Second-Order Sequence Stratigraphic Controls on the Quality of the Fossil Record at an Active Margin: New Zealand Eocene to Recent Shelf Molluscs

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New Zealand has the most complete Cenozoic molluscan fossil record in the Southern Hemisphere. In order to understand the true marine faunal history of the region, it is necessary first to identify apparent biodiversity changes that result simply from variations in the quality of the fossil record. The present study uses a range of methods to quantify both long-term, secular changes and short-term patterns of variation in sampling probability for New Zealand Cenozoic shelf molluscs. Overall, about one-third of all once-living Cenozoic species have been sampled, and average per-stage sampling probabilities are between 20% and 50%. Increase in per-stage sampling probability through time reflects the increase in outcrop area and ease of fossil recovery from older to younger stages. Short-term patterns of variation apparently are related to second-order sequence stratigraphic controls of preservation potential. Once the effects of stage duration are eliminated, patterns of stage-to-stage sampling probability reflect enhanced preservation in mid-cycle positions and, perhaps to a lesser extent, secondary post-depositional loss of stratigraphic record above and below sequence boundaries. Although this result mirrors patterns observed in Europe, it is possible that enhanced preservation mid-cycle is relatively more important at active margins, such as New Zealand, whereas secondary loss of record at the sequence boundary is more important at passive margins. Finally, it is worth noting that different methods and data compilations yield rather consistent estimates of short-term variation in sampling probability, lending confidence to the methods and suggesting that the patterns identified are likely to reflect true underlying features of the New Zealand marine fossil record.

INTRODUCTION

Since the writings of Darwin (1859), incompleteness of the fossil record has been perceived as a major barrier to the meaningful interpretation of paleobiological patterns through geological time (e.g., Newell, 1959; Raup, 1976; Paul, 1998). Despite this, the effects of large-scale preservational biases on first-order, apparent biodiversity patterns largely have been ignored since the widely cited consensus paper of Sepkoski et al. (1981). Indeed, most studies explicitly or implicitly have assumed uniform sampling and preservation over time (e.g., Sepkoski and Raup, 1986). Recently, there has been a resurgence of interest in this problem, and several workers have sought to quantify the completeness of the fossil record using a variety of methodologies (e.g., Valentine, 1989; Paul, 1998; Foote and Sepkoski, 1999; Connolly and Miller, 2001; Foote, 2003). Alongside these developments, the implications of non-random or biased incompleteness in the record have been explored in a number of papers, notably Peters and Foote (2001), Smith (2001), and Smith et al. (2001).

Estimates of the quality of New Zealand's fossil record of shelf molluscs presented herein form part of a larger study of New Zealand Cenozoic marine molluscan biodiversity. In this context, estimates of the completeness of the fossil record are important because they underpin inferences about patterns and controls of marine-mollusc biodiversity history. Given New Zealand's (paleo)oceanographic and isolated biogeographic setting, such inferences are important on a global scale because they represent the only available data from a large sector of the southwestern Pacific. Moreover, for the last 20 million years, New Zealand has straddled an active, convergent plate boundary. In contrast, other recent studies of the causes and effects of biases in the fossil record have been based largely on data from stable cratonic regions (North America and Western Europe). It is important to determine whether the fossil record of an active margin is influenced by the same geological biases that affect the records of passive margins and stable cratonic regions (c.f., Kidwell, 1988).

Beu et al. (1997) argued that New Zealand's fossil record

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of Cenozoic molluscs is extremely good—the best available in southern mid- to high latitudes. Johnson and Curry (2001) quantified the completeness for Plio-Pleistocene shelf taxa in a single, stratigraphically relatively complete New Zealand basin, inferring that 88% of all once-living mollusc species had been preserved and discovered. This figure can be judged against the global, semi-quantitative assessment of Newell (1959), who speculated that, at the time of writing, perhaps one percent of readily fossilizable species were known. Ten years later, Valentine (1970) suggested that this figure lay between 3% and 25%, and that the maximum potential completeness for readily preserved species is perhaps 50% to 75%.

The aims of the present paper are two-fold. First, a range of established methods are used to quantify per-stage sampling probabilities and the overall completeness of New Zealand's fossil record of shelf molluscs over the past 65 Ma. Two important components of temporal variation are of interest: short-term, stage-to-stage patterns, and long-term, secular changes. Second, large-scale geological factors that control sampling probability are examined. The data used essentially are complete, inasmuch as they represent the total known fossil record of shelf molluscs from New Zealand. The study is restricted to shelf taxa because these taxa dominate the fauna (>82%, data from Crampton et al., 2003; and see below). In this way, debates and uncertainties regarding the environmental locus of maximum molluscan biodiversity in the marine realm are avoided (e.g., Gray, 2001; Smith, 2001). It is also important to note that this study is focused on estimates of the quality of the fossil record, not biodiversity per se. Thus, conclusions regarding geological controls of fossil-record quality will not be confounded by truly biological variations in diversity and turnover.

With the risk of stating the obvious, when examining the issue of completeness of the record, there are certain caveats that must be borne in mind. There are two distinct components of completeness that are, in practice, hard to separate and quantify independently. First, there is interest in how complete the fossil record is—the proportion of taxa living at any time that were captured in the sedimentary archive. The vast majority of paleontological research is concerned only with the highly preservable components of any biota—the skeletonized taxa. These taxa may comprise only approximately 10% of all Phanerozoic species (Paul, 1998). The important point is that, in most studies, estimates of completeness have meaning only in the context of a specified subset of life with a particular set of sampling probabilities. The present study considers only shelly Mollusca; estimates of completeness for planktic foraminifera or annelids will be very different and subject to very different biases (e.g., Foote and Sepkoski, 1999). Second, it is desirable to know the proportion of these fossilized taxa that actually have been discovered and registered in the paleontological literature or databases. This will vary with geographic region, by age of the strata, and according to various monographic biases—for example, the fossil faunas of Europe are more thoroughly described than those of Antarctica. Therefore, estimates of completeness have a geographic and stratigraphic context that is key to understanding any particular result.

In the following discussion, "per-stage sampling probability" (R) is used to mean the average probability that any taxon ranging through an entire given stage will have been sampled and recorded at least once from that stage. In other words, this and other measures described below are aimed at the joint probability that a taxon was captured in the fossil record and has been sampled. The methods employed here cannot separate these elements. "Per-taxon per-stage sampling rate" (r) is the number of occurrences per taxon (lineage) per stage and is related to R in the following way (Foote, 2003): $R = 1 - e^{-r}$. "Completeness" is used in the sense of Foote and Raup (1996) to indicate the proportion of taxa that have been sampled and recorded at least once across all stages in the window of observation (i.e., across the entire study interval). Clearly, the relationship between per-stage sampling probability and overall completeness will depend on the average taxon duration or its inverse, the average per-stage extinction rate, $\bar{q}$. In the simplest case, if assuming an infinite window of observation, and that $\bar{q}$ is equal to the average origination rate, then:

$$\text{completeness} = \frac{\bar{r}}{(\bar{r} + \bar{q})}$$

where $\bar{r}$ is the average per-taxon per-stage sampling rate (see discussions in Foote, 1997; Solow and Smith, 1997).

MATERIALS

This study is based on Cenozoic marine gastropods, bivalves, and scaphopods from New Zealand (including the Chatham Islands). Analyses were undertaken at genus level (genera + subgenera) and species level (species + subspecies), henceforth referred to as genus and species, respectively, for convenience. Geological ages are given in terms of the 24 New Zealand Cenozoic stages, with an average duration of 2.7 m.y. (standard deviation = 2.2 m.y., maximum 9.5 m.y., minimum 0.34 m.y.; see Fig. 1; Cooper, 2004). Although age calibrations of these stages and their correlations to the international timescale have changed significantly over the past 50 years, the concepts of the stages within New Zealand have remained relatively stable over this period, and stage names have been applied consistently. For this reason, the ages of taxa, collections, and lithostratigraphic units can be compared reliably, even when dealing with data of varying vintage.

As described elsewhere (Crampton et al., 2003), the fossil record of Cenozoic molluscs in New Zealand has been remarkably well documented. This study employs two distinct datasets. The first, the synoptic dataset, comprises stratigraphic ranges and paleoecological data for 5,241 species, 1,949 of which are undescribed, and 1,272 genera of Cenozoic molluscs. These data have been compiled over several years and earlier versions of the dataset are described in Beu and Maxwell (1990), Spencer et al. (in press), and Crampton et al. (2003). The present study was restricted to soft-substrate, benthic taxa that are inferred to have been confined to, or to have ranged into, shelf water depths (i.e., less than ~200m water depth). Forms that were restricted to estuarine, rocky-substrate, bathyal, or abyssal habitats, and pelagic taxa, were excluded. Inferred paleoecological habits of each species were based on uniformitarian principles, lithofacies and faunal associations (including microfossil data), and general stratigraphical considerations (Crampton et al., 2003). The

