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## Rise and fall in diversity of Neogene marine vertebrates on the temperate Pacific coast of South America

Jaime A. Villafañá and Marcelo M. Rivadeneira

**Abstract.**—Even though Neogene outcrops along the temperate Pacific coast of South America harbor a rich marine vertebrate fossil record, no studies have examined the diversification patterns of these taxa. Here, we analyze diversification trends based on the stratigraphic ranges of 86 genera of marine vertebrates, including sharks, rays, chimaeras, marine mammals, and seabirds. The richness of genera shows a hump-shaped trend, with maximum values around the late Miocene, driven by a large pulse of origination during mid-Miocene and higher extinction rates during the Pliocene. Trends varied markedly among taxa and departed largely from expectations based on global diversification patterns. Moreover, these trends cannot be explained solely as a sampling artifact derived from sampling intensity (i.e., number of occurrences) or sedimentary rock availability (i.e., number of geologic maps). A large fraction of genera (42%) went globally extinct by the late Pliocene–Pleistocene, and the extinction was highly selective according to different ecological and life-history traits. An analysis using “randomForest” showed that taxonomic structure and the geographic midpoint of distribution could explain up to 83% of extinction of genera. The extinction was taxonomically clumped (i.e., disproportionately high in Cetacea and very low in Carcharhiniformes) and concentrated in the northern area of the temperate Pacific coast of South America. Our results suggest that the particular paleogeographic, paleoclimatic, and paleoceanographic events that took place during the Neogene along the temperate Pacific coast of South America had a significant effect on the structure of marine biodiversity.

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### Introduction

The Neogene was an epoch of major climatic and oceanographic changes that had profound effects on the diversification of the biosphere (Zachos et al. 2001). Intense tectonic, climatic, and oceanographic changes have occurred along the temperate Pacific coast of South America (TPSA hereafter) during the last 23 Myr, including the onset of the hyper-aridity of the Atacama Desert (Hartley and Chong 2002), the uplift of the Andes to their present height (Blisniuk et al. 2005; Garziona et al. 2008), the advances of glacial lobes in the fjord region of southern Chile (Glasser et al. 2008), and the activation of coastal upwelling cells along the coast of Peru and Chile (Ibaraki 1997; Tsuchi 2002; Dekens et al. 2007). Whether these strong paleoclimatic and paleoceanographic changes shaped diversification of marine biota is much less understood. For instance, recent studies have shown dramatic changes in the diversity and composition of

mollusk faunas along the TPSA during the Miocene and Pliocene (Rivadeneira and Marquet 2007; Kiel and Nielsen 2010), confirming earlier suggestions of a major faunal turnover during the Mio-Pliocene and Plio-Pleistocene transitions (Philippi 1887; Herm 1969; Zinmeister 1978).

A rich marine vertebrate fauna has been described for the TPSA over the last ~120 years, including sharks, rays, bony fish, seabirds, and marine mammals (De Muizon and Devries 1985; Long 1993; Chavez et al. 2007; Walsh and Hume 2001; Ehret et al. 2012; Carrillo-Briceño et al. 2013; Valenzuela-Toro et al. 2013). Many of these studies were aimed at understanding the evolutionary history and adaptations of the biota (De Muizon 1993; Mayr and Rubilar-Rogers 2010). In contrast, studies aimed at describing the diversification patterns are scarce, and both geographically and taxonomically restricted. For instance, Chavez et al. (2007) have shown that the

family-level composition of seabirds of Chile and Peru has maintained a remarkable similarity from the late Miocene to the present. However, seabirds seem to show a drastic decline in diversity from the Miocene to the Pliocene (Chavez et al. 2007), suggesting the disappearance of a large fraction of the species. Although the existence of a large Plio-Pleistocene vertebrate turnover has long been suggested (Valenzuela-Toro et al. 2013) it has never been statistically evaluated.

It is unknown whether diversification dynamics along the TPSA are simple reflections of global trends (Warheit 2002; Uhen and Pyenson 2007; Marx and Uhen 2010; Morlon et al. 2011; Guinot et al. 2012), or if these reveal more complex and idiosyncratic trends. Indeed, studies of invertebrates (Crampton et al. 2006; McGowan and Smith 2008) show that diversification dynamics observed in particular areas depart from global trends, highlighting the importance of considering environmental and biological processes operating at a regional scale as primary drivers of diversification. In addition, there is a growing number of studies illustrating the importance of accounting for possible sampling artifacts affecting diversification assessments, using number of formations, number of maps, and volume and availability of sediments as covariates of diversification dynamics (Peters and Foote 2002; Crampton et al. 2003; Smith and McGowan 2007; McGowan and Smith 2008; Smith et al. 2012;). Although several of these studies have concluded that several proxies of rock volume can bias estimations of diversification trends (Peters and Foote 2002; Smith et al. 2012), regional studies of cetaceans in North America and Europe have shown that diversification trends during the Cenozoic are little biased by sampling artifacts (Uhen and Pyenson 2007; Marx 2009). Hence, it cannot be assumed a priori that diversification trends of marine vertebrates at TPSA are either affected or unaffected by sampling artifacts.

The suggested Plio-Pleistocene vertebrate turnover along the TPSA (Valenzuela-Toro et al. 2013) may not have been random, and the chances of extinction may have been enhanced

by particular traits of taxa, as observed in marine bivalves (Rivadeneira and Marquet 2007). Neontological studies show that extinction risk in marine vertebrates is strongly selective for different ecological and life-history traits of species (Dulvy and Reynolds 2002; Duncan and Blackburn 2004; García et al. 2008; Field et al. 2009; Davidson et al. 2012). These traits include geographic range and body size, which are also important drivers of extinction probability in fossil invertebrates (McKinney 1997) and terrestrial vertebrates (Liow et al. 2008; Boyer 2010). Differences in these ecological and life-history attributes could be translated into phylogenetic effects, as illustrated by contrasting levels of extinction risk among higher taxonomic levels (i.e., classes, Harnik et al. 2012), but whether these differences can also be observed in the fossil record remains untested.

This study aims to provide a synthesis of the considerable volume of literature documenting paleontological records of marine vertebrates along the TPSA, reconstructing diversification trends of cartilaginous fishes, marine mammals, and seabirds at the genus-level. We evaluated whether (a) diversification departs from the global expected pattern, (b) taxonomic classes show different diversification trends, (c) diversification trends could have been shaped by sampling artifacts (i.e., outcrop area and sampling effort), and (d) the late Neogene–Pleistocene extinction of genera was selective according to intrinsic traits.

