

Selective extinction of late Neogene bivalves on the temperate Pacific coast of South America

Marcelo M. Rivadeneira and Pablo A. Marquet

Abstract.—We assessed selective extinction patterns in bivalves during a late Neogene mass extinction event observed along the temperate Pacific coast of South America. The analysis of 99 late Neogene and Quaternary fossil sites (recorded from 7°S to 55°S), yielding ~2800 occurrences and 118 species, revealed an abrupt decline in Lyellian percentages during the late Neogene–Pleistocene, suggesting the existence of a mass extinction that decimated ~66% of the original assemblage. Using the late Neogene data set ($n = 59$ species, 1346 occurrences), we tested whether the extinction was nonrandom according to taxonomic structure, life habit, geographic range, and body size. Our results showed that the number of higher taxa that went extinct was not different than expected by random. At first sight, extinction was selective only according to life habit and geographic range. Nevertheless, when phylogenetic effects were accounted for, body size also showed significant selectivity. In general, epifaunal, small-sized (after phylogenetic correction), and short-ranged species tended to have increased probability of extinction. This is verified by strong interactions between the variables herein analyzed, suggesting the existence of nonlinear effects on extinction chances. In the heavily decimated epifaunal forms, survival was not enhanced by widespread ranges or larger body sizes. Conversely, the widespread and large-sized infaunal forms tended to have lower probability of extinction. Overall, the ultimate extinction of late Neogene bivalve species along the Pacific coast of South America seems to have been determined by a complex interplay of ecological and historical (phylogenetic) effects.

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Introduction

Extinction is a primordial macroevolutionary force, removing incumbent forms and creating new ecological scenarios. Extinction does not affect all species equally, and complex interactions between extrinsic forces and the species' intrinsic attributes (i.e., physiological, life-history, and ecological traits) can potentially give rise to a plethora of selectivity patterns, as has been observed among taxa and across macroevolutionary and ecological timelines (Jablonski 1995, 2005; McKinney 1997).

Because species are nested within a taxonomic hierarchy (which reflects phylogenetic history), their physiological, life-history, and ecological traits are often shared among species within taxa (Harvey and Pagel 1991; McKinney 1997). Thus, the existence of traits associated with a high risk of extinction will

tend to be shared by most species within a taxon, making them all vulnerable to extinction (McKinney 1997). Therefore, species' extinction risk would be nonrandomly distributed across taxa, a phenomenon that has been reported in several groups at ecological time scales (Bennett and Owens 1997; Gittleman and Purvis 1998; Russell et al. 1998; Purvis et al. 2000a; Schwartz and Simberloff 2001; Jones et al. 2003). In the case of the fossil record, however, most of the selectivity analyses come from mass extinction events where random patterns are the norm (e.g., Jablonski and Raup 1995; Lockwood 2003, 2005; Jablonski 2005). In contrast, selectivity patterns during background extinctions have received considerably less attention (McKinney 1995, 1997; Smith and Roy 2006).

The late Neogene represents a time of major global environmental change (Zachos et al. 2001; Ravelo et al. 2004) that led to profound

alterations of biotas around the world. Although it has been profusely documented that several well-preserved bivalve faunas in different regions of the world experienced enhanced levels of extinction (Stanley and Campbell 1981; Raffi et al. 1985; Stanley 1986; Jackson et al. 1993; Allmon et al. 1993; Berkman and Prentice 1996; Johnson and Curry 2001; Todd et al. 2002), selectivity patterns associated with these extinctions have been largely unexplored (e.g., Stanley 1986; Smith and Roy 2006).

The late Neogene and Quaternary mollusk faunas of the temperate Pacific coast of South America (PSA) have been studied for more than a century (Philippi 1887; Herm 1969; Ortlieb et al. 1995). The bulk of paleontological research, however, has focused on the use of fossil mollusks as stratigraphic or taphonomic indicators (e.g., Covacevich and Frassinetti 1986; Frassinetti and Covacevich 1993, 1995; Le Roux et al. 2004) and paleoceanographic proxies (e.g., Ortlieb et al. 1990, 1994, 1996; Nielsen et al. 2005). Fossil mollusks have been also used to reconstruct some biogeographic features of the region (e.g., Covacevich and Frassinetti 1986; Valdovinos 1996; DeVries and Frassinetti 2003). Nevertheless, little effort has been directed at generating a synoptic picture of the macroevolutionary dynamics experienced by this biota (Herm 1969; DeVries 1985, 2001; Lindberg 1991). Preliminary evidence suggests the existence of higher extinction levels for mollusks during the late Neogene along the PSA (Herm 1969; DeVries 2001), but the existence of possible selectivity patterns remains largely unknown. Here we show that the PSA bivalve biota did experience higher levels of extinction during late Neogene, and that such extinction was strongly selective among species.

Methods

Database.—The primary information was collected from a comprehensive literature survey of paleontological studies carried out along the PSA. The data were gathered from 99 marine late Neogene–Holocene sites reported in 21 studies, ranging from late Miocene to Holocene, covering both Peruvian and Magellan marine zoogeographic provinces

(see Table S1 of the supplemental material, online at <http://dx.doi.org/10.1666/06042.s1>). Although the paleoenvironments are rather poorly known, the environments represent shallow-water habitats (i.e., coastal shelf), in wave-exposed and wave-protected areas (e.g., Herm 1969; Frassinetti and Covacevich 1995; Le Roux et al. 2005). We included only late Neogene sites with a Pliocene minimum estimated age; older Miocene faunas were not included in the present analysis. The original database included 118 species and 2798 occurrences. We followed the basic taxonomic treatment given by Herm (1969) and Valdovinos and Nielsen (unpublished manuscript), but we used recent reviews (e.g., Coan et al. 2000; Millard 2003) to assign species to higher taxonomic levels. Subgenera, when available, were considered as valid genera.

