Recovery rates of bottlenose dolphin (*Tursiops truncatus*) carcasses estimated from stranding and survival rate data

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Abstract

Recovery of cetacean carcasses provides data on levels of human-caused mortality, but represents only a minimum count of impacts. Counts of stranded carcasses are negatively biased by factors that include at-sea scavenging, sinking, drift away from land, stranding in locations where detection is unlikely, and natural removal from beaches due to wave and tidal action prior to detection. We estimate the fraction of carcasses recovered for a population of coastal bottlenose dolphins (*Tursiops truncatus*), using abundance and survival rate data to estimate annual deaths in the population. Observed stranding numbers are compared to expected deaths to estimate the fraction of carcasses recovered. For the California coastal population of bottlenose dolphins, we estimate the fraction of carcasses recovered to be 0.25 (95% CI = 0.20–0.33). During a 12 yr period, 327 animals (95% CI = 253–413) were expected to have died and been available for recovery, but only 83 carcasses attributed to this population were documented. Given the coastal habits of California coastal bottlenose dolphins, it is likely that carcass recovery rates of this population greatly exceed recovery rates of more pelagic dolphin species in the region.

Key words: bottlenose dolphin, *Tursiops truncatus*, strandings, carcass recovery, survival rates, human-caused mortality.

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Estimated levels of human-caused mortality and serious injury for cetaceans suffer from negative biases due to incomplete detection and recovery of carcasses. Contributing factors may include scavenging, drift, sinking, decomposition, natural removal from beaches due to wave action, undocumented bycatch, remoteness of cases, carcass removal or burial by municipalities prior to a stranding response, and failure to detect visible carcasses. It follows that documenting *natural* mortality through carcass recovery also suffers from negative bias for many of the same reasons. Previous carcass recovery studies have utilized abundance data, annual survival rates, tagging of carcasses at sea, and stranding numbers to estimate the degree of negative bias. Where reported, the fraction of carcass recovery is quite low, ranging from 0 to 0.062 for Gulf of Mexico cetaceans (Williams *et al.* 2011), <0.01 for North Atlantic harbor porpoises (*Phocoena phocoena*) (Moore and Read 2008), 0.039–0.13 for eastern Pacific gray whales (*Eschrichtius robustus*) (Punt and Wade 2012), 0.17 for north Atlantic right whales (*Eubalaena glacialis*) (Kraus *et al.* 2005), 0.08 for common dolphins (*Delphinus*) off France (Peltier *et al.* 2012), 0.05–0.18 for Brazilian franciscana dolphins (*Pontoporia blainvillei*) (Prado *et al.* 2013), and 0.33 for Sarasota Bay bottlenose dolphins (*Tursiops truncatus*) (Wells *et al.* 2015) (Table 1).

Our goal is to estimate the fraction of carcasses recovered for the "California coastal" population of bottlenose dolphin that occurs along the U.S. west coast and Baja California (Defran *et al.* 1999). This population is a good case study because of factors including habitat preferences, reliability and stability of abundance estimates, and population distinctness. The population has a high degree of nearshore site fidelity, with >99% of all sightings within 500 m of shore (Hanson and Defran 1993, Carretta *et al.* 1998). The population's nearshore distribution suggests that individual California coastal bottlenose dolphins may be the most likely delphinid species to strand in the region, given a mortality event. If stranding probabilities of coastal bottlenose dolphins are indeed higher than other delphinid species in the area, the population serves as an excellent "best case scenario" with respect to carcass recovery.

Table 1. Published estimates of cetacean carcass recovery rates.

