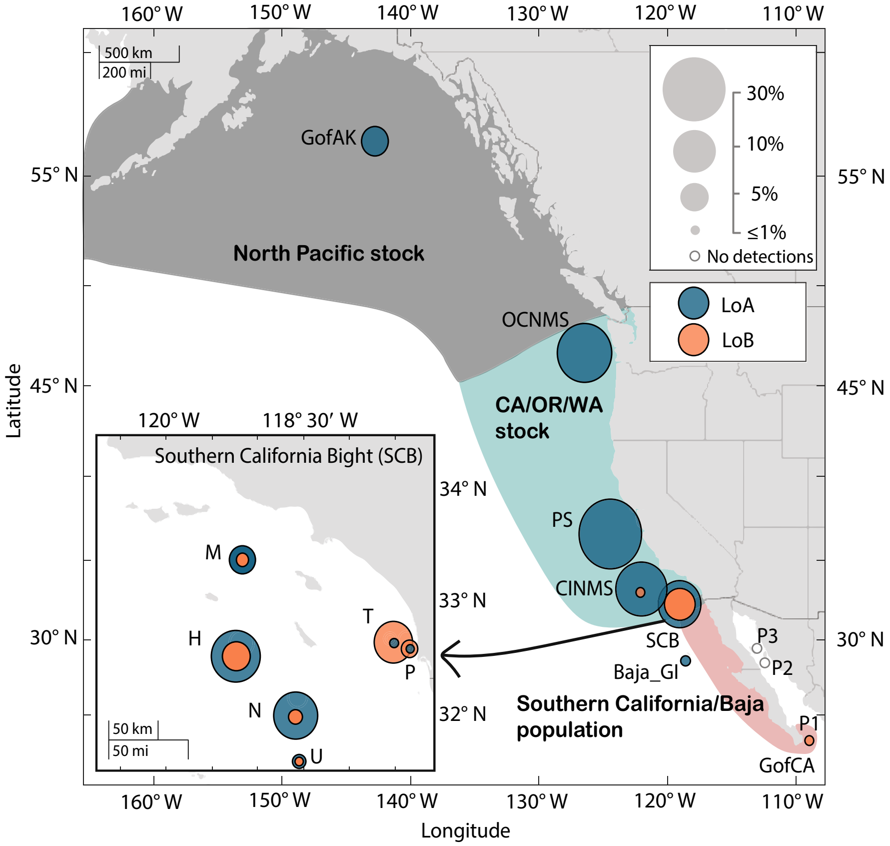


FIGURE 1 PAM sites ranging across the Northeastern Pacific overlaid with geographic boundaries of the North Pacific and CA/OR/WA Pacific white-sided dolphin management stocks and hypothesized boundaries of the cryptic Southern California/Baja population. The North Pacific stock boundaries are outlined in grey, CA/OR/WA stock boundaries are outlined in blue, and Southern California/Baja stock boundaries are outlined in pink. HARP locations are presented as circles scaled by percentage of recording days with Pacific white-sided dolphin clicks present, with blue circles representing LoA clicks and coral representing LoB clicks. The percentage of recording days with presence is summed for all sites in the Southern California Bight (SCB). The black arrow points from the summed SCB values to the inset box which displays percentages at six Southern California recording sites. LoA clicks were detected between 56.2433′ N and 31.8515′ N, with the highest percentage of click-positive recording days at PS (36.2993′ N, −122.3930′ W). LoB clicks were detected between 34.3168′ N and 23.4983′ N, with the highest percentage of click-positive recording days at SCB_T (32.8868′ N, −117.5560′ W).

and low (Baja_GI, GofCA) latitude sites spanned only the early or later years of the total recording effort (Table 1). High-frequency acoustic recording packages (HARPs) were deployed at depths of 500–1200 m, continuously recording 16-bit audio at a 200 kHz sampling rate, with an effective recording bandwidth of 10 Hz to 100 kHz for up to 1 year (Wiggins & Hildebrand, 2007). Some sites (PS, GofCA_P1, P2, P3) operated on a duty cycle of 5 min on and 10, 20 or 25 min off to extend deployment durations. HARP hydrophones were suspended 10–20 m above the seafloor.

## 2.2 | Data processing

### 2.2.1 | Click detection

For each HARP deployment, echolocation clicks were detected using customized routines in the MATLAB-based software program *Triton* (Wiggins & Hildebrand, 2007). A two-step detection approach was implemented in *Triton* following methods outlined in Soldevilla et al. (2008) and Roch et al. (2011), with the objective that all acoustic signals within an expected frequency range and duration of odontocete echolocation clicks and with an 8 dB signal-to-noise ratio would be returned (Roch et al., 2011; Soldevilla et al., 2008).

### 2.2.2 | Unsupervised clustering phase I

Outputs from the detector were passed through an unsupervised clustering algorithm developed in *Triton* to categorize consistent signal types into 5-min bin-level averages (Frasier et al., 2017). We applied a 120 dB peak-to-peak (pp) re: 1 μPa threshold to filter out low-quality detections before clustering them based on spectral and waveform similarity scores. Similarity scores were computed between all clicks detected in a 5-min time period (bin), up to a maximum of 5000 clicks for computational efficiency. For each bin, a network was formed in which clicks represented nodes connected by "edges", or linkages based on inter-click similarity scores. The weakest 95% of edges in the network were pruned to facilitate clustering, and the Chinese Whispers algorithm (Biemann, 2006) was used to identify clusters of similar clicks within the network. This algorithm iteratively assigns nodes into common clusters, seeking to maximize within-cluster similarity and minimize between-cluster similarity. A maximum of 15 clustering iterations was allowed; however, reassignments typically cease after 5–10 iterations. Clusters consisting of a minimum of 50 clicks were retained, and multiple clusters could form per time bin. If fewer than 50 clicks were detected in a 5-min bin, they were treated as a single cluster for classification purposes. If more than 5000 clicks were detected in a 5 min bin, a subsample of 5000 clicks was randomly selected for clustering and classification purposes. Each cluster's normalized mean spectrum and waveform envelope were calculated, along with the inter-click interval (ICI) between clicks, binned in 10-ms increments from 0.1 to 1 s. ICI distributions were plotted as histograms to define a modal ICI for each type within a 5-min bin.

### 2.2.3 | Unsupervised clustering phase II

Dominant signal types within a subset of four deployments were identified to form a training dataset for the development of a deep neural network for classification using a second phase of clustering. The bin level clusters were grouped using one large network (maximum size 20,000 bins) based on similarity to identify the dominant signal types (typically 5–15 types) observed across a particular deployment. Types were considered dominant if they consisted of at least 50 bins. Up to 30 iterations of the Chinese Whispers algorithm (Biemann, 2006) were allowed in this case. This step aggregated examples of the dominant signal types found in each deployment into distinct clusters (Frasier et al., 2017).

### 2.2.4 | Expert review of dominant types

An expert analyst (MA) merged the aggregated clusters of six dominant signal types across four deployments to develop a robust classifier training set. Five oceanic dolphins are commonly observed in Southern California, including long-beaked common dolphins (*Delphinus capensis*), short-beaked common dolphins (*Delphinus delphis*), bottlenose dolphins (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*) and Pacific white-sided dolphins (Bearzi, 2005; Becker et al., 2022; Campbell et al., 2015; Soldevilla et al., 2008). Soldevilla et al. (2008) determined that Risso's and Pacific white-sided dolphin echolocation clicks are acoustically distinguishable by their unique spectral banding patterns, whereas bottlenose and common dolphins are not. Here, we use the characteristic spectral peak and notch features described by Soldevilla et al. (2008) to identify Risso's dolphin (Gg) and Pacific white-sided dolphin's LoA and LoB clusters present in the phase II clustering output (Figure 2). Clusters resembling common dolphin and bottlenose dolphin clicks were categorized as unidentified dolphin (UD). Additionally, clusters for Cuvier's beaked whale (*Ziphius cavirostris*) (Zc) (Baumann-Pickering et al., 2013; Zimmer et al., 2005) and boat noise were identified and incorporated into the training dataset as non-target classes to improve classifier performance.

