

Carcasses on the coastline: measuring the ecological fidelity of the cetacean stranding record in the eastern North Pacific Ocean

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Abstract.—To understand how well fossil assemblages represent original communities, paleoecologists seek comparisons between death assemblages and their source communities. These comparisons have traditionally used nearshore, marine invertebrate assemblages for their logistical ease, high abundance, and comparable census data from living communities. For large marine vertebrates, like cetaceans, measuring their diversity in ocean ecosystems is difficult and expensive. Cetaceans, however, often beach or strand themselves along the coast, and archived data on stranded cetaceans have been recorded, in some areas, over several decades. If the stranding record is interpreted as a death assemblage, then the stranding record may represent a viable alternative for measuring diversity in living communities on directly adjacent coastlines. This study assessed the fidelity of the cetacean stranding record in the eastern North Pacific Ocean. The living community in this region has been studied for over 100 years and, recently, extensive and systematic live transect surveys using ship-based observing platforms have produced a valuable source of live diversity data. Over this same period, the U.S. Marine Mammal Stranding Program has collected and archived a record of cetacean strandings along the U.S. Pacific coastline, providing an ideal death assemblage for comparison. Using fidelity metrics commonly used in marine invertebrate taphonomy, I determined that the stranding record samples the living cetacean community with high fidelity, across fine and coarse taxonomic ranks, and at large geographic scales (>1000 km of coastline). The stranding record is also richer than the live surveys, with live-dead ratios between 1.1 and 1.3. The stranding record recovers similar rank-order relative abundances as live surveys, with statistical significance. Also, I applied sample-based rarefaction methods to generate collector's curves for strandings along the U.S. Pacific Coast to better evaluate the spatiotemporal characteristics of the stranding record. Results indicate that saturation (i.e., sampling >95% assemblage) at species, genus, and family levels occurs in less than five years of sampling, with families accumulating faster than species, and larger geographic regions (i.e., longer coastlines) accumulating taxa the most rapidly. The high fidelity of the stranding record, measured both in richness and by ranked relative abundance, implies that ecological structure from living cetacean communities is recorded in the death assemblage, a finding that parallels marine invertebrate assemblages, though at far larger spatial scales. These results have implications for studying cetacean ecology in both modern and ancient environments: first, these results imply that the stranding record, over sufficiently long time intervals, yields a richer assemblage than using line-transect methods, and faithfully records aspects of community structure; and second, these results imply that geochronologically well-constrained fossil cetacean assemblages might preserve ecologically relevant features of community structure, depending on depositional and taphonomic conditions.

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Introduction

The occurrence of beached, or stranded, marine mammals has fascinated naturalists since Aristotle. Though sometimes regarded as anomalies on the coastal landscape (Smeenk 1997), stranded (and usually dead) specimens offer fundamental anatomical and descriptive data that otherwise would not be available because of the logistical limits of studying living cetaceans in their marine habitat. Historically, strandings presented unique

opportunities for naturalists to generate detailed accounts for many species of marine mammals, and especially for cetaceans (Hunter and Banks 1787; Scoresby 1810). The advent of large-scale commercial whaling at the end of the nineteenth century radically changed the study of cetacean natural history by bringing naturalists into contact with living or freshly dead specimens (Tønnessen and Johnsen 1982), but strandings along populated coastlines continue to provoke questions about their origin and significance to this day.

The causes of cetacean strandings are poorly understood. In various circumstances, they have been attributed to disease, infections, malnutrition, or senescence (Geraci and Loundsbury 2005). Mass strandings, which are almost entirely restricted to toothed cetaceans, have been explained by a similar list of causes, but the striking peculiarity of entire stranded pods, which can consist of hundreds of individuals, has produced no shortage of hypotheses. Explanations for mass strandings include geomagnetic interference with navigation (Kirschvink 1990; Walker et al. 1992); complexities of nearshore geomorphology (Brabyn and Frew 1994); military sonar use (Cox et al. 2006; Parsons et al. 2008); and large-scale patterns in earth and ocean climate (Evans et al. 2005; Bradshaw et al. 2006). This list of possible mechanisms is not mutually exclusive, and the putative causes for strandings vary in explanatory power depending on the number of individuals stranded, the region in which the events occur, as well as any obvious anthropogenic causes (e.g., ship strikes [Douglas et al. 2008]).

The primary data source for understanding these phenomena derives from long-term records and archived stranding reports based on direct accounts along coastlines. The United Kingdom, for example, established the first systematic network for reporting cetacean strandings, with annual reports published continuously since 1913 (Sheldrick 1976; Fraser 1977). In the United States, F. W. True (1883) first proposed a framework for reporting strandings, but such a program only emerged in 1972 with the U.S. Marine Mammal Protection Act, which established a legal basis for recognizing the value of recording marine mammal strandings (Geraci and St. Aubin 1979). Since 1991, reporting in regional U.S. Marine Mammal Stranding Networks has become more uniform and consistent than previous efforts in the 1970s, which had patchy and inconsistent reporting, as well as unstandardized data archiving (Heyning 1991). Elsewhere in the world, stranding networks have become more common, with other countries, such as New Zealand and the Netherlands, adopting

coordinated research programs to document and archive marine mammal stranding data (Brabyn 1991; van der Meij and Camphuysen 2006).

Generally, stranding records have been used to provide a measure of cetacean population size and species composition in specific regions (Sheldrick 1976; Sergeant 1982; Woodhouse 1991; MacLeod et al. 2004; Gulland et al. 2005; Keiper et al. 2005; Leeney et al. 2008), but these records can also be interpreted as a death assemblage representing a sample of the cetacean community living in adjacent waters. Since the 1960s, paleoecologists have compared the composition of living communities to their accumulated, hardpart remains in an effort to understand which ecological features of living communities are incorporated into the fossil record (Johnson 1964; Kidwell and Bosence 1991; Kidwell and Flessa 1996; Kidwell 2007). Such live-dead comparisons have guided reconstructions of extinct communities by elucidating the preservational biases in fossil assemblages (Valentine 1989; Kidwell and Flessa 1996). In cases where death assemblages have been time-averaged (Walker and Bambach 1971), live-dead comparisons have revealed that certain aspects of species diversity can be reliably read from evidence in the death assemblage, when controlling for factors like transport, destruction, and taxonomic turnover (Kidwell and Flessa 1996; Kidwell 2001, 2002).

Liebig et al. (2003) were the first to explicitly use beachcast marine mammal specimens as a death assemblage when they assessed how well the remains of dead marine mammals on a 4-km-long beach near the Colorado River Delta represented the adjacent living community in the Gulf of California. Other studies, including MacLeod et al. (2005), Maldini et al. (2005), and van der Meij and Camphuysen (2006), have made similar live-dead comparisons with cetaceans, although with less explicit reference to the previous taphonomic and paleoecological literature. Here, I followed this line of thinking by considering the cetacean stranding record along the continental U.S. Pacific coastline as a death assemblage (comprising

2533 individual stranding occurrences for 26 species), and compared this record to live surveys, conducted over the same interval of time, directly adjacent to the coastline in the eastern North Pacific Ocean. Using fidelity metrics and rarefaction methods at appropriate spatial and temporal scales, I evaluated how well the cetacean stranding record compares to the richness and abundance of taxa in the living community. The results of these comparisons have implications for measuring cetacean diversity in both modern and ancient realms. For modern ecological studies, the record of stranding occurrences may prove more useful for capturing aspects of cetacean community structure than previously suspected, especially at large spatial scales. The stranding record also provides an important comparison for well-sampled fossil cetacean assemblages, especially from geochronologically constrained stratigraphic sections that match the spatiotemporal parameters of the stranding record.

Methodological Considerations

Cetacean Natural History

Diversity and Ecology.—Cetaceans possess specific characteristics that make them a useful taxonomic group for the objectives of this study. First, cetaceans are the most species-rich clade of marine mammals, with a global richness exceeding 70 recognized species (Rice 1998; Reeves et al. 2002). Cetaceans of the eastern North Pacific Ocean (hereafter abbreviated ENP) consist exclusively of marine cetacean species, even if they occasionally enter brackish water embayments. Generally, most species in the ENP are widely represented from California to Washington State, although regionally endemic species have been recognized (e.g., coastal bottlenose dolphins, *Tursiops truncatus*, distributed solely between San Francisco and San Diego [Caretta et al. 2006]). The ENP contains a relatively high percentage of global species richness, with 49% of the all species reported by Reeves et al. (2002) occurring within the boundaries of the ENP. At broad taxonomic categories, nearly all marine odontocete (toothed whale) families

are represented in the ENP, and three out of the four major clades of mysticetes (baleen whales) are also in the ENP.

Second, cetacean life history exhibits a suite of features (e.g., long life, low fecundity, large range) that have broad temporal and geographic parameters. Cetacean life spans can exceed a century for some large baleen whales (George et al. 1999), and many odontocetes can live for several decades (Evans et al. 2002; Garde et al. 2007: Table 2). Consequently, this longevity would prevent cetacean death assemblages from displaying the mixed generational signatures that occur with invertebrate death assemblages (Kidwell 2002). Also, marine cetacean species have broad geographic ranges that span relatively wide latitudinal gradients (Reeves et al. 2002), and many mysticetes, like gray whales (*Eschrichtius robustus*), undertake seasonal migrations from temperate to polar latitudes (Jones et al. 1984).

Historiography.—Although naturalists have described marine mammal species in the ENP well before the nineteenth century, the first full account of marine mammal species in this region was accomplished in 1874 by C. M. Scammon (Scheffer 1968). Based on his experiences as a whaling captain, Scammon's (1874) account provided the first general summary of marine mammals of the ENP, and formed the basis for all later descriptions of marine mammal species in the region (e.g., Scheffer 1942; Leatherwood et al. 1988). Overall, the ENP cetacean community is one of the best-studied cetacean assemblages in the world because of a history of whaling and fisheries, an emerging legacy of conservation, and a close proximity to major centers of learning.

