mean sample diversity and abundance values in the Indo-Pacific and low ones in the South Atlantic. The terminal Oligocene event (25 to 22 Ma) is indicated only by an increase in mean sample diversity in the North Atlantic. The trends of the middle Miocene (15 to 14 Ma) data are mixed, with increasing mean sample diversity restricted to the South Atlantic. A major speciation event in *Poseidonamicus* accompanied the circulation pattern changes of this key region (*14*).

To conclude, benthic deep-sea ostracode data support the presence of three major periods of flux during the past 70 million years. The Cretaceous-Tertiary boundary event is more sudden than the others. No satisfactory paleoceanographic mechanism thus far proposed can explain this event. Two other global and strong faunal changes are in agreement with known or hypothesized paleoceanographic events. Finally, three additional intervals, suggested as times of important changes, are not supported as events of global significance by our ostracode data, which suggest only localized and weak effects.

The benthic deep-sea ostracodes represent a conservative animal group living in a conservative environment. They tend to show fewer major reactions to minor paleoceanographic events of localized importance. They have persisted through critical changes in the development of the floor of the world ocean from times of parochial invasions of the depths, through the abrupt punctuation of the Cretaceous-Tertiary boundary event, into a period of confinement to these depths but with increased cosmopolitanism after the development of the psychrosphere.

RICHARD H. BENSON
RALPH E. CHAPMAN
LINDA T. DECK
Department of Paleobiology,
National Museum of Natural
History, Smithsonian Institution,
Washington, D.C. 20560

References and Notes

1. T. Birkelund and R. G. Bromley, Eds., *Cretaceous-Tertiary Boundary Events* (Univ. of Copenhagen Press, Copenhagen, 1979); R. Lewin, *Science* **221**, 935 (1983); C. B. Officer and C. L. Drake, *ibid.* **219**, 1383 (1983).
2. J. M. Luck and K. K. Turekian, *Science* **222**, 613 (1983); L. W. Alvarez *et al.*, *ibid.* **208**, 1095 (1980); J. Smit and J. Hertogen, *Nature (London)* **285**, 198 (1980).
3. W. A. Berggren, in *Climate in Earth History* (National Academy Press, Washington, D.C., 1982), pp. 118–125.
4. R. H. Benson, *Lethaia* **8**, 69 (1975).
5. B. Corliss, *Mar. Micropaleontol.* **6**, 367 (1981).
6. R. G. Douglas and F. Woodruff, in *The Sea*, C. Emiliani, Ed. (Wiley, New York, 1981), vol. 7; W. Alvarez *et al.*, *Science* **216**, 885 (1982).
7. R. J. Foster, *Nature (London)* **249**, 751 (1980).
8. S. M. Savin, in *Climate in Earth History* (National Academy Press, Washington, D.C., 1982), pp. 164–171; W. H. Berger, in *ibid.*, pp. 43–54.
9. C. G. Adams *et al.*, *Nature (London)* **269**, 383 (1977).
10. Indices used include the Shannon-Wiener and Simpson (diversity) and Sheldon's and Buzas and Gibson's equitability.
11. R. H. Benson *et al.*, in *South Atlantic Palaeoceanography*, K. Hsu, Ed. (Cambridge Univ. Press, Cambridge, in press).
12. E. C. Olson and R. L. Miller, *Morphological Integration* (Univ. of Chicago Press, Chicago, 1958). The rho-groups analysis used the Dice coefficient on generic presence-absence data.
13. Transect. DSDP stations from West to East: São Paolo Plateau (356), Rio Grande Rise (518, 517, 357, 516, 22, 21, 20, and 19), Mid-Atlantic Ridge (14, 15, 16, 5, 19, and 17), Angola Basin (522), Walvis Ridge (527, 528, 529, 525, 526, and 524), and off the west coast of Africa (363, 362, and 532).
14. R. H. Benson, *Paleobiology*, in press. Studied using resistant-fit theta-rho analysis, a form of transformational analysis [R. H. Benson *et al.*, *Paleobiology* **8**, 328 (1982)].
15. We gratefully acknowledge the comments of S. Lidgard, M. Buzas, N. Sohl, and R. Grant. This study was sponsored by the Scholarly Research Program of the Smithsonian Institution.

