

ON THE COMPLETENESS AND FIDELITY OF THE QUATERNARY BIVALVE RECORD FROM THE TEMPERATE PACIFIC COAST OF SOUTH AMERICA

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ABSTRACT

Despite the considerable knowledge gained of the patterns and processes shaping the completeness and fidelity of fossil bivalve faunas, it is still hard to generalize these patterns to the species level and to different regions around the globe. Here I analyze the completeness and fidelity of Quaternary bivalve faunas of the temperate Pacific coast of South America, summarizing >120 years of paleontological studies in the region. The degree of completeness, measured as percentage of extant forms, is only moderate. Only 45% of the 93 extant species are preserved in the Quaternary fossil record. When completeness was measured as the discoverable fraction of species (according to a non-parametric richness estimation), however, values were >88%. Missing species were not biased by shell mineralogy nor concentrated in particular taxonomic groups. Completeness was highly selective for other species traits; small size, geographic restriction, and forms inhabiting deeper areas of the shelf had lower chances of being present in the fossil record, in agreement with previous studies. A generalized linear model revealed that the effect of these variables was multiplicative—i.e., the effects of geographic range and bathymetric distribution were significant only for small-sized forms. Therefore, the moderate degree of completeness may be the consequence of a limited fossilization potential (e.g., via low preservation potential, lack of deep-shelf outcrops, or preburial down-slope transport), rather than poor sampling quality. Results suggest that the sampling effort made in the region has reached a plateau and that further progress in the completeness of species' inventories may occur only at a very slow rate.

INTRODUCTION

Evaluations of the completeness and fidelity of the fossil record are crucial in order to validate the evolutionary patterns and processes inferred from it (Allmon, 1989; Kidwell and Flessa, 1995; Foote and Raup, 1996; Greenstein et al., 1998; Alroy et al., 2001; Jablonski et al., 2003; Kidwell, 2005; Valentine et al., 2006). Recent studies have demonstrated high completeness levels (i.e., 76%) for modern genera of marine bivalves at a global scale (Valentine et al., 2006), confirming the same species-level patterns reported for certain regions (Valentine, 1989; Crampton et al., 2006). The degree of fidelity of the bivalve fossil record, however, relies strongly upon different ecological and life-history traits, including shell size, mineralogy, habitat, and geographic and bathymetric distribution (Valentine, 1989; Cooper et al., 2006; Valentine et al., 2006). Whether the insights gained can be generalized to species level and around the globe remains uncertain.

Along the temperate Pacific Coast of South America (PSA), the vast Quaternary marine terraces have yielded excellently preserved bivalve faunas, favored by the extreme hyperaridity of the Atacama Desert (Philippi, 1887; Herm, 1969; Ortlieb et al., 1990, 1994, 1995, 1996, 1997a, 1997b; Paskoff et al., 1995; Guzmán et al., 2000; Rivadeneira and Marquet, 2007; Rivadeneira and Carmona, 2008). Yet to date there has been no rigorous evaluation of the degree of completeness and fidelity of the Quaternary bivalves of the PSA. Here I analyze the completeness and

fidelity of the this record, summarizing the paleontological research that has been devoted to this task over the last ~120 years. The particular goals of this study are to (1) estimate the completeness of the bivalve fauna and (2) evaluate the fidelity of the fossil record—that is, how completeness is biased by species ecological and life-history traits.

