

Reports

Tiering in Suspension-Feeding Communities on Soft Substrata Throughout the Phanerozoic

Abstract. *Tiering of benthic marine suspension-feeding communities on soft substrata has varied throughout the Phanerozoic. Epifaunal tiering was most developed during the middle and late Paleozoic and the Triassic to Jurassic, with large-scale reductions in tiering occurring during the Permian-Triassic extinctions and after the Jurassic. Infaunal tiering reached its highest level of organization after the Paleozoic.*

Tiering, the establishment of a community structure in which different organisms are distributed vertically in space (1), is a common biological solution for resource partitioning. Temperate forest communities (2) and infaunal marine deposit-feeding communities (3) are examples where tiering can be found in disparate settings.

The role and evolution of tiering in benthic marine suspension-feeding communities are not well known, and a general model has not been developed. We describe the Phanerozoic history of tiering in suspension-feeding communities on soft substrata from nonreef, shallow subtidal shelf and epicontinental sea settings (4). Communities in only one major habitat are considered in order to eliminate effects of environmental variability, which influence community development.

The importance of tiering in Paleozoic benthic communities was initially suggested for epifaunal crinoid communities (5), and tiering has proved useful in interpreting the paleoecology of younger strata (6). However, a consistent application of a tiering model has not been followed (7).

The proposed history through the Phanerozoic of infaunal and epifaunal suspension-feeding communities is shown in Fig. 1 (8). In epifaunal communities four tier subdivisions are recognized (9). A subdivision below approximately 5 cm above the substratum has been maintained throughout the Phanerozoic by organisms feeding from water close to the sediment-water interface. This tier

was established during the Paleozoic by mollusks, brachiopods, bryozoans, corals, and echinoderms (10). After the Paleozoic mollusks, bryozoans, annelids, and corals became dominant in this tier, and brachiopods were important only locally (11).

The highest epifaunal tier at approximately 10 cm was established in the Lower and Middle Cambrian and contained blastozoan echinoderms (eocrinoids) (12) and sponges. The composi-

tion of this tier changed in the Early Ordovician to primarily bryozoans, corals, echinoderms (including crinoids, paracrinoids, cystoids, and eocrinoids), graptolites, and sponges (13). Gross composition of the 10-cm tier then remained relatively constant to the end of the Paleozoic (14). The 10-cm upper limit of this tier was maintained until at least the Middle Silurian (15). Fenestrate bryozoans of the suspension-feeding communities increased the upper level of this tier to 20 cm by at least the Early Mississippian (16).

Although no documentation is available, the upper limit of this tier must have decreased during the Permian-Triassic extinctions because fenestrate bryozoans and most stalked echinoderms became extinct at that time. Probably during the Triassic and certainly by the Jurassic, this tier was reestablished at 20 cm by corals, sponges, bivalves, alcyonarians, and bryozoans (11). The 20-cm level and gross taxonomic aspect of this tier did not change throughout the remainder of the Mesozoic and Cenozoic.

The maximum height of epifaunal tiering changed markedly throughout the Phanerozoic. By at least the Middle Cambrian it was 10 cm, and by the Middle Ordovician crinoids were probably living at least 50 cm above the substratum (17). Blastoids and cystoids remained predominantly in the tiers around 5 and 10 cm. By the Middle

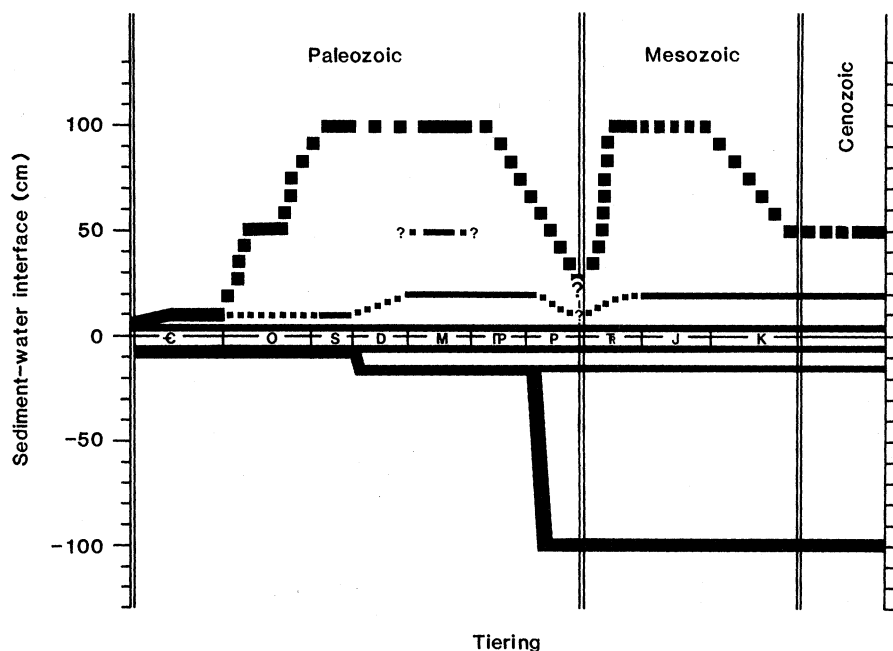


Fig. 1. Tiering in soft substrata suspension-feeding communities through the Phanerozoic. The heaviest lines represent the maximum level of tiering above or below the substratum at any time (8). Other lines represent levels of tier subdivision. Solid lines represent data, and dotted lines are inferred levels.

