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ORIGINAL RESEARCH

Echolocation repetition rate as a proxy to monitor population structure and dynamics of sperm whales

Alba Solsona-Berga, Natalie Posdaljian, John A. Hildebrand & Simone Baumann-Pickering

Scripps Institution of Oceanography, University of California San Diego, La Jolla California, 92093-0205, USA

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Correspondence
Alba Solsona-Berga, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093-0205. Tel: +1 (858) 534-8036; Fax: +1 (858) 5346-849; E-mail: asolsonaberga@ucsd.edu

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Abstract

Characterizing population structure and dynamics is critical for the conservation of endangered species. Monitoring sperm whales *Physeter macrocephalus* is especially difficult because it requires monitoring different latitudes to capture the dynamics of most populations. Since their remarkable sexual dimorphism in body size is reflected in their sounds, passive acoustic monitoring presents an opportunity to capture contiguous patterns in time, space, and over large scales. We show that the echolocation repetition rate (measured as inter-click interval, ICI) as a proxy for body length is a suitable approach for large-scale acoustic monitoring. Body length has previously been estimated from the time interval between pulses (IPI) within sperm whale echolocation clicks. These estimates can only be achieved when whales are oriented toward the recorder or directly facing away, resulting in sparse data. A representative subsample of data demonstrated that ICI and IPI are linearly correlated, allowing conversion of ICI distributions into likely body length categories. This approach was applied to three monitoring sites in the Gulf of Mexico (2010–2017), where sperm whale population structure and male movements were poorly understood. We identified three classes: large animals between 12–15 m (ICI between 0.72 and 1 sec), presumed to correspond to adult males, and small animals below 12 m (ICI between 0.44 and 0.64 sec) likely pertaining to social groups (mixed groups with adult females and their offspring), and the third class with mid-sized animals (ICI between 0.64 and 0.83 sec) believed to contain adult females or sub-adult males. Our results revealed spatial and seasonal variability of the population structure including possible male presence throughout the year and migratory patterns of the population. This approach provides a means to efficiently characterize the putative population structure of sperm whales to understand the population's geographical dynamics and population status, which is relevant under rapidly changing habitat conditions.

Introduction

Characterizing population structure and dynamics is critical for the conservation of endangered species. Many marine mammal population estimates are data-limited and lack temporal and spatial coverage. This is due in part to elusive behaviors (e.g., long and deep foraging dives or extensive migrations) which, combined with their presence in remote areas, represent logistical and economic challenges in monitoring. Studying sperm whales *Physeter macrocephalus* is especially difficult in many areas as it requires monitoring different latitudes to capture their population dynamics (Whitehead & Weilgart, 2000). Females and males have differences in social preferences and ecological needs (Best, 1979; Gowans et al., 2007), resulting in latitudinal segregation across most of their range (Lyrholm et al., 1999). This excludes the latitudinally restricted Mediterranean population, where sexes are found in sympatry (Frantzis et al., 2014; Pirotta et al., 2011), but males and females still use areas with different characteristics resulting in fine spatial scale segregation (Jones et al., 2016; Pirotta, Brotons, et al., 2020; Pirotta, Vighi, et al., 2020). However, most populations span large geographic ranges, including international borders (Rice, 1989), with different anthropogenic threats. They may encounter threats from cumulative risks of multiple stressors (e.g., anthropogenic noise, ship strikes, fisheries interactions, oil spills, and pollution; National Academic of Sciences Engineering and Medicine, 2017).

The strong sexual segregation of sperm whales is well known but their large-scale movements are still unclear (Whitehead, 2003). Females display social philopatry, and in some regions can also display geographic philopatry (Alexander et al., 2016; Engelhaupt et al., 2009), remaining in tropical and subtropical waters in social groups for cooperative care of their young (Best, 1979). They form long-lasting social units consisting of adult females, calves, and juveniles (Whitehead et al., 1991). Once male juveniles reach puberty, they gradually move to higher latitudes (Rice, 1989) forming small groups and become increasingly solitary as they mature (Best, 1979; Whitehead, 2003). Mature males travel to lower latitudes to associate with social groups in mating periods (Whitehead, 2003), resulting in large ranges for males at the population level (Gaskin, 1970; Whitehead & Weilgart, 2000). The latitudinal movements of mature males were believed to be seasonal (Best, 1979), but further studies have shown them to be labile (Whitehead, 2003). North–south migrations were observed in midlatitudes, but the seasonal movement is less evident in tropical and subtropical regions (Whitehead, 2003), where mature males have been seen at low latitudes in small numbers for a few months throughout the year (Silva et al., 2014; Whitehead, 1993). Observations of large-scale movement are limited in most regions and seasonal patterns are only explored in well-studied populations (Steiner et al., 2012; Whitehead et al., 2008). Gene distributions suggest the movement of both sexes covering substantial parts of the ocean basins, with some flux of males breeding in different basins (Alexander et al., 2016; Lyrholm et al., 1999).

