

# The high fidelity of the cetacean stranding record: insights into measuring diversity by integrating taphonomy and macroecology

Nicholas D. Pyenson<sup>1,2,\*</sup>

<sup>1</sup>*Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA*

<sup>2</sup>*Departments of Mammalogy and Paleontology, Burke Museum of Natural History and Culture, University of Washington, PO Box 353010, Seattle, WA 98195-3010, USA*

Stranded cetaceans have long intrigued naturalists because their causation has escaped singular explanations. Regardless of cause, strandings also represent a sample of the living community, although their fidelity has rarely been quantified. Using commensurate stranding and sighting records compiled from archived datasets representing nearly every major ocean basin, I demonstrated that the cetacean stranding record faithfully reflects patterns of richness and relative abundance in living communities, especially for coastlines greater than 2000 km and latitudinal gradients greater than 4°. Live–dead fidelity metrics from seven different countries indicated that strandings were almost always richer than live surveys; richness also increased with coastline length. Most death assemblages recorded the same ranked relative abundance as living communities, although this correlation decreased in strength and significance at coastline lengths greater than 15 000 km, highlighting the importance of sampling diversity at regional scales. Rarefaction analyses indicated that sampling greater than 10 years generally enhanced the completeness of death assemblages, although protracted temporal sampling did not substitute for sampling over longer coastlines or broader latitudes. Overall, this global live–dead comparison demonstrated that strandings almost always provided better diversity information about extant cetacean communities than live surveys; such archives are therefore relevant for macroecological and palaeobiological studies of cetacean community change through time.

**Keywords:** taphonomy; diversity; strandings; macroecology; fossil record

## 1. INTRODUCTION

The direct records of species occurrences, in time and space, provide the fundamental data to test hypotheses about the ecological and evolutionary processes that generate and maintain diversity [1,2]. For marine species, however, such occurrence data are notoriously deficient because of inconsistent sampling, lack of study and patchy distribution [3]. Despite their relatively large size, global distribution and iconic status, occurrence data for a large percentage of living cetaceans remain similarly poor [4], especially for pelagic species that rarely occur near shore. This gap in knowledge is highlighted by the fact that new species of living baleen and toothed whales continue to be described from museum vouchers, sighting and stranding occurrences [5–8]. Stranded cetaceans provide an especially important source of occurrence data, and the entirety of knowledge for some species of beaked whales (Ziphiidae) is based on such data [6].

Beachcast (or stranded) cetaceans are widespread occurrences across the world's coastlines. Historically, their presence has been regarded as anomalous [9], but a suite of intrinsic and extrinsic causes has now been recognized. In some cases, intrinsic and restricted

mechanisms, such as disease or senescence, cause cetaceans to strand; extrinsic mechanisms, in contrast, range across broad geographical scales. Military sonar use, for example, has been implicated in some cetacean strandings [10]; marine pollution, geomagnetic interference and geomorphological features have also been considered as putative mechanisms [11,12]. More convincingly, changes in prey resources demonstrably drive stranding occurrences, and regions with mass stranding 'hotspots' are linked with cyclical large-scale oceanographic and climatic variables [13,14].

In some countries, strandings have been recorded for multiple decades, providing a valuable archive of data [15] that can be correlated with observed changes in Earth and ocean systems [16]. The scientific networks for collecting and archiving stranding data have improved in the past 40 years [17], as advancements in research coordination, coastal surveillance and improvements in observer effort have led to standardized protocols and less patchy survey effort [18]. While the results of such programmes can provide an accounting of cetacean population size and species composition in specific regions [15,19], these records can also be considered through a taphonomic lens, where strandings represent a death assemblage that samples the nearby ecological community [20–22]. Previously, researchers have asked similar questions about the fidelity of the cetacean stranding record for discrete taxonomic groups [23], specific geographical regions or across specific spans of time

\*pyenson@si.edu

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[18,19,24], but none of these aforementioned studies used metrics to quantify fidelity in a comparable manner. Recently, Pyenson [22] explicitly implemented such fidelity metrics to demonstrate that the cetacean stranding record along the Pacific coastline of the continental US faithfully captured ecological information about the adjacent living community in the eastern North Pacific ocean.

