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## Vocal activity of tropical dolphins is inhibited by the presence of killer whales, *Orcinus orca*

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### ABSTRACT

Research has suggested killer whale (*Orcinus orca*) predation may affect cetacean vocal behavior; however, few data exist to test this hypothesis. Data collected during 40,976 km of visual and acoustic shipboard surveys in the tropical Pacific Ocean, including 1,232 detections of 13 species, were examined to determine if changes in dolphin vocal activity could be attributed to the presence of killer whales. Generalized linear models and Random Forest analyses were used to test the hypothesis that dolphin vocal activity was related to the distance and time to the nearest killer whale sighting. Both results show that dolphin vocalizations were inversely correlated with the temporal proximity of killer whales ( $P < 0.05$ ). Despite the relative rarity of killer whales in the tropics, they appear to influence vocal behavior of nearby dolphin schools. This disruption in communication may not significantly impact interactions necessary for survival in tropical waters where killer whale density is low. However, in temperate climates, where increased productivity supports a greater abundance of killer whales, this interruption in communication may have a greater impact. The lower incidence of whistling dolphins in temperate waters may be related to the greater abundance of killer whales in these areas.

Key words: killer whales, dolphin behavior, acoustic behavior, predator avoidance.

Killer whales (*Orcinus orca*) are found throughout the world's oceans, and have been shown to feed on a wide variety of prey (Forney and Wade 2006). In the eastern North Pacific and Antarctic, where these animals have been well studied, research has found several ecotypes of killer whales based on their prey preference (Ford *et al.* 1998, Pitman and Ensor 2003). Little is known of killer whales in the tropical oceans, where their abundance is relatively low (Forney and Wade 2006). They have been found to prey on dolphins, including species of the genus *Delphinus* (Brown and Norris 1956) and *Stenella* (Pitman *et al.* 2003), and may be opportunistic feeders (Baird *et al.* 2006). It is not known if tropical killer whales are also comprised of multiple ecotypes that differ in their prey preference.

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Killer whales are one of the main predators of dolphins and porpoises, and it has been suggested that mammal eating killer whales may eavesdrop on vocalizing dolphin schools as a hunting strategy (Jefferson *et al.* 1991, Barrett-Lennard *et al.* 1996, Deecke *et al.* 2005). Conversely, vocal activity of mammal eating killer whales was found to be significantly greater after a kill, suggesting that they may limit vocalizations to prevent eavesdropping by potential prey (Deecke *et al.* 2005). Previous research has suggested that killer whale predation may affect dolphin vocal behavior (Morisaka and Connor 2007, Oswald *et al.* 2008), and anecdotal reports support this. For example, when highly vocal beluga whales in Alaska were exposed to playback of killer whale sounds, they moved downriver from the sound and produced very few vocalizations (Fish and Vania 1971). Until now, however, few data existed to test the hypothesis that dolphins change their vocalization patterns to avoid detection by eavesdropping killer whales. Here we analyze data from shipboard cetacean abundance surveys in the tropical Pacific Ocean to rigorously test this hypothesis.

Dolphins produce a variety of sounds, including whistles, echolocation clicks, and burst pulses. Echolocation clicks are short broadband sounds that are relatively high-frequency and do not travel great distances (<6 km; SR, unpublished data). Dolphin whistles are social signals that are lower in frequency (<30 kHz) and travel greater distances (Janik 2000, Quintana-Rizzo *et al.* 2006). Burst pulses are click sounds with a high repetition rate, with highly variable frequency and temporal structure. The frequencies of greatest hearing sensitivity of killer whales are between 18 and 42 kHz (Szymanski *et al.* 1999), and these frequencies overlap with those for the majority of dolphin whistles.

Many of the dolphin species encountered in the tropical Pacific Ocean are found in large, vociferous schools that use whistles to communicate over large areas (Rankin *et al.* 2008b). Whistles can propagate over greater distances than echolocation clicks and may be necessary to retain group cohesion. While most dolphin schools were found to be vocal in the tropical Pacific Ocean, this was not the case for killer whales (Rankin *et al.* 2008a). Killer whales are relatively rare in the nutrient-poor tropical Pacific Ocean; however, they do occur in this area (Forney and Wade 2006, Olson and Gerrodette 2008). Using data collected by Southwest Fisheries Science Center (SWFSC) during six years of systematic shipboard visual and acoustic abundance surveys of cetaceans in the Pacific Ocean, we tested the hypothesis that the vocal activity of dolphins in the tropical Pacific Ocean is decreased in the presence of killer whales. In addition to testing this hypothesis for all dolphin species encountered, we also tested the hypothesis on the genera *Delphinus* and *Stenella*. These dolphin species are known prey of killer whales (Jefferson *et al.* 1991; Visser 1999, 2007), and produce vocalizations that are detected at relatively great distances in the tropical Pacific Ocean (Rankin *et al.* 2008a).

