

BIOTIC EFFECTS OF SEA LEVEL CHANGE: THE PLEISTOCENE TEST

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Abstract. Species diversity change, and therefore compositional changes in a biota, may be associated with changes at any of three ecological levels, involving the number of provinces within the biosphere, of communities within provinces, and of species represented within communities. Pleistocene sea level changes did not much affect the marine biosphere at any ecological level. An analysis of an extensive data set of Californian Pleistocene and Recent mollusks indicates a continuity of community and species composition during highstands of the last million years. Extensive latitudinal shifts in species' geographic ranges, associated with climatic change and not with sea level itself, created the most significant biotic changes. Extinctions were minimal, well below predicted species-area effects. Evidently, only "perched" faunas are particularly vulnerable to sea level change. Although sea level falls are commonly associated with a faunal hiatus, changes associated therewith can be referred to sea level change itself only in limited situations, and other paleobiologic explanations should be sought in most cases.

1. Introduction

Marked changes in the stratigraphic succession of marine faunas are often localized at unconformities. In some instances the faunal turnover is much greater than would be expected simply from the passage of time associated with the break in deposition. As these breaks are generally associated with regressions, it has long been suggested that factors associated with lowering sea levels were responsible for the extinctions [Chamberlin, 1898; Moore, 1954; Newell, 1967; Schopf, 1974], while Hallam [1986, 1989] has argued that factors associated with sea level rises may be responsible. During the Pleistocene, however, the marine biota withstood large and rapid sea level fluctuations without major losses, and this fact has been held to argue against the effectiveness of sea level change as an agent of extinction [Wise and Schopf, 1981; S. M. Stanley, 1984, 1988]. Here we briefly review the sorts of biotic effects that have been attributed to sea level change and discuss how the Pleistocene model may bear upon these ideas.

2. Diversity, Extinction, and Diversification

There are three levels within the ecological hierarchy that affect the capacity of the marine environment to support species [Valentine, 1973]. Diversity accommodation is provided by (1) the number of biotic provinces in the marine biosphere; (2) the number of biotic communities within the provinces; and (3) the number of species represented within the communities. Given this framework,

the more heterogeneous the environment, the higher the biotic diversity it can support, other things being equal. Thus, again referring to the ecological hierarchy, when multiple geographic barriers restrict migration or strong temperature gradients restrict species' geographic ranges, provinciality may be high. When a province contains a large number of distinctive topographic or depositional settings or biotopes, the number of communities may be accordingly high. And when a community consists of numerous habitat patches, local species diversity may be high. Clearly, a biosphere with many provinces, each of which contains many communities each composed of large numbers of species' populations, will accommodate a very high diversity of species. Any factor that reduces the number of ecological units at any hierarchical level, however, will ultimately reduce the biosphere's total species richness. The mechanisms postulated for extinctions due to sea level changes operate at one or more of these ecological levels as follows:

2.1. Number of Provinces

The eustatic draining of epicontinental seas or seaways can eliminate entire provincial or subprovincial regions. The endemic faunas adapted to the regime of the province or subprovince will clearly be lost, and species whose populations centered on the vanished environment may fail to survive in what is, for them, the marginal conditions remaining. Johnson [1974] termed such epicontinental associations "perched faunas." The elimination of perched faunas could have played a major role in extinction events, particularly during the Paleozoic when epicontinental seas were extensive and supported more than one perched fauna [see Sheehan, 1988, and references therein]. But such effects are strongly dependent on the level of endemism of those epicontinental faunas. For example, extensive Mesozoic seaways were drained repeatedly but their modest levels of endemism (only 5-10% at the generic level, and no endemic families, for bivalves in the Cretaceous Western Interior Seaway, slightly higher for some groups, lower for others [Kauffman, 1973, 1984] are insufficient to account for global extinction tallies.