The study presented herein follows this line of thought by testing the fidelity of the cetacean stranding record across the globe, using multiple coastlines from seven different countries that border nearly every large ocean basin in the world. This comparative analysis used published or publicly archived datasets from the coastlines of Australia, the Galapagos Islands (Ecuador), Greece and the Greek Archipelago, Ireland, The Netherlands, New Zealand and the United States. To ensure legitimate comparisons between stranding records and live surveys, both live and dead datasets were restricted to identical time spans (except for New Zealand, which only had death assemblage data). A total of 1 283 988 individual sighting records and 12 847 individual stranding occurrences (including New Zealand) were compiled for this study (electronic supplementary material, table S1). Fidelity metrics, which have predominantly been successful at resolving live–dead comparisons in marine invertebrate assemblages [25–27], provided a quantitative framework for comparing live–dead datasets for cetaceans [22]. Also, sample-based rarefaction analyses illuminated the sampling characteristics of strandings on different coastlines. Together, these sets of analyses quantified the spatial and temporal characteristics of the stranding record, and its ecological fidelity, across the globe.

## 2. MATERIAL AND METHODS

### (a) Strandings and sightings datasets

Raw sighting and stranding (live and dead, respectively) data were compiled from Australia, the Galapagos Islands, Greece and the Greek Archipelago, Ireland, The Netherlands, New Zealand and the United States (both Pacific and northeastern Atlantic coasts) using either published or publicly available datasets (table 1; see the electronic supplementary material for sources). Generally, the temporal coverage of stranding datasets exceeded that of sightings data; for coastlines in which the stranding records exceeded the temporal bounds of the sighting records, the former were truncated by the latter to ensure commensurate temporal comparisons. Both raw sighting and stranding data were collected at the finest possible categories, although often the taxonomic categories did not conform to standard taxonomic structure (e.g. ‘dolphin species’). Therefore, I pooled each dataset into a taxonomic hierarchy of exclusively species-, genus- and family-level data, following methods outlined by Pyenson [22].

### (b) Fidelity metrics

Taxonomic richness, compositional fidelity and ranked proportional (i.e. relative) abundance between living communities and death assemblages were measured using comparative metrics and equations described by Kidwell & Bosence [25]. Sighting data derive from multiple different platforms (including ship-based, aerial and land-based platforms); strandings occurrence data also may relate to singular strandings, mother–calf occurrences or mass strandings. Although these various

Table 1. Time range for cetacean stranding and sighting records used in this study, ranked in increasing number of years sampled. Asterisk denotes that New Zealand’s record is exclusively a death assemblage, used only in rarefaction analyses.

coastline	years sampled	total no. years
US Atlantic coast	1998–2004	7
Greece	1991–2001	11
US Pacific coast	1990–2004	15
Australia	1972–1995	24
Ireland	1981–2009	29
New Zealand*	1978–2008	31
Galapagos Islands	1971–2003	33
The Netherlands	1970–2008	39

methods carry biases, this study followed the assumptions outlined in a previous study [22], which equated sighting and stranding data, effectively scoring live–dead data as presence/absence occurrence data.

### (c) Taxonomic accumulation curves

Collection curves from the stranding data were generated using the sample-based rarefaction software package ESTIMATE-S [28]. Because year-by-year totals were not available and unfeasible to compute for both the Galapagos Islands and Ireland, respectively, these two countries were not used for this set of analyses. Accumulation curves of the stranding data, however, were computed from New Zealand’s coastline, despite lacking a comparable sightings dataset. In ESTIMATE-S, I selected the  $S_{\text{obs}}$ -value as an estimation of taxonomic richness, along with 95 per cent confidence bounds (see [22] for further details). Significant differences between different accumulation curves were determined when confidence bounds diverged as they approached saturation, a visual distinction that is analogous to a two-sample *t*-test of rarified richness values because it incorporates information about variance from both samples [29].

### (d) Coastline lengths

Coastline length data were collected from the World Resources Institute’s EARTH TRENDS database [30]. These coastline lengths derive from the World Vector Shoreline database of the US National Geospatial-Intelligence Agency, which calculated coastline lengths for the globe using a GIS database at a resolution of 1 : 250 000 km. Aside from EARTH TRENDS database, Australia’s coastline lengths derive from Geoscience Australia’s GEODATA Coast 100 K 2004 database, and the US Pacific and northeastern Atlantic datasets were computed from published coastline lengths of individual ocean-side states [31]; for more details, see the electronic supplementary material.