30 December 1983; accepted 18 April 1984

Community Recovery After Storm Damage: A Case of Facilitation in Primary Succession

Abstract. *Manipulations of early arriving, fast-growing algal stands, which appeared soon after a severe storm denuded a Southern California marine reef habitat, indicated that the dense cover protected newly settled kelp plants from excessive damage by grazing fishes. This is an example of refuge facilitation in primary succession after a major natural disturbance, a mechanism that may contribute substantially to the regeneration of a kelp forest.*

The process of community succession has been well documented (*1*), and three mechanisms have been proposed for the sequential replacement of species: facilitation, inhibition, and neutral effect (*2*). These mechanisms may work by competitive interactions between species that arrive earlier or later during the process. They may be activated by major disturbances, whether biological (predation) or physical (weather). For example, predation of sea urchins by sea otters, mediated by human exploitation, can initiate a change in the structure of coastal kelp bed communities from an open, cleared state (barren grounds) overgrazed by urchins to a densely vegetated state (kelp forest) dominated by macroalgae (*3*). Severe storm damage to subtidal reefs may start the successional process as well (*4*). At our study site in a kelp bed off the coast of Southern California, two major storms occurring 3 years apart perturbed the reef community in opposite directions. The first storm started degenerative changes from a lush kelp forest dominated by large kelps (*Macrocystis pyrifera* and *Pterygophora californica*) to a barren grounds overgrazed by sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*), and the second storm initiated regenerative changes culminating once again in the kelp forest (*5*). This gave us the opportunity to collect the first experimental evidence that facilitation—whereby an early successional dominant provides a refuge for establishment of a later one—is an important mechanism of community succession in kelp forests. We now show that early arriving, fast-growing algae enhanced the survival of young kelp plants by sheltering them from herbivorous fish.

Table 1. Survival of kelp sporophytes in treatment (filamentous algae removal) and control (unmanipulated) plots. Each plot (covering 0.1 m^2) of a treatment-control pair was located within 0.5 m of the other. The first and second trials of five replicates each were observed after 5 and 2 days, respectively. Tabulated are counts of sporophytes (plants with more than half their blade intact) and stipes (plants with little or no blade remaining). Abbreviations: MB, many bitten plants (> 50 percent); FB, few bitten plants (< 25 percent); and NB, no bitten plants. No change in number or condition of sporophytes in control plots was observed at the end of the two trials.

Beginning of trial		End of trial	
Sporophytes (number) and condition		Sporophytes (number)	Stipes (number)
Treatment	Control		
First trial (12 to 17 May 1983)			
77 MB	100 FB	0	15
35 FB	40 FB	0	21
30 FB	40 FB	0	17
77 NB	100 FB	0	55
26 FB	30 FB	No change	
Second trial (17 to 19 May 1983)			
29 FB	30 FB	2	21
39 FB	50 FB	20	10
37 FB	100 FB	4	20
56 FB	40 FB	40	8
55 FB	100 FB	14	18

In early March 1983, the second storm ravaged the area (*6*). At Naples Reef near Santa Barbara (34°25'N, 119°57'W), much of the upper surfaces on the rocky, subtidal substratum were scoured severely, leaving crustose coralline algae as the only conspicuous marine plants visible. Sections of the oil-shale ridges were broken loose, exposing large areas of virgin rock. The scouring and breakage created extensive new surfaces (*7*), much as did the first storm which struck in February 1980. Unlike the first storm, however, whose destructive power could not reach the urchins because they were protected in rocky refuges and had plenty of kelp litter to eat, the second storm decimated the population because the urchins had emerged to graze back all new plant growth and had no source of litter to exploit. Thus, by creating bare space for successful kelp settlement while destroying urchins, the second storm catalyzed the regeneration of a kelp forest (*5*).