Fossil deposits are distributed along most of PSA. Quaternary terraces are found mostly in northern and southern Peru and northern Chile, where extremely arid conditions and very sparse human settlements have favored the preservation of rich deposits. Most of those deposits have been dated with independent age controls, and the bulk of them have been assigned to interglacial periods during the early to late Pleistocene and the Holocene (Radtke 1987; Ortlieb et al. 1995; Paskoff et al. 1995). Early Pleistocene deposits have only recently been described (e.g., Ortlieb et al. 1997; Guzman et al. 2000). There are no Quaternary deposits south of 30°S, except in the Magellan region, where diverse Holocene assemblages have been described (Gordillo 1999). Late Neogene sites with Pliocene minimum estimated age are found across most of the PSA (Fig. 1), in central-south Peru (Pisco Formation: De Muizon and DeVries 1985; DeVries and Frassinetti 2003), northern Chile (La Portada Formation: Cantalamessa et al. 2005; Bahía Inglesa Formation: Marquardt et al. 2000; Coquimbo Formation: Le Roux et al. 2004, 2005), and south-central Chile (La Cueva Formation: Encinas et al. 2006; Buatois and Encinas 2006; Tubul Formation: Biro 1979). However, and in marked contrast to Quaternary deposits, independent age controls are not available for many of these units (DeVries and Frassinetti 2003). In spite of recent strati-

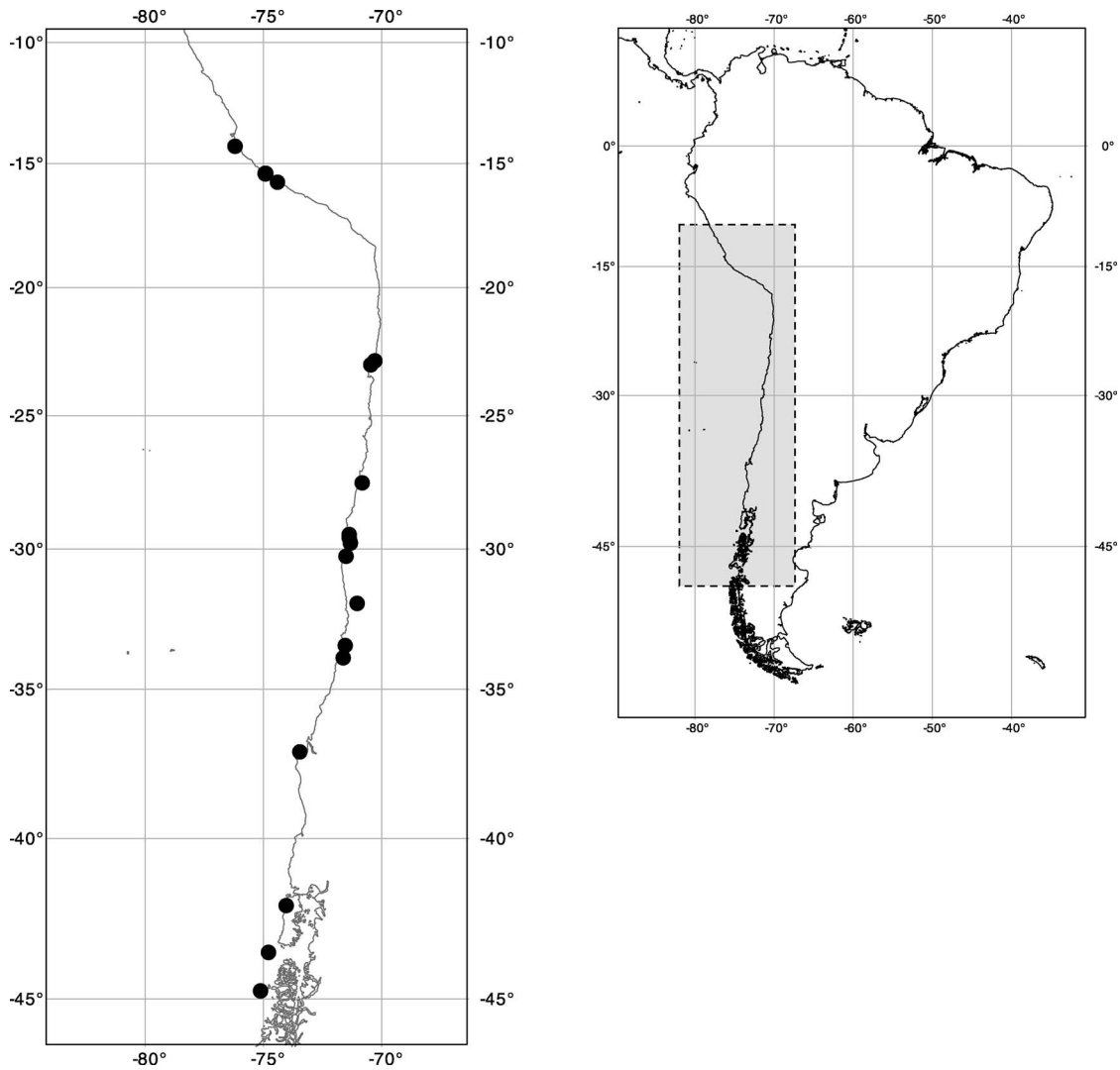


FIGURE 1. Map of the study region, along the Pacific coast of South America, showing the distribution of the 19 Pliocene sites (black circles) used to evaluate extinction and selectivity patterns (see Supplemental Table S1 for sources).

graphic analyses (Dunbar et al. 1990; Martinez-Pardo 1990; Marquardt et al. 2000; Le Roux et al. 2004, 2005; Encinas et al. 2005, 2006; Cantalamessa et al. 2005), an accurate assignment of stratigraphic ranges is not yet available for most species, hindering a detailed analysis of the macroevolutionary dynamics experienced by the fauna. The current information, though incomplete, provides a preliminary picture of the stratigraphic distribution of occurrences of the late Neogene bivalves in the region.