Silurian, if not earlier, some crinoids had stems 1 m in length (15). This 1-m level was maintained through at least the Mississippian and probably into the Pennsylvanian and Early Permian (5, 16). An additional tier at 50 cm has been proposed for Middle Mississippian crinoid communities (5, 16). Whether these Middle Mississippian communities represent an acme in epifaunal tiering in suspension-feeding communities on soft substrata has not yet been documented. During the Pennsylvanian or Permian this proposed uppermost tier must have decreased, as did the tier at 20 cm, because of extinctions. Neither the lowest position that the upper tier reached as a result of Permian-Triassic extinctions nor the pattern of recovery is preserved. Crinoids reestablished the maximum community height at approximately 1 m in communities of the European Triassic (18), and this level was probably maintained through the Jurassic. After the Jurassic, stalked echinoderms were generally not a part of shallow water communities (19), and for the first time since the Cambrian, they did not establish the upper tier of epifaunal suspension-feeding communities. Instead, beginning in the early Cretaceous, alcyonarians and sponges probably began to dominate this position (20). Since the Jurassic a maximum height of approximately 50 cm has been maintained (11), although maximum structural development in epifaunal suspension-feeding communities may be rare because of increased predation and infaunal activity (21, 22).

Infaunal suspension-feeding communities on soft substrata have a maximum of three tier subdivisions that have been recognized. Until the Devonian generally only a single tier was present at approximately 6 cm below the sediment-water interface. Trace fossil evidence (23) indicates that this tier was present in the Cambrian. Inarticulate brachiopods (24) and burrowing bivalves (25) became established in this tier during the Ordovician, and suspension-feeding gastropods possibly became constituents during the Devonian (26).

In the Devonian several bivalve taxa, particularly lucinids (27), had increased their burrowing abilities so that a tier with a limit at approximately 12 cm below the sediment-water interface was established. By the Mississippian siphonate anomalodesmatan bivalves had populated this tier, and several were able to burrow below 12 cm (28, 29). Permian anomalodesmatans (30) and possibly suspension-feeding arthropods (31) reached a depth approaching 1 m. After the Pa-

leozoic, siphonate heterodont bivalves underwent extensive diversification and, by at least the Cenozoic, reached depths of as much as 1 m (32, 33). The three-tier infaunal structure established in the Permian has remained, with few changes in gross taxonomic structure (34).

Adaptive radiations of benthic invertebrates into new tiering levels should have led to overall increases in diversity as new habitats were filled. The variations in diversity in the Phanerozoic, as described by Sepkoski (35, 36), closely parallel the trends proposed of increasing and decreasing tiering. For example, Sepkoski's (36) Cambrian fauna is characterized by relatively simple tiering of infaunal and epifaunal suspension-feeding communities on soft substrata, his Paleozoic fauna is characterized by high levels of epifaunal tiering, and his post-Paleozoic fauna is characterized by well-developed infaunal tiering. Although numerous other factors certainly play a part in determining diversity, the history of tiering suggests that tiering may have been one of the major factors controlling diversity through the Phanerozoic.