Study	Species	Area (years)	Minimum estimate of carcass recovery	Maximum estimate of carcass recovery
Kraus *et al.* (2005)	Right whale (*Eubalaena glacialis*)	NE United States (1986–2005)	—	0.17
Moore and Read (2008)	Harbor porpoise (*Phocoena phocoena*)	NE United States (1999–2003)	—	<0.01
Peltier *et al.* (2012)	Common dolphin (*Delphinus delphis*)	France (2004–2009)	—	0.08
Prado *et al.* (2013)	Franciscana dolphin (*Pontoporia blainvillei*)	Brazil (2005–2009)	0.05	0.18
Punt and Wade (2012)	Gray whale (*Eschrichtius robustus*)	Alaska to Mexico (1999–2000)	0.039	0.13
Wells *et al.* (2014)	Bottlenose dolphin (*Tursiops truncatus*)	SE United States (1993–2012)	—	0.33
Williams *et al.* (2011)	Multiple species	Gulf of Mexico (2003–2007)	0	0.062

The range of California coastal bottlenose dolphins is well-known, spanning approximately 1,000 km of coastline from Ensenada, Mexico, to San Francisco, California (Defran *et al.* 1999) (Fig. 1). Rarely, carcasses from this population are found as far north as the states of Oregon and Washington. High rates of photo-identification overlap (percent of identified individuals documented between regions) are documented between Ensenada and Santa Barbara in the southern California Bight (55% to 90%) and between the southern California Bight and Monterey Bay (>50%) (Feinholz 1996, Defran *et al.* 1999, Hwang *et al.* 2014; Fig. 1). Individual animals have traveled nearly 1,000 km between Ensenada and Monterey and rapid movements of 300 km in 5 d between San Diego and Santa Barbara are known (Hwang *et al.* 2014). From this we infer that the area from Ensenada to San Francisco includes one population. Approximately 18% of the stock's range occurs south of the U.S./Mexico border (Carretta *et al.* 2013). Based on mark-recapture movement data, individuals appear to use this entire range and exhibit limited site fidelity to any particular region (Defran *et al.* 1999, Hwang *et al.* 2014). In contrast, only 3% of animals identified near San Quintín, Mexico were also identified in the southern California Bight (Caldwell 1992, Defran *et al.* 2015), suggesting a southern limit of this population somewhere between Ensenada and San Quintín. The coastal stock of bottlenose dolphins is distinct from the offshore stock, based on morphology and genetics (Perrin *et al.* 2011, Lowther-Thielking *et al.* 2015). Of 56 haplotypes found among coastal and offshore bottlenose dolphins in the region, only one is shared by both populations (Perrin *et al.* 2011). Approximately 90% of stranding records of bottlenose dolphins along the mainland coast represent coastal stock animals (Perrin *et al.* 2011; NMFS,
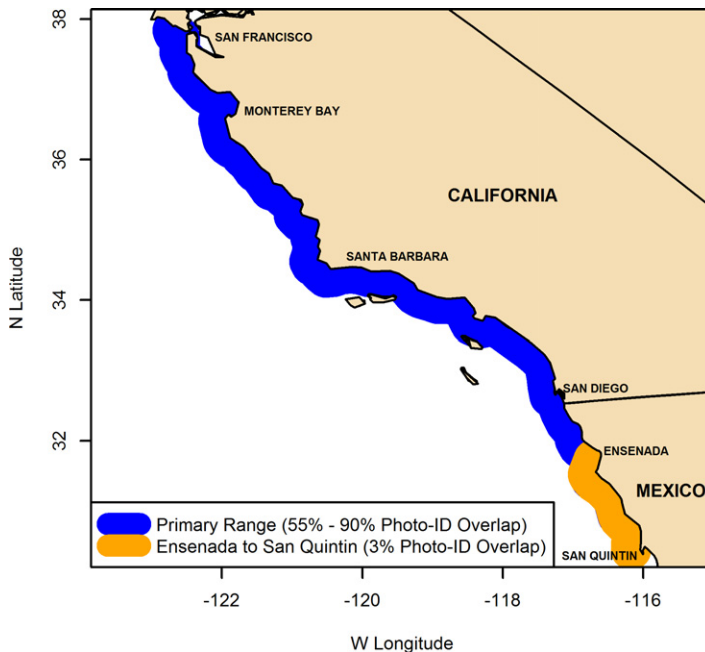

Figure 1. Normal range of California coastal bottlenose dolphins, including estimates of photo-ID match overlap between geographic regions. Photographic mark-recapture evidence indicates that individuals from the population utilize the entire coastal range.

unpublished data), despite the fact that the offshore population is estimated to be 6–7 times more abundant (Barlow 2010, Carretta *et al.* 2013).