Extinction Dynamics.—A Lyellian curve was

used to explore temporal dynamics of extinction across the late Neogene along the PSA. This was done by plotting for each fossil assemblage (grouping sites with a similar age [see Table S1 of the supplemental material]) the proportion of its fauna that is extant in the area where the site is located (based on a comprehensive literature analyses [Valdovinos 1999]), versus its estimated age. Total extinction ($100 - \text{Lyellian}\%$) was estimated for Quaternary and Pliocene times. To evaluate the possible impact of differences in the number of sites (19 Pliocene, and 80 Quaternary) on

these estimates, and to generate confidence intervals for their comparison, we generated bootstrapped estimates for the Quaternary (1000 runs) by randomly selecting 19 sites from the total pool of 80. To assess the statistical significance of the differences between the Quaternary and the Pleistocene, the estimated extinction for the latter was contrasted with the 95% confidence interval obtained from the 1000 runs.

The possible impact of extinction on total species richness in the region was explored by comparing species richness between Pliocene and Quaternary times. The analysis was done using a rarefaction analysis (EstimateS [Colwell 2005]), based on the total number of individuals and species obtained from three late Pliocene sites (Frassinetti and Covacevich 1995; Frassinetti 1997; Valdovinos and Nielsen unpublished data) and 24 Quaternary (mid-Pleistocene to Holocene) (see Table S1). We followed the "maximum number of individuals" approach (Gilinsky and Bennington 1994; Todd et al. 2002), considering each valve as an individual, with a total of ~3500 individuals for Pliocene and Quaternary assemblages. Analyses were done at two spatial scales, local (using each site independently) and regional (pooling sites within each epoch), in order to explore how differences in richness were expressed in the space hierarchy. Although the time frames encompassed by them are not exactly similar, they represent the best and only data set available to try to test the existence of temporal changes in species richness.

A major potential bias in extinction and selectivity analysis is the incompleteness of the fossil record. Indeed, the record of PSA is far from complete, especially for Pliocene deposits. If such incompleteness is also associated with preservation bias, it may create a problem in estimating both extinction and selectivity. In order to explore the effects of shell mineralogical composition on extinction estimates, species were classified as aragonite/calcite bearers, using assignments made at higher taxonomic levels (Coan et al. 2000). To test for temporal changes in the preservation potential of the bivalve faunas we compared the proportion of calcite bearers between time periods (Pliocene versus Recent, and Quater-

nary versus Recent) using a binomial test. To test whether shell mineralogy is biasing the selectivity patterns we evaluated differences in the life habit, range, and body size (see below) between calcitic and aragonitic forms using a binomial test and *t*-tests (respectively). However, the results of this analysis should be viewed with caution as differences in the incidence of aragonite/calcite species may also reflect a true pattern of differential evolutionary responses if biochemical differences are coupled with ecological differences (as may be the case, given that most calcitic forms are epifaunal).

Selectivity Patterns.—The existence of a mass extinction of late Neogene bivalve species (see "Results") provides the opportunity to test for selectivity. Thus, further analyses were performed only in the subset of 59 Pliocene bivalve species (see Table S2 of the supplemental material), based on 19 sites, and 1346 occurrences, with an average of 23 occurrences/species. A species was considered as a survivor, or extinct, if it is, or it is not, observed in the present-day record within the PSA area (obtained from the exhaustive review of Valdovinos 1999), respectively.

We tested whether the extinction was selective according to several life-history and ecological traits. These were

1. Taxonomic level: To test for taxonomic patterns of selectivity, we compared the observed number of surviving genera, families, orders, and subclasses, with the predictions of a null model, using the protocol of Smith and Roy (2006). The model was built by randomly drawing the observed number of surviving species from the original pool, and counting the number of genera, families, orders, and subclasses represented by those species. The process was repeated 10,000 times and the distributions compared with the observed estimates for each taxonomic level. We also analyzed patterns for some particularly well represented taxa. The *p*-values obtained by the multiple tests were not corrected with the traditional sequential Bonferroni adjustment (Rice 1989), because of the excessive penalization to the α -values imposed by the method (see Moran 2003 for a series of objections to

the method). Taxonomic selectivity was statistically evaluated using the 97.5th or 2.5th percentiles of the bootstrapped distributions.

2. Life habit: The life habit (infaunal/epifaunal) is a trait typically conserved at higher taxonomic levels (Jablonski 2005). This allows us to infer the life habit of each species based on information available in other data sets (e.g., Roy et al. 2000; Todd et al. 2002). Although infaunal forms exhibit various feeding strategies (filter feeders/deposit feeders), this was not considered in the analyses, because the number of deposit feeders was reduced ($n = 8$), and extinction was essentially the same for the two feeding modes.

3. Range: This was estimated for all species as the latitudinal range between their northernmost and southernmost occurrences. Because the South American coast is oriented mostly in a north-south direction between 14°S to 44°S (Fig. 1), latitudinal range was considered a good proxy of geographic range. \log_{10} range was used in all the analyses. Given that observed range may not accurately represent the “true” (i.e., absolute) range of species, owing to the incompleteness of the fossil record, we performed a simulation analysis to evaluate the sensitivity of the estimated latitudinal ranges to sampling quality (number of sampled sites). From the total number of sampled sites ($n = 19$) we generated 500 random subsets of 15, 12, 9, 6, and 3 sites, randomizing the columns (sites) and fixing the rows (species). For each run, we estimated the range as above, and calculated the Pearson product-moment correlation between the original ranges and the re-estimated ranges. The simulation showed that even after a severe truncation in the number of sampled sites, positive and significant correlation values are still obtained (Table 1). Therefore, despite the limitations of the data, relative range estimates are consistent among taxa, validating the exploration of range as a possible factor in extinction patterns.