Monitoring females and males over long periods of time requires cost-effective methods applicable to large-scale data. Sexual dimorphism is key to tracking the structure of sperm whale populations using acoustics. They have the widest degree of sexual dimorphism in body size among cetaceans (Rice, 1989) and it is reflected in their sounds (Goold & Jones, 1995). Sperm whales use sound to navigate, communicate and find prey (Gordon, 1987; Mullins et al., 1988; Norris & Harvey, 1972; Watkins & Schevill, 1977; Worthington & Schevill, 1957). The most frequently detected sounds are broadband echolocation clicks, with apparent source levels measured up to 235 dB_{rms} (Møhl et al., 2003) and 229 dB_{peak} re: 1 μPa at 1 m (Zimmer, Tyack, et al., 2005). These highly-directional clicks can be detected acoustically over large distances (range of 10–20 km) and may be produced regularly for over 80% of a dive cycle (Teloni et al., 2008; Watwood et al., 2006; Weilgart & Whitehead, 1990), although values as low as 60% have been reported in other regions (Douglas et al., 2005; Fais et al., 2016). The most supported theory is that regular clicks (or usual clicks) are primarily used for long-range prey detection (Jaquet et al., 2001; Madsen, Wahlberg, & Møhl, 2002). There is a general relationship between the repetition rate of echolocation clicks, measured as the inter-click interval (ICI), and the size across odontocete species (Jensen et al., 2018). This may be related to the maximum detection range for prey (Jensen et al., 2018) since the interval between clicks allows for an echo-return to be detected before emitting another click, and the greater the time interval between clicks the longer the range. The ability to scan large volumes of water allows larger whales to find more calorific prey in deeper layers (Goldbogen & Madsen, 2018); this can satisfy the high calorific requirements to maintain such size (Teloni et al., 2008). Males, with larger bodies, exploit a wider variety of prey than females by searching for bigger prey at larger depths or smaller, more accessible prey in aggregations at shallower depths (Isojunno & Miller, 2018; Teloni et al., 2008). This exploitation of different-sized prey at varying depths has facilitated the evolution of larger sonar structures that can increase effective detection ranges (Goldbogen et al., 2019).

The multi-pulse structure that characterizes sperm whale echolocation clicks results from the sound transmission pathways before exiting the rostrum (Cranford, 1999; Norris & Harvey, 1972). The time between the multiple pulses (referred to as the inter-pulse interval, IPI) scales with the body length of whales emitting the clicks (Gordon, 1991). The empirical derived relationship relating IPI and total length are supported by different measurements of the spermaceti organ (i.e., sound speed, nasal complex length, and photogrammetry; Flewellen & Morris, 1978; Møhl, 2001; Rhinelander & Dawson, 2004) that has led to estimates of body length (Growcott et al., 2011; Rhinelander & Dawson, 2004). When clicks are received at the sensor, the multi-pulse structure can be cluttered by additional pulses and time delays that vary with the orientation and proximity of the echolocating whale (Laplanche et al., 2006; Zimmer, Madsen, et al., 2005).

Autonomous acoustic sensors are capable of recording for months, generating large datasets of clicks detected from all angles and distances (Miller & Miller, 2018; Stanistreet et al., 2018). The algorithm presented by Beslin et al. (2018) automates the estimation of IPI from on-axis clicks but is limited by the high proportion of off-axis clicks from autonomous sensors (i.e., over 99% of recorded clicks; Beslin et al., 2018) that do not display a clear multi-pulse structure. Methods that involve averaging techniques over long click sequences have improved the consistency of IPI estimates but require distinguished clicks of the focal whales (Antunes et al., 2010; Teloni et al., 2007). The challenge is to overcome the sources of variability for body length estimation and hence population structure as the recorded clicks are received from unknown whale orientations, on a variety of acoustic sensors, and under a big data paradigm.

We describe a method to categorize acoustic encounters of sperm whales based on the distribution of distinct ICI distributions as a proxy for body length. The instantaneous repetition rate of regular clicks varies considerably during a dive. However, when averaged over several minutes or an entire dive, it is remarkably consistent (Douglas et al., 2005). We use the distinct ICI distribution as potential indicators of female and male presence and investigate if population structure can be determined on the basis of passive acoustic monitoring. We apply this method to 7 years of acoustic data from three monitoring sites in the Gulf of Mexico (GOM), where male movements and timing of breeding are largely unknown.

Methods

Data collection

Underwater sounds of sperm whales were monitored at three locations in the GOM between 2010 and 2017 (Fig. 1) using high-frequency acoustic recording packages (HARPs). HARPs are autonomous bottom-mounted instruments equipped with a hydrophone, data logger, battery power supply, and acoustic release system (Wiggins & Hildebrand, 2007). All HARPs were recorded at a sampling frequency of 200 kHz with an effective bandwidth from 10 Hz to 100 kHz. The sequential deployments over multiple years provided nearly continuous acoustic data (Appendix S1).

Echolocation click detection

We identified individual echolocation clicks of sperm whales using a multi-stage approach consisting of automated and manual evaluation processes. We detected candidate clicks using an automated multi-step detection algorithm (Solsona-Berga et al., 2020) developed in MATLAB (version R2016b, The MathWorks, Natick, MA), based on the proposed approach for odontocete clicks (Roch et al., 2011; Soldevilla et al., 2008). The detector applied a band-pass filter between 5 and 95 kHz to minimize other sources of noise. Clicks with a received level of at least 130 dB_{pp} were retained to maintain a consistent detection range, remaining well above background noise. We removed other odontocete clicks based on spectral characteristics (Solsona-Berga et al., 2020). Sperm whale clicks can be easily distinguished from other odontocete clicks because of their lower-frequency content and long ICI. One of the difficulties is that their signals are similar to impulse cavitation sounds produced by vessel propellers. We detected ship passages using an automated classifier based on average power spectral densities and an adaptive received level threshold to detect passages above

