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Acoustic evidence that harbor porpoises (*Phocoena phocoena*) avoid bottlenose dolphins (*Tursiops truncatus*)

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Along the West Coast of the United States, harbor porpoises (*Phocoena phocoena*) and coastal common bottlenose dolphins (*Tursiops truncatus*) overlap in distribution from Point Conception to San Francisco Bay in a narrow coastal band (Wells *et al.* 1990; Hansen and Defran 1993; Carretta *et al.* 1998, 2001). This overlap is relatively recent. Increased water temperatures in California during the 1982–1983 El Niño event prompted a northward range expansion of coastal bottlenose dolphins past Point Conception into central California (Hansen 1990, Wells *et al.* 1990). Harbor porpoises occur in distinct populations along the California coast (Calambokidis and Barlow 1991, Chivers *et al.* 2002, Carretta *et al.* 2009), whereas coastal bottlenose dolphins move throughout their range and comprise a single population (Defran *et al.* 1999, Hwang *et al.* 2014).

In California and in other regions where these species overlap, interspecies aggression has been observed (Ross and Wilson 1996, Dunn *et al.* 2002, Cotter *et al.* 2012). Between 1991 and 1993 in Moray Firth, Scotland, blunt force trauma associated with bottlenose dolphin attacks was the largest contributor to stranded harbor porpoise mortality (Ross and Wilson 1996). Bottlenose dolphin attacks on harbor porpoises have also been documented in Cardigan Bay, Wales (Jepson and Baker 1998) and in Monterey Bay, California (Cotter *et al.* 2012, Wilkin *et al.* 2012). The first documented stranding of a harbor porpoise killed by bottlenose dolphins in California occurred in July 2005. Between 2007 and 2009 researchers witnessed three bottlenose dolphin attacks on harbor porpoises in Monterey Bay (Cotter *et al.* 2012). These attacks involved 23 individual bottlenose dolphins, 21 of which were known

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to be males. Observed attacks occurred in the late summer and early fall, during the possible breeding season for bottlenose dolphins.

In Monterey and Santa Cruz counties between 2005 and 2011, 179 harbor porpoise strandings were documented. Of these, 43 of 68 stranded porpoises in which cause of death could be determined presented signs of blunt force trauma, at least 28 of which were consistent with attacks by bottlenose dolphins.² In California between 1998 and 2010, 54 of 216 stranded porpoises in which cause of death was determined presented signs of blunt force trauma consistent with attacks by bottlenose dolphins (Wilkin *et al.* 2012). In 2007 an apparent increase in harbor porpoise strandings in central California triggered the declaration of an Unusual Mortality Event (UME) and the stranding rate was more than twice the mean annual rate of the previous decade during 2008 and 2009. During this time, stranding rates were highest from June to November and blunt force trauma was the most common diagnosed cause of death (Wilkin *et al.* 2012). Taken together, the findings from California suggest that in this region a relatively sudden onset of aggression towards harbor porpoise was executed by a few male bottlenose dolphins.

Hypothesized drivers for bottlenose dolphin attacks on harbor porpoise can be broadly divided into ecological and behavioral explanations (Ross and Wilson 1996, Cotter *et al.* 2012). Possible ecological drivers include prey competition and feeding interference, whereas possible behavioral drivers include object-oriented play to practice fighting or infanticidal behaviors, with high levels of testosterone and a skewed sex ratio perhaps contributing to heightened aggression in male bottlenose dolphins (Ross and Wilson 1996, Cotter *et al.* 2012).