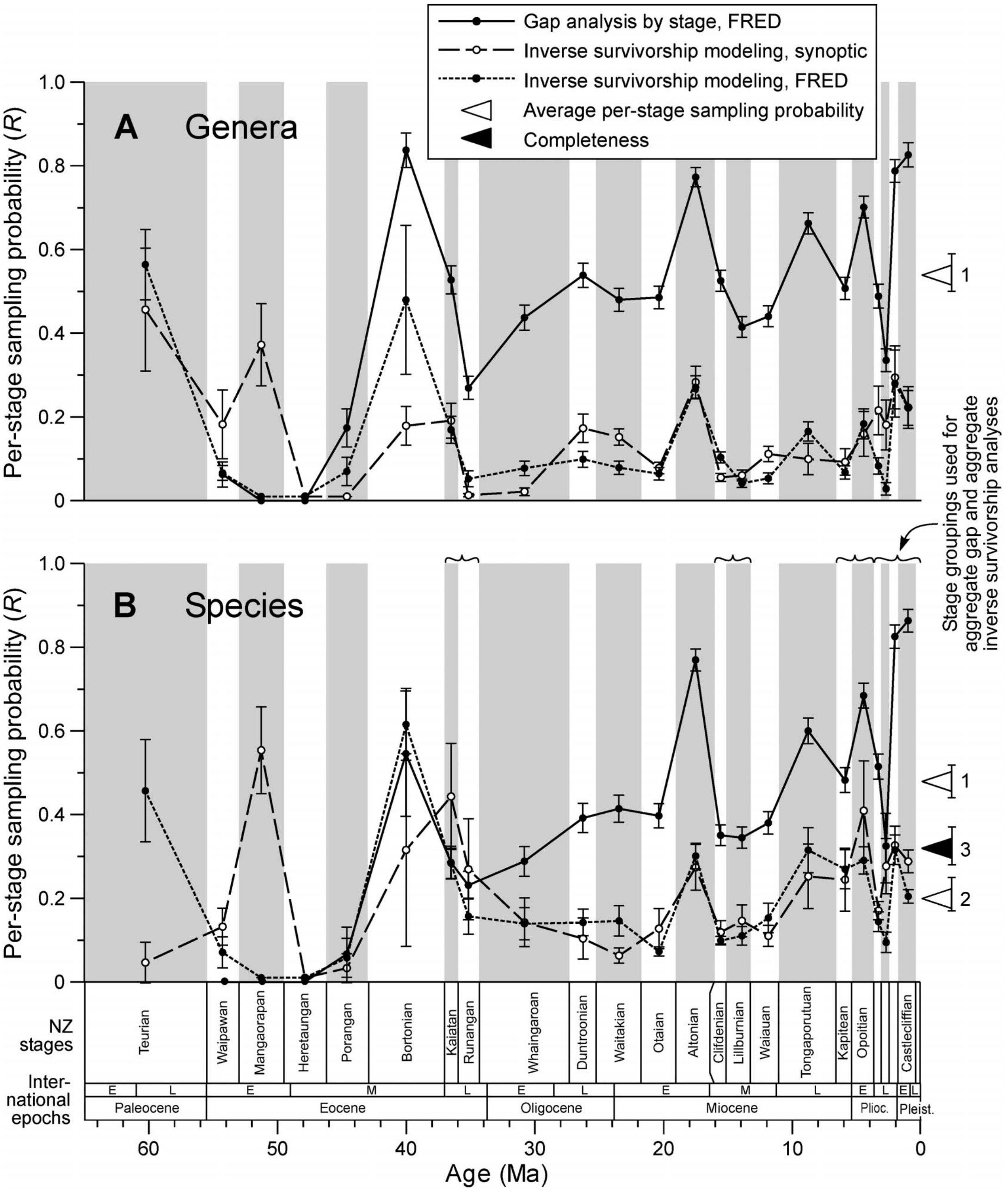

FIGURE 1—Plots of per-stage sampling probability (R), average per-stage sampling probability ($\bar{R}$), and completeness against geological time for genera (A) and species (B) of New Zealand Cenozoic shelfal molluscs (see Appendix 1). In this and subsequent plots, both the New Zealand stages and international epochs are shown on the x-axis. For clarity, New Zealand stages are indicated with gray and white bars. The six youngest stages are, in ascending order, the Opoitian, Waipipian, Mangapanian, Nukumaruan, Castlecliffian, and Haweran. R was derived using gap analysis by stage (FRED dataset) and inverse survivorship modeling (synoptic and FRED datasets); data points are shown ± 1 standard error. $\bar{R}$ was derived using aggregate gap analysis (labeled 1) and aggregate inverse survivorship modeling (labeled 2, for species only); 95% confidence intervals are shown. Note that for the calculation of $\bar{R}$, the shortest stages were grouped as indicated at the top of the species plot. Completeness for species only was derived using aggregate inverse survivorship modeling (labeled 3); the 95% confidence interval is shown.

study was restricted in this manner because extra-shelf marine molluscs are greatly underrepresented in the New Zealand fossil record. This reflects the relatively low abundance of fossiliferous estuarine, bathyal, and abyssal facies, and/or the low abundance of mollusc fossils within those facies. Although the quality of the record of bathyal and deeper fossils is of interest, this should be assessed independently of the shelf record.

In addition, data from areas north of Auckland were excluded (northernmost New Zealand). This is because these comparatively rich faunules apparently represent a distinct biogeographic component in the New Zealand mollusc fauna that is not represented elsewhere in the country (Beu and Maxwell, 1990; Maxwell, 2002). Because the Northland faunules are restricted to just a brief interval of time—they are essentially all Otaian to Altonian in age (Early Miocene, 21.7–16.0 Ma)—their inclusion in the analyses would have biased estimates of completeness and sampling probability for those stages. Following these adjustments, the synoptic dataset contains 2,985 species, of which 1,091 are undescribed, and 917 genera.

The second dataset used in this study was derived from the New Zealand Fossil Record File Electronic Database (the FRED dataset; see Crampton et al., 2003). The FRED contains 6,154 collection lists of Cenozoic molluscs. Each list records all taxa identified in a particular collection (a collection being a sample taken by one or more paleontologists from a single locality on a single occasion). Given differences in sampling and recording practices between paleontologists and over time, a single locality might comprise a single bed or horizon, several beds, or an entire outcrop. Stratigraphic ages assigned to collection lists in the FRED are based on paleontological content (including microfossils) and, in some cases, stratigraphic context, and are given at the resolution of New Zealand stages. As was done for the synoptic dataset, the FRED data were culled to include only soft-substrate, benthic, shelf taxa, and to exclude 167 collections from Northland.

The raw collection lists contain data of varying vintage and quality. Prior to analysis, all lists were edited and updated, both by hand and using automated pre-processing routines. First, all lists prepared by Suter in the early Twentieth Century were eliminated because they are known to be taxonomically unreliable (Beu and Maxwell, 1990). Second, collection lists that are not dated to single-stage resolution (i.e., span two or more stages; 39% of all lists at stage resolution) also were eliminated. Analyses in which such collections were retained and assigned randomly to one or other of their possible stages during repeated trials, using assignment weights for each stage proportional to the relative stage duration, introduced excessive noise and were comparatively poorly constrained; these results are not reported here. Third, duplicated data (i.e., multiple lists for a single collection deriving from full or partial re-examination) were amalgamated or culled so that each valid taxonomic occurrence was represented just once for any given collection. Fourth, questionable or uncertain taxonomic assignments were treated in the same way as unambiguous identifications. In other words, open nomenclature, inverted commas, or question marks simply were removed from the taxonomic names. Fifth, new or un-named species-level taxa that are identified in the original lists using an alphanumeric modifier or manuscript name were regarded as valid taxa during analysis. This means, for example, that "*Turritella* n. sp. a" was regarded as a single, valid species across all collections in which it is listed. This assumption will be violated in some unknown proportion of cases. The approach is justified, however, because the vast majority of the taxonomic lists were created by just a few taxonomists and, in many instances, the alphanumeric identifiers have been used consistently to represent the same species-level taxon, even by different taxonomists. (In fact, 76% of the faunal lists were prepared by just three taxonomists: A.G. Beu, C.A. Fleming, and J. Marwick. Of the remaining lists, 16% do not record the identifier and 8% were compiled by 49 different paleontologists.) Lastly, all taxonomic names were checked against a list of synonyms and, if necessary, junior synonyms were replaced by their revised names. Following these adjustments, the FRED dataset analyzed here contains 5,741 collection lists, 2,059 species, and 827 genera.

Information on New Zealand's Cenozoic stratigraphic record has been compiled for this study from a synthesis of sedimentary patterns that was, itself, based on a series of synoptic basin studies (King et al., 1999; and references therein). King et al. (1999) employed 39 relatively evenly spaced and representative transects across New Zealand's eight major Cenozoic sedimentary basins and, for each transect, summarized chronolithostratigraphic patterns. Importantly, they used only significant or representative lithostratigraphic units that best characterize the major features of basin history; they ignored those that have restricted geographic extent or those considered synonyms of other included units. For the present study, a list of all sedimentary units thus identified by King et al. (1999) was compiled; these vary in formal rank from member to group. Units that do not crop out onshore were excluded. Because of the synthetic nature of this compilation, the authors judge that it better characterizes the New Zealand sedimentary rock record than similar lists based simply on all named formations (e.g., Crampton et al., 2003; and references therein). In particular, the designation of formation rank is somewhat subjective, and will be influenced by the level of knowledge of a given region or basin, the degree of chronostratigraphic control, and the extent to which a particular stratigrapher is a splitter or a lumper. In contrast, the units included in the present analysis are likely to have relatively comparable status in a hierarchy of paleogeographic and genetic significance. However, they need not be similar in terms of thickness, outcrop area, or volume. The present list will not capture all valid, comparable lithostratigraphic units, but it will include the representative subset that is intersected in the transects of King et al. (1999).

For each of these units, information on age (in terms of New Zealand stages), distribution (by sedimentary basin), major sedimentary facies, and inferred environment of deposition was compiled. Most of the data on age, distribution, and facies were taken directly from King et al. (1999). Information on environment of deposition was taken from individual basin studies used as sources by King et al. (1999) and from the primary literature; key references are too numerous to be listed here but can be found in the New Zealand on-line stratigraphic lexicon (<http://data.gns.cri.nz/stratlex/index.jsp>). The present study focused on the following stratigraphic parameters derived from this compilation: numbers of units that were deposited, entirely or in part, on the shelf; and numbers of these shelf units that are dominated by carbonate, siliciclastic-mud (clay and silt), or coarse-siliciclastic facies (sand, conglomerate, and breccia).

METHODS

Existing methods for estimating the quality of the fossil record typically employ either just the observed stratigraphic ranges of taxa, encoded as the stages of first and last occurrence, or, additionally, information on occurrences within those ranges. Using the synoptic (first and last occurrences) and FRED (occurrences within ranges) datasets, this study was able to use both general approaches and three different methods. The methods used have been described elsewhere and are not detailed here; for full explanations, the reader should consult the cited references.

Gap Analysis

First, using the FRED dataset, range-through taxa—those taxa that are known to range through a given stage and both its boundaries—can be used to estimate the per-stage sampling probability, R. This method has been applied widely to diverse fossil groups (e.g., Paul, 1982, 1998; Allmon, 1989; Harper, 1998; Foote, 2001; Jablonski et al., 2003; an application of the method in a cladistic context is presented in Smith, 1988). Henceforth, this approach is referred to as "gap analysis by stage." For each stage, the number of range-through taxa actually recorded in that stage is determined as a proportion of the total known number of range-through taxa. Because range-through taxa had the potential to be preserved at any point within a given stage, the proportion that have left no record is an estimate of the overall probability of non-preservation in that stage. Binomial standard errors are calculated as:

$$SE(R) = \sqrt{R(1 - R)/X}$$

where X is the total number of known range-through taxa (Foote, 2001).

This approach also can be used to approximate average per-stage sampling probability, $\bar{R}$, for the entire Cenozoic record by summing, for all range-through taxa in all stages, the number of recorded stage occurrences and dividing this by the sum of the total known durations (aggregate gap analysis). These summations exclude stages of first and last occurrence that will, of course, by definition contain taxon occurrences (cf., Paul, 1982; see Foote and Raup, 1996, p. 128). In this way, the individual terms of the calculation consider only those stages over which a taxon has known freedom to occur or not, and ignore unsampled and unknowable range extensions beyond the first- and last-occurrence records. To make the results of this analysis exactly comparable to aggregate inverse survivorship analysis (see below), uneven stage durations were minimized by grouping the shortest stages to create 17 time bins, as shown on Figure 1 (average bin duration 3.8 m.y., standard deviation 2.0 m.y., maximum 9.5 m.y., minimum 1.7 m.y.). Ninety-five-percent confidence limits were calculated using the binomial standard error (equation given above).

Inverse Survivorship Modeling

Second, estimates of r (per-taxon per-stage sampling rate) were obtained using the inverse survivorship modeling approach of Foote (2003). This method uses maximum likelihood parameter estimation based on forward and backward survivorship probabilities derived from observed ranges of taxa (for an explanation of survivorship analysis in this context, see Foote, 2001). The method ignores occurrences within ranges. Because the parameter space is large and the number of possible solutions enormous, maximum likelihood optimization cannot be exhaustive but must employ a gradient-based search algorithm (Foote, 2005). In addition to r, the model also yields estimates of extinction and origination rates, although these are not discussed here. The method assumes stochastically uniform probabilities across all taxa within a stage, but is fully varying between stages. Importantly, either continuous or pulsed turnover can be modeled—in other words, it can be assumed either that origination and extinction were concentrated at stage boundaries, or that they occurred at a constant per-capita rate throughout a given stage (Foote, 2003, 2005). In the case of both New Zealand Cenozoic molluscs and the global marine fossil database of Sepkoski (2002), the pulsed model is supported more strongly than the continuous model (Foote, 2005). For this reason, in the present discussion, only the results for pulsed turnover are reported, although this subject will be explored in more detail elsewhere. In the present study, both the FRED and synoptic datasets were analyzed using this method. Standard errors were estimated using 100 bootstrap replicates.