## 3. RESULTS

### (a) Taxonomic richness

Generally, stranding records were richer than live surveys for most coastlines around the world (table 2). Both US coasts and Australia possessed death records richer than live surveys at every taxonomic level. Australia collected the most dead species of any country (39 species), although the US Atlantic coast had the highest dead : live (D : L) value in the entire analysis with 1.67 at the species level. For most countries, D : L values were

Table 2. Live and dead taxonomic richness, grouped by taxonomic category and by coastline, calculated in this study. Dead:live ratios, which provide a relationship between the raw number of exclusively dead and live taxa in a given assemblage, are ranked in increasing values.

taxa	coastline	dead	live	dead : live
species	Galapagos	13	21	0.62
	The Netherlands	16	16	1.00
	Greece	10	10	1.00
	Ireland	20	17	1.18
	US Pacific	26	20	1.30
	Australia	39	28	1.39
	US Atlantic	25	15	1.67
genera	Galapagos	12	17	0.71
	The Netherlands	13	15	0.87
	Greece	9	10	0.90
	Ireland	16	15	1.07
	US Pacific	20	18	1.11
	Australia	24	20	1.20
	US Atlantic	16	13	1.23
families	The Netherlands	5	7	0.71
	Galapagos	5	5	1.00
	Greece	5	5	1.00
	Ireland	5	5	1.00
	US Pacific	8	7	1.14
	Australia	8	7	1.14
	US Atlantic	7	6	1.17

highest at fine taxonomic levels, where the difference between the number of dead and living taxa was the greatest; the maximum D:L values decreased as taxonomic levels coarsened from genus to family levels. Some coastlines, however, were exceptions to these trends. Both The Netherlands and Greece had coastlines with D:L ratios equal to 1.0 at the species and family levels, although both of their genus-level ratios were less than 1.0. The Galapagos Islands death assemblage was never richer than live surveys, at any taxonomic level. The Netherlands, with the longest time series among all the countries sampled, was the only country with a D:L ratio less than 1.0 at the family level (five dead to seven living families).

### (b) Compositional fidelity

Compositional fidelity metrics quantified the relative contribution of uniquely dead or uniquely live taxa found in each assemblage (LD and DL, respectively), and included a correction for abundant dead taxa as well ( $DL_a$ ; see [22,25] for equations and details). The stranding record had more uniquely dead taxa than uniquely living taxa found in live surveys when  $LD > DL$ ; when  $LD < DL$ , the stranding record failed to record as many uniquely living taxa as live surveys did (figure 1).  $DL_a$  values indicated the degree to which the presence of dead taxa was driven by their relative abundance. Both US coasts, Ireland and Australia all showed depressed DL relative to LD values (figure 1), across nearly all taxonomic levels (except for Ireland at the family level, where  $DL = LD$ ). In contrast, The Netherlands, Greece and particularly the Galapagos Islands all showed inflated or equivalent DL relative to LD values, across species, genus and family levels (see the electronic supplementary

material, figure S1).  $DL_a$  values exceeded 90 per cent for all countries and taxonomic levels, and increased with coarser taxonomic levels.  $DL_a$  values always surpassed DL values, although the two metrics were identical for certain taxonomic levels of the coastlines of The Netherlands, Greece and the Galapagos Islands. At the family level, all three metrics were equal for Greece and the Galapagos Islands, a finding that matched the 1.0 D:L ratios for these countries, in terms of taxonomic richness.

### (c) Abundance metrics

Histograms of ranked proportional abundance in figure 2 show the results of live and dead rankings of proportional abundance, for each coastline, over commensurate time periods at the family level. These histograms assumed that live abundance occurrences were equivalent to dead abundance occurrences, following the rationale outlined by Pyenson (p. 462 of [22]). The visualization in figure 2 was supported by rank-order abundance tests, which examined the statistical correlation between ranked proportional abundances using Spearman correlations (table 3). This live–dead comparison demonstrated that the most abundant living families in most coastlines were preserved in the same rank order in the stranding record. Both US coasts, The Netherlands and Ireland all had identical rank-order proportional abundances for at least the top three most abundant families in both live and dead assemblages (The Netherlands and Ireland had identical order for the top five most abundant families). All four of these aforementioned coastlines showed relatively strong correlations that were also significant (table 3), except for the US Atlantic coast at the family level. Greece preserved the same suite of top three most abundant families between the living and the dead, with ranks switched for second and third most abundant families (Physeteridae and Ziphiidae); these rank correlations for Greece were strong, even if the family-level concordance was not significant. The Galapagos preserved the same most abundant family (Delphinidae) across the live–dead comparison, while switching the second- through fourth-ranked families, yielding nonetheless strong correlation coefficients. Lastly, Australia showed the least correspondence between living and dead ranked abundances, with no matching in abundant families, a pattern also observed in the genus-level data. Although species-level correlations were significant for Australia, the correlation coefficients across all taxonomic levels were the lowest of any coastline in this study.