All of the proposed ecological explanations hinge on some form of competition for resources, for which evidence in California is weak. Spitz *et al.* (2006) reported qualitative similarities in diet composition of bottlenose dolphins and harbor porpoise in the Bay of Biscay, but quantitative examination found strong evidence that diet profiles were distinct between these two species. There has been no comprehensive comparative study of the diets of bottlenose dolphins and harbor porpoise on the U.S. West Coast (Cotter *et al.* 2012). The most relevant available data indicate that bottlenose dolphins in California feed primarily on surfperches (family *Embiotocidae*) and croakers (family *Sciaenidae*; Defran *et al.* 1999 and references therein), whereas harbor porpoises in this region feed mainly on market squid (*Doryteuthis opalescens*) and small forage fish (Cotter *et al.* 2012 and references therein). Harbor porpoise stomachs collected from stranded animals in Monterey Bay contained primarily northern anchovy (*Engraulis mordax*), spotted cusk-eel (*Chilara taylori*), rockfish (family *Sebastes*), and market squid (Dorfman 1990, Sekiguchi 1995, Byrd 2001). More recent analyses of stranded animals in central California confirmed northern anchovy, market squid, and sardine (*Sardinops sagax*) as harbor porpoise prey items.³ Although not conclusive, these data indicate that harbor porpoise are generalists and may have seasonal or inter-annual variation in preferred prey types. The limited evidence for dietary overlap in combination with known differences in depth distributions for these two species indicate that competition for resources is an improbable explanation for the observed bottlenose dolphin aggression in California.

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The prevailing hypothesis for bottlenose dolphin aggression towards harbor porpoises is that it is either a misdirection of infanticidal tendencies or a way of developing infanticidal behaviors (Patterson *et al.* 1998, Kaplan *et al.* 2009, Cotter *et al.* 2012). In Moray Firth, Scotland, stranded bottlenose dolphin calves presented internal and external injuries consistent with infanticide (Patterson *et al.* 1998) at the same time that harbor porpoise strandings were dominated by dolphin-inflicted blunt force trauma (Ross and Wilson 1996). Infanticide also has been observed in bottlenose dolphins in Virginia (Dunn *et al.* 2002) and Florida (Kaplan *et al.* 2009). It is likely that infanticidal behavior was previously observed in bottlenose dolphins but was documented by researchers as play rather than aggression (Dunn *et al.* 2002). In some of these instances, attacked individuals of both species have been similarly sized (100–150 cm; Ross and Wilson 1996, Patterson *et al.* 1998, Dunn *et al.* 2002). This link with infanticide is supported by some observations that aggressors are males (Kaplan *et al.* 2009, Cotter *et al.* 2012) who may use infanticide as a strategy to gain reproductive access to females (Kaplan *et al.* 2009). In California 92% of bottlenose dolphin aggressors in observed attacks were known or putative males, and there was 40% overlap in bottlenose dolphin identity between attacks (Cotter *et al.* 2012). However, there may be other explanations for the observed interspecies aggression since not all stranded harbor porpoises with dolphin-inflicted injuries fall within this size range (Wilkin *et al.* 2012), bottlenose dolphins have been observed attacking other delphinids (*e.g.*, Barnett *et al.* 2009), and infanticide has never been documented in bottlenose dolphins in California (Cotter *et al.* 2012).

In the present study, we investigated whether this documented conflict between bottlenose dolphins and harbor porpoises in California affected harbor porpoise behavior within the nearshore environment where habitat overlap occurs with bottlenose dolphins. We expected to find lower densities of harbor porpoises when bottlenose dolphins were present than when they were absent.

We used data from moored click detectors (C-PODs; Chelonia Ltd., <http://www.chelonia.co.uk>) which were deployed at a study site in Monterey Bay (Fig. 1) to quantify the relative presence of harbor porpoises as well as bottlenose dolphins. These data were collected as part of a separate study but provided an opportunity to examine the acoustic behavior of both species within a few kilometers of the sites where bottlenose dolphin attacks on harbor porpoises were observed by Cotter *et al.* (2012) in previous years. Our instruments were moored in Monterey Bay at 36°52'53"N, 121°50'31"W approximately 15 m deep and 6 m above the sea floor. We used a mooring design that required diver installation and retrieval but allowed C-PODs to be serviced by hand from a small boat. Our C-POD installation was active from 7 October to 30 December 2011, for a total of 2,016 one-hour sample periods. On 1 November we serviced the mooring and exchanged C-PODs.