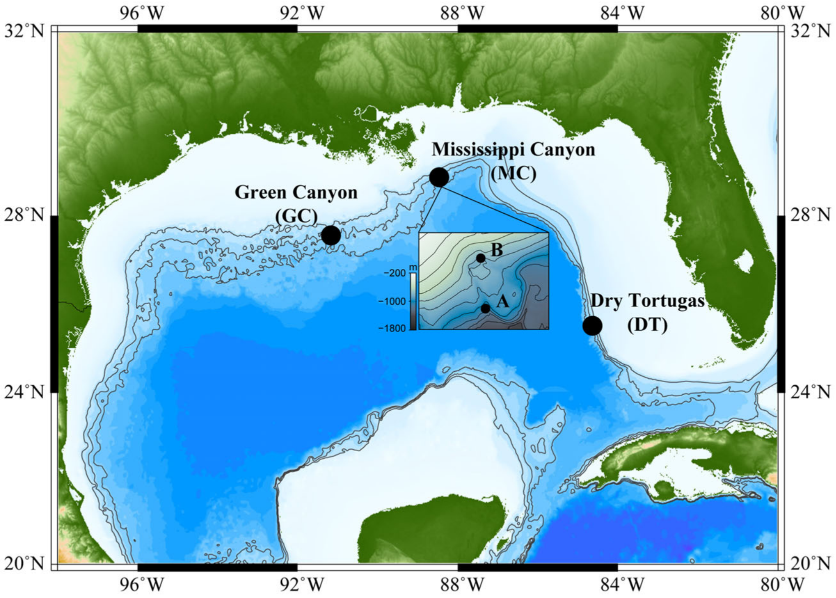

Figure 1. Map of recording site locations in the Gulf of Mexico with green/brown representing land masses, and white/blue representing water (Amante & Eakins, 2009). The three sites are named based on the federal lease block in which they are located: Green Canyon (GC, at 1100 m), Mississippi Canyon (MC, location A at 980 m and location B at 800 m), and Dry Tortugas (DT, at 1300 m). Contours are at 500, 1000 and 1500 m. Inset map showing two different locations for monitoring at the MC site with a color scale representing seafloor depth (Wessel et al., 2019).

background noise (Solsona-Berga et al., 2020) and excluded clicks within those periods of ship passages.

We manually removed the remaining false positive detections using the open-source software *DetEdit* (Solsona-Berga et al., 2020) to ensure that retained clicks were attributable to sperm whales. This software provides interactive displays that show detections in relation to one another and compares and contrasts different features. This assisted editing facilitated the quality control of large numbers of detections.

Acoustic body length estimation

A subset of 176 encounters (a dive cycle of about 45 min) with echolocating sperm whales from multiple years across all sites was selected randomly and used to examine the relationship between ICI distribution and whale body length in the GOM. We manually measured the IPIs and ICIs of click sequences in our data subset using the software *Triton* (Wiggins & Hildebrand, 2007). Analysts referred to the spectrogram and waveform to randomly select click sequences during periods with consistent ICI that had little variability in time from one click to another (i.e., <200 msec), indicating they came from the same whale and were clearly distinguishable from other interleaved click sequences based on the variability of amplitude between consecutive clicks. The displayed click trains were band-pass filtered between 5 and 95 kHz to clarify the clicks and their pulse structure from noise. A total of 402 clicks were manually measured from different days (n = 127) and all sites. Manual measurements of ICI were done by selecting the start time of each click. Clicks that occurred with consistent intervals (variability below 200 msec) were considered suitable for measurement. Clicks were measured when at least five consecutive clicks were consistent. Manual measurements of IPI were done by selecting the time of the highest amplitude of each pulse. Clicks were considered suitable for measurement when at least three pulses were clearly identified. The slope of a linear-fit between mean ICI and IPI was used to predict acoustic animal lengths corresponding to ICI distributions. Following the methods of Giorli and Goetz (2020), we determined the acoustic body length for animals with IPIs less than 4 msec using the Gordon (1991) equation derived from whales less than 11 m (females, juveniles, and calves) and the Growcott et al. (2011) equation derived from larger whales with IPIs greater than 4 msec.

Inter-click interval classification

We calculated ICIs as the time difference between sequential clicks and developed a method to minimize the instantaneous fluctuations and capture the consistency of ICIs in time across encounters. We obtained ICI distributions over 5-min windows by computing a histogram with a 25-msec bin width, restricted to values between 0.3 and 1.4 sec (Fig. 2A). The use of histograms allowed us

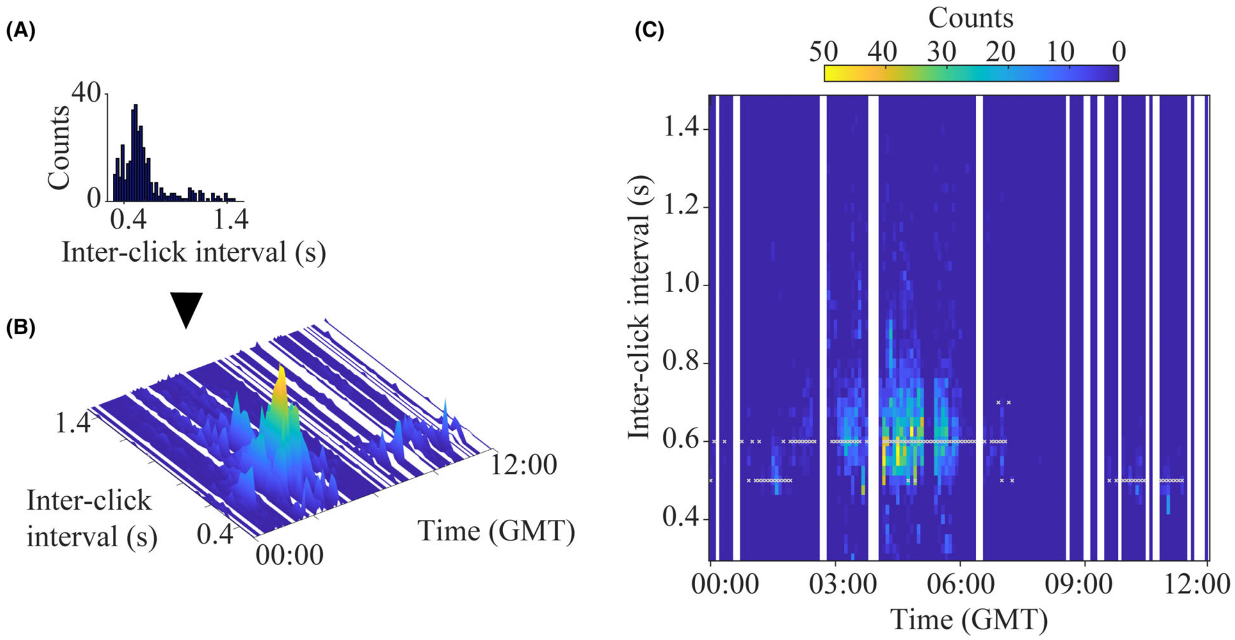

Figure 2. Method to classify ICI distributions: (A) ICI histograms, 25 msec bin width over 5-min time bins, (b) concatenated in time with the count in color. (c) ICI distribution visualization (ICIgrams) for successive 5-min time bins. White points represent histogram mode (dominant ICI band with 100 msec bin width).