Abundance estimates of the coastal stock are based on three different photographic mark-recapture estimates between 1987 and 2005 and appear stable over a 20 yr period, with approximately $300-400$ marked individuals (Dudzik 1999, Dudzik *et al.* 2006) (Table 2). Such a stable population size facilitates comparison of annual stranding data with expected carcass numbers, in contrast with a population where abundance may be changing rapidly.

Estimation of annual dolphin deaths requires data or assumptions about life history parameters such as annual survival rate. While survival rates for the California coastal population are not currently estimated, other bottlenose dolphin populations (both captive and wild) have been studied, from which published estimates of survival can be used in tandem with abundance data to estimate the number of carcasses available to strand.

Methods

Our analysis focuses on the years 1995–2006, when both reliable abundance estimates and stranding numbers of coastal bottlenose dolphins were available. We reviewed the literature to obtain survival rate estimates for bottlenose dolphins, which are used in combination with abundance data from the California coastal population to estimate the expected number of deaths annually. The number of carcasses recovered annually by stranding networks is compared to the number of expected deaths estimated *via* Monte Carlo simulations and used to estimate the fraction of carcasses recovered.

Strandings

Stranding records of bottlenose dolphins from the U.S. west coast were obtained from several institutions: NOAA Fisheries Southwest Fisheries Science Center, Los Angeles County Museum, Santa Barbara Museum of Natural History, Moss Landing Marine Laboratories, Long Marine Lab (UC Santa Cruz), The Marine Mammal Center, California Academy of Sciences, Oregon State University, Cascadia Research Collective, and the Washington Department of Fish and Wildlife. Stranding records were available as early as 1935, however, we focus on the time period beginning in 1995 for a few reasons. First, 1995 represents the first year that systematic accounting of human-caused mortality for U.S. marine mammal populations was required after 1994 revisions to the Marine Mammal Protection Act (MMPA) (Barlow *et al.* 1995).

Table 2. Estimates of California coastal bottlenose dolphin abundance and coefficients of variation (CV) obtained from photo-ID mark-recapture studies. Estimates represent only marked animals in the population.

Years	Estimated abundance (CV)	Source
1987–1989	354 (0.04)	Dudzik (1999)
1996–1998	356 (0.09)	Dudzik (1999)
2004–2005	323 (0.12)	Dudzik *et al.* (2006)

Second, new field efforts designed to estimate the abundance of the California coastal bottlenose dolphin stock began in 1996 (Dudzik 1999). Third, stranding networks in the region were well-established by this time. Stranding reporting and documentation was much-improved compared with earlier decades and facilitated by increased cell phone use and improved education and outreach efforts with local lifeguards and other coastal authorities compared to earlier periods. In previous decades, it was not uncommon for local municipalities to bury cetacean carcasses or relocate them to landfills before marine mammal experts were contacted. This may still occur on occasion, but public and municipal cooperation is improved, and from a historical perspective, the percentage of strandings reported to biologists today is probably at its highest.