C-PODs have been used in a variety of acoustic monitoring applications (*e.g.*, Galus *et al.* 2012, Teilmann and Carstensen 2012, Benke *et al.* 2014). C-PODs record narrow-band high-frequency (120–140 kHz) porpoise echolocation clicks and mid-frequency (30–60 kHz) dolphin echolocation clicks. C-PODs detect and record only echolocation signals; therefore we have no information about other odontocete vocalizations, including whistles. Summary information for each echolocation signal detected is stored on a flash memory card. In postprocessing, the data were extracted using the C-POD software v. 2.024 and signal detections were classified into echolocation click trains using a manufacturer-supplied KERNO classifier (Tregenza 2012). The KERNO classifier identifies trains based on similarity of successive interclick intervals and the coherence of click parameters including peak frequency and

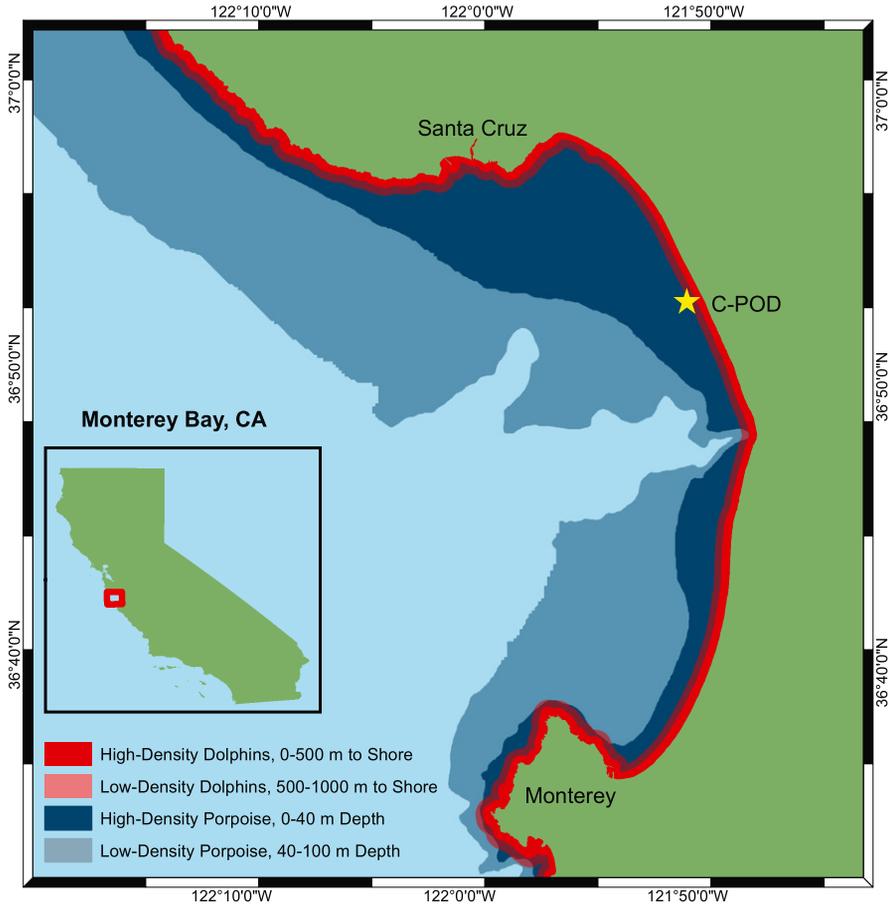


Figure 1. Study site in Monterey Bay, California. The yellow star indicates the position of the C-POD mooring. The approximate distribution of bottlenose dolphins is indicated in red (dark red: high density, 0–500 m from shore; light red: low density, 500–1,000 m from shore). The approximate distribution of harbor porpoises is indicated in blue (dark blue: high density, 0–40 m depth; medium blue: low density, 40–100 m depth).

duration. The inclusion of inter-click interval as a detection criterion reduces the false positive error rate since high-frequency noise from sediment or surf conditions is not patterned like cetacean click trains. For our analyses, we filtered the data to include only the highest quality echolocation click trains.