### (d) Accumulation curves

Taxonomic accumulation curves, also known as collector's curves, elucidated the temporal scale at which different stranding records sampled their source communities. Accumulation curves with confidence boundaries that remained open through time reflect a lack of sampling saturation; curves with tapered terminations indicated that the stranding record approached a complete sampling of the available alpha diversity. At the species level, both New Zealand and The Netherlands demonstrated saturated curves, with a levelling of the mean values and a tapering in their confidence boundaries, as their stranding records both exceed 25 years of sampling (see the electronic supplementary material).

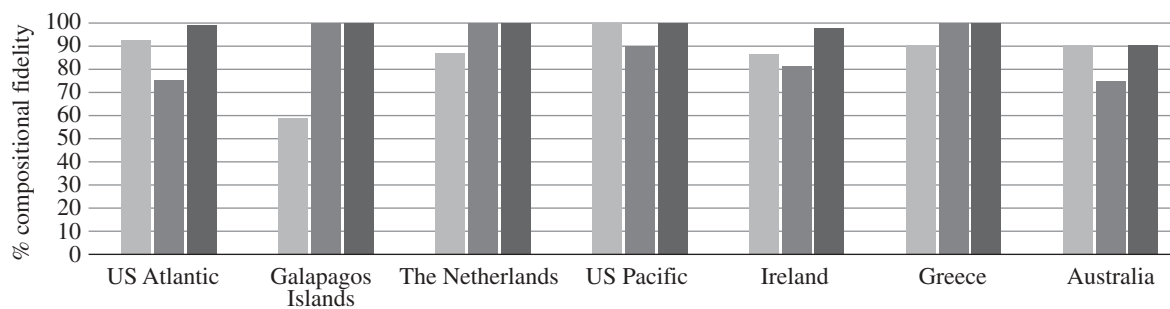


Figure 1. Compositional fidelities for different live–dead records across the globe, at the generic level. Light grey indicates live–dead (LD) values, medium grey indicates dead–live (DL) values and dark grey indicates abundance-corrected dead–live values (DL<sub>a</sub>). Countries are ranked, left to right, in increasing coastline size. See the electronic supplementary material for compositional fidelities at other taxonomic levels.

Notably, all other countries at this taxonomic level exhibited open confidence boundaries, with rapidly increasing rates of sampling. At the generic level (figure 3), both New Zealand and The Netherlands tapered noticeably after 20 and 15 years, respectively, although the US Pacific coast showed the most dramatic pinching, as its assemblage reached full saturation after 10 years. Otherwise, Australia and Greece showed little tapering in their genus-level curves, although the US Atlantic tapered slightly, despite its short sampling interval. Lastly, at the family level nearly every coastline exhibited accumulation curves that reached saturation near the end of their sampling interval, except for two: The Netherlands, which reached saturation over 50 per cent before the end of its sampling; and New Zealand, which showed no dramatic tapering to its curve (see the electronic supplementary material, figure S2).

#### 4. DISCUSSION

Historically, cetacean strandings have been interpreted as semaphores for local species diversity and abundance, marine pollution or oceanographic changes [9,12]. Given the challenges of sampling large, mobile obligate aquatic organisms in their natural habitat, strandings have also provided the unusual opportunity to glean important data about the identity, morphology and diversity of cetacean communities, in lieu of more difficult and expensive sea-based survey work. Similarly, taphonomists have studied cetacean strandings to understand the processes and pathways of decay, and how skeletal elements are differentially preserved in a marine environment [20,21,32,33]. Instead of focusing on the actualistic data related to bones on the beach, I used the sampling provided by this taphonomic pathway to measure how well strandings reflected the diversity of living cetacean communities, as a precursor study [22] did for the US Pacific coast. By compiling a live–dead dataset from coastlines around the world, I effectively conducted a study in ‘spreadsheet taphonomy’ to resolve the major characteristics that drive the high fidelity of cetacean death assemblages to their source communities. Key findings are elaborated below.