Other Candidate Marine Vertebrates.—In spatiotemporal terms, cetaceans live at the same scales as other large marine vertebrates like sharks, pinnipeds, and sea turtles (Eckert and Stewart 2001; Reeves et al. 2002; Hart et al. 2006). Sea turtles and sharks in the ENP strand in numbers so small as not to be useful for the purposes of this study. Pinnipeds (seals, sea lions, and walruses) seem like plausible candidates because they generally strand in large numbers and their strandings

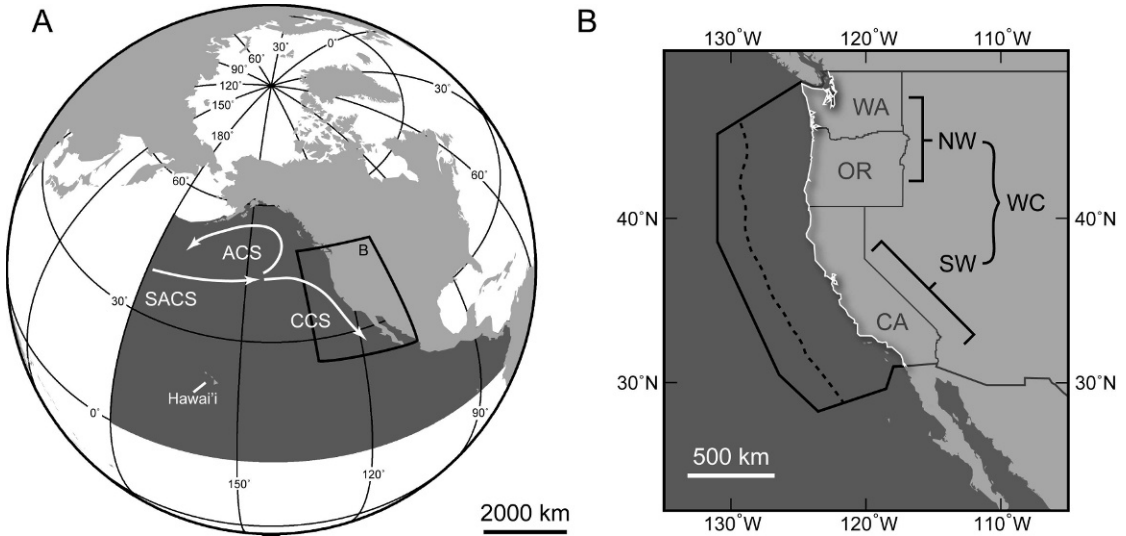


FIGURE 1. A, Orthographic projection of Earth, oriented on the eastern North Pacific Ocean (shaded in gray) with large-scale, temperate latitude physical oceanography. Abbreviated current systems follow Francis and Hare (1994): SACS, the Subarctic Current System; ACS, the Alaska Current System; and CCS, the California Current System. B, Mercator projection of the Pacific coastline of North America. Stranding regions abbreviations represent Northwest (NW) and Southwest (SW) regions, following each state's participation in the U.S. Marine Mammal Stranding Network. West Coast (WC) represents the summation of both NW and SW regions. U.S. state abbreviations represent California (CA), Oregon (OR) and Washington State (WA). Dashed line represents the U.S. Economic Exclusion Zone; the distal solid line represents the limits of the study transects conducted by Barlow and Forney (2007). Base maps generated using Online Map Creator, Martin Welnel, 2008.

occur in the same regions in which cetacean strandings are recorded (Cordaro 1997; Greig et al. 2005). Pinnipeds, however, have important limitations. Because they spend significant portions on their lives on land and are philopatric to their rookeries (Reeves et al. 2002), their geographic distributions are concentrated near select haul-out areas. This patchiness in distribution, at local to regional scales, is compounded by the decimation of many pinniped populations during historical times, which has dramatically reduced and/or altered their ranges (Moss et al. 2006). Although pinnipeds strand in numerically greater abundances than cetaceans, ENP pinnipeds have a much lower overall species richness along the U.S. Pacific coast, with no more than six pinniped species stranding in the regional stranding networks of the U.S. Pacific coastline (see data from sources in Methods).

Geographic Parameters of Live Surveys and Strandings Records

The ENP essentially represents the north-eastern quadrant of the Pacific Ocean,

bounded by the continental coastline of North America from Alaska to Panama (Fig. 1A). Several major oceanographic current systems are included in the broad latitudinal cross-section of the ENP region, and the physical and biological oceanography of the ENP and current systems have been intensively studied for more than 100 years (Benson and Rehbock 2002). Excluding Alaska and Hawaii (see justification in "Methods"), the U.S. Pacific coastline (i.e., the source of the death assemblage) is most directly affected by the California Current System, which runs from 50°N to 25°N, resulting in extensive nutrient upwelling that occurs from the coast of Washington State to southern California (Mann and Lazier 1996). The physical oceanography of the ENP thus provides a unique way to sample the diversity of living cetaceans, in contrast to other possible regions with stranding records that occur at the confluence of two or more current systems (e.g., New Zealand).

The large scale of living cetacean habitats highlights the importance of studying the death assemblage at commensurate scales.

For the purposes of this study, the continental U.S. Pacific coastline was used as a proxy for sampling the cetaceans living in the adjacent waters of the ENP. The U.S. Marine Mammal Stranding Network divides the U.S. Pacific coastline into the following regions: Southwest (the entirety of California's coastline); Northwest (Oregon's and Washington State's coastlines); and Alaska, which includes only its own coastline (Fig. 1B). This study will address only the Southwest and Northwest stranding regions, as explained in the "Methods" section.

The geomorphology of the U.S. Pacific coastline varies from California to Washington. General coastlines of the SW and NW regions are 1352 km and 729 km long, respectively (NOAA 1975), but tidal coastlines, which are a product of different geological and tectonic histories, differ dramatically. In California, tidal coastline, which includes the San Francisco Bay system, is 5515 km long. The large embayment system in Washington State increases its tidal coastline over 19 times more than its general length (4870 km from 253 km); for Oregon, the tidal coastline length is four times greater (2269 km from 476 km). Unfortunately, the available stranding record data in this study do not provide information about tidal conditions at stranding events, and thus it is not feasible to evaluate this bias of the stranding record any further.

Temporal Scale of Both the Strandings and Live Surveys

Prior to 1972, there were no U.S. federal laws to guide the collection of marine mammal stranding data along American coastlines (Geraci and St. Aubin 1979). Thus, the record of U.S. Pacific coast strandings before this time likely does not provide a thorough or accurate sample of all strandings that actually occurred. It is worth noting that Norman et al. (2004) demonstrated that the compilation of stranding records from Washington and Oregon, over several decades, provided a legitimate sampling of the adjacent living community (using data from 1930–2002). Maldini et al. (2005) demonstrated the same for toothed whale strandings in Hawaii,

during 1937–2002. Such compilations, however, are rare and difficult to generate, and mostly lack corresponding live survey data necessary for live-dead comparisons. After 1972, marine mammal strandings were reported using general guidelines, but the spatial coverage of the stranding networks was inconsistent within and between regions (Reynolds and Odell 1991). After 1991, network reporting increased its coverage across the United States, using taxonomic identifications that were widely recognized or sufficient (Heyning 1991; see MacLeod et al. 2005, for a similar rationale). The 1970s also mark the end of commercial, industrial whaling in waters of the ENP, and thus this aspect of human impact on the cetacean community may be constrained, although the effects of whaling on some ENP cetacean species remain apparent on levels of abundance, especially for some species of large baleen whales (Clapham et al. 1999; Reeves and Smith 2006).

Biases in the Stranding Record

Annual data reported by the U.S. marine mammal stranding networks provide, at face value, a consistent census of the occurrence of cetaceans along U.S. coastlines; whether such occurrence provides faithful data for understanding the diversity and abundance of cetaceans living near these coastlines is the focus of this study. Stranding occurrences themselves, however, have hidden biases and factors that are broadly related to aspects of cetacean natural history, human impacts, and stranding reporting.

Types of Strandings.—Cetacean strandings consist of different combinations of species and number of individuals, depending on the stranding event. For example, a single stranding event may consist of a single individual from one species, a mother-calf pair, a mass stranding of a single species, or a mass stranding of multiple species (Simmonds 1997; Hohn et al. 2006). Mass strandings are rare for mysticetes (Sergeant 1982: p. 27; Hohn et al. 2006) but they are more common among odontocetes, whose high degree of sociality may play a large role (Sergeant 1982). Large-scale oceanographic events may also

play a role (Evans et al. 2005), although the effect of such changes in the ENP during the interval of time considered in this study will be addressed in a subsequent study.

Human-Related Strandings.—Human impacts on cetaceans arise from interactions with fisheries and the shipping industry. Specifically, smaller cetaceans species may become entangled in fishing gear, and larger species, like balaenopterids, are often victims of ship strikes (Douglas et al. 2008). These events may create an artificially high number of stranding events near fishing grounds or along shipping lanes, which concentrate near human population centers. Environmental catastrophes, like massive oil spills or toxic algal blooms, may also increase the likelihood of stranded cetaceans. In the ENP, Carretta et al. (2006: p. 297) noted that from 1998 to 2002 the proportion of human-related strandings was 0.07% for pinnipeds and 10% for cetaceans (Carretta et al. 2006). Carretta et al. (2005: Table 2) also reported that specific human-related mortalities caused by fisheries primarily affected a select few species. For the ENP, Carretta et al. (2005) indicated that gillnets seem to affect only common dolphins (*Delphinus* spp.) and northern right whale dolphins (*Lissodelphis borealis*), both of which are highly abundant. Given the limitations of the available strandings data (see “Methods”), the data in this study could not be vetted for human-related impacts.

Reporting Biases.—Biases in reporting may affect the accuracy of the stranding record. For example, an individual may strand multiple times during its lifetime (assuming successfully refloating by timely rescuers), which would register multiple counts of the same species in the stranding record. Generally, live strandings are rare, and individuals stand a small chance of survival without significant human intervention (Geraci and Lounsbury 2005). Although a stranded cetacean may be a striking and unusual feature along the coastline, the chances of its occurrence being observed and reported are related to the accessibility of the shoreline to observers (Evans 1976).

Observer Population Size.—Human population density, in a given region, provides a

substantial pool of potential observers to record marine mammal strandings along the coastline. Population changes, and attendant changes in observer intensity and coverage, may thus affect the number of strandings reported, as MacLeod et al. (2005: p. 478) asserted for the Scottish coast. Increases in human population density can also improve stranding reporting, as indicated by CeTAP (1982) and Sergeant (1982) for coastal surveys along the North Atlantic Ocean.

In this study, observer intensity was ostensibly related to the rate of population growth along the U.S. Pacific Coast during the time interval of the available live-dead data. The population concentration in counties along the U.S. Pacific coastline is high relative to other coastlines with similar upwelling regions (e.g., the west coasts of Africa and South America). Between the turn of the century and the 1970s, the U.S. population increased dramatically, and it is possible that this growth correlates with increased the number of reported strandings over this period. Such biasing factors will be more thoroughly considered in subsequent work.

Methods

Data Sources

Death Assemblage.—This study used cetacean stranding data recorded by the U.S. Department of Commerce marine mammal stranding network, which is archived and published in the annual Marine Mammal Assessment volumes issued by the Department of Commerce to the U.S. Congress. The U.S. marine mammal stranding network is divided into different regions, with landlocked states roughly designated by proximity to a coastal state. Along the coastline of the ENP, there are four regions: the Southwest region (SW), whose coastline is composed entirely of California; the Northwest region (NW), whose coastline includes Oregon and Washington State; Alaska; and Hawaii. Although data from all regions of the marine mammal stranding network are published annually for the National Oceanic and Atmospheric Administration (NOAA) Fisheries in the Marine Mammal Protection Act Annual

TABLE 1. List of cetacean taxa in this study, with both taxonomic and common names (Rice 1998, with modifications following Reeves et al. 2002). Other compilations (e.g., Leatherwood et al. 1988) list more species in the ENP; the list of taxa presented here pertains only to those cetaceans sampled in the living or death assemblage over the time period included in this study (1990–2005). Explanation of symbols: †, dead only in SW region; ‡, dead only in NW region; ◇, living only in SW region; *, not alive in any region; ‡, found dead as a species, but only diagnosable alive at generic level. Note that total number of taxa listed here (27) differs from subtotals of dead and living taxa in the ENP.