4. Body size: Following previous studies (e.g., Stanley 1986; Roy et al. 2001; Smith and Roy 2006), body size was estimated as the \log_2 of the geometric mean of the maximum length and height of the shell of each species. All the estimates correspond to the largest Pliocene

TABLE 1. Results of a simulation analysis (500 runs) testing the effects of sampling bias in range estimation. This effect was assessed by evaluating the correlation (Pearson's r) between the original ranges for each of the 59 species studied and the estimated range under different levels of reduction in sample size obtained by subsampling a given fraction of the total sites. Positive correlation values indicate a good correspondence between the original and truncated sizes across species. See text for details.

Subsampled sites (% of total)	r (95 % CI)
15 (79%)	0.96 (0.70–1.00)
12 (63%)	0.90 (0.55–0.97)
9 (47%)	0.66 (0.40–0.93)
6 (32%)	0.49 (0.27–0.78)
3 (16%)	0.34 (0.10–0.58)

valve reported in the literature (Herm 1969; Watters and Fleming 1972; Frassinetti and Covacevich 1995; Frassinetti 1997; Valdovinos and Nielsen unpublished manuscript). The number of valves sampled was variable (from a only few to thousands of valves), but often sample size used to estimate the maximum length was missing, so it is not possible to estimate a priori the impact of sampling size on body size estimates. However, three lines of evidence strongly suggest that our body size estimates are robust, supporting the validity of our analysis: First, because the estimates of maximum body size in a population depend on the sampling intensity (i.e., a positive relationship between maximum body size and sampling size), the body size of underrepresented species (i.e., with fewer occurrences) should be biased. This is not the case, however—the relationship between total number of occurrences and body size (estimated as indicated above) is not significant ($r = 0.10$, $n = 59$, $p = 0.44$). Second, and following the same reasoning as before, the comparatively better studied Quaternary species should appear larger on average than their Pliocene counterparts. However, the body sizes of Quaternary species (estimated independently using the same protocols as above) and Pliocene forms showed no significant differences (t -test: $t = 1.98$, d.f. = 113, $p = 0.39$). Finally, if the body size of Pliocene species really was underestimated, then we should expect that for the surviving genera in the region (i.e., genera present in both Pliocene and Recent assemblages,

$n = 20$) present-day species should be significantly larger than their Pliocene counterparts. Again, differences in the maximum body size between Pliocene and Recent were not statistically significant (paired t -test: $t = 2.09$, d.f. = 19, $p = 0.80$). Although our three lines of evidence provide *necessary*, but not *sufficient*, evidence for the robustness of our body size estimates, they suggest that qualitatively our general conclusions should not be affected by sampling artifacts.

Two kinds of statistical analyses were conducted to establish the existence of selectivity patterns. First, we assessed the effect of each explanatory variable separately. Life-habit selectivity was tested using a binomial test. The roles of range and body size were evaluated using a GLM (generalized linear model, i.e., logistic regression), where survival was the dependent binary variable, and the errors were assumed to follow a binomial distribution (Crawley 2005). Second, all the variables were integrated in a multiple logistic regression, where we tested the significance of both additive and multiplicative terms. Life habit was considered as a categorical variable, and levels were coded as 0 (epifaunal) and 1 (infaunal). The final best model was chosen after backward elimination of less significant terms, minimizing the Akaike Information Criterion (AIC) (Crawley 2005). The advantage of this method is that it allows us to test the relative importance of each factor, as well as the existence of nonlinear trends evident from the significant interaction between explanatory terms (Crawley 2005). All analyses were done using the R statistical software (R Development Core Team 2005).

Phylogenetic Effects.—We used two different but complementary analyses to assess the existence of phylogenetic inertia on the range and body size. First, a Moran's autocorrelation analysis was used to evaluate whether differences in body size among species are related to their taxonomic distance. This method has been suggested as a good analytical strategy to assess the existence of a phylogenetic signal on quantitative traits when phylogenetic information is not available (see Gittleman and Kot 1990, and Smith et al. 2004 for

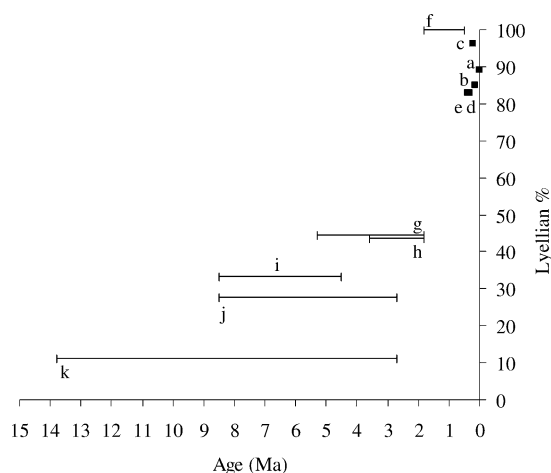


FIGURE 2. Lyellian percentages in late Neogene–Holocene bivalve assemblages along the temperate Pacific coast of South America. Sites have been grouped into temporal assemblages according to their respective ages, indicated by different letters (see Table S1 in supplemental material for sources for each temporal assemblage). Horizontal bars indicate the maximum and minimum ages assigned to each formation/site.

examples of its application). A typical phylogenetic signature is evident by the decay in the rescaled Moran's I toward higher taxonomic levels (Gittleman and Kot 1990). Analyses were conducted using the package APE (Paradis et al. 2005). In addition, a hierarchically nested ANOVA, using orders, families, and genera as nesting levels (Smith et al. 2004), was conducted for body size and range. A variance component analysis was used to assess the percentage of variance explained at each level. A small amount of explained variance is interpreted as a high level of similarity among taxa, and hence high phylogenetic inertia. Both approaches (Moran's I and nested ANOVA), as well as any other method that depends on a taxonomic classification, might be affected by paraphyletic trends, but they are the only approaches available.