## Methods

### Database

We obtained information on the stratigraphic ranges of 86 genera, representing at least 124 species of marine vertebrates (cartilaginous fishes, marine mammals, and seabirds) from 48 Neogene (Miocene–Pliocene) outcrops along the temperate Pacific coast of South America encompassing most of the modern Peruvian biogeographic zone (Fig. 1). These sites represent mostly shallow-water habitats (i.e., coastal shelf), in wave-exposed and wave-protected areas (Herm 1969; Le Roux et al. 2005). The data set gathered was based on an exhaustive bibliographical compilation,

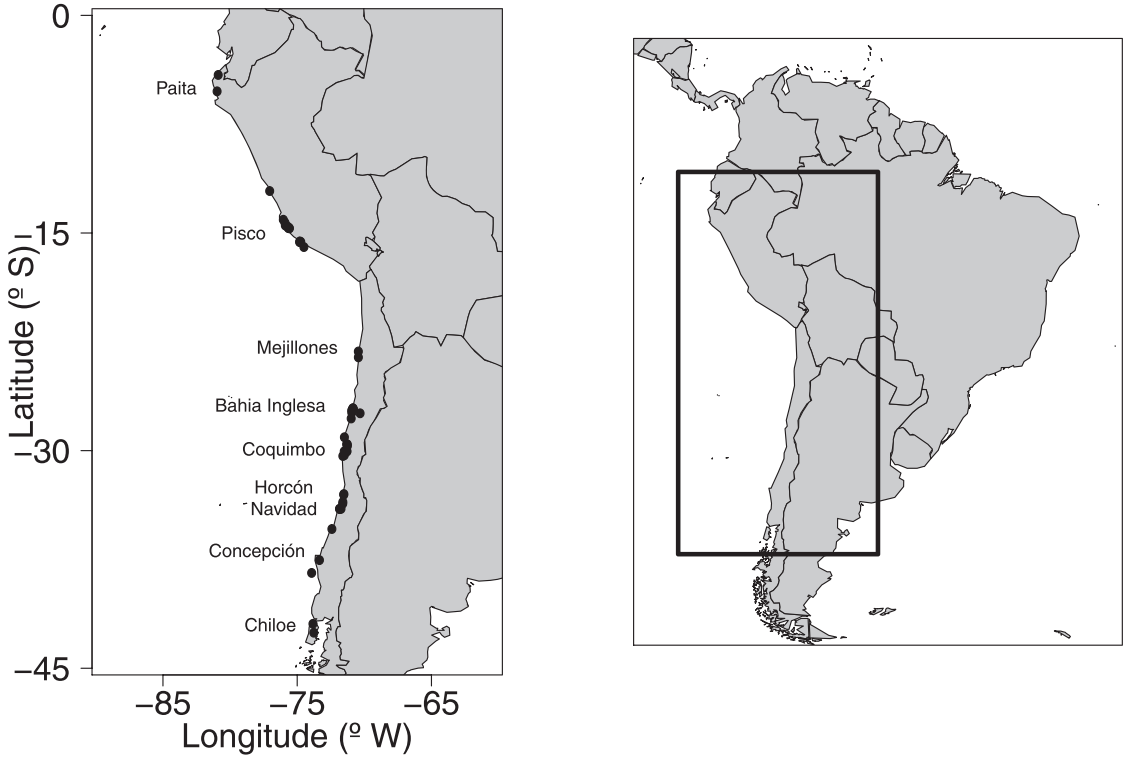


FIGURE 1. Map of the study region on the temperate Pacific coast of South America, showing the location of the Neogene fossiliferous sites analyzed here.

including more than 71 papers, unpublished theses, and technical reports (many available only in Spanish), complemented with data taken from the Paleobiology Database (via Fossilworks). The new compiled information, including references and the names and ages of localities, was uploaded to the Paleobiology Database. The stratigraphic ranges were constructed from the ages of the localities, using only those sites with ages well resolved up to age or sub-epoch.

#### Macroevolutionary Dynamics

We estimated the diversification rates (standing richness, origination, and extinction) for nine time intervals (i.e., Miocene and Pliocene ages), based on first and last appearances of genera and assuming an effectively complete sampling. Origination and extinction rates were estimated using the “face value” mini-cohort approach proposed by Foote (2000), which ignores singletons.

$$q = -\ln[N_{bt}/(N_{bt} + N_b)]$$

$$p = -\ln[N_{bt}/(N_{bt} + N_t)]$$

where  $q$  is the extinction rate per million years,  $p$  is the origination rate per lineage per million years,  $N_{bt}$  is the number of taxa crossing both bottom and top interval boundaries,  $N_b$  is number of taxa crossing the bottom boundary and last appearing in an interval, and  $N_t$  is number of taxa crossing the top boundary and first appearing in an interval. This approach assumes no sampling bias, which is clearly unwarranted in our data set (but see below), but in the absence of estimations of relative abundance of species this is the best possible approach. Analyses were carried out using the library *stratigraph* in R (R Development Core Team 2014).

We tested whether diversification trends were affected by outcrop availability and sampling effort. We used the number of maps

available for each time interval, extracted from the Geologic Map of Chile (SERNAGEOMIN 2003, 1:1000000 scale) as a proxy of outcrop availability. The number of maps has been used as a proxy of outcrop availability by several previous studies (Smith and McGowan 2005; McGowan and Smith 2008; Lloyd 2012; Lloyd et al. 2012). A single map is basically a spatial polygon with a given age. However, the age precision of each map is variable, and often a map cannot be assigned unambiguously to a single time unit. Given this limitation, for instance, a polygon assigned to the Miocene had to be assigned to all Miocene ages. In the same manner, a polygon with a Pliocene age was assigned to Zanclean and Piacenzian. The total number of maps per age is obtained by summing across all polygons. Using area instead of number of maps yielded the same results, because these variables are tightly correlated ( $r = 0.91$ ,  $n = 9$ ,  $p = 0.007$ ). We could not use maps for Peru because the available temporal resolution of most of polygons was too coarse (e.g., "Neogene"), and so we used the number of maps of Chile as a proxy of outcrop availability of the entire region. This assumption seems reasonable, because the number of occurrences as well as the genus richness in Peru and Chile are strongly correlated ( $r = 0.80$ ,  $n = 9$ ,  $p = 0.001$ ;  $r = 0.83$ ,  $n = 9$ ,  $p = 0.007$ , for the number of occurrences and genus richness, respectively). We used the total number of occurrences per time interval as a coarse proxy of sampling effort. However, in many cases the number of maps and occurrences could not be unambiguously assigned to single subepochs, and so temporal trends reflect maximum possible values. A significant correlation between diversification trends and the number of maps or sampling effort may suggest bias (i.e., non-biological signatures) in the observed trends.

We estimated regional-scale departures of the diversification rates from a global diversification null model. We used 454 Neogene genera of the three major taxa studied (cartilaginous fishes = 84, marine mammals = 303, seabirds = 67), with stratigraphic ranges obtained from the Paleobiology Database (major contributors: Pilleri 1986; Domning

and Pervesler 2001; Koretsky 2001; Uhen 2007). We re-estimated the diversification rates in random stratified samples of 86 genera of the global data set in a total of 10,000 runs, stratifying by the number of genera of each major taxon on the TPSA. We assumed that "anomalies" existed in the regional dynamics of diversification if the observed rates were different from the 95% confidence interval of the global diversification null model. Analyses were repeated separately for each class.