MATERIALS AND METHODS

Database

The information was collected from a comprehensive literature review. The occurrences of bivalve species were recorded in 43 Pleistocene and Holocene fossiliferous sites reported from southern Peru to central Chile (15°–30°S, Fig. 1) using published information (see Supplementary Data 1¹). Taphonomic analyses suggest that all of these sites correspond to coastal shallow-water (i.e., upper shelf) paleoenvironments (Herm, 1969; Rivadeneira and Carmona 2008). Only non-extralimital species (i.e., species still present in the study region) were considered for further analyses. In addition, a database of distribution and ecological attributes of all present-day bivalve species inhabiting the coastal shelf (<200 m) was compiled for the area between 15° and 30°S, using information available in the literature (see Supplementary Data 2¹). Millard's classification (Millard, 2001) was used to assign species to higher taxonomic levels. For a total of 93 species, the following data were recorded: (1) body size, (2) geographic range, (3) bathymetric midpoint, and (4) shell mineralogy. Body size was measured as the log₂ of the geometric mean between shell maximum length and maximum height, following Roy et al. (2000). Geographic range was measured as the log₁₀ of the difference between the southernmost and northernmost latitude (including limits outside the study region). Bathymetric midpoint was measured as the log₁₀ of the average between the maximum and minimum recorded depth distribution, including those for which the maximum depth was deeper than 200 m. Species were also classified according to their bathymetric midpoints in two categories: upper shelf (≤100 m depth) and lower shelf (>100 m depth). Finally, species were categorized according to shell mineralogy (aragonite or calcite), based on general literature (Moore, 1969, 1971; Taylor et al., 1969, 1973; Coan et al., 2000) and assuming the mineralogy from congeneric forms. This assumption seems reasonable, since shell mineralogy tends to be highly conserved among species within a genus and among genera within a family (Taylor et al., 1969, 1973). The entire database and sources are given in the Supplementary Data.¹

Analyses: Completeness of Fossil Record

The completeness of the bivalve species inventory was assessed using two complementary methods: extant forms and discoverable species. First, the completeness was evaluated as the percentage of the living

¹ www.paleo.ku.edu/palaios

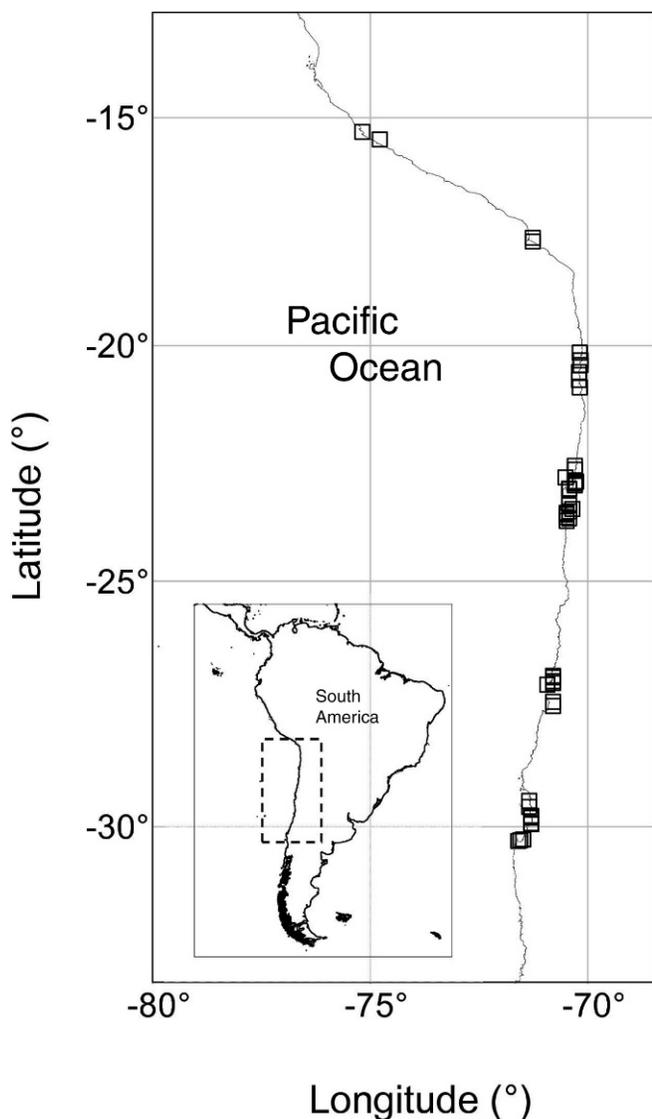


FIGURE 1—Map showing study region and 43 Quaternary fossiliferous localities analyzed; localities shown as open squares; see sources in Supplementary Data 1¹.