We used acoustic data exclusively to quantify harbor porpoise and bottlenose dolphin presence in the study area. At our study location, bottlenose dolphins and harbor porpoises are the only commonly encountered odontocetes. To confirm species identifications, we used data collected during six days of cliff-top observations and six days of aerial line-transect surveys that were conducted as part of a separate study. During both of these visual surveys we observed harbor porpoises and bottlenose dolphins in the vicinity of the C-POD and did not observe any other odontocetes. Therefore, we have attributed all narrow-band high-frequency click trains to harbor porpoise and

all mid-frequency click trains to bottlenose dolphins. The maximum detection range of a C-POD for harbor porpoise is approximately 400 m, whereas bottlenose dolphins may be detected from more than 1,000 m (Chelonia Ltd. 2012).

Since the number of echolocation click trains increases nonlinearly with harbor porpoise density, we used a relative rather than absolute metric of echolocation activity. Before analysis, echolocation click trains were binned into one-hour periods. We chose hour-long sampling periods to reduce autocorrelation in the data set while also preserving the signal of bottlenose dolphin encounters, which occur on timescales of one to a few hours. Echolocation click trains were reported as either a Proportion of Positive Minutes (PPM) or as a count of positive minutes in each hour. A positive minute was defined as containing at least one echolocation click train. Additionally, in some analyses bottlenose dolphins were counted simply as absent or present for each hour. The C-PODs also recorded *in situ* temperature measurements every minute, which were averaged for each hour period. Because our instruments were moored successively rather than in tandem, we are unable to quantify possible instrumental differences in sensitivity. However, our chosen metric of PPM is robust to variation in instrumental sensitivity (Benke *et al.* 2014).

To validate our data set, we randomly selected a subsample of 1,000 min for manual confirmation. We calculated a false positive error rate for harbor porpoise positive minutes of 4% and a false positive error rate for bottlenose dolphin positive minutes of 0%. The false negative error rate is likely high for both species, however, for our application it is preferable to avoid false detections in the data set at the potential expense of missed detections.

Preliminary examination of the data indicated a negative relationship between harbor porpoise presence and bottlenose dolphin presence. To explore this relationship, we examined changes in harbor porpoise PPM during discrete encounters with bottlenose dolphins using a boxplot (Fig. 2). Encounters were defined as single or consecutive hours with bottlenose dolphins present. We collated one- ($n = 65$), two- ($n = 28$), and three-hour ($n = 7$) bottlenose dolphin encounters and calculated harbor porpoise vocal activity before (T0), during (T1–T3), and after (T2–T4) these encounters. Qualitatively, we found that harbor porpoise acoustic presence at our study site decreased during bottlenose dolphin encounters. We performed a randomization test (Efron and Tibshirani 1993) to examine whether this observed pattern of lower mean harbor porpoise PPM when bottlenose dolphins were present (mean PPM = 0.06) compared with when they were absent (mean PPM = 0.18) could have occurred by chance (Fig. 3). This was accomplished by shifting the record of bottlenose dolphin presence to a new, randomly generated starting time and recalculating the mean harbor porpoise PPM when bottlenose dolphins were artificially present. We repeated this process 10,000 times to produce the distribution shown in Figure 3. Our randomization procedure was designed to preserve autocorrelation in the original time series. The randomization test results indicated that the observed harbor porpoise mean PPM was significantly less when bottlenose dolphins were present compared with the distribution of values expected by chance alone ($P = 0.0002$) thus the observed pattern was extremely unlikely to have occurred by chance.