### 2.2.5 | Deep neural network training and testing

Aggregated examples of Risso's and Pacific white-sided dolphin categories were pooled across four deployments: three in the Southern California Bight (SCB_H_61, SCB_H_66, SCB_E_65, Table 2), and one in the Olympic Coast National Marine Sanctuary (OCNMS_QC_12). At the time of training, composite clusters from additional sites were not available and were, therefore, not included in the model. For the background UD, Boat and Zc categories, examples were pulled only from the SCB_H_61 deployment, which had the best representation of all six categories. Some types are more common than others (e.g. UD), therefore, to balance the dataset, we drew 500 examples from each category to form the training set. The Boat and Zc categories, and the combined LoB category, contained fewer than 500 bin-level examples (Table 2). Therefore, those categories were randomly resampled to reach the 500 sample target size. The 3000 bin-level examples (500 × 6 categories) were split into 66% training and 33% testing. The model was trained to automatically discriminate LoA and LoB click types found between Southern California and Washington. While other distinct Pacific white-sided dolphin click types may exist, or there may be a latitudinal gradient in spectral variation (Soldevilla et al., 2017), investigation of such hypotheses was outside the scope of this analysis.

The deep neural network ran as an add-on package in *Triton* using MATLAB's *Deep Learning Toolbox* and was trained on spectral averages, mean waveform envelope and ICI distributions of the 5-min-level clusters representing the six signal categories. Labels were numerically encoded for the network, which comprised four 512-node fully connected layers, featuring 50% dropout, leaky ReLU activations and a Softmax output layer, limited to 15 training epochs. Performance using this architecture, further detailed in Frasier (2021), was evaluated based on accuracy, precision and recall on the testing dataset. Additionally, we tested model performance on novel data by comparing its labels with an expert analyst's (MA) manual annotations for three deployments (SCB_P_35, SCB_H_29 and CINMS_C_33) (Tables S2–S4). We selected this wide range of test deployments to investigate the potential for domain shift, or cases when differences between the training data and target (novel) data result in reduced performance (Ben-David et al., 2010).

## 2.3 | Data analysis

### 2.3.1 | Signal review and timeseries generation

The data processing workflow for each deployment included signal detection, Phase I clustering and classification of bin-level averages

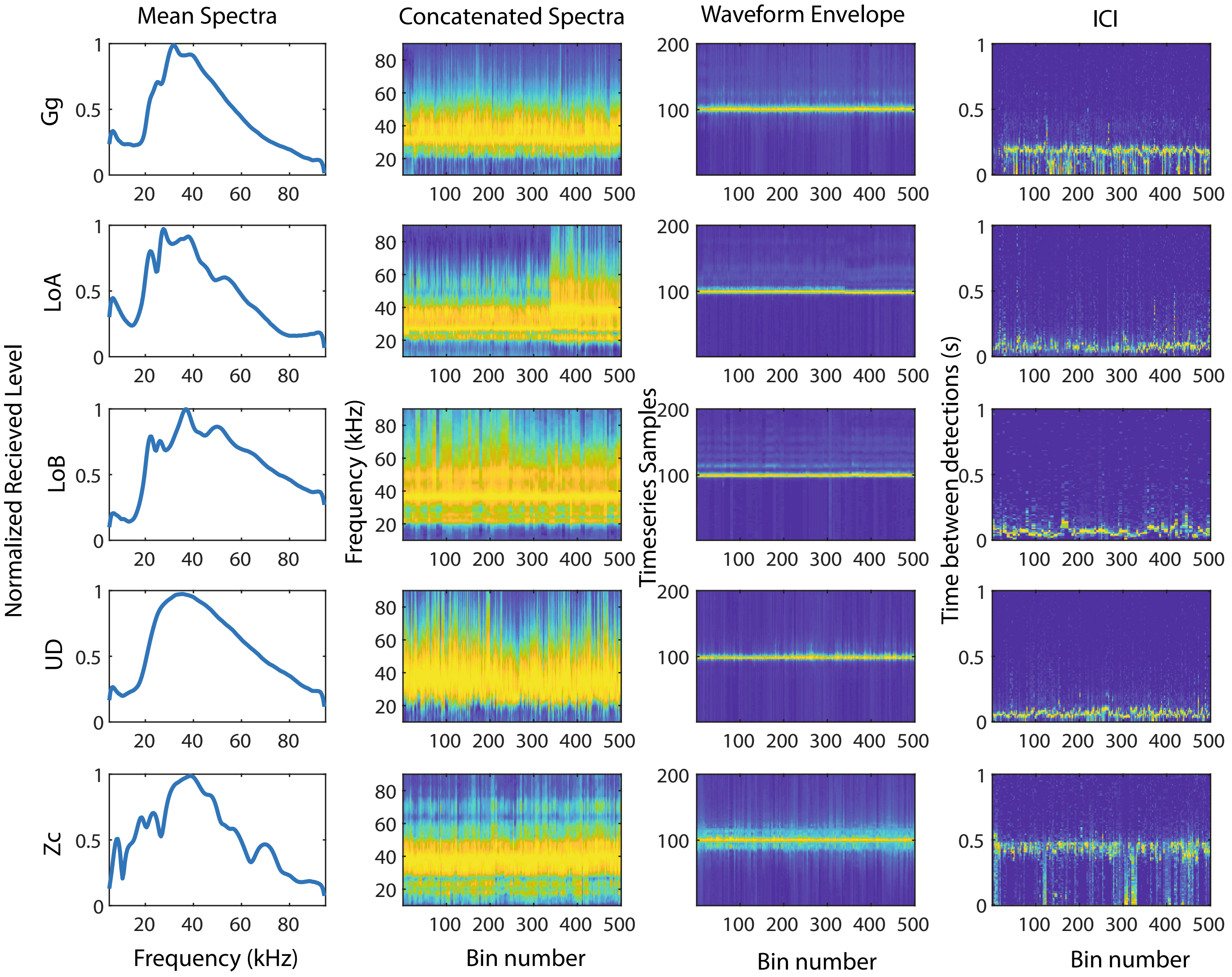


**FIGURE 2** Bin-level examples for five odontocete categories: Risso's dolphin (Gg, row 1), Pacific white-sided dolphin (LoA, row 2), Pacific white-sided dolphin (LoB, row 3), unidentified dolphin (UD, row 4) and Cuvier's beaked whale (Zc, row 5). Columns display unique spectral and temporal properties of each signal category. Species-specific spectral banding patterns evident in Gg, LoA, LoB and Zc categories concatenated spectrum plots. Gg peaks at 30 and 40 kHz, LoA peaks at 22, 27.5 and 39 kHz, LoB peaks at 22, 26 and 37 kHz and Zc peaks at 18, 22 and 40 kHz.

using the trained network. LoA, LoB and Gg labels were evaluated by three expert analysts, including co-authors MA and AA, using the *DetEdit* interface (Solsona-Berga et al., 2020), enabling review and re-classification of mislabelled clusters.

We implemented a final received level threshold of 123 $\mathrm{dB_{pp}}$ re:1 µPa to maintain consistency in detection thresholds across recording sites. The initial 8 dB SNR threshold may have excluded high-amplitude low-SNR clicks, resulting in non-linear detection curves (Figures S1 and S2). If no clicks are missed, a theoretical detection curve would scale linearly with dB amplitude as more clicks are detected further away from the hydrophone (Hildebrand et al., 2019). By thresholding above 123 $\mathrm{dB_{pp}}$ re:1 µPa, we retained only the highest quality detections and effectively restricted our detection range at each site.