species having a fossil record in the region, following the method of extant forms of Valentine (1989). A binomial proportion confidence interval (CI 95%) was also estimated. This method assumes that the true species composition has remained unchanged from Pleistocene to the recent, an assumption that seems reasonable, considering the low proportion of species extinctions during the Pleistocene in the region (Rivadeneira and Marquet, 2007). A rarefaction analysis (Colwell and Coddington, 1994; Gotelli and Colwell, 2001) was carried out in order to evaluate the effect of sampling effort on the estimations, using sites as surrogates of sampling effort (i.e., sample-based rarefaction curves; Colwell et al., 2004).

Because many species may not have left a fossil record or their fossilization potential is very low, and hence they will never be discovered, they need to be removed from the completeness estimation. In the second method used, the discoverable completeness is calculated as the percentage of recorded fossil species out of the total estimated (extrapolated) fossil richness. Previous studies have taken advantage of nonparametric estimators, commonly used in ecological analyses (Colwell and Coddington, 1994; Gray, 2000; Curtis et al., 2002), in order to extrapolate the fossil richness (e.g., Wing and DiMichele, 1995; Wang and Dodson, 2006; Rivadeneira and Carmona, 2008). Here, the extrapolated richness was estimated using the Chao 2 (bias-corrected

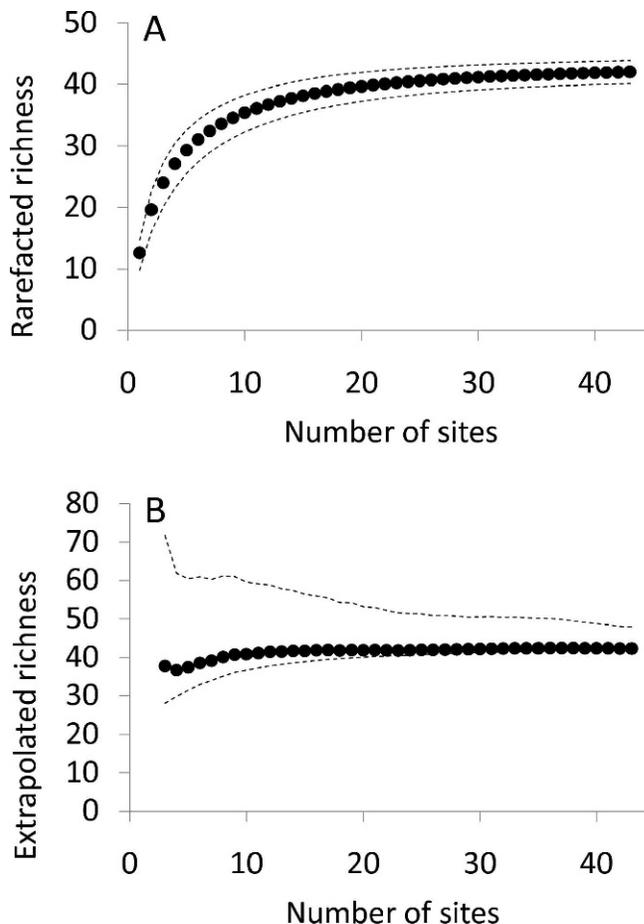


FIGURE 2—Bivalve species richness in Quaternary deposits of the Pacific coast of South America. Rarefacted richness (A) and extrapolated richness (B) (nonparametric Chao 2 index) as a function of the sampling effort (number of sites sampled). Dotted lines show 95% confidence intervals.

