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Aragonite bias, and lack of bias, in the fossil record: lithological, environmental, and ecological controls

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Abstract.—Macroevolutionary and macroecological studies must account for biases in the fossil record, especially when questions concern the relative abundance and diversity of taxa that differ in preservation and sampling potential. Using Cenozoic marine mollusks from a temperate setting (New Zealand), we find that much of the long-term temporal variation in gastropod versus bivalve occurrences is correlated with the stage-level sampling probabilities of aragonitic versus calcitic taxa. Average sampling probabilities are higher for calcitic species, but this contrast is time-varying in a predictable way, being concentrated in stages with widespread carbonate deposition.

To understand these results fully, we link them with analyses at the level of individual point occurrences. Doing so reveals that aragonite bias is effectively absent in terrigenous clastic sediments. In limestones, by contrast, calcitic species have at least twice the odds of sampling as aragonitic species. This result is most pronounced during times of widespread carbonate deposition, where the difference in the per-collection odds of sampling species is a factor of eight. During carbonate-rich intervals, calcitic taxa also have higher odds of sampling in clastics. At first glance this result may suggest simple preservational bias against aragonite. However, comparing relative odds of aragonitic versus calcitic sampling with absolute sampling rates shows that the positive calcite bias during carbonate-rich times reflects higher than average occurrence rates for calcitic taxa (rather than lower rates for aragonitic taxa) and that the negative aragonite bias in limestones reflects lower than average occurrence rates for aragonitic taxa (rather than higher rates for calcitic taxa).

Our results therefore indicate a time-varying interplay of two main factors: (1) taphonomic loss of aragonitic species in carbonate sediments, with no substantial bias in terrigenous clastics; and (2) an ecological preference of calcitic taxa for environments characteristic of periods with pervasive carbonate deposition, irrespective of lithology per se.

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Introduction

Biogenic carbonate is precipitated in various polymorphs as discrete layers or functional components in molluscan shells. These polymorphs dissolve at different rates in seawater: in order of increasing solubility, low- and moderate-Mg calcite, aragonite, high-Mg calcite (Canfield and Raiswell 1991), although relative solubilities are affected by microstructural surface area and shell organic content (Walter 1985; Glover and Kidwell 1993). Mineralogical composition is typically conserved at the level of biological families or higher (Carter 1990a). For this reason, studies relying on the relative numbers of individuals or species from different higher taxa are potentially susceptible to taphonomic distortion. Such studies are pervasive in paleobiology and include ecological interpretation of relative abundance distributions within communities (Powell and Kowalewski 2002; Peters 2004a,b; Wagner et al. 2006; Cherns and Wright 2009), analysis of trophic structure (Dunne et al. 2008), documentation of major changes in global ecosystems (Vermeij 1977; Signor and Brett 1984), modeling of macroevolutionary dynamics (Sepkoski 1981, 1984), and inference of evolutionary rates from taxonomic structure (Foote 2012).

All else being equal, dominantly aragonitic or high-Mg calcitic shells are expected to suffer

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greater post-mortem taphonomic and diagenetic destruction on the seafloor and during early burial than shells composed dominantly of low-Mg calcite. Widespread evidence supports this expectation for the case of aragonite and, in particular, for carbonate-rich environments (Nelson 1978; Palmer and Wilson 2004; James et al. 2005; Kidwell et al. 2005; Cherns et al. 2011). This evidence has driven a general assumption, also supported by many empirical studies, that the fossil record is pervasively and perhaps profoundly biased against organisms with mineralogically less stable shells (Harper 1998; Brachert and Dullo 2000; Cherns and Wright 2000, 2009; Smith and Nelson 2003; Wright et al. 2003; James et al. 2005; Caron and Nelson 2009; Cherns et al. 2011; Hendy 2011). Estimates of the magnitude of the bias, in terms of the loss of species with more reactive shells, are on the order of less than 10% to ~50% in studies of local and regional diversity (Koch and Sohl 1983; Cherns and Wright 2000; Bush and Bambach 2004).

In contrast, a number of recent studies have argued that the bias is relatively small or negligible at larger spatial and temporal scales (Kidwell 2005; Crampton et al. 2006a; Kowalewski et al. 2006; Valentine et al. 2006; Rivadeneira 2010). For example, Kidwell (2005) showed that global data on bivalve genera do not support the hypothesis that those with less stable shell mineralogy have shorter durations or significantly more stratigraphic singletons. Her interpretation, in part, was that data at this scale contain substantial redundancy and that recrystallization of aragonite to calcite can actually increase long-term preservation potential. Other work has shown, also with global data at the genus level, that temporal patterns of occurrence frequency are not clearly predicted as artifacts of mineralogy or other aspects of shell structure (Behrensmeyer et al. 2005; Kosnik et al. 2011).

Thus the question of scale is critical (Kosnik et al. 2011). At the scale of alpha diversity in an individual bed, preservation potential will be determined by the interplay of shell durability, time spent in the taphonomically active zone, and the local taphonomic and diagenetic environments (Koch and Sohl 1983; Smith and Nelson 2003; Cherns et al. 2008, 2011). In contrast, when considering presence/absence data at regional to global scales over long time spans, sampling potential of a given species will also reflect the abundance and geographic and stratigraphic ranges of the species, time scale of analysis, redundancy in the fossil record, and factors relating to the nature of the environmental and rock records. Importantly, as noted above, dissolution of aragonite need not always result in complete destruction of fossils, and various processes promote preservation of originally aragonitic fossils in altered form (McAlester 1962; Bush and Bambach 2004; Kidwell 2005; Kidwell et al. 2005; Kowalewski et al. 2006; Cherns et al. 2008; Tomašových and Schlögl 2008; Caron and Nelson 2009).

Here, we compare temporal variation in sampling probability of dominantly aragonitic versus dominantly calcitic marine mollusk species at the regional spatial scale (~10^6 km^2) and the temporal scale of stratigraphic stages (~2.4 million years on average). We then interpret these results in light of local, bed-level data, where we explicitly consider the lithology of each collection as well as the attributes of individual species. We explain the observations in terms of both preservational and ecological factors and conclude that spatiotemporally localized sampling in this study system is broadly consistent with the regional picture. Importantly, at both the regional and local scales, preservational bias is effectively absent in terrigenous clastic sediments and is otherwise time-varying and predictable on the basis of gross features of the rock record, and large segments of the record show no appreciable bias.

Materials and Methods

Nature and Sources of Data.—Our data set represents the exemplary fossil record of New Zealand Cenozoic midlatitude mollusks that occupied marine shelf environments (Crampton et al. 2006a). This record derives from a single first-order, transgressive-regressive, mixed siliciclastic-temperate carbonate stratigraphic sequence (King et al. 1999; Crampton et al. 2006b). Data were downloaded from the New Zealand Fossil Record File Electronic

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Database (FRED: http://www.fred.org.nz/). We restricted the analysis to bivalves, gastropods, and scaphopods that are inferred to have inhabited level-bottom environments at shelf depths (0–200 m water depth; see Crampton et al. 2006a) and excluded pelagic, littoral, and estuarine taxa. The following data were eliminated prior to analysis: fossil lists prepared by identifiers of unknown or doubtful expertise, all uncertain identifications (including "cf." and "aff." modifiers), collections that could not be dated to a single time bin, and collections lacking information on enclosing rock type. Following these adjustments, our database contains 2951 collections that were used to characterize the stratigraphic record (Table A1), where each collection derives from a single locality (nearly always a single bed or narrow stratigraphic interval) that was sampled by one person or team on a single occasion. The time bins used in this study are stages of the New Zealand geological timescale, updated from Hollis et al. (2010). To analyze species sampling, we further restricted the data to include only occurrences of taxa that have information on shell composition (>99%) and are resolved to the species level, leaving a database of 16,007 species-level occurrences of 1466 species from 2494 collections.

Data on the abundance and distribution of living marine mollusks occupying the shelf around New Zealand were extracted from the database of the Museum of New Zealand Te Papa Tongarewa. We used information relating to 16,330 geographically localized samples of 335 species that are shared with our fossil data set and have known shell composition.

Biological Attributes of Species.—Following Crampton et al. (2006a), mollusks were classified as calcitic if their shell includes a substantial calcitic component that could, in the absence of aragonite, be identified to species level. Aragonitic taxa are those that would not be identifiable following aragonite loss (and assuming no replacement by other minerals or formation of molds). We note that our compositional categories differ somewhat from those adopted in other studies of taphonomic bias (e.g., Kidwell 2005), but are designed to reflect the real-world process of documenting the fossil record, with its emphasis on species identification. Nearly all identifications of aragonitic taxa are based on preserved shell material rather than molds (Crampton et al. 2006a: p. 518).