Detections were binned into hourly intervals, with 'click-positive' bins indicating any number of detected clicks in a bin. This binning facilitated initial visualization of diel and long-term patterns (Figures S3–S7). Timeseries were generated at each site using the *Tethys* (Roch et al., 2016) package in MATLAB. Detections were then grouped into 'click-positive days' indicating that at least one click-positive hour was present during that day, to analyse the spatial biogeographic patterns of the LoA and LoB click types. We illustrated the percentage of recording days with Pacific white-sided dolphins present at each site as scaled circles and overlaid current stock boundaries defined by NMFS (Figure 1; Carretta et al., 2022).

### 2.3.2 | Analysis of diel patterns

To test whether LoA clicks occurred more frequently at night and LoB clicks during the day, we binned detections into minutes per hour, labelling each hour as 'day' or 'night' using Rstudio's (Rstudio

**TABLE 2** Signal category, deployment number and number of 5-min bin-level training examples that were used as input for the deep neural network. Each category contained less than or equal to 500 examples, where 66% were used for training and 33% were used for testing. For the Gg, LoA and LoB categories, examples from multiple deployments were included to increase variability.

| Signal category | Deployment number | Number of bin-level training examples |
|---|---|---|
| Boat | SCB_H61 | 18 |
| Gg | SCB_H61 | 392 |
| | OCNMS12QC | 108 |
| LoA | SCB_H61 | 78 |
| | SCB_H66 | 54 |
| | SCB_E65 | 83 |
| | OCNMS12QC | 285 |
| LoB | SCB_H61 | 77 |
| | SCB_H66 | 73 |
| UD | SCB_H61 | 500 |
| Zc | SCB_H61 | 377 |

Team, 2022) *suncalc* package. Day and night hourly detections were summed and divided by recording effort, being the total number of day or night recording hours. We applied one-sided *t*-tests to the scaled diel activity values to test whether the mean difference in LoA activity was greater during the night than day, and whether the mean difference in LoB activity was less during the night than day, as was observed in Soldevilla et al. (2010) and Henderson et al. (2011).

### 2.3.3 | Analysis of seasonal and spatial patterns

We analysed the seasonal patterns of Pacific white-sided dolphins by converting daily detections into the number of days with presence per season. Seasons were categorized into Winter (December–February), Spring (March–May), Summer (June–August) and Fall (September–November), focusing on sites with at least 25% recording effort for a given season. To investigate the relationship between click type presence, season and latitude, we built generalized additive models (GAMs) for both LoA and LoB clicks using the *mgcv* package (Wood, 2011) in RStudio. These models, designed to handle non-linear seasonal interactions and latitudinal influences, used the number of click-positive days per season as the response variable, applying a Tweedie distribution (Wood et al., 2016) for zero-inflation adjustment. The GAMs were constructed using a tensor product smooth term to capture the interaction between season and latitude, allowing us to investigate variation in seasonality with latitude. Model diagnostics were performed to assess the quality of the fits and the significance of each term. Contour plots were generated to visually represent the spatial-seasonal interactions and display large-scale biogeographic patterns.

### 2.3.4 | Analysis of interannual and environmentally driven patterns

We examined interannual variations in Pacific white-sided dolphin acoustic presence at three long-term monitoring sites in Southern California. Building upon the results of Henderson et al. (2014), we applied generalized linear models (GLMs) at sites CINMS, SCB_H and SCB_N to test the null hypothesis of no correlation between climate drivers and Pacific white-sided dolphin presence. We selected the ONI and NPGO as covariates as they are associated with sea-surface temperature deviations and biological productivity in the California Current. The climate data were sourced from NOAA's National Weather Service Climate Prediction Center and http://www.o3d.org/npgo/, respectively (Di Lorenzo et al., 2008). We calculated a 3-month running average of the NPGO variable to match the resolution of the ONI and seasonal dolphin presence. Each GLM, fitted with a Tweedie distribution to handle zero inflation, included linear coefficients for both ONI and NPGO, with diagnostic assessments to evaluate model fits. Additionally, we examined the relationship between Pacific white-sided dolphin acoustic presence and the extreme marine heatwave event of 2014–2016 (Leising et al., 2015). We used Kruskal–Wallis and Dunn's post-hoc tests to assess the null hypothesis that Pacific white-sided dolphin presence was the same before, during and after the 2014–2016 marine heatwave event at the aforementioned long-term monitoring sites.

## 3 | RESULTS

We analysed 163 HARP deployments between the Gulf of California and the Gulf of Alaska, representing 57 cumulative years of recording effort. The majority of effort occurred in Southern California at sites CINMS, SCB_H and SCB_N, where recording was nearly continuous between 2009 and 2021.

### 3.1 | Classifier performance

The classification accuracy of the deep neural network was 99.6% on the test dataset and testing recall and precision were above 98% for each category (Table 3). However, these metrics overestimate the model's performance because they are estimated using the highest quality examples aggregated from a subset of sites by the phase II clustering process. On truly novel and minimally curated bin-level clusters consisting of one or more clicks, the model's precision ranged from 22% to 75% for the LoA category, and 0.67% to 67% for the LoB category reflecting a relatively high false positive rate (Tables S2–S4). Recall ranged from 83% to 92% for the LoA category and 100% for the rare LoB category. Given these results, all LoA and LoB labels were manually reviewed to remove false positives.

**TABLE 3** Confusion matrix for bin-level classifier on testing dataset with 500 examples from each category. Bold values along the diagonal indicate how many of the total were correctly identified and adjacent rows and columns represent false positives or false negatives for each category.

| | | True class | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Category** | **Boat** | **Gg** | **LoA** | **LoB** | **UD** | **Zc** | **Precision** |
| Predicted class | Boat | **500** | 2 | 0 | 0 | 0 | 0 | 99.60% |
| | Gg | 0 | **492** | 0 | 0 | 1 | 0 | 99.80% |
| | LoA | 0 | 0 | **497** | 0 | 0 | 0 | 100% |
| | LoB | 0 | 0 | 1 | **500** | 0 | 0 | 99.80% |
| | UD | 0 | 6 | 2 | 0 | **499** | 0 | 98.40% |
| | Zc | 0 | 0 | 0 | 0 | 0 | **500** | 100% |
| | Recall | 100% | 98.40% | 99.40% | 100% | 99.80% | 100% | **99.60%** |

**TABLE 4** Results of paired *t*-tests comparing diel activity patterns of the LoA and LoB click types across sites. Alternative hypothesis corresponds to true mean difference in normalized diel activity, compared across all sites.

| Paired *t*-test | Alternative hypothesis | Mean difference | *t* | df | *p*-value |
|---|---|---|---|---|---|
| LoA | True mean difference is greater than 0 | 64.16 | 3.41 | 11 | **.0029** |
| LoB | True mean difference is less than 0 | −15.30 | 2.02 | 11 | **.034** |

Significant differences are indicated by bold *p*-values (<.05).

## 3.2 | Biogeographic patterns

### 3.2.1 | Geographic distribution

The Pacific white-sided dolphin LoA click type was detected at 11 of the 14 study sites (Figure 1), including the northern locations (GofAK, OCNMS, PS), CINMS, all Southern California Bight sites and Guadalupe Island (Baja_GI), but not at the Gulf of California sites (GofCA P1, P2, P3). Daily detection frequencies varied, with the highest at OCNMS (29.3% of days) and PS (29.5%). LoA clicks were detected at the CINMS station on 24.7% of days, and in the Southern California Bight, detections ranged from 1% to 16.5% with greater values trending towards offshore sites (Figure 1). The southernmost LoA detection was at Baja_GI, present on less than 1% of recording days. Conversely, LoB clicks were observed at eight sites, predominantly in the Southern California Bight, with isolated detections at CINMS and GofCA_P1. The highest presence of LoB clicks was observed at the inshore site SCB_T (9.3% of days). LoB clicks were not detected at GofAK, PS, OCNMS, Baja_GI, GofCA_P2 or GofCA_P3.