version) nonparametric estimator (Chao and Lee, 1992):

$$\hat{S}_{Chao\ 2} = S_{obs} + \left(\frac{m-1}{m}\right) \left(\frac{Q_1(Q_1-1)}{2(Q_2+1)}\right),$$

where S_{obs} = observed richness, m = samples (sites), Q_1 = the number of species present in only one site, and Q_2 the number of species present in only two sites. The variance is estimated as:

$$\begin{aligned} var(\hat{S}_{Chao\ 2}) = & \hat{S}_{Chao\ 2} + \left(\frac{m-1}{m}\right)^2 \frac{Q_1(2Q_1-1)^2}{4(Q_2+1)^2} \\ & + \left(\frac{m-1}{m}\right)^2 \frac{Q_1^2 Q_2(2Q_1-1)^2}{4(Q_2+1)^4}. \end{aligned}$$

Then the lower 95% bound = $S_{obs} + \frac{T}{K}$ and the upper 95% bound = $S_{obs} + TK$,

$$\text{where } T = \hat{S}_{Chao\ 2} - S_{obs}, \text{ and } K = e^{\left(1.96 \left(\log\left(1 + \frac{var(\hat{S}_{Chao\ 2})}{T^2}\right)\right)\right)^{1/2}}.$$

All the analyses were done using the software Estimates, freely available online (Version 7.5, R.K. Colwell, <http://purl.oclc.org/estimates>).

Analyses: Fidelity of Fossil Record

The degree of fidelity of the bivalve fossil fauna was evaluated using different ecological and life-history traits. To test for taxonomic

TABLE 1—Representation of different bivalve clades in the Quaternary fossil record. The percentage of missing species within each clade (species without fossil record) did not differ from that expected just by random; ns = nonsignificant.

Clade	Number of species	Missing species	% missing species
Anomalodesmatans	5	5	100 ^{ns}
Arcoids	3	0	0 ^{ns}
Heteroconchs	63	32	51 ^{ns}
Lucinoids	1	1	100 ^{ns}
Mytiloids	10	4	40 ^{ns}
Protobranchs	7	6	86 ^{ns}
Pteriomorphs	4	3	75 ^{ns}

patterns of fidelity, I compared the observed number of missing species (i.e., species without a fossil record) within each clade (following the classification used by Valentine et al., 2006) with the predictions of a null model, using the same statistical protocol adopted by previous studies (Smith and Roy, 2006; Valentine et al., 2006; Rivadeneira and Marquet, 2007). The model was built by randomly drawing the observed number of missing species from the original pool and counting the clades represented by those species. The process was repeated 10,000 times and the distributions compared with observed estimates for each taxonomic level. Taxonomic selectivity was statistically evaluated using the 97.5 or 2.5 percentiles of the

bootstrapped distributions. The degree of fidelity was also evaluated by comparing the body size, geographic range, bathymetric midpoint, and shell mineralogy in living species with and without a fossil record using a two-sample t-test and a chi-square test, on the already log-transformed variables (see above and Supplementary Data 2¹) in order to ensure assumptions of homoscedasticity and normality.

Finally, the four variables were combined in a generalized linear model (GLM), using a binary response (1 = with fossil record; 0 = without fossil record) and assuming multiplicative effects. This method is analogous to a linear multiple regression, but it allows the use of a binary response variable (Crawley, 2007). The final model was the one maximizing the Akaike Information Criterion (AIC) and included only significant terms. All the analyses were performed using the software R (Team, 2007).

RESULTS

According to the extant forms method, only 45% (95% CI: 35%–55%) of present-day species (42 out of 93) had a fossil counterpart in the Pleistocene record. Even at the generic level, the completeness is moderated (52% [95% CI: 40%–65%], 37 out of 71 genera). The rarefaction curve shows a marked saturation pattern (Fig. 2A), and very few species were added to the pool after sampling >30 sites. The extrapolation curve showed the same trend; at increasing levels of