Finally, $\bar{R}$ and completeness were estimated using the approach of Foote and Raup (1996) and the extension of this method developed by Foote (1997; aggregate inverse survivorship modeling or FreqRat of Foote and Raup, 1996). This approach exploits useful relationships between the frequency distributions of observed taxon ranges, the estimated extinction rate, and the overall per-time bin sampling probability. Again, the method ignores occurrences within ranges. It assumes stochastically constant extinction and sampling probabilities through time and that the original distribution of taxon durations was exponential (i.e., survivorship was exponential), although Foote and Raup (1996) inferred that it is robust to modest violations of all these assumptions. The method also assumes sub-equal stage durations; thus, the shortest stages were grouped, as described above for aggregate gap analysis, and shown on Figure 1. The calculations were performed using maximum likelihood parameter estimation as described by Foote (1997). Using this approach, 95% confidence limits are approximated by the three-unit maximum likelihood support region, as explained in Foote (1997, and references therein). Both the FRED and synoptic datasets were analyzed using this method.

RESULTS

In the following discussion, comparisons between different time series using correlation coefficients all employ first differences between successive stages (i.e., the value for a stage minus the value for the preceding stage). This is necessary because, without first differencing, such time series exhibit serial or autocorrelation—any point on the series is likely to be correlated with points immediately before and after (McKinney, 1990). Such autocorrelation may, in turn, induce spurious correlations between different time series. First differencing is a statistically conservative and simple, but effective, way to detrend the series and circumvent this problem. In effect, first differencing means that comparisons examine short-term, stage-to-stage patterns of variation. Henceforth, this procedure is referred to as detrending.

Relationships between first differences for each data series are assessed using Pearson's product-moment correlation coefficient. Use of this coefficient assumes that data are normally distributed. This assumption appears to be justified—using Lilliefors test, none of the data series discussed here is likely to be significantly non-normal. For post-hoc comparisons of several correlation coefficients, in order to account for and control inflation of type I error rates arising from multiple comparisons, individual significance levels are adjusted for family-wise errors using the false discovery rate procedure (Curran-Everett, 2000). In such cases, definition of the family of comparisons in question is determined by the hypotheses and relationships being tested and is explained in the associated table captions (for discussions of these issues, see Rice, 1989; Cabin and Mitchell, 2000). Henceforth, significance levels for correlation coefficients are indicated as follows: "*" signifies $p < 0.05$; "**" signifies $p < 0.01$; "***" signifies $p < 0.001$.

Per-stage sampling probability is expected to increase with increasing stage duration: the longer the stage, the greater the chance for a particular taxon to be preserved at least once. Indeed, the New Zealand mollusc data bear this out—correlation coefficients between R (estimated by gap analysis) and stage duration for genera and species are 0.464* and 0.442*, respectively (data detrended). The same holds true for the New Zealand stratigraphic parameters, which comprise counts of stratigraphic units that also are expected to correlate with stage duration. In contrast, r represents a per-stage rate, and therefore can be normalized for stage duration. In the following discussion, it is convenient to consider both quantities; conversions between the two utilize the equation given in the introduction. Given that stages represent, in the present context, the finest practically resolvable units of time available, then R yields a meaningful measure of relative quality of the fossil record in different stages. In other words, it is useful to know that the fossil record of stage x is twice as good as that of stage y, even if this difference is caused, in part, by differences in stage durations. On the other hand, calculation of r/m.y. allows assessment of the absolute magnitude of changes in the quality of the fossil record through time. Plots of r/m.y. and R are expected to reveal different features of New Zealand's Cenozoic molluscan fossil record.

Because of the expected positive relationships between stage duration and some of the parameters of interest, partial correlation coefficients that are insensitive to the effects of stage duration have been employed where relevant. In other words, these correlation coefficients are based on the residuals from linear regressions of each parameter against stage duration (all calculated using the detrended data). In the text, partial correlation coefficients are identified as such.

Estimates of Per-Stage Sampling Probability (R)

Estimates of R based on gap analysis by stage for genera and species are shown in Figure 1 and Appendix 1. By definition, using this method, R cannot be calculated for the first and last stages. Unsurprisingly, both curves show a progressive increase in R from the early Eocene to the Pleistocene that matches the increase in outcrop area (Crampton et al., 2003; and discussed below). Values of R for genera are higher than those for species by, on average, ~8%. This is to be expected, given that for every species record there is a corresponding genus record, but not vice versa. For both taxonomic ranks, there are conspicuous and statistically significant peaks in R in the Bortonian, Altonian, Tongaporutuan, and Castlecliffian stages. Thus, for example, from this method, it would be inferred that of the species of level-bottom, shelf molluscs that actually lived during the Altonian and have been recorded at least once in the FRED dataset, 77% are present in at least one collection from the Altonian. In contrast, only half this number (~40%) has been recorded from the following Clifdenian Stage.

The results of inverse survivorship modeling are shown on Figures 1–2. In general, the estimates of R from this method are poorly constrained and inconsistent for stages older than about the Kaiatan; this reflects the relatively sparse data for these older stages. If the results of gap analysis are compared by stage to both sets of results from inverse survivorship modeling, then a number of patterns are evident.

First, estimates of R derived by inverse survivorship modeling are relatively low compared to those calculated using gap analysis (Fig. 1). In fact, the generic curves for inverse survivorship modeling are inconsistently low even in comparison to their corresponding species-level curves. This suggests that the values of R calculated using inverse survivorship modeling are underestimates, at least in the case of genera, and possibly for both taxonomic levels. Second, curves for the inverse survivorship method fail to detect the long-term trends that are evident in the results from gap analysis. Possible explanations for these differences between survivorship analysis and other methods are given in the discussion below. Third, and in contrast, short-term, stage-to-stage patterns of variation in R are similar between the two methods and two datasets; most partial correlation coefficients are significant (compare Figures 1, 2, and Table 1). For each taxonomic level, certain key features of the curves are identified consistently. In the case of genera, these features are peaks or marked increases in R in the Bortonian–Kaiatan, Altonian, Nukumaruan, and, to a lesser extent, Duntroonian. For species, peaks or increases occur in the Bortonian, Altonian, Tongaporutuan, Opoitian, and Nukumaruan stages. Clearly, however, there are also some differences between the plots. For each taxonomic level, if the detrended data and partial correlation coefficients (Fig. 2, Table 1) are considered, then it can be seen that the shapes of the two curves derived from the FRED dataset are more similar to each other than either is to the curve for the synoptic dataset. Patterns of short-term variation derived for the FRED dataset using the two methods are very similar indeed, and really differ only in magnitude (Fig. 2). In other words, short-term signals in the data appear to be robust to the methods of estimation used here.

From these results, both a method effect and a database effect can be identified in the estimates of R. The method effect relates to the differences in magnitude between the two sets of estimates and the detection of a long-term trend by gap analysis by stage but not by inverse survivorship modeling. The database effect relates to differences between datasets in patterns of stage-to-stage variation in R. Most importantly, it should be stressed that the differ-

TABLE 1—Partial correlation coefficients (Pearson's product-moment correlation coefficient) between estimates of *R*, outcrop area (from Crampton et al., 2003), number of shelfal lithostratigraphic units, and numbers of shelfal units that are characterized by mudstone, sandstone, or carbonate contents (see Appendix 2). Entries above the diagonal are for all stages from the Mangaorapan to the Castlecliffian (Early Eocene–Pleistocene, see Fig. 2); entries below the diagonal are for the Otaian to the Castlecliffian (Neogene). Correlation coefficients are based on the residuals of regressions of the detrended data against stage duration. All significant correlations ("*" signifies $p < 0.05$; "**" signifies $p < 0.01$; "***" signifies $p < 0.001$) are shown in bold. Significance levels have been adjusted for family-wise error rates; for comparisons between different estimates of *R*, the family is taken to include just those estimates and the number of tests is 15; for comparisons between *R* and lithostratigraphic data, the number of tests is 45.

			Gap analysis by stage FRED dataset		Inverse survivorship modeling Synoptic dataset	
			R. species	*R.* genera	*R.* species	*R.* genera
Gap analysis by stage	FRED dataset	*R.* species		**0.910*****	0.336	**0.571***
		R. genera	**0.956*****		0.329	**0.516***
Inverse survivorship modeling	Synoptic dataset	*R.* species	0.461	0.486		**0.719*****
		R. genera	**0.760****	0.592	0.302	
	FRED dataset	*R.* species	**0.870*****	**0.825****	0.558	**0.744***
		R. genera	**0.946*****	**0.961*****	0.544	**0.727***
Outcrop area			0.129	0.268	0.344	−0.153
Number of shelfel units			0.521	0.451	0.594	0.665
Shelfal units, mudstone			0.265	0.198	0.466	0.535
Shelfal units, sandstone			0.609	0.643	0.602	0.441
Shelfal units, carbonate			0.205	0.119	0.089	0.358

ent methods and datasets agree well in their estimates of stage-to-stage variation in sampling probability, *R*.

Estimates of Per-Taxon, Per-m.y. Sampling Rate (*r*)

Estimates of *r*/m.y. derived from gap analysis by stage (Fig. 3, Appendix 1) reveal a secular motif that is different from the pattern shown by *R*. Once the effects of stage duration are taken into account, *r*/m.y. for both genera and species shows an exponential increase towards the Recent, with rapidly accelerating rates of sampling from the Late Miocene onwards. Conspicuous peaks in *r*/m.y. occur in the Kaiatan, Altonian–Clifdenian, Waipipian, and Nukumaruan stages. With the exception of the Altonian, these peaks do not correspond to the peaks in *R*, noted above—clearly, the latter result, to a great extent, from long stage durations.

Considering the plots for *r*/m.y. for inverse survivorship modeling, again it can be seen that they are similar in general shape to those derived from gap analysis, but conspicuously lower in magnitude through the Oligocene to Recent. Correlation coefficients between the two pairs of curves are 0.711*** for genera and 0.187 for species. The low correlation between the species curves results, to a large extent, from anomalous patterns of change in the three late Pliocene stages; if these stages are ignored, then the correlation coefficient increases to 0.619**.

Estimates of Average Sampling Probability ($\bar{R}$) and Completeness

Using aggregate gap analysis, average per-stage sampling probability, $\bar{R}$, was estimated for both genera and species; these values are 0.54 (95% CI: 0.50–0.59) and 0.48 (95% CI: 0.44–0.52), respectively (Fig. 1).

Using aggregate inverse survivorship modeling, $\bar{R}$ and completeness were calculated for species. Although the synoptic and FRED datasets were examined in this way, it appears that species durations in the FRED dataset are significantly and, most probably, spuriously longer than those in the synoptic data (Fig. 4). Indeed, as calculated using aggregate inverse survivorship modeling, the average species duration is 5 million years for the synoptic data and 17 million years for the FRED data. The long average duration determined for the FRED dataset almost certainly reflects, to a large extent, the effects of taxonomic lumping and the presence of dustbin taxa in this set. Although such biases were reduced by the data-cleaning routines described previously, they were not eliminated. To remove the effects of taxonomic lumping entirely would require reexamination of a large amount of fossil material—a time-consuming task that is beyond the scope of the present study. The average duration of 5 million years determined for species in the synoptic dataset is well within the range determined for marine molluscs elsewhere (e.g., Stanley and Yang, 1987; Foote and Raup, 1996). Thus, the estimates of $\bar{R}$ and completeness derived from the synoptic dataset are favored here: 0.20 (95% CI: 0.17–0.25) and 0.32 (95% CI: 0.28–0.37), respectively (Fig. 1). If just the Neogene is considered, then the corresponding values of $\bar{R}$ and completeness are 0.28 (95% CI: 0.2–0.35) and 0.41 (95% CI: 0.35–0.48).