Clade	Family	Genus	Species	Status	Common name	
Mysticeti	Balaenidae	<i>Eubalaena</i>	<i>japonica</i>	†*	Right whale	
		<i>Balaenoptera</i>	<i>musculus</i>	†	Blue whale	
	Balaenopteridae	<i>Balaenoptera</i>	<i>physalus</i>		Fin whale	
		<i>Balaenoptera</i>	<i>borealis</i>	§	Sei whale	
		<i>Balaenoptera</i>	<i>edeni</i>	◇	Bryde's whale	
		<i>Balaenoptera</i>	<i>acutorostrata</i>		Minke whale	
		<i>Megaptera</i>	<i>novaeangliae</i>		Humpback whale	
		<i>Eschrichtius</i>	<i>robustus</i>		Gray whale	
Odontoceti	Delphinidae	<i>Delphinus</i>	<i>delphis</i>	†	Common dolphin	
		<i>Globicephala</i>	<i>macrorhynchus</i>	◇	Short-finned pilot whale	
		<i>Grampus</i>	<i>griseus</i>		Risso's dolphin	
		<i>Lagenorhynchus</i>	<i>obliquidens</i>		Pacific white-sided dolphin	
		<i>Lissodelphis</i>	<i>borealis</i>		North right whale dolphin	
		<i>Orcinus</i>	<i>orca</i>		Killer whale	
		<i>Stenella</i>	<i>coeruleoalba</i>		Striped dolphin	
		<i>Steno</i>	<i>bredanensis</i>		Rough-toothed dolphin	
		<i>Tursiops</i>	<i>truncatus</i>	◇	Bottlenose dolphin	
		Kogiidae	<i>Kogia</i>	<i>breviceps</i>	‡	Pygmy sperm whale
			<i>Kogia</i>	<i>simus</i>	†‡	Dwarf sperm whale
			Phocoenidae	<i>Phocoena</i>	<i>phocoena</i>	
	<i>Phocoenoides</i>	<i>dalli</i>			Dall's porpoise	
	Physeteridae	<i>Physeter</i>	<i>macrocephalus</i>		Sperm whale	
	Ziphiidae	<i>Berardius</i>	<i>bairdii</i>		Baird's beaked whale	
		<i>Mesoplodon</i>	<i>stejnegeri</i>	‡	Stejneger's beaked whale	
		<i>Mesoplodon</i>	<i>carlhubbsi</i>	†‡	Hubbs' beaked whale	
		<i>Mesoplodon</i>	<i>peruvianus</i>	†‡	Pygmy or Peruvian beaked whale	
		<i>Ziphius</i>	<i>cavirostris</i>	◇	Cuvier's beaked whale	

Report Archive (available at <http://www.nmfs.noaa.gov/pr/laws/mmpa/annual.htm>), the regional data may be subsequently revised and corrected (J. Cordaro personal communication 2008).

Data archived from the U.S. marine mammal stranding network for the regions in this study consisted primarily of reported strandings with taxonomic identifications at the highest possible resolution. In most cases, taxonomic identifications were made at the species level, but some categories included generic or supra-familial level identifications. The raw data, as downloaded from NOAA websites, consisted of a list of mixed taxonomic ranks, which reflects the difficulty in diagnosing stranded specimens in the field. For the analyses presented in this study, these raw data were compiled into uniform rank sets of species-, genus-, and family-level data, which included only identifications relevant to the respective taxonomic rank.

(The modification procedures to the raw data are reported in Appendix 1). With the exception of *Balaenoptera*, *Kogia*, and *Mesoplodon*, stranded species belong to genera that are monotypic in the ENP. Family-level groupings are also monophyletic groupings (May-Collado and Agnarsson 2006) (see Table 1 for scientific and common names).

Individual stranding occurrence data, per taxonomic category, were treated as individual events, i.e., one individual per occurrence. In reality, individual occurrences reported to the stranding network may consist of multiple individuals; the raw NOAA data sets online provide no information about this possibility. Also, this study assumed that stranding individuals were necessarily dead, and that the individual was not refloated by human intervention or by tides. Lastly, this study made no assumption with respect to the cause of individual cetacean strandings. In reality, strandings may include natural

mortalities and human-related strandings. Many odontocetes, and especially beaked whales (Ziphiidae), seem highly vulnerable to ocean noise and military sonar (Cox et al. 2006; Parsons et al. 2008). Large mysticetes, like blue whales (*Balaenoptera musculus*), seem susceptible to mortality from ship strikes (Douglas et al. 2008).

Of the available stranding network regions along the whole U.S. Pacific coast, only the NW and SW regions were selected for this study. Both of these coastlines have consistent reporting on an annual basis. In contrast, the Alaska region has a much smaller population (and thus a much smaller pool of potential observers), and year-to-year observer consistency is lacking. Both the NW and SW regions have relatively accessible coastlines, whereas the Alaska coastline south of 59°N is inaccessible by foot (Martin 2004). Notably, the living cetacean community in Alaska is highly endemic, consisting of Holarctic species like belugas (*Delphinapterus leucas*) and bowhead whales (*Balaena mysticetus*), which rarely range into temperate waters. Lastly, the comparison of Alaska with the NW and SW regions may not be legitimate because the regions are driven by different current systems. The stranding network of Hawaii was also excluded from this study because of its restricted geographic sampling in comparison with NW and SW regions (Maldini et al. 2005). Because this study aimed to analyze stranding data at the scale of continental coastlines, both the individual NW and SW regions were pooled into a larger data set of the California-Oregon-Washington or West Coast coastline, termed hereafter WC (Fig. 1B).

Stranding data for this study were collected during 1990–2004 for the NW region and during 1990–2005 for the SW region. For uniformity, WC data thus covered 1990–2004. The NW region data were collected as a composite from two different tabulations, and the SW region data were collected from the SW regional NOAA (see Appendix 1 for details). Pre-1990 stranding data were inconsistently collected by SW and NW regions, and thus were not used in this study. Notably, by including post-1990 data, the

resultant data set included the most recently described cetacean species in the ENP, the pygmy beaked whale (*Mesoplodon peruvianus*) (Reyes et al. 1991). In sum, this study considered the death assemblage at three different taxonomic levels (species, genera, and families) across three different geographic scales (NW, SW, and WC regions).

Living Community.—Because of the intense interest in the natural history of ENP cetaceans for fisheries research, live relative abundance data exist for the same regions that have death assemblage data sets (i.e., stranding records). Cetacean live abundance data have been traditionally measured by using line-transect methods (Buckland et al. 2001), which use an array of visual and acoustic tools (Evans and Hammond 2004). Such methods have been used consistently by NOAA's Southwest Fisheries Science Center for estimating marine mammal abundance in the California Current System since the 1990s (Appler et al. 2004). The first comprehensive survey of living marine mammals within an approximately 500 km envelope of U.S. Pacific coastline was conducted by researchers in 1996, and the culmination of several, successive efforts since that time were recently reported in Barlow and Forney (2007). Specifically, Barlow and Forney (2007) conducted a series of line-transect surveys at different times during 1990–2005, generating a set of cetacean live abundance data unrivalled for any other large geographic region of the world in its consistency and scope. The authors surveyed the ENP with detailed line-transects in 1991, 1995, 1996, 2001 and 2005, ranging a total of 15 years. Lacking individual year samples like those of the stranding record, I compared the cumulative abundance data over the entire survey period (1991–2005) with cumulative stranding record data, which were collected over the same time range, though shifted by one year (1990–2004).

The taxonomic coverage in Barlow and Forney's (2007) surveys was not entirely complete, and they noted that their data sets lacked live abundance data for three primarily coastal cetacean species: gray whales, harbor porpoises (*Phocoena phocoena*), and the coastal stock of bottlenose dolphins. The

supplemental live abundance data for each of these species were collected from additional references listed in Appendix 2. Also, I modified the taxonomic categories of the live survey data set to develop a hierarchy parallel with the death assemblage data set. Modifications to the ranks and subsequent data sets follow protocols listed in Appendix 3.

Lastly, it is important to note that the live survey data were collected using different types of methods. Although data from all methods were treated equivalently in this study, the sum total of cetacean live data was collected through a combination of ship-, aerial-, and land-based surveys (Barlow and Forney 2007). With each collection method, ocean conditions may reduce visibility and thus surveying effectiveness, but it is difficult to control for such biases or to assess them in a rigorous and consistent manner.

Analysis

Fidelity

Paleobiologists and taphonomists interested in comparing the differences in diversity between dead and living assemblages have developed a series of comparative measurements that have been termed fidelity metrics (Kidwell and Bosence 1991; Kidwell and Flessa 1996; and references therein). Fidelity metrics use the differences in species occurrence, richness, and abundance to quantify how well living assemblages mirror dead ones, and vice versa, and are used to measure in particular composition fidelity, richness fidelity, and relative abundance fidelity (Kidwell and Bosence 1991).

Compositional Fidelity.—This group of fidelity metrics describes the overall assemblage-wide similarities between dead and living assemblages. Specifically, this metric involves three different comparative calculations: the percentage of taxa found in the living assemblage that are also found in the death assemblage (live-dead); the percentage of taxa found in the death assemblage that are also found in the living assemblage (dead-live); and the percentage of individuals of the taxa in the death assemblage that are also found in

the living assemblage (an abundance-based dead-live measure).

The live-dead metric (*LD*) follows an equation described by Kidwell and Bosence (1991). In this expression, N_l equals the number of exclusively live taxa, and N_s equals the number of taxa shared among the living and death assemblages. For the percentage of living taxa that are also represented in the death assemblage, the equation is

$$LD = \frac{N_s \times 100}{(N_l + N_s)}. \quad (1)$$

The dead-live metric (*DL*) expresses the number of dead taxa that are also represented in the living assemblage. In this calculation, N_d equals the number of exclusively dead taxa, and follows the equation described by Kidwell and Bosence (1991), using the same values from the previous equation:

$$DL = \frac{N_s \times 100}{(N_d + N_s)}. \quad (2)$$

Lastly, Kidwell and Bosence (1991) provided an equation to describe an abundance-corrected version of equation (2) that accounts for the number of individuals of the dead taxa that also represented in the living assemblage (DL_a). This equation has been clarified from its original articulation (Kidwell and Bosence 1991: p. 138) to indicate that the denominator includes the dead abundance of *both* N_d and N_s . Here, the number of dead individuals of each value is abbreviated by “# d. i.”:

$$DL_a = \frac{\# \text{ d. i. } N_s \times 100}{(\# \text{ d. i. } N_d + \# \text{ d. i. } N_s)}. \quad (3)$$

The resultant values from these three equations are reported in a comparative fashion, across geographic regions and taxonomic ranks.

Taxonomic Richness.—Though live-dead studies generally focus on species or generic richness, I broadened the taxonomic categories used in this study to those that are available in both the stranding record and living assemblage data (e.g., species, genera, and families). Richness, in this study, referred to the simple, raw count of taxa within a given taxonomic category and region. For the death assemblage, cumulative richness values were collected from the accumulated strandings record along the ENP during 1990–2004 (no new taxa were

recorded in the SW region 2005 stranding data). For the living community, richness values derived from Barlow and Forney's (2007) compilation from 1991–2005, in addition to the three coastal species that lacked abundance their data set (see Appendix 2). Comparisons between the death and living assemblages were expressed as simple ratios, following Lockwood and Chastant (2006). Given the difficulties in assembling the living data set, rarefaction analyses of abundance data from the living community would not be appropriate or meaningful; rarefaction of the time-series strandings data are discussed below.

Abundance Fidelity.—To compare the relative abundances of taxa in the living and death assemblage, raw abundance data were tabulated for all taxonomic categories in each region, for both the living and death assemblages. Given the stark differences in the magnitude of absolute living abundance data (10^0 – 10^5 individuals, within a region), these values were interpreted as proportional percentages of the total abundance. Dead abundance values were also reported as proportions. Proportional abundances were calculated by taking the percentage of each taxon's occurrence, by region. Discrepancies in survey consistency limited live-dead abundance comparisons to the total year range of both living and death assemblage data, rather than year-by-year comparisons. Raw abundance values were also ranked, starting with a value of 1 for the most abundant taxon, providing rank-order abundances. Raw, ranked and proportional abundances are standard values that have been widely used in paleobiological analyses of diversity (e.g., Kidwell 2001, 2007; Alin and Cohen 2004; Lockwood and Chastant 2006).