A corollary of the elimination of perched faunas, although perhaps played out at a lower hierarchical level, is that geographically restricted forms should suffer greater extinction than widespread forms, which indeed appears to have been the rule during many extinction events [Sheehan, 1986; Westrop, 1989; Jablonski, 1989 and references therein]. However, sea level drops may actually increase diversity when they allow barriers to emerge and fragment shallow sea provinces and thus enhance speciation probabilities [see Hallam 1984, p. 231 for examples].

2.2. Number of Communities

At the community level, sea level changes are presumed to cause extinction through a reduction in environmental heterogeneity as habitat types are eliminated. This is the

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Paper number 90JB00602
0148-0227/91/90JB-00602\$05.00

least well-documented biotic effect of sea level change: for the open shelf, it is not even clear whether sea level rises or falls would be more conducive to net global increases in environmental heterogeneity. Reefs and bioherms are the most frequently cited examples of community level destruction during sea level changes; carbonate buildups can be stranded and killed by a sea level fall (as argued for Mesozoic reefs by G. D. Stanley [1988]), or can be drowned by a sea level rise [see Hallock and Schlager, 1986]. At the end of the Permian, extirpation of reef and biohermal structures evidently removed their entire complex of associated communities [see Jablonski, 1986a, and references therein], and calcareous level bottom substrata were virtually eliminated as well [Kummel, 1973]. This is certainly a good example of a great reduction in environmental heterogeneity at the community level, but it is far from certain that the extinction was forced primarily by sea level change. If that were the case, it might be expected that reef-associated taxa, caught in the destruction of the reef biotope, would be more severely affected than nonreef taxa. However, Raup and Boyajian [1988] found reef and nonreef genera to have highly correlated extinction records, with little difference in magnitude or timing. The preferential extinction in the tropics often cited in the literature [e.g., Jablonski, 1986a, S. M. Stanley, 1988] thus requires further documentation and could have been triggered at other levels in the hierarchy [Jablonski, 1986b]: disruption of tropical provinces with concomitant loss of endemics or population loss owing to excursions in temperature or other environmental variables, for example.

2.3. Number of Species

At the level of species accommodation within communities, there are two principal suggestions as to how sea level fluctuations can drive diversity changes. One idea is simply an extension of the role of environmental heterogeneity to within-biotope level; sea level change might restrict or enhance the range of habitats within areas inhabited by a community. The other idea involves the "species-area effect," the claim that as habitable area increases, so does the number of species that can be accommodated, even if environmental heterogeneity remains constant.

Quantitatively, the species-area effect [MacArthur and Wilson, 1963, 1967] is usually expressed as $N = kA^z$, where N is the number of species and A is the area available to them. The interpretation of k and z is controversial; Connor and McCoy [1979] consider them fitted constants with little biological significance. The exponent z has been subject to much comparative study and is generally held to account for differences between taxa; area clearly has a different significance to, say, littorines of the rocky intertidal and naticids of the sandy shore. Owing to the way taxa are deployed on the globe, or for other reasons still poorly understood, z is not independent of latitude or the size of the area under study [Martin, 1981]. The coefficient k has received much less attention and is somewhat problematic [see Connor and McCoy, 1979; Gould, 1979] but is taken to account for other environmental features that govern species diversity. For example, tropical communities can contain over an order of magnitude more species than Arctic communities within an equal area, and k would tend to normalize for this difference.

Empirical curves of rising species numbers with increasing area can be fairly well described by the MacArthur-Wilson equation, and the species-area effect has been widely invoked to explain extinctions associated with sea level drops, up to and including the largest extinction of the Phanerozoic at the end of the Paleozoic [Schopf, 1974; Simberloff, 1974; Wyatt, 1987; Sheehan, 1988]. However,

the explanatory power of the species-area equation is limited: any number of models predict the observed relationship (see Connor and McCoy [1979] and Boecklin and Simberloff, 1986, for reviews). Thus there is no generally accepted method for separating the effects of area per se from those of environmental heterogeneity, for in the real world the range of habitat conditions will almost inevitably increase with increasing environmental area and decrease as the area shrinks. The fitted curves with their values of k and z , then, are really species-area-heterogeneity curves.