##### (a) *Death assemblages sample cetacean diversity better than live surveys*

First, death assemblages were richer than surveys of living communities, at all taxonomic levels, for coastlines

longer than approximately 2000 km. These results hold for both total compilations of live–dead taxa (table 2) and metrics that account for the relative contribution of uniquely dead or uniquely living taxa in their respective assemblages (figure 2; electronic supplementary material, S1). For coastlines shorter than this threshold, the stranding record failed to recover a richer assemblage than living surveys did, even if temporal sampling exceeded several decades. Previous studies have noted the high richness of the cetacean stranding record, including its effectiveness at sampling both common and rare species better than live surveys, but results presented herein demonstrate how this pattern extends to coastlines elsewhere in the world, especially when coastlines exceed approximately 2000 km in length.

Besides richness, live–dead abundance comparisons (figure 3) showed that the stranding record faithfully samples the relative abundances of common and rare taxa, even at coarse taxonomic levels. Such a result is relatively striking, even if ranked order of relative abundances for uncommon taxa do not precisely correspond (which may be expected given their low relative abundances). For the majority of coastlines longer than approximately 2000 km in this analysis, monotypic taxonomic groups played an important role in driving the high fidelity of the death assemblages (i.e. the coastlines of Ireland, US Pacific and Australia). For example, Phocoenidae in Australia was represented entirely by one dead occurrence of *Phocoena diotropica*; for the US Pacific coast, a single dead occurrence of *Eubalaena japonica* represented Balaenidae in the entire death assemblage; and for Ireland and the northeastern US Atlantic coast, death records represented unique occurrences for some ziphiid genera (e.g. *Ziphius*, *Mesoplodon*). Shorter coastlines, however, such as The Netherlands, for example, generally showed depauperate death assemblages because they lacked death records for families represented by singletons in their communities (e.g. Monodontidae, Balaenidae). Such absences also lowered the contribution of uniquely dead taxa for compositional metrics in these coastlines.

##### (b) *Community structure recorded by cetacean strandings*

Second, the stranding record preserves clear features of cetacean community structure, mostly independent of spatial and temporal sampling. Although living and dead assemblages differed in absolute abundance by several