A diatom layer grew on all surfaces immediately after the storm, while filamentous and leafy seaweeds appeared within a few weeks. A clear dichotomy of algal composition by surface type existed. On old surfaces containing crustose coralline algae, most foliage was composed of blades and filaments of red algae. This assemblage resembled algal turf typical of Southern California subtidal habitats (*8*) and appeared to be regenerating from basal fragments that had survived the scouring. Scattered throughout the red algal turf were small patches of filamentous brown algae: *Giffordia, Ectocarpus*, and others. On new surfaces, however, filamentous browns formed dense stands. By late April, the teardrop-shaped blades of small kelp sporophytes (*Macrocystis* and *Pterygophora*) were visible all over the reef, although the greatest densities were on new surfaces.

Earlier studies (*9*), direct observations, and stomach-content analyses showed that two grazing fishes, *Medialuna californiensis* and *Girella nigricans*, eat leafy algae including young kelp sporophytes, and many of the distal tips of the new sporophyte blades were cut off in the crescent patterns typical of fish bites. Sporophytes hidden within stands of filamentous brown algae apparently suffered less fish predation than sporophytes associated with regenerating red algal turf.

To test for the role of filamentous browns in helping kelp sporophytes survive fish grazing, filamentous algae were removed from stands of kelp sporophytes on new surfaces to compare sporophyte survival between removal and unmanipulated control plots. To supplement this experiment, nondisruptive quadrat samples were taken in unmanipulated areas to compare (i) the height of filamentous algae to the percentage of sporophytes with fish bites and (ii) the density of sporophytes between new and old surfaces.

Overall, nine of ten removal plots (*10*) suffered conspicuous fish damage, whereas no observable change occurred in sporophyte numbers in any control plot (Table 1). The four removal plots grazed during the initial trial (5 days) had no undamaged sporophytes; only a few stipes had parts of their blades remaining (Table 1). In the second trial (2 days), the damage was not so severe, but there were bladeless stipes in all removal plots; no bladeless stipes were found in any of the plots before the manipulations or in control plots at any time (Table 1) (*11*).

In the 28 nondisruptive quadrat samples from old surfaces, where turf height averaged 1.4 ± 0.1 (S.E.M.) cm, 94 percent of the 86 sporophytes examined had fish bites (Fig. 1). In the 30 quadrats from new surfaces, where turf height averaged 11.5 ± 1.6 cm ($N = 20$ random probes with a ruler), 59 percent of the 1674 sporophytes examined were damaged [*G*-test of independence (*12*): $G = 27$, $P < 0.005$] (Fig. 1).

These experiments and observations, including a natural experiment (*13*), indicate that young kelp plants growing within stands of filamentous algae receive some protection from herbivorous fish. The plants are more vulnerable when they grow among the shorter red algal turf on old surfaces. Since the grazing fishes had filamentous browns as well as kelps in their guts, the mechanism responsible for this protection does not appear to involve the fishes' general avoidance of filamentous browns. Instead, the fish may find it more difficult to spot and pick out sporophytes from within the undulating assemblage of plants (*14*).

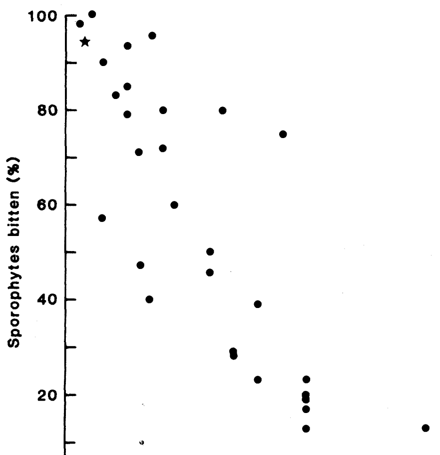

Fig. 1. Relation between height of the brown filamentous algal turf on new rock surfaces and the percentage of kelp sporophytes that had been bitten by fish. Quadrats for each observation measured 0.1 m^2 and 30 quadrat samples were observed on new surfaces. The 28 quadrat samples observed on old, regenerating surfaces are represented by a single point because the data were consistent. The correlation coefficient (*r*) for new surfaces is −0.82 ($P < 0.01$). (●), New surfaces; (★), mean for old surfaces.