### Extinction Selectivity

The existence of a large extinction during the late Neogene (see "Results") provides the opportunity to test for selectivity patterns. A genus was considered as a survivor if it is observed in the present-day record within the TPSA area. To establish the modern presence of each genus we used information collected from Fishbase ([www.fishbase.org/](http://www.fishbase.org/)), Aquamaps ([www.aquamaps.org/](http://www.aquamaps.org/)), and the Ocean Biogeographic Information Systems ([www.iobis.org/](http://www.iobis.org/)). We tested whether the extinction was selective with regard to several traits: (a) phylogenetic relatedness, (b) geographic range size, (c) midpoint of geographic distribution, (d) body size, and (e) maximum age. Taxonomy (i.e., classes and orders) was used as a coarse proxy for phylogenetic relatedness among genera. To test for taxonomic patterns of selectivity, we compared the observed number of extinct genera across classes and orders with the predictions of a null model, following the protocol of Rivadeneira and Marquet (2007). The model was built by randomly drawing the observed number of extinct genera from the original pool, and then counting the number of genera expected to go extinct for each class and order. The process was repeated 50,000 times and the distributions compared with the observed estimates for each taxonomic level. Range size was estimated for all species as the latitudinal range between their northernmost and southernmost occurrences. Because the TPSA is oriented mostly in a north-south direction (Fig. 1), latitudinal range was considered a good proxy of geographic range. Previous numerical experiments suggest that this measure is robust to sampling incompleteness

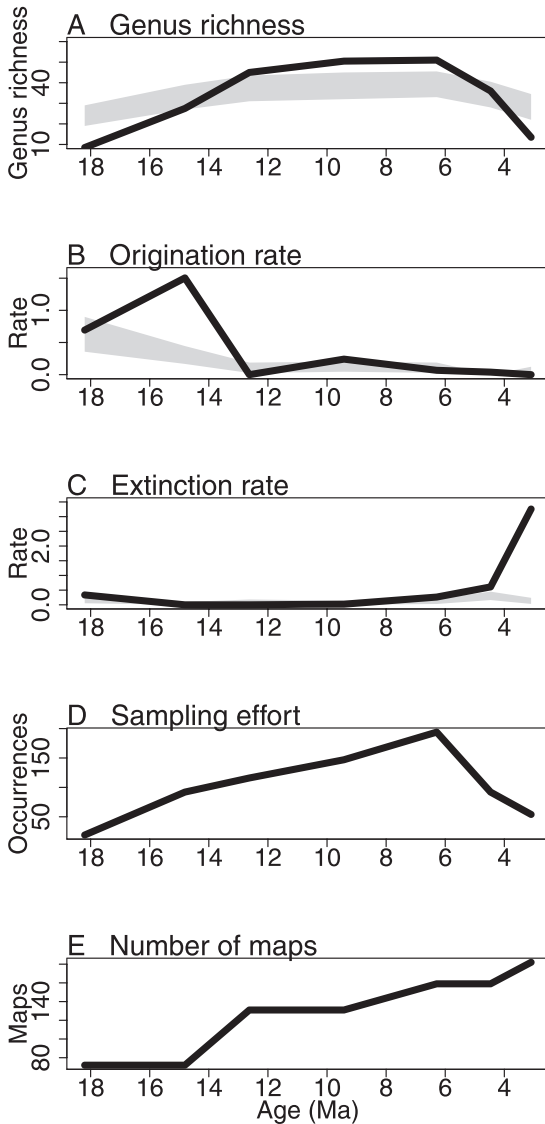


FIGURE 2. Genus-level diversification trends for all marine vertebrate taxa combined during the Neogene on the temperate Pacific coast of South America. A, Standing richness. B, Origination rate. C, Extinction rate. D, Number of occurrences. E, Number of geologic maps. The gray areas enclose the 95% confidence intervals of 10<sup>6</sup> runs of a global diversification null model of diversification (see text for details).

(Rivadeneira and Marquet 2007). Because the geographic ranges are likely to extend beyond the study area, this proxy represents a relative measure of the geographic range, as customary in macroecological studies (Gaston and Blackburn 2000). Similarly, we calculated the midpoint of the latitudinal distribution. We

obtained information on the maximum length and weight for all the genera analyzed, using online databases including Fishbase (fishbase.org), Avibase (avibase.bsc-eoc.org), Animal Diversity (animaldiversity.ummz.umich.edu), BirdLife International (birdlife.org/), and Encyclopedia of Life (eol.org/). We obtained information for all taxa except five genera of sharks for which we did not find a direct estimation of weight. We estimated body weight for those five genera by using a mass-length allometric relationship based only on Chondrichthyes ( $r^2 = 0.83$ ,  $n = 26$  genera). We only used body mass as a predictor of extinction because body mass is strongly correlated to body length ( $r = 0.98$ ,  $n = 80$ ,  $p < 0.0001$ ). Observed maximum age was the midpoint of the oldest interval where the genus was present. The data set is provided in the Appendix.

The existence of selectivity in the late Neogene extinction was evaluated with random forest modeling (Breiman 2001; Liaw and Wiener 2002), using extinction as a binary response (0: survivor, 1: extinct) and traits as predictors (see Davidson et al. 2012 for a recent application in recent marine mammals). Analysis was carried out using the library *randomForest* in R (R Development Core Team 2014). We selected an optimal set of predictor variables by optimizing the area-under-the-response-operator-curve (AUC), using the backward elimination based on the initial ranking of the variables proposed by Calle et al. (2011) and implemented in the library *AUCRF* in R (R Development Core Team 2014).

## Results

The observed diversification trends show important departures from the global null model (Fig. 2). Overall, the number of genera increased during the Miocene, reaching maximum values around the late Miocene, and then decreasing toward the Pliocene (Fig. 2A). The diversity peak was higher than expected with the null model. In parallel, diversity was lower than the null-model expectation during periods of low richness (early and mid-Miocene and late Pliocene). Origination rate showed two major pulses ca. 15 and 9 Ma,

TABLE 1. Spearman moment-product correlation for diversification trends between paired taxa. Significant values ( $p < 0.05$ ) are in bold.

Variable	Seabirds – marine mammals	Seabirds – Chondrichthyes	Marine mammals – Chondrichthyes
Genus richness	<b>0.86</b>	<b>0.95</b>	<b>0.90</b>
Origination rate	-0.19	-0.27	0.78
Extinction rate	0.37	0.27	0.03

which were higher than predicted by the null model (Fig. 2B). Extinction rate showed a main pulse during the late Pliocene, much higher than the null-model prediction (Fig. 2C).