Results

Quaternary faunas show a remarkable similarity to present-day biotas. In contrast, all the late Neogene faunas bear little resemblance to modern assemblages, suggesting the existence of an abrupt species extinction event at some point during the Pliocene (Fig. 2). Overall, 66% of the late Neogene (39 out of 59)

species are no longer present in the region (95% confidence intervals assuming binomial distribution: 54–78%), suggesting a large extinction event. In contrast, only 26% of Quaternary species (17 out of 79) can be considered regionally extinct (95% CI: 12–30%). When we controlled for the number of sites analyzed, extinction in the Quaternary still remained much lower (95% CI: 6–29%) than in the Pliocene. Although the current state of paleontological information is insufficient to assess the exact timing and synchrony of this mass extinction event, it may have occurred at some point during the late Pliocene to early Pleistocene. Coupled with this extinction event is a decline in species richness from the late Neogene to the present (Fig. 3). At a regional scale (Fig. 3A), the rarefaction curves show that species richness could have been higher (~50%) during the Pliocene than during the Quaternary, suggesting that speciation and/or immigration events during the Pleistocene did not totally compensate for the loss of species. These differences persisted at a local scale, although they were not so extreme (Fig. 3B). Indeed, mean rarefacted richness ($n = 100$) was only marginally different between time periods (ANOVA: $F_{1,13} = 4.66$, $p = 0.08$).

Extinction estimates varied by shell mineralogy (binomial test: $\chi^2 = 4.63$, d.f. = 1, $p = 0.03$), being much higher in calcitic (89%) than in aragonitic forms (56%). A low proportion of species in both Pliocene and Quaternary deposits had a calcite shell (31% and 23%, respectively); however, the differences were not significant (binomial test: $\chi^2 = 0.68$, d.f. = 1, $p = 0.41$). These proportions were slightly higher than observed in the present-day shallow-water fauna of the region (18%), but the differences were not significant (Pliocene vs. Recent, binomial test: $\chi^2 = 2.55$, d.f. = 1, $p = 0.11$; Quaternary vs. Recent, binomial test: $\chi^2 = 0.32$, d.f. = 1, $p = 0.57$). This suggests an elevated preservation potential in the Pliocene and Quaternary fossil record. Differences in extinction estimates according to shell mineralogy might be linked to the strong correlation between shell composition and life habit: all calcitic species (18 out of 18) were epifaunal, and almost all aragonitic forms (39 out of 41) were infaunal (see below). Conversely,

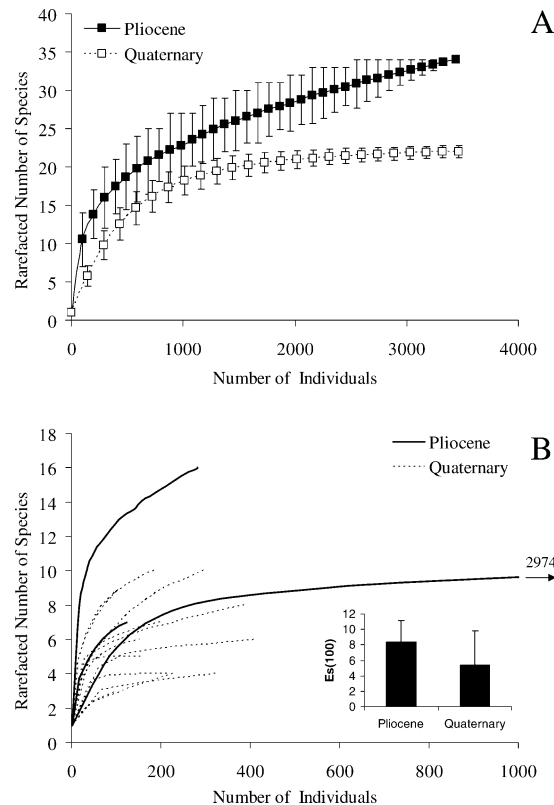


FIGURE 3. Rarefaction curves (EstimateS 7.5 [Colwell 2005]) for the number of bivalve species in Quaternary (late Pleistocene–Holocene) and late Pliocene assemblages based on number of individuals reported in several sites (see text). A, Regional-level analysis, pooling all the information across sites (bars indicate the 95% confidence intervals based on 1000 randomizations). B, Local-level analysis, showing rarefaction curves for each site. The inset indicates the mean rarefacted richness ($n = 100$ individuals) for Pliocene and Quaternary assemblages (bars indicate the 95% CI).

neither body size (t -test: $t = -1.945$, d.f. = 57, $p = 0.06$) nor range (t -test, $t = -0.492$, d.f. = 57, $p = 0.62$) was different between aragonitic and calcitic forms, indicating that shell mineralogy is not masking selectivity patterns.

Species survival was in general not selective across taxonomic levels; the observed numbers of surviving genera, families, orders, and subclasses were not different than expected by chance (Fig. 4). Nevertheless, extinction did not affect all taxa equally, particularly at higher taxonomic levels. The Subclass Pteriomorpha was heavily depleted (85% of species, 17 out of 20 went extinct), experiencing losses that were even higher than expected by chance alone ($p = 0.02$, 10,000 bootstrapped values).