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References and Notes

1. Tiering is often described as stratification [for example, E. P. Odum, *Fundamentals of Ecology* (Saunders, Philadelphia, 1971)], but we avoid the use of stratification because of its geological connotations.
2. R. MacArthur and J. MacArthur, *Ecology* 42, 594 (1961).
3. J. S. Levinton and R. K. Bambach, *Paleobiology* 1, 97 (1975).
4. The trophic classification of K. R. Walker and R. K. Bambach [*Lethaia* 7, 67 (1974)] is followed except that corals are considered suspension-feeders and not carnivores. Both body and trace fossils that have consistently been interpreted as representing suspension-feeding organisms are included. Data used to complete this history come from a survey of more than 1100 references dealing with taxonomy and paleoecology of benthic organisms. Many of the references document periods of little or no change in tiering or were inappropriate because (i) preservation was incomplete during the period, (ii) tiering reconstructions were not attempted, or (iii) the studies were not of soft substrata suspension-feeding communities. No data were rejected. Approximately 35 references are cited that document especially well-developed tiering or changes in tiering. Temporal coverage is incomplete, as indicated in Fig. 1, because of a poor fossil record for certain time intervals.
5. N. G. Lane, *J. Paleontol.* 37, 1001 (1963); N. G. Lane, *Univ. Calif. Publ. Geol. Sci.* 99, 82 (1973).
6. T. E. Stump, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 17, 177 (1975); A. Hoffman, *Acta Geol. Pol.* 27, 227 (1977).
7. The high-level suspension-feeder designation of K. R. Walker [*J. Paleontol.* 46, 82 (1972)] has been applied to a variety of organisms at a variety of levels: 1 m in crinoid communities (5, 16) and several millimeters in Paleocene brachiopod communities [H. R. Feldman, *J. Paleontol.* 51, 86 (1977)].
8. This diagram displays the characteristic maximum tiering attained at any one time. Not all communities would have shown all of this tiering, but maximum epifaunal or infaunal tiering may have developed in mature communities in environmentally predictable settings. We treat characteristic community structure developed through the Phanerozoic. Examples could probably be cited in which an organism at some particular time exceeds the tiering bounds outlined, especially in settings other than those of soft substrata suspension-feeding communities.
9. We do not presume that the tier heights are absolute levels rigidly conformed to by organisms. Rather, they represent logical subdivisions of the community structure which appear to be significant. We may be subdividing a continuum, which is acceptable but only further research could document this.
10. W. B. N. Berry, *J. Geol.* 82, 371 (1974).
11. W. S. McKerrow, Ed., *The Ecology of Fossils* (MIT Press, Cambridge, Mass., 1978).
12. J. Sprinkle, *Mus. Comp. Zool. (Harv. Univ.) Spec. Pub.* (1973).
13. K. R. Walker, *J. Paleontol.* 44, 928 (1970); R. Titus and B. Cameron, *ibid.* 50, 1209 (1976).
14. After the Ordovician the primary stalked echinoderms in lower tiers were crinoids, blastoids, and cystoids. Cystoids became extinct by the end of the Devonian. A brief history of stalked echinoderms in the 10-cm tier is given in T. J. Frest and H. L. Strimple [*Southeast. Geol.* 19, 157 (1978)].
15. R. Watkins and J. M. Hurst, *Paleobiology* 3, 207 (1977).
16. W. I. Ausich, *J. Paleontol.* 54, 273 (1980).
17. J. Sprinkle, personal communication.
18. H. C. O. Linck, *Naturwiss. Monatsschrift Deutsch. Naturk.* 62, 225 (1954).
19. D. L. Meyer and D. B. Macurda, Jr., *Paleobiology* 3, 74 (1977); R. C. Moore, *Univ. Kans. Paleontol. Contrib. Pap.* 17 (1967).
20. At times byssate free-swinging bivalves and other epizoans attached to algae and sea grasses formed an upper level after the Paleozoic [D. C. Rhoads, I. G. Speden, K. M. Waage, *Bull. Am. Assoc. Pet. Geol.* 56, 1100 (1972); M. D. Brasier, *Palaeontology* 18, 681 (1975)].
21. G. J. Vermeij, *Paleobiology* 3, 245 (1977).
22. C. W. Thayer, *Science* 203, 458 (1979).
23. Trace fossils include *Bergaueria*, *Arenicolites*, and *Inhizocorallium* [W. Hantzschel, in *Treatise on Invertebrate Paleontology, Part W, Miscellaneous Supplement 1, Trace Fossils and Problematika*, C. Teichert, Ed. (Geology Society of America and Univ. of Kansas Press, Lawrence, 1975)]. Other trace fossils interpreted to have been made by suspension-feeders, such as the so-called *Skolithos* group and U-shaped vertical burrows with spreite, were employed at greater depths during this time but are characteristic of high-energy (intertidal) environments, and the lengths of burrows may not be accurate indicators of burrowing depth because of the common upward adjustment reaction of burrowers to high sedimentation rates in such environments.
24. M. J. S. Rudwick, *Living and Fossil Brachiopods* (Hutchinson, London, 1970).
25. J. Pojeta, Jr., *U.S. Geol. Surv. Prof. Pap.* 695, 1 (1971).
26. E. L. Yochelson, *Smithson. Contrib. Paleobiol.* 3, 231 (1971).
27. S. M. Stanley, *Annu. Rev. Earth Planet. Sci.* 3, 361 (1975).
28. B. Runnegar, *J. Paleontol.* 48, 904 (1974).
29. S. M. Stanley, *ibid.* 46, 165 (1972).
30. D. E. Hattin [*Kans. State Geol. Surv. Bull.* 124, 1 (1957)] reported anomalodesmatan bivalves referred to *Allorisma* in burrows as deep as 1 m.
31. C. K. Chamberlain and J. Baer [*Brigham Young Univ. Geol. Stud.* 20, 79 (1973)] reported specimens this size of the trace fossils *Ardelia* and *Ophiomorpha*, possibly formed by suspension-feeding thalassinid shrimp.
32. S. M. Stanley, in *Patterns of Evolution as Illustrated by the Fossil Record*, A. Hallam, Ed. (Elsevier, Amsterdam, 1977), p. 209.
33. R. D. Barnes, *Invertebrate Zoology* (Saunders, Philadelphia, 1974).
34. Possible exceptions are groups, such as the polychaetes, for which information from the fossil record is lacking.
35. J. J. Sepkoski, Jr., *Paleobiology* 5, 222 (1979).
36. —, *ibid.* 7, 36 (1981).
37. We thank N. G. Lane for thoughtful discussions during the initiation of ideas that led to this research and E. L. Yochelson, D. E. Hattin, N. G. Lane, J. Pojeta, Jr., and anonymous referees for instructive comments on an earlier draft of this report.

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