Shell size measurements used here are based on updated data from Crampton et al. (2010); each species was assigned a single size value based on the maximum linear dimension of an average adult shell. For the purposes of the present study, we binned size measurements into three categories: small (≤10 mm), medium (>10 mm and ≤ 32.5 mm), and large (>32.5 mm). These arbitrary divisions were designed to divide the spectrum of size so that roughly equal numbers of species fall into each category. For analyses involving size, we omitted two species that are relevant to those analyses but lack size information.

Stratigraphic and Lithologic Data.—The stratigraphic record was characterized in two ways, regional and site-specific (Table A1). First, we compiled collection lithological data from the FRED "carbonate" field, which is coded into three categories based mainly on subjective field determinations: "limestone," "calcareous," and "non-calcareous," the latter two designations being for siliciclastic rocks. (Strictly speaking, limestone refers to rocks consisting of >50% calcium carbonate.) Here, we simplified this classification to just two categories: "limestone" and "siliciclastic" (the latter being the calcareous plus non-calcareous categories in FRED), and used these data to calculate the proportion of limestone collections in each stage. Thus, lithological data associated with particular collections were used as a proxy for the immediate substrate habitat occupied by a particular species at a given site as well as to characterize the regional extent of carbonate deposition.

Second, for each stage, we tabulated the number of 1:50,000 topographical map sheets that are represented by fossil collections with known lithology, and calculated the proportion of these map sheets that contain at least one limestone collection. This measure provides a simple proxy for the regional geographic extent of limestone in each stage.

For each measure of carbonate extent, we calculated uncertainties as conventional binomial standard errors: $SE = (p[1-p]/n)^{0.5}$,

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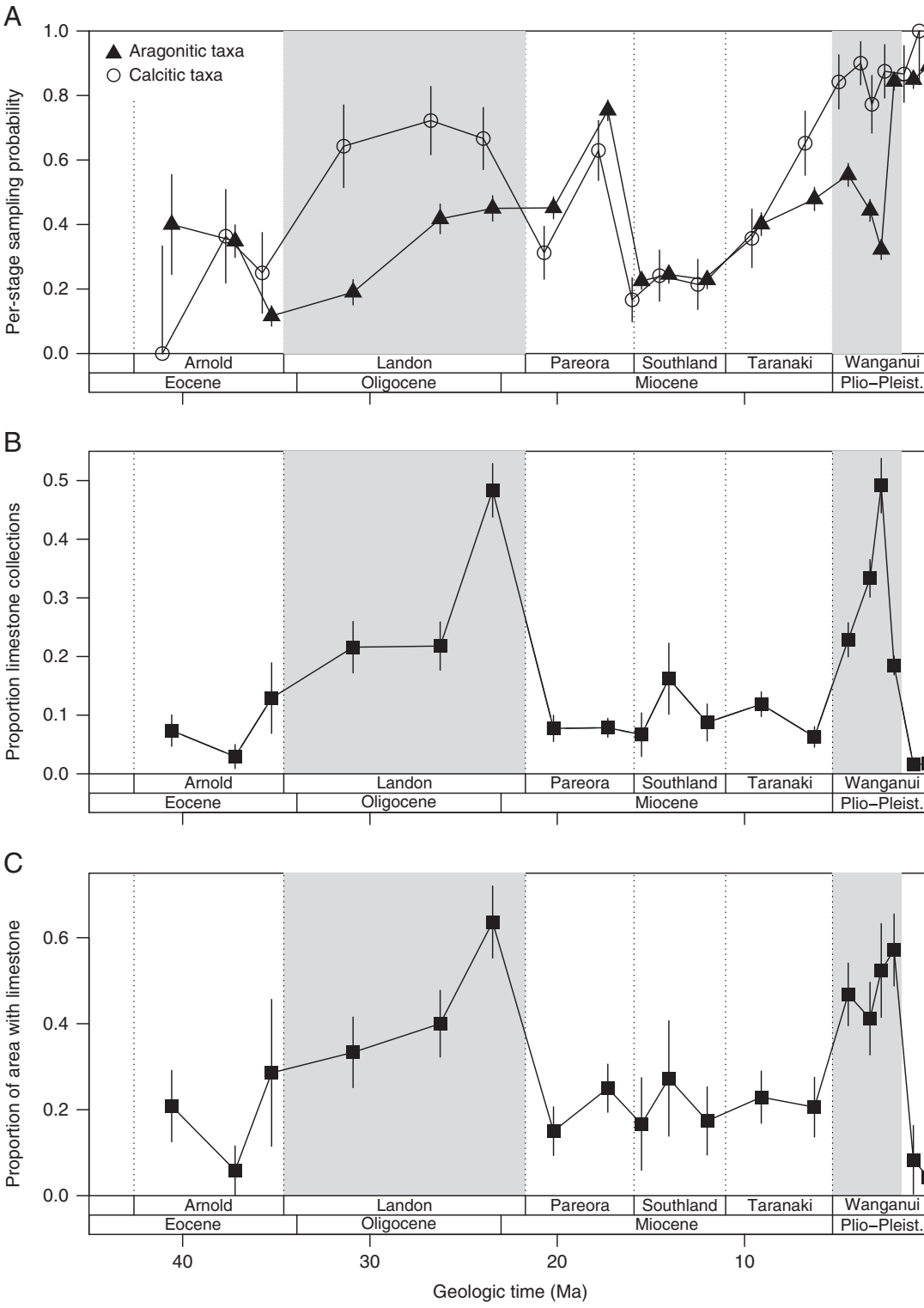

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where p is the observed proportion and n is the sample size. The one exception is that, for a very small number of cases in which $p = 0$ or $p = 1$, we used the Wilson confidence interval (Agresti and Coull 1998: eq. 2) for $z = 1$ and treated one-half this interval as an approximation of the standard error (Table A1). In Figure 1A, where this is relevant, we plot the full confidence interval.

We are interested in the regional and local (bed-scale) effects of carbonate substrate on the distribution and sampling of species, but also on the broader environmental impacts of widespread carbonate deposition. To examine this, we identified two intervals of time during which deposition and sampling of shelfal limestones were relatively extensive: latest Eocene to earliest Miocene (34.6 Ma–21.7 Ma) and Pliocene to early Pleistocene (5.3 Ma–1.63 Ma) (Fig. 1). These designations were based on proportions of limestone collections and of map sheets containing limestones (Table A1), but were also informed by our knowledge of New Zealand's geological history. These carbonate-rich intervals were used to test the idea that times conducive to carbonate formation might have influenced the species composition of collections, whether original or preserved, irrespective of the substrate type occupied by a particular species.

Limestone formations are present outside these carbonate-rich intervals, but many of these other occurrences are of limited geographic and volumetric extent and/or were deposited at water depths of >200 m (Kamp and Nelson 1988), and they have had a relatively small influence on the preserved shelfal macrofossil record (Fig. 1). We note that the Runangan Stage (36.4 Ma–34.6 Ma) arguably could be included in the older of the two carbonate-rich intervals, but we have not done so because it is poorly sampled and measurements are subject to large uncertainties. We acknowledge that the two carbonate-rich intervals identified represent times of very different regional paleogeographic and tectonic regimes. The older interval represents peak first-order transgression during the latter stages of passive-margin subsidence of the Zealandian continent, during which temperate limestone was deposited over much of the now-exposed New Zealand landmass (King et al. 1999). In contrast, Plio-Pleistocene limestones were deposited in a range of active tectonic settings related to the modern Australia-Pacific plate boundary (Kamp and Nelson 1987, 1988; Beu 1995; Caron and Nelson 2009). Despite these differences, if the two intervals are treated separately in our analyses, principal results and conclusions remain the same (results not shown here).

Regional and Local Sampling Statistics.—Per-stage sampling probability (R) is the average probability that any species ranging through an entire stage has been sampled and recorded at least once from that stage. We estimated R separately for aragonitic and calcitic species using the standard gap statistic of Paul (1982), as modified by Foote and Raup (1996). Because pre-middle Eocene data are sparse, R is reported only for post-40 Ma (late Middle Eocene) faunas.

To compare regional and local scales and to test for ecological and taphonomic effects, we need to examine occurrences collection by collection. Thus, for each collection in each stage, we tabulated the presence or absence of every species that first appears before that stage and last appears after the stage. The number of species-by-collection combinations represents the total number of sampling opportunities for a given stage. For each opportunity, we scored an indicator variable, R_{coll}, equal to 0 if the species is absent from the collection and 1 if it is present. In contrast to the net per-stage sampling probability, this approach analyzes sampling on a per-collection basis and therefore implicitly factors out the effects of uneven sampling

FIGURE 1. Species sampling probability (A) and distribution of limestone (B, C) in the New Zealand Cenozoic shelf fossil and stratigraphic records. Divisions on the abscissa are international series (Gradstein et al. 2012) and series of the New Zealand geological timescale (Hollis et al. 2010). Stages with widespread carbonate deposition are shaded gray. All panels show plus or minus one standard error, except as noted in Materials and Methods. A, Per-stage sampling probability calculated separately for calcitic and aragonitic species. B, Proportion of limestone collections in the FRED data set. C, Proportion of sampled 1:50,000 map sheets containing at least one limestone collection. Stages when calcitic taxa are better sampled than aragonitic taxa tend to be those with widespread carbonate deposition.

