PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Constancy and Change of Life in the Sea [and Discussion]

J. B. C. Jackson and P. R. Sheldon

Phil. Trans. R. Soc. Lond. B 1994 **344**, 55-60
doi: 10.1098/rstb.1994.0051

Constancy and change of life in the sea

J. B. C. JACKSON

Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, U.S.A.

SUMMARY

Most marine species appear abruptly in the fossil record and persist unchanged for millions of years. Speciation and extinction commonly occur in pulses so that groups of species come and go as ecological units that dominate the seascape for millions of years. Dramatic turnover of mollusc, coral and planktonic foraminifera species occurred throughout tropical America about two million years ago in apparent response to the onset of northern hemisphere glaciation. In contrast, subsequent glacial cycles, temperature fluctuations and sea-level change had little lasting biological effect. There is no necessary correlation between the magnitude of environmental change and the subsequent ecological and evolutionary response.

1. INTRODUCTION

Uniformatarianism is the null hypothesis of geology, and gradual speciation by natural selection the null hypothesis of evolution. Ecology is the link between the two. The expectation is that gradual changes in earth processes drive gradual shifts in species and communities. Many ecological and evolutionary trends are in agreement with this scenario (Overpeck *et al.* 1992), but much new evidence suggests that changes in climate may be abrupt and unstable, with lasting effects on the subsequent climate and biota (Crowley & North 1988; Kennett & Stott 1991). Sudden environmental change may underlie the nearly universal occurrence of discontinuities in morphology and community composition which mark the age, stage and epoch boundaries of the geological timescale which traditionally have been attributed to the imperfections of the fossil record (Darwin 1859; Levinton 1988). Here I review evidence that communities of molluscs, reef corals and planktonic foraminifera have changed very little since the end of the Pliocene approximately two million years (Ma) ago. After at least eight Ma of relative faunal stability, turnover of Late Pliocene faunas required only a few hundred thousand years (Ka).

2. PATTERNS OF SPECIATION

There are now several palaeontological studies of patterns and rates of morphological change in the sea that allow distinction between punctuated and gradual speciation (Gould & Eldredge 1993). The best data are for Neogene to Recent marine invertebrates which have the advantage of an excellent fossil record and numerous fossil species that are still alive for comparison. Planktonic foraminifera exhibit both gradual and punctuated speciation (Wei & Kennett 1988), whereas cheilostome bryozoans are exclusively punctuated (Cheetham 1986; Jackson & Cheetham 1994). Most gastropod molluscs are punctuated, although there is one good example of gradualism (Michaux 1989; Geary 1990). Bivalve molluscs consistently exhibit morphological stasis but patterns and rates of changes in morphology at speciation have not been described (Stanley & Yang 1987). Based on these and other studies, cases of punctuation and stasis outnumber gradual evolution by more than ten to one for the over 100 species examined in detail. Thus, for all practical purposes, species of marine invertebrates exist as discrete packages in space and time whose durations and distributions can be usefully counted and compared.

3. THE TIMING OF SPECIATION AND EXTINCTION

Almost all living, well-skeletonized species of foraminifera, corals, bivalves and snails have persisted without obvious morphological change for 2 Ma and the majority for longer. This alone constitutes compelling evidence for evolutionary stasis in the sea, and demonstrates that speciation and extinction do not occur at random over time. The best data are for planktonic foraminifera which have been sampled intensively worldwide as part of the Deep Sea Drilling Program (Kennet & Srinivasan 1983; Berggren *et al.* 1985). Median species durations for the 44 known species of Neogene globigeriniids is 10.4 Ma (range 1.0–34.9) and for the 50 globorotaliids is 4.4 Ma (range 1.0–23.7) (Stanley *et al.* 1988). Despite these long durations, however, 39% of globogerinid and 20% of globorotaliid species died out between 3 and 2 Ma ago.