### 3.2.2 | Diel patterns

Analysis of diel patterns showed significant differences in day and night acoustic activities. The one-sided *t*-test suggested that LoA clicks occurred significantly more frequently at nighttime (mean difference = 64.16, $p = .0029$) (Table 4). Conversely, LoB clicks occurred significantly more frequently during the daytime (mean difference = −15.30, $p = .034$) (Table 4). The scaled site-specific patterns in Figure 3 indicate that LoA clicks are detected more often during nighttime at northern and central California sites OCNMS, PS and CINMS (Figure 3). In the Southern California Bight, a slight preference for nighttime activity was evident at SCB_H. As suggested by the one-sided *t*-test, the scaled activity of the LoB click type was greater during the daytime, indicating an inverse relationship to LoA clicks, especially evident at SCB_T (Figure 3).

### 3.2.3 | Seasonal-spatial patterns

Pacific white-sided dolphin LoA and LoB click presence exhibited seasonal site-specific spatial variability (Figure 4a1–a4). LoA presence was greater off the coast of Central California and Southern California during winter and spring, with minimal presence detected at Baja_GI during spring. Seasonal presence increased at OCNMS and GofAK during the summer and fall, suggesting a north–south seasonal migration. The GAM revealed a significant non-linear relationship between LoA presence and the interaction between season and latitude (Table 5) and predicted the greatest LoA presence during summer at mid to higher latitudes, ranging from 35° to 45° N (Figure 4a5). The model's smooth term captured 19.8% of the variance, suggesting that additional ecological dynamics play a role in shaping the biogeographic distribution of LoA's presence.

LoB click presence peaked at inshore stations in the Southern California Bight during fall and winter, with minimal detections in the Gulf of California during winter and spring (Figure 4b1–b4). The GAM

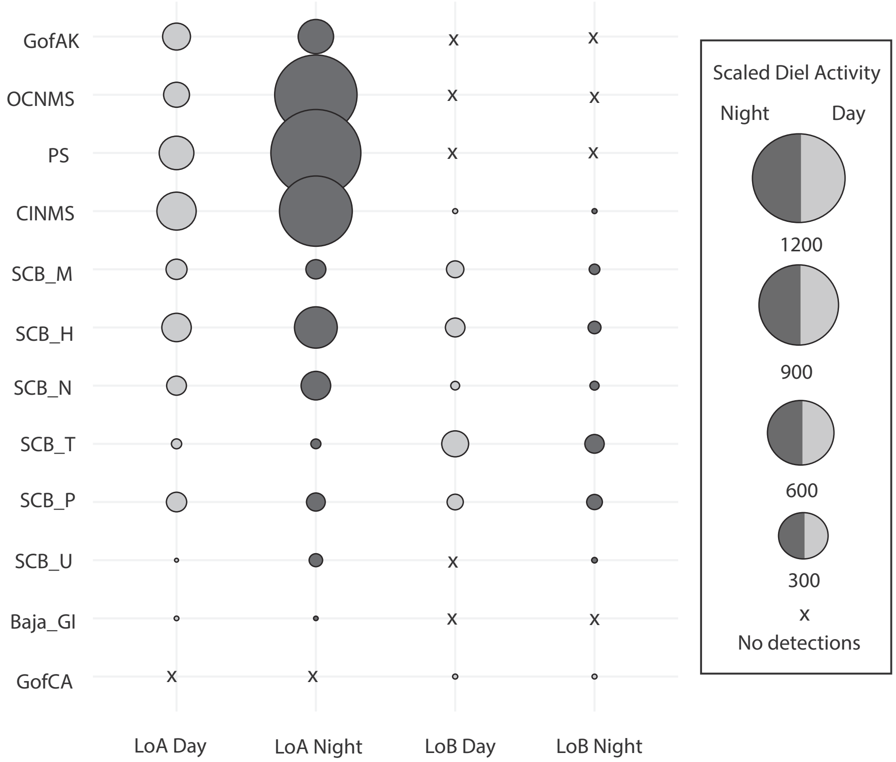


**FIGURE 3** Site-specific scaled diel activity. Each recording site is represented on the *y*-axis, and diel activity of each click type is represented on the *x*-axis. Dark grey circles represent nighttime and light grey circles represent daytime, with circle size representing scaled presence throughout the diel recording periods. Scaled diel presence is the total number of click positive minutes per hour divided by the total number of recording hours.

model results for LoB indicated a significant non-linear relationship between seasonal presence and latitude (Table 5), with predictions concentrated in the southern half of the species' geographic range during winter, spring and extending into fall (Figure 4b5). However, the lack of temporal overlap between Southern California and Gulf of California (GofCA) stations makes it challenging to resolve LoB's seasonal patterns across the region, especially when considering interannual variability. The LoB model accounted for 22.4% of the variance in presence, indicating that while the model captures some of the ecological dynamics, others may play a significant role in determining LoB's presence across the region.

### 3.2.4 | Interannual patterns and environmental drivers

Biogeographic patterns at three long-term monitoring sites in Southern California showed significant changes in LoA and LoB acoustic presence, particularly during and following the 2014–2016 marine heatwave and El Niño (Figure 5). Notably, LoB presence was detected for the first time at site CINMS during the fall of 2018, and again in the fall of 2019 (Figure 5). There were marked differences in dolphin presence before, during and after the heatwave at all sites (Figure 6, Table 6) and the post-hoc analyses further highlighted these shifts. At site CINMS, LoA presence decreased during the heatwave, with no significant differences detected in periods before and after the event (Figure 6a). At SCB_H, LoA presence decreased significantly during and post-heatwave, while LoB presence significantly increased post-heatwave, marking a notable shift in dominance between click types (Figure 6b). At SCB_N, LoA presence was significantly higher before the heatwave compared to during and after, whereas LoB presence showed no significant changes across these periods (Figure 6c).

The shifts in presence coincided with inflection points of the ONI and NPGO indices (Leising et al., 2015; Wells et al., 2017), suggesting that interannual changes in Pacific white-sided dolphin presence are driven by large-scale climate phenomena. Our GLMs further substantiated this link (Figure 7, Table 7). At site CINMS, LoA was slightly negatively correlated with the NPGO and ONI. At site SCB_H, LoA was positively correlated with the NPGO, while LoB was negatively correlated, highlighting different environmental conditions favouring the two click types. LoA presence was negatively correlated with the ONI and positively correlated with the NPGO at SCB_N, indicating a preference for cooler, nutrient-rich conditions typically found during La Niña phases in Southern California. LoB, however, was not significantly correlated with either environmental driver at site SCB_N. These findings may highlight how Pacific white-sided dolphins navigate climate phases in the Eastern North Pacific, shifting their distribution in response to dynamic ocean conditions (Henderson et al., 2014).

## 4 | DISCUSSION

Results from this study add additional support to the hypothesis that Pacific white-sided dolphins produce population-specific echolocation clicks. LoA clicks were detected throughout the study region, with seasonally specific peak occurrences off Point Conception,