## METHODS

Six systematic visual and acoustic line-transect cetacean surveys of cetacean abundance were conducted in the tropical Pacific Ocean between 2000 and 2007 (Fig. 1). Survey trackline design varied by survey; however, visual and acoustic data were collected systematically for all surveys (see Rankin *et al.* 2008a for additional information on survey methods). Survey vessels were diesel-powered NOAA

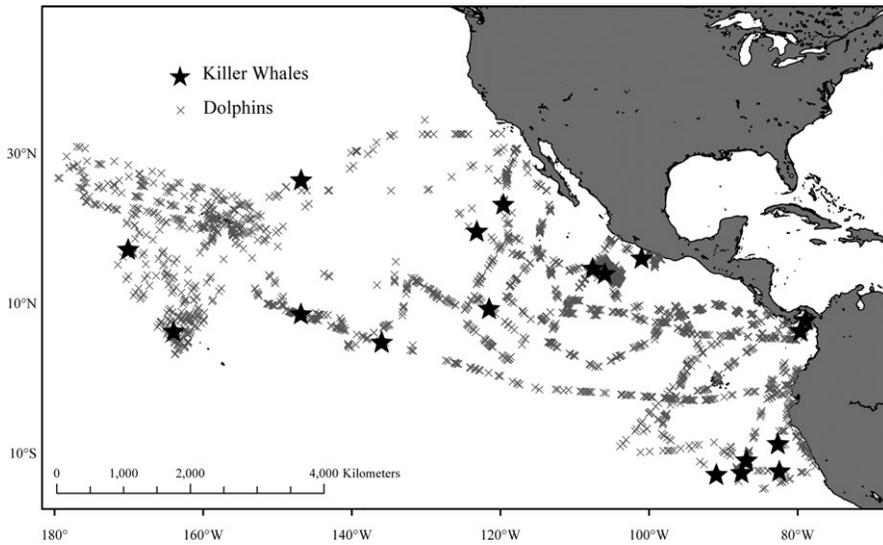


Figure 1. Map of study area in the tropical and sub-tropical Pacific Ocean. Dolphin detections are shown as a gray “X” and killer whales sightings are shown as black stars.

research vessels with dual propellers, including R/V *David Starr Jordan* (52 m), R/V *McArthur* (53 m), and the R/V *McArthur II* (68 m). Visual observation methods followed a standard SWFSC protocol that has been used since the 1980s (Kinzey *et al.* 2000). A team of six experienced visual observers rotated between two “big-eye” 25 × 150 binoculars and one data-recording position. Visual observation occurred during daylight hours in Beaufort sea states 0–5. When animals were sighted by the visual observation team, the ship approached them for species identification and group size estimation.

A towed hydrophone array was used for acoustic detection of cetacean vocalizations. The array was typically towed 200–300 m behind the ship during daylight hours and in sea states less than Beaufort 7. Several array configurations were used, each with its own specifications (see Rankin *et al.* 2008a for details). The five-element “Sonatech” array (Sonatech, Inc., Santa Barbara, CA) had a flat frequency response from 2 kHz to 45 kHz ( $\pm 4$  dB at  $-132$  dB re  $1 \text{ V}/\mu\text{Pa}$ ), the three-element high-frequency (HF) array (Sonatech, Inc.) had a flat frequency response from 2 kHz to 120 kHz ( $\pm 3$  dB at  $-164$  dB re  $1 \text{ V}/\mu\text{Pa}$ ), and the “SWFSC” array had a flat frequency response from 500 Hz to 30 kHz ( $\pm 5$  dB at  $-155$  dB re  $1 \text{ V}/\mu\text{Pa}$ ).