Molluscs from the Caribbean coast of western Panama and Costa Rica show a similar pattern (figure 2; Jackson *et al.* 1993). The median duration of 395 genera and subgenera common enough to be

Figure 1. Stratigraphic ranges of 395 subgenera of molluscs from the Caribbean coast of Costa Rica and western Panama. Timescale: R, Recent, 0 Ma; P, Pleistocene, 0–1.6 Ma ago; PP, Plio-Pleistocene boundary, 1.6–1.8 Ma ago; LLP, late Late Pliocene, 1.8–2.5 Ma ago; ELP, early Late Pliocene, 2.5–3.5 Ma ago; EP, Early Pliocene, 3.5–5.3 Ma ago; late Late Miocene, 5.3–6.8 (by interpolation) Ma ago; middle Late Miocene, 6.8–8.2 Ma ago.

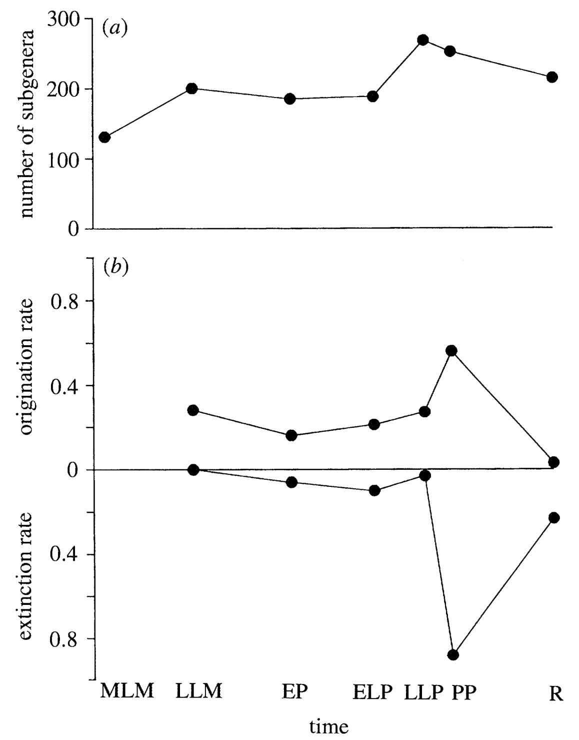

Figure 2. Diversity, origination and extinction of 395 subgenera of molluscs. Timescale as in fig. 1. The origination rate at time t equals the number of taxa that first appear at t, divided by the total number of taxa at t, divided by the time between t and $t-1$. The extinction rate at t equals the number of taxa present at $t-1$ that are absent at t and thereafter, divided by the total taxa at $t-1$, divided by the time between t and $t-1$.

analysed is 5.2 Ma (range 0.2–8.2 Ma for all but nine taxa known only from the Recent). Extinction rates were low until the end of the Pliocene about 2 Ma ago when 18% of the taxa disappeared (figures 1 and 2). Origination rate also doubled at the same time, so that altogether there was a 30% turnover of the fauna at the generic and subgeneric level within about 200 Ka. There are no known younger (Pleistocene) fossil faunas in the region, so that the end-Pliocene faunas can only be compared directly with the Recent. Nevertheless, 36% of these taxa went extinct some time during the Early Pleistocene, so that turnover lasted longer than 200 Ka. Two-thirds of Early Pliocene species of molluscs from the southeastern United States also went extinct at the end of the Pliocene (Stanley & Campbell 1981; Stanley 1986), but were replaced by new species as diversity did not decline (Allmon *et al.* 1993). As for the Isthmus, the average durations of these younger species are unknown for lack of Pleistocene fossils. Such data are available for 747 fossil species from California, however, where the extinction rate over the past million years is only 13% (Valentine 1989; Valentine & Jablonski 1991).

Finally, Budd *et al.* (1994*a,b*) revised the stratigraphy and taxonomy of 175 species of Caribbean reef corals over the past 24 Ma. Their median duration is approximately 7 Ma (range 150 Ka–24 Ma). As for the other groups, there was a pulse of extinction at the end of the Pliocene, when extinction rates increased nearly ten-fold, and only 36% of the 106 species alive between 4–2 Ma ago survived to the present. The only subsequent Pleistocene extinctions were of *Stylophora* and *Pocillopora*. Some other groups did not experience exceptional turnover or extinction at the end of the Pliocene. Only six of 107 common benthic foraminifera from the Caribbean coast of Panama went extinct, and no common species evolved during the past 3 Ma (Collins 1994).