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TABLE 1. Results of multiple logistic regression. In all models, R_{coll} = indicator variable showing whether species is (1) or is not (0) found in a given collection, M = shell mineralogy (aragonite, calcite), S = shell size (small, medium, large; analyses presented for small and large species relative to medium), L = collection lithology (siliciclastic, limestone), T = incidence of shelf carbonate (carbonate-poor, carbonate-rich). $L{:}T$ indicates a non-additive interaction between the factors. Data from Table A2.

	Data	Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	p-value
1	All mollusks	$R_{coll} \sim M + L + T$	103,746	0.074	M	0.78	0.025	$\ll$0.001
2					L	−0.69	0.033	$\ll$0.001
3					T	0.04	0.020	0.040
4		$R_{coll} \sim M + L + T + L{:}T$	103,741	0.926	M	0.78	0.025	$\ll$0.001
5					L	−0.87	0.077	$\ll$0.001
6					T	0.03	0.020	0.187
7					L:T	0.22	0.085	0.009
8	Aragonitic taxa	$R_{coll} \sim L + T$	85,682	0.601	L	−1.09	0.043	$\ll$0.001
9					T	−0.15	0.022	$\ll$0.001
10		$R_{coll} \sim L + T + L{:}T$	85,683	0.399	L	−1.01	0.088	$\ll$0.001
11					T	−0.14	0.022	$\ll$0.001
12					L:T	−0.11	0.101	0.273
13	Calcitic taxa	$R_{coll} \sim L + T$	17,136	0.121	L	0.17	0.054	0.002
14					T	0.90	0.049	$\ll$0.001
15		$R_{coll} \sim L + T + L{:}T$	17,132	0.879	L	−0.18	0.159	0.262
16					T	0.86	0.052	$\ll$0.001
17					L:T	0.40	0.170	0.019
18	Siliciclastic lithologies during carbonate-poor stages	$R_{coll} \sim M + S$			M	0.07	0.044	0.140
19					S (small)	0.04	0.040	0.361
20					S (large)	−0.02	0.032	0.470
21	Siliciclastic lithologies during carbonate-rich stages	$R_{coll} \sim M + S$			M	1.00	0.039	$\ll$0.001
22					S (small)	−0.39	0.045	$\ll$0.001
23					S (large)	−0.08	0.033	0.011
24	Limestone lithologies during carbonate-poor stages	$R_{coll} \sim M + S$			M	0.63	0.181	<0.001
25					S (small)	−0.86	0.369	0.019
26					S (large)	0.61	0.184	<0.001
27	Limestone lithologies during carbonate-rich stages	$R_{coll} \sim M + S$			M	2.13	0.071	$\ll$0.001
28					S (small)	−0.35	0.146	0.018
29					S (large)	0.59	0.084	$\ll$0.001

between stages. In total, there are about 480,000 species-by-collection combinations in our data set, for all stages extending back to the base of the Cenozoic. Our approach tacitly assumes that biogeographic sampling failure (i.e., differential sampling of species reflecting variation in geographic range) will be stochastically uniform with respect to shell mineralogy and size, an assumption we discuss below. For each sampling opportunity, we also tabulated lithology as a proxy for substrate type, assignment to carbonate-poor or carbonate-rich intervals (irrespective of whether the enclosing rock of any particular fossil collection was limestone or siliciclastic sediment), shell mineralogy of the species, and shell size. R_{coll} data are summarized in Table A2.

To examine relationships between per-collection sampling, shell mineralogy, substrate type, and limestone-rich intervals, we used multiple logistic regression, coding R_{coll} as the response variable and the other factors as predictor variables. In interpreting the results (Table 1), note that calcitic mineralogy is

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compared with aragonitic, so that a positive regression coefficient implies greater odds of sampling of calcitic taxa. Likewise, other regression
coefficients reflect the log odds ratio of sampling in limestones versus siliciclastic lithologies, and carbonate-rich versus carbonate-poor time intervals. For shell size, both small and large shells are compared with medium shells, so that there is an implicit ordering in this three-state variable. For various partitions of the data, we tested a range of models of increasing complexity. Although we examined a number of models involving interactions between factors, we restricted interaction terms to those that are relatively simple. Thus, we examined the interaction between lithology and carbonate-rich times to test whether, say, preservation in limestones was enhanced or diminished during times of widespread carbonate deposition on the shelf. We are interested primarily in effect sizes, assessed using the estimates of regression coefficients, but we also cite AIC values and Akaike weights as aids to model selection. For simplicity, many models that are uninformative or essentially duplicate other results are not reported.

Because regional and local sampling statistics are based on the presence or absence of species with first appearance before a given stage and last appearance after that stage, only the 625 species with a range of three or more stages, accounting for 11,036 occurrences in 2426 collections, are included in these analyses. If we compare the total occurrence count in Table A2 for each combination of factors (class, mineralogy, size, and so on) with the count for this longer-ranging subset of species, the two track each other very well (Spearman rank-order correlation coefficient: 0.96; $p \ll 0.001$).

All analyses were carried in R, version 2.14.1 (R Development Core Team 2011).

Results

Regional, Stage-level Analyses.—Figure 1A shows time series of per-stage sampling probabilities (R) for aragonitic and calcitic mollusk species. This reveals times when calcitic taxa have much higher sampling probabilities than aragonitic species, supporting the notion of profound relative bias, and other times when sampling probabilities are approximately equal and bias is not evident. The potential significance of this observation, in terms of macroevolutionary or macroecological inference, is illustrated quite simply by changes in the relative frequency of gastropods and bivalves through time. Given that shelf-dwelling gastropod species are almost entirely aragonitic (99.3%) whereas 15% of bivalves are calcitic, it stands to reason that periods of time with better sampling of aragonitic taxa should have a higher proportion of gastropod species and occurrences (Fig. 2). The Spearman rank-order correlation between time series of ($R_{calcite} - R_{aragonite}$) and the proportion of sampled species that are gastropods is equal to −0.63 (one-tailed $p = 0.0025$); for occurrences the correlation is equal to −0.80 (one-tailed $p \ll 0.001$); for genera it is equal to −0.63 (one-tailed $p = 0.002$). Thus a substantial part of the temporal variation in relative representation of gastropods in the record is potentially explained by changes in the sampling probabilities of

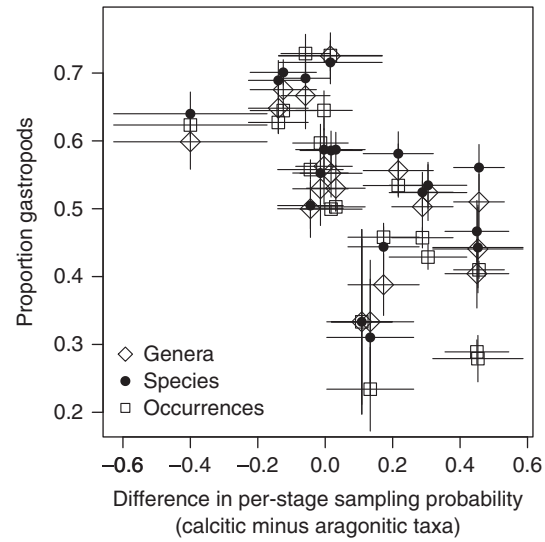

FIGURE 2. Difference in per-stage sampling probability (R) for calcitic versus aragonitic species (from Fig. 1A), plotted against proportion of taxa and occurrences that are gastropods versus bivalves. Error bars are plus or minus one standard error; for the ordinate this is the binomial standard error; for the abscissa it is estimated as $[SE(R_{calcite})^2 + SE(R_{aragonite})^2]^{0.5}$. Stages with better sampling of aragonitic species tend to have a higher proportion of gastropods.