to graphically capture one or multiple mode distributions in each window while still showing the wide range of variation. We restricted the ICI range on the upper boundary to minimize ICIs caused by some of the clicks within the click train not being detected. Values below the lower boundary of the ICI range were ignored to minimize the influence of interleaved click sequences from multiple animals clicking at the same time, resulting in perceived short ICIs. We developed a custom graphical user-interface tool (Fig. 2C) based on MATLAB (MathWorks, Natick, MA) to display time series of ICI histograms as a heatmap, similar to the agglomeration of ICI histograms referred to as ICIgrams by Miller and Miller (2018). Comparable to a spectrogram, the interface displayed each 5-min window ICI distribution over time, with warmer colors where ICI bins had higher counts representing the mode. To enhance distributional differences in the display, for each 5-min window we computed a histogram with 10 ICI bins of 100-msec bin width, referred to as ICI-bands, where each 100-msec bin was centered on the first decimal from 0.4 to 1.4 sec. The ICI band with the highest count was displayed with a cross mark to highlight the mode in each 5-min window (Fig. 2C). If a 5-min window had a bimodal distribution with equal counts, cross marks were displayed on both modes. An interactive panel displayed the ICIgrams for one day, providing the context needed to intuitively annotate large batches of data by selecting single or multiple 5-min windows and attributing each time window to a heuristic group of modal ICIs. Heuristics were essentially assumptions regarding the typical clicking rate behavior of sexes and maturity levels and were based on ICI ranges of dive cycles reported in the literature (Appendix S2). Using this display, trained analysts (ASB, NP) recognized repetitive clicking rate patterns across time and subjectively ascribed them to one of the three heuristic groups: (1) fast-clicking (modal ICI <0.6 sec), (2) medium-clicking (0.6 > modal ICI <0.8), (3) slow-clicking (modal ICI >0.7), 4) indecisive (less than 5 consecutive windows with a consistent ICI). Less than 3% of categorized events were classified as indecisive. All decisions were evaluated and agreed upon by both analysts.

Statistical analysis

We examined temporal patterns of each ICI class at each site using generalized additive models (GAMs) with total presence in minutes per day as the response variable and Julian day and year as the predictor variables for seasonal and multi-year trends. During 2010–2013 at site MC, the HARP was deployed at a mean depth of 980 m southwest of a seamount (location A, Fig. 1, Appendix S1). Beginning in 2014, the hydrophone was deployed 15 km north of its previous location, at a depth of 800 m north of the seamount (location B). These locations were modeled as different sites (Appendix S3). GAM analysis was carried out using the *mgcv* package (Wood, 2011) in R (R Core Team, 2019). Due to the zero-inflated nature of the data, we used a Tweedie distribution with a logistic link function. The smoothing function for Julian day was estimated by a cyclic cubic regression spline and limited up to six degrees of freedom to help interpretability of the four seasons and allow for unique conditions during season transitions. Year was modeled with a thin-plate spline with no restrictions. We employed the restricted maximum likelihood (REML) to optimize the level of smoothing (Marra & Wood, 2011).

Results

A 7-year dataset of sperm whale detections

We collected a total of 16 years of acoustic data from three sites in the GOM region (GC, MC, and DT). Sperm whale clicks were automatically detected in large numbers during all deployments at each site, with click counts ranging from 8600 to over 11 million analyst-confirmed detections per deployment (Appendix S1).

Acoustic body length estimation

To characterize the relationship between ICI distributions and body length from our subset, we correlated the mean ICI and IPI for 176 click trains and converted the mean IPIs into acoustic body lengths. The subset was composed of 44 click trains from GC, 43 from MC, and 88 from DT. Between all three sites, mean ICIs ranged between 0.43 and 1.32 sec, and mean IPIs ranged between 1.73 and 7.30 msec. Although some scatter is observed, there is a positive relationship between IPI and ICI (line of best fit: IPI = 0.004*ICI + 0.9, $R^2 = 0.5$; $\rho = 0.7$, $p < 0.001$: Spearman's correlation coefficient; Fig. 3). This corresponded to acoustic body length estimates between 7.3 and 15.4 m (Fig. 3). The slope between ICI and body length suggests that a 0.7 m increase of size is associated with a 0.1 sec increase in ICI (line of best fit: body length = 0.006*ICI + 6.3, $R^2 = 0.5$; $\rho = 0.7$, $p < 0.001$: Spearman's correlation coefficient; 3).

ICI distributions

We inspected a total of 1081 days of ICIgram plots, with 306 days of detections from GC, 683 days from MC, and 92 days from DT. ICIs varied considerably within each encounter but a dominant clicking rate was observed across most encounters, regardless of the received levels of the detected clicks (Fig. 4). Three different classes of

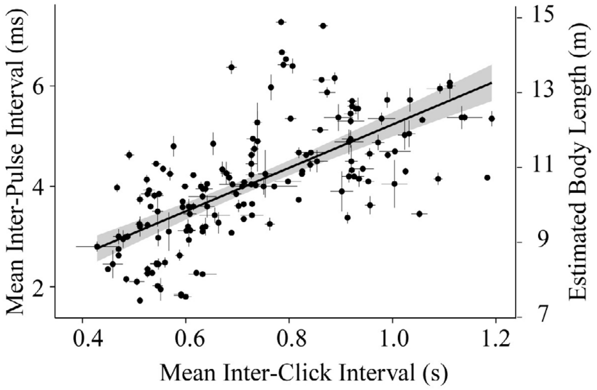

Figure 3. Relationship between ICI and IPI/sperm whale estimated body length. Each point represents a click train with mean values and error bars indicate the standard error of the mean. Linear regression (black line) with confidence intervals (shaded area).

