Marine Mammal Science

MARINE MAMMAL SCIENCE, 28(1): E1–E15 (January 2012)

DOI: 10.1111/j.1748-7692.2011.00474.x

"Porpicide" in California: Killing of harbor porpoises (*Phocoena phocoena*) by coastal bottlenose dolphins (*Tursiops truncatus*)

MARK P. COTTER
University of Massachusetts at Dartmouth,
285 Old Westport Road,
North Dartmouth, Massachusetts 02747-2300, U.S.A.
and
Okeanis,
P. O. Box 583,
Moss Landing, California 95039, U.S.A.
E-mail: markpcotter@hotmail.com

DANIELA MALDINI
Okeanis,
P. O. Box 583,
Moss Landing, California 95039, U.S.A.

THOMAS A. JEFFERSON
Clymene Enterprises,
5495 Camino Playa Malaga,
San Diego, California 92124, U.S.A.

ABSTRACT

Between 2007 and 2009, we witnessed three aggressive interactions between harbor porpoises and bottlenose dolphins in Monterey Bay, California. This is the first time such aggression has been documented in the Pacific, and the first time a harbor porpoise was collected immediately after witnessing its death, inflicted by bottlenose dolphins. Of the bottlenose dolphins present, 92% were males either confirmed (61%) or putative (31%). Since 2005, 44 harbor porpoise deaths inflicted by bottlenose dolphins were documented in California. Aberrant behavior was rejected as a cause of aggression, based on widespread documentation of similar behaviors in other populations of free-ranging bottlenose dolphins. The evidence for interspecies territoriality as a form of competition for prey was weak: there is little dietary overlap and there are differences in bottlenose dolphin and harbor porpoise distribution patterns in California. Object-oriented play was plausible as a form of practice to maintain intraspecific infanticidal skills or a form of play to maintain fighting skills between male associates. Contributing factors could be high-testosterone levels, as attacks occurred at the height of the breeding season, and/or a skewed operational sex ratio. Ultimately, we need more information about bottlenose dolphin social structure at the time of the aggression.

Key words: bottlenose dolphin, *Tursiops truncatus*, harbor porpoise, *Phocoena phocoena*, California, Monterey Bay, attack, aggression, kill, mortality.

Aggressive, non-predatory interactions between sympatric species of odontocetes have been often documented in the wild (Jefferson *et al.* 1991, Shane 1995, Herzing 1996, Ross and Wilson 1996, Weller *et al.* 1996, Herzing and Johnson 1997, Baird 1998, Orr and Harwood 1998, Patterson *et al.* 1998, Alonso *et al.* 2000, Herzing *et al.* 2003, Wedekin *et al.* 2004, Barnett *et al.* 2009). The reasons for these conflicts are often unclear and the ultimate causes may be complex. Bottlenose dolphins (*Tursiops truncatus*) have been implicated in attacks, some of which were fatal, on a variety of species such as estuarine dolphins (*Sotalia guianensis*: Terry 1984, Wedekin *et al.* 2004, Acevedo-Gutierrez *et al.* 2005), Atlantic spotted dolphins (*Stenella frontalis*; Herzing 1996, Herzing and Johnson 1997, Herzing *et al.* 2003), and harbor porpoises (*Phocoena phocoena*: Ross and Wilson 1996, Jepson and Baker 1998, Wilson *et al.* 2004, Jepson 2005). Barnett *et al.* (2009) recently reported fatal attacks by bottlenose dolphins along the United Kingdom's coastline on short-beaked common dolphins (*Delphinus delphis*), striped dolphins (*Stenella coeruleoalba*), juvenile long-finned pilot whales (*Globicephala melas*), and Risso's dolphins (*Grampus griseus*). In addition, infanticide has been recorded within bottlenose dolphin groups in Scotland (Patterson *et al.* 1998) and on the United States' East Coast (Dunn *et al.* 2002).

Aggressive interactions between bottlenose dolphins and harbor porpoises are often fatal for the porpoise and have been reported around the United Kingdom (Ross and Wilson 1996, Jepson and Baker 1998). Despite some direct observations of attacks (Ross and Wilson 1996), little information exists to date regarding the identity or sex of the bottlenose dolphins responsible.

We report on three interactions between Pacific coastal bottlenose dolphins and harbor porpoises in Monterey Bay, California. Aggressive interactions between bottlenose dolphins and harbor porpoises have not been documented before in the Pacific Ocean. A unique feature of our observations is that attacks were witnessed directly by the research crew, and that all animals participating in the attacks were known individual bottlenose dolphins that were part of a long-term investigation. This enabled us to evaluate these occurrences in some detail.

Methods

Study Area

Monterey Bay (Fig. 1) is located along the central California coast between Santa Cruz to the north, and Point Piños to the south. It is part of the Monterey Bay National Marine Sanctuary and is California's second largest bay. The Bay is approximately 37 km long, north to south, and 16 km wide, east to west. California coastal bottlenose dolphins range between San Quentin, Mexico, and San Francisco, California, and the same individuals move throughout this range (Feinholz 1996, Defran *et al.* 1999).

The dolphins are limited in distribution to the coastal strip in a ribbon-like fashion between the shoreline and 500 m offshore (Defran *et al.* 1999), except for Santa Monica Bay (Bearzi *et al.* 2009) where coastal dolphins are occasionally seen feeding a few kilometers offshore.