For 1995–2006, we reviewed 92 bottlenose dolphin mainland stranding records from the U.S. west coast from the States of California, Oregon, and Washington. A majority of strandings occurred in California ($n = 91$), none in Oregon, and one in Washington. We strived to account for all stranding records during this time, but cannot guarantee that records are all-inclusive. Strandings from offshore islands were rare and were not included in this analysis, as stranding response effort there is minimal and opportunistic. Population identity (coastal *vs.* offshore) is not known for every stranding because many lack genetic or skeletal material. Perrin *et al.* (2011) reported finding 56 haplotypes among California coastal and offshore bottlenose dolphin populations, with only one shared haplotype. Of 80 mainland strandings examined by Perrin *et al.* (2011), 73 (91%) were assigned to the coastal population based on having haplotypes known only from coastal reference animals. A larger data set of genetic determinations from strandings along the California, Oregon, and Washington mainland coast between 1953 and 2013 shows that 94% (163/173) of animals have a high probability of being from the coastal population (NMFS, unpublished data). Likewise, during our study period, 54 of 61 (88%) mainland strandings for which genetic material was available were assigned to the coastal population, while the remaining 31 animals were not assigned to any population, usually because genetic material was insufficient or lacking. Based on the historic ratios of bottlenose dolphin carcasses from the mainland that were identified as coastal *vs.* offshore stock animals, we prorated the number of observed mainland strandings by 0.90 to correct for the approximately 10% that represent offshore animals. This implies that of the 92 mainland strandings recorded between 1995 and 2006, approximately 83 animals were from the coastal population.

Dolphin Abundance

We estimate mean dolphin abundance from 1995 to 2006, using the two most recent estimates from Table 2. Our analysis period extends one year before and after field data were collected for those abundance estimates, with the assumption that abundance did not change significantly during the 1 yr periods before and after each field study. Mean abundance for the period is calculated as the geometric mean of the 1996–1998 and 2004–2005 abundance estimates, in the same manner used in Pacific marine mammal stock assessment reports (Carretta *et al.* 2013). The resulting mean estimate (and CV) is 339 animals (CV = 0.07). This estimate represents only *marked* animals in the population (those with distinctive dorsal fins). Dudzik *et al.* (2006) estimated that the fraction of marked animals in the population was 0.63, but did not report a variance for this value. Using the sample sizes of marked ($n = 164$) and unmarked ($n = 97$) animals given by Dudzik *et al.* (2006), we assume that the

fraction of marked animals in the population is a binomial random variable with mean = 0.63 (see *Simulations* below). This fraction marked represents a correction factor to estimate "true" population size, such that mean abundance is estimated as 339 animals divided by 0.63, or approximately 538 animals.

Annual Survival Rate

Bottlenose dolphins are among the most-studied cetaceans, with long-term studies of small populations yielding a variety of survival rate estimates, including some age- and sex-specific estimates (DeMaster and Drevenak 1988, Hersh *et al.* 1990, Wells and Scott 1990, Small and DeMaster 1995, Stolen and Barlow 2003, Currey *et al.* 2009, Nicholson *et al.* 2012). We reviewed the literature for bottlenose dolphin survival rate estimates, including wild and captive populations. Large differences in annual survival for animals ≤1 yr old (calves) and older animals was apparent from multiple studies, with the lowest annual survival rates found among calves (Table 3).

Simulations

Monte Carlo methods were used to simulate abundance (N_{sim}) and annual survival rate (S) for each year from 1995 to 2006. Annual abundance was modeled as a log-normal random deviate with a mean of 339 animals, a CV = 0.07, and a sample size of 1,000. Simulated annual abundance was divided by the fraction of marked animals in the population (Fr_{marked}), reported as 0.63 by Dudzik *et al.* 2006), to correct for the unmarked portion of the population not reflected in mark-recapture estimates. No estimate of uncertainty was given for Fr_{marked}, but the number of marked ($n = 164$) and unmarked ($n = 97$) animals was reported, from which we generated a binomial random variable to represent the fraction of the population marked for each of 1,000 uncorrected annual abundance estimates. The resulting distribution of Fr_{marked} has a mean of 0.63 with an approximate 95% confidence interval of 0.57 to 0.69.

Roughly 18% of the population's range occurs in Mexican waters where we do not have reliable stranding data, thus, all simulated abundances were multiplied by a

Table 3. Published estimates of annual survival rates for captive and wild bottlenose dolphin populations. Only estimates based on wild populations are used in the present study.