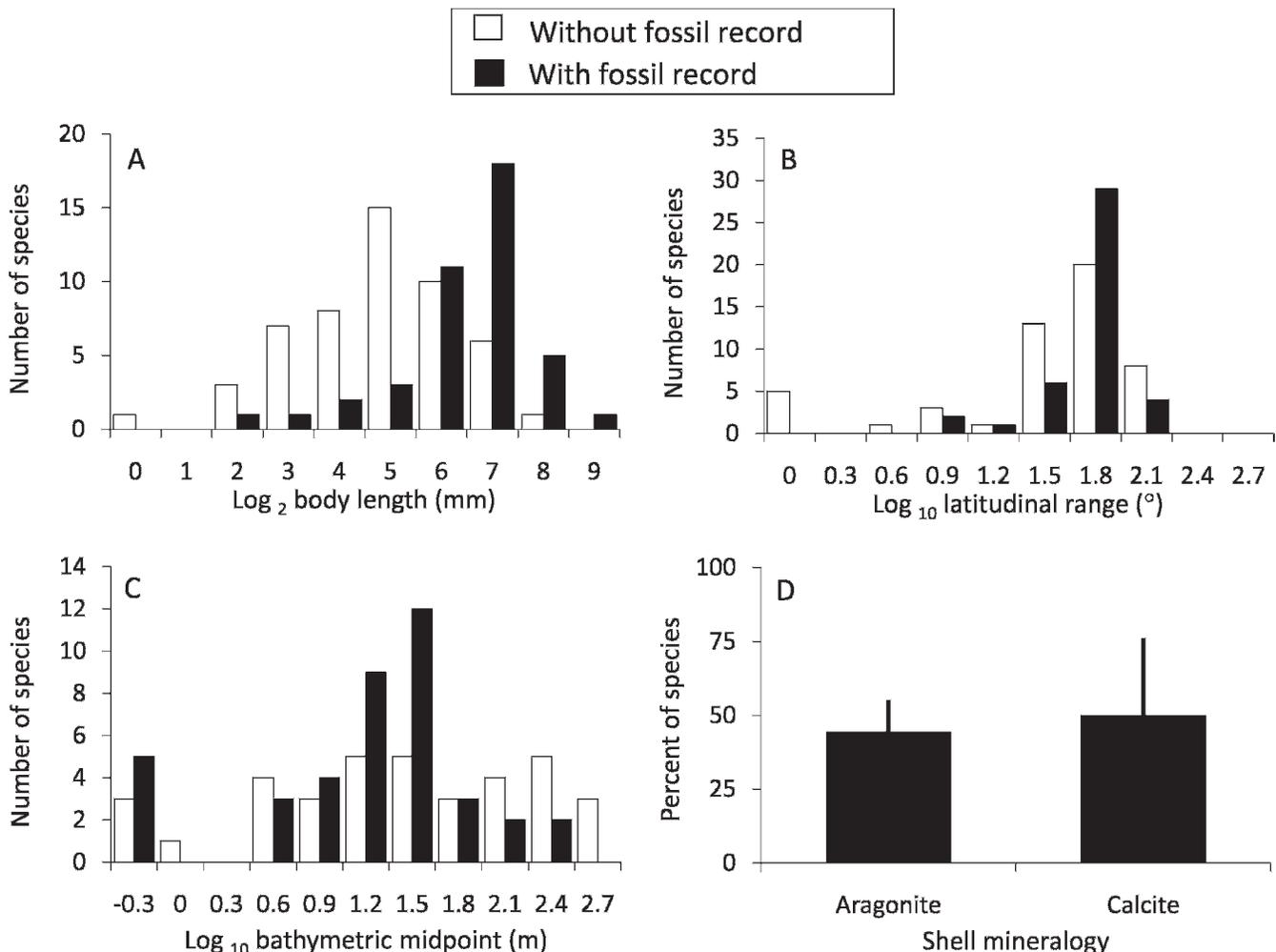


FIGURE 3—Bias in the bivalve fossil record according to different ecological traits: body length (A), latitudinal range (B), midpoint of bathymetric distribution (C), and shell mineralogy (D), with vertical bars indicating the 95% binomial proportion confidence interval.