Kelp sporophytes were beginning to grow beyond the height of the filmentous algae by mid-May, indicating that the refuge from fish predation was only temporary (*15*). Therefore, we suggest that by the time kelps outgrow their protective mask they have attained a refuge by virtue of their size. Qualitative observations made during the quadrat sampling indicated that smaller sporophytes (< 10 cm tall) were being selectively attacked in the midst of larger individuals (> 10 cm).

The greater density of sporophytes observed on new surfaces may also increase the chances of plants to escape fish predation because of their size. The density of kelp sporophytes on old surfaces (30.8 plants per square meter, $N = 28$ quadrats 0.1 m^2 in area) was far less than that on new surfaces (558 per square meter, $n = 30$) (*16*). Earlier studies of turf interactions have indicated that coverings of red algae or crustose corallines inhibit the recruitment of kelp sporophytes (*17*). We suggest that a second mechanism—the cropping of the few exposed sporophytes that happen to recruit to such turf—acts together with recruitment inhibition to reduce further the chances of establishment of kelps on old surfaces.

Facilitation has been found to occur mainly during primary succession on new surfaces (*2*). Early-successional organisms may alter the composition of the substratum to make it more suitable for recruitment of later forms (*18*) or to provide protection from physical trauma such as desiccation (*19*). Our evidence supports the idea that facilitation is most likely to occur during primary succession. The role of early-successional species, however, is expanded to include protection from predation on young individuals of later successional forms. Other studies have shown that established sessile organisms may provide refuges from predation in fouling communities and rocky intertidal habitats (*20*), but our discoveries appear to be the first example of refuge facilitation in primary succession after a major natural disturbance. This process may commonly contribute to regrowth of kelp (*21*).

LARRY G. HARRIS
Department of Zoology, University of New Hampshire, Durham 03824
ALFRED W. EBELING
DAVID R. LAUR
ROBERT J. ROWLEY
Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara 93106