Study	Area	Population type	Annual survival rate (age class)
Currey *et al.* (2009)	Doubtful Sound, New Zealand	Wild	0.862 (<1 yr) 0.937 (adults)
DeMaster and Drevenak (1988)	Various display facilities	Captive	0.61 (<1 yr) 0.93 (all ages)
Hersh *et al.* (1990)	Florida	Wild	0.908–0.931 (all ages)
Nicholson *et al.* (2012)	Australia	Wild	0.95 (all ages)
Small and DeMaster (1995)	Various display facilities	Captive	0.666 (<1 yr) 0.948 (adults)
Stolen and Barlow (2003)	Florida	Wild	0.836 (<1 yr) 0.902 (all ages)
Wells and Scott (1990)	Florida	Wild	0.81 (<1 yr) 0.96 (adults)

"range correction factor" ($R_f = 0.82$) to reflect only those carcasses available to strand on U.S. beaches. This is equivalent to assuming that animals are equally likely to utilize areas in southern California and Mexico, which is supported by high resighting rates of individuals between southern California and Mexico (Defran *et al*. 1999, Hwang *et al*. 2014). If on average, more than 18% of the population occurs south of U.S./Mexico border, this approach would overestimate the number of carcasses available to strand on U.S. beaches, which would negatively bias carcass recovery estimates. Insufficient fine-scale and short-term movement data for individual dolphins in this population are available to test this assumption.

Annual survival rate (S) was allowed to vary as a uniform random variable for each of 1,000 N_{sim}, with lower and upper limits taken from the literature (Table 3). Separate survival rates were assumed for two different age classes: animals ≤1 yr old and animals >1 yr. Calf survival (S_{calf}) ranged between 0.81 and 0.862 and adult survival (S_{adult}) ranged between 0.937 and 0.96, based on published values for wild populations only (Table 3).

Use of separate estimates of survival for calves and adults required knowledge about the fraction of calves in the population. Hansen (1990) and Weller (1991) found that calves (defined as animals ≤1 yr old) represented 7% and 11%, respectively, of all individuals photographed in the California coastal population. Values from other coastal bottlenose dolphin populations are similar, with calves representing between 8% and 11% of animals (Würsig 1978, Shane *et al*. 1986, Campbell *et al*. 2002, Stolen and Barlow 2003). The fraction of calves in the population (Fr_{calf}) was based on sampling with replacement from a uniform distribution ranging from 0.07 to 0.11, and was allowed to vary for each of 1,000 values of N_{sim}. The fraction of adult animals (Fr_{adult}) is simply $1 - Fr_{calf}$. The expected number of carcasses available to strand each year ($C_{expected}$) is a simulated distribution of 1,000 values derived from N_{sim}, Fr_{calf}, Fr_{adult}, S_{calf}, and S_{adult}, and can be expressed as:

$$C_{expected} = C_{calf} + C_{adult} \tag{1}$$

where

$$C_{calf} = N_{sim}/Fr_{marked} \cdot R_f \cdot (1 - S_{calf}) \cdot Fr_{calf} \tag{2}$$

and

$$C_{adult} = N_{sim}/Fr_{marked} \cdot R_f \cdot (1 - S_{adult}) \cdot Fr_{adult} \tag{3}$$

where $C_{expected}$ = expected dolphin carcasses in year y; C_{calf} = expected calf carcasses in year y; C_{adult} = expected adult carcasses in year y; N_{sim} = simulated abundance in year y, Lognormal(mean = 339, CV = 0.07); Fr_{marked} = fraction of population that is marked, Binomial(mean = 0.63, 95% CI = 0.58–0.69); Fr_{calf} = fraction of calves in the population in year y, Uniform(0.07–0.11); Fr_{adult} = fraction of adults in the population in year y, Uniform(0.89–0.93); S_{calf} = annual calf survival rate in year y, Uniform(0.81–0.862); S_{adult} = annual adult survival rate in year y, Uniform(0.937–0.96); and R_f(0.82) represents the fraction of carcasses assumed to occur in U.S. waters at any one time.