4. EVOLUTION AND ENVIRONMENT

Many long-term evolutionary trends in the sea were probably due to interactions among species almost regardless of fluctuations in the physical environment (Vermeij 1987; Jackson & McKinney 1990). On the other hand, synchronous turnover of faunas is more closely tied to changes in climate and oceanographic conditions. The most likely explanation for the massive Plio-Pleistocene turnover of tropical western Atlantic foraminifera, corals and molluscs is climatic cooling due to the onset of northern hemisphere glaciation (Stanley & Campbell 1981; Stanley 1986; Stanley *et al.* 1988), with new estimates for tropical sea surface temperatures during glacial maxima of 5–6°C below present values (Beck *et al.* 1991; Guilderson *et al.* 1994). Independent evidence for the cooling hypothesis comes from the geographic and habitat distributions of extinct and surviving species of bivalves and

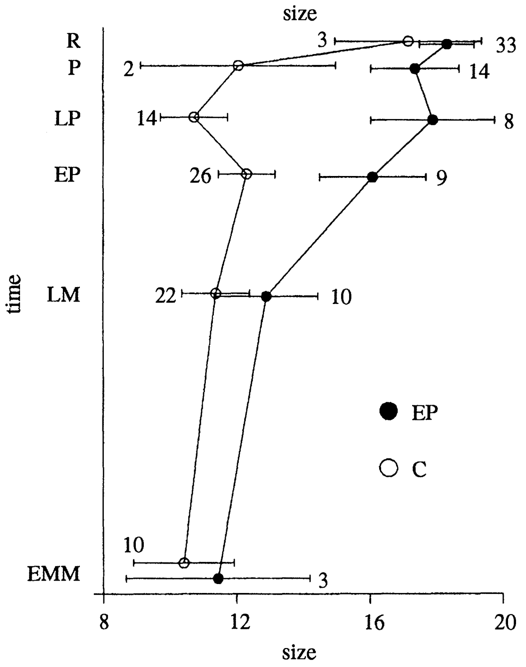

Figure 3. Trends in strombinid shell size (square root height × width in mm) in the eastern Pacific (EP) and Caribbean (C). Numbers of species at each interval indicated alongside standard error bars. Ages: R, Recent; P, Pleistocene; LP, Late Pliocene; EP, Early Pliocene; LM, Late Miocene, EMM, Early and Middle Miocene combined.