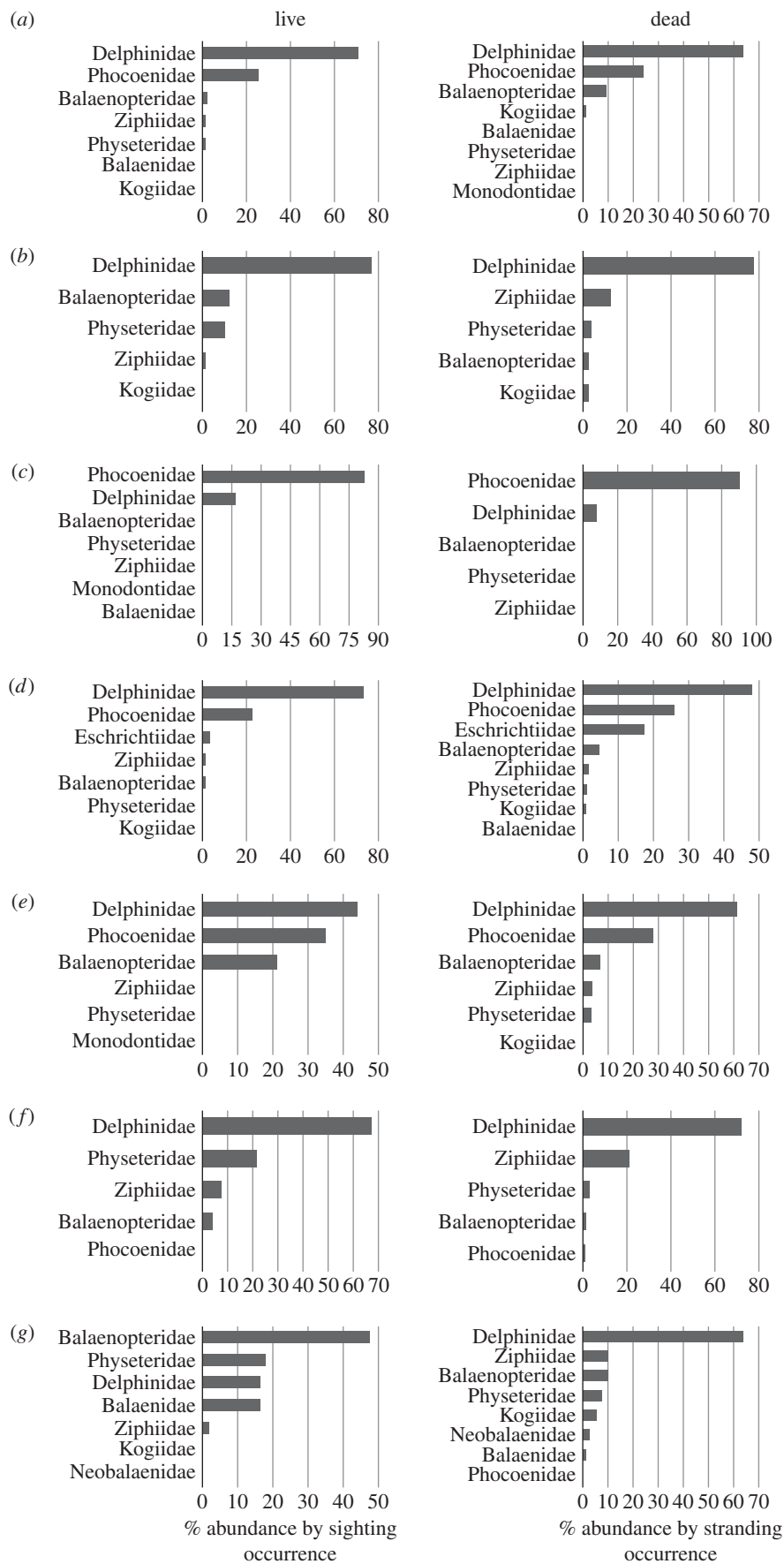


Figure 2. Rank-order family-level abundances of cetaceans for both living and death assemblages from different coastlines around the world. Live–dead pairs are ranked, top to bottom, in increasing coastline size. Abundance values are percentages of total number of sighting occurrences (live) or total number of stranding occurrences (dead), in both cases reflecting relative abundance. (a) US Atlantic, (b) Galapagos Islands, (c) The Netherlands, (d) US Pacific, (e) Ireland, (f) Greece and (g) Australia.

Table 3. Spearman's rank-order correlation tests on ranked relative abundance values from living and death assemblages in this study. Results are grouped by taxonomic rank and by coastline; coefficient represents values for Spearman's  $r$ ; and  $p$ -values are one-tailed. Bold indicates  $p > 0.01$  and represents correlations that are not significant.

	coefficient	$p$ -value	$n$
<b>US Atlantic coast</b>			
species	0.593	0.0006	27
genera	0.797	0.0001	17
families	0.762	<b>0.014</b>	8
<b>The Netherlands</b>			
species	0.818	<0.0001	18
genera	0.818	0.001	15
families	1	<0.0001	7
<b>Ireland</b>			
species	0.708	0.0001	21
genera	0.61	0.0036	18
families	0.964	0.0003	7
<b>Australia</b>			
species	0.411	0.0034	42
genera	0.422	<b>0.0159</b>	26
families	0.595	<b>0.0598</b>	8
<b>Galapagos Islands</b>			
species	0.714	0.001	21
genera	0.789	0.001	17
families	0.6	<b>0.1424</b>	5
<b>US Pacific coast</b>			
species	0.725	<0.001	19
genera	0.725	<0.001	18
families	0.976	<0.001	8
<b>Greece</b>			
species	0.855	<0.001	11
genera	0.83	0.0014	10
families	0.9	<b>0.0187</b>	5

orders of magnitude, live–dead ranked relative abundance comparisons revealed strong and significant correlations at nearly all taxonomic levels. For example, both living and death assemblages recorded the same dominant taxonomic groups from the shortest coastline (northeastern US Atlantic) through to the second longest (Greece), with only Australia showing a decoupling between live and dead relative abundance patterns. Both US coasts, The Netherlands and Ireland all showed identical rank-order proportional abundances for at least the top three most abundant families in both live and dead assemblages (the top five most abundant families for The Netherlands and Ireland showed identical ranked order). Similar to the results from live–dead richness comparisons, these patterns indicated that regional death assemblages, from approximately 1000–15 000 km in length, recorded the abundance structure of living cetacean communities. Coastlines longer than those of Ireland and Greece (approx. 6000–15 000 km; electronic supplementary material, table S1) probably lost the correspondence between live–dead relative abundances because of scaling effects (elaborated below). The faithful preservation of rank-order