Signals from the array were equalized using a Mackie CR1604-VLZ mixer and recorded using a Tascam DA-38 eight-channel digital recorder (sample rate 48 kHz). Sounds were monitored by an acoustic technician both aurally, using headphones, and visually, using real-time scrolling spectrographic software (ISHMAEL, Mellinger 2001). Acoustic localization of dolphin schools was performed based on the convergence of bearing angles plotted on Whaltrak, a custom-written plotting program. Bearing angles to vocalizing dolphin schools were calculated using the phone-pair bearing algorithm in ISHMAEL (Mellinger 2001). All data presented here are based on monitoring within the limitations of the hydrophones and recording equipment; only sounds detected

between 2 kHz and 24 kHz were included in the analyses. A dolphin school was determined to be vocal if sounds within this bandwidth could be confirmed through localization (minimum of 3–5 individual vocalizations required for localization). All call types detected within this frequency range were considered.

We used generalized linear models (GLM) (McCullagh and Nelder 1989) using the *glm* package in R (R Development Core Team 2010) to test the hypothesis that the vocal activity of dolphin schools was related to the distance and time to the nearest killer whale detection. Distance was calculated as the great circle distance between a dolphin sighting and the nearest killer whale sighting within the survey. Time was calculated as the shortest time between a dolphin sighting and a killer whale sighting, regardless of whether the killer whale sighting occurred prior to or after the sighting under consideration. Because line-transect survey effort is designed to emphasize detection of cetaceans for abundance estimates, dolphin behavioral data other than basic information on vocal behavior were not collected in a systematic manner and thus were not used in this analysis.

The GLM was structured as a logistic model where the response variable was vocal activity of each dolphin group (vocal/not vocal within the 2–24 kHz bandwidth), and the predictor variables were the log transformations of the group size, distance to killer whale, time to killer whale, distance  $\times$  time, distance  $\times$  group size, time  $\times$  group size, and distance  $\times$  time  $\times$  group size. Group size was included because vocal activity was highly correlated to group size in a study that included the data presented here (Rankin *et al.* 2008b). GLMs were run on the overall data set including all dolphins detected during these tropical surveys, and a subset of these data including only dolphins of the genera *Stenella* and *Delphinus*.

For the same two data sets, we also conducted a Random Forest analysis (Breiman 2001) as implemented in the *randomForest* package in R (Liaw and Wiener 2002) on the same response and predictor variables. Random Forest is an ensemble tree-based method that extends standard Classification and Regression Tree (CART) methods by creating a collection of classification trees (the forest). The classification uncertainty of each tree is assessed using randomly selected cases which are withheld during its construction (the out-of-bag or OOB cases). The importance of each predictor variable is determined by evaluating the decrease in prediction accuracy when those variables are permuted. This decrease is averaged over all trees to produce the final measure of importance. For both data sets, 1,000 trees were grown, which were assessed to be sufficient based on stability of the OOB error rate. Because we had so few predictor variables, we set the *mtry* parameter, or the number of predictors randomly selected at a node for splitting, to two. In order to balance sample sizes between categories and ensure that all of the variability within each category was adequately represented, an equal number of vocal and nonvocal sightings were used to build each tree based on half of the frequency of the smaller category ( $n = 184$  for the entire data set and 52 for the *Stenella/Delphinus* subset). The significance of the importance measures were assessed with 1,000 permutations of the response variable using the *rfPermute* package for R.

## RESULTS

Data on the vocal activity of dolphin encounters were collected during 40,976 km of visual and acoustic shipboard surveys in the tropical and

subtropical Pacific Ocean, including 1,232 dolphin sightings of 13 species (Fig. 1). A total of 921 of these dolphin schools were vocal (74.7%). Dolphin species seen on these surveys included striped dolphins (*Stenella coeruleoalba*), rough-toothed dolphins (*Steno bredanensis*), spinner dolphins (*Stenella longirostris*), spotted dolphins (*Stenella attenuata*), bottlenose dolphins (*Tursiops truncatus*), pilot whales (*Globicephala* spp.), pygmy killer whales (*Feresa attenuata*), false killer whales (*Pseudorca crassidens*), dusky dolphins (*Lagenorhynchus obscurus*), Risso's dolphins (*Grampus griseus*), Fraser's dolphins (*Lagenodelphis hosei*), short-beaked common dolphins (*Delphinus delphis*), and long-beaked common dolphins (*Delphinus capensis*). The mean acoustic detection distance of these combined detections was 4.6 km (range 0.01–18.52 km), and the mean group size was 83 animals (range 1–2,800). Sixty-seven of these sightings were on days in which killer whales were sighted. The mean distance to a killer whale sighting was 984 km (range 4–5,870 km), and the mean time to a killer whale sighting was 12 d (range 0.01–87 d). There were a total of 19 detections of killer whale groups during the combined surveys.