Diversification trends showed marked differences among taxa (Table 1, Fig. 3); richness was significantly correlated between seabirds and marine mammals ( $r = 0.86$ ,  $p < 0.05$ ), between seabirds and cartilaginous fishes ( $r = 0.95$ ,  $p < 0.05$ ), and between marine mammals

and cartilaginous fishes ( $r = 0.90$ ,  $p < 0.05$ ). Standing richness of seabirds and cartilaginous fishes reached a maximum during the middle and late Miocene, which was higher than expected with the global null model (Fig. 3A,C). In contrast, marine mammals showed a secular increase that did not differ from the expected trend, with the exception of the early Miocene (Fig. 3B). Taxa showed different trends of origination; only marine mammals and cartilaginous fishes had similar origina-

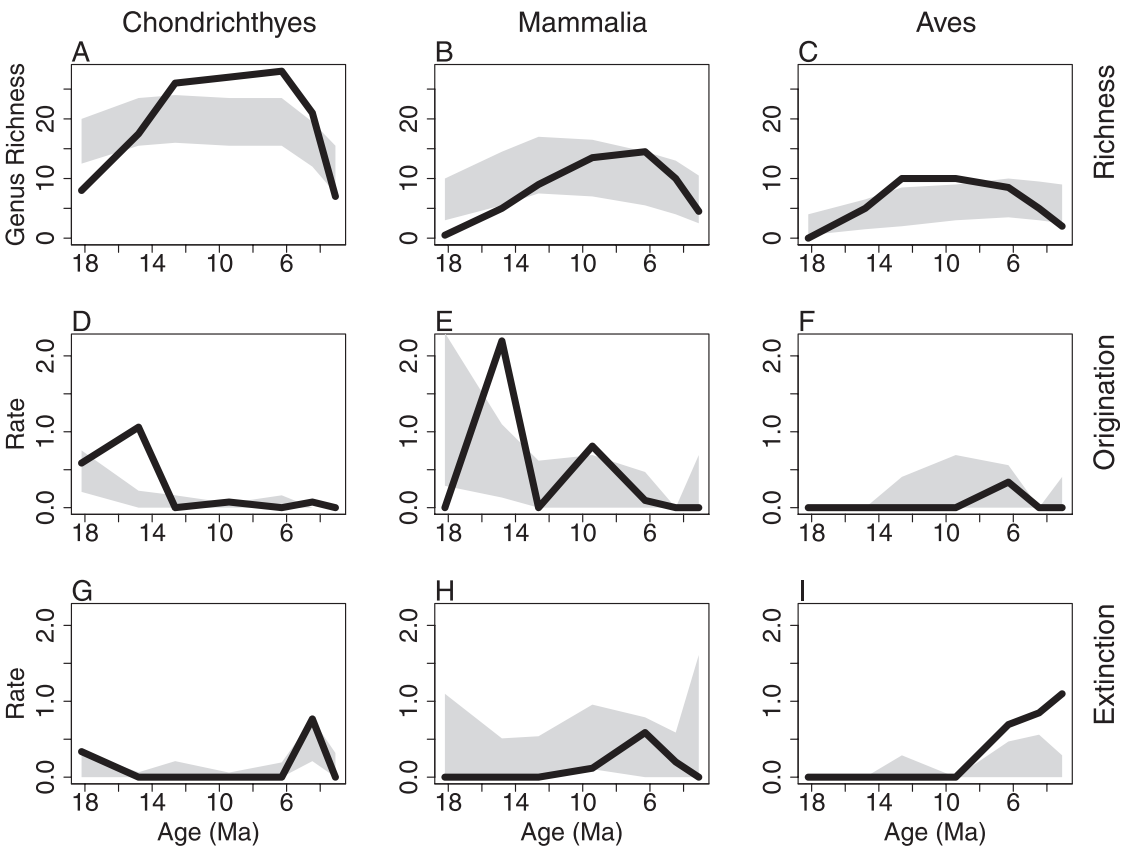


FIGURE 3. Genus-level diversification trends for three classes of marine vertebrates during the Neogene on the temperate Pacific coast of South America. Standing richness (A, B, C), origination rate (D, E, F), and extinction rate (G, H, I) for Chondrichthyes (A, D, G), Mammalia (B, E, H), and Aves (C, F, I). The gray areas enclose the 95% confidence intervals of  $10^6$  runs of a global diversification null model of diversification (see text for details).

TABLE 2. Spearman moment-product correlation between diversification trends of taxa versus the number of maps and number of occurrences during the Neogene. Significant values ( $p < 0.05$ ) are in bold.

Taxon	Variable	No. of maps	No. of occurrences
All	Genus richness	0.31	<b>0.93</b>
	Origination rate	<b>-0.84</b>	0.29
	Extinction rate	0.59	-0.40
Chondrichthyes	Genus richness	0.19	<b>0.92</b>
	Origination rate	<b>-0.87</b>	-0.65
	Extinction rate	0.04	-0.13
Marine mammals	Genus richness	0.52	<b>0.91</b>
	Origination rate	-0.57	-0.36
	Extinction rate	0.42	<b>0.77</b>
Seabirds	Genus richness	0.26	<b>0.80</b>
	Origination rate	0.30	0.75
	Extinction rate	<b>0.83</b>	-0.48

tion rates ( $r = 0.78$ ,  $p < 0.05$ , Table 1). Despite marked differences in the absolute rates, cartilaginous fishes and marine mammals showed a main pulse of origination during the mid-Miocene (Fig. 3D,E), higher than the null model. Seabirds showed a single pulse of origination ca. 6 Ma that was not different from that predicted by the null model (Fig. 3F). The extinction rate showed marked differences among taxa (Figs. 3G–I), and the correlation values were not significant in any case (Table 1). Cartilaginous fishes exhibited a single pulse of extinction toward the late Pliocene (Fig. 3G), which was similar to the global extinction trend. Similarly, a single pulse of extinction occurred in marine mammals toward the early Pliocene (Fig. 3H). In contrast, the extinction rate in seabirds increased steadily through time, ending with a major extinction during the late Pliocene (Fig. 3I).

Diversification trends showed a variable correlation with the number of geologic maps available and the number of occurrences per stage (Table 2, Fig. 2C,D). On the one hand, the number of maps was significantly correlated with the origination rate ( $r = -0.84$ ,  $p < 0.05$ ) of overall taxa. The number of maps was correlated with origination rate for cartilaginous fishes ( $r = -0.87$ ,  $p < 0.05$ ) and extinction rate for seabirds ( $r = 0.83$ ,  $p < 0.05$ ). On the other hand, the number of occurrences was positively and strongly correlated with richness for all taxa ( $r = 0.93$ ,  $p < 0.05$ ), seabirds

( $r = 0.80$ ,  $p < 0.05$ ), mammals ( $r = 0.91$ ,  $p < 0.05$ ), and cartilaginous fishes ( $r = 0.92$ ,  $p < 0.05$ ). Origination and extinction rate were not significantly correlated with the occurrences in any case (Table 2).