Possible explanations for the observed decrease at our study site include niche partitioning (*i.e.*, habitat characteristics drive changes in species presence) and avoidance behavior (*i.e.*, harbor porpoises avoid potential aggression by bottlenose dolphins by either changing their distribution or their acoustic behavior).

Harbor porpoise and bottlenose dolphins have little diet overlap and different depth distributions, supporting a lack of competition for resources, and have

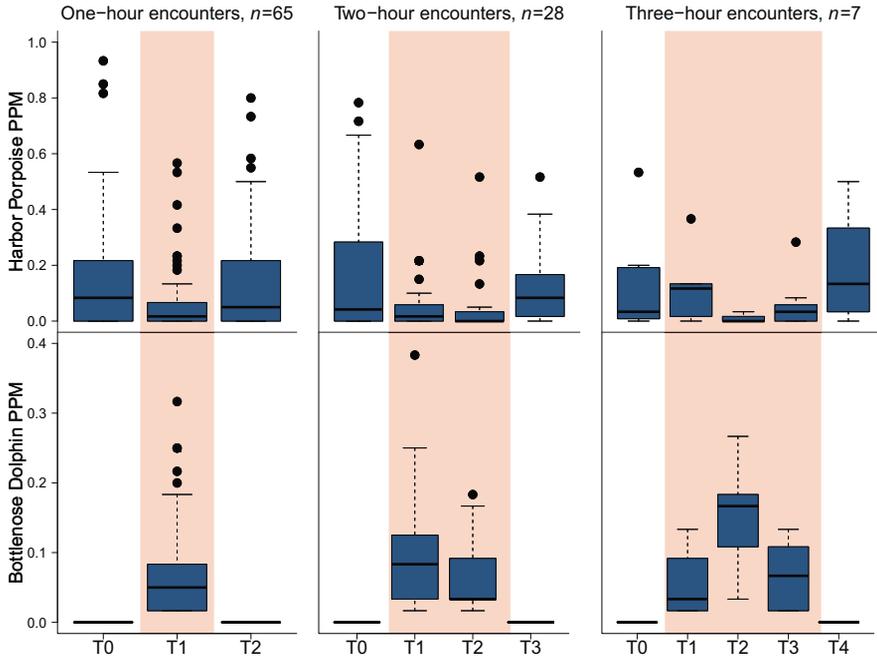


Figure 2. Box-and-whisker plots illustrating changes in the Positive Minutes (PPM) per hour for harbor porpoise (top panels) and bottlenose dolphins (bottom panels) before, during, and after all one-, two-, and three-hour bottlenose dolphin encounters in Monterey Bay. The black horizontal line indicates the median PPM value in each time period, while the blue shaded region represents the range between the first and third quartiles. The dashed lines show the range of the minimum and maximum values and the dots are outlier points that are more than 1.5 times the interquartile range beyond the first and third quartiles. T1 represents the onset of bottlenose dolphin presence and the red shaded regions indicate hours when bottlenose dolphins were present. At T0 and at the final period in each plot (T2, T3, or T4, depending on length of encounter), bottlenose dolphins were absent. Qualitatively, harbor porpoise PPM decreases when bottlenose dolphins are present and increases after they depart.

fundamentally different ecological niches. Best available data indicate that suitable habitat for both species is defined primarily in terms of depth, proximity to shore, and temperature (Fig. 1; Barlow 1988, Forney 1999, Carretta *et al.* 2001). Coastal bottlenose dolphins are found primarily within 1 km of shore (Hansen 1990, Defran *et al.* 1999), whereas harbor porpoise are less constrained by distance from shore and are more broadly distributed throughout waters 0–100 m deep, with greatest densities in depths from 0 to 40 m (Barlow 1988, Carretta *et al.* 2001, Forney *et al.* 2001). Because depth and proximity to shore are static, and temperature does not change rapidly enough to explain the observed changes in relative dolphin and porpoise presence, we do not believe that changes in habitat suitability could drive the observed periods of simultaneous increase in bottlenose dolphin presence and decrease in harbor porpoise presence in Monterey Bay.