There were a total of 572 schools of the genera *Delphinus* and *Stenella*, of which 469 were vocal (82%). The mean group size was 137 (range 1–2,540). Twenty-five of these sightings were on days in which killer whales were sighted. The mean distance to a killer whale sighting was 864 km (range 8–3,980 km), and the mean time to a killer whale sighting was 11 d (range 0.02–76 d).

The results of the GLM for the overall data set of tropical dolphins (including 1,232 detections of 13 species) showed a significant relationship between the vocal activity of dolphins and the time to a killer whale sighting, as well as the interaction effect between time to a killer whale sighting and group size ( $P < 0.05$ , Table 1). The GLM results for the *Stenella/Delphinus* subset was significant based on the time to a killer whale sighting, as well as the time  $\times$  group size interaction ( $P < 0.05$ , Table 1). This logistic regression (Fig. 2) shows an increase in the probability that a dolphin school was vocal with increasing time to a killer whale sighting for the overall data set of tropical dolphins and the subset of *Stenella* and *Delphinus* species. The effect of the presence of killer whales could be detected up to

Table 1. Results of Generalized Linear Models.  $P$ -values are given for the predictor variables for the overall data set of tropical dolphins, and for a subset containing detections of the genus *Stenella* and *Delphinus*. Values in bold indicate that they are significant at the 0.05  $\alpha$ -level. Group size was included as a predictor variable due to its known relationship to vocal behavior. "Time" and "distance" in interaction terms are in reference to the nearest killer whale sighting.

Predictor variables	$P$ -value	
	Tropical dolphins	<i>Stenella/Delphinus</i> spp.
Group size	0.278	0.098
Distance to killer whale	0.354	0.425
Time to killer whale	<b>0.017</b>	<b>0.005</b>
Distance $\times$ time	0.258	<b>0.016</b>
Distance $\times$ group size	0.411	0.353
Time $\times$ group size	<b>0.020</b>	<b>0.010</b>
Distance $\times$ time $\times$ group size	0.224	<b>0.026</b>

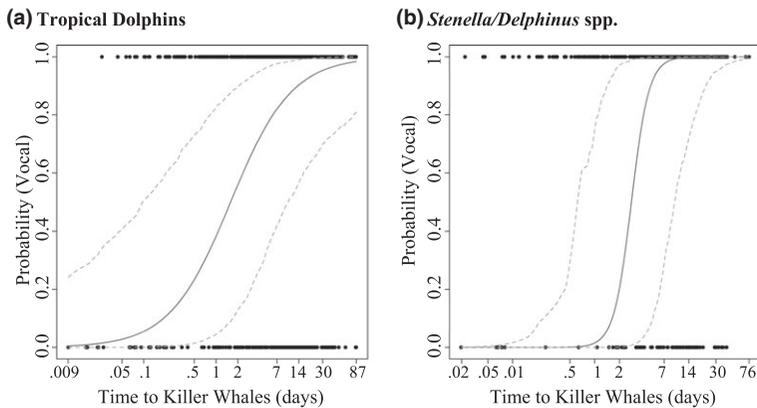


Figure 2. Logistic regression plot showing the relationship between the probability that a dolphin school was vocal and the number of days (log scaled) to the nearest killer whale sighting (solid line), with 95% confidence intervals (dashed lines) for (A) overall data set of tropical dolphins and (B) subset containing detections of the genera *Stenella* and *Delphinus*.

1.5 d for the overall combined species (Fig. 2a), and for 2 d for the subset of *Stenella* and *Delphinus* (Fig. 2b). The logistic regression of vocal activity on time  $\times$  group size interaction also showed a sharp, but inverse sigmoidal form, with a decreasing probability of being vocal corresponding to increasing values of the interaction term (results not shown).