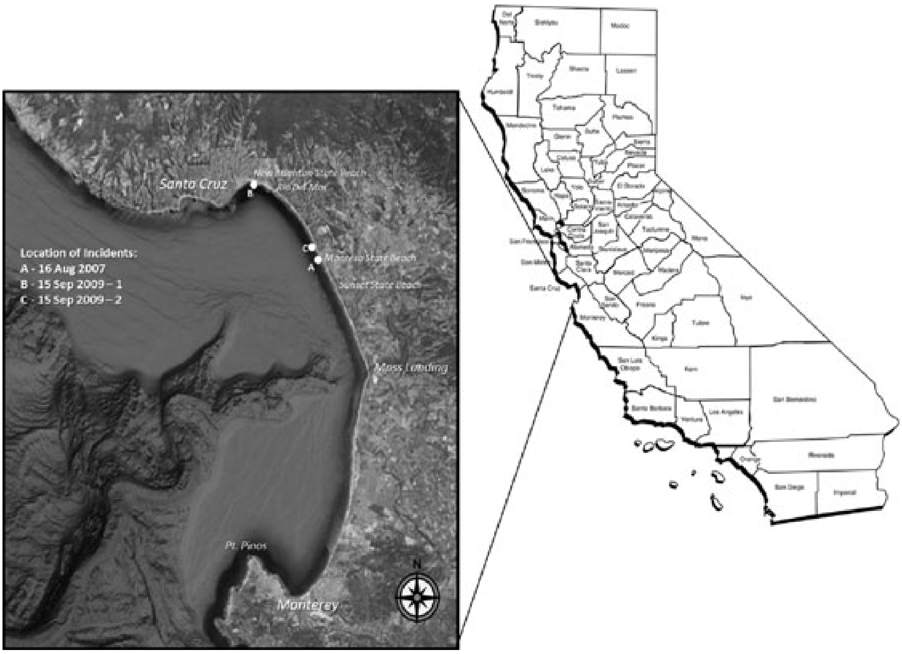

Figure 1. Map of California and its counties and map of the study area (Monterey Bay) with locations and dates of the three bottlenose dolphin/harbor porpoise interactions.

Data Collection

The Monterey Bay coastal bottlenose dolphin population has been the subject of a long-term investigation since 1990 (Feinholz 1996). The study includes regular boat-based surveys of the coastal strip between the shoreline and 1 km offshore. During the surveys, photo-identification, behavioral, bathymetric, and environmental data were collected, as well as other data on cetacean sightings. Biopsy samples of specific individual bottlenose dolphins were collected during an investigation of health and contaminant levels, and to determine sex for social structure analysis (Jefferson, Maldini and Cotter, unpublished data).

Observations on interactions between bottlenose dolphins and harbor porpoises were collected opportunistically as part of the surveys. When these interactions occurred, the boat moved slightly away from the interacting animals to be able to better document the behaviors. Photographic and cinematographic documentation were collected *ad libitum* and detailed notes were recorded. Digital video and photographs were analyzed to identify individual animals and specific behavioral sequences. The entire database and social structure analysis derived from data collected between 2006 and 2008 was used to interpret the events (Maldini and Cotter, unpublished data). The sexes of individual bottlenose dolphins involved in the attacks were either verified by genetic analysis of biopsy samples already available, confirmed by visual inspection of genital slits, inferred by the presence of calves accompanying females, or presumed (for males) by association, behavior, and size. Age class was estimated based on size and/or on historical data on the animal. Stranding information for harbor porpoises was obtained from the California Marine Mammal Stranding Network web site (http://swr.nmfs.noaa.gov/psd/strand/strandings.htm, accessed March 2010) and from Wilkin.[1]

Results

Strandings

Harbor porpoise stranding records along the California coast have been maintained by the California Marine Mammal Stranding Network since 1990. Detailed harbor porpoise necropsy reports are available consistently since at least 1998 (at least 347 necropsies conducted). Between 1990 and 2009, 470 harbor porpoise strandings have been reported by the stranding network (http://swr.nmfs.noaa.gov/psd/strand/strandings.htm; Wilkin[1]).

The stranding of a harbor porpoise killed by bottlenose dolphins, as confirmed through necropsy, was first recorded in California in July 2005, the only occurrence that year. No trauma cases were recorded in 2006. Between 2007 and 2009, 125 harbor porpoises were found stranded between Humboldt County (northern end) and San Luis Obispo County (southern end), an approximately 450 km coastal strip where coastal bottlenose dolphins and harbor porpoises overlap in range. Of these harbor porpoises, 44 (35%) had sustained traumatic injuries from interactions with bottlenose dolphins. Most of the trauma-related porpoise strandings occurred in San Luis Obispo County (32%) and in Santa Cruz County, Monterey Bay (61%). These strandings comprised 53% of all harbor porpoise strandings in Monterey Bay. All trauma-related strandings occurred between the months of July and November and 64% were in August and September. Trauma-related strandings occurred with higher frequency between Sunset State Beach and New Brighton State Beach in Santa Cruz County, the northern portion of Monterey Bay (Fig. 1).

Average length of the porpoises killed in Monterey Bay was 139.9 cm (54–168 cm). Thirty-one percent were females, 62% were males, and 8% were of unknown sex. Based on Lockyer *et al.*'s (2001) classification of harbor porpoise age-classes, which relies on total length, 19% of harbor porpoises killed by dolphins were adults, 59% were subadults, and 22% were calves.

Documented injuries included multiple fractures of the ribs, spinal column, skull, scapula and tympanic bulla, and lung and soft tissue lacerations and contusions. What distinguishes these injuries from those potentially inflicted by boat strikes is their bilateral nature, which points to a deliberate attack by another animal. The widespread rake-marks on both dorsal and ventral surfaces of the skin (Fig. 2) were diagnostic and consistent with bottlenose dolphin average intertooth distance (Sigler[2] , Ross and Wilson 1996). The trauma-related injuries found on one harbor porpoise that was collected immediately after it was killed by bottlenose dolphins (and the event was witnessed by the authors), were similar to the injuries recorded in all other trauma cases attributed to bottlenose dolphins along the California coast.