Out of 86 genera present during the Neogene, 36 (42%; 95% CI = 31–53%) went globally extinct at some point during the Pleistocene. The random forest model was 83% accurate (measured as a pseudo- $r^2$ ) in predicting extinction of genera. Variable selection analysis showed that few variables were relevant in the model (Fig. 4), with taxonomic order and class being the most important followed by the midpoint of latitudinal distribution of genera (Fig. 4). Maximum age, latitudinal range, and body size did not improve the accuracy of the model. Extinction had a marked taxonomic signature; it was very different among classes, being much more pronounced in marine mammals (79% [64–91%]), followed by seabirds (25% [7–52%]) and cartilaginous fishes (3% [0–17%]) (Fig. 4B). The very low extinction of cartilaginous fishes—lower than expected under a taxonomically random extinction—was largely driven by the absence of extinctions in Carcharhiniformes (Table 3). Conversely, the extinction of marine mammals was much larger than expected by a taxonomically random extinction, and it was mostly due to the extremely high loss of Cetacea—77% of genera (24 out of 31; Table 3). Extinction probability was related to the midpoint of latitudinal distribution; the chance of going extinct for genera with midpoints north of 21°S was roughly three times greater than for genera with midpoints south of 21°S (67% [41–81%] vs. 24% [13–38%]) (Fig. 4C).

## Discussion

Even though Neogene outcrops along the TPSA harbor a rich marine vertebrate fossil record (De Muizon and Devries 1985; Canto et al. 2010), this study is the first attempt to synthesize and understand the macroevolutionary diversification trends in the region. The main findings of our study are that (1) diversification trends show a marked “regional imprint” (i.e., departures from the global pattern), (2) diversification patterns vary



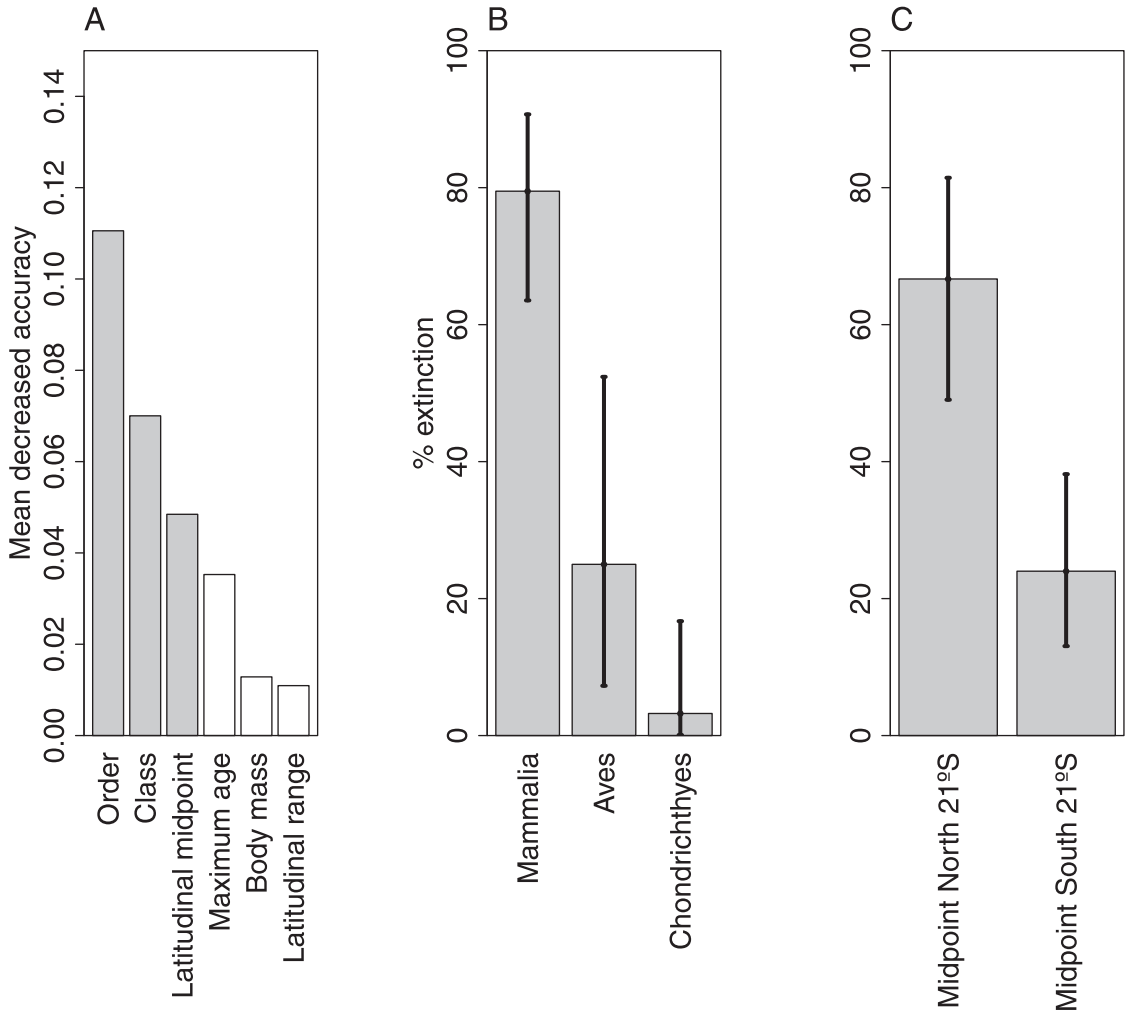


FIGURE 4. A, Variable importance (mean decreased accuracy) of a random forest analysis considering the importance of taxonomic structure (classes, orders), midpoint of latitudinal distribution, maximum age, body size, and geographic range for marine vertebrates during the Neogene on the temperate Pacific coast of South America. Black bars represent significant values ( $p < 0.05$ ). B, C, Percentage of genus extinction according to classes (B) and midpoint of latitudinal distribution (C). Error bars correspond to 95% confidence intervals.

among taxa, (3) diversification cannot be explained by sampling artifacts, and (4) the massive loss of genera was highly selective for ecological and life-history traits.

Diversification trends, for each taxon and for all taxa combined, showed marked deviations from global patterns. Although the overall shape of genus richness mirrors the global pattern, e.g., as seen for marine mammals and seabirds (Marx and Uhen 2010; Morlon et al. 2011), the richness peak is much higher than predicted. Similarly, peaks of origination and extinction are unusual, and

are not mere reflections of global trends. These departures of the diversification trends from the global diversification null model may be explained by the particular climatic and oceanographic events that occurred along the TPSA during the Neogene. The main pulse of origination was coeval with the Miocene climatic optimum (Zachos et al. 2001) and the onset of coastal upwelling cells associated with the Humboldt Current System (Ibaraki 1997; Tsuchi 2002), suggesting that warm and highly productive waters may have favored the appearance and coexistence of new forms.

TABLE 3. Taxonomic selectivity in the extinction of genera, for classes and orders of marine vertebrates. Lower and upper CI corresponds to the 95% CI expected number of extinctions based on 50,000 runs (ns = nonsignificant).