This study made the explicit assumption that death assemblage abundances (i.e., individual stranding occurrences) were equivalent to individual values from cumulative live survey abundances. These live survey abundances specifically included estimated abundance, N , in Barlow and Forney (2007) and minimum population estimate, N_{\min} , in Carretta et al. (2006). In theory, such equivalency between living and dead values is valid, but

in reality the N values from live surveys were not true measurements of actual, living abundance. Instead, N is a calculation derived from a series of other variables (Barlow and Forney 2007). Nonetheless, for the purposes of this study, N provided a reasonably good assessment of relative cetacean abundance in the ENP. Moreover, there exists no other variable that is equally comprehensive (taxonomically, geographically, and temporally).

Taxonomic Collection Curves for Strandings

To measure and compare the accumulation of different cetacean taxa at different geographic scales along the U.S. Pacific coast, I used EstimateS (Colwell 2006) to generate collection curves from the stranding data. EstimateS is sample-based form of rarefaction that generates collector's or accumulation curves based on iterative resampling of separate collections of richness data (or, in this study, stranding occurrences). EstimateS resamples the original data set with Monte Carlo resampling, which randomly accumulates reiterations of the original data set, thereby computing a sample-based accumulation curve (generally described as a species accumulation curve). Sample-based rarefaction is more appropriate for the time-series stranding data in this study than are standard individual rarefaction analyses (e.g., analytical rarefaction) that sample from a single pool of data without replacement (Colwell and Coddington 1994; Gotelli and Colwell 2001). In general, species accumulation curves measure alpha diversity directly, but such absolute sampling produces jagged curves because occurrence data are naturally patchy. By resampling with replacement, EstimateS smoothes collection curves and provides confidence intervals for comparison with other collection curves. In this manner, EstimateS also provides an assessment of beta diversity (i.e., richness between samples) that could not be achieved with standard rarefaction analyses alone (Colwell et al. 2004).

The input data file for EstimateS contained cetacean stranding occurrences for a given stranding network region (NW, SW, or WC) that were grouped by year and sorted by taxonomic level. Although the NW and SW

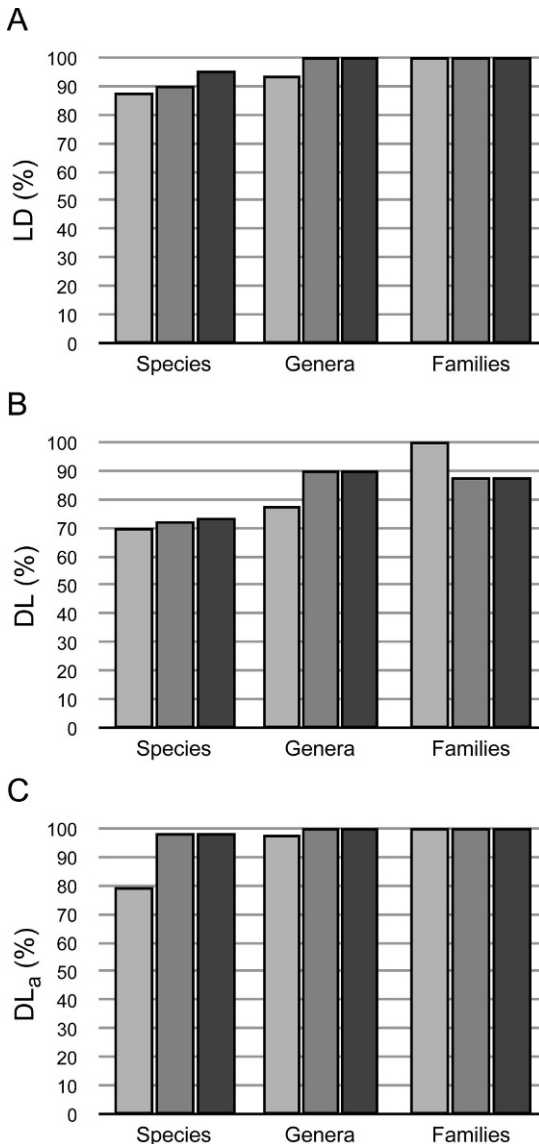


FIGURE 2. Compositional fidelity metrics, following those of Kidwell and Bosence (1991), comparing living and death assemblages in the ENP. A, Live-dead results (LD). B, Dead-live results (DL). C, Abundance-corrected dead-live results (DL_a). Light gray denotes NW, dark gray denotes SW, and black denotes WC regions.

regions share many cetacean species, some cetacean species are unique to each region over the time-series (Table 1). The WC data set combined data from both NW and SW regions by including taxa unique to either region and also summing shared occurrences. In EstimateS, I selected nominal parameters, including 50 randomization runs, a strong

hash encryption for the random number generator, and randomization without replacement. EstimateS produces an S_{obs} value as an estimation of taxonomic richness, along with 95% confidence bounds around this value. For this study, significance between different accumulation curves occurred when both curves moved outside of the other's confidence limits, as they reached their maximal values. This visual distinction approximates a two-sample t -test on the rarified richness values because it incorporates information about the variance from both samples (Davis and Pyenson 2007).

Results

Compositional Fidelity

Three sets of fidelity metrics (Kidwell and Bosence 1991) were applied to the total set of stranding and live-survey data, producing the following groups of results: dead-live comparisons; live-dead comparisons; and abundance-corrected live-dead comparisons.

Live-Dead.—Live-dead comparisons specifically determined the percentage of taxa from the living assemblage that were also found in the death assemblage (Fig. 2A). Across all taxonomic ranks, the WC region showed the highest fidelity (i.e., live-dead percentage), followed by SW and NW regions, in decreasing order. Compositional fidelity increased successively with each higher taxonomic group, ranging from 87.5–95% for species-level comparisons, to 93–100% for genera, and culminating in 100% values for families. These results indicate that nearly all living taxa were represented in the death assemblage. In fact, live-dead fidelity was absolutely perfect, with all living taxa in the death assemblage, when both (a) generic and familial taxonomic levels were considered and (b) coastline lengths were greater than the SW region (approximately 1300 km of general coastline; Fig. 2A).

Dead-Live.—Dead-live comparisons asked the precise inverse of live-dead comparisons: What percentage of taxa from the death assemblage were also found in the living assemblage (Fig. 2B)? Dead-live values were lowest for species (70–73%), and the ranges

for genera and families overlapped one another (77–90% for genus and 87.5–100% for family levels). Dead-live values increased for larger geographic regions at both species and genus levels. At the family level, the NW region had 100% dead-live values, although SW and WC regions had lower values, and these family-level data were lower than the genus level (87.5% versus 90%) for both SW and WC regions. The depressed dead-live fidelity values for the latter two regions can be directly attributed to the influence of the North Pacific right whale (*Eubalaena japonica*) data, as explained further below.

Abundance-Corrected Dead-Live.—Kidwell and Bosence's (1991) abundance-corrected metric (see eq. 3 above) is shown in Figure 2C. Across all taxonomic levels, the abundance-corrected dead-live comparisons showed that >79% of dead individuals were from taxa also represented in the living assemblage. Except for species levels in the NW, all other abundance-corrected values for dead-live values for species, genera, and families exceeded 97%, but none actually reached 100%.

The sole taxon present in the death assemblage of the SW and WC regions that was not represented in the living assemblage was the North Pacific right whale, which is the sole representative of its family, Balaenidae, in the ENP. A brief, but intense interval of nineteenth-century whaling in the North Pacific Ocean decimated populations of North Pacific right whales. Evidence for illegal hunting of this species by Soviet whaling fleets, following a 1935 moratorium, suggests that Soviet hunting may have irreversibly damaged the long-term status of this species (Brownell et al. 2001). Most strikingly, no North Pacific right whale calves have been observed in the ENP within the last century (Clapham et al. 1999; see Appendix 4), and sightings of adults are extremely unusual (Gendron et al. 1999; Waite et al. 2003). The single occurrence of *Eubalaena* in the death assemblage, out of >2000 individual strandings, explains two unusual aspects of the dead-live comparisons (Fig. 2B,C): its occurrence in the SW region prevented dead-live values in both SW and WC from reaching 100%, and it prevented the

TABLE 2. Live and dead taxonomic richness, grouped by geographic region and taxonomic category. Dead:live ratio provides a relationship between the number of dead and live taxa.

Taxa	Region	Dead	Live	Dead:Live
Species	WC	26	20	1.30
	SW	25	20	1.25
	NW	20	16	1.25
Genera	WC	20	18	1.11
	SW	20	18	1.11
	NW	18	15	1.20
Families	WC	8	7	1.14
	SW	8	7	1.14
	NW	7	7	1.00

abundance-corrected dead-live values from reaching 100%.

Taxonomic Richness

Comparisons between the raw number of dead and living taxa in each assemblage (Table 2) revealed that the stranding death assemblage was richer than the living community. With one exception, dead:live ratios increased with both larger geographic regions and more resolved taxonomic groups, demonstrating that coastline lengths greater than the NW region (approximately 700 km) had death assemblages that better represented the living community than live surveys, even at broad taxonomic scales. The highest dead:live ratio in this series of comparisons occurred in the WC region for species-level data (1.3); the lowest ratio occurred in the NW region (1.0) for family-level data, where the number of dead families was exactly equal to those found alive.

Abundance Fidelity

The last set of fidelity metrics addressed the correspondence between the death and living assemblages in terms of relative abundance (both proportional and rank-order), based on raw abundance data from live surveys and stranding occurrences.

Ranked Proportional Abundance.—For ranked abundance distributions, only the NW region had more dead taxa than living ones (Table 3). Even though most of the death assemblages were richer than their living counterparts (Table 2), larger geographic regions (SW and WC) had just as many taxa in

TABLE 3. Rank-order abundances for live surveys (live) and stranding record (dead) of cetacean species in the ENP. These rank-order abundances were identical for both species and genus levels because all of the most dominant species belong to monotypic genera in the ENP; see text for further details. The number of taxa falling below the threshold of 5% is indicated by n in each list.

	NW Abundance (%)		SW Abundance (%)		WC Abundance (%)	
Live	<i>Phocoenoides dalli</i>	40.07	<i>Delphinus delphis</i>	75.18	<i>Delphinus delphis</i>	61.13
	<i>Phocoena phocoena</i>	31.09	<i>Phocoenoides dalli</i>	7.42	<i>Phocoenoides dalli</i>	13.84
	<i>Eschrichtius robustus</i>	7.37	n = 16	<5.00	<i>Phocoena phocoena</i>	8.54
	<i>Lagenorhynchus obliquidens</i>	6.55			n = 15	<5.00
	<i>Lissodelphis borealis</i>	5.11				
	n = 10	<5.00				
Dead	<i>Phocoena phocoena</i>	40.22	<i>Delphinus delphis</i>	38.39	<i>Delphinus delphis</i>	30.23
	<i>Eschrichtius robustus</i>	25.49	<i>Phocoena phocoena</i>	19.05	<i>Phocoena phocoena</i>	22.62
	<i>Phocoenoides dalli</i>	17.58	<i>Eschrichtius robustus</i>	16.07	<i>Eschrichtius robustus</i>	18.88
	n = 15	<5.00	<i>Tursiops truncatus</i>	7.05	<i>Tursiops truncatus</i>	5.7
			n = 16	<5.00	<i>Phocoenoides dalli</i>	5.65
				n = 15	<5.00	

living rank-order abundances as the death assemblages. (In general, these results pertain to proportional abundances for all taxa with relative abundances $\geq 5\%$; taxa that fell below this threshold were not reported).