Note that the presence of spurious range extensions in the FRED dataset will have affected the gap analysis. This effect may have resulted in underestimation of *R* for this method. Preliminary examination of the data suggests that spurious range-extensions of the greatest concern—those that involve several stages—commonly are based on a single, outlying occurrence record. For the stages between this outlier and the true range, therefore, the taxon in question will be recorded as a missing range-through, thus reducing the calculated value of *R*. If these errors are distributed randomly, then patterns of stage-to-stage variation should not have been affected unduly.

Application of aggregate inverse survivorship modeling to the FRED genus-level data is not straightforward for two reasons. First, these data do not show exponential survivorship and, on theoretical grounds, are not expected

TABLE 1—Continued.

	FRED dataset		Outcrop area	Number of shelfal units	Shelfal units, mudstone	Shelfal units, sandstone	Shelfal units, carbonate
	R. species	*R.* genera					
Gap analysis by stage	**0.841*****	**0.904*****	0.144	0.065	−0.063	0.343	−0.119
	0.884***	**0.954*****	0.092	0.026	−0.193	0.425	−0.157
Inverse survivorship modeling	0.321	0.290	0.201	0.063	0.073	0.163	−0.163
	0.485*	**0.497***	−0.055	0.077	−0.035	0.261	−0.050
		0.950***	−0.145	−0.052	−0.116	0.177	−0.169
	0.897***		−0.035	−0.048	−0.162	0.286	−0.198
Outcrop area	−0.073	0.159					
Number of shelfal units	0.513	0.552					
Shelfal units, mudstone	0.303	0.316					
Shelfal units, sandstone	0.488	0.665					
Shelfal units, carbonate	0.254	0.180					

to do so (Raup, 1975). Second, the window of observation is short compared with genus durations. Whereas Foote and Raup (1996) estimated $\bar{R}$ for non-exponential distributions assuming an infinite window of observation, and Foote (1997) estimated $\bar{R}$ for exponential distributions with a finite window of observation, there is no generally accepted method to estimate $\bar{R}$ for non-exponential distributions and a finite window.

Comparisons Between Short-Term Variations in Sampling Probability (R) and the Stratigraphic Record

Major features of New Zealand's Cenozoic marine stratigraphic record are summarized in Figure 5 and in Appendix 2. The number of lithostratigraphic units that were deposited on the shelf peaked in the Early Oligocene—just before the time of first-order maximum marine flooding in the latest Oligocene (King et al., 1999). The rock record is dominated by shelfal units, although bathyal and abyssal units form a significant component in the Oligocene and Miocene. Of the shelfal units, siliciclastic facies dominate, with sandstone and conglomerate forming the largest fraction. Temperate carbonate facies (e.g., Nelson, 1988) are a significant component in the Oligocene and Early Miocene, the interval that has been interpreted as the condensed section associated with first-order maximum marine flooding (see below).

Partial correlations between R and the stratigraphic record are summarized in Table 1. None of these correlations is significant—a reflection, in part, of the large number of post-hoc, simultaneous comparisons being undertaken. Furthermore, correlations for the entire Cenozoic generally are lower than those for the Neogene. Examination of the table reveals, however, that two sets of partial correlations are relatively strongly developed.

First, for the Neogene, R is relatively strongly correlated with the total number of shelfal lithostratigraphic units. This is expected because estimates of R are based on shelf taxa. Previous studies have assumed that the number of units is likely to be a proxy for both facies heterogeneity and outcrop area (Peters and Foote, 2001; Crampton et al., 2003). Data presented here tend to support this conclusion: the lithostratigraphic units are known to correspond to distinctive facies associations, and they are significantly correlated with outcrop area (partial correlation coefficient between total outcrop area—data from Crampton et al., 2003—and total number of marine lithostratigraphic units = 0.474*). Analyses, in which facies information was included more explicitly by summing the numbers of distinct sedimentary facies for each unit to yield a facies heterogeneity index, had a negligible impact on the correlations cited in Table 1. Curiously, R is not correlated with the number of units if the entire Cenozoic is considered. This suggests that, in contrast to the Neogene, the number of Paleogene units is not a significant determinant of the quality of the fossil record. This result may reflect biases in the stratigraphic and/or paleontological records in the Paleogene—for example, lumping of units in the older part of the stratigraphic succession might mask correlations. Alternatively, there may be secular variations in some other underlying geological factor(s) affecting the relationship between the number of units and R. This discrepancy cannot be explained using existing data.

Second, there are relatively strong partial correlations between most estimates of R and the number of shelfal sandstone units. These correlations, interpreted below, are strong for the Neogene window, but also are evident for the entire time series. With a few exceptions, partial correlations between R and either mudstone or carbonate units are generally low. Whereas the temporal distributions of mudstone and carbonate units undoubtedly hold paleogeographic and stratigraphic interest, for the purposes of this study, it is most useful to focus below on the relatively strong correlations shown by sandstone units.

INTERPRETATION AND DISCUSSION

Overall Quality of the Fossil Record and Long-Term Secular Trends

Estimates of completeness and $\bar{R}$ from this and other studies, derived using a variety of methods, are summarized in Table 2. These estimates seem to define two broad groupings. First, those based on Paleogene molluscs from the U.S. Gulf and Atlantic coasts, Pliocene molluscs from Jamaica, and the global dataset of Foote and Sepkoski (1999) are in reasonable agreement with the results presented here. Second, the remaining estimates are all considerably higher. Some of these discrepancies can be explained by differences in methodology (see note on Table 2 regarding Valentine's 1989 study) and/or by the short and

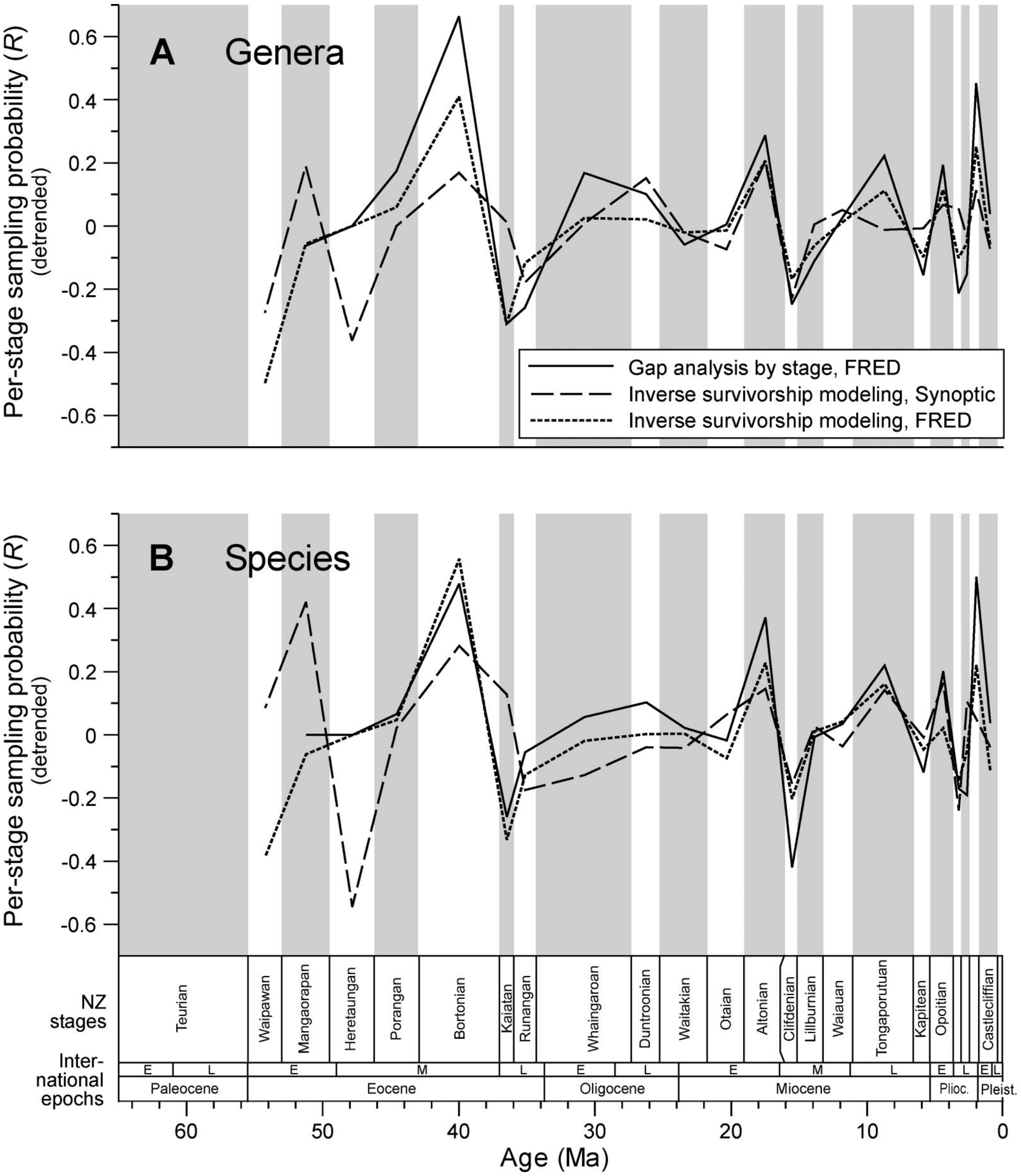

FIGURE 2—Plots of *R* (detrended) for genera (A) and species (B) of the synoptic and FRED datasets as derived by gap analysis by stage and inverse survivorship modeling against geological time (data calculated from Appendix 1). Timescale (x-axis) as for Figure 1.

geologically recent time window under study (Valentine, 1989; Johnson and Curry, 2001). Of note is the study by Foote and Raup (1996) of Jurassic bivalves from Europe: their estimated completeness for species of 90% may reflect nothing more than the relatively expansive Jurassic stratigraphic record in Europe combined with a long history of intense paleontological study.

At the coarsest scale, a previous study has shown that the apparent record of New Zealand Cenozoic molluscan biodiversity is influenced by the number of collections obtained from each time interval (Crampton et al., 2003). The number of collections is, in turn, related to the area of sedimentary rock available for sampling. This result is mirrored here: sampling improves through time, and the youngest stages have, on average, more-complete fossil records than the older stages (Figs. 1, 3). This trend in sampling probability reflects both the increase in outcrop area through the Cenozoic and, probably, the general reduction in induration and concomitant increase in ease of fossil recovery moving up the stratigraphic column. These observed relationships between the fossil record, outcrop area, and geological age are entirely predictable. From the results presented above, however, it is now possible to extend this analysis and attempt to identify the major geological factors that determine short-term, stage-to-stage variations in per-stage sampling probability (R) and sampling rate (r) for the New Zealand Cenozoic molluscan fossil record.