TABLE 2—Summary of the multiple logistic regression (best-reduced model) between the binary response variable (1 = with fossil record, 0 = without fossil record) and several ecological traits: \log_2 body size (w), \log_{10} latitudinal range (r), and \log_{10} bathymetric midpoint (z). The final model included only significant additive and multiplicative terms; d.f. = degrees of freedom, AIC = Akaike Information Criterion.

Term	Estimate	Std. error	z-value	P-value
Intercept	-2.118	0.988	-2.144	0.032
r	1.532	0.733	2.089	0.037
r * z	-2.635	0.685	-3.847	0.000
r * w * z	0.496	0.141	3.530	0.000

Null deviance: 128.058 (92 d.f.)

Residual deviance: 96.769 (89 d.f.)

AIC = 104.77

sampling, the Chao 2 estimated richness increased in similarity to the observed richness (Fig. 2B). When the sampling effort is maximized (i.e., 43 sites), the upper 95% CI of the Chao 2 index predicts that up to five species would remain unknown from the fossil record. Therefore, the discoverable completeness was >88%.

The number and percentage of missing species was variable across different clades (Table 1). Missing species are distributed across all clades except in arcoid bivalves. Some species-poor clades (i.e., anomalodesmatans and lucinoids) are completely unrepresented in the fossil record. In the most speciose clades (heteroconchs and mytiloids), the percentage of missing species ranged between 40% and 51%. Despite the number and percentage of missing species varying across clades, these numbers were not different than those expected based on the null model.

Other species traits showed different responses. On average, species without a fossil record were smaller than species with a fossil counterpart: t-test $_{0.05} = -4.92$, degrees of freedom (d.f.) = 91, $p < 0.001$ (Fig. 3A). In addition, species without a fossil record had shorter latitudinal ranges: t-test $_{0.05} = -2.25$, d.f. = 91, $p = 0.027$ (Fig. 3B). For instance, no single species with a latitudinal range of less than $\sim 6^\circ\text{S}$ had a fossil record. The chances of being present in the fossil record were also associated with the bathymetric midpoint of distribution; species without a fossil record tended to be those with deeper midpoints of bathymetric distribution: t-test = 2.12, d.f. = 91, $p = 0.036$ (Fig. 3C), and only 19% of the lower-shelf species had a fossil record, compared with the 51% of the upper-shelf species, a difference that was statistically significant ($\chi^2 = 4.23$, d.f. = 1, $p = 0.04$). Finally, aragonitic and calcitic forms had similar degrees of completeness—44% and 50%, respectively (Fig. 3D), not differing from the random expectation ($\chi^2 = 0.01$, d.f. = 1, $p = 0.92$).

The GLM revealed that the different variables operate both additively and multiplicatively (Table 2). Shell mineralogy did not figure as a significant variable in the final model. The only additive variable included in the best reduced model was the latitudinal range (GLM, coefficient = 1.532, $p = 0.037$; Table 2). The effect of body size and bathymetric midpoint was evident only in the multiplicative terms. The negative coefficient value of the interaction term between latitudinal range and bathymetric midpoint (GLM, coefficient = -2.635, $p < 0.001$; Table 2) indicated that even species with larger latitudinal ranges can have a low probability of being present in the fossil record if they also have deeper midpoints of bathymetric distribution (Fig. 4). The interaction between latitudinal range and bathymetric midpoint was also modulated by body size (GLM, coefficient = 0.496, $p < 0.001$; Table 2). In addition, in small-sized forms (below the median, <26 mm), species with larger latitudinal ranges and shallower bathymetric distribution had a higher chance of being present in the fossil record (Fig. 4A). In contrast, in large-sized species (≥ 30 mm) the chances of fossilization were relatively independent of the latitudinal range and bathymetric midpoint (Fig. 4B).