Class	Order	Total genera	Extinct genera	Expected extinction (null model)		
				Lower CI	Upper CI	Interpretation
Aves	Odontopterygiformes	1	1	0	1	ns
	Pelecaniformes	4	1	0	3	ns
	Procellariiformes	4	0	0	4	ns
	Sphenisciformes	5	1	1	4	ns
	All combined	4	16	3	10	ns
Chondrichthyes	Carcharhiniformes	8	0	1	6	Lower than expected
	Chimaeriformes	1	0	0	1	ns
	Echinorhiniformes	1	0	0	1	ns
	Heterodontiformes	1	0	0	1	ns
	Hexanchiformes	2	0	0	2	ns
	Lamniformes	4	1	0	4	ns
	Myliobatiformes	5	0	0	4	ns
	Odontaspidida	3	0	0	3	ns
	Orectolobiformes	2	0	0	2	ns
	Pristiophoriformes	1	0	0	1	ns
	Rajiformes	1	0	0	1	ns
	Squaliformes	1	0	0	1	ns
	Squatiformes	1	0	0	1	ns
	All combined	1	31	9	17	Lower than expected
	Mammalia	Carnivora	5	4	0	4
Cetacea		31	24	9	17	Higher than expected
Sirenia		2	2	0	2	ns
Xenarthra		1	1	0	1	ns
All combined		31	39	12	21	Higher than expected

Paleoclimatic and paleoceanographic conditions were drastically altered during the Pliocene when the Humboldt Current System reached its modern conditions; paleoceanographic reconstructions and modeling suggest that sea-surface temperature collapsed between 1.7 and 4.4°C, during the mid Pliocene (Dekens et al. 2007; Dowsett and Robinson 2009; Garreaud et al. 2010), whereas primary productivity increased abruptly ca. 2 Ma (Suto et al. 2012). Although this transition from warmer to cooler upwelling conditions has also been observed in other eastern boundary ecosystems (Dekens et al. 2007), the onset of the hyper-aridity of the Atacama Desert (Hartley and Chong 2002; Garreaud et al. 2010) during the Pliocene likely created a unique set of environmental conditions hostile to coastal biodiversity, particularly seabirds and marine mammals. Marine transgressions induced by tectonic subsidence may have destroyed coastal habitats, especially sheltered habitats (Herm 1969; Valenzuela-Toro et al. 2013). In addition, gastropods and bivalves, prey for larger vertebrates, experienced extremely elevated extinction rates at the species

level (Rivadeneira and Marquet 2007; Kiel and Nielsen 2010), suggesting that trophic cascades may have also triggered vertebrate extinction. The marked departures of the diversification trends from a global null expectation mirror similar conclusions drawn for invertebrates (Crampton et al. 2006; McGowan and Smith 2008), supporting the idea that global-scale analyses of diversification cannot properly capture the complex relationships between environmental forcing and biotic responses at evolutionary time scales. In addition, diversification trends were highly variable among classes, highlighting the importance of intrinsic traits interacting with climate in shaping diversity patterns through time (Alroy 2010; Ezard et al. 2011).

Possible sampling artifacts (i.e., preservation bias and/or insufficient sampling) may affect the robustness of the diversification trends, for instance explaining the low richness during the early Miocene and late Pliocene (Fig. 2A,B,C). Other authors have considered possible sampling artifacts such as the number of maps and the volume and availability of sediments (Crampton et al 2003;

Smith and McGowan 2007; McGowan and Smith 2008; Smith et al. 2012), in some cases finding relationships between global diversity curves and sampling bias. Like us, Uhen and Pyenson (2007) and Marx (2009) found no evidence of a control of outcrop area and the diversity of Cenozoic marine mammals, in North America and Western Europe, respectively. In our case, the number of maps (a proxy of outcrop availability) was correlated only with overall origination rate, but the negative sign of the correlation implies that the low origination rate recorded during the late Miocene and Pliocene could not be linked to an insufficient amount of sedimentary rock. Moreover, within each taxon diversification trends (richness, origination, and extinction) were largely uncoupled from the temporal variation in number of maps. The positive correlation between richness and number of occurrences, observed in all genera combined and within each taxon, might reflect changes in the relative abundance of genera, and not necessarily insufficient sampling. This is reinforced by the lack of relationship between richness and number of maps. This combined evidence suggests that, although further paleontological sampling will likely increase the diversity of fossil inventories the observed diversification patterns reported here are robust and cannot be attributed to sampling artifacts.

Our analyses confirm the existence of a major vertebrate turnover occurring during the Neogene–Pleistocene transition (Valenzuela-Toro et al. 2013), when 42% of genera went globally extinct. The precise timing of this massive loss remains unknown, because it is beyond the temporal resolution of our analysis. Vertebrate fossil assemblages are rare and/or undersampled in the vast Pleistocene deposits of Peru and Chile (e.g., Valenzuela-Toro et al. 2013). Moreover, our results showed that extinctions were not random with respect to the ecological and life-history traits of genera, a pattern also demonstrated by neontological studies in cartilaginous fishes (Dulvy and Reynolds 2002; García et al. 2008; Field et al. 2009), marine mammals (Davidson et al. 2012) and seabirds (Duncan and Blackburn 2004). Rather, extinction was highly selective

for taxonomic relatedness and midpoint of latitudinal distribution, as revealed by the high accuracy of the random forest model (pseudo- $r^2 = 0.83$ ). First, taxonomic relatedness i.e., orders and classes, was by far the most important driver of extinction; it is also an important variable conditioning the extinction risk in modern species (García et al. 2008; Davidson et al. 2012). The extinction ranking among classes (marine mammals > seabirds > cartilaginous fishes) mirrors the relative risk faced by modern species (Harnik et al. 2012). At the ordinal level, the selectivity was largely driven by the large and disproportionate extinction of cetaceans, one of the marine groups facing the highest extinction risk in modern oceans (Harnik et al. 2012). On the other hand, extinction was unusually low among Carcharhiniformes, which could be attributed to the lack of endemic genera along the TPSA during the Neogene. Second, the higher extinction observed for taxa distributed in the northern region (i.e., midpoint of latitudinal distribution north of 21°S) could be attributed to geographic differences in large thermal anomalies in sea-surface temperature, as predicted by paleoceanographic models for the mid-Piacenzian (Dowsett and Robinson 2009); for instance, in the northern TPSA zone (i.e., 6–22°S) the mean SST anomaly was 5.3°C, much higher than in the southern TPSA zone (i.e., 24–42°S), where the mean thermal anomaly was 3.5°C. This lends support to the cooling effect as one primary driver of the late Neogene–Pleistocene faunal turnover, induced by the modern onset of coastal upwelling cells (Dekens et al. 2007).