3. Pleistocene Sea Level Effects

The living and Pleistocene molluscan faunas of the extratropical eastern Pacific are as well known in combination as any in the world and therefore form a good test case for the effects of Pleistocene sea level changes on benthic faunas. We can examine effects at each level in the ecological hierarchy.

3.1. Number of Provinces

Each of the provinces recognized in the modern biota can be traced back through the Pleistocene [Valentine, 1961; Addicott, 1966; Kennedy, 1978] and with one exception have not involved geographic barriers. The exception is the very low-diversity region in the Arctic and Subarctic, where the Bering Land Bridge was exposed during low sea levels. The Pleistocene record of low sea levels is, however, completely unknown there, and the remaining high-latitude Pleistocene record sufficiently poor that the provincial consequences of the Bering barrier, if any, have not been identified in the highstand record.

3.2. Number of Communities

Data are particularly good for the Californian Province region, where Pleistocene communities have been extensively studied [e.g., Woodring et al., 1946; Valentine, 1961; Valentine and Mallory, 1965]. At the scale at which Recent marine communities are usually studied, all living associations are recorded in the Pleistocene, and continuity, despite sea level oscillations, is the rule. It might be assumed that rocky shore communities would be especially at risk during glacial lowstands, given that shorelines were well out on the shelf, in areas now receiving only silts and clays. However, these associations, including rock cliff, rock rubble, and tide pool elements, can be traced as species-rich faunas in the Pleistocene highstand deposits and are equally rich today.

Another shoreline association that might be thought to be at risk during Pleistocene sea level fluctuations, as it is very patchily distributed in small discontinuous areas and is of relatively low diversity, is the coastal marsh community. However, as far as can be determined from Pleistocene molluscan fossils, this community also emerged from lowered sea levels much as it had been during previous highstands. In both of these cases the record speaks to the continuity of environments that was clearly maintained during the sea level fluctuations and thus to significant continuity in the processes of sediment transport and deposition that are so important in determining the distribution of the invertebrate community biotopes.

3.3. Number of Species

The Pleistocene extinction of species within molluscan communities has recently been reviewed for the Californian Province region, based on 747 species recorded as fossils [Valentine, 1989a]. Summed over the past million years, the

extinction rate has been about 13%, a figure that agrees closely with average extinction rate curves for the late Neogene [Stanley et al., 1980]. Accurate dating of the fossiliferous Pleistocene deposits is not sufficiently complete to permit the tracing of extinction rates within this interval. However, faunas from terraces deposited during isotopic substage 5e, about 125,000 years B.P. contain no more than 3% extinct forms, a level of extinction that agrees well with figures given for the western Atlantic by Stanley and Campbell [1981]. Extinction rates may have been higher elsewhere, as in the important local late Pliocene to early Pleistocene extinctions in the tropical Western Atlantic [Stanley and Campbell, 1981; Stanley, 1986], but the Californian rates are as low as any that have been recorded, despite the narrowness of the Californian shelf relative to the shelf in the Western Atlantic [Stanley, 1984]. Indeed, since the average Cenozoic rates are lower than those of earlier Eras [Raup and Sepkoski, 1982], the Pleistocene extinction rates are at or near the Phanerozoic minimum. Not only were community associations preserved during the sea level swings, but there appears to have been no within-biotope habitat loss, at least none with a discernible effect.

Using the species-area expression to calculate expected effects of decreased habitat area is not straightforward, for it depends greatly upon the selection of coefficients and exponents and of course on the values chosen for shelf area lost during glacial episodes. Estimation of this area involves assumptions as to the shelf width during low sea levels, based on reconstruction of the shelf slope and on the position of the thermocline; the position at which the thermocline intercepts the sea floor probably determine the outer margin of the shelf environment as perceived by the benthos [see Jablonski and Valentine, 1981]. Wise and Schopf [1981], using an estimate of sea level fall of 134 m and a series of assumptions of other parameters, estimated a drop in species diversity of 13.5% at low seastand.