For each year, the estimated fraction of carcasses recovered is simply the observed number of strandings (prorated by 0.90 to account for some animals being of offshore origin) divided by the mean of $C_{expected}$. 95% confidence limits for the fraction of

carcasses recovered are calculated as number of stranding events divided by the 2.5th and 97.5th percentiles of $C_{expected}$.

Results

Over the 12 yr study period, 92 stranded bottlenose dolphin carcasses were documented on the mainland. After prorating for the proportion historically identified as coastal (*vs*. offshore) stock animals, 83 strandings were assumed to originate from the coastal stock. The number of expected deaths for this same period was 327 animals (78 calves and 249 adults). Calves represented 24% of the expected carcasses over the study period, which is less than that documented from long-term stranding data (38%). Estimated carcass recovery for all ages averaged 0.25 (95% CI = 0.20–0.33) over the 12 yr study period (Table 4). Annually, carcass recovery estimates ranged from 0.099 to 0.46 (Table 4), reflecting annual variability in carcass numbers found ashore under an assumption of stable population size. Simulated annual deaths (calves and adults combined) represented 6% of the estimated population size, which is equivalent to an annual all-ages survival rate of 0.94. The mean number of expected deaths each year ($n = 27$) converges towards a single value because we assumed a fixed population size over the study period and simulation sample sizes were sufficient to result in such convergence.

Discussion

With the exception of an embayment population of Florida bottlenose dolphins where carcass recovery was estimated to be 0.33 (Wells *et al.* 2015), carcass recovery estimates for California coastal bottlenose dolphins from this study (0.25) are higher than values found for other cetaceans (Table 1). This is not surprising, considering the coastal habits of the population, the effectiveness of stranding networks, and the high density of human activity along this coast. Our results are case-specific to this particular population and stranding network characteristics, but likely represent a maximum carcass recovery rate for dolphin species along the U.S. west coast. One caveat to our estimates is that they reflect background rates of mortality in the absence of an unusual or mass mortality event, such as those associated with morbillivirus (Lipscomb *et al.* 1994).

Both natural and anthropogenic mortality are represented in strandings, but confirming evidence of anthropogenic mortality is sometimes difficult due to carcass decomposition or the cryptic nature of the evidence (*e.g.*, gill net marks that may not be detected by responders). Our results contain the implicit assumption that stranding probability is equal for natural and anthropogenic mortality, but this may not be true. In a study of harbor porpoise, Moore and Read (2008) suggested that natural mortality involves processes such as predation and starvation that may have lower stranding probabilities than previously healthy gill net-caught animals discarded at sea that are more likely to float. They also found evidence of age-biased mortality for animals caught in gill nets compared to beach strandings representing an unknown mix of natural and anthropogenic mortality. Given the extremely coastal habits of California coastal bottlenose dolphin and infrequent interaction with gill nets that

Table 4. Observed and prorated numbers of strandings, expected carcass numbers, and estimated fraction of carcasses recovered for the period 1995–2006. Prorated strandings may not be whole numbers because observed strandings were prorated by 0.90 to account for some strandings originating from the offshore population.