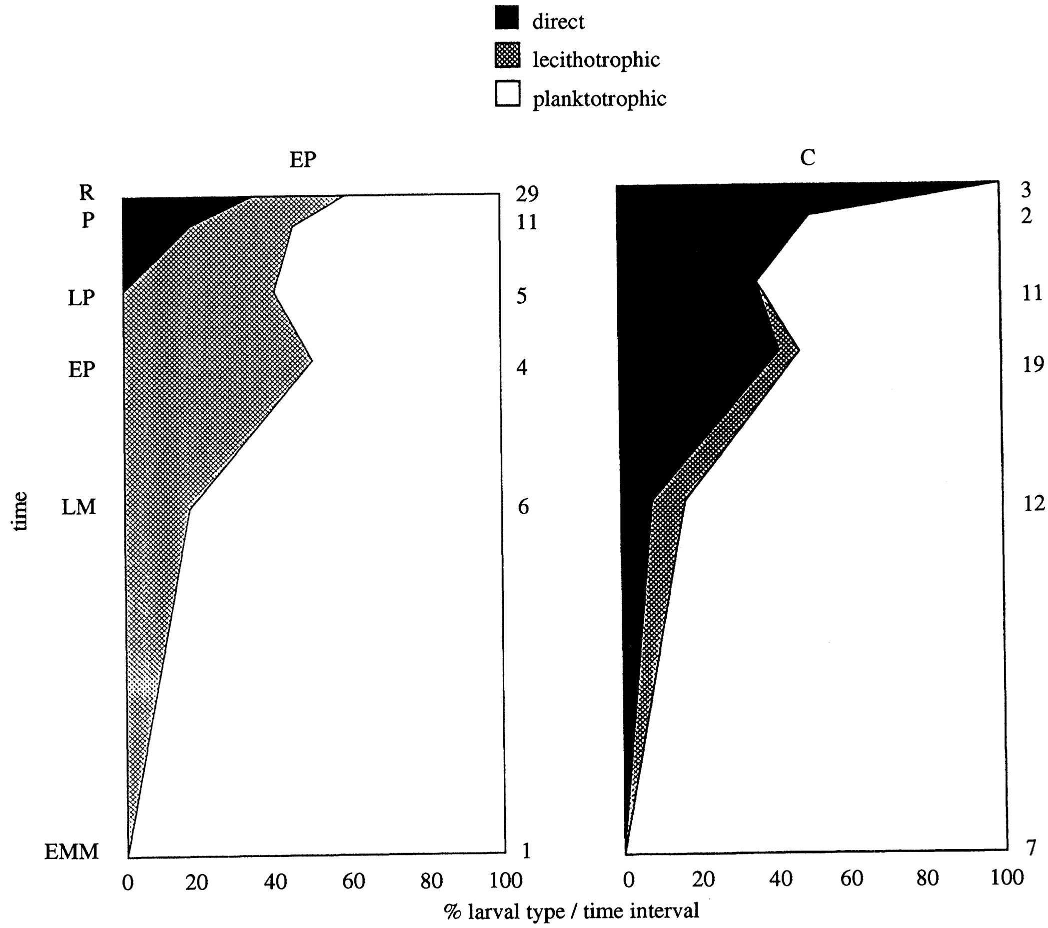

Figure 4. Trends in relative frequency of species inferred to possess planktotrophic larvae (feed in plankton for several weeks), lecithotrophic larvae (non-feeding, drift in plankton about one week) and direct development (no free larval stage) in the eastern Pacific (EP) and Caribbean (C). Numbers of species at each interval indicated to right of boxes for each ocean. Age intervals as in figure 3.

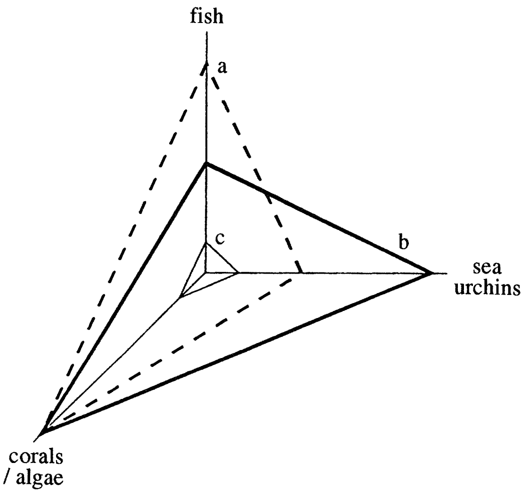

Figure 5. Model of the response of Caribbean coral reef communities to overfishing and sea urchin disease. For details see text.

planktonic foraminifera (Stanley 1986; Stanley *et al.* 1988) and altitudinal shifts in tropical terrestrial vegetation (Bush *et al.* 1992; Colinvaux 1994).

Differences in patterns and rates of Plio-Pleistocene turnover between oceans further implicate refrigeration as an important factor. Extinction of eastern Pacific molluscs at the end of the Pliocene was less than in the tropical western Atlantic (Jackson *et al.* 1993), and was preceded by different evolutionary trends in adult size and larval development (Jackson *et al.* 1994; figures 3 and 4). Molluscan size and development vary with differences in primary production and food availability (Vance 1973; Vermeij 1978; Jablonski & Lutz 1983), and the data in figures 3 and 4 agree well with inferred Pliocene increase in seasonality and upwelling in the eastern Pacific based on oxygen isotopic variation in mollusc shells, but more localized or ephemeral upwelling in the Caribbean (Teranes *et al.* 1994). Disappearance of well-developed eastern Pacific coral reefs after the Miocene (Budd 1989) also agrees with the inferred difference in seasonality between the two oceans.

Upwelling causes seasonal differences in temperature that may exceed 10°C even in the tropics (D'Croz *et al.* 1991). Thus Late Pliocene molluscs in the eastern Pacific were probably exposed to comparable seasonal temperature decreases that exceed estimates of a 5–6°C drop in winter sea surface temperatures due to glaciation. In contrast, Late Pliocene Caribbean species would not have been similarly preadapted to temperature decrease. Once past the initial thermal filter of glacial cooling, however, subsequent rapid rise and fall of sea level and temperatures had a negligible effect on Caribbean molluscan or reef coral extinction and diversity (figure 2; Budd *et al.* 1994*a*).