Geological Controls on Short-Term Variations in the Quality of the Fossil Record

Unsurprisingly, R is determined in part by stage duration: the longer the stage, the more likely it is that any tax-

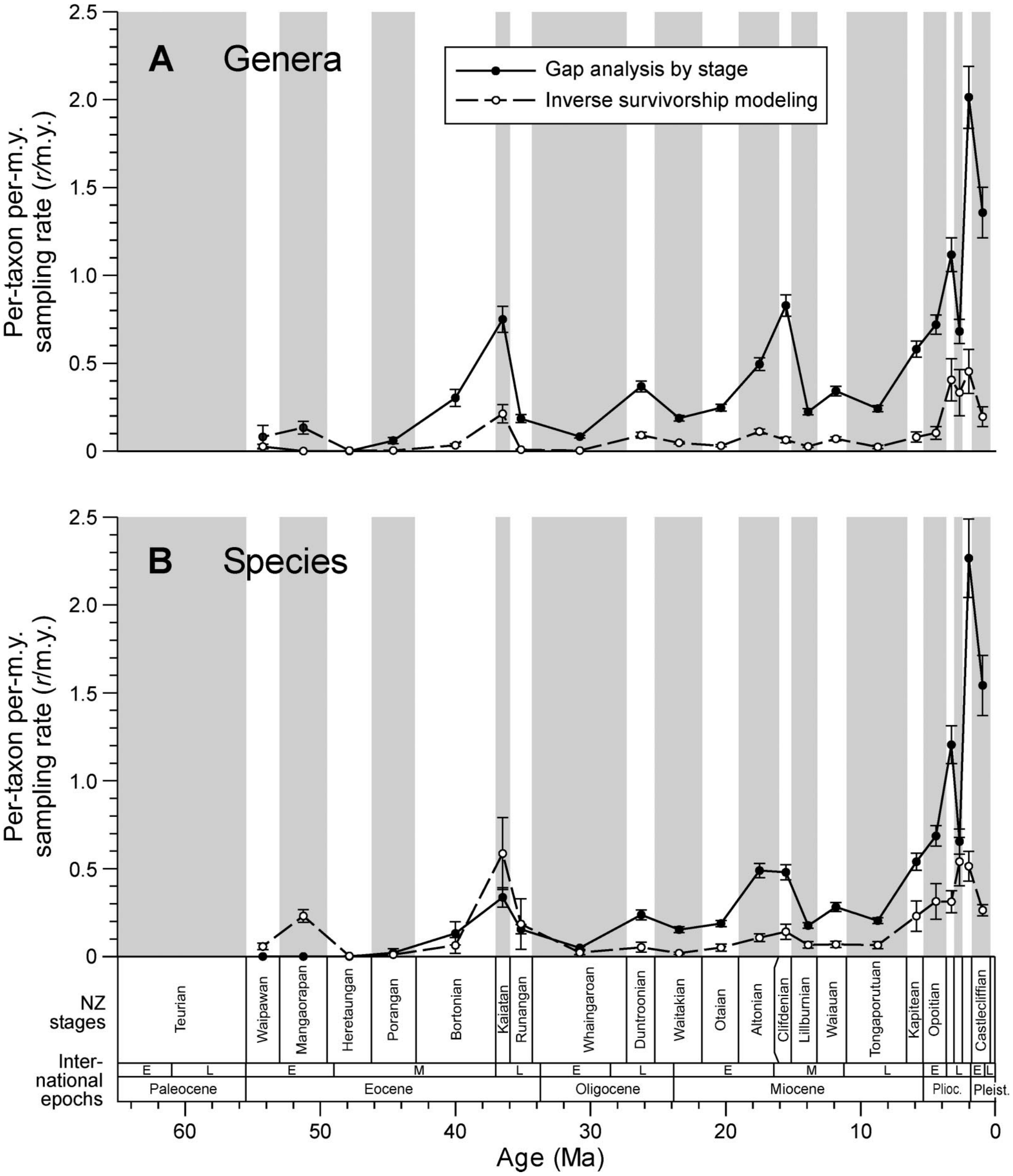

FIGURE 3—Plots of *r*/m.y. for genera (A) and species (B) of the synoptic and FRED datasets as derived by gap analysis by stage and inverse survivorship modeling against geological time (see Appendix 1). Timescale (x-axis) as for Figure 1. For clarity, *r*/m.y. as derived by inverse survivorship modeling is shown for the synoptic dataset only; the curve for the FRED dataset is omitted.

on alive during that time will have been sampled. Indeed, by comparison with *r*/m.y., it is clear that nearly all of the conspicuous peaks in R result from long stage durations. As noted previously, this fact does not necessarily diminish the utility of R as a measure of record quality if the time bins being used represent the finest practicable units of temporal resolution available.

In contrast to the long-term trend, results presented above indicate that once the effects of stage duration are eliminated (by regressing on stage duration), short-term fluctuations in R apparently are insensitive to changes in detrended outcrop area. This result is based on measurements of total outcrop area per stage; at present, outcrop area cannot be determined by paleoenvironmental setting, and it is possible that conclusions based on data thus resolved would be rather different. If true, however, then this result is unexpected. Given this apparent lack of correlation and the significant correlations between shelfal units and R, and if it is accepted that the number of lithostratigraphic units codes primarily for both outcrop area and facies heterogeneity, then for the Neogene data presented here, it can be argued that facies heterogeneity *per se* might be a significant determinant of short-term variation in R. This inference seems reasonable, but the relationship does not hold true for the Paleogene mollusc record in New Zealand and requires testing using more highly resolved areal and paleoenvironmental data.

Second-Order Sequence Stratigraphic Cycles and Stage-by-Stage Variations in Sandstone Units: On Figure 6, the numbers of shelfal sandstone units are plotted together

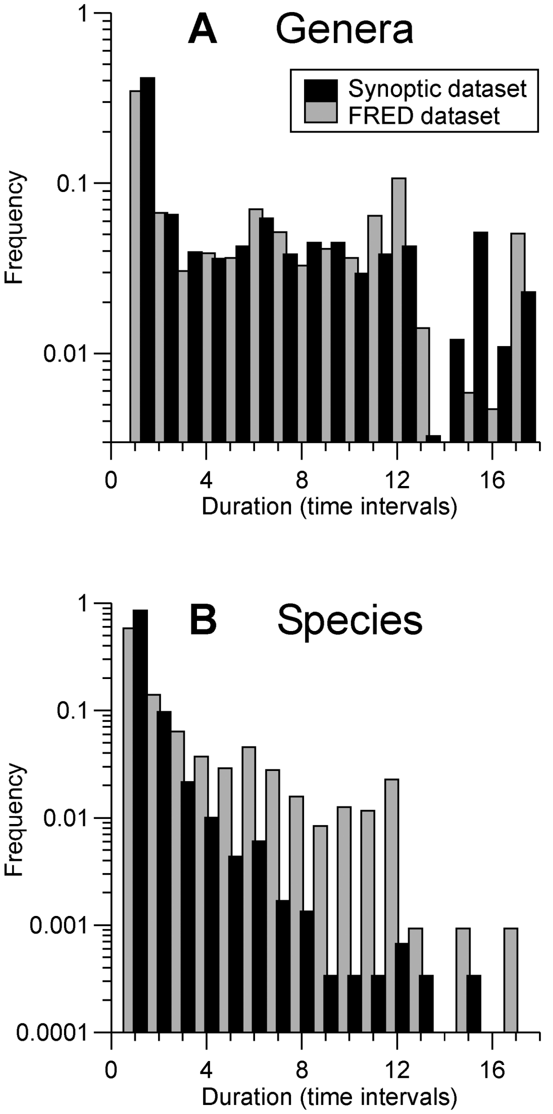

FIGURE 4—Frequency distributions of taxic durations for the synoptic and FRED datasets. Durations are given in terms of the grouped stages of the New Zealand geological timescale indicated on Figure 1.

with the generalized, second-order cycle boundaries of King et al. (1999; see also Carter, 1988a, b; for a discussion of regional variations, see Kamp et al., 2004). A striking feature of this figure is the quasi-periodic shape of the sandstone-units curve and the apparent coincidence of abrupt increases in sandstone units with second-order cycle boundaries. The nature and origin of these second-order cycles are summarized here (after King et al., 1999):

(1) Cycle 3 corresponds to a period of post-rift, thermal subsidence and passive margin development. The cycle is transgressive in character.
(2) The base of cycle 4 marks the regional marine flooding surface associated with first-order flooding of the New Zealand microcontinent. The cycle corresponds to the time of maximum submergence and culmination of passive-margin development. The cycle includes a relatively high proportion of carbonate rocks (Fig. 5).
(3) The base of cycle 5 corresponds to the downlap surface of the first-order highstand/regressive systems tract. This surface marks a base-level fall and the onset of uplift and erosion of clastic source areas coincident with the inception of a discrete, convergent plate boundary through New Zealand. Cycle 5 is regressive in character.
(4) The base of cycle 6 marks a major transition in tectono-sedimentary patterns that relates to a change in plate-boundary configuration. A significant tectonic pulse was manifested by a base-level fall and uplift and erosion within New Zealand. Again, the cycle is regressive in character.
(5) Cycle 7 is strongly regressive in character, and marks an increase in the tempo of convergent-margin uplift. Again, the base of the cycle marks a base-level fall.

As is clear from these descriptions, all the cycles are essentially tectonic in nature—a general characteristic of second-order sequences—and King et al. (1999) suggested that their cycles 3 to 7 were not significantly influenced by eustasy.

From the discussion above and Figure 6, it is concluded that the base of each of cycles 4 to 7 is marked by an abrupt increase in the number of sandstone formations that were deposited at shelf depths on the New Zealand microcontinent. For cycles 5 to 7, this pattern is easily explained by pulses of clastic sedimentation related to tectonic uplift and erosion. Although these second-order cycles, as envisaged in a general sense by Vail et al. (1991) and more specifically King et al. (1999), do not necessarily correspond to complete base-level oscillations, the sandstone signatures also can be interpreted in a classic sequence-stratigraphic sense as comprising shelf sandstones of stacked third- or higher-order sequences within the second-order transgressive systems tract. The sandstone pulse associated with the base of cycle 4 is somewhat different, and probably results from the abundance of greensands overlying the first-order regional flooding surface (King et al., 1999; and references therein).

Relationships Between R*, Sandstone Units, and Second-Order Cycles*: In Figure 6, plots of *R* and the numbers of shelfal sandstone units are compared. Conspicuous on this figure is the general similarity in the shapes of the family of *R* curves and the sandstone-units curve. Late Oligocene and Early Miocene peaks in *R* appear to lag similar peaks in sandstone units by one stage—a factor that undoubtedly reduces the correlation coefficients—whereas Late Miocene and younger peaks are coincident at stage resolution.