Monterey Bay is at the northern end of the range of bottlenose dolphins (Hansen 1990, Defran *et al.* 1999). As water temperatures decreased during our study period the frequency of bottlenose dolphin encounters decreased. Bottlenose dolphin pres-

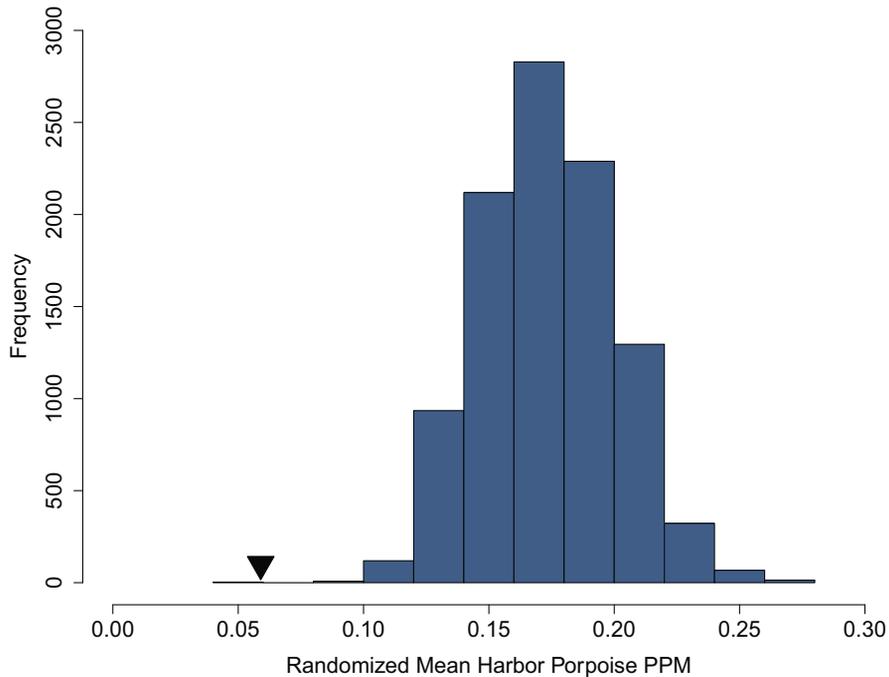


Figure 3. Blue bars indicate the randomization distribution of mean harbor porpoise Positive Minutes (PPM) during bottlenose dolphin encounters (mean = 0.18). The black arrow is the true mean harbor porpoise PPM during bottlenose dolphin encounters (mean = 0.06). There are no possible randomizations that result in a lower-than-observed mean PPM value when bottlenose dolphins are present.

ence at our study site could be considered as a stochastic occurrence moderated by temperature. We were interested in modeling the effect of bottlenose dolphin presence on counts of harbor porpoise positive minutes, but were concerned that changes in habitat might affect dolphin and porpoise presence. To explicitly include possible environmental influences, we included both dolphin presence and temperature as predictor variables of harbor porpoise positive minutes.

Because of the large proportion (29%) of zeros and overdispersion of counts in the harbor porpoise acoustic record, the data do not fit standard negative binomial or Poisson distributions. We tested for the goodness-of-fit of Generalized Linear Models specified with negative binomial and Poisson distributions using a chi-square test on the residual deviance and degrees of freedom. These tests indicated that models fitted using these distributions did not fit the data (chi-square tests, $P < 0.05$). Therefore, we chose a zero-inflated negative binomial (ZINB) model (Zeileis *et al.* 2008). This is a two-part model, with zeros generated by a binomial model with a logit link and counts generated by a negative binomial model with a log link. This model formulation allows zeros to be generated by either part of the model. Results of the ZINB model indicated that the data contained significantly more zeros than expected under standard distributions and that the data are overdispersed (Theta = 0.49). We use Akaike's Information Criterion (AIC) to choose between possible combinations of predictor variables in the ZINB model formulation (Table 1).