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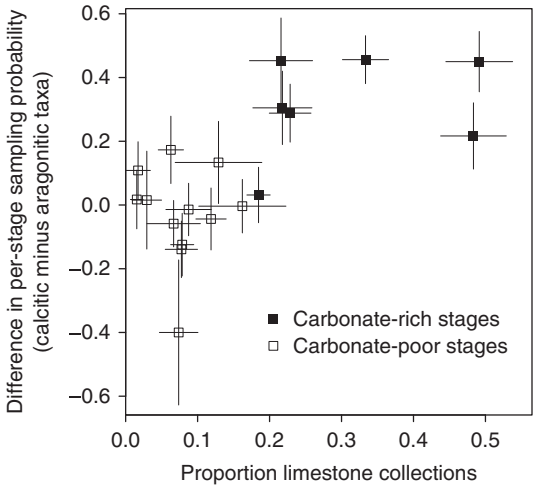

FIGURE 3. Difference in per-stage sampling probability (R) for calcitic versus aragonitic species (from Fig. 1A), plotted against proportion limestone collections (from Fig. 1B). Error bars are plus or minus one standard error; for the abscissa this is the binomial standard error; for the ordinate it is estimated as $[SE(R_{calcite})^2 + SE(R_{aragonite})^2]^{0.5}$. Consistent with Fig. 1, the spatial extent of carbonate deposition predicts the difference between calcite and aragonite sampling probabilities.

aragonitic and calcitic taxa. The difference in sampling depicted in Fig. 1A is not merely a reflection of the relative representation of bivalves and gastropods, however, for we see the same pattern within bivalves (Fig. A1).

Times of relative bias against aragonitic fossils correspond broadly to times when limestone is both more widespread and highly sampled (Figs. 1, 3, A2). Taken at face value, these patterns support the inference that aragonite dissolution is particularly pervasive in New Zealand temperate carbonate settings, but it is essential to test this inference explicitly by analyzing collection-level data. It is also possible that the results reflect ecological preferences of different species, either aversion of aragonitic taxa to environments that are widespread during carbonate-rich intervals or affinity of calcitic taxa for such environments. This possibility too must be explored at the level of individual collections, to which we now turn.

Local, Collection-level Analyses.—Results of the logistic regressions are shown in Table 1. In the following discussion, specific inferences are cross-referenced to key regression models by line number in the table. When interpreting this table, effect sizes can be gauged from the magnitude of regression coefficients, and relative model fits can be assessed using Akaike weights. Positive or negative coefficients indicate positive or negative regression relationships for the second factor state relative to the first. For example, in line 1, the regression coefficient is 0.78, indicating that sampling of calcitic species is favored relative to sampling of aragonitic species. Specifically, the odds of sampling calcitic taxa are $\exp(0.78) = 2.2$ times as high as the odds of sampling aragonitic taxa; this relationship is statistically significant ($p \ll 0.001$).

Models including all data support the regional- and stage-scale interpretation of bias against aragonitic shells and in limestones (lines 1, 2, 4, 5), but indicate somewhat better sampling overall from limestones deposited during carbonate-rich times (line 7). This last result shows a statistical interaction; there is a combined effect of limestone lithology during carbonate-rich times that surpasses the additive effects of the two factors. The Akaike weights also indicate better support for the model with the interaction term. Looking just at aragonitic taxa, we find strong bias against sampling in limestones, and a comparatively modest effect of carbonate-rich intervals (lines 8–12). In other words, presence of aragonitic taxa is influenced much more by the immediate substrate than by abundant carbonate in the wider environment. Calcitic taxa, on the other hand, are mainly affected by the nature of the wider environment and are relatively better sampled during carbonate-rich times (lines 13–17). Calcitic taxa also seem to drive the interaction between limestone lithology and carbonate-rich intervals (lines 7, 17).

The regression coefficients pertain to *relative* odds of sampling, for example of calcitic versus aragonitic taxa. To put these into context, it helps to examine *absolute* sampling proportions as well (Table 2). These show that for several partitions of the data there is a characteristic sampling rate similar to the overall rate of about 2.3% per species per collection. Aragonitic species, however, stand out for having low sampling rates in limestones, during both carbonate-poor and carbonate-rich times, but slightly lower in the latter. Calcitic taxa stand out for having higher sampling rates during carbonate-rich times, an effect that is enhanced in limestones. Thus the inferences based on

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TABLE 2. Absolute sampling rates for mollusks partitioned by shell mineralogy, lithology, and carbonate-rich versus carbonate-poor time intervals.

Mineralogy	Lithology	Time	No. of sampling opportunities	No. sampled	Proportion sampled	Standard error
Aragonitic	Siliciclastic	Carbonate-poor	186,892	4660	0.025	0.00036
		Carbonate-rich	167,765	3645	0.022	0.00036
	Limestone	Carbonate-poor	14,377	133	0.0093	0.00080
		Carbonate-rich	63,574	458	0.0072	0.00034
Calcitic	Siliciclastic	Carbonate-poor	23,659	621	0.026	0.0010
		Carbonate-rich	16,568	994	0.060	0.0018
	Limestone	Carbonate-poor	1951	43	0.022	0.0033
		Carbonate-rich	6556	482	0.074	0.0032
Combined data			481,342	11,036	0.023	0.00022

relative odds are consistent with the absolute sampling proportions.

We emphasize again that sampling is analyzed here at the level of individual collections. Thus, for example, the per-species, per-collection sampling rate in limestones need not be higher in carbonate-rich stages simply because there are more limestones during those stages.

Next we partitioned the data by lithology and general environment and included shell size as a factor. Remarkably, for siliciclastic sediments deposited during carbonate-poor times, neither shell mineralogy nor size significantly biases the odds of sampling (Table 1: lines 18–20). In marked contrast, there is apparently a significant bias against aragonitic taxa in both siliciclastic lithologies deposited during carbonate-rich times and in limestone deposited at any time (Table 1: lines 21, 24, 27). However, looking at the absolute sampling rates (Table 2), we see that the relatively low odds of sampling aragonitic taxa in clastic lithologies during carbonate-rich times are primarily caused by enhanced sampling of calcitic taxa rather than reduced sampling of aragonitic forms. *Thus, there is effectively no sampling bias against aragonitic taxa in siliciclastic lithologies.*

Finally, there is a bias against small- and medium-sized shells, relative to large, in limestones (Table 1: lines 25–26, 28–29), and bias against small mollusks in siliciclastic lithologies during carbonate-rich intervals (Table 1: line 22). The preservational bias against smaller sizes is consistent with previous work on Cenozoic mollusks of New Zealand (Cooper et al. 2006) and with suggestions of a more general size-related bias in mollusks (Kidwell and Bosence 1991; Cherns and Wright 2011).

Discussion

In analyzing the factors that contribute to species sampling, we have assumed that biogeographic sampling failure does not vary systematically with salient factors such as shell composition, but this assumption could be violated if aragonitic or calcitic taxa had larger geographic ranges on average. To test this assumption, we examined the geographic ranges of living mollusks around New Zealand. Using maximum great-circle distance as a measure of geographic range and ignoring 26 species recorded from a single occurrence, we find that there is a modest difference in the geographic ranges of aragonitic and calcitic taxa of about 16%: the 25 calcitic taxa have a median range of 1573 ± 115 km, and the 284 aragonitic taxa have a median range of 1325 ± 43 km (median plus or minus one standard error, based on bootstrap resampling). These estimates must be regarded as provisional because of sampling biases that are particular to the living fauna and will not affect our fossil data. For example, 83% of the occurrences are from the water depth range of 0–100 m and only 17% are from the outer half of the shelf depth range; this reflects the relative ease of sampling in shallow water. Similarly, there is relatively sparse sampling of some sectors of the shelf, in particular off the northwestern South Island and part of the western North Island. Taken at face value, the biogeographic bias in the living fauna is small compared to the mineralogical effect sizes documented in the fossil record (Table 1) and is therefore unlikely to dominate these effects. Most importantly, we know from the fossil

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TABLE 3. Abundances of living mollusks, per species per sample, from the Te Papa database. Standard error of median based on bootstrap resampling of the samples.

Data	No. of species	No. of samples	Median abundance	Standard error
All species	335	16,231	3	~0.0
Calcitic species	25	1907	3	~0.0
Aragonitic species	310	14,324	3	~0.0
Bivalves	119	7022	4	0.17
Gastropods	214	8954	2	0.26
Calcitic bivalves	22	1712	3	0.059
Aragonitic bivalves	97	5310	5	0.046
Calcitic gastropods	3	195	2	0.17
Aragonitic gastropods	211	8759	2	0.26

record that there are times when no bias can be detected (Table 1: lines 18–20; Table 2), which indicates that any significant shell-composition-related biogeographic effects are not a persistent feature of the fauna.

Similarly, locality data on living mollusks do not support the idea that geographic range varies systematically with body size in a way that is likely to produce the sampling results we have documented. Small, medium, and large species have median ranges of 1324 ± 98 km, 1087 ± 122, and 1387 ± 80 km, respectively. One of the main effects we document is that small species have lower odds of sampling than medium or large species (Table 1: lines 21–29), a result that would not be predicted from the larger geographic ranges of small versus medium species or the nearly identical ranges of small versus large species.