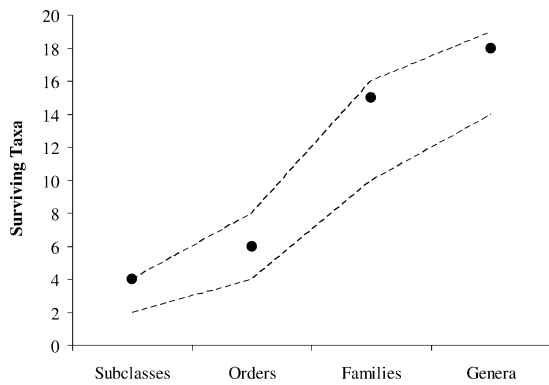


FIGURE 4. Number of observed taxa surviving at different taxonomic level (black circles). Dotted lines shows the expected number of extinctions at each level (2.5th and 97.5th percentiles), based on 10,000 bootstrapped values. See "Methods" for details.

At ordinal level, over 92% of ostreoids (12 out of 13) went extinct, a proportion significantly higher than expected by chance (bootstrapped values, $p = 0.02$). Conversely, in the veneroids the loss of species (52%, 14 out of 27) was lower than expected by chance (bootstrapped values, $p = 0.03$). At both family and generic levels extinction effects were not biased toward a particular taxon.

The ecological and life-history traits examined showed different effects upon extinction selectivity patterns (Fig. 5). Life-habit effect on the proportion of extinct species was marginally significant (binomial test: $\chi^2 = 3.63$, d.f. = 1, $p = 0.056$; Fig. 5A). Epifaunal forms were devastated by extinction (85%, 17 out of 20), whereas extinction was less intense, although still very high, in infaunal species (56%, 22 out

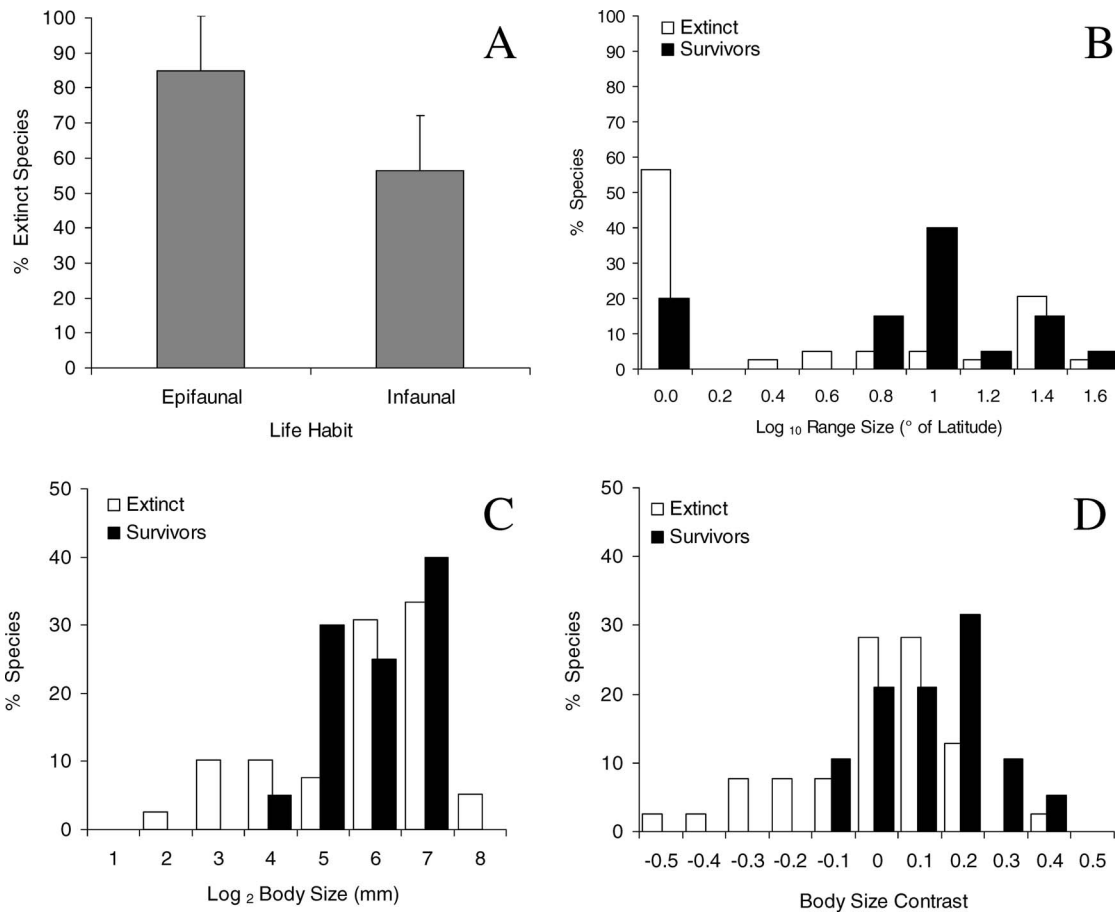


FIGURE 5. Selectivity patterns of the mass extinction according to several ecological and life-history traits. A, Life habit. B, Range. C, Original body size. D, Body size contrasts. See text for details. Error bars in A indicate the 95% confidence intervals based on binomial errors.

TABLE 2. Results of the autocorrelogram and nested ANOVA analyses used to evaluate the existence of phylogenetic inertia on species body size and range. Values in bold: $p > 0.05$; ns (nonsignificant): $p > 0.05$.

Variance source	Rescaled Moran's <i>I</i>	% Variance explained nested ANOVA
Body size		
Orders within subclasses	-0.14	56
Families within orders	0.33	22
Genera within families	0.48	0
Species within genera	0.35	22
Range		
Orders within subclasses	-0.02 ns	0
Families within orders	0.01 ns	0
Genera within families	0.05 ns	40
Species within genera	0.26 ns	60

of 39). Extinction was selective according to range; extinct species had smaller ranges than surviving forms (GLM: coefficient = 1.11, d.f. = 57, $p = 0.03$, Fig. 5B). Body size showed no relationship with extinction probability (GLM: coefficient = 0.09, d.f. = 57, $p = 0.63$, Fig. 5C).