For comparative purposes, although the approach is fraught with pitfalls and uncertainties, we can perform similar calculations for the Californian Province. Given a shelf length of 988 km from Point Conception, California, to Isla Cedros, Mexico, and an average shelf width of 7 km (estimated from data of Emery [1960] and Shepard [1963]) we estimate Δ at 6916 km². Few z values are available for marine benthos: $z = 0.21$ for both California coastal fishes and global shallow water bryozoans [Horn and Allen, 1976; Schopf et al., 1978], and so we take z values to fall at the low end of the 0.2-0.4 range observed for organisms generally [Connor and McCoy, 1979]. Wise and Schopf [1981]

adopted Preston's [1962] theoretical z value of 0.26. Given a present-day diversity of about 800 species, we find k for a plausible range of z values (Table 1, columns 1 and 2).

The Californian shelf, as recognized on physiographic grounds [Dietz and Menard, 1951], is not only narrower than average but terminates at a depth that is much shallower than average (ranging from 250 to 480 feet off southern California [see Emery, 1960, p. 37; Shepard, 1963, p. 224 ff]). Assuming an average depth of 110 m, the average seaward shelf slope is 54 arc min, rather steep (the global average estimated by Shepard [1963] is 7 arc min.). The continental and basinal slopes bordering the shelves are quite steep also, probably averaging well over 10° [Emery, 1960, p. 39]. Thus if sea levels fell from between 60 and 150 m as sometimes estimated for glacial intervals, shelf area would be reduced at those times to between from about half to less than a tenth of its present area, assuming that the shelf edge depth is considered to remain at a water depth of 110 m on the slope. In Table 1 (columns 3 and 4) we calculate the numbers of species predicted by the species-area equation following a reduction of shelf area of 50% and 75%. For these very conservative estimates, the losses range from 13% to about 30% of the species. For a shelf area reduction of 90% the reduction in species is predicted as 37% at a z value of 0.20.

It is clear that if the low seastands could in fact accommodate only the lower levels of diversity predicted, the faunal adjustments did not involve species extinctions to any extent that can be detected. Sea level drops that occurred about as rapidly as is possible in the ocean and that are evidently comparable in magnitude with any during the Phanerozoic have failed to produce any species-area-heterogeneity extinctions. What possible explanations are there for this apparent lack of response of the shelf fauna to important sea level changes?

One possibility is that the effects have accrued gradually, beginning with earlier Neogene sea level oscillations, and that the brief intervals between falls have been insufficient for faunal replenishment. The present fauna, in this scenario, is already adjusted to conditions at low sea level. It is not possible definitively to rule out such a history. In fact there is no clear evidence of any replacement species. All shallow sea species that are common or of ecological importance in present-day communities are found in the Californian Pleistocene [Valentine, 1989]. If new species have joined the fauna lately they are quite rare or otherwise obscure. There is certainly sufficient time available during relative highstands that new species could be evolved (that

TABLE 1. Expected Loss of Molluscan Species for the Californian Province Owing to Effects of Area (and Heterogeneity) During a Pleistocene Sea-Level Fluctuation, Using the Equation $N = kA^z$

z	k	50% Decrease in Δ	75% Decrease in Δ
0.20	136.50	696 (13.0% loss)	606 (24.3% loss)
0.22	114.37	687 (14.1% loss)	590 (26.3% loss)
0.24	95.83	678 (15.3% loss)	574 (28.3% loss)
0.26	80.31	668 (16.5% loss)	559 (30.3% loss)

Area of Californian Province now ~6917 km² (shelf length = 988 km and average shelf width = 7 km), present-day diversity about 800 species, taken as starting value. As both z and the diversity are specified, the percent of species lost as area decreases is independent of the absolute size of the starting area.

is, evolution is known to be capable of producing morphospecies at this time scale) but whether they should be evolved is a question that cannot be answered at present.