dominant ICI distributions recurred across all sites with similar received level distributions (Fig. S1), suggesting the possible presence of whales with different body lengths (Fig. 5). Class A was characterized by a dominant ICI distribution with a mode at 0.46 sec (median 0.51 sec, IQR 0.20 sec, Fig. S1A), class B at 0.68 sec (median 0.72 sec, IQR 0.19 sec), and class C at 0.80 sec (median 0.83, IQR 0.27 sec). ICI variability within each encounter was observed when multiple animals were clicking simultaneously (i.e., class A Fig. 5A, Fig. S2), when several clicks within a period of echolocation were not detected (Fig. 5C, Fig. S2), and in periods where the ICI variability was caused by the animal dive behavior (i.e., descent phase, Fig. S3). Such variabilities were reduced when displayed in time series of modal ICI distributions of 5-min windows. Despite the notable difference between the three classes, there may be short bouts when dominant ICI distributions might be associated with individual animal behavior (Fig. S4). However, these exceptions become trivial with large datasets that markedly display the three classes of ICI distributions.

The ICI-body length relationship was used to categorize the three classes of consistent ICI distributions into approximate body length ranges. Class A with dominant ICIs between 0.5 and 0.7 sec corresponded to small animals between 9 to 11 m, equivalent to adults in social groups (adult females and their offspring) reported by Jochens et al. (2008) in the GOM region. Class C with dominant ICIs between 0.7 and 1 sec which we hypothesized corresponds to adult males between 12 to 15 m. Although class B was easily distinguished in the ICIgrams, the length ranges for class B overlapped with those of the other two classes. Hence, a maturity class was not distinguishable based on the relationship of ICI and acoustic length and was referred to as mid-size animals (larger than A and smaller than C).

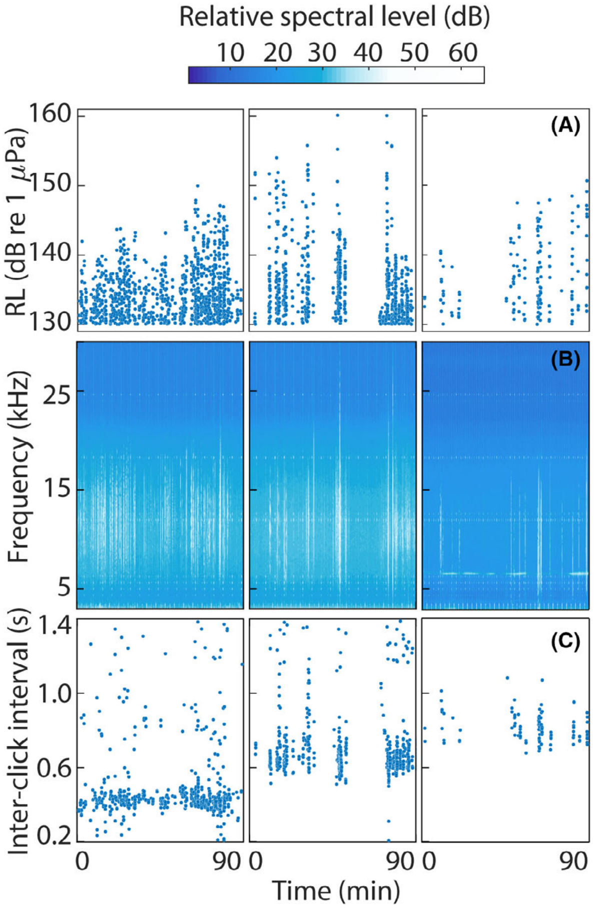

Figure 4. Three sperm whale encounters with distinctive echolocation repetition rates. (A) Received levels from each echolocation click, (B) long-term spectral average (average 1000 non-overlapped Hann-windowed spectra every 5 sec), and (C) ICIs from echolocation click detections.

Population structure exhibit different temporal and spatial patterns

All three classes of dominant ICI distribution were detected across all sites with notable differences in temporal and spatial daily detection. Presumed social groups (class A) were the most prevalent group in the GOM region: they were commonly detected at MC and GC (64 and 42% of recording days, respectively) and were less frequent at DT (14% recording days, Fig. 6). While high rates of detection of social groups occurred during much of the year at MC and GC, there was a significant increase in detections during the fall (Fig. 7). GC also had a peak in detection in early spring and a decrease in late winter. At DT social groups were detected seasonally from May to August persistently during all years (Figs. 6 and 7). There was a decrease in the daily detection of social groups in the last 2 years at MC. There was an