One factor that is likely to be important but for which we do not have data from the fossil collections is numerical abundance; all else being equal, we would expect more-abundant species to have better chances of sampling. To test for systematic differences in abundance between groups of mollusks, we extracted specimen counts from samples of living mollusks and tabulated the median number of specimens per species per sample (Table 3). We find no appreciable difference between the median abundance of calcitic versus aragonitic species; both medians are equal to 3 (two-tailed Wilcoxon test: $p = 0.572$). Thus, if these abundances are representative of calcitic and aragonitic species in general, we infer that the effects of mineralogy documented herein do not simply reflect underlying effects of abundance. In fact, if we focus on bivalves, within which both mineralogies are well represented, we see that aragonitic taxa are more abundant (Table 3). All else being equal, this would predict better sampling of aragonitic taxa in the fossil record, quite the opposite of what we find.

Lithification can reduce the chances of recovering fossil material from a sample and affect the body-size distribution of recovered shells (e.g., Koch and Sohl 1983; Hendy 2009; Sessa et al. 2009). It seems unlikely a priori that lithification exerts a major control on our results, simply because so few collections come from unlithified sediments prior to the Nukumaruan stage (2.4 Ma) (Crampton et al. 2006a: Fig. 5). We can nonetheless assess the effects of lithification on sampling by considering the subset of collections (~82%) that have information on degree of induration, coded in FRED as unconsolidated, moderately soft, moderately hard, and hard, but bearing in mind that these categories have probably not been applied consistently by collectors. For siliciclastic lithologies, the four categories account for 5.8%, 64.4%, 22.9%, and 6.9% of the collections, respectively. For limestones, the corresponding figures are 2.4%, 29.1%, 39.0%, and 29.4%. Although limestones are more heavily indurated on average, lithology and the other factors we have shown to influence sampling are not mere proxies for lithification. We can see this by repeating regression analyses with lithification as an additional factor (Tables A3–A8). These regressions show that lithification, as expected, reduces the odds of sampling, and that models including lithification as a factor generally have substantially better fit. The effects of other

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factors are about the same, however, regardless of whether lithification is included in the regressions. In these analyses, we have treated lithification as a binary factor, contrasting unconsolidated sediments with all other categories, but we attain similar results (not shown) if we contrast unconsolidated plus moderately soft samples with moderately hard plus hard samples, or if we consider all four categories as distinct levels of an induration factor.

There are of course other controls on sampling that we have not considered, including sequence-stratigraphic context. Limestone formation in the study system is influenced by a complex interplay of eustatic sea level, tectonic setting, sediment supply, current regime, and availability of hard substrates for bioclast producers (Nelson 1978; Kamp and Nelson 1987, 1988; Beu 1995). We have previously documented higher per-species sampling probabilities around the middle of second-order cycles (Crampton et al. 2006b), but sequence-stratigraphic control will also likely be important at temporal scales finer than those we can document with our stage-level data.

Although not central to our study, our data allow additional analyses bearing on the relative representation of bivalves and gastropods (Fig. 2). We carried out a further logistic regression, using only gastropods and bivalves and adding class as a factor to the results shown on lines 4–7 of Table 1. The results (Table A9) show that gastropod species have odds of sampling at the collection level about 11% lower than bivalves and that adding class membership to the regression yields a model with substantially better support. Body size is also correlated with class membership; the median size of bivalves (32.5 mm) is significantly larger than that of gastropods (17 mm) (Wilcoxon test: $p \ll 0.001$). We therefore added class as a factor to the regressions that partitioned data by lithology and time interval and included body size (see Table 1: lines 18–29). In all four cases, sampling odds are lower for gastropods even when the effects of mineralogy and size are taken into account (Tables A10–A13). In three cases, the regression coefficient for class membership is statistically significant, and adding class as a factor leads to a substantial increase in support. At this point we do not know definitively why, all else being equal, gastropods have lower odds of sampling, but it is reasonable to put forth lower abundance as a live hypothesis: the same data on living species used to compare aragonitic and calcitic taxa show that bivalves have twice the average abundance as gastropods per species per locality (Table 3) (two-tailed Wilcoxon test: $p \ll 0.001$). This difference stands to reason given that gastropod species in our data are largely within carnivorous trophic guilds, whereas bivalves are mainly filter feeders (Crampton et al. 2010: p. 213). The database on abundances does not include the relative numbers of articulated and disarticulated bivalves, which would be necessary to estimate how many individuals are represented by a given number of shells. It is likely that the count of bivalves needs to be adjusted downward (Gilinsky and Bennington 1994; Kowalewski et al. 2002), but only the most pessimistic assumptions would lead us to divide the bivalve counts in half and conclude that bivalves and gastropods are equally abundant.

Our emphasis here has been on whether taxa are sampled within an interval during which they are known to have existed. We previously suggested (Crampton et al. 2006a) that, because the proportion of aragonitic taxa does not trend markedly, aragonite loss does not shape the long-term biodiversity trajectory of Cenozoic mollusks in New Zealand. Our present conclusions differ from those of Crampton et al. (2006a: Fig. 5) because the earlier study did not specifically examine relative differences in sampling probabilities of aragonitic and calcitic taxa, and data were displayed only as the overall proportion of aragonitic taxa, a presentation that unfortunately mutes the signals described in the present study. We note, however, that Figure 5 of Crampton et al. (2006a) does reveal variation in the proportion of aragonitic species that is consistent with the patterns of sampling probability shown in the present study (Figs. 1A, 2). In particular, the difference between calcitic and aragonitic sampling probabilities (Fig. 2) is a strong predictor of the proportion of aragonitic species sampled in a stage (Crampton et al. 2006a: Fig. 5) (Spearman $r = -0.79$, $p \ll 0.001$).

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On the whole, the effects of aragonite sampling bias in New Zealand mollusks are consistent at the scale of spatiotemporally localized collections and at the regional- and stage- scales. Stage-level sampling probabilities (Fig. 1) suggest that aragonite bias is most pervasive during times of widespread carbonate deposition, and analysis of collection-level data (Table 1) supports this inference. The analysis of sampling at the collection scale, however, allows us to resolve the nature of bias in this system in more detail and to quantify the components of bias. In particular:

1. Mollusks living on siliciclastic substrates experience no significant sampling bias against aragonitic taxa.
2. There is a strong bias against aragonitic mollusks living on carbonate substrates; judging from the effect during carbonate-poor stages, this bias reduces the odds of sampling aragonitic taxa by about one-half (Table 1: line 24). This result is expected and was predicted by earlier studies at both temperate and tropical latitudes (e.g., Nelson 1978; Brachert and Dullo 2000; Kidwell et al. 2005; Best et al. 2007; Best 2008).
3. There is also a bias in favor of calcitic taxa, regardless of substrate and in addition to effects of lithology per se, during times of widespread limestone deposition; judging from the effect in clastic lithologies, this bias increases the odds of sampling calcitic taxa by ~170% (Table 1: line 21). Effects (2) and (3) combine to give odds of sampling calcitic taxa during limestone-rich intervals that are ~8 times as high as for aragonitic taxa (Table 1: line 27).
4. Relative to medium-sized mollusks, there is significant bias against small and for large mollusks in limestones, and bias against small taxa in siliciclastic lithologies deposited during carbonate-rich intervals. The size bias decreases the odds of sampling small mollusks by ~30% to ~60% and increases the odds of sampling large mollusks by ~80% (Table 1: lines 22, 25, 26, 29).
5. Gastropods are somewhat more poorly sampled than bivalves, even when we account for mineralogy and body size, a result that likely reflects lower numerical abundance. This last effect is generally small relative to the effect of shell composition (Table A9).

The preference of calcitic taxa for carbonate-rich times in general, not just for limestones, is an unexpected result. The higher absolute sampling rates of calcitic taxa, rather than reduced rates for aragonitic taxa (Table 2), point to an original ecological preference rather than a taphonomic effect. We can gain some insight into the ecological effect by looking at sampling rates of calcitic taxa family by family (Table 4). Weighing the sampling rates with the number of opportunities for sampling, it appears that the bivalve families Ostreidae and Pectinidae are the dominant contributors. This stands to reason given that widespread oyster banks and oyster-pecten-barnacle associations are known to be major features of the carbonate-rich intervals (Nelson 1978; Beu 1995). More generally, Nelson (1978: p. 758) reported a dominance of epifaunal versus infaunal bivalves in New Zealand Cenozoic limestones. Again we emphasize, however, that it is not simply limestones per se but carbonate-rich times more broadly that account for the higher sampling rates of calcitic taxa (Tables 1, 2). Mytilidae, which we have categorized as calcitic on account of their mixed mineralogy, have low sampling rates overall but especially in limestones. These results make sense in light of the generally high aragonitic component in this family (Carter 1990b). High sampling rates of epitoniids partly reflect the fact that the Cenozoic record of calcitic gastropods in New Zealand is dominated by *Cirsotrema*, whose species are mainly large-bodied.