5. PROSPECTS FOR MARINE DIVERSITY

Changes in marine species and communities are coordinated and discontinuous. This was as true 380 Ma ago in the Devonian (Brett *et al.* 1990) as in the Neogene, and on the land (Vrba 1985) as in the sea. Species appear and disappear as morphologically discrete packages that come and go in surprising synchrony. Shifts in biotas are due to major changes in climate, but, once they occur, new biotas persist more-or-less intact for millions of years despite repeated occurrences of the same climatic fluctuations. Thus continued Pleistocene cycles of low and high temperatures had little evolutionary effect (Potts 1984; Valentine 1989) because, once through the initial thermal filter, all that was left were eurythermal species.

What can these insights tell us about the prospects for marine diversity in the face of increasing human disturbance? Consider the case of Caribbean coral reefs where the abundance of live corals has decreased precipitously over the last 20 years with accompanying increase in macroalgae (Lessios 1988; Knowlton 1992). Caribbean reefs had been heavily exploited for at least 500 years previously with superficially little effect. Early good observers (Sloane 1701; Dampier 1729) described extraordinarily abundant populations of large vertebrates (manatees, turtles, groupers) and molluscs (conchs, pearl oysters) that have not been seen anywhere in abundance for at least a century. Yet turtle was the principal supply of meat eaten in Jamaica during the 18th century (Catesby 1731; Long 1774) until they were virtually eliminated, just as the Maori eliminated the moas of New Zealand (Burney 1993). Manatees, turtles, jewfish and conchs are not as dramatic as giant sloths and mammoths, but there is little doubt that they have been hunted to virtual extinction with the same efficiency.

As far as one can reconstruct from the Holocene record and the first detailed descriptions of reefs in the 1950s (Goreau 1959; Jackson 1992), the virtual disappearance of large vertebrates and conchs had little if any direct effect on the composition of Caribbean reef communities. Abundant smaller predatory and herbivorous fishes consumed sea urchins, other invertebrate grazers and algae, and the ratio of corals to macroalgae was still high (plane a in figure 5). Subsequently intense subsistence fishing associated with rapidly rising human populations decreased both predatory and grazing fishes, resulting in a dramatic increase in invertebrate grazers such as the sea urchin *Diadema antillarum* (Hay 1984). However, this sea urchin also severly regulates algal growth, so that coral abundance remained high (plane b in figure 5).

In 1983, mass mortality of *Diadema* (Lessios 1988) left the reefs without any efficient grazers. This sudden and dramatic shift in the relative abundance of different consumers and their prey permitted enormous increase in unpalatable macroalgae that are progressively overgrowing corals throughout the Caribbean (plane c in figure 5), and reef communities appear to be at least temporarily locked into a macroalgal community state (Knowlton 1992). To make things worse, increased nutrients due to use of fertilizers, decreased coral abundance due to major storms, sedimentation associated with deforestation, toxins and oil spills, and mass bleaching of corals (Woodley *et al.* 1981; Cortes & Risk 1985; Tomascik & Sander 1987; Brown 1990; Hallock 1988; Guzman *et al.* 1991) all help to further lower thresholds for macroalgal dominance over corals (Knowlton 1992). At the rate things are going, there may be very few Caribbean corals to be affected by global climate change (Smith & Buddemeier 1992).

There is a disturbing parallel to this grisly story and the long-term persistence followed by rapid turnover described for Plio-Pleistocene marine communities. Threshold effects on the scale of entire biotas are irreversible.

The ideas for this paper germinated during a sabbatical year at Wolfson College and the Department of Zoology, University of Oxford. Tony Coates, Tom Cronin, Helena Fortunato, Nancy Knowlton and Paul Morris gave much helpful advice. Helena Fortunato and Xenia Guerra prepared the figures. This work was supported by the National Geographic Society, the Kugler Fund of the Basel Naturhistorische Museum, National Science Foundation and STRI.