The results of the Random Forest analysis found that the classification error was well below what would be expected by chance alone; the error rate from the out-of-bag samples was 30% for the overall data set of the tropical dolphins and 27.6% for the subset including *Stenella* and *Delphinus* species (Table 2). In the overall data set including all tropical dolphin species, group size was ranked as being the most important predictor, followed by the interaction terms of group size and distance to a killer whale sighting (Table 3). The pattern of variable importance was different for the *Stenella/Delphinus* subset. In the latter data set, the distance and time to a killer whale sighting interaction was the most important predictor, followed by the time and group size interaction (Table 3).

Table 2. Random Forest confusion matrices and classification error for (A) overall detections and (B) for a subset containing detections of the genus *Stenella* and *Delphinus*. The out-of-bag error rate is 30% for the overall data set of tropical dolphins and 27.6% for the subset of *Stenella/Delphinus* species.

	Not vocal	Vocal	Classification error
(A) Tropical dolphins			
Not vocal	251	116	0.316
Vocal	253	612	0.292
(B) <i>Stenella/Delphinus</i> spp.			
Not vocal	59	44	0.427
Vocal	114	355	0.243

Table 3. Importance of predictor variables from Random Forest as measured by mean decrease in accuracy for (A) the overall data set of tropical dolphins and (B) the subset containing detections of the genus *Stenella* and *Delphinus*. Variables are sorted in order of decreasing importance for each data set. All variables had permutation  $P$ -values  $< 0.05$  (note: values represent variable importance, *not*  $P$ -values). “Time” and “distance” in interaction terms are in reference to the nearest killer whale sighting.

Predictor variables	Variable importance
(A) Tropical dolphins	
Group size	0.041
Distance $\times$ group size	0.0324
Distance $\times$ time $\times$ group size	0.0274
Time to killer whale	0.0245
Distance $\times$ time	0.0228
Time $\times$ group size	0.0225
Distance to killer whale	0.0145
(B) <i>Stenella/Delphinus</i> spp.	
Distance $\times$ time	0.0223
Time $\times$ group size	0.0193
Time to killer whale	0.0183
Distance $\times$ time $\times$ group size	0.0182
Group size	0.017
Distance $\times$ group size	0.012
Distance to killer whale	0.0104

Permutation tests on Random Forests for both the overall data set and the *Stenella/Delphinus* subset indicated that all measures had significant ( $P < 0.05$ ) importance scores (Table 3).

## DISCUSSION

Our results show that the vocal behavior of tropical dolphins is significantly influenced by their proximity to killer whales, despite the relative rarity of killer whales in our study area. While both the GLM and the Random Forest analyses showed the significance of group size as well as time to nearest killer whale sighting in predicting vocal activity, the two methods highlight different aspects of the data. As shown in Figure 2, the GLM shows that the relationship between the probability that dolphin schools were vocalizing and time to killer whale sighting can be well-described by a simple logistic model. In other words, despite the relative rarity of groups of killer whales in the tropical Pacific Ocean ( $n = 19$  groups for this study), they appear to have strong and predictable influence on the vocal activity of nearby dolphin schools. Nearby dolphin schools had a lower probability of vocalizing within the sensitive hearing range of killer whales.

Conversely, because it is not constrained by a parametric model, the Random Forest analysis is better able to explore the utility of weak predictors, such as distance to a killer whale sighting, which was nonsignificant in the GLM. As such, the permutation test found that all variables play a significant role in predicting vocal activity in both data sets. The Random Forest also identified important differences between the effects of killer whales in the two data sets. In

the overall data set, group size, or an interaction term containing it, was one of the first three most important predictors of vocalization. This finding agrees with results from previous studies (Rankin *et al.* 2008b). Conversely, in the *Stenella Delphinus* subset, time to killer whale sighting and its interactions with distance and group size were found to be more important in predicting vocal activity than group size alone, again suggesting that these species are especially attuned to the presence of killer whales.

As identified by the results, the predictor variables of time and distance to a killer whale sighting are not necessarily comparable. The predictor variable of distance to a killer whale sighting may be complicated by factors related to how survey tracklines are covered and by transit to/from a port. For example, a killer whale sighting detected within a short distance of a port-of-call may be close in geographic proximity to a large number of dolphin schools that were detected during the transit *to* and *from* the port. While the distance may be small, the time to the killer whale sighting may be several days at the minimum, and up to several months at the maximum (for surveys that start and end in a given port). In fact, killer whales were detected near port calls in Mexico and Panama (Fig. 1). Given the low density of killer whales, a single detection of this kind could affect the results of either analysis. This is highlighted by the fact that the distance to a killer whale sighting was found to be the least important variable in the Random Forest analysis for both data sets (Table 3), while both the GLM and Random Forest found the effect of a killer whale sighting on a nearby dolphin school well represented by time.