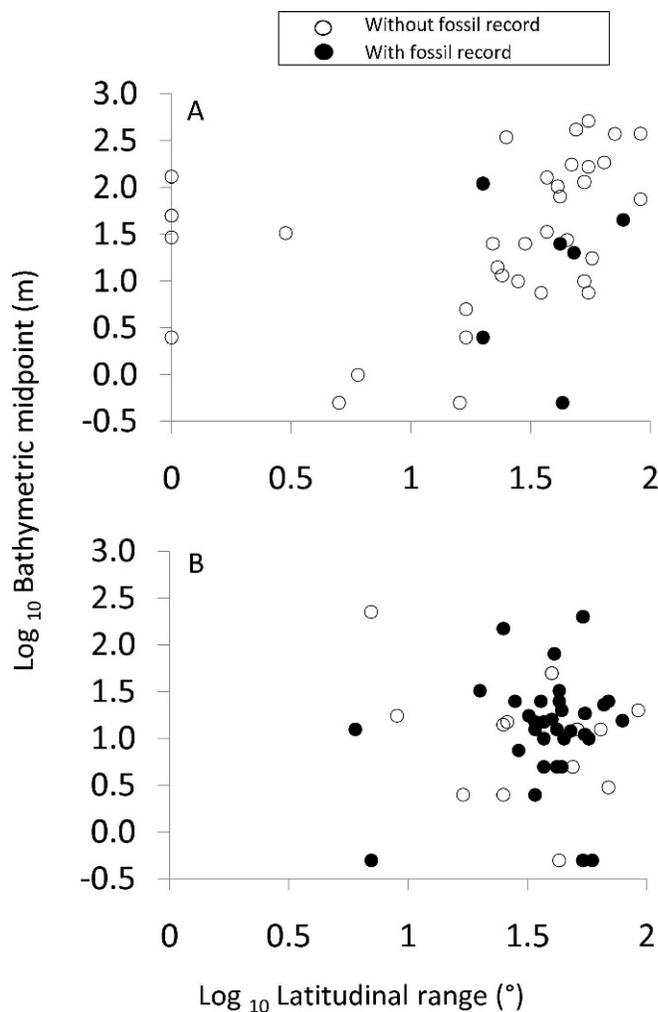


FIGURE 4—Interaction between latitudinal range and midpoint of bathymetric distribution determining bias in the bivalve fossil record in (A) small-sized species (below median, <26 mm) and (B) large-sized species (above median, ≥ 26 mm).

DISCUSSION

The two methods used to evaluate the degree of species completeness of the Pleistocene bivalve faunas of the PSA provide a novel view of the patterns and processes shaping the quality of the fossil inventories in the region. On one hand, using the method of extant forms, the species-level completeness is only moderate (45%) in comparison with the 30%–88% reported for other mollusk faunas of the Plio–Pleistocene around the globe (Valentine, 1989; Crampton et al., 2006). On the other hand, a different scenario is revealed when the discoverable species method (Fig. 2) is applied. In this study, both rarefaction and extrapolation curves suggest that current sampling efforts have documented most of the discoverable species. The upper 95% CI of the Chao 2 index suggests that up to five new species may be added to the inventory and thus completeness may be >88%. Taken together, this evidence suggests that the moderate degree of completeness (according to the extant forms methods) is more associated with a limited preservation potential rather than with a poor quality sampling (further paleontological surveys would require a very large sampling effort in order to improve the quality of the species inventories).

Not all the species had the same probabilities of being recorded in the fossil record. Indeed, missing species were not a random subset of the total pool of species, but were highly correlated to several species' traits. Typically, missing species tended to be small sized, geographically restricted, and inhabitants of deeper shelf zones, as shown by previous

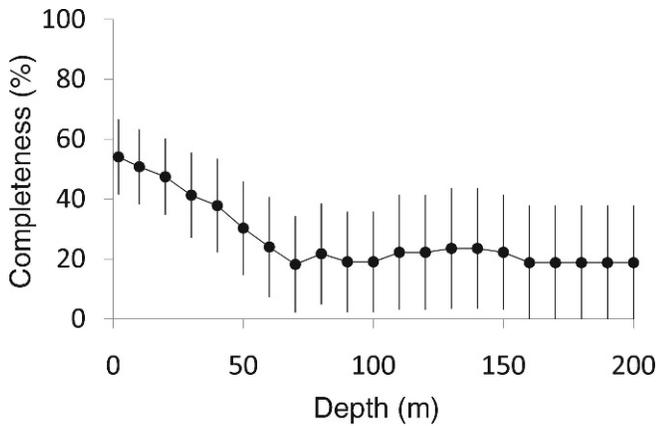


FIGURE 5—Bathymetric variation in the average degree of completeness across the coastal shelf (vertical bars indicate the 95% binomial proportion confidence interval).