[1]Unpublished data from Sarah Wilkin, NOAA, Southwest Regional Office, 501 West Ocean Boulevard, Suite 4200, Long Beach, CA.

[2]Personal communication from Teri Sigler, University of California Santa Cruz, Long Marine Laboratories, 100 Shaffer Road, Santa Cruz, CA, 28 September 2009.

Figure 2. Rake marks on an adult harbor porpoise stranded in Santa Cruz County.

Observed Interactions

Three bottlenose dolphin/harbor porpoise interactions were witnessed directly between 2007 and 2009: two of unknown fate, and one resulting in the death of the porpoise, which was collected for examination. The events are described in detail below.

Event 1

On 16 August 2007 at 1210, a school of 10 adult bottlenose dolphins (Table 1, Group A) was sighted north of Sunset Beach (36.89033°N, 121.83860°W; Fig. 1) at a depth of 10 m. Male dolphin Poke, confirmed as a male by biopsy (Table 1, Subgroup A1) was sighted milling approximately 100 m from the other nine bottlenose dolphins while in close association (*i.e.,* swimming in echelon formation similar to mother/calf pairs, *sensu* McBride and Kritzler 1951) with an adult harbor porpoise. The harbor porpoise appeared to be trying to get away, but the bottlenose dolphin prevented any attempt at evasion by keeping pace with the porpoise and maintaining its position next to it. Once, the harbor porpoise swam away and came within 3 m of the research vessel. Male Poke quickly positioned itself between the porpoise and the vessel and nudged the porpoise away with its snout. Bottlenose dolphin Poke and the harbor porpoise surfaced together throughout the encounter. Our vessel left the scene at 1244 (25 min after first contact with the school) while the harbor porpoise was still with the dolphin. Throughout the encounter, all bottlenose dolphins traveled in a southerly direction at 0.46 km/h.

On 15 September 2009, we recorded the following two separate events and described four different aggressive behaviors by bottlenose dolphins toward harbor

Table 1. Identity of bottlenose dolphins present during interactions with harbor porpoises in Monterey Bay, California. Sexes were verified by biopsy (B), visual inspection of genital slit (V), presence of calves (C) or presumed (P) by association and behavior over time and relative body size. The Groups of bottlenose dolphins encountered are identified by a capital letter (A or B), and the subgroup that interacted with harbor porpoises is indicated by a capital letter and number corresponding to the order in which the interaction occurred (*i.e.*, A1).

Dolphin name	Sex	Minimum age	16 August 2007 group	15 September 2009 1 group	15 September 2009 2 group
Ake'akamai	♂ (B)	Adult	A		
Allure	♂ (B)	20+		B	B
Avalanche	♂ (P)	Adult		B	B4
Bat	♂ (P)	Adult		B	B3
Brandy	♀ (C)	11+	A		
Falco	♂ (V)	Adult		B	B
Gumpy	♂ (P)	11+		B	B
Kahuna	♂ (V)	Adult	A		
Kelp	♂ (V)	Adult		B2	B
Mako	♂ (P)	11+		B	B
Medusa	♂ (V)	Adult	A	B	B4
Naissance	♂ (V)	Adult		B2	B
Nibble	♂ (B)	Adult	A	B	B
Nii	♂ (P)	11+		B	B
Poke	♂ (B)	Adult	A1	B	B
Pursuit	♂ (P)	Adult		B	B
Quadrat	♀ (C)	16+	A		
Rapier	♂ (B)	Adult		B	B
Phyto	♂ (B)	Adult		B	B3
Tidbit	♂ (B)	Adult	A		
Tikanawa	♂ (P)	Adult	A		
Twinky	♂ (V)	Adult		B	B3
Unity	♂ (B)	15+	A		

porpoises (see Table 2 for description of behaviors and Fig. 3 for photographic documentation).

Event 2

At 0906 a school of 16 adult bottlenose dolphins (Table 1, Group B) was sighted off Rio del Mar (36.97356°N, 121.93060°W; Fig. 1), 10–15 m from the shoreline, while interacting with an adult harbor porpoise. The interaction was visible at a distance because the water was agitated by tall splashes as a result of the dolphins chasing the porpoise.

At 0908 14 bottlenose dolphins left the interaction with the harbor porpoise. The remaining two bottlenose dolphins, male Naissance and male Kelp (Table 1, Subgroup B2) continued the interaction.

At 0913 Kelp and Naissance displayed synchronous and cooperative behaviors which resulted in the harassment of the porpoise (Table 2, Fig. 3).

From 0915 to 0924, within 9 min, the bottlenose dolphins engaged in sandwiching four times, tossing three times, and ramming and drowning several times (Table 2,

Table 2. Definitions of behaviors displayed by bottlenose dolphins while harassing harbor porpoises between 2007 and 2009.

Behavior	Description
Sandwiching	Squeezing the harbor porpoise between the left and right flank of two bottlenose dolphins in a forceful movement that lifts the porpoise's body out of the water. The intensity and power of this maneuver may cause bilateral hematomas of varying severity and bilateral rib fractures.
Drowning	Repeatedly lifting a dolphin's upper body out of the water at a 45° angle and letting it forcefully drop on top of the porpoise's head, pushing it underwater. Also positioning a dolphin's rostrum underneath the flukes of the porpoise and lifting the dolphin's head out of the water, effectively keeping the head of the porpoise underwater. Both techniques are effective in tiring and disorienting the porpoise, and in preventing it from breathing.
Tossing	Partially or completely throwing the porpoise out of the water with fast and violent maneuvers, using either the rostrum or the fluke to hit it. Often performed in sequence. This tactic produces loud noises as the porpoise is violently hit on both sides, and often sends the victim somersaulting out of the water.
Ramming	Hitting the porpoise at fast speed with the rostrum and the side of the body, often repeatedly and sometimes by multiple animals at the same time.