Live and dead abundance comparisons for species and genera were identical because all of the dominant species belong to genera that are monotypic in the ENP; the only difference between species- and genus-level results was in the number of taxa falling below the threshold of 5%. (Results reported here pertain equally to both species and genus abundances, although only results for species are mentioned). In the NW region, the three most abundant taxa (harbor porpoises, Dall's porpoise [*Phocoenoides dalli*], and gray whales) dominated both living and death assemblages, together constituting $>78\%$ of the total cetacean abundance in both assemblages. In the SW region, there was a poor correspondence among living and dead species except for the common dolphin (*Delphinus delphis*), which alone accounted for 75% of living cetacean species and for 38% of stranded species in that region. For the whole coastline (WC), the two most dominant species were common dolphins and harbor porpoises, accounting for $>50\%$ of abundance in both living and death assemblages. Overall, it is noteworthy that, at species and genus levels, living and death assemblages were dominated by nearshore species. In contrast, abundances of pelagic species (e.g., balaenopterids and ziphiids) were 2% or less.

Patterns in ranked proportional abundances at the family level mostly parallel those in genus- and species-level comparisons (Fig. 3). The rank-order of the top three most dominant families (Delphinidae, Phocoenidae, and Eschrichtiidae) was identical for both living and death assemblages in SW and WC regions; in the NW region, the second and third most abundant taxa switched ranks between living and death assemblages. Across all regions, delphinids and phocoenids dominated both living and death assemblages, constituting 90–94% of the living community and 65–77% of death assemblages. Eschrichtiidae was the third most dominant taxon in all living assemblages, as well as in every death assemblages except for the NW region, where it ranked second (Fig. 3). (Eschrichtiidae includes only *Eschrichtius*, among living mysticetes). The other extant families of cetaceans in the ENP include Ziphiidae, Balaenopteridae, Balaenidae, Physteridae, and Kogiidae. These families were consistently rare in both living and death assemblages, with living and death abundances at or below 1%, and thus differences in rank position between different regions or assemblages at such low levels are likely not ecologically meaningful. Balaenopterids, for example, were consistently the fourth most abundant taxon in the death assemblage of every region, ranging from 4.49 to 4.74%, although they were slightly less abundant than ziphiids in the living data (Fig. 3). These similarities and differences were also

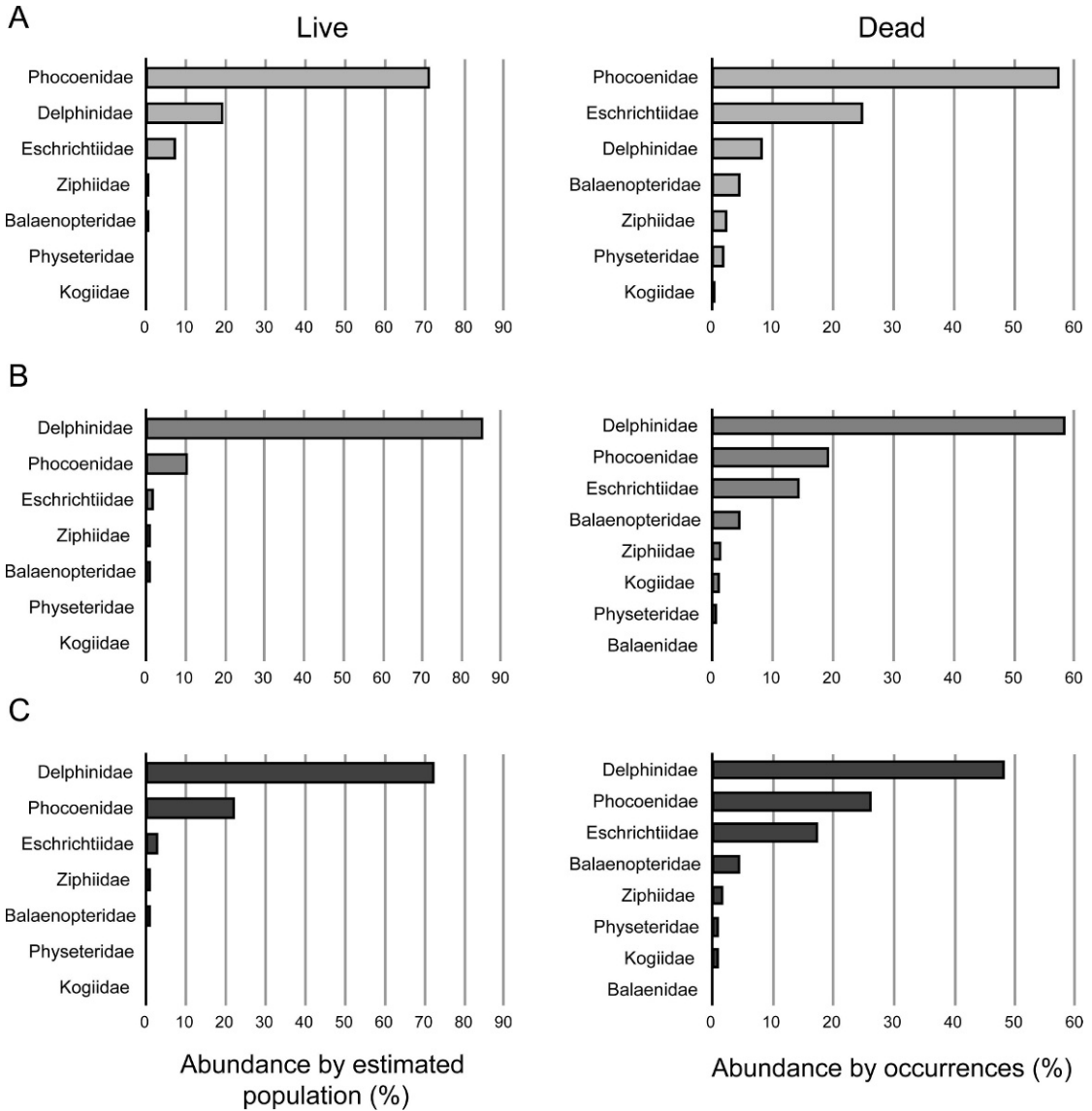


FIGURE 3. Rank-order cetacean family-level abundances of both living and death assemblages, grouped by region. Abundance values are percentages of total number of estimated individuals (live) or total number of stranding occurrences (dead). A, NW. B, SW. C, WC. Light gray denotes NW, dark gray denotes SW, and black denotes WC regions.

consistent at genus and species levels (Table 3), although family level patterns provide the best sense of presence-absence data for ranked abundance.

Rank-Order Abundance Tests.—Rank-order abundances from live surveys and individual stranded occurrences were plotted for geographic regions and taxonomic categories to illuminate fidelity correlations with statistical strength. Spearman correlations between

rank-order live and dead abundances were significant for every geographic region and for every taxonomic rank, except for the NW region at the species level ($r = 0.512$; $p = 0.059$; Table 4). Within each taxonomic level, correlation coefficients increased with region size. By region, species- and genus-level coefficients were fairly close to one another: $r = 0.512$ and 0.578 , respectively, for the NW region; $r = 0.680$ and 0.666 for the

TABLE 4. Spearman rank-order correlation tests on ranked relative abundance values from both living and death assemblages of cetaceans in the eastern North Pacific Ocean. See text for definitions of regions.

	NW			SW			WC		
	Coefficient	<i>p</i> value	<i>n</i>	Coefficient	<i>p</i> value	<i>n</i>	Coefficient	<i>p</i> value	<i>n</i>
Species	0.512	0.059	14	0.68	0.002	18	0.725	<0.001	19
Genera	0.578	0.029	14	0.666	0.002	18	0.725	<0.001	18
Families	0.929	<0.001	7	0.929	<0.001	7	0.964	<0.001	7

SW region; and *r* values were identical (0.725) for the WC region. Family-level correlation coefficients were unusually high, with *r* ranging from 0.929 to 0.964. It is likely that these high values reflect the small number of families (*n* = 7) available for such comparisons, as compared with lower taxonomic ranks.

Taxonomic Accumulation Curves

Accumulation curves of stranded cetaceans were grouped by taxonomic level, which allowed sampling regimes over different lengths of coastline (i.e., spatial scales) to be compared. Overall, across all taxonomic groups, the NW region had the lowest richness, followed by the SW region and then the WC region (Fig. 4A–C). The SW and WC regions were closer in richness than to the NW region, although the distinction was not statistically significant for any taxonomic rank after sampling more than 3–4 yr, according to the overlap in confidence limits. As taxonomic categories increased in rank (from species to families; Fig. 4A–C), confidence boundaries tapered dramatically and more quickly as the accumulation curves raced toward sampling the entire assemblage (i.e., saturation). Essentially, these results confirm the intuitive prediction that higher taxonomic categories accumulate taxonomic groups faster than lower, more resolved categories.

For the accumulation of stranded species, the confidence boundaries of the SW curve were encompassed by those of the WC curve after 4 yr of sampling (Fig. 4). After the same duration of sampling, the upper confidence boundary of the NW region overlapped into the SW and WC limits, suggesting that these curves were not significantly different as each region approached a full sample. Stranded species richness, however, was much lower in

the NW region than in the SW and WC regions. For species accumulation, there was a slight tapering of the confidence boundaries for the SW curve after about 10 yr of sampling. The confidence boundaries for the genus-level accumulation curves for each region were similar in overlap to the species accumulation curves, except the WC region fell within the SW region confidence boundaries after 5 yr of sampling and accumulating about 20 genera (Fig. 4B). The dramatic tapering of the WC boundaries after sampling for 5 yr indicates that generic richness approached saturation (20 genera) in less time than species richness, especially for coastlines with lengths greater than 1300 km (Fig. 4A,B). In the generic sampling curves, the upper confidence limit of the NW region overlapped with the lower bounds of both the SW and WC regions. Although the NW curve ultimately sampled a lower generic richness, after 3 yr, the NW region was not statistically different from the SW curve; also, after 8 yr, the NW region was not statistically different from the WC curve (Fig. 4B). Lastly, the accumulation curves at the family level were all strongly tapered after a mere 2 yr of sampling, indicating that saturation at this taxonomic level was rapidly reached in comparatively little time, relative to lower taxonomic levels (Fig. 4C).

Discussion

High Fidelity of the Cetacean Stranding Record

Fidelity metrics pioneered in paleoecological analyses of marine invertebrate assemblages were used in this study to measure how well the stranding record of cetaceans along the U.S. Pacific coast samples the living cetacean community in the ENP. Each of the three different kinds of fidelity metrics

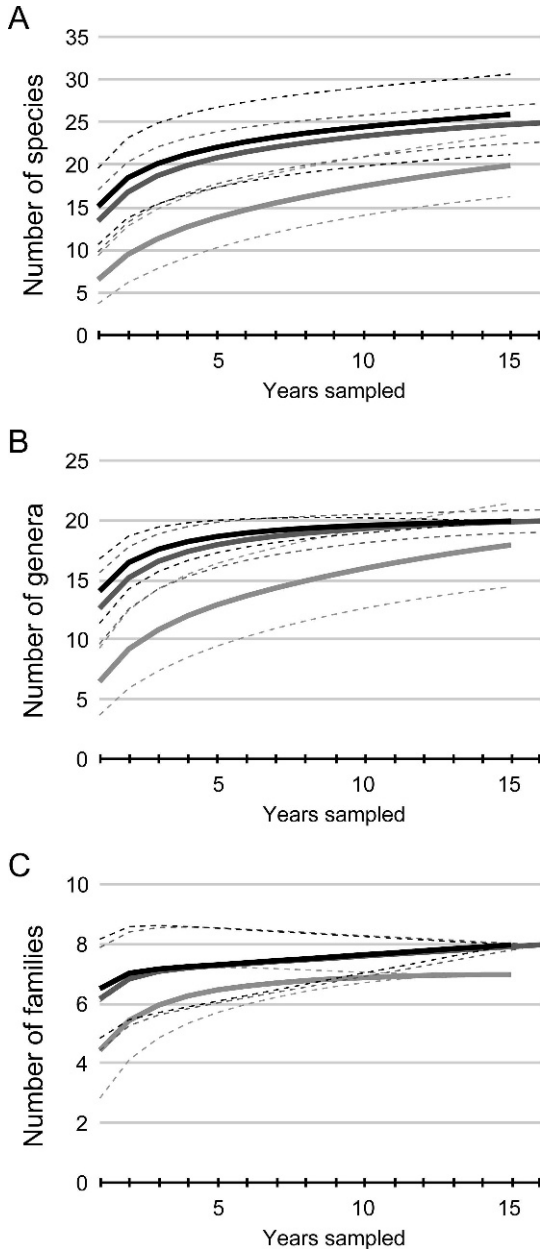


FIGURE 4. Accumulation curves of species (A), genera (B), and families (C) of cetaceans in the eastern North Pacific Ocean. NW region in light gray, SW region in dark gray, and WC region in black. Collector's curves were computed using EstimateS (Version 8.0.0, R. K. Colwell, <http://purl.oclc.org/estimates>). Dashed lines represent 95% confidence boundaries computed for each stranding region.