Many of the dolphin species encountered in the tropical Pacific Ocean are found in large, spread out schools (Wade and Gerrodette 1993). The acoustic detection distance of dolphin schools in the tropical Pacific Ocean is large enough that sounds would be detected from sighted dolphin schools if they were producing sounds. Whistles, which can propagate over several kilometers, may be necessary to retain group cohesion. This type of long distance communication may also serve as a dinner bell to any killer whales in the area, and our results show that these dolphins were less likely to be vocal in the presence of killer whales. Due to the relative rarity of killer whales in the tropics, it is unlikely that these infrequent disruptions to communication significantly impact interactions necessary for survival. However, in temperate climates, where increased productivity supports a greater abundance of killer whales, this interruption in communication may have a greater impact on survival. Small odontocetes in temperate waters may need to develop alternative antipredator strategies, such as adapting their vocal behavior to avoid detection by killer whales. In fact, many dolphin species in the temperate north Pacific Ocean have a relatively low rate of whistle production (Oswald *et al.* 2008, Rankin *et al.* 2008b) or likely do not produce whistles (Rankin *et al.* 2007), and porpoise produce only narrow-band, high-frequency click sounds that are entirely above the hearing of killer whales.

The data presented here were collected during cetacean abundance surveys, with survey methods designed to maximize the detection of animals. Nonetheless, not all animals are detected on the trackline, even in the best of conditions (Barlow *et al.* 2001). Therefore, it is likely that many groups of dolphins and killer whales were missed, adding variance to our data. Additional factors other than the presence of the killer whales may have also influenced the vocal behavior of dolphins. For example, it has been shown that dolphin vocal behavior can be related to vessel noise (Lesage *et al.* 2006, Nowacek *et al.* 2007), species (Rankin *et al.* 2008b), and

behavioral state (Herzing 1996, Janik 2009, Henderson *et al.* 2012). The vessels used in this survey were of similar size, and all animals detected within this study would have been exposed to similar levels of ship noise. This study found a strong relationship between the vocal activity of the combined species of dolphins related to the proximity of killer whales, and this relationship was even greater for the subset of species from the genera *Stenella* and *Delphinus*. Our sample sizes did not allow for the examination of each species independently; however, it is likely that this relationship varies by species. Likewise, behavioral state may also influence vocal activity, yet behavioral data were not collected systematically during these surveys and therefore not included in the analysis.

Of course, it is possible that the dolphins are not reacting to the killer whales that were actually seen on our survey. Rather, they could be reacting to the presence of an aggregation of killer whales at some scale that we are not able to detect with our surveys. In this case, the interpretation of the zone of influence (both in space and time) is different but no less real. We see no signs of spatial aggregation of killer whales in our sighting data, but sightings of killer whales are too rare for this to be detected with our data.

Given the large scale of our study area and our line-transect survey design it would be impossible to adequately address all of the potential factors that might influence the vocal behavior of each dolphin group encountered. Nonetheless, our analyses demonstrate a clear relationship of dolphin vocal behavior to the proximity of killer whales. Changes in vocal activity related to factors not included in our analyses would be expected to increase the variance in our data and thus make this pattern more difficult to detect.

Our results suggest that the zone of influence that a killer whale may have on the vocal activity of dolphins (up to 2 d, Fig. 2) is greater than would be expected given simple passive detection of their sounds (Miller 2006, Rankin *et al.* 2008a). In addition, mammal-eating killer whales are known to be silent much of the time, often vocalizing only after a kill (Deecke *et al.* 2005). Alarm calls have been found to elicit strong behavioral responses in terrestrial mammals and birds (Klump and Shalter 1984, Griesser 2008, Macedonia and Evans 2010), and the existence of alarm calls has been suggested for cetaceans (Pitman *et al.* 2001, Lesage *et al.* 2006). It is possible that dolphins might produce alarm calls in the presence of killer whales, essentially broadcasting their presence even if the killer whales themselves are silent. This broadcast range may be increased further if the dolphins were fleeing the killer whales or if other dolphin schools respond to the alarm calls with additional alarm calls. Further research should consider the use of alarm calls by dolphins, and how other dolphin schools react to these types of calls from conspecifics.

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