Fig. 3). All behaviors were carried out at high speed while chasing the harbor porpoise, which was trying to escape.

At 0928 there was a lull in activity. The porpoise was no longer visible. The two bottlenose dolphins started traveling south at a slow pace. There was no evidence of a kill, nor visual confirmation of the porpoise's health status. The research vessel followed the bottlenose dolphins south.

Event 3

At 0930 the same school of 16 dolphins which engaged in Event 2 (Table 1, Group B) was resighted 600 m south of the vessel (36.9057°N, 121.8509°W; Fig. 1): male Twinky, male Phyto, and putative male Bat (Table 1, Subgroup B3) inshore, and 13 others slightly offshore. The research vessel traveled south in proximity to the threesome all the way to Manresa State Beach (36.9246°N, 121.8551°W; Fig. 1).

At 1026 the threesome started pursuing a harbor porpoise. Based on the analysis of our digital photographs for scars and other distinguishing marks, this harbor porpoise was not the same animal as in the previous incident and was identified as a male when the carcass was retrieved.

From 1029 to 1035 the threesome "corralled" the porpoise 30 m from shore (Table 2). Subsequently, these dolphins repeatedly displayed sandwiching, ramming, and drowning behaviors (Table 2). Twice the porpoise was tossed out of the water. The porpoise was still alive at this point, albeit sluggish and seemingly incapacitated.

At 1038 seven of the bottlenose dolphin offshore joined in the aggression. The porpoise was dealt a series of violent fluke slaps (ramming). Throughout the

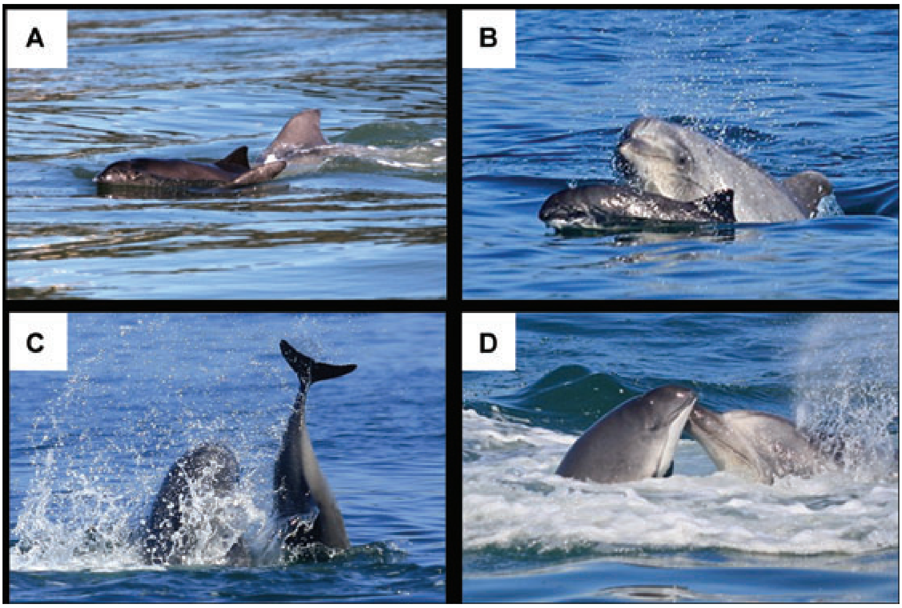

Figure 3. Examples of aggressive behaviors by bottlenose dolphins on harbor porpoises in Monterey Bay, California. (A) sandwiching, (B) drowning, (C) tossing, and (D) ramming. Refer to Table 2 for a definition of each behavior.

observation period, no blood was seen and the bottlenose dolphins did not appear to bite or rake the porpoise with their teeth.

From 1039 to 1043 tossing occurred twice (Table 2). The porpoise appeared weak, exhibiting atypical surfacing.

At 1046 the porpoise appeared to be dead, and floated motionless either horizontally or vertically in the water. The dolphins continued to push it around, and the porpoise was observed several times just below the surface, belly-up.

At 1104 all bottlenose dolphins started traveling south at a slow pace and showed little interest in the now-dead porpoise, except for male Medusa and putative male Avalanche (Table 2, Subgroup B4). Medusa and Avalanche stayed behind and started to "handle" the carcass. They pushed it around and underwater with their rostra for up to a minute at a time. Medusa was observed making genital contact with the porpoise.

At 1107 Medusa actively pushed the porpoise carcass with its rostrum to within 1 m of the stern of our boat and then logged (sat motionless) sideways at the surface, looking up, at about 2–3 m distance from the vessel. Avalanche was positioned 4–5 m away (at the bow of the vessel), also logging at the surface and looking up. Both animals watched as our crew hoisted the dead porpoise out of the water and onto the boat. Both dolphins vocalized repeatedly using a combination of clicks and whistles while continuing to log and looking at the boat for the duration of the carcass retrieval.

At 1108 interaction and observations ended. The dead harbor porpoise was transferred to the stranding network coordinator for necropsy. The porpoise did not have any rake marks or external trauma on the body.

Social Context

All dolphins involved in the events were full-grown adults. Sixty-one percent were confirmed males and 31% were putative males. During Event 1 in 2007, only male Poke was seen interacting with the porpoise. Poke was also present in both the 2009 events. Of the 16 dolphins present at Event 2 and 3 in 2009, 11 were confirmed males and 5 were putative males (Table 1).