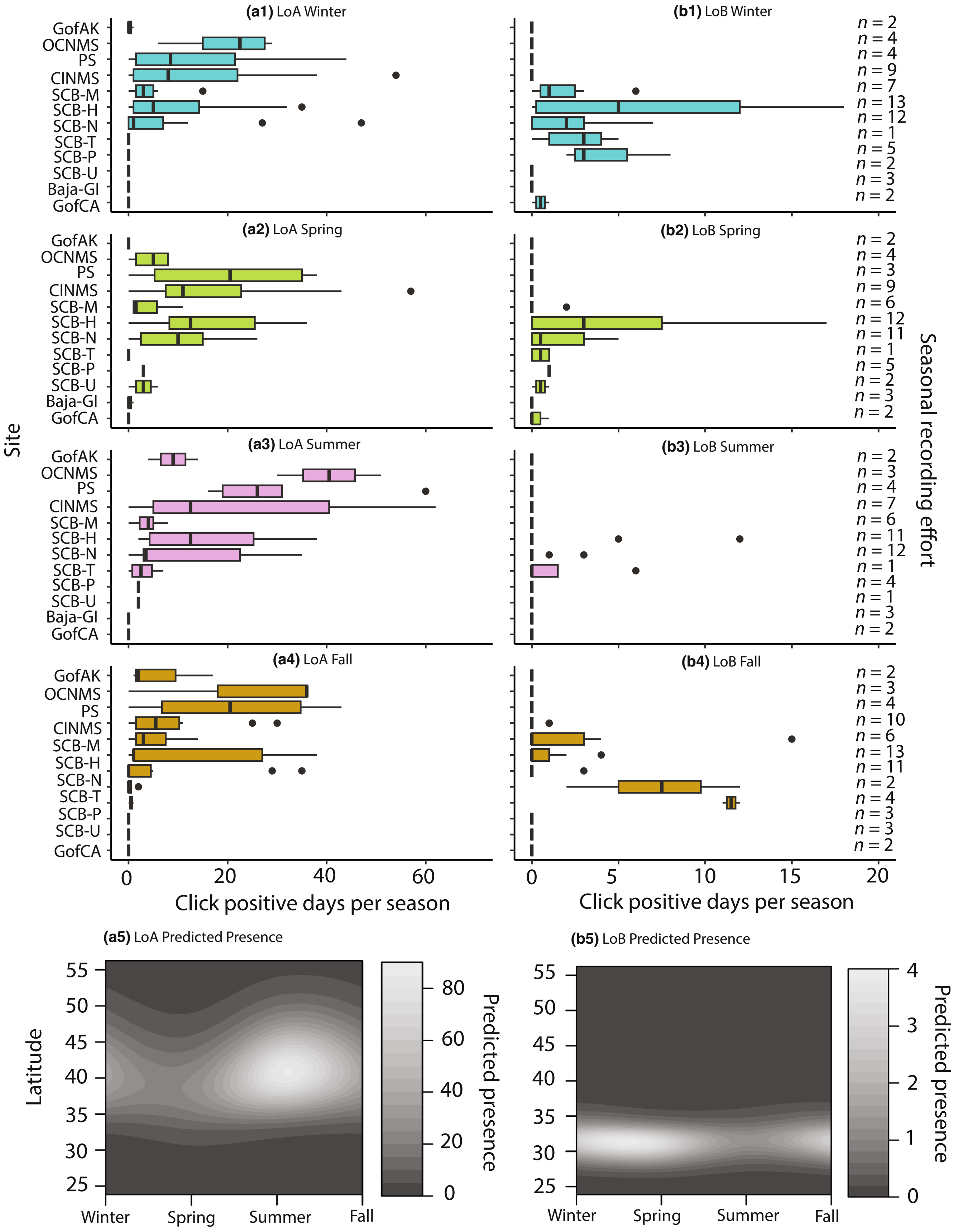

(a1) LoA Winter
(a2) LoA Spring
(a3) LoA Summer
(a4) LoA Fall
(b1) LoB Winter
(b2) LoB Spring
(b3) LoB Summer
(b4) LoB Fall
GofAK
OCNMS
PS
CINMS
SCB-M
SCB-H
SCB-N
SCB-T
SCB-P
SCB-U
Baja-GI
GofCA
Site
0
20
40
60
0
5
10
15
20
Click positive days per season
Click positive days per season
n = 2
n = 4
n = 4
n = 9
n = 7
n = 13
n = 12
n = 1
n = 5
n = 2
n = 3
n = 2
n = 2
n = 4
n = 3
n = 9
n = 6
n = 12
n = 11
n = 1
n = 5
n = 2
n = 3
n = 2
n = 2
n = 3
n = 4
n = 7
n = 6
n = 11
n = 12
n = 1
n = 4
n = 1
n = 3
n = 2
n = 2
n = 3
n = 4
n = 10
n = 6
n = 13
n = 11
n = 2
n = 4
n = 3
n = 3
n = 2
Seasonal recording effort
(a5) LoA Predicted Presence
(b5) LoB Predicted Presence
Latitude
55
50
45
40
35
30
25
Winter
Spring
Summer
Fall
80
60
40
20
0
Predicted presence
4
3
2
1
0
Predicted presence

**FIGURE 4** Site-specific seasonal presence of LoA and LoB click types with recording effort bin counts displayed. (a1–a4) Site-specific boxplots of LoA click positive days for winter, spring, summer and fall. (a5) Contour surface map displaying predicted LoA presence as a function of season and latitude, based on a Poisson GAM. Seasonal changes are represented cyclically, latitude ranges from site GofCA to GofAK and the grey scale represents predicted number of click-positive days. (b1–b4) Site-specific boxplots of LoB click positive days for winter, spring, summer and fall. (b5) Contour surface map displaying predicted LoB presence as a function of season and latitude, based on a Tweedie GAM. Seasonal changes are represented cyclically, latitude ranges from site GofCA to GofAK and the grey scale represents predicted number of click-positive days.

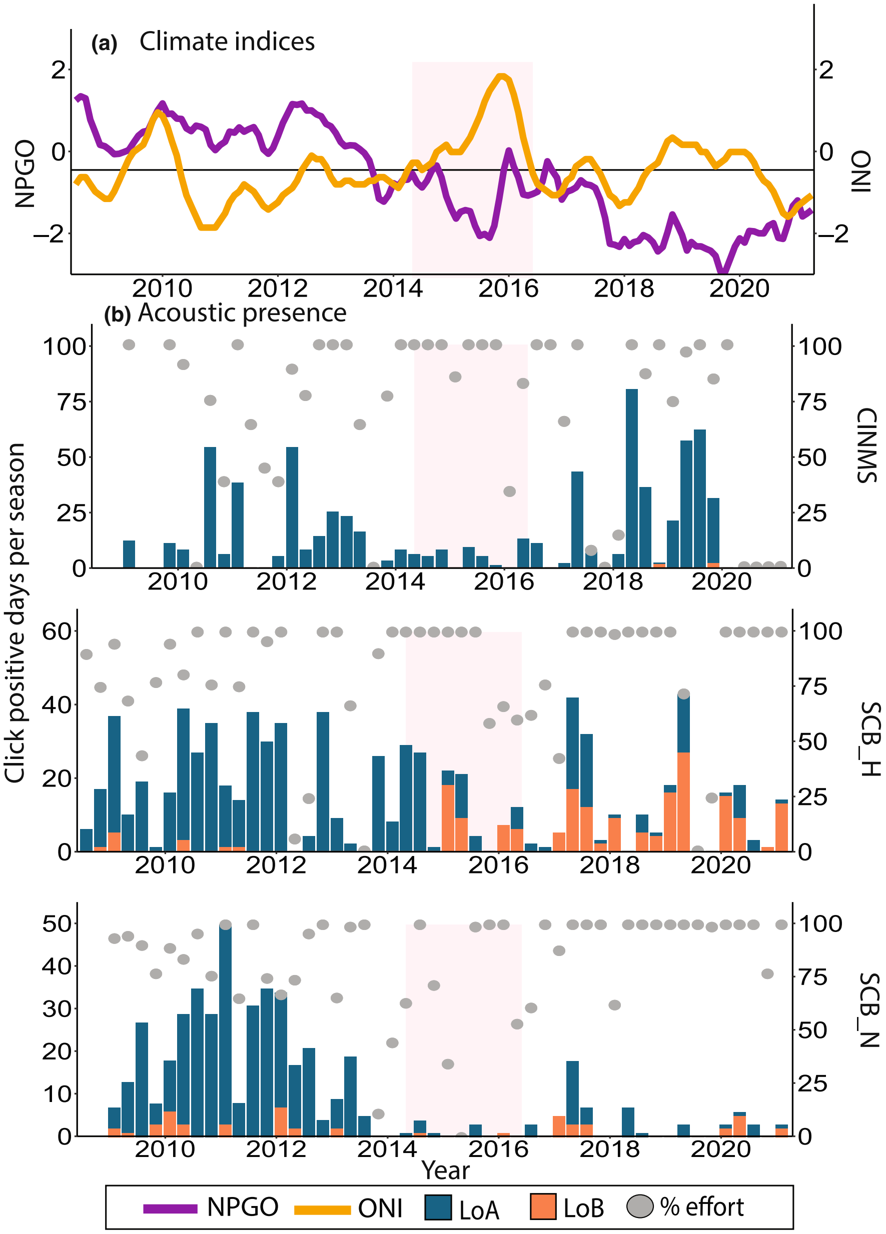
**TABLE 5** Summary of spatial-seasonal GAM model results for LoA and LoB presence.

| Model | Smooth term | EDF | Ref. df | *F* | *p*-value | Deviance explained |
|---|---|---|---|---|---|---|
| LoA | te (Season, latitude) | 5.8 | 8 | 9.3 | **<2E-16** | 19.8% |
| LoB | te (Season, latitude) | 4.8 | 8 | 3.8 | **5.93E-06** | 22.4% |

*Note*: te represents the tensor product smooth term.