Given the relatively high correlations between short-term variations in *R* and sandstone units (both statistical and visual) and the interpretation of sandstone-unit variations given above, it is further suggested that the quality of the molluscan fossil record is related to second-order sequence stratigraphic signals. For cycles 4, 5, and, to a lesser extent, 6, peaks in *R* occur in the mid-part of each cycle (cycle 7 is discussed below). This pattern is in keeping with theoretical predictions and empirical observations from sequence stratigraphy. First, for third- and higher-order sequences, diverse fossil assemblages are concentrated in the condensed section that results from sediment starvation at the top of the transgressive systems tract (TST), just below the maximum flooding surface (MFS) in the

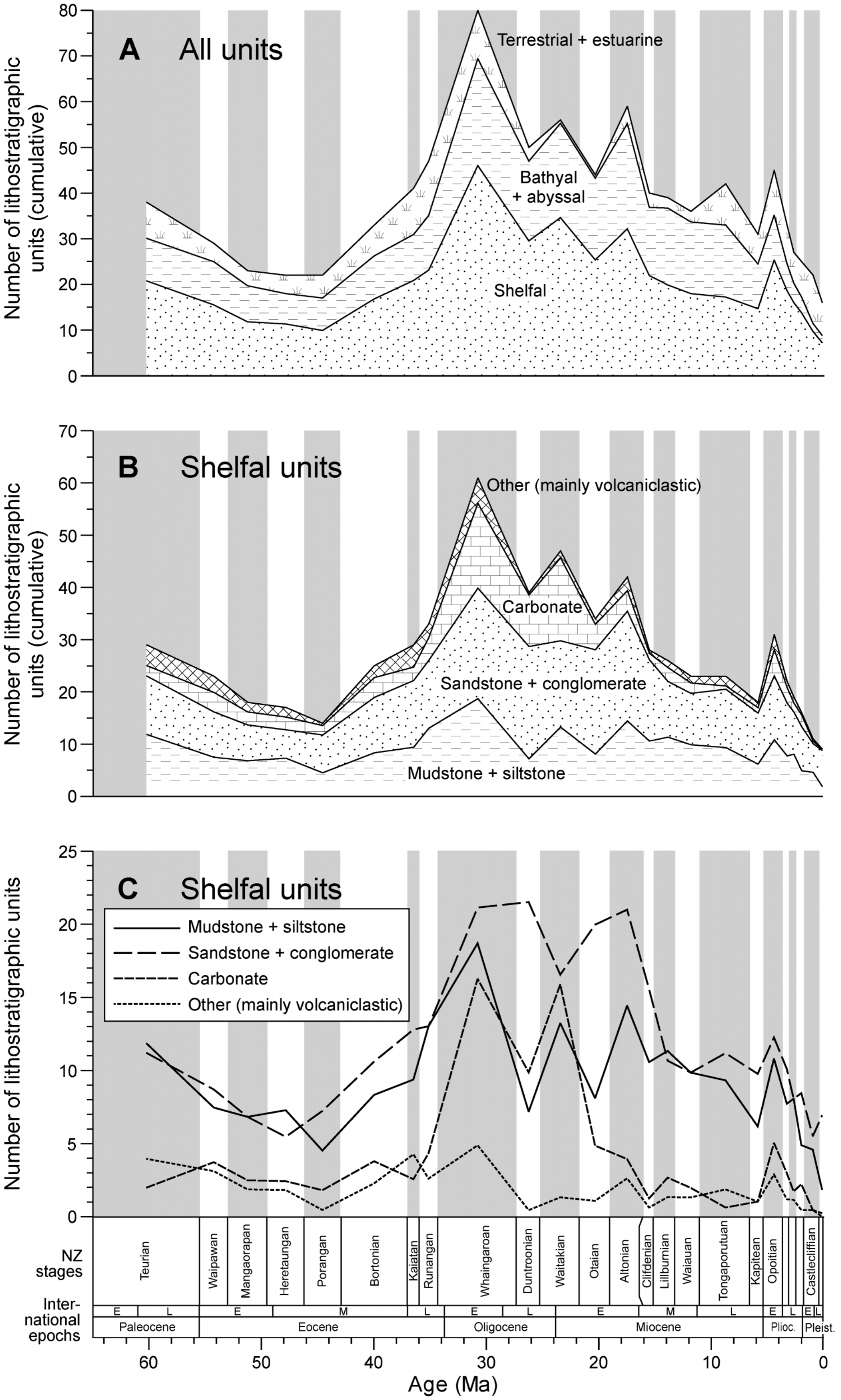

FIGURE 5—Plots of major features of the New Zealand stratigraphic record against geological time (see Appendix 2). Timescale (x-axis) as for Figure 1. (A) Cumulative plot showing breakdown of representative lithostratigraphic units into bathyal + abyssal, shelfal, and terrestrial + estuarine units. (B) Cumulative plot showing principal lithofacies of shelfal units. (C) As for B, but data shown as non-cumulative values.

TABLE 2—Comparisons of estimates of completeness and $\bar{R}$ from this and other studies, derived using a variety of methods. *Note these figures, based on the proportion of living taxa found in the adjacent onshore Pleistocene strata, excluded Recent taxa that were considered to have low fossilization potential or to be very rare. Therefore, Valentine's (1989) estimates of completeness will be inflated compared to those of the present study. † = per-5 m.y. interval; § = per-stage, with an average stage duration of 5.3–5.5 m.y.; ‡ = per-stage (grouped), with an average stage duration of 3.8 m.y.; †† = per-stage (grouped), with an average stage duration of 3.1 m.y.

Region	Taxonomic group	Stratigraphic interval	Completeness (%)		Per-interval sampling probability (%)		Reference
			Genera	Species	Genera	Species	
US Gulf and Atlantic coastal plains	Molluscs	Paleogene		30–50			Allmon, 1989
California	Molluscs	Pleistocene	83	77			Valentine, 1989*
Europe	Bivalves	Jurassic		90		87†	Foote and Raup, 1996
Global	Bivalves	Phanerozoic	84				Harper, 1998
Jamaica	Molluscs	Pliocene	91	50			Paul, 1998
Global	Bivalves	Phanerozoic			45–53§		Foote and Sepkoski, 1999
Global	Gastropods	Phanerozoic			42–56§		Foote and Sepkoski, 1999
Wanganui Basin, NZ	Shelf molluscs	Plio-Pleist		88			Johnson and Curry, 2001
NZ	Shelf molluscs	Cenozoic		32	<54‡	20–48‡	Herein
NZ	Shelf molluscs	Neogene		41		28††	Herein

mid-cycle position (the backlap shellbed of Kidwell, 1991; Kondo et al., 1998). These fossils have high preservation potential because they are mantled subsequently by regressive deposits. In the case of the second-order cycles discussed here, peaks in R in mid-cycle positions may reflect the stacking of successive third- and higher-order condensed backlap shellbeds. Second, these results bear out the theoretical predictions of Holland (2000, fig. 5, and references therein), who modeled the clustering of lowest and highest occurrences near the MFS. Likewise, using empirical evidence from Mesozoic and Cenozoic sedimentary rocks of Western Europe, Smith (2001) argued that the apparent standing diversity of fossil marine animal genera is controlled strongly by second-order sequence stratigraphic architecture. In particular, he also suggested that on the shelf, lowest and highest occurrences tend to cluster at flooding surfaces at the top of stacked TSTs (i.e., close to the maximum flooding surface). Clusters of lowest and highest occurrences will correspond to peaks in R identified here. This follows because, in response to uneven sampling probabilities and compared to levels of true origination and extinction, apparent lowest occurrences will tend to be displaced up-section and apparent highest occurrences down-section, from levels of relatively low sampling probability to levels of high sampling probability. Thus, for New Zealand Cenozoic molluscs, extinction data show the expected pattern: peaks in apparent extinction rate (q) typically coincide with stages of maximum sampling probability (Fig. 7); corresponding sets of R and q measurements are all significantly correlated (Table 3).

Smith and co-workers (Smith et al., 2001) went on to propose that during periods of high sea level, shallow-water facies are deposited on craton interiors as thin, condensed, and perched successions that are highly prone to erosional destruction during subsequent sea-level falls and sequence boundary formation. They suggested that the resultant loss of diverse, shallow-water faunas from the fossil record could result in apparent, but spurious, mass extinctions. Again, this reasoning accords well with the theoretical modeling of Holland (1995, 2000) and Holland and Patzkowsky (1999, 2002). In addition, this pattern of fossil-record destruction was predicted in a qualitative way by Valentine (1989), who argued that incompleteness of the fossil record in well-preserved groups mainly reflects the loss of fossiliferous rock rather than failure of taxa to enter the fossil record. Curiously, however, the present study does not detect Holland's (2000, fig. 5) predicted clustering of lowest and highest occurrences close to the sequence boundary (Figs. 6, 7). Instead, consistently low values of R and q close to the tops of cycles in the New Zealand mollusc data suggest that within the upper part of the highstand systems tract (HST), low diversity, low abundance, and taphonomic destruction *in situ* (Kidwell, 1991; Kondo et al., 1998) have been more important than subsequent, wholesale erosional removal of strata at the sequence boundary. Similarly, low values of R at the base of some cycles—notably cycles 4 and 5—probably reflect faunal dilution by high sediment fluxes, in particular the sandstone pulses already discussed.

To summarize, therefore, whereas it is accepted that some erosional loss of the HST may occur at the overlying sequence boundary, evidence discussed above also indicates that patterns of sampling result equally from enhanced preservation potential mid-cycle. In other words, for New Zealand Cenozoic shelf molluscs, temporal variations in the quality of the fossil record at the second-order scale seem to be the result of primary depositional variations in preservation potential and, perhaps to a lesser extent, secondary post-depositional loss of stratigraphic record. This difference in emphasis may reflect no more than the expected differences in stratigraphic records between an active, convergent margin, as studied here, and a passive margin, as discussed by Holland, Smith, and co-workers. Thus, on the passive margin of a stable craton, accommodation space is limited. In contrast, on an active margin, subsidence, creation of accommodation space, and filling of that space are likely to be ongoing processes in locally forming basins.

For cycle 7, the pattern described above is complicated by the presence of two peaks in both R and sandstone units in the Opoitian and Nukumaruan stages. This complexity probably results from the discrimination of third-order cycles not resolved by King et al. (1999). Specifically, the base of the Nukumaruan Stage, at 2.4 Ma, was ap-

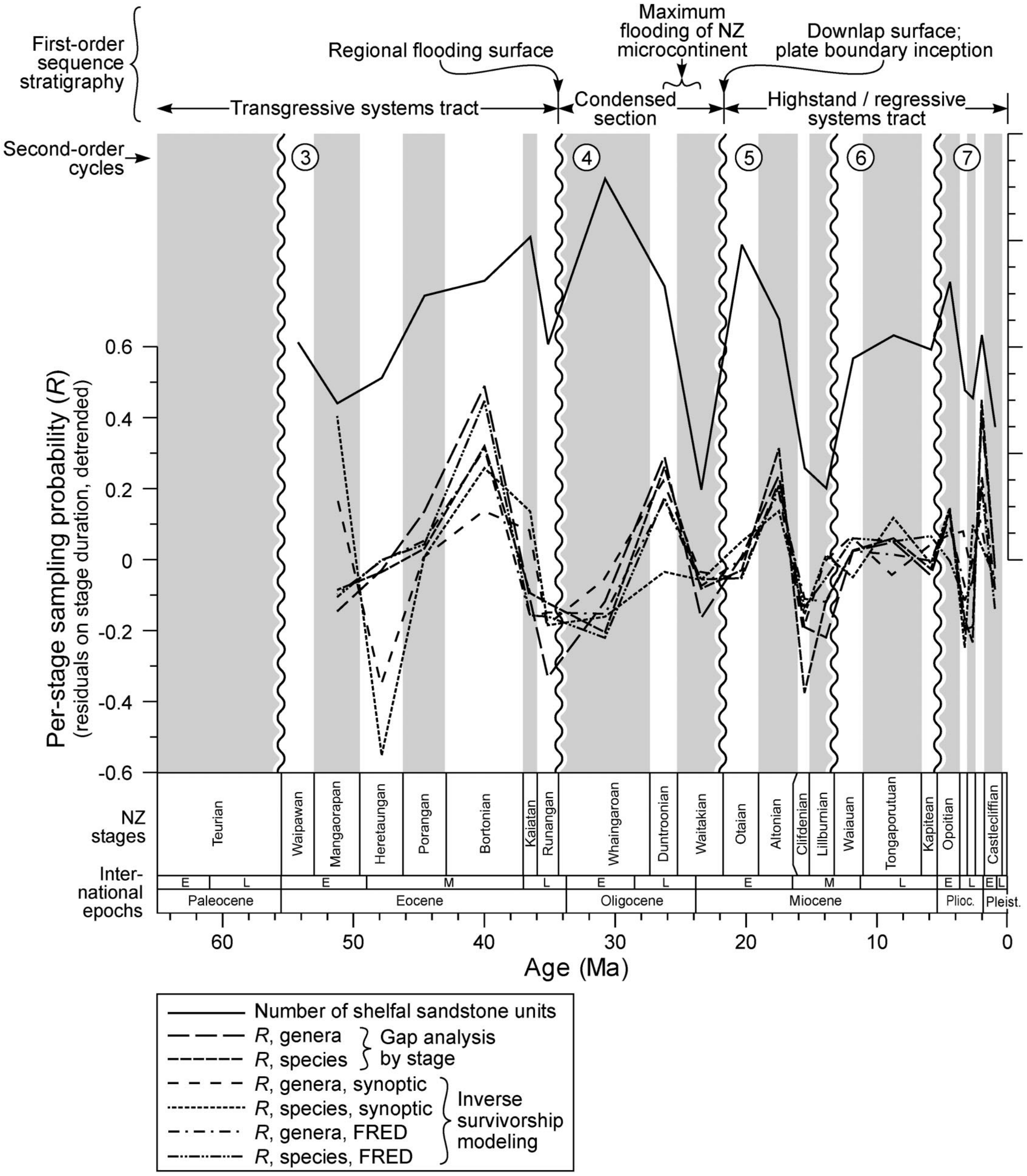

FIGURE 6—Plots of *R* and numbers of shelfal sandstone units against geological time. Timescale (x-axis) as for Figure 1. All data have been detrended and standardized for stage duration. Correlations between the curves are shown in Table 1. Also shown are the principal first- and second-order sequence stratigraphic interpretations of King et al. (1999). Second-order cycles are numbered as in that publication (see also Carter, 1988a).