In Event 2, two males, Kelp and Naissance, engaged in a prolonged aggressive interaction with the porpoise. In Event 3, two of the first three dolphins to engage in aggressive interaction were confirmed males (Phyto and Twinky). The two dolphins that handled the porpoise after it was dead were a confirmed male (Medusa) and a putative male (Avalanche).

There was a 40% overlap in the identity of the bottlenose dolphins present during harbor porpoise interactions in 2007 and 2009. In fact, the same group of 16 dolphins was involved in both events in 2009, one hour apart, in two separate locations, suggesting that the same individuals engage in this activity repeatedly.

Discussion

Intra- and interspecific aggression can be costly, and, as such, would be expected to be expressed only in circumstances when clear advantages can be gained by the individual (Lorenz 1963). However, the causal factors for such interactions may be different in different locations and a more detailed analysis of local evidence, we believe, is the best approach to understanding this behavior. Critical to this discussion is the fact that all the bottlenose dolphins involved in the attacks were either known adult males or putative males. This is the first time the sex of the attackers has been confirmed in such interactions.

To limit the discussion to plausible forms of aggression, we excluded antipredatory and predatory aggression (harbor porpoises do not prey on bottlenose dolphins and *vice versa*); defensive aggression by bottlenose dolphins (harbor porpoises are unlikely to initiate aggression on bottlenose dolphins given the differences in body size); and maternal aggression (the attackers were all either males or putative males). The hypotheses we explore are: (1) aberrant behavior, (2) interspecies territoriality, (3) prey competition or feeding interference (as suggested by Spitz *et al.* 2006), (4) object-oriented play with infanticide and practicing fighting skills as triggers, and (5) other potential contributing factors. Ultimately, the motivation for these aggressions could be complex and depend on multiple combined factors.

Aberrant Behavior

Aberrant behavior, in the context of our discussion, is a behavior that is outside of the behavioral repertoire considered typical of the species in question, according to current knowledge. Based on this definition, we exclude aberrant behavior as an explanation for attacks on harbor porpoises.

Reports involving aggressive interactions between bottlenose dolphins and other cetacean species have been numerous and geographically widespread. The attack tactics we have witnessed are similar in execution and sequence to those described in other geographic areas, specifically the United Kingdom, in conjunction with harbor porpoise attacks (Ross and Wilson 1996, Jepson and Baker 1998), and Virginia, United States in conjunction with interspecific infanticide (Dunn *et al.* 2002). Both of these observations support the notion that these patterns are part of the natural repertoire for the genus *Tursiops*.

Interspecies Territoriality

The seasonality and the geographic extent of harbor porpoise/coastal bottlenose dolphin interactions along the California coast mirror harbor porpoise distribution patterns and the seasonality of harbor porpoise movements. Harbor porpoises and bottlenose dolphins overlap in geographic range only between Point Conception, the southern limit of harbor porpoise distribution (Gaskin 1984) and Mendocino County, the northern limit of California coastal bottlenose dolphin distribution (Feinholz 1996, Fig. 1). While coastal bottlenose dolphins are restricted to depths $\leq$15 m (Defran and Weller 1999), harbor porpoises have highest densities in waters $\leq$60 m (Carretta *et al.* 2001) and range no deeper than 110 m (Barlow *et al*. 1998). Aggressive interactions were recorded only in late summer and fall when harbor porpoise densities are highest (Sekiguchi 1995, Barlow *et al*. 1998). Because of body size and a tendency to be solitary or in small groups, harbor porpoises are unlikely to present a threat to bottlenose dolphins, and the only possible conflict in overlapping ranges could come from competition for food.

Prey Competition and Feeding Interference

In the North Atlantic, interactions between bottlenose dolphins and harbor porpoises have been attributed to interference competition based on the extent of geographic and dietary overlap (Spitz *et al.* 2006). No comprehensive study on either coastal bottlenose dolphin diet or dietary overlap with harbor porpoises exists for the Pacific coast.

Based on stomach samples, harbor porpoises in the Pacific feed mainly on market squid (*Loligo opalescens;* Walker *et al.* 1998), Pacific sardine (*Sardinops sagax*), Pacific herring (*Clupea pallasii*), Pacific hake (*Merluccius productus*), and smelt (Wilke and Kenyon 1952, Scheffer 1953, Fink 1959). Prey items sizes range from 80 to 371 mm in length and from 4 to 317 g in weight (Walker *et al.* 1998).

Pacific coast bottlenose dolphins were documented eating at least 25 species. The families *Embiotocidae* (surf perches) and *Sciaenidae* (croakers) comprised 75% of the fish identified, and market squid may be taken when seasonally abundant in inshore waters (Norris and Prescott 1961, Walker 1981, Hanson and Defran 1993). Bottlenose dolphins feed on a larger and wider variety of prey than harbor porpoises. In addition, harbor porpoises have a much wider depth range.

In contrast, direct competition exists between California sea lions (*Zalophus californianus*) and bottlenose dolphins. In the Southern California Bight, Bearzi (2006) found pinnipeds associated with dolphins in 53% of her encounters. Monterey Bay is home to a large population of seals and sea lions year-round. However, aggressive interactions with pinnipeds and pinniped strandings resulting from trauma inflicted by bottlenose dolphins have not been documented. The food competition hypothesis is also weakened by the concentration in space (northern Monterey Bay) and time

(August 2008 primarily) of porpoise/dolphin aggressive interactions, unless specific and currently unknown resource limitations were present at those specific times and places. In addition, the fact that only male dolphins participated in the documented interactions favors alternative hypotheses.