Significant terms are indicated by bold *p*-values (<.05).

**FIGURE 5** (a) Climatic variations in NPGO and ONI 3-month running means between 2009 and 2021. Purple line denoting NPGO and orange denoting ONI, with light pink box highlighting the time period of the 2014–2016 marine heatwave. (b) Pacific white-sided dolphin acoustic presence at three long-term monitoring stations in the SCB. Number of LoA and LoB click-positive days per season are represented as stacked blue and coral bars, respectively. Percent of recording effort for that season is represented by gray circles.



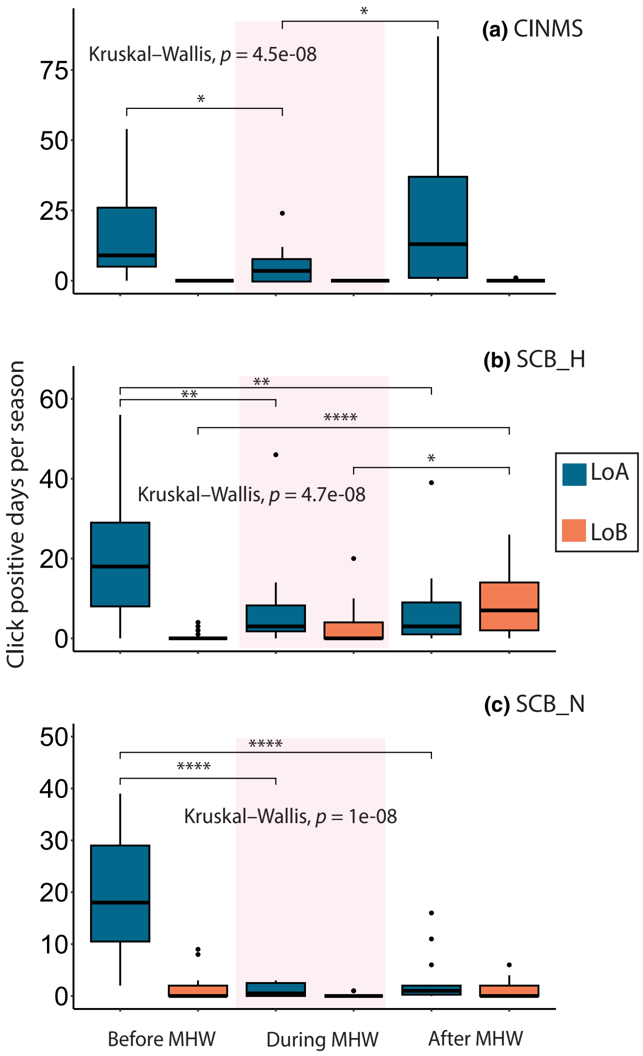


**FIGURE 6** Boxplots displaying the distribution of LoA (blue) and LoB (coral) presence before, during and after the 2014–2016 marine heatwave (MHW) event at three long-term monitoring stations including CINMS, SCB_H and SCB_N. Results of Kruskal–Wallis test displayed for each site and significant Dunn's post-hoc test pairwise comparisons displayed as asterisks (*$p < .05$; **$p < .01$; ***$p < .001$). Time period before the MHW event spans recording effort at each site between (07/01/2008–12/31/2013), during the MHW event spans recording effort at each site between (01/01/2014–12/31/2016) and after the MHW event spans recording effort at each site between (01/01/2017–09/30/2021). LoA boxplots are in blue and LoB in coral, with the MHW event time period highlighted in light pink.

**TABLE 6** Summary of Kruskal–Wallis test results comparing LoA and LoB presence before, during and after the 2014–2016 MHW event at long-term Southern California monitoring stations.

| Site | Chi-squared | df | *p*-value |
|---|---|---|---|
| CINMS | 42.6 | 5 | **4.49E-08** |
| SCB_H | 42.5 | 5 | **4.65E-08** |
| SCB_N | 45.7 | 5 | **1.03E-08** |

Significant differences are indicated by bold *p*-values (<.05).

Point Sur and Washington. LoB clicks were detected seasonally throughout the Southern California Bight and at the southernmost tip of the Gulf of California. Soldevilla et al. (2010) put forward multiple hypotheses to explain the significance of the two distinct click types, and our results most consistently match the population-specific click hypothesis, stating that LoA clicks are produced by the CA/OR/WA population, and LoB clicks are produced by the Southern California/Baja population. It is possible that anatomical differences in cranial shape (Walker et al., 1986) between the populations result in the unique spectral content of each click type (Cranford et al., 1996; Soldevilla et al., 2008, 2010). Here, we address the results of each of our hypotheses and put into context the ecological relevance of our findings.

### 4.1 | Supporting evidence for the population-specific click hypothesis

The geographic distribution of the LoA click type is associated with the geographic distribution of the CA/OR/WA population laid out by Walker et al. (1986) cranial morphometric comparisons and Lux et al. (1997) genetic distinctions. The majority of LoA presence was detected within the CA/OR/WA stock boundaries (Figure 1). LoA clicks were also detected during summer and fall in the Gulf of Alaska. However, our automated approach would not have distinguished these from potential variants representative of another acoustically distinct population, which Lux et al. (1997) found genetic evidence for off the coast of British Columbia and Alaska. Therefore, it remains unclear whether the LoA clicks detected at GofAK were in fact those of a separate North Pacific population, and future studies should investigate the spectral and temporal content of these clicks in greater detail. One LoA encounter was detected at the Baja_GI site although no LoB clicks were detected there throughout the 4-year recording period. The Baja_GI LoA detection occurred during the spring (Figure 4), corresponding to a time of year when LoA presence peaked in the Southern California Bight, suggesting that the CA/OR/WA Pacific white-sided dolphin population may migrate further south than originally hypothesized.