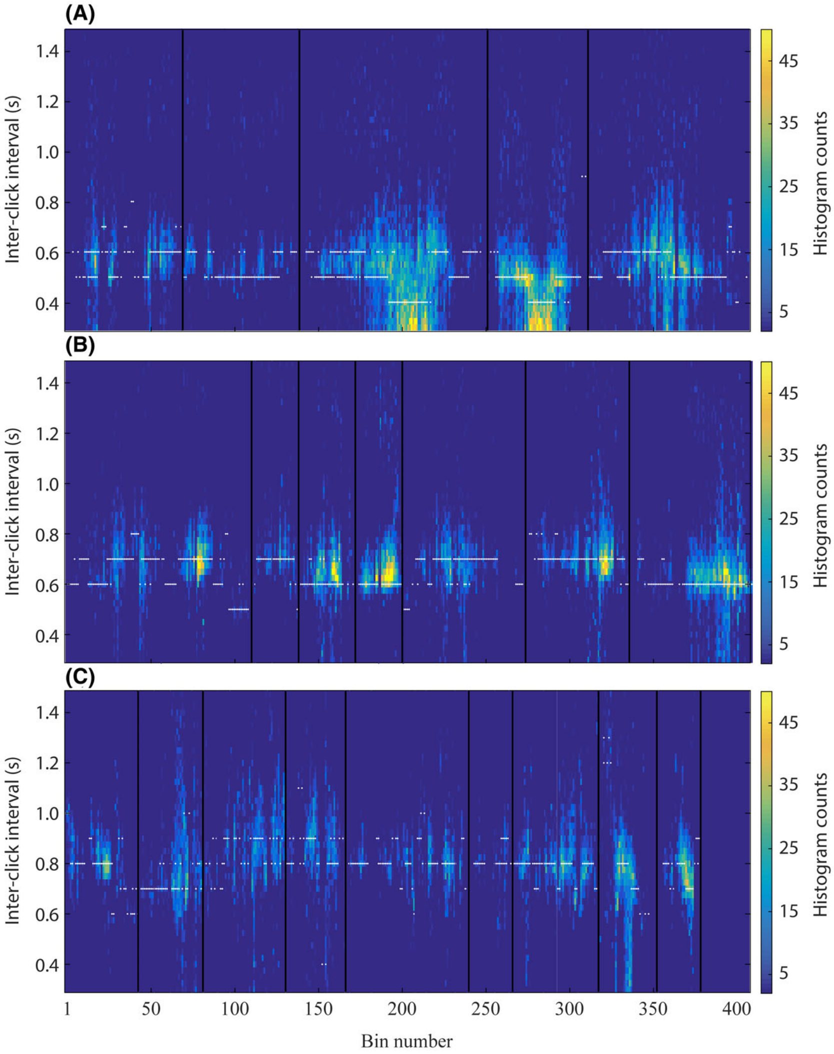

Figure 5. Concatenated ICIgrams of the three classes, A, B, and C (corresponding plots a, b, and c) over several encounters. Encounter boundaries are indicated by a black line. ICI distributions for each 5 min time bin with the color scale representing histogram counts.

overall increase in GC and DT, with a decrease from 2013 to 2015 in GC, and 2014 in DT.

Mid-size whales (class B) were detected in low numbers across all sites (<10% of recording days, Fig. 6). At GC and MC there was a slight peak in late summer (Fig. 7). While our model shows an increase in detections in late summer at both locations A and B at MC, only location B had a significant peak in detections. Both locations were modeled as different sites so location A had less than 3 years of data. There was no interannual change in the number of daily detections of mid-size animals at GC and DT, while at MC there was an increase in 2016.

Presumed adult males (class C) were detected throughout the year and in the lowest numbers at GC and DT (3% of recording days, Fig. 6). At GC, there was a significant peak in detections during late summer and an increase in the number of daily detections over the monitoring years. Adult males were detected more regularly at MC, although detection levels were also low (6% of recording days). There was a decrease in the number of daily detections from 2010 to mid-2011, followed by an increase in the subsequent years.

Discussion

Inferring population structure through ICI distributions

Our results suggest that ICI can be used as a proxy for sperm whale body length, with increasing ICI scaling with body size. Acoustic body lengths were estimated from the measured IPIs within click sequences from a subset of