Table 1. Partial list of zero-inflated negative binomial (ZINB) model parameters for the binomial and negative binomial portions of the model with their degrees of freedom (DF) and AIC scores. A “+” indicates that both variables were included, whereas a “×” indicates that both variables and their interaction term were included in the model. The best model is in bold.

Binomial model (zeros)	Negative binomial model (counts)	DF	AIC
Temperature	Temperature	5	12,768.71
Dolphin Presence	Dolphin Presence	5	12,731.62
Temp × Dolphin	Temp × Dolphin	9	12,692.38
Temp × Dolphin	Temp + Dolphin	8	12,692.48
Temp + Dolphin	Temp × Dolphin	8	12,708.23

The best model includes temperature, dolphin presence, and their interaction to model the binomial process (probability of occurrence), and temperature and dolphin presence without their interaction to model the count (number of acoustic detections given occurrence). The model with interaction terms in both parts of the model had a slightly better AIC score ($\Delta\text{AIC} = 0.10$) but the interaction term was not significant in the count portion of the model (Z -test, $P = 0.14$). The best-fit model, with 95% confidence intervals, is shown in Figure 4. Both the presence of dolphins and temperature were significant in both parts of this best model (Z -test, $P < 0.05$ for all coefficients). The models including either only temperature or only dolphin presence performed poorly, indicating that neither is adequate to explain harbor porpoise acoustic activity.

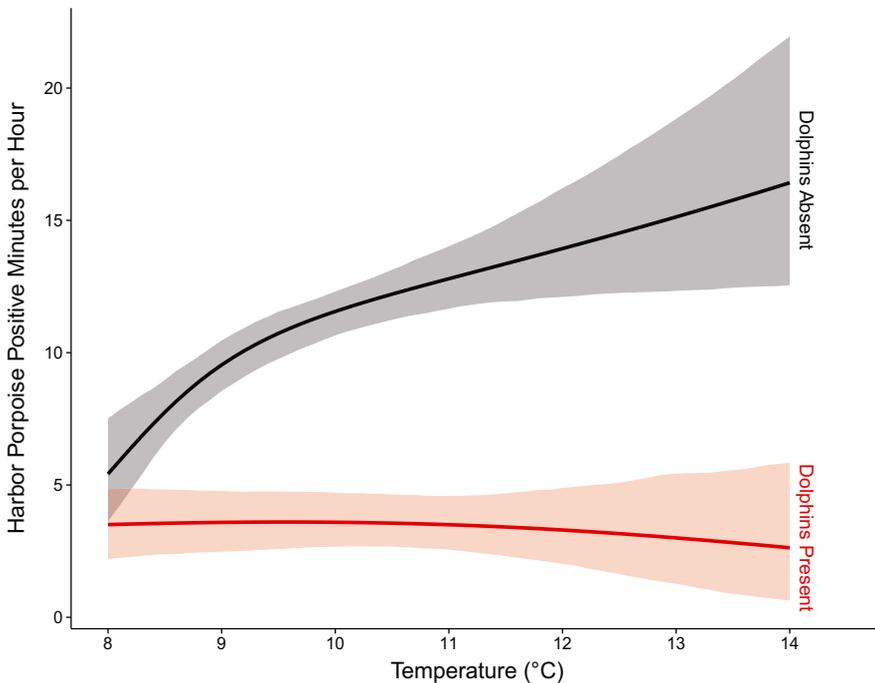


Figure 4. Fitted zero-inflated negative binomial (ZINB) model (red: dolphins present; black: dolphins absent) with 95% confidence intervals (shaded areas) indicating that harbor porpoise positive minutes per hour increased with temperature when dolphins were absent.

Our model predicts that when bottlenose dolphins are present, harbor porpoise acoustic activity is reduced by 52% at relatively low temperatures and by 82% at higher temperatures compared with when bottlenose dolphins are absent. Temperature decreased during our study, so this result may reflect seasonal changes in the relative abundances of harbor porpoises and bottlenose dolphins at our study site. Our data indicated that both species were relatively more abundant in October than in December. The magnitude of the harbor porpoise response to bottlenose dolphin presence may be heightened when both species are relatively more abundant.