REFERENCES

Allmon, W.D., Rosenberg, G., Portell, R.W. & Schindler, K.S. 1993 Diversity of coastal plain mollusks since the Pleistocene. *Science*, *Wash.* **260**, 1626–1629.

Beck, J.W., Edwards, R.L., Ito, E. *et al.* 1992 Sea-surface temperature from coral skeletal strontium/calcium ratios. *Science*, *Wash.* **257**, 644–647.

Berggren, W.A., Kent, D.V., Flynn, J.J. & Van Couvering, J.A. 1985 Cenozoic chronology. *Geol. Soc. Am. Bull.* **96**, 1407–1418.

Brett, C.E., Miller, K.B. & Baird, G.C. 1990 A temporal hierarchy of paleoecologic processes within a Middle Devonian epeiric sea. *Paleont. Soc. Spec. Publ.* **5**, 178–209.

Brown, B.E. (ed.) 1990 Coral bleaching: special issue. *Coral Reefs* **8**, 153–232.

Budd, A.F. 1989 Biogeography of Neogene Caribbean reef corals and its implications for the ancestry of eastern Pacific reef corals. *Mem. Ass. Australas. Palaeontols* **8**, 219–230.

Budd, A.F., Johnson, K.G. & Stemann, T.A. 1994*a* Stratigraphic distributions of genera and species of Neogene to Recent Caribbean reef corals. *J. Paleont.* (In the press.)

Budd, A.F., Johnson, K.G. & Stemann, T.A. 1994*b* Plio-Pleistocene turnover and extinctions in the Caribbean reef coral fauna. In *Evolution and environment in tropical America* (ed. J. B. C. Jackson, A. G. Coates & A. F. Budd). University of Chicago Press. (Submitted.)

Burney, D.A. 1993 Recent animal extinctions: recipes for disaster. *Am. Sci.* **81**, 530–541.

Bush, M.B., Piperno, D.R., Colinvaux, P.A. *et al.* 1992 A 14,300-yr paleoecological profile of a lowland tropical lake in Panama. *Ecol. Monogr.* **62**, 251–275.

Catesby, N. 1971 *The natural history of Carolina, Florida and the Bahama islands.*

Cheetham, A.H. 1986 Tempo of evolution in a Neogene bryozoan: rates of morphologic change within and across species boundaries. *Paleobiology* **12**, 190–202.

Colinvaux, P.A. 1994 Quaternary environmental history and forest diversity in the neotropics. In *Evolution and environment in tropical America* (ed. J. B. C. Jackson, A. G. Coates & A. F. Budd). University of Chicago Press. (Submitted.)

Collins, L.S. 1994 Environmental changes in Caribbean shallow waters relative to the closing tropical American seaway. In *Evolution and environment in tropical America* (ed. J. B. C. Jackson, A. G. Coates & A. F. Budd). University of Chicago Press. (Submitted.)

Cortes, J. & Risk, M.J. 1985 A reef under siltation stress: Cahuita, Costa Rica. *Bull. Mar. Sci.* **36**, 339–356.

Crowley, T.J. & North, G.R. 1988 Abrupt climate change and extinction events in earth history. *Science*, *Wash.* **240**, 996–1002.

Dampier, W. 1729 *A new voyage around the world* (reprint). New York: Dover Publ.

Darwin, C. 1859 *On the origin of species by natural selection.* London: John Murray.

D'Croz, L., Del Rosario, J.B. & Gomez, J.A. 1991 Upwelling and phytoplankton in the Bay of Panama. *Rev. Biol. Trop.* **39**, 233–241.

Geary, D.H. 1990 Patterns of evolutionary tempo and mode in the radiation of *Melanopsis* (Gastropoda; Melanopsidae). *Paleobiology* **16**, 492–511.

Goreau, T.F. 1959 The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* **40**, 67–90.

Gould, S.J. & Eldredge, N. 1993 Punctuated equilibrium comes of age. *Nature*, *Lond.* **366**, 223–227.

Guilderson, T.P., Fairbanks, R.G. & Rubenstone, J.L. 1994 Tropical temperature variations since 20 000 years ago: modulating inter-hemispheric climate change. *Science*, *Wash.* **263,** 663–665.