(compositional fidelity, richness and abundance) demonstrated an extremely faithful representation of living taxa in the stranding record. Compositional fidelity (live-dead,

dead-live and abundance-corrected dead-live comparisons) increased with greater geographic scale and broader (higher) taxonomic categories (Tables 2, 3, Fig. 2). As with most taphonomic studies of invertebrate assemblages (Valentine 1989; Kidwell and Bosence 1991; Kidwell 2002), live-dead values in this study were higher than dead-live values, reflecting the greater richness of the cetacean death assemblage. On the whole, these compositional fidelity metrics compare favorably with similar fidelity metrics compiled from a variety of other marine and freshwater assemblages, including those belonging to mollusks, crustaceans, and echinoids (Kidwell and Flessa 1996: pp. 437–438). Taxonomic richness comparisons showed that the richness values generated from line-transect surveys in every region were depressed relative to values from the stranding record, except for the NW region (where family-level richness values in living and death assemblages were equal). This result suggests that the stranding record does a better job of sampling both common and rare cetacean taxa than line-transect surveys do, especially at large spatial scales. Lastly, relative abundance comparisons demonstrated that the stranding record adequately captured ecologically meaningful data about the structure of living cetacean communities in the ENP. The striking correspondence between living and death assemblages in the structure of abundances, which was statistically significant for nearly all taxonomic groupings (Table 4), indicates that rank-order abundances from living cetacean communities are recorded relatively intact in death assemblages, a finding that parallels decades' worth of work on marine invertebrate assemblages (Kidwell 2001, 2002). Although higher percentages were registered in the live assemblages than in the death assemblages, the same cetacean taxonomic groups were dominant in both, with delphinids, phocoenids, and gray whales ranking as the most dominant taxa.

Interestingly, these three families are composed mostly of coastal and nearshore species. The low abundances of pelagic species in both the living and death assemblages mirror the findings of Barlow and Forney's (2007)

live surveys. Balaenopterids were rare, and, moreover, identifications from a distance at sea do not generally permit the distinction between species like sei whales and Bryde's whales (*Balaenoptera borealis* and *B. edeni*, respectively). Other pelagic and uncommon taxa, such as beaked whales, were represented by extremely low abundances in live surveys, although they were decidedly more common than balaenopterids (which are also known as rorquals). Large pelagic cetaceans (e.g., right whales, rorquals, and sperm whales, collectively the so-called great whales) were the targets of sustained whaling in the North Pacific Ocean (see below), which depleted their populations drastically (Clapham et al. 1999; Reeves and Smith 2006). As a consequence, however, more is known about their natural history than might otherwise be the case: in contrast to the great whales, the natural history of pygmy sperm whales and many species of beaked whales, for example, is still poorly understood (Guan 2007). In part, this knowledge gap derives from the large habitat of these pelagic taxa, which equals or exceeds the boundaries of the ENP (Reeves et al. 2002). Despite these issues, the basic fidelity metrics used in this study indicate that the stranding record recovers a faithful snapshot of cetacean community diversity in the ENP when fidelity can be assessed at regional-continental scales.

Collection Curves and Spatiotemporal Sampling Scales

Ecologists have developed different types of rarefaction methods to measure diversity from data sets that are pooled in different ways (Colwell and Coddington 1994; Gotelli and Colwell 2001). The stranding record represents time-series data from multiple pools, and therefore sample-based rarefaction approaches will yield more accurate collector's curves than other rarefaction methods (Colwell et al. 2004). The smoothed, computed collector's curves produced from the stranding records in this study are similar to those produced by MacLeod et al. (2005), who used Monte Carlo simulations to analyze the accumulation of stranded cetacean species along the coast of northwest Scotland

between 1948 and 2003. MacLeod et al. (2005) specifically sought to understand the difference between an expected species accumulation curve and the actual accumulation of stranded species over a 48-yr period. The statistical difference between the two curves, MacLeod et al. (2005) argued, indicated a shift in cetacean community composition (based on the timing of new species' appearances in their time-series) that they correlated with oceanographic and climatic changes. Several important assumptions underlie such comparisons (as identified in previous sections), including the potential linkage of cetacean stranding with decadal-scale periodicity in climate change (Evans et al. 2005) and the impacts of fisheries (Leeney et al. 2008). Although the high fidelity of the stranding record at large geographic scales reinforces the legitimacy of such live-dead comparisons, detailed examination of such potentially correlated factors ought to drive future studies.

Rarefaction analyses presented here demonstrated that longer coastline lengths and higher taxonomic categories accumulate taxa more rapidly than smaller coastline lengths and more-resolved categories. Sample-based rarefaction analyses conducted here provide legitimate comparisons of such data because they explicitly aim to standardize comparisons for differences in sample size, sampling regime, or, in the case of this study, coastline lengths (see Gotelli and Colwell 2001, for further discussion). In general, the WC and SW regions sampled richness better than NW region. Given the similarities in richness between the SW and WC regions (with the SW contributing more shared and more unique species than the NW to the WC region), it is not surprising that rarefaction analyses produced nearly identical collection curves for the WC and SW regions for species- through family-level data. Nonetheless, this study showed that sub-decadal (<10 yr) sampling regimes might be sufficient to sample cetacean diversity from species through family levels, depending on the length of coastline sampled. Large coastlines (>1000 km long), as in the SW and WC regions, will likely sample richness relatively

rapidly; smaller coastline lengths, at the scale of 10^0 – 10^2 km in length, might require slightly more time (10–15 yr) to accumulate a saturated sample at genus and species levels.

Further Considerations

Legacy of Whaling on Cetacean Abundances in the ENP.—Although the data in this study post-date major whaling eras in the North Pacific Ocean, the massive effects of the whaling industry on cetacean populations in the ENP are evident in the results. Most strikingly, the absence of balaenids in the living surveys and their presence in the stranding record can be directly attributed to the long history of whaling on right whales in the North Pacific (Brownell et al. 2001) (see Appendix 4). Whaling has occurred in the ENP for centuries in many forms, including that as practiced by Native Americans, shore-based whaling, and industrial, ship-based whaling (Reeves and Smith 2006). Although small odontocetes (the most abundant dead and living taxa in this study) were not explicit targets, larger mysticetes and sperm whales were systematically hunted. Recent studies that have attempted to generate pre-whaling population estimates for these species in the North Atlantic Ocean have concluded that populations of *Balaenoptera* spp. and humpback whales (*Megaptera novaengliae*) were 6–20 times more abundant before whaling than they are now (Roman and Palumbi 2003). Although the exact parameters used for these estimates have been the subject of much debate (Alter et al. 2007), there is little doubt that the *magnitude* of the change in abundance of whaled cetacean species has been accurately reported, and that populations of great whales were many times larger in the historical past, prior to whaling (Jackson 2006). For cetacean species in the ENP, the most affected species are large *Balaenoptera* spp., *Megaptera* and *Eubalaena japonica* (Clapham et al. 1999) (see also Appendix 4). It is unclear if abundances of sperm whales (*Physeter macrocephalus*) have recovered to pre-whaling numbers (Clapham et al. 1999), but gray whales appear to have recovered (Moore et al. 2001). Interestingly, recent studies suggest that the large discrepancy

between the stable, current population size and historical estimates of gray whales reflects fundamental changes in the function of ENP ocean ecosystems (Alter et al. 2007). Regardless, given the good correspondence in proportional cetacean species and generic abundances between the living and dead assemblages of the ENP (Table 4, Fig. 3), historical changes do not appear to be a serious issue so long as temporal collection is sufficiently long and spatial collecting is sufficiently widespread. However, for reconstructing the relative or proportional abundances of other cetacean assemblages, especially those in the fossil record, such changes may be important.

Marine Mammal Death Assemblages.—By considering stranded marine mammals as a kind of death assemblage (Liebig et al. 2003, 2007), previous authors have used coastlines as an analog of transects, in order to sample the adjacent marine environment. Transect lines generally sample a cross-section of environments (Buckland et al. 2001), and because emergent beaches are clearly not the regular habitat of obligate aquatic marine mammals, transect lines may be less adequate as an analogy for strandings than traps. In fidelity studies, natural traps are laterally restricted catchment areas that provide snapshots of diversity, with some degree of time-averaging. These snapshots of diversity, however, do not necessarily reflect the original habitat of the community, and include a variety of phenomena like tar pits, caves, amber inclusions, and bogs (Brain 1988; Elias 1990; Fall 1992; Henwood 1993; Hadly 1999). Carnivore abundance data from the Pleistocene La Brea tar pits, for example, preserve analogs of unique predator aggregations that can be observed or replicated in modern environments (e.g., Carbone et al. 1999). Hadly (1999) demonstrated that the mammal assemblage from Lamar Cave, a late Holocene cave deposit in Wyoming, better sampled the taxonomic richness of the surrounding extant, non-volant mammal assemblage than traditional raptor pellet or carnivore scat-based sampling regimes (Hadly 1999). Although a nearshore bias might be expected in the composition of a marine mammal death

assemblage on a beach, the results presented here showed that even rare pelagic taxa were sampled in the death assemblage at rank and proportional abundances that matched live, ship-based surveys. In contrast, Liebig et al. (2003) recovered mostly resident and migrant species in their death assemblage (six residents or migrants out seven dead cetacean species), with very few rare pelagic species (Liebig et al. 2003: Table 1). Thus, even though beaches do not provide in-habitat sampling, the high fidelity and richness of the stranding record data presented here, along with preservation of ecologically relevant data at large spatial scales, indicate that coastlines can be considered as traps for marine mammal death assemblages.

Differential Preservation of Cetacean Carcasses.—The death assemblage in this study consisted entirely of individual occurrences tallied from 1990 to 2004. Out of analytical necessity, this record was averaged over this time interval for comparison with live surveys, but such tallied time-averaging is not comparable to the actual time-averaging that occurs with carcasses on coast. In other words, taphonomic processes operating in intertidal environments (e.g., scavenging, dispersal, and dismemberment) would likely prevent a carcass stranded in 1990 from persisting on a particular beach until 2004 (in the absence of human-mediated alteration). This strong gradient in differential preservation, with attendant time-averaging, bears on understanding how carcasses from stranded cetaceans may become incorporated into the fossil record.