studies (Cooper et al., 2006; Valentine et al., 2006). These traits were also positively correlated, as the latitudinal range of a species is positively correlated with its body size (Pearson product-moment correlation coefficient, $r = 0.42$, $n = 93$, $p < 0.001$). This interaction between traits was also revealed by the GLM analysis. Only in small-sized forms did the latitudinal range and bathymetric distribution increase the chances of being present in the fossil record; large geographic range and short bathymetric midpoint of distribution are needed to maximize chances of fossil preservation (Fig. 4A). By contrast, in large-sized bivalves, this potential was not enhanced by the other variables.

Missing species, however, were not clustered significantly in particular clades (e.g., Valentine et al., 2006), which could be explained by the low taxonomic inertia of the studied variables (i.e., latitudinal range and bathymetric midpoint), with the bulk of variation explained at the generic and specific levels (Rivadeneira and Marquet 2007). Taken at face value, this may represent good news for studies comparing the taxonomic composition in modern versus Pleistocene assemblages in the region (Rivadeneira and Carmona, 2008) because the subset of species recorded by the fossil record should not be taxonomically biased. In spite of the lack of significance of the taxonomic selectivity, however, entire clades are poorly represented in the fossil record (protobranchs, pteriomorphs) or are not represented at all (anomalodesmatans, lucinoids; Table 1). Because these missing taxa tend to inhabit deeper zones of the shelf and slope, the degree of completeness (measured as extant forms) shows a bathymetric gradient (Fig. 5). Completeness is moderate (40%–60%) only at depths <20 m; below 70 m it is only ~20% on average.

The ultimate cause for the moderate degree of completeness of bivalve faunas and the observed biases in missing species may be strongly associated with the existence of a very narrow coastal shelf (i.e., a few kilometers) along most of the Pacific coast of South America (Figueroa and Moffat, 2000; Thiel et al., 2007). The existence of a narrow shelf also implies a very steep slope, which increases the chances of preburial down-slope transport, as suggested by several analyses (Donovan, 2002; Dominici and Zuschin, 2005; Kidwell, 2008). In addition, Pleistocene deposits along PSA are typically from shallow-water environments (Herm, 1969; Le Roux et al., 2005), and currently there are no deep-shelf fossiliferous outcrops described within the region. Therefore, chances of recovering fossil remains of many small-sized forms that typically inhabit deeper zones of the shelf and are geographically restricted might be very low. This hypothesis is supported by the findings of a recent sampling program undertaken at 24 new Pleistocene sites in northern Chile, which added only one new species, *Nuculana (Saccella) cuneata* (Sowerby), to the inventory (Rivadeneira and Marquet, 2007; Rivadeneira and Carmona, 2008). This species is small (10 mm), inhabits deeper areas of the shelf (mid-

bathymetric distribution = 110 m), and is endemic to Peru and north-central Chile. A further comparison of the completeness of bivalve faunas in regions with shelves of different sizes may also be used to formally evaluate this hypothesis.

In conclusion, the Pleistocene bivalve fauna of the temperate PSA shows a moderate degree of completeness. The most likely cause for the moderate completeness seems to be a low fossilization potential (e.g., via low preservation potential, lack of deep-shelf outcrops, or preburial down-slope transport), rather than insufficient sampling effort. The species-sampling curve has entered a plateau zone (i.e., it is mostly saturated), predicting that paleontological progress will occur at a very slow pace in the future (Fig. 2). Any significant increase in species inventories will demand a vast amount of paleontological effort.

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