Comparing their spatial distributions, the Southern California/Baja population appears to produce the LoB click type as hypothesized by Soldevilla et al. (2010). Our results suggest that the Southern California/Baja population prefers coastal inshore habitats as demonstrated by the peak in LoB acoustic presence at sites SCB_T and SCB_P, in the San Diego Trough and off of Point La Jolla. Species distribution models of Pacific white-sided dolphins in Baja California waters predict the highest densities near shore, with increasing density further offshore in Southern California Bight waters (Becker et al., 2022). Relative abundance estimates from Becker et al. (2022) were less accurate in the Southern California Bight region, possibly due to the differing habitat preferences between the two overlapping populations (Becker et al., 2022). Together, these findings suggest that animals observed nearshore off San Diego

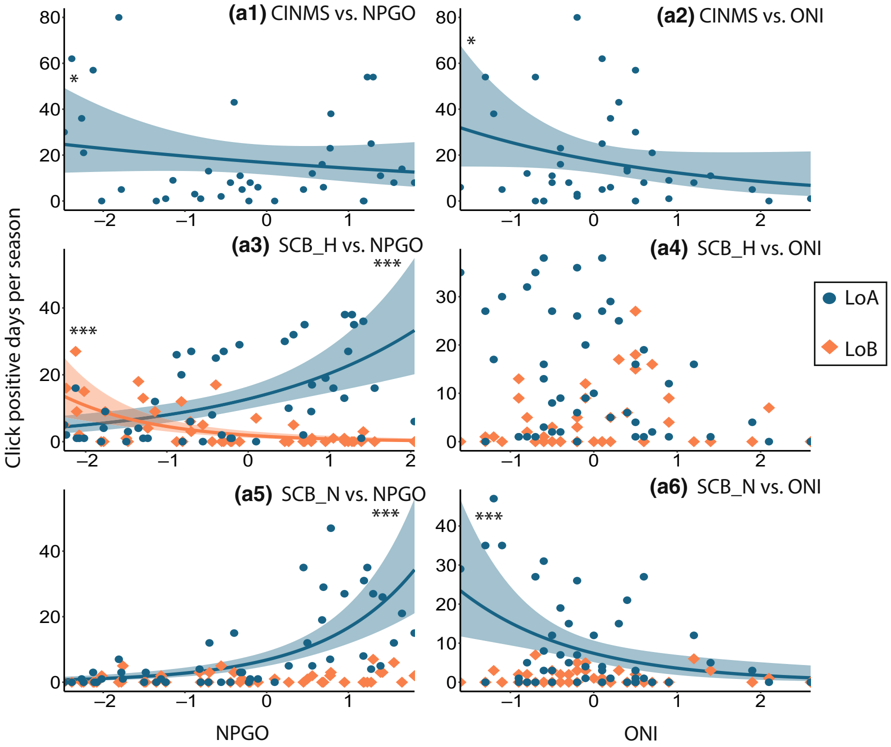


**FIGURE 7** Site-specific GLMs from long-term monitoring SCB stations. The models are overlaid with Pacific white-sided dolphin acoustic presence in seasonal bins, plotted against corresponding climate index indices such as blue circles and coral diamonds. Only significant linear relationships ($p < .05$) are plotted for each click type, station and per index, with significance codes displayed as asterisks (*$p < .05$; **$p < .01$; ***$p < .001$) for each fit.

**TABLE 7** Summary of environmental GLMs for LoA and LoB presence at sites CINMS, SCB_H and SCB_N.

| Model | Coefficient | Estimate | Standard error | *t*-value | *p*-value |
|---|---|---|---|---|---|
| LoA ~ ONI + NPGO @ CINMS | ONI | −0.58 | .17 | −2.66 | **.012** |
| | NPGO | −0.29 | .14 | −2.05 | **.048** |
| LoA ~ ONI + NPGO @ SCB_H | ONI | −0.32 | .16 | −1.97 | .055 |
| | NPGO | 0.41 | .11 | 3.69 | **.001** |
| LoA ~ ONI + NPGO @ SCB_N | ONI | −0.55 | .19 | −2.91 | **.006** |
| | NPGO | 0.82 | .13 | 6.29 | **1.16E-07** |
| LoB ~ ONI + NPGO @ SCB_H | ONI | 0.23 | .22 | 1.06 | .293 |
| | NPGO | −0.84 | .18 | −4.71 | **2.49E-05** |
| LoB ~ ONI + NPGO @ SCB_N | ONI | −0.01 | .28 | −0.037 | .971 |
| | NPGO | 0.35 | .19 | 1.82 | .076 |

Significant terms are indicated by bold *p*-values (<.05).

and Baja California are more likely from the Southern California/Baja population, whereas animals observed offshore in the Southern California Bight are more likely from the CA/OR/WA population.

In a study by Kanes et al. (2024) Pacific white-sided dolphin pulsed calls (Henderson et al., 2011) were detected year-round throughout a 2-year study period (2013–2015) near Barkley Canyon offshore of Vancouver Island, British Columbia. Kanes et al. (2024) findings demonstrated that Pacific white-sided dolphin pulsed call presence was greatest during summer months, with a majority of activity during nighttime and dawn periods. Our analysis of diel and seasonal patterns of echolocation clicks corroborate and extend these findings across different geographic locations. Expanding upon the notion that echolocation click rate can serve as an indicator of behavioural state in odontocetes (Madsen et al., 2005), our study employed a methodology that assumes higher echolocation rates to infer increased foraging potential (Nowacek, 2005; Van Parijs & Corkeron, 2001). The significant nocturnal bias in echolocation activity, especially at sites OCNMS, PS and CINMS (Figure 3), implies that foraging activities are more intense at night in these habitats and suggests that animals producing LoA clicks may be consuming vertically migrating mesopelagic fish and squid when they are accessible at the surface, which has been proposed for other delphinid species (Caruso et al., 2017; Rice et al., 2021). Our results support the hypothesis that differences in diel activity may be evidence of habitat-based niche partitioning between the populations (Henderson et al., 2011; Soldevilla et al., 2010). In Southern California, the CA/OR/WA population appears to favour offshore, nocturnal foraging locations whereas the Southern California/Baja population appears to favour inshore, diurnal foraging locations. Coupling Henderson et al. (2011) behavioural patterns with the diurnal acoustic activity suggests that during daytime hours in Southern California, the CA/OR/WA population may be seen exhibiting resting or social behaviours, whereas the Southern California/Baja population may be seen foraging Henderson et al. (2011).

Furthermore, Pacific white-sided dolphin clicks detected in Southern California consistently separated into two distinct clusters: LoA and LoB. Previous studies have documented odontocete species exhibiting adaptive control over the source-level, inter-click interval and frequency content of their echolocation clicks (Au et al., 1985, 1995; Houser et al., 1999; Ladegaard et al., 2019; Simon et al., 2007). During object detection and discrimination tasks in captive settings, Au et al. (1985, 1995) and Houser et al. (1999) documented multiple click types varying in frequency content produced by individual animals. If the two Pacific white-sided dolphin echolocation click types were purely indicative of adaptive control in a single population, more intermediate click types would likely have been observed during the clustering step. Additionally, 5 min bin-level encounters of each click type tended to occur separately. The absence of intermediate click types and minimal mixed encounters lends further support to the hypothesis that Pacific white-sided dolphin LoA and LoB click types are representative of two distinct populations whose echolocation frequency spectra are shaped by their distinct skull and melon morphology (Soldevilla et al., 2008, 2010; Walker et al., 1986).

Our seasonal-spatial GAM models display how Pacific white-sided dolphin acoustic presence varies seasonally with latitude (Figure 4). We demonstrate that the CA/OR/WA population's presence increases off Central and Southern California during winter and spring and shifts northward during summer and fall (Figure 4). Previous studies observed similar seasonal patterns in the region (Becker et al., 2019; Forney & Barlow, 1998; Henderson et al., 2014; Rice et al., 2021), yet ours is the first to delineate these patterns at the population level. Presence of the LoB click type, likely produced by the Southern California/Baja population, increases at coastal inshore sites in Southern California during fall and winter, suggesting that while there may be sympatry in terms of shared geographical space, it is likely structured temporally, with each population favouring different habitats during different times of the year. The Southern California/Baja population seems to prefer inshore habitats during the fall and winter, while the CA/OR/WA population is more frequently found offshore during winter and spring. However, it remains unclear whether the Southern California/Baja Population moves further offshore of Southern California, or further south into Baja California during summer months. The peak in coastal inshore presence of the southern population in fall and winter may be influenced by the dynamics of the Southern California Counter-current. This inshore current transports warm water from Baja California and is linked to distinct community assemblages (Lavenberg & Ebeling, 1967), with increased strength during fall and winter seasons (Collins et al., 2000; Lynn & Simpson, 1987).