We found no evidence of selectivity for geographic range, maximum age, or body size. Geographic range is one of the traits most consistently associated with extinction risk in modern and fossil invertebrates and vertebrates (Jablonski 2005; Payne and Finnegan 2007; Davidson et al. 2012). On the one hand, it is plausible that the functional relationship between extinction risk and range size changed its form during large extinction events; i.e., a geographic range size that confers protection against extinction during background times would be less effective during mass extinctions (Jablonski 2008). The

onset of the modern conditions of the Humboldt Current during the late Neogene necessarily implies that a huge ecosystem transformation occurred across a major geographic expanse (i.e., northern Peru to southern Chile, 5–42°S); hence, large latitudinal ranges did not enhance chances of survival of genera. On the other hand, body size is frequently cited as an important factor in the extinction risk in modern marine vertebrates (Dulvy and Reynolds 2002; Davidson et al. 2012), with larger forms typically being at higher risk than smaller ones because of different constraints in physiology, ecology, and life-history traits (Peters 1983; Brown et al. 2004). However, several paleontological studies (McKinney 1997; Jablonski 2005) have shown no relationship between extinction and body size. The lack of a significant relationship between extinction risk and body size implies that traits buffering or enhancing extinction risk may not be perfectly represented by body size. Indeed, taxonomy and life-history traits were more important than body size per se in explaining the extinction risk of modern marine mammals (Davidson et al. 2012). In addition, comparing body sizes across different classes assumes some sort of universal scaling between extinction risk and body size, which is unwarranted (del Monte-Luna and Lluh-Belda 2003). Indeed, the largest body size estimated for cartilaginous fishes (*Carcharocles*) is comparable to those estimated for cetaceans (see Appendix), but the intensity of genus extinction in cartilaginous fishes was remarkably low. Finally, the age of first appearance was not related to survival, in contrast to what is observed in marine invertebrates during the entire Phanerozoic (Finnegan et al. 2008).

New paleontological studies will provide data for further refinements of the present analyses, including (1) species-level assessment of diversification trends, (2) more precise dating of events, and (3) a more robust test of the role of environmental drivers based on new paleoceanographic reconstructions. Although future paleontological surveys are much needed in order to increase the quality of fossil inventories, our analysis provides the first step to a deeper understanding of the

diversification patterns of marine vertebrates during the late Cenozoic along the temperate Pacific coast of South America.

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Appendix  
Summary of ecological and life-history traits of 86 genera used for the analysis of extinction selectivity.

Class	Order	Family	Genus	Length (cm)	Weight (kg)	Latitudinal range (° latitude)	Midpoint of latitudinal distribution (°S, southeastern Pacific coast)	Extinct (1 = yes, 0 = no)	Age, min	Age, max
Mammalia	Carnivora	Phocidae	<i>Acrophoca</i>	150	105	12	-21	1	5.332	11.608
Mammalia	Cetacea	Physeteridae	<i>Acrophyseter</i>	400	500	1	-16	1	5.332	7.246
Chondrichthyes	Myliobatiformes	Myliobatidae	<i>Aetobatus</i>	330	230	26	-17	0	3.6	15.97
Chondrichthyes	Myliobatiformes	Myliobatidae	<i>Aetomyliatus</i>	240	200	1	-27	0	5.3	16
Mammalia	Cetacea	Kentriodontidae	<i>Atocetus</i>	900	4000	1	-14	1	11.608	13.65
Mammalia	Cetacea	Phocoenidae	<i>Australiiflux</i>	220	120	1	-14	1	7.246	11.608
Mammalia	Cetacea	Balaenidae	<i>Balaena</i>	1800	100,000	1	-42	0	2.588	15.97
Mammalia	Cetacea	Balaenopteridae	<i>Balaenoptera</i>	2900	173,000	23	-27	0	2.588	15.97
Mammalia	Cetacea	Kentriodontidae	<i>Belonodelphis</i>	275	235	1	-14	1	11.608	13.65
Chondrichthyes	Orectolobiformes	Brachaeluridae	<i>Brachaelurus</i>	122	12	1	-27	0	5.3	16
Chondrichthyes	Cetacea	Pontoporiidae	<i>Brachydelphis</i>	255	185	13	-21	1	5.332	15.97
Chondrichthyes	Chimaeriformes	Callorhynchidae	<i>Callorhynchus</i>	125	12	18	-25	0	2.6	23
Chondrichthyes	Carchariniiformes	Carcharhinidae	<i>Carcharhinus</i>	420	347	29	-18	0	2.588	15.97
Chondrichthyes	Odontaspida	Odontaspidae	<i>Carcharias</i>	370	159	23	-16	0	2.588	15.97
Chondrichthyes	Lamniiformes	Lamnidae	<i>Carcharodes</i>	3000	103,000	30	-19	1	3.6	16
Chondrichthyes	Odontaspida	Carcharodontidae	<i>Carcharodon</i>	540	3230	18	-25	0	2.588	15.97
Chondrichthyes	Lamniiformes	Cetorhinidae	<i>Cetorhinus</i>	900	4000	3	-29	0	3.6	16
Aves	Procellariiformes	Procellariidae	<i>Daption</i>	39	0.5	1	-27	0	1.8	11.6
Chondrichthyes	Myliobatiformes	Dasyatidae	<i>Dasyatis</i>	430	300	23	-16	0	5.3	15.97
Mammalia	Cetacea	Delphinidae	<i>Delphinus</i>	250	235	20	-25	0	2.588	15.97
Aves	Procellariiformes	Diomedetidae	<i>Diomedea</i>	150	12	1	-27	0	5.332	7.246
Chondrichthyes	Echinorhniiformes	Echinorhinidae	<i>Echinorhinus</i>	400	200	1	-27	0	2.6	15.97
Aves	Sphenisciformes	Spheniscidae	<i>Eudyptula</i>	33	2	1	-27	0	7.2	16
Aves	Procellariiformes	Procellariidae	<i>Fulmarus</i>	48	1	12	-21	0	5.332	16
Chondrichthyes	Carchariniiformes	Carcharhinidae	<i>Galeocerdo</i>	750	807	11	-9	0	5.3	15.97
Chondrichthyes	Carchariniiformes	Triakidae	<i>Galeorhinus</i>	193	45	6	-30	0	2.6	15.97
Chondrichthyes	Orectolobiformes	Ginglymostomatidae	<i>Ginglyostoma</i>	430	110	1	-4	0	5.3	11.61
Mammalia	Cetacea	Delphinidae	<i>Globicephala</i>	760	4000	1	-33	0	2.588	15.97
Mammalia	Carnivora	Phocidae	<i>Hadrokoris</i>	350	600	1	-15	1	5.332	7.246
Chondrichthyes	Carchariniiformes	Hemigaleidae	<i>Hemipristis</i>	240	500	13	-10	0	5.3	23
Mammalia	Cetacea	Delphinidae	<i>Hemisyrtrachelius</i>	980	10,000	12	-21	1	3.6	7.246
Chondrichthyes	Heterodontiformes	Heterodontidae	<i>Heterodontus</i>	152	21	20	-24	0	2.6	23.03
Chondrichthyes	Hexanchiformes	Hexanchidae	<i>Hexanchus</i>	482	590	17	-24	0	2.6	16
Mammalia	Carnivora	Otariidae	<i>Hydrarchos</i>	230	350	1	-16	1	5.332	7.246
Mammalia	Cetacea	Kentriodontidae	<i>Incaetus</i>	275	235	1	-16	1	20.4	23
Chondrichthyes	Odontaspida	Carcharodontidae	<i>Isurus</i>	417	506	28	-28	0	2.6	23.03
Mammalia	Cetacea	Kogiidae	<i>Kogia</i>	350	400	1	-27	0	2.6	16
Chondrichthyes	Lamniiformes	Lamnidae	<i>Lamna</i>	350	230	1	-34	0	15.97	23.03

Appendix. Continued.