Moran's and nested ANOVA analyses show a marked phylogenetic signature in body size, but not in range (Table 2). Body size shows a positive and significant autocorrelation at subgenus/genus and family levels, but at ordinal level, Moran's *I* values become significantly negative (Table 2). For range, Moran's *I* values at all taxonomic levels were low and not significant. The nested ANOVA analysis showed similar trends. For body size, most of variation is concentrated at ordinal level (56%), whereas for range most of the variability is residual (60%).

The previous analyses only allow us to identify possible phylogenetic inertia on a set of given traits, not its effect on selectivity patterns. Because no phylogenetic hypothesis is available for the data set, true independent contrasts are not possible. We therefore had to use a different approach to account for the marked phylogenetic inertia in body size: we used the standardized body size at ordinal level as a proxy of an independent contrast of body size. Ordinal level was chosen because it explains most of variability in body size. This was calculated as the $(S_s - S_o)/S_o$, where S_s is the species body size, and S_o is mean ordi-

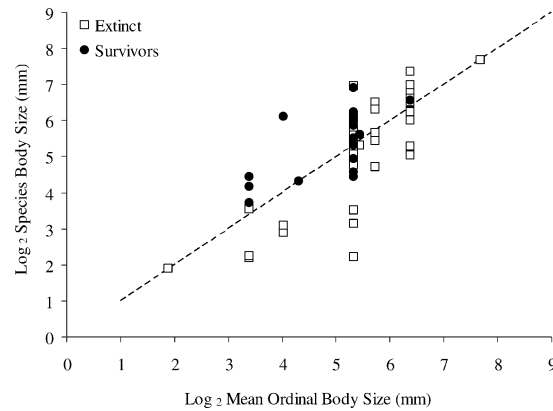


FIGURE 6. Phylogenetic effects on body size selectivity. Points above the dotted line (slope = 1) correspond to species with a body size above the average ordinal body size.

nal size (calculated using all the species in the order). The existence of strong phylogenetic inertia on body size has a marked effect on the detection of selectivity patterns (Fig. 6). Within orders, the body size of survivors was in general above the mean ordinal body size. Indeed, the intercept of the regression curves between species and mean ordinal body sizes was significantly higher in survivors (ANCOVA: $F = 8.40$, d.f. = 1, 55, $p = 0.005$). No differences in the slope were detected ($F = 2.84$, d.f. = 1, 55, $p = 0.097$). Similar results were obtained when the selectivity analysis was redone using the body size contrast (GLM: coefficient = 6.702, d.f. = 57, $p = 0.008$), showing that larger species are less extinction prone (Fig. 5D).

The multiple logistic regression shows that the effects of range and body size contrast on species survival probability were dependent on life habit (Table 3). For epifaunal species no trait or combination of traits showed a significant effect on species survival. In infaunal forms, conversely, survival was enhanced in large-sized (after phylogenetic correction) and widespread forms (Table 3). The interaction between body size and range is verified in that for widespread species (i.e., ranges above the median), body size had no significant effect on survival (GLM: coefficient = -0.976, d.f. = 16, $p = 0.242$). In contrast, for species with restricted ranges (i.e., below or equal to the median) body size had a direct

TABLE 3. Results of the logistic regression analysis (best reduced models) between species survival and life-history and ecological traits (life habit, range, body size contrast). Analyses were done for the complete data set, and separately for infaunal and epifaunal forms. Significant values ($p < 0.05$) are in bold.

Term	Estimate	SE	Z-value	<i>p</i> -value
Complete data set (AIC: 20.47; residual deviance: 12.48; d.f.: 16)				
Intercept	-1.736	0.522	-3.328	0.001
Life habit × Body size contrast	22.482	8.644	2.601	0.009
Life habit × Range	1.374	0.407	3.375	0.001
Life habit × Body size contrast × Range	-11.709	4.084	-2.867	0.004
Infaunal only (AIC: 53.42; residual deviance: 34.27; d.f.: 35)				
Intercept	-1.740	0.943	-1.845	0.065
Body size contrast	22.505	10.213	2.204	0.028
Range	3.168	1.320	2.399	0.016
Body size contrast × Range	-26.987	11.172	-2.416	0.016
Epifaunals only (AIC: 20.47; residual deviance: 12.48; d.f.: 16)				
Intercept	-3.015	1.853	-1.628	0.104
Body size contrast	4.117	14.468	0.285	0.776
Range	1.074	1.882	0.571	0.568
Body size contrast × Range	2.453	11.712	0.209	0.834

effect on species survival (GLM: coefficient = 0.944, d.f. = 19, $p = 0.024$).

Discussion

In agreement with similar claims that date back more than a century (Philippi 1887; Herm 1969; DeVries 1985, 2001) our results strongly support the existence of a mass extinction event that may have taken ~66% of species along the PSA during the late Neogene, probably during the Pliocene/Pleistocene transition. High levels of species extinction in Pliocene bivalves have been also recorded in other regions (Mediterranean [Raffi et al. 1985]; Caribbean [Allmon et al. 1993; Jackson et al. 1993]; Antarctic [Berkman and Prentice 1996]; New Zealand [Johnson and Curry 2001]). Inflation of species loss by a “pseudoextinction” artifact (i.e., morphologically identical species have different names across different epochs or stages) is unlikely, because the bulk of the species identification has been generated by researchers who have carefully examined several epochs and geographic regions (e.g., Herm 1969; Watters and Fleming 1972; Valdovinos 1996; Guzman et al. 2000). The magnitude of this extinction (66%), however, is much larger than reported for other late Neogene bivalves along the eastern Pacific coast (California [Stanley et al. 1980; Stanley 1986]; Ecuador [Landini et al. 2002]), and it may be one of the causes of the extreme im-

poverishment of the present-day bivalve fauna in the southeastern Pacific region (Herm 1969; Crame 2000; Valdovinos et al. 2003). However, the lack of precise dating for many Pliocene deposits precluded a statistical evaluation of the Lyellian curve and its comparison with other temperate biotas. Therefore, emerging temporal dynamics must be analyzed with caution. Although further sampling along the PSA is needed to improve the temporal resolution and spatial extent of this event, our results are unlikely to be radically altered, as there is little evidence of incompleteness due to preservation potential and sampling effort as suggested by our shell mineralogy and rarefaction analyses. Changes in richness were not so evident at a local (site) scale, suggesting that spatial turnover (beta diversity) might have been enhanced during the Pliocene. Unfortunately, the dearth of Pliocene sites presently available does not allow for a test of this potential explanation.