Year	Observed strandings	Prorated strandings	Mean expected deaths	L95 expected deaths	U95 expected deaths	Mean expected calves	Mean expected adults	Mean *Fr* recovered	L95 *Fr* recovered	U95 *Fr* recovered
1995	8	7.2	27.2	20.8	34.8	6.6	20.6	0.26	0.21	0.35
1996	5	4.5	27.1	21.3	34.2	6.5	20.6	0.17	0.13	0.21
1997	3	2.7	27.1	20.8	34	6.5	20.6	0.1	0.079	0.13
1998	5	4.5	27.3	21.2	34.3	6.5	20.8	0.16	0.13	0.21
1999	3	2.7	27.2	21.1	34.2	6.5	20.7	0.099	0.079	0.13
2000	10	9	27.2	20.7	34.4	6.5	20.7	0.33	0.26	0.43
2001	12	11	27.3	21	34.4	6.5	20.7	0.4	0.31	0.52
2002	11	9.9	27.2	21	34.3	6.5	20.7	0.36	0.29	0.47
2003	7	6.3	27.3	21.4	34.7	6.5	20.8	0.23	0.18	0.29
2004	14	13	27.3	21.1	34.5	6.5	20.8	0.46	0.37	0.6
2005	7	6.3	27.3	21.1	35.1	6.5	20.7	0.23	0.18	0.3
2006	7	6.3	27.2	21.1	33.9	6.5	20.8	0.23	0.19	0.3
All years	92	83	327	253	413	78	249	0.25	0.2	0.33

are fished at least 3 mi (4.8 km) from shore, we believe that any differences in stranding probabilities for natural and anthropogenic mortality are likely to be small.

Levels of uncertainty in carcass recovery estimates are likely underestimated. The fraction of the coastal bottlenose dolphin population that occurs in U.S. waters at any one time is unknown and cannot be estimated without tracking individual dolphin movements. Rather, we assume that 18% of coastal bottlenose dolphin carcasses are unavailable to U.S. west coast stranding networks, based on the fraction of their known range that occurs south of the U.S./Mexico border. Our method of estimating carcass recovery is crude compared with multivariate models that consider factors such as drift, wind, buoyancy, and decomposition (Peltier *et al.* 2012, 2013; Prado *et al.* 2013). However, while it is interesting to know *why* all carcasses are not recovered, we reduce the problem to a simple metric of *how many* carcasses are recovered relative to the expected number, similar to the work of Williams *et al.* (2011). The reasons behind negative biases in carcass recovery are interesting subjects, but are not necessary to develop correction factors for stranding numbers.

Length data for strandings collected during 1995–2006 were available for only 42 of 92 records, so a direct comparison of observed and expected carcass numbers for calves and adults is not possible. Length-at-age data are not available for this population, but two animals from this population as large as 168 cm and 171 cm have been aged at <1 yr (NMFS, unpublished data). By comparison, Read *et al.* (1993) reported a lower-bound length of 171 cm for 1-yr-old bottlenose dolphins in Sarasota Bay. When a larger data set (*n* = 162) of mainland bottlenose dolphin strandings from 1948 to 2013 is examined, a distinct modal length of 125 cm is apparent, corresponding to high numbers of neonate strandings compared to other age classes (Fig. 2). If animals <1 yr old are assumed to be <170 cm, then approximately 38% of all strandings between 1948 and 2013 represent calves (Fig. 2). From simulations, the fraction of expected calf carcasses is 0.24 (78/327) (Table 4), which is considerably less than the fraction of calves (0.38) observed from long-term stranding data. If we assume that 38% of the 83 strandings attributed to the coastal population between 1995 and 2006 are animals <1 yr old, then 32 calves are represented. The number of expected calves from simulations is 78 over the same period, implying a calf recovery fraction of 0.41. The corresponding estimate of carcass recovery for
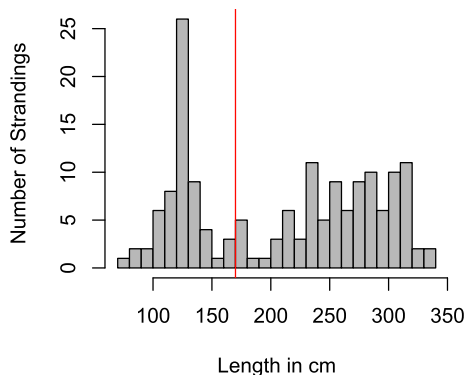

Figure 2. Distribution of dolphin lengths recorded for 162 stranded specimens of *Tursiops truncatus* along the mainland U.S. west coast, 1948–2013. Vertical red line delineates approximate length of animals <1 yr old (≤170 cm).