The general agreement we find between local- and regional-scale aragonite bias stands in contrast to recent studies reporting that aspects of shell durability for marine brachiopods, bivalves, and gastropods, as recorded in the Paleobiology Database, do not consistently and positively predict frequency of occurrence or temporal trends in occurrence (Behrensmeyer et al. 2005; Kosnik et al. 2011). These studies differ from ours in three salient ways: in them, occurrence data were aggregated at the genus level, data were global in scope, and time intervals were longer than the stages we have

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TABLE 4. Sampling statistics for principal calcitic families.

Family		All data	Siliciclastics	Limestones	Carbonate-rich stages	Limestones in carbonate-rich stages
Epitoniidae (Gastropoda)	No. of sampling opportunities	2777	2332	445	1221	331
	Proportion sampled	0.031	0.027	0.054	0.054	0.073
	Standard error	0.0033	0.0034	0.011	0.0065	0.014
Limidae (Bivalvia)	No. of sampling opportunities	4379	3540	839	2860	735
	Proportion sampled	0.0048	0.0054	0.0023	0.0063	0.0072
	Standard error	0.0010	0.0012	0.0017	0.0015	0.0019
Mytilidae (Bivalvia)	No. of sampling opportunities	11,503	9539	1964	5789	1548
	Proportion sampled	0.012	0.012	0.0087	0.013	0.0090
	Standard error	0.0010	0.0011	0.0021	0.0015	0.0024
Ostreidae (Bivalvia)	No. of sampling opportunities	3729	3030	699	1978	577
	Proportion sampled	0.15	0.14	0.19	0.21	0.23
	Standard error	0.0058	0.0063	0.0015	0.0092	0.017
Pectinidae (Bivalvia)	No. of sampling opportunities	21,661	17,827	3834	9615	2890
	Proportion sampled	0.055	0.048	0.088	0.083	0.10
	Standard error	0.0015	0.0016	0.0046	0.0028	0.0057
Pinnidae (Bivalvia)	No. of sampling opportunities	2984	2514	470	1268	338
	Proportion sampled	0.044	0.050	0.011	0.073	0.015
	Standard error	0.0038	0.0044	0.0047	0.0073	0.0066
Propeamussiidae (Bivalvia)	No. of sampling opportunities	1701	1445	256	393	137
	Proportion sampled	0.013	0.012	0.016	0.010	0.022
	Standard error	0.0027	0.0029	0.0078	0.0051	0.013

used. These differences all tend in the same direction—toward increasing redundancy in the data, evening out temporal and spatial variation in sampling, and therefore mitigating the effects of compositional and structural bias. Given that we see some similar results at the genus and species level (Fig. 2) and that times of extensive limestone formation extend for several stages, we tentatively suggest that expanding from the regional to the global scale—where, in particular, spatial variation in carbonate versus clastic extent should be evened out—may have more of an effect than aggregating data at coarser taxonomic or temporal scales.

Our study has successfully linked the local scale with the regional scale, uncovering underlying reasons for regional-scale bias that could not have been detected without the finer-scale analysis. Likewise, dissecting the Paleobiology Database into subsets of regional species pools that are stratigraphically well-defined may bring us closer to documenting relationships between regional and global patterns and therefore to understanding the complexity of sampling at a hierarchy of scales.

Conclusions

Our key finding is that, among Cenozoic mollusks of New Zealand, the occurrence of aragonitic versus calcitic taxa reflects an interplay of both diagenetic loss of aragonite and original ecology. Specifically, whereas there is no bias against aragonitic taxa in siliciclastic lithologies, calcitic taxa are preferentially favored both in limestones and in carbonate-rich environments regardless of lithology. The former preference reflects preservational bias and doubles the sampling odds of calcitic taxa relative to aragonitic. The latter reflects original ecology and increases calcitic sampling odds by a factor of nearly three. In limestones deposited during carbonate rich times, the sum of these effects plus their interaction yields odds of sampling that are eight times as high for calcitic taxa.

If our results hold more generally, they imply that, with respect to aragonite dissolution, unbiased data on faunal composition at the local and regional scale in temperate settings can be extracted from dominantly siliciclastic marine

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rock records, whereas fossil assemblages from carbonate-rich settings must be interpreted with caution because of the conflation of ecological signals and taphonomic bias.

Our results allow us to draw a number of other conclusions. Data from living species yield no evidence for a systematic difference in numerical abundance between calcitic and aragonitic taxa, suggesting that mineralogy is not an alias for abundance. We do, however, find that gastropod species have median abundances about one-half as high as those of bivalves; this difference may help explain the result that, even controlling for shell mineralogy and body size, fossil gastropods have lower sampling rates than fossil bivalves. The general agreement we find between regional and local preservational effects complements recent studies at the genus level and global scale showing that shell composition is not an overriding factor in patterns of taxonomic occurrence. For the questions addressed here, we suggest that the difference between regional and global scales is more important than that between the species and genus levels or between shorter (~stage) and longer (~series) time scales.

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Appendix

TABLE A1. Lithologic and taxonomic sampling statistics.

Series	Stage	Age at base of stage (Ma)	No. of collections*	No. of limestone collections	Proportion of limestone collections	Standard error	No. of maps	No. of maps containing clastics	Proportion of maps containing clastics	Standard error
Wanganui	Haweran	0.34	58	1	0.017	0.017	24	23	0.958	0.041
	Castlecliffian	1.63	194	3	0.015	0.009	12	12	1.000	0.038
	Nukumaruan	2.4	574	106	0.185	0.016	35	33	0.943	0.039
	Mangapanian	3	116	57	0.491	0.046	21	18	0.857	0.076
	Waipipian	3.7	216	72	0.333	0.032	34	30	0.882	0.055
	Opoitian	5.3	210	48	0.229	0.029	47	41	0.872	0.049
Taranaki	Kapitean	7.2	191	12	0.063	0.018	34	33	0.971	0.029
	Tongaporutuan	11	236	28	0.119	0.021	48	47	0.979	0.021
Southland	Waiauan	12.7	80	7	0.088	0.032	23	22	0.957	0.043
	Lillburnian	15.1	37	6	0.162	0.061	11	9	0.818	0.116
	Clifdenian	15.9	45	3	0.067	0.037	12	11	0.917	0.080
Pareora	Altonian	18.7	280	22	0.079	0.016	60	58	0.967	0.023
	Otaian	21.7	142	11	0.077	0.022	40	38	0.950	0.034
Landon	Waitakian	25.2	120	58	0.483	0.046	33	25	0.758	0.075
	Duntroonian	27.3	101	22	0.218	0.041	40	33	0.825	0.060
	Whaingaroan	34.6	88	19	0.216	0.044	33	29	0.879	0.057
Arnold	Runangan	36.4	31	4	0.129	0.060	7	7	1.000	0.063
	Kaiatan	39.1	68	2	0.029	0.020	17	16	0.941	0.057
	Bortonian	42.6	95	7	0.074	0.027	24	23	0.958	0.041

Stage	No. of maps containing limestone	Proportion of maps containing limestone	Standard error	No. of aragonitic taxa extant	No. of aragonitic taxa sampled	Proportion of aragonitic taxa sampled	Standard error	No. of calcitic taxa extant	No. of calcitic taxa sampled	Proportion of calcitic taxa sampled	Standard error
Haweran	1	0.042	0.041	83	74	0.892	0.034	5	5	1.000	0.083
Castlecliffian	1	0.083	0.080	166	141	0.849	0.028	15	13	0.867	0.088
Nukumaruan	20	0.571	0.084	179	151	0.844	0.027	16	14	0.875	0.083
Mangapanian	11	0.524	0.109	223	72	0.323	0.031	22	17	0.773	0.089
Waipipian	14	0.412	0.084	214	95	0.444	0.034	20	18	0.900	0.067
Opoitian	22	0.468	0.073	195	108	0.554	0.036	19	16	0.842	0.084
Kapitean	7	0.206	0.069	192	92	0.479	0.036	23	15	0.652	0.099
Tongaporutuan	11	0.229	0.061	192	77	0.401	0.035	28	10	0.357	0.091
Waiauan	4	0.174	0.079	232	53	0.228	0.028	28	6	0.214	0.078
Lillburnian	3	0.273	0.134	253	62	0.245	0.027	29	7	0.241	0.080
Clifdenian	2	0.167	0.108	262	59	0.225	0.026	30	5	0.167	0.068
Altonian	15	0.250	0.056	183	138	0.754	0.032	27	17	0.630	0.093
Otaian	6	0.150	0.056	217	98	0.452	0.034	32	10	0.313	0.082
Waitakian	21	0.636	0.084	160	72	0.450	0.039	24	16	0.667	0.096
Duntroonian	16	0.400	0.077	115	48	0.417	0.046	18	13	0.722	0.106
Whaingaroan	11	0.333	0.082	100	19	0.190	0.039	14	9	0.643	0.128
Runangan	2	0.286	0.171	103	12	0.117	0.032	12	3	0.250	0.125
Kaiatan	1	0.059	0.057	89	31	0.348	0.051	11	4	0.364	0.145
Bortonian	5	0.208	0.083	10	4	0.400	0.155	2	0	0.000	0.167

*Total collection count is lower than that cited in the text, because not all stages are included here.