In the past decade, the Eastern North Pacific has experienced extreme climatic events, including a severe marine heatwave starting in late 2013, followed by the strongest El Niño on record in 2015–2016 (Jacox et al., 2016). Following these heatwaves, coupled with steadily rising temperatures, range expansions have been documented for zooplankton and sub-tropical fishes (Cavole et al., 2016; Leising et al., 2015; Wells et al., 2017), as well as oceanic dolphins including short-beaked common dolphins and striped dolphins (Becker et al., 2019). Our findings suggest that a range expansion may be occurring for the Southern California/Baja Pacific white-sided dolphin population, while a range contraction out of the Southern California Bight may be occurring for the CA/OR/WA population. Notably, the detection of LoB clicks at site CINMS in the fall of 2018 and 2019 – beyond the known range of the Southern California/Baja population – lends further support to the possibility of a northward range expansion in response to changing oceanographic conditions. The inverse relationships between both click types and environmental drivers support the hypothesis that the click types represent distinct populations, and that those populations may favour opposing oceanographic conditions (Figure 7). Our findings indicate that the LoA click type, associated with the CA/OR/WA population, shows a preference for cooler, nutrient-rich waters typically found during La Niña conditions, as evidenced by their negative correlation with the ONI and positive correlation with the NPGO in the Southern California Bight. This suggests a reliance on strong upwelling-driven productivity that characterizes such periods. Alternatively, at site CINMS, the CA/OR/WA LoA click type was weakly negatively correlated with both the ONI and NPGO. The timeseries in Figure 5 indicates that LoA presence has increased at site CINMS in recent years. We hypothesize that this may be further evidence of a range contraction, meaning, the CA/OR/WA population may be staying further north to remain within their preferred cool-temperate habitat rather than entering the warmer waters of the Southern California Bight, thus resulting in the weak negative correlation with the ONI and NPGO during this timeframe. Additionally, the apparent negative relationship between the NPGO index and Pacific white-sided dolphin acoustic presence at CINMS is consistent with results from Henderson et al. (2014), who found a positive correlation between the PDO and Pacific white-sided dolphin visual presence, hypothesizing that this may be evidence of a range contraction as warmer conditions bring animals to closer to shore.

Conversely to LoA, the LoB click type, associated with the Southern California/Baja population, exhibits a positive correlation with the ONI and a negative correlation with the NPGO in the Southern California Bight, suggesting a preference for warmer, less productive conditions that prevail during El Niño phases or positive phases of the NPGO. However, as the climate continues to change rapidly, the meaning of large-scale derived climate indices such as the NPGO and PDO may change unpredictably (Litzow et al., 2020; Werb & Rudnick, 2023) and future work should incorporate meso-scale environmental drivers to predict oceanic dolphin presence. Finally, the significant differences in LoA and LoB presence before, during and after the 2014–2016 marine heatwave highlight the profound effect this extreme event may have had on the geographic distribution of the two populations.

The CA/OR/WA and Southern California/Baja Pacific white-sided dolphin populations remain visually indistinguishable; however, our work demonstrates that they may be acoustically distinguishable by the two click types described in Soldevilla et al. (2008). Here, we have provided support to resolve the geographic boundaries of each stock, as well as elucidating biogeographic range shifts throughout a decade of environmental change in Southern California. Passive acoustic monitoring is used in this context as a valuable tool for population-level cetacean assessments and we encourage future policy and management directives to integrate our findings when developing tailored management approaches for each stock. Additionally, integrating environmental DNA sampling (Suarez-Bregua et al., 2022) alongside PAM and visual surveys offers a promising avenue for future research. Such a multidisciplinary approach would not only enrich the lines of evidence (Martien et al., 2019) available across sampling platforms but also provide deeper insight into stock structure and geographic boundaries. This comprehensive understanding is critical, particularly in light of potential climate-driven range shifts, as it will inform and refine population-level management and conservation strategies, ensuring they are adaptable and effective in the face of new environmental challenges.

## 4.2 | Limitations

Our study relied on automated detection and classification of echolocation clicks and manual removal of false positives. This technique, while greatly increasing the efficiency of our data processing pipeline, resulted in some missed detections. We assessed missed detection rates by comparing analyst labels with automatically generated labels in three test deployments outside of the source domain, spanning multiple years and locations not included in the training data. Recall, or the true positive rate, ranged from 83% to 92% for the LoA category and 100% for the LoB category (Tables S2–S4). These findings suggest an expected recall of over 83% for LoA and 100% for LoB categories across our study, acknowledging possible fluctuations in other untested datasets. By removing all false positives, our study achieved 100% precision. While potential biases between analysts were not explicitly addressed, they are presumed to be minimal due to the consistent training and methodology imparted to all three analysts. Despite potential limitations, the amalgamation of automated detection and manual validation was an efficient, consistent and robust methodology for examining the spatiotemporal distribution of Pacific white-sided dolphins across diverse biogeographic regions, encompassing over 50 cumulative years of data.

Recording periods and total recording durations varied across different sites (Table 1). We adjusted for recording effort in our spatial and diel analysis and selected sites with periods of full recording effort for our interannual timeseries analysis. However, the variability in recording effort, particularly along the latitudinal gradient of our study sites, may have obscured the true seasonal-spatial patterns, especially when considering interannual variability. Seasonal recording effort was considered complete if at least 25% of the seasonal bin had recording activity. This threshold, while necessary to include all sites in our analysis, may have influenced the apparent seasonal patterns to favour sites and seasons with complete recording periods.

Our findings support the previous hypotheses that Pacific white-sided dolphins produce population-level echolocation clicks and partition the Southern California Bight habitat in time and space. Nonetheless, alternative hypothesis cannot be completely rejected. The differences in spatial distribution in the Southern California Bight could reflect specific acoustic signals being used by the same animals in different habitats based on prey composition. Detection of the LoA click type at Baja_GI presents confounding evidence for the hypothesis that the clicks are population specific. It is possible that the Southern California/Baja population could produce the LoA click type in certain regions, or when hunting certain prey items. Although, with only one encounter of Pacific white-sided dolphins at this site during three continuous years of recording effort, the most parsimonious explanation is that the species is rare in this region and environmental conditions were favourable for the CA/OR/WA animals to venture further south resulting in detection at Baja_GI.

# 5 | CONCLUSIONS

Here, we demonstrate how long-term PAM can be used to study population-level species dynamics. The biogeographic patterns of Pacific white-sided dolphins described in this study support the hypothesis that the CA/OR/WA and Southern California/Baja populations are acoustically distinct, and exhibit spatial and temporal niche partitioning in the Southern California Bight. The implications of this research are especially important in the context of extreme climatic events witnessed in the Eastern North Pacific over the past decade. Our results suggest a potential range expansion of the southern population and a range contraction of the northern population in response to warming ocean conditions. As the marine environment continues to change rapidly, dynamic and innovative management strategies will be increasingly called upon to protect species and their ecosystems. Long-term passive acoustic monitoring is a valuable tool for establishing baselines and should be further integrated into protected species management as we navigate this period of unprecedented environmental change.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

## PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13903.

## DATA AVAILABILITY STATEMENT

Binned hourly detections and deployment metadata from each recording site are publicly available on Dryad. Binned hourly detections contain counts of click-positive minutes per hour for each click type at each site where they were detected (https://doi.org/10.5061/dryad.95x69p8rj).

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## BIOSKETCH

The researchers involved in this project use acoustic methodologies to understand cetacean species distributions and population dynamics, trophic interactions and adaptations to changing environmental conditions (Scripps Acoustic Ecology Lab, Scripps Machine Listening Lab).

Author contributions: SB-P, ACMK, KEF and MNA designed the project. SB-P and KEF oversaw data acquisition. KEF designed the machine learning approach implemented by MNA. MNA and AA performed acoustic analysis, and MNA performed statistical analysis, wrote the manuscript text and prepared the figures. SB-P, ACMK, KEF and AA reviewed all figures, analysis and writing. All authors contributed to the final manuscript.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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