adults (assuming that 51 of 83 coastal animal strandings were adults) is 51 recovered/ 249 expected = 0.20. Both observed (38%) and simulated (24%) percentages of calf carcasses are high relative to the percent of calves observed in the population at any one time (7%–11%) (Hansen 1990, Weller 1991), implying that calf recovery rates are relatively high compared to adults. Differences in stranding probabilities by age probably exist, especially if currents and beach conditions favorable to deposition overlap with calving seasonality. For example, the long-term stranding data for 1948–2013 includes 62 strandings <170 cm in length, 48 (77%) of which stranded during the 4 mo spring/summer period of May–August. By comparison, only 46% of "large" carcasses (>170 cm) were collected during this same 4 mo period. These observations imply a seasonal peak in calving, spring/summer ocean conditions conducive to beach deposition of carcasses, or both. Spring and summer are characterized by gentle wave action conducive to deposition, in contrast to autumn and winter conditions more favorable to erosion and removal of objects from beaches. Although newly born calves are seen year-round in this population, calving seasonality is not well-studied. If calving seasonality coincides with summer beach conditions favorable for deposition (and detection due to increased human presence), then high calf recovery levels are not surprising.

Another potential contributing factor to higher calf recovery estimates is that simulated calf survival estimates from wild populations are optimistically high because field researchers fail to detect all births. Wells and Scott (1990) noted that birth rates can be underestimated, especially if field efforts are far enough apart in time such that neonates that die soon after birth have no chance of being counted by researchers unless they strand. Studies of captive calves indicate that a large percentage of neonates die within days of birth (Venn-Watson *et al.* 2011) and this may apply to wild births too. The lower bound of 0.81 for wild calf survival (Wells and Scott 1990) used in our simulations resulted in approximately 6–7 expected calf carcasses annually. Had we included *captive* calf survival estimates in our simulations, annual calf survival could have ranged as low as 0.61 (DeMaster and Drevenak 1988) and the expected number of calf carcasses would have increased to 10–11 annually, representing approximately one-third of annual expected carcasses, which is in close agreement with long-term stranding observations.

Our estimates of carcass recovery (0.25, 95% CI = 0.20–0.33) for an extremely coastal dolphin population suggests that observed anthropogenic mortality values of dolphins in this region derived from strandings should be corrected to account for unobserved mortality. This assumes that the probability of stranding is equal for natural and human-caused deaths, an assumption that is difficult to test. Our estimates have implications for developing carcass recovery correction factors for other more pelagic dolphin species in the region that might be less likely to strand (Perrin *et al.* 2011). Context clues as to the degree of negative bias in carcass recovery for more pelagic dolphins in this region are apparent when abundance and strandings are considered across multiple populations. Perrin *et al.* (2011) noted that a coastal bottlenose dolphin carcass is 50 times more likely to reach shore than an offshore ecotype, based on differences in estimated abundance for each population and assuming similar mortality rates. Danil *et al.* (2010) reported that the more pelagic common dolphin (*Delphinus delphis* and *D. capensis* combined) accounted for 43% of cetacean stranding records in San Diego County, while bottlenose dolphins (largely coastal animals) represented 16% of records. This yields a crude stranding ratio of 2.6 common dolphins for every bottlenose dolphin. In Santa Barbara County, the ratio of common dolphin to bottlenose dolphin strandings is approximately 10:1 (Santa

Barbara Museum of Natural History, unpublished data). Estimates of common dolphin abundance (both species combined) in southern California waters are approximately 400,000 animals (Barlow 2010, Carretta *et al.* 2011), compared with approximately 500–600 animals for coastal bottlenose dolphins. The ratio of common dolphin to bottlenose dolphin abundance is roughly 700:1 and expected stranding ratios should reflect relative abundance if both groups had equal stranding probabilities. Taken in context, abundance and strandings data imply a very low probability of stranding for the extremely abundant, but more pelagic common dolphins.

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