We showed that in spite of the high levels of species loss, the Pliocene bivalve mass extinction along the PSA was highly selective. Taken together, our results suggest that species survival emerges from the interaction between ecological and historical (phylogenetic) components (e.g., Marquet et al. 2004). This is apparent in that (1) the effect of body size was evident only when phylogenetic effects were removed, and (2) the effects of life history and

ecological traits upon survival probability are nonlinear, as shown by the multiple logistic regression analysis (Table 3). For instance, range and body size affect the chances of extinction but mostly in infaunal forms. In the massively devastated epifaunal forms (85% went extinct), even large-sized and widespread forms were doomed to extinction. We hypothesize that this is indicative of a negative association between selectivity and the intensity of the extinction event, such that non-selective mass extinctions (Jablonski and Raup 1995; Jablonski 2005) hold for very severe events. The precise nature of this relationship (i.e., whether it is monotonic or there are thresholds) requires further study. However, even in the less devastated infaunal forms, survival cannot be easily explained in terms of linear responses to range or body size: above a certain range and body size, survival was not selective according to these variables.

The masking of body size selectivity by phylogenetic effects is noticeable. In addition to supporting the recent findings of Smith and Roy (2006) for the late Neogene pectinids of the California region, it suggests that the conclusions regarding the lack of size-related effects during mass extinctions (e.g., Jablonski and Raup 1995; Lockwood 2005) might be sensitive to the inclusion of phylogenetic effects. In vertebrates, species with large body size tend to be more prone to extinction (e.g., Purvis et al. 2000b; Cardillo et al. 2005; Alroy et al. 2001; Dulvy and Reynolds 2002), which is at odds with the pattern reported here (see also Smith and Roy 2006, but see Stanley 1986, and Norris 1991). The ultimate mechanism explaining the enhanced survival of large-sized bivalves remain uncertain, but it may be related to particular advantages conferred by enhanced fecundities (Roy et al. 2001) and reduced energetic requirements per unit mass (Peters 1983).

Despite the existence of a marked pattern of selective extinction, the removal of higher taxonomic levels was in general not different from random (Fig. 4). Although this may appear at first sight as a contradiction, it can be explained by the way in which species' traits are nested within and across the taxonomic hierarchy, i.e., the relative importance of evolu-

tionary inertia on these traits. Range (measured as latitudinal range) appears largely independent of the evolutionary history, and hence its effect on chances of extinction was much clearer, supporting the notion that enhanced range increases survival during mass extinction events (Jablonski and Raup 1995; Banerjee and Boyajian 1996; McKinney 1997). At the same time, the lack of evolutionary inertia observed in range implies that no particular taxonomic group would have, on average, higher chances of going extinct or surviving, thus explaining the lack of taxonomic selectivity of the extinction; i.e., the loss of higher-level taxa was not different than expected by chance.

The significant effect of life habit upon the extinction selectivity pattern offer some clues about the potential mechanisms involved. The enhanced survival of infaunal forms, dominants in modern anaerobic environments, suggests that the development of anoxic conditions could be the cause of the mass extinction (e.g., see discussion in McRoberts and Newton 1995). Anoxic conditions (<1 ml O₂/l) can be found at very shallow depths along the modern coasts of Peru and north-central Chile (~60 m on average [Morales et al. 1999]). The extremely shallow oxygen minimum zone (OMZ) found in the region is considered the shallowest in the entire global ocean (Levin 2003; Helly and Levin 2004), and it might explain the very depauperate mollusk fauna in the region (Valdovinos et al. 2003; Rivadeneira unpublished data). Although the existence of a very shallow OMZ might be linked to the very high productivity of the Humboldt Upwelling Ecosystem, established during the mid to late Miocene (Ibaraki 1997; Tsuchi 1997, 2002), there is no direct paleoceanographic evidence linking the onset of the modern OMZ conditions with the late Neogene mass extinction. Moreover, the onset of anoxic conditions might not have been important in the southern PSA (south of 37°S), where OMZ is well below the coastal shelf (Levin 2003; Helly and Levin 2004), and where a different set of processes (e.g., advances of glacial armadas toward coastal areas) could have been more important (e.g., Valdovinos et al. 2003). Available information does not allow

us to rule out other competing hypotheses either, such as cooling and destruction of protected areas/bays (Herm 1969) or intrinsic differences in the evolutionary rates between epifaunal and infaunal forms (Jablonski 2005).

We show evidence of strong selectivity in bivalve species extinction during the late Neogene in the PSA. Our results also show that the fate of species emerges as the result of a complex (i.e., nonlinear) interplay between ecological (i.e., size, habit, and range) and historical (phylogenetic) factors. Much more could be learned about the species' responses to mass disturbances by embracing, rather than avoiding, the natural complexity of the system. Although many questions about the extinction event and the species' responses remain open (e.g., the timing and duration of the event, geographical extent and synchrony, ultimate causes, recovery dynamics, and the role played by other traits, such as larval type, shell morphometry) our results provide new insights and the first steps toward a more comprehensive understanding of the macroevolutionary dynamics of bivalves along the temperate Pacific coast of South America.

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