Guzman, H.M., Jackson, J.B.C. & Weil, E. 1991 Short-term ecological consequences of a major oil spill on Panamanian subtidal reef corals. *Coral Reefs* **10**, 1–12.

Hallock, P. 1988 The role of nutrient availability in bioerosion: consequences to carbonate buildups. *Palaeogeogr. Palaeoclim. Palaeoecol.* **63**, 275–291.

Hay, M.E. 1984 Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* **65**, 446–454.

Jablonski, D. & Lutz, R.A. 1983 Larval ecology of marine benthic invertebrates: paleobiological implications. *Biol. Rev.* **58**, 21–89.

Jackson, J.B.C. 1992 Pleistocene perspectives on coral reef community structure. *Am. Zool.* **32**, 719–731.

Jackson, J.B.C. & Cheetham, A.H. 1994 Phylogeny reconstruction and the tempo of speciation in cheilostome Bryozoa. *Paleobiology*. (In the press.)

Jackson, J.B.C., Jung, P., Coates, A.G. & Collins, L.S. 1993 Diversity and extinction of tropical American mollusks and emergence of the Isthmus of Panama. *Science*, *Wash.* **260**, 1624–1626.

Jackson, J.B.C., Jung, P. & Fortunato, H. 1994 Paciphilia revisited: transisthmian evolution of the *Strombina* Group (Gastropoda: Columbellidae). In *Evolution and environment in tropical America* (ed. J. B. C. Jackson, A. G. Coates & A. F. Budd). University of Chicago Press. (Submitted.)

Jackson, J.B.C. & McKinney, F.K. 1990 Ecological processes and progressive macroevolution of marine clonal benthos. In *Causes of evolution* (ed. R. M. Ross & W. D. Allmon), pp. 173–209. Chicago: University of Chicago Press.

Kennett, J.P. & Srinivasan, M.S. 1983 *Neogene planktonic Foraminifera, a phylogenetic atlas.* Stroudsburg, Pennsylvania: Hutchinson Ross Publ.

Kennett, J.P. & Stott, L.D. 1991 Abrupt deep-sea warming, paleoceanographic changes and benthic extinctions at the end of the Palaeocene. *Nature*, *Lond.* **353**, 225–229.

Knowlton, N. 1992 Thresholds and multiple stable states in coral reef community dynamics. *Am. Zool.* **32**, 674–682.

Lessios, H.A. 1988 Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *A. Rev. Ecol. Syst.* **19**, 371–393.

Levinton, J. 1988 *Genetics, paleontology and macroevolution.* Cambridge University Press.

Long 1774 *History of Jamaica, or general survey of the ancient and modern state of that island.* London: T. Loundes.

Michaux, B. 1989 Morphological variation of species through time. *Biol. J. Linn. Soc.* **38**, 239–255.

Overpeck, J.T., Webb, R.S. & Webb, T., III 1992 Mapping eastern North American vegetation change of the past 18 ka: no-analogs and the future. *Geology* **20**, 1071–1074.

Potts, D.C. 1984 Generation times and the Quaternary evolution of reef-building corals. *Paleobiology* **10**, 48–58.

Sloane, H. 1701 *A voyage to the islands Madera, Barbados, Neives, St. Christophers and Jamaica with the natural history of the herbs and trees, four-footed beasts, fishes, birds, insects, reptiles, etc. of the last of those islands*. London.

Smith, S.V. & Buddemeier, R.W. 1992 Global change and coral reef ecosystems. *A. Rev. Ecol. Syst.* **23**, 89–118.

Stanley, S.M. 1986 Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the western Atlantic bivalve fauna. *Palaios* **1**, 17–36.

Stanley, S.M. & Campbell, L.A. 1981 Neogene mass extinction of western Atlantic molluscs. *Nature, Lond.* **293**, 457–459.

Stanley, S.M., Wetmore, K.L. & Kennett, J.P. 1988 Macroevolutionary differences between the major clades of Neogene planktonic foraminifera. *Paleobiology* **14**, 235–249.

Stanley, S.M. & Yang, X. 1987 Approximate evolutionary stasis for bivalve morphology over millions of years: a multivariate, multilineage study. *Paleobiology* **13**, 113–139.