Object-Oriented Play: Infanticide

Patterson *et al.* (1998), suggest that attacks on porpoises are a form of object-oriented play aimed at practicing skills used in infanticidal attacks. Infanticide in vertebrates has been documented extensively in the literature (see review by Hausfater and Hrdy 1984) and is considered a strategy that enhances the reproductive success of the infanticidal male by providing access to an otherwise reproductively unavailable female. When access to females is limited, a male with infanticidal skills may have more chances at mating by inducing estrous in females. In fact, Connor *et al.* (1996) reported that female bottlenose dolphins became sexually receptive within 7–11 d of the loss of their calves. Considering that male–female consortships may last several weeks (Connor *et al.* 1996), infanticide is a viable strategy for males. However, females have counter-strategies such as going into a sham-estrous during periods of high male harassment or having multiple estrous cycles to avoid being monopolized by a single male or male pair (Connor *et al.* 1996).

Infanticide has been documented along the East Coast of the United States (Dunn e*t al.* 2002) and in the United Kingdom (Patterson *et al.* 1998), where it may be frequent, based on indirect evidence provided by trauma-related bottlenose dolphin calf strandings. Patterson *et al.* (1998) suggested the trigger for bottlenose dolphin aggression could be the harbor porpoise's small size, which is similar to the size of a bottlenose dolphin calf. Supporting this hypothesis is the fact that the majority of porpoises killed in the United Kingdom are between 100 and 150 cm long (Ross and Wilson 1996, Jepson and Baker 1998). This pattern was similar in California, although all-age classes were included among the stranded porpoise carcasses with trauma-related injuries, including adults up to 163 cm in length, both males and females. Another argument in support of this hypothesis is the fact that all bottlenose dolphins engaging in the aggressive interactions we documented were either males or putative males.

However, in California, there are no records of bottlenose dolphin calves with injuries similar to those sustained by harbor porpoises (Cordaro[3]) and overall, documented bottlenose dolphin strandings are rare, making it difficult to determine true mortality rates. In addition, we have followed 30 females between 2006 and 2009, and only three appear to have lost their calves (Cotter and Maldini, unpublished data). Causes of death were unknown. An infanticidal male would have to contend with the female to gain access to the calf. It is possible that females in Monterey Bay are extremely successful at protecting their calves from attacks. Females with calves in Monterey Bay almost exclusively travel in nursery schools, and the presence of many females may provide an extra level of protection through female cooperation and strength in numbers against coalitions of males (Cotter and Maldini, unpublished data).

[3]Personal communication from Joe Cordaro, NOAA, Southwest Regional Office, 501 West Ocean Boulevard, Suite 4200, Long Beach, CA, 28 September 2009.

Object-Oriented Play: Practice Fighting

In bottlenose dolphin societies, where males tend to form lifelong bonds, and in some locations, coalitions to gain access to females, male sexual-competition is high (Connor *et al.* 2000, Mann and Sargeant 2003, Connor and Whitehead 2005). Bonds and coalitions are the highest form of cooperation within these populations, and male reproductive success, as well as survival in general, depends on the strength and coordination of these units (de Waal and Harcourt 1992; Connor *et al.* 1992*a*, *b*). Direct fighting between large male dolphins has a high cost, may result in injury to one or more of the males and, ultimately, be a disadvantage. However, maintaining fighting skills may be necessary for a dolphin to prevail when these skills are needed (Möller *et al.* 2001). Directing aggression toward a smaller individual of a different species may be the best strategy to practice fighting skills without incurring the cost of fighting a large conspecific. Additionally, coordinating an attack on a harbor porpoise may fine-tune coordination among close male associates and may provide an indirect bonding mechanism.

Other Factors

Other factors may have played a role in triggering the attacks on porpoises. Aggression by male bottlenose dolphins could have been driven by high levels of testosterone (Higgins and Tedman 1990, Rose *et al.* 1991). In California, harbor porpoises come close to shore and overlap in distribution with coastal bottlenose dolphins in the summer, which coincides with the estimated height of the breeding season for bottlenose dolphins in Monterey Bay, based on the time of sighting of new calves each year and on a 12 mo gestation period (Cotter and Maldini, unpublished data). High levels of testosterone have been linked to heightened aggression in males for several species of vertebrates, including humans (Archer 1988) and ultimately measuring stress hormones in California coastal bottlenose dolphins may be important in weighing different hypotheses. However, in the United Kingdom, where the two species overlap in distribution year-round, there was no strong seasonality in the frequency of bottlenose dolphin aggression on harbor porpoises (http://www.ukstrandings.org, accessed June 2010; Jepson[4]).

A skewed male–female ratio may also lead to heightened aggression patterns driven by the presence of a low number of available females for a larger population of males. The inability of low ranking or less experienced males to access females may lead to “frustration” expressed in the form of aggression (Le Boeuf and Campagna 1994). Interestingly, both 2008 and 2009 appeared to be periods of low female availability in Monterey Bay where the male/female ratio was approximately 1:1 for known sex individuals but the operational sex ratio may have been closer to 3:1 (Cotter and Maldini, unpublished data).

In conclusion, ultimate explanations for complex behaviors are difficult to find. In this case, knowing the sex and the social composition of the bottlenose dolphin groups perpetrating the attacks may have added a layer of understanding to this difficult question. Nonetheless, a more detailed analysis of social structure, reproductive status and stress hormone levels may be needed. It is likely that multiple factors may have played a role in the expression of this aggressive behavior.

[4]Personal communication from Dr. Paul Jepson, Zoological Society of London, Regent’s Park, London, NW1 4RY, UK, June 2010.