A second, related possibility is that lowstands may not be sufficiently long to produce all of the extinction required by the species-area relation; faunal adjustments can hardly be instantaneous, although we are dealing with many thousands of generations here. Nevertheless we know little about relaxation times (the time it takes a fauna to adjust to diversity level appropriate to available area), in that it is difficult to predict diversity losses when sea levels oscillate over geologically rapid time scales. Boecklin and Simberloff [1986] review some of the uncertainties and alternative models for faunal responses to reductions in habitable areas.

A third possibility is that the Californian Pleistocene fauna was quite different in composition during low sea levels, and that local extinctions (that is, extinction of local populations but not of entire species) were in fact common, so that the lowstand communities were depauperate compared with highstand communities. However, populations of the locally extinguished species survived, either in deeper water or to the south in warmer waters, and then returned during high seastands, when the capacity of the wider shelf to accommodate species increased and the temperatures rose. Species immigrating from the north during glacial times should be fewer than those being restricted to more southerly latitudes, so local diversity would drop. In fact, latitudinal range shifts of a great many species (113 between provinces, many more within provinces) are known from the Californian high sea level record [Valentine, 1989a], indicating that extensive latitudinal migration has indeed been common during the Pleistocene and the scenario outlined above is a plausible one.

On the other hand, a retreat to deeper-water environments would not be likely for much of the fauna, for example for the rocky shore species that are so well represented during highstands. Unfortunately, we do not have any lowstand faunas to confirm the character of any migrations during glacial times. The suggestion here, however, is that any real effects of the species-area-heterogeneity relation were mitigated by latitudinal migration; they were absorbed biogeographically and not evolutionarily.

A fourth possibility is simply that habitat area per se is not a very important parameter in the survival of marine invertebrates, so that the implications of the species-area curve are invalid for benthic faunas (except perhaps at extremely small areas). Most shelf species have geographically broad ranges parallel to shore, but very narrow ranges in an onshore-offshore direction, so that narrowing of the onshore-offshore dimension, even to a small fraction of its present value, may have little impact on invertebrate species. The present lack of correlation between species diversity and shelf width from area to area suggests that this may be the case [Stanley, 1984] (see also Schopf et al. [1978], who were unable to detect a significant species-area relationship in marine bivalves).

4. Concomitant Effects

Sea level changes can bring or accompany environmental perturbations beyond simple area effects, and those might also have biotic consequences. Perhaps most important is the change in climatic amelioration that must accompany extensive flooding or exposure of continents [Valentine and Moores, 1970, 1972]. Drowning of extensive continental areas should enhance climatic stability, zonally or even globally; this in turn would tend to stabilize many diversity-governing factors, such as primary

productivity. Draining of such areas would have the opposite effect. Sea level changes that happened to alter the exposed continental area to a great extent, such as a drop from a highstand well up on the craton where gradients are gentle, would have a particularly strong effect on the diversity and composition of the marine fauna. These major effects, though surely real, are difficult to disentangle from other factors, paleogeographic ones, for example, but new generations of climate models may permit a quantitative assessment. Barron and Washington [1984] and Crowley et al. [1986] present models testing the role of exposed land area in global climate; Crowley and North [1988] specifically disavow the end Cretaceous regression as an agent of sufficient climatic change to produce the accompanying mass extinction.

Other ancillary effects that may be important locally include changes in runoff and therefore in sediment and nutrient supplies to the shelf, changes in salinity, and the introduction of novel predators, competitors, and parasites. Most of these effects would have their greatest impact in areas that are enclosed by ecological and/or geographic barriers, so that a large fraction of the fauna is endemic or strongly centered in the affected region.