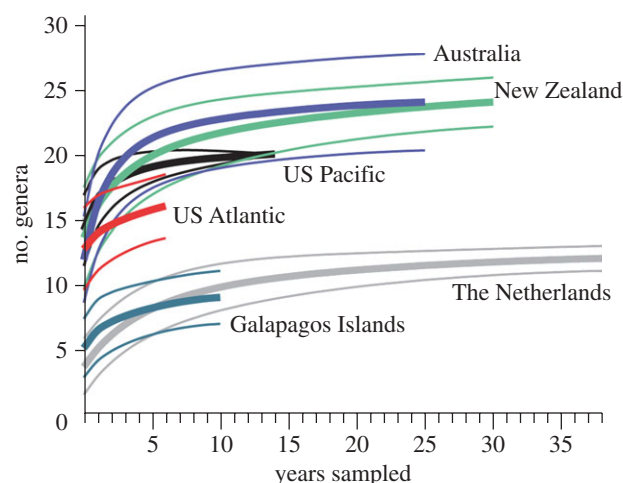


Figure 3. Generic accumulation curves generated from sample-based rarefaction curves of stranding data. Strandings from Ireland and the Galapagos Islands could not be used in this analysis, although New Zealand's strandings were included. See the electronic supplementary material for accumulation curves at other taxonomic levels.

relative abundances from living cetacean communities is a finding that parallels decades' worth of work on marine invertebrate assemblages [34,35]; in this study, I argue that the results strongly suggest that cetacean death records universally preserve such fidelity at a regional scale.

### (c) *Temporo-spatial scaling*

Very few live surveys have the logistical capacity to sample cetacean diversity at a scale commensurate with their natural habitats, which can range in scope from embayments to ocean basins. Stranding records, however, can easily approach such scales in linear dimensions, which is probably an important factor that explains how their sampling regimes generate high fidelities. Results from comparisons of sample-standardized collector's curves indicate that extended temporal sampling (beyond 10 years) generally enhances taxonomic sampling, especially at genus and species levels. Notably, such protracted temporal sampling assists short and medium-length coastlines (i.e. approx. 1000–2000 km) in producing saturated death assemblages. However, extended temporal sampling had little effect on Australia, the longest coastline, which reached saturation only when it sampled at the coarsest taxonomic level. The Netherlands, which had the most protracted temporal sample of any coastline in this study (39 years), produced saturated death assemblages at every taxonomic scale, although such an extensive time interval seems to have had little effect on sampling rare species, as The Netherlands ranked among the least faithful countries for live–dead comparisons of richness. Unusually, New Zealand was the only coastline never to reach saturation, despite its long coastline length (approx. 17 000 km) and time interval (31 years; electronic supplementary material).

In contrast, increased spatial sampling, especially for coastlines oriented over broad latitudinal transects, improved taxonomic sampling. Coastlines that were latitudinally restricted, such as The Netherlands, the Galapagos Islands and even Greece, generally failed to adequately sample richness, even with protracted temporal sampling (table 2). By contrast, coastlines that sampled greater than 4° of latitude generally produced

richer death assemblages. For example, the northeastern US Atlantic coast, which is roughly the same length as The Netherlands and sampled for the shortest amount of time in this study, nonetheless ranked among the highest D:L ratios. At the largest coastline scale, the continent of Australia generated a rich and saturated death assemblage (table 2 and figure 3), but failed to recover ranked abundances with any kind of correspondence to living communities (figure 2). This ecological non-correspondence at long coastline lengths (i.e. New Zealand and Australia) may result from sampling cetacean diversity at geographical scales that necessarily incorporate different ocean current systems. I tested this idea by sub-sampling Australia's dataset using two states (Queensland and Western Australia; 13 347 and 20 781 km long, respectively) that shared similarly shaped coastlines and ranged across commensurate latitudes, while bordering independent current systems (electronic supplementary material). The live–dead ranked abundances of the two states were either roughly equal or stronger than those for the whole of Australia (electronic supplementary material, table S3). More importantly, unlike the entire coastline of Australia, these sub-continental-scale coastlines did recover similarly dominant groups in both live and dead assemblages, with rare taxa accounting for much smaller proportional abundances (see the electronic supplementary material, figure S3). Thus, coastlines bordering multiple current systems appear to sample different communities and conflate ranked abundances, suggesting that cetacean community structure is tied more to local–regional scales than to continental ones.