Intact (or relatively complete) cetacean carcasses on the beach are relatively unusual phenomena, from a taphonomic perspective, because their relatively large size provides an excellent resource for scavengers (Long and Jones 1996), well before landfall. If a cetacean carcass persists in the water column, many skeletal elements may become distributed far away from the carcass, via dismemberment that occurs near openings like the oral cavity (Schäfer 1972). Skeletal elements that survive scavenging to become buried, either on the seafloor or on a beach, are those that (1) separate from the rest of the body easily, early in decay, and (2) are durable and strongly

constructed. For cetaceans, skeletal elements from the auditory complex (e.g., tympanic bullae and periotics) and larger elements (like mandibles, humeri, and other cranial and thoracic elements) correspond to these latter categories and consequently dominate the cetacean fossil record. Semi-articulated or completely articulated skeletons are rare (Fordyce and Muizon 2001). Fossils of stranded cetaceans are unknown or unreported, although stranded sub-fossils have been reported from a Holocene site in Australia (Kemper et al. 1997).

Given the known taphonomy of cetacean carcasses, it is likely that fidelity decreases dramatically in these first steps of the taphonomic pathway from carcasses on the coast to bones on the beach. Testing this prediction requires tracking the fate of individual specimens from carcass to bones, and such a program is a feasible, though somewhat prolonged, exercise. The high fidelities of the first steps in cetacean taphonomy mean that time-averaging in marginal marine environments (e.g., a beach or subtidal shoreface) does not entirely destroy ecologically relevant signals of the original source cetacean community. Recovering such signals in the fossil record would require sampling within candidate stratigraphic horizons whose sedimentological context is well understood. Recently, Peters et al. (2009) provided such an example with upper Eocene marine mammal-bearing units of Wadi Al-Hitan, in Egypt. Through systematic study, this region has produced >1000 vertebrate skeletons, many of which belong to *Dorudon* and *Basilosaurus*, early obligately aquatic stem cetaceans. By carefully assessing the sequence stratigraphy of fossil-bearing strata, Peters et al. (2009) showed that the distribution of fossil cetaceans, in section, was the product of sedimentary processes (e.g., sediment starvation) operating over a protracted period of time, rather than short-term episodes of accumulation (e.g., mass strandings). The range of depositional environments preserved at Wadi Al-Hitan is broader than in the intertidal zone, and it is possible that fidelity patterns change across broad environmental gradients. Testing such a prediction is most tractable

through the fossil record. For example, in Wadi Al-Hitan, Peters et al. (2009) found changes in relative abundance patterns of *Dorudon* and *Basilosaurus* across different water depths that were tied to sequence stratigraphic changes. Disentangling these signals from biological factors (i.e., habitat preference) remains an ongoing challenge.

Physical and Environmental Factors Affecting Estimates of Cetacean Diversity.—Among many factors, large-scale oceanographic processes play a large role in structuring the distribution of carcasses on coastlines (Norman et al. 2004). Hart et al. (2006) demonstrated that patterns of sea turtle (Cheloniidae) strandings on the eastern seaboard of the United States strongly correlated with the experimental distribution of drift bottles on the same coastline, suggesting that the same physical oceanographic conditions favor both bottle and sea turtle carcass landfalls in some areas, while disfavoring them in others (Hart et al. 2006). Bibby and Lloyd (1977) and Bibby (1981), in studying the pattern of seabird carcass landfalls in the North Sea, also adopted a similar approach, concluding that wind vectors primarily predicted the landfalls of carcasses over a protracted period of time. It may be concluded that landfalls of cetacean carcasses follow similar oceanographic regimes, as Sergeant (1982) suspected: "I believe that the animals [on shoaling coasts] can be regarded as 'drift bottles' that inevitably tend to arrive at such times" (Sergeant 1982: p. 37). This analogy, however, is not entirely appropriate. On taphonomic grounds, cetacean carcasses are poor candidates as long-distance floaters. With the exception of rorquals, cetaceans lack large internal cavities that provide air or gas repositories sufficient for flotation. Balaenids float because of the high proportion of fat in their blubber; rorquals can float, in the process of their decomposition, if their ventral throat cavity fills with gas, but such flotation devices are not persistent (Schäfer 1972; Tønnessen and Johnsen 1982). Moreover, these carcasses provide excellent resources for scavengers, decreasing their likelihood of landfall prior to dismemberment. Thus, the landfall of identifiable cetacean carcasses (i.e., dead, not live

strandings) indicates a propinquity of death in time and space (1–2 days and 10^0 – 10^2 km). Any predictability for carcass landfalls (or strandings) has been demonstrated only in unique regions, like southeastern Australia, where the linkage between large-scale oceanographic cycles and cetacean strandings has been supported with a record of events at the decadal scale (Evans et al. 2005).

Whether the landfall of cetacean carcasses can be predicted in the ENP is secondary to more critical issues about the existing stranding record data. Given the broad geographic binning of the data in this study (e.g., coastlines of whole states), it was not possible to directly evaluate the impact of latitudinal gradients across the cetacean community in the ENP. Not all living cetacean species in the ENP are randomly distributed along the U.S. Pacific coastline, and stranding data with more precise geographic resolution (e.g., county-level occurrences) will help future work discern any such biases or patterns.

The heterogeneity of the eastern North Pacific Ocean is well documented by a suite of variables (e.g., sea surface temperature, salinity and productivity changes) and indices (e.g., North Pacific Index, Pacific Decadal Oscillation) that record changes in the physical and biological oceanography (Mantua and Hare 2002). Within the time interval examined in this study, another major regime shift occurred in the North Pacific Ocean, between 1998–2002 (Chavez et al. 2003, Peterson and Schwing 2003). Such large-scale oceanographic changes are correlated spatially and temporally with specific cetacean species distributions in the CCS (Tynan et al. 2005), but the timeframe of most of these studies is shorter than the period of most large-scale changes (Chavez et al. 2003), and such studies must surmount serious issues of oceanographic variability (Forney 2000). Major oceanographic and climate changes in the Bering Sea have had a measurable impact on the entire composition of marine vertebrate communities between 1997–2004 (Grebmeier et al. 2006); given the magnitude of projected climate change in the future, attendant oceanographic changes may seriously restructure the composition of major marine vertebrate communities,

including those of cetaceans (Whitehead et al. 2008). Future work, already in progress, will better resolve potential linkages between large-scale oceanographic changes and the taxonomic composition of the cetacean strandings along the U.S. Pacific coast.

Conclusions and Implications

1. The Importance of Carcasses on the Coast

Live-dead comparisons have been conducted informally in marine mammalogy since its inception because marine mammalogists have long assumed that the composition and condition of stranded marine mammal species on the coastline reflected ecologically meaningful information about the living community in the adjacent habitat. This study evaluated how well cetacean strandings record the ecological structure and composition of communities living in adjacent waters by using metrics explicitly developed for live-dead studies. This study explicitly merged cetacean ecology and taphonomy in a direct, measurable way by combining tools pioneered in marine ecosystems (Kidwell and Flessa 1996) with a focus on large mammals, whose taphonomic pathways are better understood in terrestrial environments (Behrensmeier 1978). Dead, beachcast marine mammals have been objects of taphonomic study since Schäfer's (1972) seminal work, but consideration of the ecological information recorded in their death assemblages has occurred mainly without consideration by paleoecologists, at least until studies by Liebig et al. (2003, 2007).

2. Cetacean Strandings Faithfully Record Richness and Abundance Data at Large Spatial Scales

Fidelity metrics used in this study demonstrated that cetacean death assemblages faithfully recorded the taxonomic richness and relative abundances of living cetaceans in the ENP, over a 15-year interval. This live-dead fidelity, though for assemblages at much larger scales, is comparable to values recorded for marine invertebrates. Notably, the fidelity of cetacean death assemblages increased with coastline length, a result likely

attributable to the large scale of cetacean habitats. Sample-based rarefaction analyses of the stranding data demonstrated that, depending on the taxonomic resolution, 5–10 yr of sampling produced a saturated tally of the entire death assemblage. It is unclear if the temporal scale of such a sampling regime is adequate to surmount the effects of oceanographic changes or sampling biases, but the results do suggest a temporal span longer than is usual for marine mammal census studies (e.g., Tynan et al. 2005). At nearly all coastline lengths in this study (i.e., >700 km), cetacean death assemblages were richer than transect surveys of living communities (capturing both rare and common species), a finding that highlights the value of studying death assemblages for understanding assemblage-wide ecological questions.

The ENP, in particular, offered a unique opportunity to investigate live-dead metrics because of the existence of two unique records (archived stranding data and line-transect survey data) that provided regular and successive pools of sampling at comparable scales. The high fidelity of relative abundance data, at multiple taxonomic levels, suggests that cetacean death assemblage preserve ecologically relevant information about the structure of living communities. Moreover, because taxonomic rank among cetaceans actually reflects monophyletic groups, the preservation of family-level ecological signals in the death assemblage suggests an evolutionary component to the structure of cetacean communities that can be investigated in the fossil record. Taxonomic consistency has been undervalued in many studies of living cetacean ecology, and significant ecological distinctions between major clades of cetaceans (e.g., mysticetes versus odontocetes; delphinids versus ziphiids) merit further investigation using data from well-sampled regional assemblages (e.g., Barlow et al. 2008, for the ENP).

3. Implications for Studying Fossil Cetacean Assemblages

Death assemblages are additionally important because they provide a basis for understanding what components of living commu-

nities may be preserved in the fossil record (Kidwell and Flessa 1996). The stranding of cetacean carcasses on the coast is just the first step along a taphonomic pathway that is followed literally by bones on the beach (Liebig et al. 2003), which is then followed by the burial and incorporation of the surviving parts into the fossil record. Although emergent coastlines are not source habitats for obligately aquatic cetaceans, the stranding record is analogous to natural traps, like tar pits and bogs, which sample living biota from adjacent source communities. The cetacean fossil record notably lacks a surfeit of reported assemblages from beach deposits (Uhen and Pyenson 2007), and such high-energy environments are unlikely to preserve diagnostic skeletal material (Fordyce and Muizon 2001). Nonetheless, there is no reason to suspect that the general fidelity of cetacean death assemblages is not also represented in other nearshore deposits (subtidal, shoreface, and shelf accumulations) that predominate the cetacean fossil record (Uhen and Pyenson 2007). In an example from the Eocene, Peters et al. (2009) demonstrated how careful stratigraphic control, coupled with detailed lateral sampling, can begin to disentangle physical, environmental overprints from potentially genuine paleoecological signals available in abundant fossil assemblages.

Two major issues remain before data from stranding can be integrated into studies of fossil assemblages: (1) resolving the equivalency of spatial and temporal sampling in the stranding record; and (2) sampling fossil cetacean assemblages that have solid stratigraphic and geochronologic constraints. For the first issue, if cetacean strandings faithfully reflect living communities at large spatial scales, it is possible that restricted spatial sampling, over much longer temporal scales, would produce similar results. Hadly and Maurer (2001) demonstrated that the accumulation of mammal species in Lamar Cave, over time, paralleled the accumulation of mammals from mountain ranges across the Great Basin of North America. Because the species distributions of Lamar Cave and the Great Basin had similar exponents in a fitted

power relationship, Hadly and Maurer (2001) argued that caves were like "islands in time," which sampled communities in the same way that mountain ranges sample the geographic ranges of a pool of species. Recently, ecologists have adopted this approach for a variety of time- and space-series studies, demonstrating the equivalency of sampling species through time and across space, given certain scaling parameters (e.g., Adler et al. 2005). Because strandings seem to possess the same taphonomic attributes as caves, the stranding record may also demonstrate such equivalency in sampling over time and space, especially if large sampling scales can be substituted for temporal spans approaching that of the geologic record. Empirical demonstration of such a relationship will, however, require more finely resolved geographic data about stranding occurrences, at least for the stranding record along the U.S. Pacific Coast.