5. Implications for Ancient Faunas

The attribution of ancient extinctions associated with lowered sea levels to the sea level changes themselves is not easily justified. The clearest cases are those that involve the elimination of an entire provincial regime with its fauna (e.g., the demise of the North American fauna in the end Ordovician extinction [see Sheehan, 1988; Branchley, 1984]). Marine invertebrate faunas that are not perched, however, are unlikely to suffer extinction from sea level change itself; associated features such as climatic change (which of course may itself cause sea level fluctuations) are more likely to be responsible for the often cited association between extinctions and sea level drops [Jablonski, 1986a]. Cases in which faunas are so localized by various barriers that any local extinctions are tantamount to total extinction, trapped faunas, are obviously highly vulnerable to any local environmental deterioration, but whether or not they are vulnerable to a species-area change remains moot.

To account for extinctions that are associated with sea level change, Hallan [1986, 1989] has proposed that conditions associated with sea level rises might often have been responsible. If a transgression caused the spread of anoxic bottom waters onto expanding shelves, it might extirpate much of the biota, which would have a lowered diversity in any event from its restriction to lowered shelf area during the preceding regression [Hallam, 1989]. Although the Pleistocene data are not supportive of an areal effect, any association of transgressions with a rise in an anoxic layer would successfully couple sea level change with an extinction factor. A coupling is also suggested by Brinkhuis and Zachariasse [1988] for paleoceanographic conditions similar to those of the Late Cretaceous, when there is evidence that deep waters were generated largely in shallow marginal seas. In such a setting, lowering of sea level would reduce deep-water sources, reduce the thermal gradient and lower productivity. It is possible that extinction would be promoted among the shelf benthos in such a situation. Our data simply do not speak to these models.

Eustatic sea level curves alone, then, may have relatively little to offer to the paleobiologist, who instead needs data on the lateral movement of strandlines and on changes in the total area of exposed land or shallow seas. Giving a starting position of extensive inundation of the continents, a relatively modest drop in sea level could have far greater effect on both the marine and terrestrial biota, directly via

destruction of unique habitats and endemic centers, and indirectly via climatic forcing, than the larger sea level drops in a world dominated by pericontinental seas. As several authors have pointed out [Hallam, 1984; Brenchley, 1984; Jablonski, 1986a; Sheehan, 1988] this may be the key to the contrast between the Pleistocene and the Paleozoic responses to comparable sea level fluctuations. An encouraging approach is taken by Wyatt [1987], who shows that a given sea level drop will expose a lesser percentage of a large continent than a small continent, owing to differences in their respective hypsometric curves. Consequently, different continents will have different transgression-regression histories in response to a single eustatic trend, and the areal consequences of a given magnitude of sea level change will differ between times of fragmented and of amalgamated continents.

A final generality about Phanerozoic faunas that might bear on sea level effects is that earlier benthic faunas were dominated by clades with high "background extinction" rates. These early clades were replaced as dominant elements by those with intermediate extinction rates and these in turn by low-rate clades [see Raup and Sepkoski, 1982; Sepkoski, 1984; Van Valen, 1984, 1985; Valentine, 1989b and references therein]. Thus, long-term success has accrued to clades with the best strategies of extinction resistance. On the other hand, clades with high turnover rates and thus the best strategies of diversification are most capable of exploiting environments that are newly invaded or newly opened by extinction, as in the early Cambrian and the early Triassic, when the high-turnover trilobites and ammonoids, respectively, were most successful. Thus, as M. Cooper (personal communication 1990) has pointed out, early in the Phanerozoic or following massive extinctions, environmental changes associated with sea level change may have been somewhat more effective agents of extinction than they were during the Pleistocene. The study of extinction remains one of the most complex problems in paleobiology.

Acknowledgments. Michael R. Cooper, University of Durban-Westville, South Africa, and Alan Hull, University of California, Santa Barbara, perceptively discussed the ideas herein and suggested improvements. Research from which these ideas have grown is supported by NSF grants EAR84-17011 (to D.J. and J.W.V.) and EAR87-21192 (to J.W.V.).

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(Received October 19, 1989;
revised March 1, 1990;
accepted March 1, 1990.)