Teranes, J.L., Geary, D.H. & Bemis, B.E. 1994 The oxygen isotopic record of seasonality in Neogene bivalves from the Central American Isthmus. In *Evolution and environment in tropical America* (ed. J. B. C. Jackson, A. G. Coates & A. F. Budd). University of Chicago Press. (In the press.)

Tomascik, T. & Sander, F. 1987 Effects of eutrophication on reef-building corals. II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. *Mar. Biol.* **94**, 53–75.

Valentine, J.W. 1989 How good was the fossil record? Clues from the California Pleistocene. *Paleobiology* **15**, 83–94.

Valentine, J.W. & Jablonski, D. 1991 Biotic effects of sea level change: the Pleistocene test. *J. geophys. Res.* **96**, 6873–6878.

Vance, R.R. 1973 On reproductive strategies in marine benthic invertebrates. *Am. Nat.* **107**, 339–352.

Vermeij, G.J. 1978 *Biogeography and adaptation*. Cambridge, Massachusetts: Harvard University Press.

Vermeij, G.J. 1987 *Evolution and escalation*. Princeton University Press.

Vrba, E.S. 1985 African Bovidae: evolutionary events since the Miocene. *S. Afr. J. Sci.* **81**, 263–266.

Wei, K.-Y. & Kennett, J.P. 1988 Phyletic gradualism and punctuated equilibrium in the late Neogene planktonic foraminiferal clade *Globoconella*. *Paleobiology* **14**, 345–363.

Woodley, J.D., Chornesky, E.A., Clifford *et al.* 1981 Hurricane Allen's impact on Jamaican coral reefs. *Science, Wash.* **214**, 749–755.

Discussion

P. R. SHELDON (*Department of Earth Sciences, The Open University, U.K.*). Stasis – with inferred punctuational speciation – is undoubtedly a common feature of the fossil record. However, there is some evidence that, on geological timescales and for physical variables, the more unstable the environment, the more that lineages are prone to stasis, and conversely, the more stable the environment, the more that lineages tend to evolve continuously (Sheldon 1993). Most of the fossil record comes from relatively dynamic, shallow marine settings, and we could gain the impression that, unless extreme, any forthcoming climatic and other physical changes are not likely to pose a particularly serious threat for most species. Does Professor Jackson consider that the above hypothesis might be generally true and, if so, that there are important implications for species living on land in the tropics and in the deeper sea, namely that such species might be more susceptible to perturbation and thus perhaps to extinction?

Reference

Sheldon, P.R. 1993 Making sense of microevolutionary patterns. In *Evolutionary patterns and processes* (ed. D. R. Lees & D. Edwards) (Linn. Soc. Symp. Vol. **14**), pp. 19–31. London: Academic Press.

J. B. C. JACKSON. The hypothesis appears to confuse the variance in environmental conditions characteristic of a particular habitat with that which may be associated with climatic change. The evolutionary response of a species to a pervasive change in its environment should increase with the magnitude and novelty of the *relative to pre-existing conditions*. From this perspective, both the deep sea (Kennett & Stott 1991) and terrestrial tropics (Bush *et al.* 1992; Colinvaux 1994) are apparently no more or less stable climatically or evolutionarily than are shallow marine environments. Thus sub-Saharan African Bovidae experienced great extinction and speciation at the onset of northern hemisphere glaciation about 2.5 Ma ago (Vrba 1981), just as did reef corals (Budd *et al.* 1994a), whereas subsequently more extreme Pleistocene climatic fluctuations had little evolutionary effect on either group. In contrast, a rapid rise in tropical sea surface temperatures (SSTs) of only 2–3° above present values could be catastrophic for most reef corals whose upper thermal tolerance is typically only a few degrees above present seasonal maxima (Smith & Buddemeier 1992). This is because tropical SSTs have almost certainly been 5 and 6° below present values for most of the past 2.5 Ma (Beck *et al.* 1992; Emiliani 1992; Guilderson *et al.* 1994), so that higher temperatures are beyond the evolutionary experience of modern corals.

References

Emiliani, C. 1992 Pleistocene paleotemperatures. *Science, Wash.* **257,** 12462.

Smith, S. V. & Buddemeier, R. W. 1992 Global change and coral reef ecosystems. *A. Rev. Ecol. Syst.* **23,** 89–118.