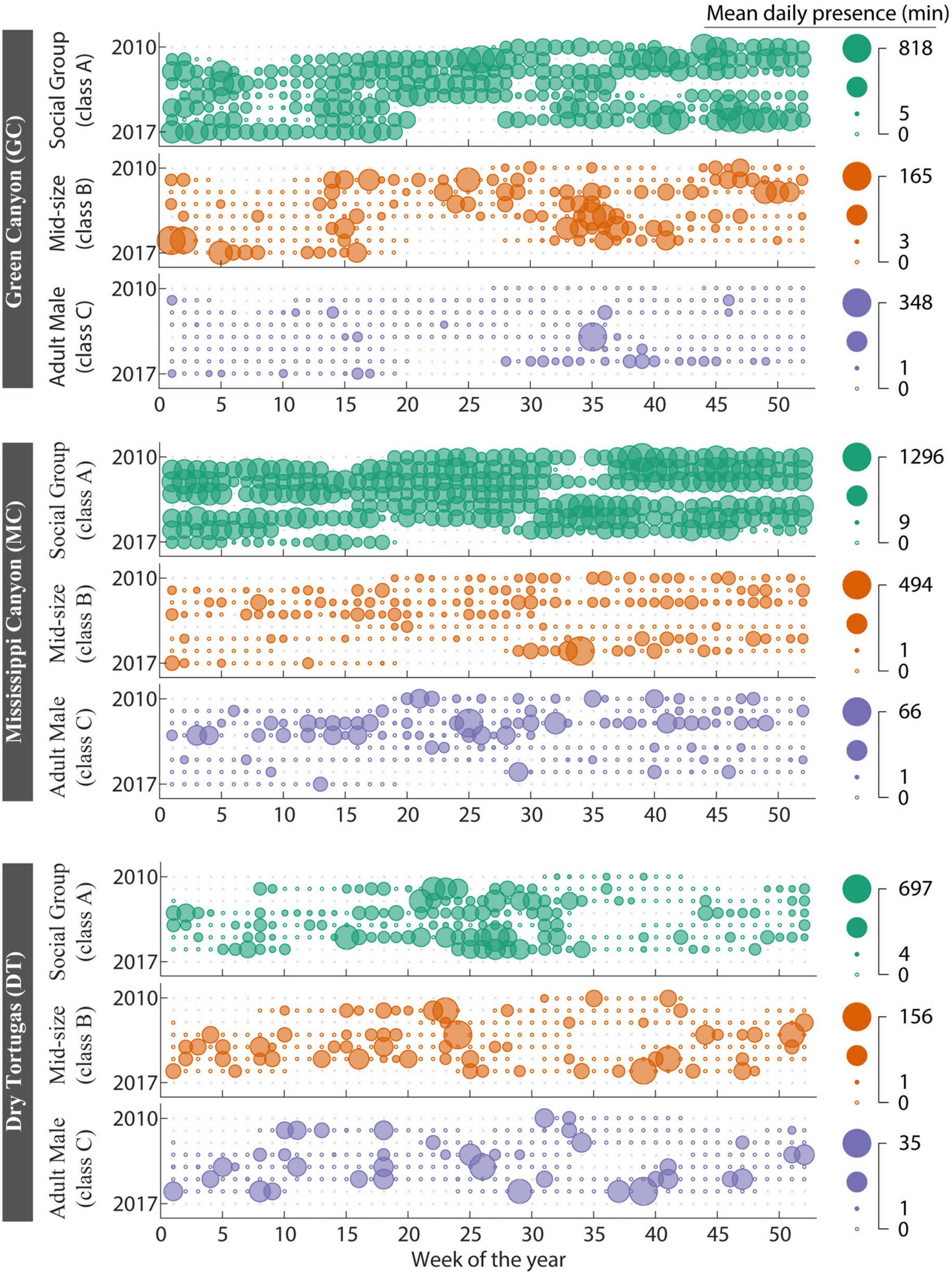

Figure 6. The daily presence of the three classes is categorized as putative social groups (class A in green), mid-size (class B in orange), and adult male (class C in purple) showing the variation in time at three sites of the Gulf of Mexico. Y axis is year and x axis is week. Bubble sizes indicate mean daily presence in minutes per week (note variable scale and minimum circle size indicating no presence), and x marks indicate times of no recording effort.

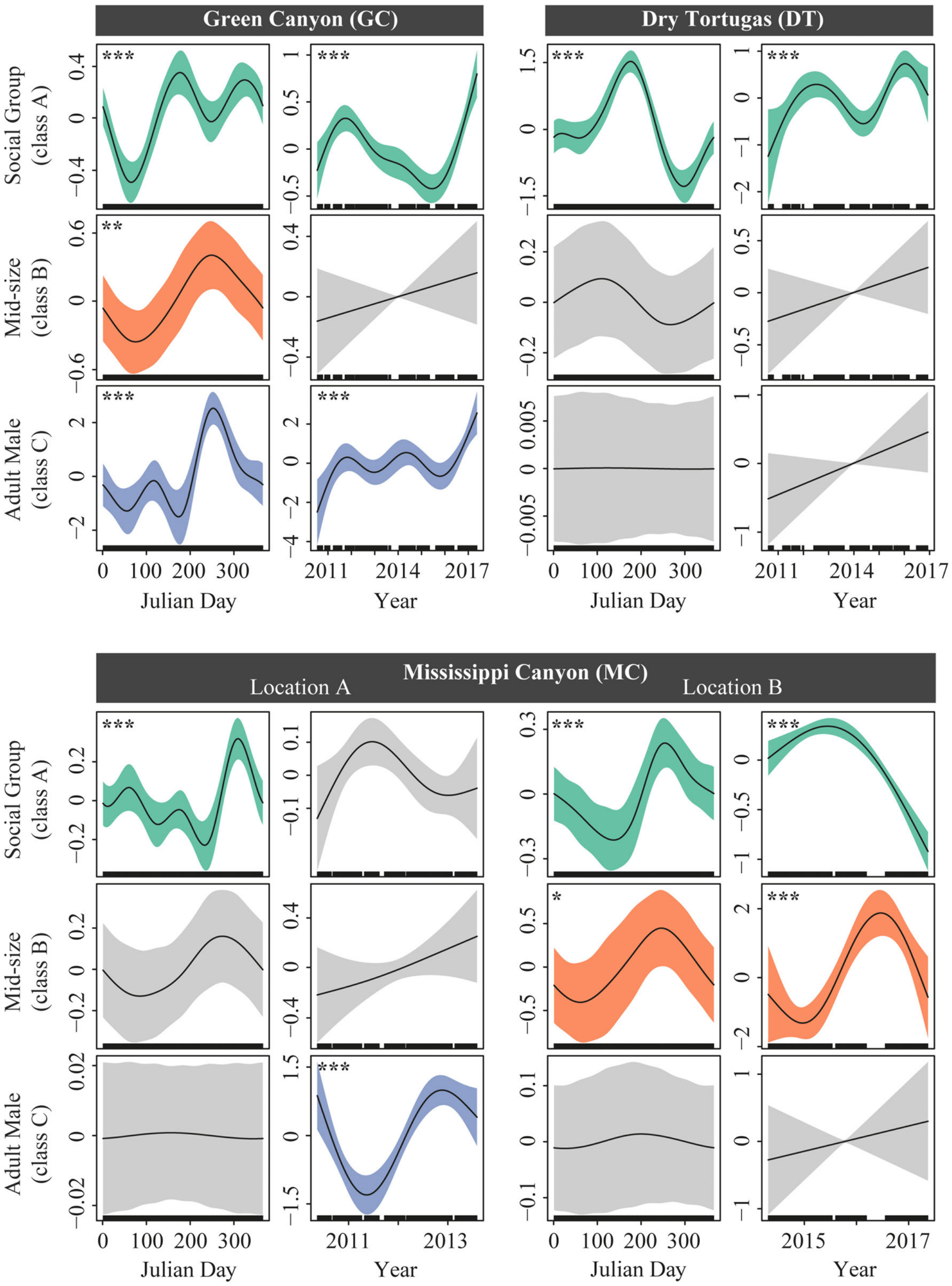

Figure 7. Generalized additive model plots for seasonal and multi-year variability of each class at three sites in the Gulf of Mexico. The solid line is the estimated smooth function, with a 95% confidence interval (shaded area). Rug plots (at the bottom of each individual plot) denote distribution. The zero in the y-axis indicates no effect of the predictive variable and quantifies the contribution made to the fitted values for that smooth function. Star indicates *p*-value significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) with plots in color having a significant *p*-value, others are shown in gray.

encounters. We used the linearly correlated, well-established allometric relationships between IPI and the head length of the animal to estimate total body length. Measured IPIs for an individual can vary on the order of 0.2 msec, related to the dynamics of the soft structure of the sperm whale nose (Bøttcher et al., 2018). The net result is a size error estimate of about 0.3 m (Bøttcher et al., 2018). The whale's distance to the sensor and orientation also affect IPI measurements (Zimmer, Madsen, et al., 2005). Such variation was a potential source of observed scatter in our observations relating to IPI and ICI. Even with this variability, estimated sizes in our study were consistent with those reported for the GOM (Collum & Fritts, 1985; Jaquet, 2006), although sizes from mature males are rarely reported for this area. Large animals were present in our study area, with similar sizes (approximately 14–15 m) to those solitary animals seen in the GOM from aerial surveys (Collum & Fritts, 1985), thus providing more evidence for the presence of breeding mature males in the GOM.