Acknowledgments

We would like to thank Joe Cordaro and Sarah Wilkin at NOAA, Teri Sigler and Dr. Dave Casper at Long Marine Lab, and Dr. Frances Gulland at The Marine Mammal Center for assistance with stranding information. Cyndi Browning, Ron Eby, Gary Haskins, Robert Scoles, Alessandro Ponzo, and Andrew Walsh provided help in the field. A special thanks to Barbara Scoles for filming the behaviors. We acknowledge Earthwatch Institute and an anonymous funder for the grants supporting the field portion of the project in 2007. Work was conducted under NOAA Letter of Agreement 877–1831. Biopsy sampling was conducted under Permit 13392 from NOAA Fisheries. Opinions expressed in the paper are solely the opinions of the authors and not necessarily the opinions of NOAA personnel or members of any other subsidiary agency indirectly involved in this work.

Literature Cited

Acevedo-Gutierrez, A., A. Diberardinis, S. Larkin, K. Larkin and P. Forestell. 2005. Social interactions between tucuxis and bottlenose dolphins in Gandoca-Manzanillo, Costa Rica. Latin American Journal of Aquatic Mammals 4:49–54.

Alonso, J. M., A. Lopéz, A. F. González and M. B. Santos. 2000. Evidence of violent interactions between bottlenose dolphin (*Tursiops truncatus*) and other cetacean species in NW Spain. Proceedings of the 14th Annual Conference of The European Cetacean Society. Cork, Ireland, 2–5 April 2000. Pp. 105–106.

Archer, J. 1988. The behavioral biology of aggression. Cambridge Studies in Behavioral Biology. Cambridge University Press, New York, NY.

Baird, R. W. 1998. An interaction between pacific white-sided dolphins and a neonatal harbor porpoise. Mammalia 62:129–137.

Barlow, J., P. S. Hill, K. A. Forney and D. P. Demaster. 1998. U.S. Pacific marine mammal stock assessments: 1998. U.S. Department of Commerce, NOAA Technical Memorandum, NOAA-TMNMFS-SWFSC-258, 40 pp. Available from Southwest Fisheries Science Center, P. O. Box 271, La Jolla, CA 92038.

Barnett, J., N. Davidson, R. Deaville, R. Monies, J. Loveridge, N. Tregenza and P. D. Jepson. 2009. Postmortem evidence of interactions of bottlenose dolphins (*Tursiops truncatus*) with other dolphin species in South-West England. Veterinary Record 165:441–444.

Bearzi, M. 2006. California sea lions use dolphins to locate food. Journal of Mammalogy 87(3):606–617.

Bearzi, M., C. Saylan and A. Hwang. 2009. Ecology and comparison of coastal and offshore bottlenose dolphins (*Tursiops truncatus*) in California. Journal of Marine and Freshwater Research 60:584–593.

Carretta, J. V., B. L. Taylor and S. J. Chivers. 2001. Abundance and depth distribution of harbor porpoise (*Phocoena phocoena*) in northern California determined from a 1995 ship survey. Fishery Bulletin 99:29–39.

Connor, R. C., and H. Whitehead. 2005. Alliances II. Rates of encounter during resource utilization: A general model of intrasexual alliance formation in fission-fusion societies. Animal Behaviour 69:127–132.

Connor, R. C., R. A. Smolker and A. F. Richards. 1992*a*. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). Proceedings of the National Academy of Sciences 89:987–990.

Connor, R. C., R. A. Smolker and A. F. Richards. 1992*b*. Dolphin alliances and coalitions. Pages 414–443 *in* A. H. Harcourt and F. B. M. DeWaal, eds. Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, UK.

Connor, R. C., A. F. Richards, R. A. Smolker and J. Mann. 1996. Patterns of female attractiveness in Indian Ocean bottle-nose dolphins. Behaviour 133:37–69.

Connor, R. C., A. J. Read and R. Wrangham. 2000. Male reproductive strategies and social bonds. Pages 247–269 *in* J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead, eds.

Cetacean societies: Field studies of dolphins and whales. University of Chicago Press, Chicago, IL.

Defran, R. H., and D. W. Weller. 1999. Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (*Tursiops truncatus)* off San Diego, California. Marine Mammal Science 15:366–380.

Defran, R. H., D. W. Weller, D. L. Kelly and M. A. Espinosa. 1999. Range characteristics of pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California Bight. Marine Mammal Science 15:381–393.

de Waal, F. B. M., and A. H. Harcourt. 1992. Coalitions and alliances: A history of ethological research. Pages 233–257 *in* A. H. Harcourt and F. B. M. de Waal, eds. Coalitions and alliances in humans and other animals. Oxford University Press, Cambridge, UK.

Dunn, D. G., S. G. Barco, D. A. Pabst and W. A. Mclellan. 2002. Evidence for infanticide in bottlenose dolphins of the western North Atlantic. Journal of Wildlife Diseases 38:505–510.

Feinholz, D. M. 1996. Northern range extension, abundance, and distribution of Pacific coastal bottlenose dolphins (*Tursiops truncatus gilli*) in Monterey Bay, California. M.S. thesis, San Jose State University, San Jose, CA. 88 pp.

Fink, B. D. 1959. Observation of porpoise predation on a school of Pacific sardines. California Fish and Game 45:216–217.

Gaskin, D. E. 1984. The harbor porpoise (*Phocoena phocoena* L.): Regional populations, status, and information on direct and indirect catches. Report International Whaling Commission 34:569–586.

Hanson, M. T., and R. H. Defran. 1993. The behavior and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. Aquatic Mammals 19:127–142.

Hausfater, G., and S. B. Hrdy. 1984. Infanticide: Comparative and evolutionary perspectives. Aldine Publishing Company, New York, NY.

Herzing, D. L. 1996. Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*. Aquatic Mammals 22:61–79.

Herzing, D. L., and C. M. Johnson. 1997. Interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985–1995. Aquatic Mammals 23:85–100.

Herzing, D. L., K. Moewe and B. J. Brunnick. 2003. Interspecies interactions between Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*, on Great Bahama Bank, Bahamas. Aquatic Mammals 29:335–341.