#### (d) *Sampling biases*

The legacy of multiple whaling eras [36], especially across a global dataset, can explain the relatively low abundances of right whales (*Eubalaena* spp.) in this study, although longer coastlines (both US coasts) did recover this taxon in their death assemblages, whereas The Netherlands did not. Despite the depressed abundances of several rorquals (Balaenopteridae) relative to their estimated pre-whaling abundances [37], the death record recovered their richness and abundance from live surveys with high fidelity, across the globe. Although this study assumed that multiple survey platforms were equivalent, survey transects at sea and sightings from the shore may not precisely be comparable, and thus these differences appear to be sufficiently averaged by sampling regimes across decadal time scales and greater than 2000 km of coastline. For example, although both US coasts were surveyed using aerial and sea-based platforms, their D:L ratios did not differ dramatically from those of Australia and Ireland, which were primarily shore-based surveys. Any type of live survey, however, is contingent on observer effort. Transect surveys have developed statistical metrics to account for such effects, but similar checks have not been conducted on the stranding record. Because coastal population growth (a proxy for observer effort) has increased over the course of stranding network data collection, one might expect stranding occurrences to increase through time, although it remains unclear whether increases in observer effort impact diversity metrics. Recent work [38] has examined such factors, including correlations with known oceanographic changes, such as the El Niño Southern Oscillation.

## 5. IMPLICATIONS

Individual coastlines in this dataset ranged from small island archipelagos to entire continents; each live–dead set sampled timeframes that varied between 7 and 35 years. As may be expected given these broad spatial and temporal parameters, cetacean diversity varied in richness, abundance and composition. Moreover, living assemblages collectively sampled several magnitudes (approx.  $10^3$ ) more individual occurrences than death records. Despite these differences, live–dead analyses produced measurable insights into the macroecological significance of cetacean strandings by clarifying specific features that yield faithful cetacean death assemblages. These findings imply that ecologists seeking taxonomic compilations for specific regions ought to consult archived stranding data, which are comparatively less expensive and logistically challenging than transect surveys. Notably, the best results will arise from water bodies adjacent to long coastlines, with large latitudinal gradients, and that have collected data for greater than 10 years. Protracted temporal sampling assists in the recovery of cetacean diversity data from source communities, but it is secondary to the aforementioned criteria. The high fidelity of the cetacean record highlights the value of such natural history archives for ecological monitoring, macroecological analyses and conservation management. However, there is still a need to resolve the specific taphonomic pathways generating such fidelity, which can only be accomplished by continued actualistic work on carcasses cast along the coast.

The preservation of key aspects of cetacean community diversity (i.e. richness and ranked abundance) in the stranding record carries important implications for studying cetacean diversity in the fossil record. Strandings are less analogous to transect surveys than they are to natural traps (e.g. the Rancho La Brea tar pits [39]), which provide snapshots of diversity from laterally restricted catchment areas, along with some degree of time-averaging. Natural traps, like strandings, do not necessarily reflect the original source habitats, but they demonstrably sample diversity better than surveys in many cases (e.g. [40]). Although beach environments are poorly represented in the cetacean fossil record [41], the fidelity of the stranding record offers the possibility that carcasses accumulating in near-shore shelf settings might preserve similar diversity features, especially over broad spatio-temporal scales. Extensive lateral sampling of cetacean-bearing rock units would be ideal, although it is unclear how much would be required. Recent work [38] has investigated the precise space–time sampling relationships of the stranding record to better understand if sampling through space can be substituted for sampling through time, as has been demonstrated in terrestrial mammal communities [42]. If so, then it is possible that time-averaged cetacean-bearing rock units (e.g. [43]) may share some component of the high fidelity to their source communities. Consequently, measures of relative abundance and richness from such strata may reflect the structure of extinct cetacean communities, if additional taphonomic and sedimentologic biases can be controlled.

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