ICI may vary as a function of behavior during a dive. This typically occurs during terminal buzzes (ICI <0.1 sec; Teloni et al., 2008), at the descent phase of a dive (<15 min of the dive cycle) with steadily decreasing ICIs (Madsen, Wahlberg, & Møhl, 2002; Thode et al., 2002; Zimmer et al., 2003), where whales tend to target the seafloor and potential prey layers that were located during previous dives (Fais et al., 2015) and the ascent phase (Madsen, Payne, et al., 2002). Therefore, ICIs of regular clicks can range considerably, however, a fairly consistent rate of clicking is maintained for the majority of a dive (Douglas et al., 2005; Madsen, Payne, et al., 2002; Zimmer et al., 2003). Transforming the ICIs into time series of modal ICI distributions of 5-min windows, or ICIgrams, allowed us to reduce the variability caused by the whale behavior during the dive. Even with the variability in ICI distribution of several 5-min windows from multiple animals clicking or clicks being missed in a click sequence, the ICIgrams still represented the characteristic click repetition rate of the whale within the duration of an encounter. We found three dominant ICI distributions, categorized as classes A, B, and C. The three classes were found at all sites with similar level distributions. Lower received levels will indicate that detected clicks were fainter and, therefore, further from the sensor. Our results show that the difference in received level did not correlate to the three classes, and therefore classes were not related to the distance to the receiver, both horizontally and vertically.

Our results from a subset of data relating the body length ranges with ICI suggest that larger whales tend to click at a slower rate than smaller whales. Sperm whales in the Azores Islands had distinctive clicking rates (Gordon, 1991), with adult males having slower rates (ICI ~ 0.85 sec) than females (ICI ~ 0.51 sec) which was also revealed in our markedly distinct classes and positively correlated ICI-body length relationship. However, individual animal behavior may vary and in the study by Teloni et al. (2008), while three out of the four male sperm whales foraging off northern Norway had long ICIs during deep and shallow dives, one animal that comprised 2% of the clicks in their study did not. While our method may not exactly capture the variability of individual animals, it still provides an efficient tool for big data to learn about population structure or contribute to acoustic density estimation (*i.e.*, click rate estimation).

Based on the ICI-body length relationship, class A may be associated with social groups which matched animal sizes of adult females reported in the GOM that are on average 1.5–2 m smaller than the global adult female mean (Jaquet, 2006; Jochens et al., 2008). Class C may be associated with adult males which had similar sizes to adult males reported in the Atlantic (Miller, 2004; Santos et al., 1999), and to those few males reported in the GOM (the solitary animals observed from aerial surveys of 14–15 m and one tagged whale of 12.4 m; Collum & Fritts, 1985; Miller, 2004). Even though the ICI distributions of class B were well differentiated from the other two classes, corresponding whale sizes to those ICI ranges were not distinct enough to determine sexual maturity and are similar to both large females and sub-adult males. However, given their distinct separation from class A, the mid-size class may represent the presence of sub-adult male groups, which are often found in temporary aggregations of smaller "bachelor" schools (Best, 1979). Observations of several bachelor males in the GOM had average sizes of 11-m in length (Jochens et al., 2008).

Population structure in the Gulf of Mexico

The three classes were detected across all sites with variations in their temporal and spatial presence. Putative social groups were common in the northern sites (GC and MC), site MC being the most utilized. These sites are close to the core areas of social units reported in the northwestern and central GOM (Jochens et al., 2008). Jochens et al. (2008) described that tagged whales ($n = 52$) of adult females and juveniles moved irregularly without migratory patterns in that general area. However, we observed consistent seasonal patterns of the presumed social groups in the summer months at DT over the course of 7 years, and an increase in presence at MC and GC during fall, and early spring at GC. These spatial and temporal patterns suggest that there is a migratory pattern in the GOM region. A decrease in presence of the putative social groups at MC in the summer months indicates that a portion of whales moves away from the area to another part of the GOM, perhaps to the DT region, where strong seasonality was noted. This distinct migration pattern could be linked to oceanographic conditions associated with prey availability or breeding. However, no peak presence of the presumed adult males was observed except in late summer at GC. Instead, adult males were present throughout the year in low proportions at all sites, making the reason for this migratory pattern more complex. These results suggest that as in the South Pacific and the Gulf of California, the breeding season is extensive, encompassing most months of the year where males rove between groups of females staying only a few hours or days with each group (Coakes, 2004; Jaquet & Gendron, 2009; Whitehead, 1990).

Our results highlight the capability to monitor the population structure and dynamics at a large-scale from passive acoustic monitoring using dominant ICI distributions as a proxy for body length. Application of this method to the GOM provides the ability to detect the presence of presumed adult males in the area and new insights into spatial and seasonal variability of the population. A major step forward would involve automating the process of classifying dominant ICI distributions through the use of computer learning algorithms that automatically recognize consistent patterns.

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Data Accessibility

Acoustic detections used for this study are archived by the Gulf of Mexico Research Initiative at https://data.gulfresearchinitiative.org/data/R4.x267.180:0012 maintained by the Gulf Research Initiative Information and Data Cooperative.

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Supporting Information

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

Appendix S1 Gulf of Mexico acoustic recording specifications.
Appendix S2. Echolocation repetition rates from multiple studies of sperm whales.
Appendix S3. Summary of generalized additive models.
Appendix S4. Violin plot of inter-click interval and received level distributions per class.
Appendix S5. ICIgram examples with different ICI variability scenarios.