TABLE 3—Partial correlation coefficients (Pearson's product-moment correlation coefficient) between estimates of *R* and estimates of extinction rate, *q*, based on the FRED and synoptic datasets (see Table 1 and Fig. 10 for further explanation). Only comparisons that relate estimates of *R* and *q* for the same dataset are shown. Indications of significance level as for Table 1; significance levels have been adjusted for family-wise error rates for 6 tests.

		Gap analysis by stage FRED dataset		Inverse survivorship modeling Synoptic dataset		FRED dataset	
		R. species	*R.* genera	*R.* species	*R.* genera	*R.* species	*R.* genera
FRED dataset	*q.* species	0.707***				0.513*	
	q. genera		0.712***				0.676***
Synoptic dataset	*q.* species			0.688***			
	q. genera				0.883***		

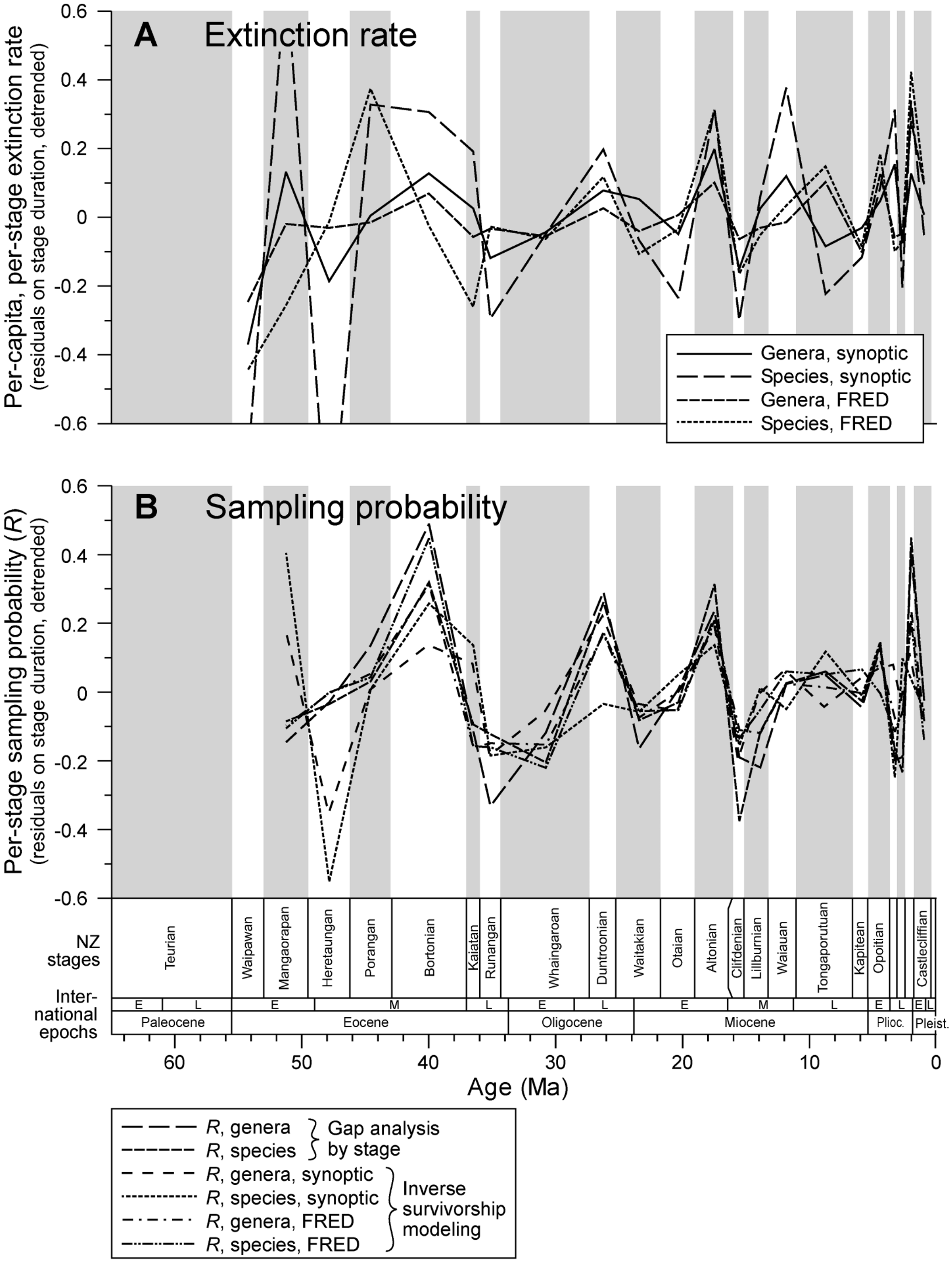

FIGURE 7—Comparison of extinction rate and *R*. Timescale (x-axis) as for Figure 1. (A) Estimates of extinction rates, *q*, for genera and species in the FRED and synoptic datasets plotted against geological time. Estimates of *q* have not been corrected for sampling effects but, following the procedures for *R*, have been detrended and recalculated as the residuals of a regression on stage duration. Extinction was computed initially as a per-capita, per-stage rate (Foote, 2000) and assumed pulsed turnover (Foote, 2003). Differences between the extinction curves and detailed consideration of extinction dynamics in New Zealand Cenozoic molluscs will be discussed in a future contribution. (B) Estimates of *R* derived from gap analysis by stage and inverse survivorship modeling for genera and species of the FRED and synoptic datasets (curves as for Fig. 6).

proximately coincident with onset of shortening in the lower North Island (Kelsey et al., 1995) that may have influenced the rich stratigraphic and fossil records in the adjacent Wanganui and East Coast basins. In addition, however, the abrupt increase in *R* at the base of the Nukumaruan Stage is also coincident with the onset of significant Northern Hemisphere glaciation and concomitant increase in the amplitude of eustatic sea-level fluctuations. These oceanographic changes are reflected, for example, in the abundance and styles of cyclothemic siliciclastic and carbonate sedimentary rocks in the East Coast and Wanganui basins (Beu, 1995; Naish and Kamp, 1995). With existing stage-resolution data, the relative importance of these factors in the generation of abrupt changes in R in the Pliocene and Pleistocene molluscan fauna of New Zealand cannot be determined.

Comments on Methods of Estimating the Quality of the Fossil Record

Estimates of sampling probability from the inverse survivorship modeling are problematic in three ways. First, they do not show the secular trend evident in estimates from gap analysis and in the quantity of shelf record. Second, they are lower than direct estimates based on gap analysis. Third, the estimates for genera are, in many cases, lower than those for species. The reasons for these discrepancies are not completely clear, but some suggestions are offered here.

Regarding the secular trend, ideal models of turnover and sampling (Foote, 2000) predict that many aspects of the expected pattern of first and last appearances should reflect short-term variation in sampling rather than long-term trends. Therefore, it can be hypothesized that the model-based method of estimating R may capture short-term variation in sampling adequately, but may not be sufficiently sensitive to detect longer-term trends.

The inverse survivorship method assumes that all taxa in a stage are characterized by the same origination and extinction rates. Foote (2001) found that analysis of simulated data incorporating taxonomic heterogeneity in origination and extinction correctly captured short-term variation in the quality of sampling, but consistently underestimated its magnitude. Since it is almost certain that the New Zealand mollusc data include taxa with different characteristic turnover rates, this may help explain why the estimates of R from survivorship modeling are lower than those from gap analysis.

Taxonomic heterogeneity also may help to explain the paradox that genus-level sampling rates from the survivorship method are lower than those at the species level. Mathematical modeling of origination and extinction predicts that the chance of a genus becoming extinct depends, in part, on the time since origin of the genus: all else being equal, older genera are expected to have a lower probability of extinction per unit time (Kendall, 1948). Several empirical studies support this expectation (e.g., Raup, 1978; Baumiller, 1993). The expectation holds even if the extinction probability of constituent species is age-independent. Thus, because the genera that coexist in a stage have a wide distribution of ages, genera may be expected to exhibit greater heterogeneity in origination and extinction rates than do their constituent species. This in turn implies, by the argument of the previous paragraph, that their sampling rates may be underestimated more severely by the survivorship method than are the species-level sampling rates.

Extensive simulation analyses would be necessary to test whether these explanations indeed hold true. In the meantime, it must be emphasized again that all the methods employed here produce comparable short-term patterns in probability of sampling per stage. Therefore, the analyses presented here are confidently resolving true stage-to-stage signals of sampling probability.

Finally, it is worth noting that other relatively sophisticated methods for estimating average per-stage sampling probability and completeness have been described recently by Solow and Smith (1997) and Connolly and Miller (2001). The first of these was applied to New Zealand data by Johnson and Curry (2001). Both these approaches have the advantage in that they use information about the distributions of occurrences within taxon ranges, and thus have the potential to yield more tightly constrained parameter estimates than the two modeling approaches used here (inverse survivorship and aggregate inverse survivorship modeling). The first method, described by Solow and Smith (1997), requires information to be expressed in continuous time (or thickness), a condition that is not met by the New Zealand data, which have stratigraphic ranges expressed in discrete stages (indeed, the same holds true for many paleontological datasets). Hence, this method has not been applied here. The second approach, based on the family of ecological techniques grouped under the heading of capture-mark-recapture analysis, resembles inverse survivorship modeling used herein (see Foote, 2005), but makes some strict assumptions regarding the data—assumptions that might be hard to satisfy in many paleontological contexts (but see Connolly and Miller 2001a, b, 2002). Although this approach has been tried as part of the present study, further work is required to demonstrate its applicability to the New Zealand mollusc data.

SUMMARY AND CONCLUSIONS

For the past 20 years, most studies of paleobiodiversity have assumed uniform sampling and preservation over time. Recent research based on European and North American data has questioned this assumption, and has suggested that some important features of the apparent fossil record may be the result of biased incompleteness (e.g., Peters and Foote, 2001; Smith, 2001; Smith et al., 2001). This issue is central to any interpretation of biological history and represents a major challenge to paleobiologists.