For the second issue, any candidate fossil cetacean assemblage used in comparison with the strandings record will require precise constraints on the amount of time- and space-averaging recorded in stratigraphic section (Kidwell and Behrensmeyer 1993). Cetacean-bearing marine deposits usually lack geochronologically useful sequences, which are more abundant in the terrestrial rock record (e.g., volcanic tuffs). Consequently, the time encompassed in many cetacean-bearing marginal marine rocks is primarily constrained by biostratigraphic correlation using assemblages of mollusks, foraminifera, or diatoms, which have broad geologic age ranges (e.g., epoch-stage scales) (Fordyce 2002). Nonetheless, some assemblages, like those from the middle Miocene Sharktooth Hill bonebed, in the San Joaquin Basin of central California, have decent temporal resolution. For the Sharktooth Hill bonebed, sedimentological, biostratigraphic, magnetostratigraphic and taphonomic data all indicate that the unit formed in less than 700 Kyr (Pyenson et al. 2009). The broad expanse of the bonebed (~50 km²) raises the possibility that this time- and space-averaging sufficiently sampled middle Miocene cetacean diversity, judging from the parameters of the death assemblages studied here. Further

paleoecological investigations will require strong geologic constraints to understand the temporal and spatial scales at which fossil cetacean assemblages are preserved, and how comparable they are to death assemblages like the stranding record.

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Appendix 1

Modifications to Stranding Data from Stranding Regions

Stranding record data from two regions (NW and SW) are archived at regional stranding network offices of the National Oceanic and Atmospheric Administration (NOAA). Data for the NW region lacked a complete 1990–2004 series, and thus data were pooled from two different sources: NOAA Marine Mammal Protection Act (MMPA) data, which consists of annual reports submitted to U.S. Congress; and archived data posted online by the NW regional office online (<http://www.nwr.noaa.gov/Marine-Mammals/Stranding-Information.cfm>). The NOAA MMPA data, covering 1990–1998, were tabulated and inputted; these data were added to more recent stranding records, from 1999–2004, available on the NW regional office website. Errors in summation were noted and changed as needed (e.g., 1996 totals were miscalculated in the MMPA reports). Data collected directly from the NW stranding network website more accurate than the NOAA data because they have been thoroughly vetted and checked with actual records archived with the regional headquarters.

Stranding data for the SW region for 1990–2005 were available online directly from the SW regional stranding office (<http://swr.nmfs.noaa.gov/psd/strand/strandings.htm>). Data for 2005 were corrected for a duplication of fin whale (*Balaenoptera physalus*) occurrence. Also, after 2001, the SW region began splitting *Delphinus* spp. records into three different groupings (J. Cordaro personal communication 2008), to reflect revisions in the

taxonomy of the common dolphin (Heyning and Perrin 1994; Jefferson and Waerebeek 2002): long-beaked common dolphin (*Delphinus capensis*), short-beaked common dolphin (*Delphinus delphis*), and unidentified common dolphins (*Delphinus* spp.). To standardize these post-2001 occurrences with pre-2001 data, I converted all post-2001 occurrences of any of the three *Delphinus* groupings into *D. delphis* occurrences, thereby making these stranding data comparable with the live abundance data sets.

Raw stranding data from the NW and SW regions were stratified into three sets that approximately reflect three taxonomic hierarchies: species-, genus-, and family-level data. Suprafamilial- to subordinal-level data are essentially uninformative for the purposes of this study.

Species.—Beginning with the raw data, I pooled all permutations of *Delphinus* species groupings under *Delphinus delphis*. I deleted any category qualified with “unidentified.”

Genera.—I pooled all species as well as unidentified *Mesoplodon* and unidentified *Kogia* into their respective genera. Otherwise, I deleted any category qualified by “unidentified.”

Families.—I pooled all genera into their respective families. Also, I pooled unidentified balaenopterid, unidentified beaked whale, unidentified dolphin and unidentified phocoenid as separate counts within Balaenopteridae, Ziphiidae, Delphinidae and Phocoenidae, respectively. Lastly, I deleted the following categories: unidentified whale; unidentified cetacean; unidentified odontocete; and unidentified baleen whale.

Appendix 2

Sources for Additional Live Species Abundance Data

The main reference for species abundance data in the ENP (Barlow and Forney 2007) did not include live abundance data for three primarily coastal cetacean species: gray whales, harbor porpoises, and the coastal stock of bottlenose dolphins. Live abundance data for these taxa were compiled from references listed below. Where pertinent, I have also indicated the survey platform used to generate abundance data.

Gray Whales.—In the eighteenth and nineteenth centuries, gray whale populations in the ENP suffered massive declines from shore-based whaling (Jones et al. 1984). Granted clemency from international whaling in 1949, and later U.S. federal protection by the Endangered Species Act in 1972, the eastern ENP gray whale population rebounded dramatically during the mid to late twentieth century (Jones et al. 1984). Since the 1950s, gray whale abundance data have been collected using land-based surveys (Rugh et al. 1999), primarily from specific points along the U.S. Pacific Coast (e.g., Granite Canyon, Monterey County, California). These stationary points provide a repeatable and consistent means of estimating population size during the annual migration of gray whales from Baja California to the shelf of the Bering Sea. Recently, debates have focused on whether gray whales have returned to pre-whaling population sizes, with estimates of historical population size varying several magnitudes depending on the source data (i.e., analyses based on visual surveys versus mitochondrial haplotype data). Survey-based analyses suggest that current population size (~18,000–22,000 individuals) is close to pre-whaling conditions (Rugh et al. 2005; Swartz et al. 2006); estimates using molecular data place pre-whaling population size between 96,000 and 118,000 individuals (Alter et al. 2007).

For the purposes of this study, I used the lower bound of Rugh et al.’s (2005) estimation for population size (18,000) as the abundance value for living gray whales in the WC region. These data derive from the 2001–2002 survey season. During 1999–2000, a massive stranding event in ENP gray whales occurred, with a sevenfold increase in the number of total strandings reported for the whole coastline of North America (Gulland et al. 2005). Though the causes of these die-offs remain poorly understood, the increase in strandings occurred mostly outside of the

continental U.S. stranding networks, namely in Baja California and Alaska (Gulland et al. 2005). Thus, the impact of the 1999–2000 did not fundamentally alter the abundances recorded in live survey and stranding record data used in this study (Gulland et al. 2005: Table 2). More broadly, Rugh et al. (2005) and Swartz et al. (2006) have indicated that the estimated population of ENP gray whales dropped from about 30,000 individuals in the 1990s to a more or less stable 20,000 individuals since 2001–2002 (Moore et al. 2001; Wade 2002). Given these details, a lower bound of 18,000 individuals is not unreasonable. For NW and SW regions, I divided the 18,000 estimate by two, producing live abundance values of 9000 individuals for each region.

Harbor Porpoises.—I collected abundance data provided by Carretta et al. (2006), who used aerial surveys as opposed to the ship-based surveys used by Barlow and Forney (2007) in the ENP. Specifically, I tabulated all harbor porpoise stock data listed by Carretta et al. (2006: Appendix 3 and p. 312), using the reported N_{\min} values (population estimates) as equivalent to N in Barlow and Forney (2007). Such equivalence is legitimate because Carretta et al.’s (2006) values for other species listed in their summary of abundance are similar to the abundance values reported by Barlow and Forney (2007). Estimates for harbor porpoise populations listed by Carretta et al. (2006) were then summed to produce a total abundance measure for all harbor porpoise species in California (i.e., Morro Bay, Monterey Bay, San Francisco-Russian River, and Northern CA/Southern OR stock areas) and Oregon-Washington (i.e., Northern California/Southern Oregon, Oregon/Washington Coast, and Washington Inland Waters stocks). To generate a partition of the data that corresponds to the SW and NW stranding networks, all area stocks were pooled in their respective regions. The Northern California/Southern Oregon area value was divided in half, and one-half was added each to the SW and NW regions.

Bottlenose Dolphins.—Coastal populations of bottlenose dolphins are entirely restricted to the central and southern California coastline (Carretta et al. 2006: Fig. 8, Appendix 2, p. 307), and therefore the abundance data need only be added to the live abundance data for the SW region. As with harbor porpoises, the coastal bottlenose dolphin abundance data were collected by aerial survey.

Appendix 3

Compiling Live Abundance Data from Surveys

The data set on live cetacean abundance derives from Barlow and Forney (2007: Tables 5, 6), which lists abundance (N or population estimate) data for nearly all cetacean species in the ENP. Regional areas from Barlow and Forney (2007: Table 5) were pooled in the following manner to build regions comparable with the stranding record: Southern, Central, and Northern California were pooled into the SW region, and Oregon and Washington were pooled in the NW region. WC data were generated by a simple addition of the NW and SW sets. To generate taxonomically uniform sets of data, I made the following modifications to the live abundance data:

Species.—First, I added the three coastal species mentioned in Appendix 2 to their respective regions. Raw data for offshore and coastal bottlenose dolphins were combined together into one category, *Delphinus delphis*, to be consistent with the time-series from the stranding record (see Appendix 1). In addition to deleting “unidentified” categories, I also deleted *Kogia* spp. and *Mesoplodon* spp. from the species-level data set.

Genera.—For genus-level data, I pooled all species into their respective genera. From the raw data categories, these modifications also included pooling sei or Bryde’s whale category into *Balaenoptera*, *Kogia* spp. into *Kogia*, and *Mesoplodon* spp. into *Mesoplodon*. At this level, I also deleted all “unidentified” categories.

Families.—For family-level data, I pooled all genera into their respective families. From the raw data categories, I pooled unidentified roqual [sic], unidentified beaked whale, and unidentified dolphin into Balaenopteridae, Ziphiidae, and Delphinidae, respectively. Lastly, I deleted all “unidentified” categories.

Appendix 4

The Occurrence of *Eubalaena japonica*

Right and bowhead whales are among the most endangered species of living cetaceans (Clapham et al. 1999). Several centuries of whaling have decimated right whales (*Eubalaena* spp.), whereas bowheads (*Balaena mysticetus*) remain relatively abundant throughout their Holarctic distribution (Reeves and Smith 2006). North Atlantic right whales (*Eubalaena glacialis*) teeter on the brink of extinction, with ~300 individuals remaining (Kraus et al. 2005). In the North Pacific Ocean, the distributions of *Eubalaena* and *Balaena* rarely overlap (Reeves et al. 2002), although the range of North Pacific right whales (*Eubalaena japonica*) has been

dramatically reduced by nineteenth-century whaling, and the population does not seem to have recovered (Brownell et al. 2001; Sheldon et al. 2005). In a major contribution, Brownell et al. (2001) reviewed all reported sightings and strandings of *E. japonica* known at that time. They vetted unsubstantiated reports and compiled thorough lists of sightings and strandings of *E. japonica* in the North Pacific Ocean. For the ENP, they concluded that *Eubalaena* strandings were limited to two known occurrences, in 1916 and in 1995, the latter of which was included in this study. A more precise account of the 1995 occurrence, detailed in NOAA archives, described a *Eubalaena* skull discovered on beachfront property ~3 km north of Crescent City, California, on 27 January 1995. It is unclear whether this specimen represents a stranding, ship-strike, or some other event, but its occurrence in the death assemblage is legitimate. The age of this stranding, however, is uncertain; an estimate by J. Cordaro (personal communication 2009) places it no more than ten but less than 100 years old.