We hypothesized that harbor porpoises passively detect bottlenose dolphin vocalizations in Monterey Bay and respond by reducing vocalization rates or leaving the area. The narrow-band high-frequency echolocation clicks of harbor porpoises have evolved independently in three odontocete lineages (Madsen *et al.* 2005). It has been suggested that use of these frequencies by harbor porpoises prevents passive acoustic detection by killer whales (Madsen *et al.* 2005, Rankin *et al.* 2013) whose hearing sensitivity declines above 100 kHz (Szymanski *et al.* 1999). Rankin *et al.* (2013) found that the vocal activity of dolphins decreased with proximity to killer whales, indicating that they used stealth to avoid passive detection and predation by killer whales.

Harbor porpoises have sensitive hearing in the range from 16 to 140 kHz (Kastelein *et al.* 2002), so they are able to hear echolocation clicks of bottlenose dolphins, which range in frequency from 30 to 110 kHz (Wahlberg *et al.* 2011). Bottlenose dolphin hearing is most sensitive in the range of 15–110 kHz (Johnson 1967, Brill *et al.* 2001, Popov *et al.* 2007) although they have limited hearing up to 150 kHz (Popov *et al.* 2007) and there is evidence that high-frequency hearing diminishes with age (Houser and Finneran 2006). Free-ranging harbor porpoise echolocation clicks are produced at a peak frequency of 129–145 kHz with a source level of 191 dB (Villadsgaard *et al.* 2007). Clicks with these parameters would attenuate in Monterey Bay seawater at a rate of approximately 40 dB per km (Fisher and Simmons 1977). Bottlenose dolphin hearing cutoff frequencies are 80 dB at 130 kHz (Popov *et al.* 2007). From these parameters, we might estimate that, bottlenose dolphins would be able to hear harbor porpoises echolocating within about 2 km. However, experimental work on the propagation of artificial harbor porpoise clicks in harbor porpoise habitats has found transmission loss of 61 dB at ranges of 200 m (DeRuiter *et al.* 2010) indicating that the true bottlenose dolphin detection range of harbor porpoise echolocation clicks may be <500 m. Since bottlenose dolphins could be passively or actively detecting harbor porpoises, we are unable to resolve whether harbor porpoises are responding to bottlenose dolphin presence by leaving the nearshore area or by reducing vocal activity to avoid detection.

In summary, our data indicated that harbor porpoise avoided bottlenose dolphins in Monterey Bay, possibly to reduce their risk of being attacked. There are two potential effects of bottlenose dolphin aggression on harbor porpoises in Monterey Bay. First, mortality that results from bottlenose dolphin attacks may directly impact harbor porpoise populations. The Monterey Bay population is approximately 3,715 individuals and appears to be increasing following past impacts from gill net bycatch (KAF, unpublished data). During the UME of harbor porpoises off central California, blunt force trauma was the most common identified cause of death (Wilkin *et al.* 2012), however, if this additional source of mortality was causing population declines, we would be unlikely to detect it given the frequency of past survey efforts and the precision of abundance and trends (Forney *et al.* 1991). The second potential impact of bottlenose dolphin aggression on harbor porpoises is a reduction in fitness as a result of exclusion from suitable habitat in the nearshore environment. This impact would

be difficult to quantify. The population of coastal bottlenose dolphins in California is estimated to be 323 individuals (Dudzik *et al.* 2006). Cotter *et al.* (2012) reported the identities of 23 individual bottlenose dolphins that have participated in attacks, suggesting a minimum involvement of 7% of the bottlenose dolphin population. If this behavior continues to spread through the coastal bottlenose dolphin population in California, direct mortality and habitat exclusion could negatively impact harbor porpoise populations.

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