Using New Zealand's very good fossil record of Cenozoic shelf molluscs—which is approximately 32% complete at the species level—this study has quantified long- and short-term variations in sampling probability. The long-term, secular increase can be explained simply by the increase in outcrop area and ease of fossil recovery from older to younger stages. Short-term, stage-to-stage variations in sampling probability are, unsurprisingly, influenced strongly by stage duration: the longer the stage, the greater the probability that any taxon will have been preserved and sampled. Much more importantly, once the effects of stage duration are eliminated, it is apparent that short-term patterns of sampling probability are related to second-order sequence stratigraphic cycles. Temporal variations in the quality of the fossil record at the second-order scale seem to reflect enhanced preservation potential mid-cycle and, perhaps to a lesser extent, secondary post-depositional loss of stratigraphic record above and below the sequence boundary. Whereas this result mirrors patterns observed in Europe (Smith, 2001; Smith et al., 2001), it may be that enhanced preservation mid-cycle is relatively more important in New Zealand and secondary loss of record at the sequence boundary is more important in Europe. This difference may reflect no more than the expected contrast in stratigraphic records between an active, convergent margin, as studied here, and a largely passive margin, as discussed by Smith and colleagues. Thus, on a passive margin, accommodation space is limited and erosional loss of record is likely to be significant; in contrast, on an active margin, subsidence, creation of accommodation space, and filling of that space are likely to be ongoing processes in locally forming basins.

Finally, it is worth noting that short-term variations in the quality of the New Zealand molluscan fossil record have been estimated at the genus and species levels, using two quite different methods and two different data compilations. The six resultant sets of analyses yield rather consistent patterns of variation. This result suggests that the methods are robust and that the patterns identified likely reflect true underlying features of the New Zealand marine fossil record.

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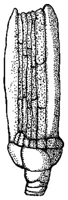

APPENDIX 1 Estimates of per-stage sampling probability (R) and per-taxon per-million-year sampling rate (r/m.y.) for species and genera of New Zealand Cenozoic shelfal molluscs as derived by gap analysis by stage and inverse survivorship modeling. Results are for the synoptic and FRED datasets. Correlations of New Zealand stages to the international timescale are shown on Figure 1. Note that for inverse survivorship modeling, values of $R = 0.01$ and corresponding values of $SE(R) = 0$ represent the lower bound permitted in the model optimization (Foote, 2003).

New Zealand stages	Age of stage base (Ma)	Gap analysis by stage FRED dataset							
		Species				Genera			
		R	$SE(R)$	r/my	$SE(r/\text{my})$	R	$SE(R)$	r/my	$SE(r/\text{my})$
Haweran	0.34	—	—	—	—	—	—	—	—
Castlecliffian	1.63	0.863	0.027	1.543	0.171	0.826	0.029	1.357	0.143
Nukumaruan	2.40	0.825	0.028	2.267	0.224	0.788	0.027	2.014	0.176
Mangapanian	3.00	0.325	0.028	0.654	0.072	0.336	0.027	0.681	0.069
Waipipian	3.60	0.515	0.030	1.205	0.107	0.488	0.029	1.117	0.096
Opoitian	5.28	0.684	0.030	0.686	0.059	0.701	0.026	0.719	0.054
Kapitean	6.5	0.482	0.030	0.540	0.049	0.507	0.027	0.580	0.046
Tongaporutuan	11.0	0.600	0.030	0.204	0.018	0.663	0.025	0.242	0.017
Waiauan	12.7	0.380	0.027	0.281	0.026	0.440	0.025	0.342	0.027
Lillburnian	15.1	0.345	0.025	0.176	0.016	0.415	0.025	0.223	0.018
Clifdenian	16.0	0.350	0.025	0.479	0.043	0.526	0.025	0.828	0.061
Altonian	19.0	0.770	0.026	0.489	0.040	0.773	0.023	0.494	0.035
Otaian	21.7	0.397	0.029	0.187	0.018	0.486	0.027	0.246	0.020
Waitakian	25.2	0.414	0.033	0.153	0.016	0.480	0.028	0.187	0.016
Duntroonian	27.3	0.392	0.035	0.237	0.028	0.539	0.029	0.368	0.031
Whaingaroan	34.3	0.288	0.035	0.049	0.007	0.438	0.030	0.082	0.008
Runangan	36.0	0.231	0.033	0.155	0.026	0.269	0.028	0.185	0.023
Kaiatan	37.0	0.286	0.039	0.336	0.056	0.528	0.034	0.750	0.074
Bortonian	43.0	0.545	0.150	0.131	0.067	0.838	0.041	0.303	0.049
Porangan	46.2	0.067	0.064	0.022	0.022	0.174	0.046	0.060	0.018
Heretaungan	49.5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mangaorapan	53.0	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Waipawan	55.5	0.000	0.000	0.000	0.000	0.063	0.030	0.026	0.013
Teurian	65.0	—	—	—	—	—	—	—	—

APPENDIX 1 Extended.

Inverse survivorship modeling Synoptic dataset								Inverse survivorship modeling FRED dataset							
Species				Genera				Species				Genera			
R	*SE*(*R*)	*r*/my	*SE* (*r*/my)	*R*	*SE*(*R*)	*r*/my	*SE* (*r*/my)	*R*	*SE*(*R*)	*r*/my	*SE* (*r*/my)	*R*	*SE*(*R*)	*r*/my	*SE* (*r*/my)
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.288	0.028	0.263	0.031	0.223	0.055	0.195	0.056	0.205	0.016	0.177	0.019	0.222	0.042	0.194	0.046
0.327	0.043	0.514	0.085	0.294	0.065	0.453	0.125	0.316	0.036	0.493	0.052	0.280	0.080	0.426	0.111
0.277	0.058	0.540	0.138	0.181	0.062	0.333	0.132	0.094	0.024	0.165	0.048	0.028	0.015	0.048	0.027
0.171	0.031	0.312	0.063	0.216	0.054	0.405	0.119	0.144	0.024	0.259	0.056	0.083	0.020	0.144	0.040
0.409	0.093	0.313	0.102	0.159	0.050	0.103	0.036	0.291	0.033	0.204	0.027	0.184	0.036	0.121	0.023
0.244	0.076	0.230	0.087	0.093	0.032	0.080	0.029	0.270	0.046	0.257	0.057	0.067	0.016	0.057	0.015
0.252	0.065	0.065	0.020	0.100	0.038	0.023	0.010	0.315	0.054	0.084	0.015	0.165	0.023	0.040	0.005
0.110	0.026	0.069	0.017	0.112	0.017	0.070	0.012	0.153	0.035	0.098	0.024	0.053	0.013	0.032	0.008
0.146	0.037	0.066	0.018	0.060	0.013	0.026	0.006	0.110	0.022	0.049	0.010	0.042	0.010	0.018	0.005
0.119	0.034	0.141	0.044	0.055	0.013	0.063	0.016	0.099	0.010	0.116	0.016	0.103	0.013	0.121	0.020
0.274	0.045	0.107	0.022	0.283	0.030	0.111	0.014	0.301	0.031	0.119	0.011	0.271	0.027	0.105	0.010
0.128	0.045	0.051	0.020	0.078	0.015	0.030	0.006	0.073	0.011	0.028	0.005	0.064	0.015	0.025	0.006
0.063	0.019	0.019	0.006	0.152	0.020	0.047	0.007	0.146	0.036	0.045	0.012	0.079	0.016	0.023	0.005
0.104	0.051	0.052	0.028	0.173	0.028	0.090	0.017	0.142	0.032	0.073	0.018	0.099	0.019	0.050	0.010
0.142	0.068	0.022	0.012	0.021	0.009	0.003	0.001	0.139	0.038	0.021	0.007	0.077	0.017	0.012	0.003
0.269	0.159	0.185	0.144	0.013	0.005	0.008	0.003	0.157	0.043	0.101	0.037	0.052	0.019	0.032	0.013
0.443	0.103	0.586	0.205	0.191	0.041	0.212	0.052	0.283	0.036	0.333	0.099	0.169	0.032	0.185	0.064
0.315	0.163	0.063	0.045	0.179	0.038	0.033	0.008	0.615	0.086	0.159	0.016	0.480	0.178	0.109	0.035
0.033	0.034	0.011	0.011	0.010	0.000	0.003	0.000	0.058	0.047	0.019	0.015	0.070	0.034	0.023	0.011
0.010	0.000	0.003	0.000	0.010	0.000	0.003	0.000	0.010	0.000	0.003	0.000	0.010	0.000	0.003	0.000
0.554	0.053	0.231	0.036	0.373	0.075	0.133	0.037	0.010	0.000	0.003	0.000	0.010	0.000	0.003	0.000
0.132	0.040	0.057	0.019	0.182	0.124	0.081	0.066	0.071	0.037	0.029	0.028	0.066	0.018	0.027	0.016
0.046	0.046	0.005	0.005	0.457	0.080	0.064	0.017	0.457	0.122	0.064	0.014	0.564	0.084	0.087	0.009

APPENDIX 2 Data used to characterize the New Zealand Cenozoic stratigraphic record. All numerical values represent numbers of lithostratigraphic units. Columns 1–3 have been adjusted to account for units that span more than one paleoenvironment (i.e., columns 1–3 sum to the total number of units recorded from each stage). Columns 4–7 have been adjusted to account for units that include more than one characteristic lithofacies (i.e., columns 4–7 sum to column 2).

New Zealand stages	Bathyal + abyssal units	Shelfal units	Terrestrial + estuarine units	Shelfal units, mudstone + siltstone	Shelfal units, sandstone + conglomerate	Shelfal units, carbonate	Shelfal units, other facies
Hawera	1.6	7.2	7.2	1.5	5.5	0.2	0.0
Castlecliffian	1.8	9.7	10.6	4.0	4.8	0.4	0.4
Nukumaruan	3.4	13.8	7.8	4.2	7.3	1.9	0.4
Mangapanian	4.2	16.0	6.8	6.8	6.8	1.5	1.0
Waipipian	5.9	18.6	8.5	6.5	8.6	2.5	1.0
Opoitian	9.8	25.4	9.8	8.8	10.0	4.1	2.4
Kapitean	9.8	14.7	6.5	5.0	8.0	0.8	0.8
Tongaporutuan	15.8	17.3	9.0	7.0	8.4	0.5	1.4
Waiauan	15.7	18.0	2.3	7.7	7.7	1.5	1.0
Lillburnian	16.8	19.9	2.3	8.7	8.2	2.0	1.0
Clifdenian	14.9	22.0	3.1	8.3	12.2	1.0	0.5
Altonian	23.0	32.2	3.8	11.1	16.1	3.0	2.0
Otaian	17.9	25.4	0.7	6.0	14.9	3.6	0.8
Waitakian	20.6	34.6	0.7	9.8	12.2	11.7	1.0
Duntroonian	17.4	29.5	3.0	5.4	16.3	7.5	0.3
Whaingaroan	23.4	46.0	10.6	14.1	16.0	12.3	3.7
Runangan	11.9	23.1	11.9	9.1	9.1	3.0	1.8
Kaiatan	10.1	20.9	10.1	6.7	9.2	1.8	3.1
Bortonian	9.4	16.8	6.7	5.6	7.1	2.6	1.5
Porangan	7.1	9.9	5.0	3.2	5.1	1.3	0.3
Heretaungan	6.7	11.3	4.0	4.9	3.6	1.6	1.2
Mangaorapan	7.9	11.8	3.3	4.5	4.5	1.6	1.2
Waipawan	9.4	15.5	4.0	5.0	5.9	2.5	2.1
Teurian	9.3	20.8	7.9	8.5	8.0	1.4	2.8