TABLE A2. Summary of collection-level occurrence data.

Factor combination*,†	No. of occurrences	No. of sampling opportunities (through-ranging species)	No. of occurrences (through-ranging species)
Bi;Ar;Sm;Si;C-p	739	16,238	524
Bi;Ar;Sm;Si;C-r	515	18,466	400
Bi;Ar;Sm;Ls;C-p	8	1167	4
Bi;Ar;Sm;Ls;C-r	41	6919	27
Bi;Ar;Md;Si;C-p	976	28,355	778
Bi;Ar;Md;Si;C-r	714	26,140	587
Bi;Ar;Md;Ls;C-p	27	2207	14
Bi;Ar;Md;Ls;C-r	83	9,634	52
Bi;Ar;Lg;Si;C-p	1243	36,930	911
Bi;Ar;Lg;Si;C-r	942	32,651	725
Bi;Ar;Lg;Ls;C-p	80	2845	59
Bi;Ar;Lg;Ls;C-r	211	12,580	173
Bi;Ar;Unk;Si;C-p	16	184	1
Bi;Ar;Unk;Si;C-r	0	782	0
Bi;Ar;Unk;Ls;C-p	0	3	0
Bi;Ar;Unk;Ls;C-r	0	266	0
Bi;Ca;Sm;Si;C-p	5	574	3
Bi;Ca;Sm;Si;C-r	0	108	0
Bi;Ca;Sm;Ls;C-p	0	58	0
Bi;Ca;Sm;Ls;C-r	1	65	1
Bi;Ca;Md;Si;C-p	167	4643	126
Bi;Ca;Md;Si;C-r	291	3912	289
Bi;Ca;Md;Ls;C-p	3	365	2
Bi;Ca;Md;Ls;C-r	66	1420	64
Bi;Ca;Lg;Si;C-p	561	17,000	471
Bi;Ca;Lg;Si;C-r	754	11,658	663
Bi;Ca;Lg;Ls;C-p	58	1414	41
Bi;Ca;Lg;Ls;C-r	489	4740	393
Bi;Ca;Unk;Si;C-p	4	0	0
Bi;Ca;Unk;Si;C-r	1	0	0
Bi;Ca;Unk;Ls;C-p	0	0	0
Bi;Ca;Unk;Ls;C-r	0	0	0
Ga;Ar;Sm;Si;C-p	1089	23,644	528
Ga;Ar;Sm;Si;C-r	531	23,059	301
Ga;Ar;Sm;Ls;C-p	15	1639	5
Ga;Ar;Sm;Ls;C-r	67	8116	36
Ga;Ar;Md;Si;C-p	1378	35,696	829
Ga;Ar;Md;Si;C-r	1330	35,030	868
Ga;Ar;Md;Ls;C-p	41	2681	25
Ga;Ar;Md;Ls;C-r	145	13,264	82
Ga;Ar;Lg;Si;C-p	1766	44,810	1079
Ga;Ar;Lg;Si;C-r	1254	31,489	756
Ga;Ar;Lg;Ls;C-p	51	3767	26
Ga;Ar;Lg;Ls;C-r	143	12,723	86
Ga;Ar;Unk;Si;C-p	67	236	0
Ga;Ar;Unk;Si;C-r	7	0	0
Ga;Ar;Unk;Ls;C-p	0	4	0
Ga;Ar;Unk;Ls;C-r	2	0	0
Ga;Ca;Sm;Si;C-p	0	0	0
Ga;Ca;Sm;Si;C-r	0	0	0
Ga;Ca;Sm;Ls;C-p	0	0	0
Ga;Ca;Sm;Ls;C-r	0	0	0
Ga;Ca;Md;Si;C-p	1	0	0
Ga;Ca;Md;Si;C-r	0	0	0
Ga;Ca;Md;Ls;C-p	0	0	0
Ga;Ca;Md;Ls;C-r	0	0	0
Ga;Ca;Lg;Si;C-p	24	1442	21
Ga;Ca;Lg;Si;C-r	47	890	42
Ga;Ca;Lg;Ls;C-p	0	114	0
Ga;Ca;Lg;Ls;C-r	27	331	24
Ga;Ca;Unk;Si;C-p	2	0	0
Ga;Ca;Unk;Si;C-r	0	0	0
Ga;Ca;Unk;Ls;C-p	0	0	0

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TABLE A2. *Continued*

Factor combination*,†	No. of occurrences	No. of sampling opportunities (through-ranging species)	No. of occurrences (through-ranging species)
Ga;Ca;Unk;Ls;C-r	0	0	0
Sc;Ar;Sm;Si;C-p	1	184	0
Sc;Ar;Sm;Si;C-r	1	0	0
Sc;Ar;Sm;Ls;C-p	0	3	0
Sc;Ar;Sm;Ls;C-r	0	0	0
Sc;Ar;Md;Si;C-p	10	615	10
Sc;Ar;Md;Si;C-r	8	148	8
Sc;Ar;Md;Ls;C-p	0	61	0
Sc;Ar;Md;Ls;C-r	2	72	2
Sc;Ar;Lg;Si;C-p	0	0	0
Sc;Ar;Lg;Si;C-r	0	0	0
Sc;Ar;Lg;Ls;C-p	0	0	0
Sc;Ar;Lg;Ls;C-r	0	0	0
Sc;Ar;Unk;Si;C-p	3	0	0
Sc;Ar;Unk;Si;C-r	0	0	0
Sc;Ar;Unk;Ls;C-p	0	0	0
Sc;Ar;Unk;Ls;C-r	0	0	0
Total	16,007	481,342	11,036

*Bi, Bivalvia; Ga, Gastropoda; Sc, Scaphopoda; Ar, aragonitic; Ca, calcitic; Sm, small; Md, medium; Lg, large; Unk, size unknown; Ls, limestone lithology; Si, siliciclastic lithology; C-p, carbonate-poor time interval; C-r, carbonate-rich interval.
†Scaphopods are exclusively aragonitic.

TABLE A3. Multiple regression results using only aragonitic taxa and comparing the model of Table 1 (lines 8–9) with one that also includes lithologic hardness (H) as a factor (unconsolidated versus moderately soft, moderately hard, and hard).

Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	*p*-value
$R_{coll} \sim M + L + T$	70472	~0	L	−0.96	0.047	$\ll 0.001$
			T	−0.16	0.024	$\ll 0.001$
$R_{coll} \sim M + L + T + H$	70026	~1.0	L	−0.92	0.048	$\ll 0.001$
			T	−0.17	0.024	$\ll 0.001$
			H	−0.90	0.038	$\ll 0.001$

TABLE A4. Multiple regression results using only calcitic taxa and comparing the model of Table 1 (lines 15–17) with one that also includes lithologic hardness (H) as a factor (unconsolidated versus moderately soft, moderately hard, and hard).

Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	*p*-value
$R_{coll} \sim M + L + T + L{:}T$	13721	0.056	L	−0.01	0.17	0.955
			T	0.90	0.057	$\ll 0.001$
			L:T	0.23	0.18	0.208
$R_{coll} \sim M + L + T + L{:}T + H$	13716	0.944	L	0.002	0.17	0.990
			T	0.90	0.058	$\ll 0.001$
			L:T	0.22	0.18	0.215
			H	−0.32	0.11	0.004

TABLE A5. Multiple regression results using only siliciclastic lithologies during carbonate-poor stages, and comparing the model of Table 1 (lines 18–20) with one that also includes lithologic hardness (H) as a factor (unconsolidated versus moderately soft, moderately hard, and hard).

Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	*p*-value
$R_{coll} \sim M + S$	42591	~0	M	0.044	0.048	0.364
			S (small)	0.042	0.042	0.317
			S (large)	−0.056	0.035	0.108
$R_{coll} \sim M + S + H$	42037	~1.0	M	0.059	0.049	0.226
			S (small)	0.016	0.042	0.703
			S (large)	−0.028	0.035	0.421
			H	−1.20	0.045	$\ll 0.001$

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TABLE A6. Multiple regression results using only siliciclastic lithologies during carbonate-rich stages, and comparing the model of Table 1 (lines 21–23) with one that also includes lithologic hardness (H) as a factor (unconsolidated versus moderately soft, moderately hard, and hard).

Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	*p*-value
$R_{coll} \sim M + S$	32834	0.184	M	1.03	0.043	$\ll 0.001$
			S (small)	−0.38	0.052	$\ll 0.001$
			S (large)	−0.096	0.038	0.012
$R_{coll} \sim M + S + H$	32831	0.816	M	1.03	0.044	$\ll 0.001$
			S (small)	−0.38	0.52	$\ll 0.001$
			S (large)	−0.095	0.38	0.012
			H	−0.16	0.54	$\ll 0.001$

TABLE A7. Multiple regression results using only limestone lithologies during carbonate-poor stages, and comparing the model of Table 1 (lines 24–26) with one that also includes lithologic hardness (H) as a factor (unconsolidated versus moderately soft, moderately hard, and hard).

Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	*p*-value
$R_{coll} \sim M + S$	1555.7	3×10^{-5}	M	0.77	0.19	$\ll 0.001$
			S (small)	−1.14	0.44	0.010
			S (large)	0.52	0.20	0.008
$R_{coll} \sim M + S + H$	1535.0	~1.0	M	0.80	0.19	4.4×10^{-5}
			S (small)	−1.15	0.44	0.0096
			S (large)	0.54	0.20	0.0067
			H	−2.41	0.39	$\ll 0.001$

TABLE A8. Multiple regression results using only limestone lithologies during carbonate-rich stages, and comparing the model of Table 1 (lines 27–29) with one that also includes lithologic hardness (H) as a factor (unconsolidated versus moderately soft, moderately hard, and hard).

Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	*p*-value
$R_{coll} \sim M + S$	7033.4	4×10^{-6}	M	2.03	0.80	$\ll 0.001$
			S (small)	−0.29	0.15	0.061
			S (large)	0.50	0.092	$\ll 0.001$
$R_{coll} \sim M + S + H$	7008.6	~1.0	M	2.03	0.080	$\ll 0.001$
			S (small)	−0.28	0.15	0.063
			S (large)	0.50	0.092	$\ll 0.001$
			H	−0.91	0.16	$\ll 0.001$

TABLE A9. Multiple regression results using bivalves and gastropods only, and comparing the model of Table 1 (lines 4–7) with a model that also includes class (C) as a factor.

Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	*p*-value
$R_{coll} \sim M + L + T + L{:}T$	103541	2×10^{-7}	M	0.78	0.025	$\ll 0.001$
			L	−0.87	0.077	$\ll 0.001$
			T	0.024	0.020	0.233
			L:T	0.22	0.085	0.010
$R_{coll} \sim M + L + T + L{:}T + C$	103516	~1.0	M	0.72	0.027	$\ll 0.001$
			L	−0.87	0.077	$\ll 0.001$
			T	0.022	0.020	0.291
			L:T	0.22	0.085	$\ll 0.001$
			C (Gastropoda)	−0.12	0.021	0.010

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TABLE A10. Multiple regression results using only bivalves, gastropods, and siliciclastic lithologies during carbonate-poor stages, and comparing the model of Table 1 (lines 18–20) with a model that also includes class (C) as a factor.

Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	*p*-value
$R_{coll} \sim M + S$	49217	4×10^{-7}	M	0.065	0.044	0.146
			S (small)	0.038	0.040	0.343
			S (large)	−0.026	0.032	0.414
$R_{coll} \sim M + S + C$	49188	~1.0	M	−0.014	0.047	0.764
			S (small)	0.044	0.040	0.268
			S (large)	−0.026	0.032	0.412
			C (Gastropoda)	−0.16	0.029	$\ll$0.001

TABLE A11. Multiple regression results using only bivalves, gastropods, and siliciclastic lithologies during carbonate-rich stages, and comparing the model of Table 1 (lines 21–23) with a model that also includes class (C) as a factor.

Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	*p*-value
$R_{coll} \sim M + S$	42475.6	0.555	M	1.00	0.039	$\ll$0.001
			S (small)	−0.38	0.045	$\ll$0.001
			S (large)	−0.082	0.033	0.014
$R_{coll} \sim M + S + C$	42476.1	0.445	M	0.98	0.041	$\ll$0.001
			S (small)	−0.38	0.045	$\ll$0.001
			S (large)	−0.085	0.034	0.012
			C (Gastropoda)	−0.041	0.033	0.21

TABLE A12. Multiple regression results using only bivalves, gastropods, and limestone lithologies during carbonate-poor stages, and comparing the model of Table 1 (lines 24–26) with a model that also includes class (C) as a factor.

Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	*p*-value
$R_{coll} \sim M + S$	1899.0	0.003	M	0.62	0.18	0.0006
			S (small)	−0.87	0.37	0.018
			S (large)	0.60	0.18	0.0011
$R_{coll} \sim M + S + C$	1887.2	0.997	M	0.34	0.19	0.074
			S (small)	−0.85	0.37	0.021
			S (large)	0.62	0.18	0.0008
			C (Gastropoda)	−0.64	0.17	0.0003

TABLE A13. Multiple regression results using only bivalves, gastropods, and limestone lithologies during carbonate-rich stages, and comparing the model of Table 1 (lines 27–29) with a model that also includes class (C) as a factor.

Model	AIC	Akaike weight	Factor	Regression coefficient	Standard error	*p*-value
$R_{coll} \sim M + S$	8772.8	0.006	M	2.14	0.071	$\ll$0.001
			S (small)	−0.34	0.15	0.021
			S (large)	0.59	0.084	$\ll$0.001
$R_{coll} \sim M + S + C$	8762.5	0.994	M	2.00	0.079	$\ll$0.001
			S (small)	−0.34	0.15	0.020
			S (large)	0.59	0.084	$\ll$0.001
			C (Gastropoda)	−0.30	0.088	0.00051

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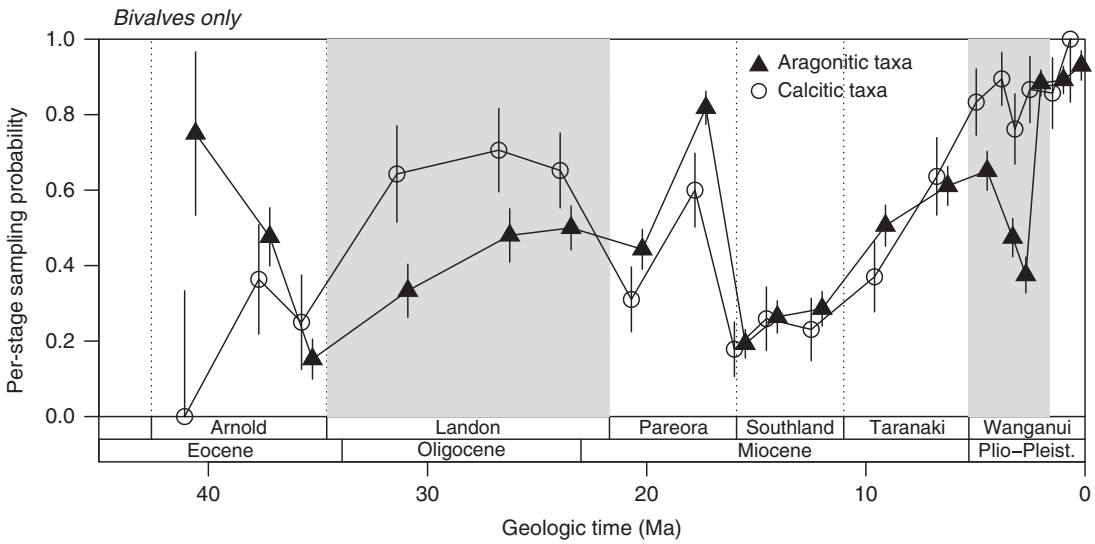

FIGURE A1. Per-stage sampling probability of aragonitic and calcitic bivalves; compare to Fig. 1A. Results of Fig. 1A hold within bivalves, indicating that the difference between aragonitic and calcitic sampling is not merely a reflection of the sampling of gastropods versus bivalves.

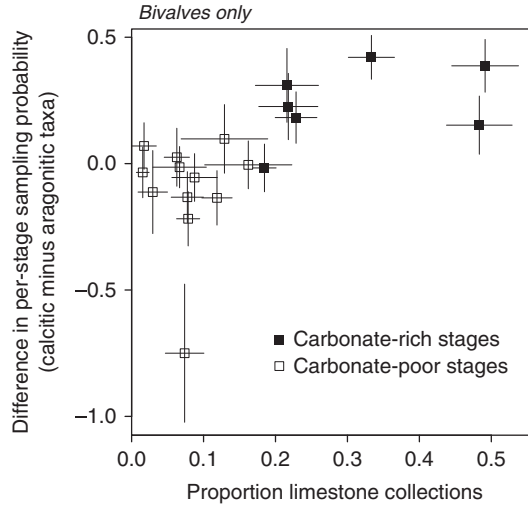

FIGURE A2. Difference in per-stage sampling probability for calcitic versus aragonitic bivalves (from Fig. A1), plotted against proportion limestone collections (from Fig. 1B). As indicated by Fig. A1, temporal variation in the difference between aragonitic and calcitic sampling transcends the difference in sampling between gastropods and bivalves.

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