Higgins, L. V., and R. A. Tedman. 1990. Effect of attacks by male Australian sea lions on mortality of pups. Journal of Mammalogy 71:617–619.

Jefferson, T. A., P. J. Stacey and R. W. Baird. 1991. A review of killer whale interactions with other marine mammals: Predation to co-existence. Mammal Review 21:151–180.

Jepson, P. D., ed. 2005. Cetacean strandings investigation and co-ordination in the UK: Final report to DEFRA for the period 1st January 2000–31st December 2004. Available at http://randd.defra.gov.uk/Document.aspx?Document=Wp01011_8244_Frp.pdf (accessed February 2010).

Jepson, P. D., and J. R. Baker. 1998. Bottlenosed dolphins (*Tursiops truncatus*) as a possible cause of acute traumatic injuries in porpoises (*Phocoena phocoena*). Veterinary Record 143:614–615.

Le Boeuf, B. L., and C. Campagna. 1994. Protection and abuse of young in pinnipeds. Pages 257–276 *in* S. Parmigiani and F. Vom Saal, eds. Infanticide and parental care. Harwood Academic Publishers, London, UK.

Lockyer C., M. P. Heide-Jørgensen, J. Jensen, C. C. Kinze and T. Buus Sørensen. 2001. Age, length and reproductive parameters of harbor porpoises *Phocoena phocoena* (L.) from West Greenland. ICES Journal of Marine Science 58:154–162.

Lorenz, K. 1963. On aggression. Harvest Publications, Harcourt Brace & Company, San Diego, CA.

Mann J., and B. L. Sargeant. 2003. Like mother, like calf: The ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). Pages 236–266 *in* D. Fragaszy and S. Perry, eds. The biology of traditions: Models and evidence. Cambridge University Press, Cambridge, UK.

McBride, A. F., and H. Kritzler. 1951. Observations on pregnancy, parturition, and post-natal behavior in the bottlenose dolphin. Journal of Mammalogy 32:251–266.

Möller, L. M., L. B. Beheregaray, R. G. Harcourt and M. Krützen. 2001. Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. Proceedings of the Royal Society of London B 268:1941–1947.

Norris, K. S., and J. H. Prescott. 1961. Observations of Pacific cetaceans of Californian and Mexican waters. University of California Publications in Zoology 63:291–401.

Orr, J. R., and L. A. Harwood. 1998. Possible aggressive behavior between a narwhal (*Monodon monoceros*) and a beluga (*Delphinapterus leucas*). Marine Mammal Science 14:182–185.

Patterson, I. A. P., R. J. Reid, B. Wilson, K. Grellier, H. M. Ross and P. M. Thompson. 1998. Evidence for infanticide in bottlenose dolphins: An explanation for violent interactions with harbor porpoises? Proceedings of The Royal Society of London B 263:1167–1170.

Rose, N. A., C. J. Deutsch and B. J. Le Boeuf. 1991. Sexual behavior of male northern elephant seals: III. The mounting of weaned pups. Behaviour 19:171–192.

Ross, H. M., and B. Wilson. 1996. Violent interactions between bottlenose dolphins and harbor porpoises. Proceedings of The Royal Society of London B 263:283–286.

Sekiguchi, K. 1995. Occurrence, behavior and feeding habits of harbor porpoises (*Phocoena phocoena*) at Pajaro Dunes, Monterey Bay, California. Aquatic Mammals 21:91–104.

Scheffer, V. B. 1953. Measurements and stomach contents of eleven delphinids from the Northeast Pacific. The Murrelet 34:27–30.

Shane, S. H. 1995. Relationship between pilot whales and Risso's dolphins at Santa Catalina Island, California, USA. Marine Ecology Progress Series 123:5–11.

Spitz, J., Y. Rousseau and V. Ridoux. 2006. Diet overlap between harbor porpoise and bottlenose dolphin: An argument in favor of interference competition for food? Estuarine Coastal and Shelf Science 70:259–270.

Terry, R. P. 1984. Intergeneric behavior between *Sotalia fluviatilis guianensis* and *Tursiops truncatus* in captivity. Zeitschrift für Säugetierkunde 49:290–299.

Walker, W. A. 1981. Geographical variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern North Pacific. Administrative Report LJ-81-03C NMFS, SWFC, San Diego, CA. 52 pp.

Walker, W. A., M. B. Hanson, R. W. Baird and T. J. Guenther. 1998. Food habits of the harbor porpoise, *Phocoena phocoena*, and Dall's porpoise, *Phocoenoides dalli*, in the inland waters of British Columbia and Washington. Marine Mammal Protection Act and Endangered Species Act Implementation Program 1997. AFSC Processed Report 98-10. National Marine Fisheries Service, Seattle, WA. Pp. 63–75.

Wedekin, L. L., F. G. Daura-Jorge and P. C. Simoes-Lopes. 2004. An aggressive interaction between bottlenose dolphins (*Tursiops truncatus*) and estuarine dolphins (*Sotalia guianensis*) in southern Brazil. Aquatic Mammals 30:391–397.

Weller, D. W., B. Würsig, H. Whitehead, *et al*. 1996. Observations of an interaction between sperm whales and short-finned pilot whales in the Gulf of Mexico. Marine Mammal Science 12:588–594.

Wilke, J., and K. W. Kenyon. 1952. Notes of the food of fur seal, sea lion, and harbor porpoise. Journal of Wildlife Management 16:396–397.

Wilson, B., R. J. Reid, K. Grellier, P. M. Thompson and P. S. Hammond. 2004. Considering the temporal when managing the spatial: A population range expansion impacts protected areas-based management for bottlenose dolphins. Animal Conservation 7:331–338.

Received: 2 June 2010
Accepted: 17 January 2011