Class	Order	Family	Genus	Length (cm)	Weight (kg)	Latitudinal range (° latitude)	Midpoint of latitudinal distribution (°S, southeastern Pacific coast)	Extinct (1 = yes, 0 = no)	Age, min	Age, max
Mammalia	Cetacea	Physeteroidea	<i>Leviathan</i>	1750	57,000	1	-14	1	11,608	13,65
Mammalia	Cetacea	Phocoenidae	<i>Lomacetus</i>	220	120	1	-15	1	7,246	11,608
Mammalia	Cetacea	Ziphiidae	<i>Messapicetus</i>	1300	15,000	1	-14	1	11,608	13,65
Mammalia	Sirenia	Dugongidae	<i>Metaxytherium</i>	250	200	1	-5	1	11.6	23
Mammalia	Cetacea	Cetotheriidae	<i>Miocapera</i>	621	3500	1	-15	1	7,246	11,608
Mammalia	Cetacea	Cetotheriidae	<i>Morenocetus</i>	1800	10,000	1	-33	1	2,588	15,97
Aves	Pelecaniformes	Sulidae	<i>Morus</i>	94	2.6	1	-15	0	3.6	11.6
Chondrichthyes	Myliobatiformes	Myliobatidae	<i>Myliobatis</i>	183	82	38	-23	0	2.6	23.03
Mammalia	Sirenia	Dugongidae	<i>Nanosiren</i>	200	150	12	-21	1	5.332	11,608
Mammalia	Cetacea	Ziphiidae	<i>Nazacetus</i>	1300	15,000	1	-14	1	11,608	13,65
Chondrichthyes	Carchariniformes	Carcharhinidae	<i>Negaprion</i>	380	184	1	-4	0	5.3	11,61
Mammalia	Cetacea	Ziphiidae	<i>Ninziphius</i>	1300	15,000	1	-15	1	5.332	7,246
Chondrichthyes	Hexanchiformes	Hexanchidae	<i>Notorhynchus</i>	300	107	2	-29	0	5.3	15,97
Mammalia	Cetacea	Odobenocetopsidae	<i>Odobenocetops</i>	210	650	1	-16	1	5.332	7,246
Chondrichthyes	Lamniiformes	Odontaspidae	<i>Odontaspis</i>	450	289	7	-30	0	5.3	23.03
Aves	Procellariiformes	Procellariidae	<i>Pachyptila</i>	28	0.2	1	-27	0	5.3	16
Aves	Sphenisciformes	Spheniscidae	<i>Palaeospheniscus</i>	75	5	11	-22	1	5.3	16
Chondrichthyes	Carchariniformes	Hemigaleidae	<i>Paragaleus</i>	140	17	1	-27	0	5.3	23
Aves	Odontopterygiformes	Pelagornithidae	<i>Pelagornis</i>	125	29	13	21	1	5.332	16
Aves	Pelecaniformes	Phalacrocoracidae	<i>Phalacrocorax</i>	94	4	15	-20	0	2,588	16
Mammalia	Cetacea	Cetotheriidae	<i>Piscobalaena</i>	1500	83,000	1	-16	1	5.332	11,608
Mammalia	Cetacea	Cetotheriidae	<i>Piscocetus</i>	2900	173,000	1	-16	1	5.332	7,246
Mammalia	Cetacea	Phocoenidae	<i>Piscolithax</i>	220	120	1	-16	1	5.332	11,608
Mammalia	Carnivora	Phocidae	<i>Pisophoca</i>	150	105	11	-21	1	5.332	11,608
Mammalia	Cetacea	Cetotheriidae	<i>Plestocetopsis</i>	150	105	1	-34	1	2.6	16
Mammalia	Cetacea	Balaenopteridae	<i>Plestocetus</i>	2900	173,000	1	-34	1	16	23
Mammalia	Cetacea	Pontoporiidae	<i>Pliopontus</i>	255	185	14	-23	1	2,588	11,608
Mammalia	Cetacea	Pontoporiidae	<i>Pontistes</i>	255	185	1	-27	1	5.332	11,608
Chondrichthyes	Carchariniformes	Carcharhinidae	<i>Prionace</i>	400	206	1	-27	0	2.6	5,332
Chondrichthyes	Pristiophoriformes	Pristiophoridae	<i>Pristiophorus</i>	137	16	20	-24	0	2.6	23.03
Aves	Procellariiformes	Procellariidae	<i>Puffinus</i>	47	0.9	1	-4	0	2,588	3.6
Aves	Sphenisciformes	Spheniscidae	<i>Pygoscelis</i>	72	6	1	-27	0	3.6	15,97
Chondrichthyes	Rajiformes	Rajidae	<i>Raja</i>	244	91	1	-27	0	5.3	15,97
Aves	Pelecaniformes	Sulidae	<i>Ramphastula</i>	94	2.6	1	-16	1	5.332	7,246
Chondrichthyes	Myliobatiformes	Myliobatidae	<i>Rhinoptera</i>	213	23	1	-27	0	5.3	15,97
Mammalia	Cetacea	Kogiidae	<i>Scaphokogia</i>	350	400	1	-16	1	5.332	11,608
Aves	Sphenisciformes	Spheniscidae	<i>Spheniscus</i>	70	4	13	-21	0	2,588	16
Chondrichthyes	Carchariniformes	Sphyrnidae	<i>Sphyrna</i>	610	450	13	-21	0	2.6	15,97



## Appendix. Continued.

Class	Order	Family	Genus	Length (cm)	Weight (kg)	Latitudinal range (° latitude)	Midpoint of latitudinal distribution (°S, southeastern Pacific coast)	Extinct (1 = yes, 0 = no)	Age, min	Age, max
Mammalia	Cetacea	Squalodontidae	<i>Squalodon</i>	180	50	1	-30	1	3.6	11.608
Chondrichthyes	Squaliformes	Squalidae	<i>Squalus</i>	160	24	1	-34	0	15.97	23.03
Chondrichthyes	Squatiformes	Squatinae	<i>Squatina</i>	200	80	7	-30	0	2.6	23
Mammalia	Cetacea	Delphinidae	<i>Stenella</i>	260	160	1	-16	0	5.332	7.246
Aves	Pelecaniformes	Sulidae	<i>Sula</i>	92	2	13	-21	0	5.332	16
Aves	Sphenisciformes	Spheniscidae	<i>Thalassarche</i>	99	4	1	-27	0	7.2	16
Mammalia	Xenarthra	Nothrotheriidae	<i>Thalassocnus</i>	182	226	15	-20	1	2.588	11.608
Mammalia	Carnivora	Otariidae	<i>Otaria</i>	350	300	1	-27	0	0.01	2.588
Mammalia	Cetacea	Phocoenidae	<i>Phocoena</i>	250	76	1	-40	0	0.01	2.588

\* Body weight estimated.