References and Notes

1. F. E. Clements, *Carnegie Inst. Washington Publ.* **242**, 1 (1916); F. L. Golley, *Ecological Succession* (Dowden, Hutchinson, and Ross, Stroudsburgh, Pa., 1977); H. S. Horn, in *Theoretical Ecology*, R. M. May, Ed. (Sinauer, Sunderland, Mass., ed. 2, 1981), p. 253; E. P. Odum, *Science* **164**, 262 (1969).
2. J. H. Connell and R. O. Slatyer, *Am. Nat.* **111**, 1119 (1977).
3. C. A. Simenstad, J. A. Estes, K. W. Kenyon, *Science* **200**, 403 (1978).
4. T. F. Goreau, *Ecology* **40**, 67 (1959); J. D. Woodley *et al.*, *Science* **214**, 749 (1981); R. K. Cowen, C. R. Agegian, M. S. Foster, *J. Exp. Mar. Biol. Ecol.* **64**, 189 (1982).
5. A. W. Ebeling, D. R. Laur, R. J. Rowley, in preparation.
6. P. K. Dayton and M. J. Tegner [*Science* **224**, 283 (1984)] give a general summary of this storm and other effects of the recent strong El Niño climatic anomaly on the Southern California kelp community.
7. New surfaces are surfaces of virgin rock exposed for the first time during the storm; old surfaces are those containing coralline algal crusts, indicating that they had been in place for some period before the storm.
8. W. J. North, *Nova Hedwigia* (Suppl.) **42**, (1971); M. S. Foster, *Mar. Biol.* **32**, 313 (1975); M. Neushul, M. S. Foster, D. A. Coon, J. W. Woessner, B. W. W. Harger, *J. Phycol.* **12**, 397 (1976); B. W. W. Harger, thesis, University of California, Santa Barbara (1979); P. K. Dayton *et al.*, *Ecol. Monogr.*, in press.
9. J. C. Quast [*Calif. Dep. Fish Game Fish Bull.* **139**, 109 (1968)] found kelp in guts of these fishes.
10. The exceptional treatment was on a surgy, exposed slope, which may have discouraged fish grazing.
11. The zone of meristomatic growth is at the junction of sporophyte blade and stipe. Since blades can regenerate from stipes, bladeless stipes may survive.
12. R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, ed. 2, 1981), p. 737.
13. A sea star (*Patiria miniata*) was found feeding on a patch of new surface and had cleared a swath through the dense stand of filamentous algae, leaving only the kelp sporophytes. All sporophytes in the swath had been cropped down to 4 cm, while the filamentous algae and sporophytes were about 12 cm in height on both sides of the swath.
14. Alternatively, fish may have been attracted by the disturbance of plot manipulation. However, the same grazing differential was observed on the unmanipulated surfaces in quadrat samples.
15. W. L. Montgomery, T. Gerrodette, L. D. Marshall, *Bull. Mar. Sci.* **30**, 901 (1980).
16. Similar differences in sporophyte densities were found between old and new surfaces in permanent quadrats established by D. Laur several years before the storm.
17. W. P. Sousa, *Ecol. Monogr.* **49**, 227 (1979); W. P. Sousa, S. C. Schroeter, S. D. Gaines, *Oecologia (Berlin)* **48**, 279 (1981); D. Breitburg, *Ecology*, in press.
18. T. Turner, *Am. Nat.*, **121**, 729 (1983).
19. B. A. Menge, *Oecologia (Berlin)* **34**, 17 (1978).
20. G. Russ, *J. Exp. Mar. Biol. Ecol.* **42**, 55 (1980); P. S. Petraitus, *Ecology* **64**, 522 (1983).
21. J. S. Stephens, Jr., observed widespread kelp recruitment and survival in dense vegetation on new rock surfaces created off Los Angeles by the 1983 storm, and W. J. North noted that outplanting young kelp among such vegetation may alleviate damage from fish grazing (personal communications).
22. We thank R. Bray, J. C. Connell, M. Hixon, S. Holbrook, R. Larson, R. Schmitt, and J. S. Stephens, Jr. for reviewing the manuscript. Supported by a University of New Hampshire–University of Maine National Oceanic and Atmospheric Administration Sea Grant (L.G.H.) and NSF grant OCE82-08183 (A.W.E. and D.R.L.).

30 January 1984; accepted 24 April 1984

Bishop Tuff Revisited: New Rare Earth Element Data Consistent with Crystal Fractionation

Abstract. *The Bishop Tuff of eastern California is the type example of a high-silica rhyolite that, according to Hildreth, supposedly evolved by liquid-state differentiation. New analyses establish that the Bishop Tuff "early/late" rare earth element trend reported by Hildreth mimics the relations between groundmass glasses and whole rocks for allanite-bearing pumice. Differences in elemental concentrations between whole rock and groundmass are the result of phenocryst precipitation; thus the data of Hildreth are precisely those expected to result from crystal fractionation.*

Considerable interest has been focused recently on the Bishop Tuff because it is the type example of a major high-silica rhyolitic magma that supposedly evolved by liquid-state diffusion. The tuff was the subject of an exhaustive petrologic study by Hildreth (*1, 2*), who concluded that crystal fractionation played no important role in establishing preeruptive chemical gradients in the Bishop Tuff magma chamber. Hildreth proposed that the magma differentiated in the liquid state, and he coined the term "thermogravitational diffusion" to encompass liquid-state fractionation processes such as Soret separation and diffusion of cations complexed with volatile components. Hildreth (*3*) and Mahood and Hildreth (*4*) have treated high-silica rhyolites as a class distinct from less silicic rocks because they believe that liquid-state mechanisms played a leading role in the evolution of high-silica rhyolites.

The thermogravitational mechanism is admittedly poorly understood (*1–4*), and the model is not even qualitatively testable. Rhyolites and granites that supposedly have evolved by liquid-state diffusion are usually identified on the basis of a comparison of their geochemical enrichment patterns to that of the Bishop Tuff (*5*). The rare earth element (REE) trends are thought to be especially important in the recognition of rock suites affected by thermogravitational diffusion; in the Bishop Tuff the light REE decrease and the heavy REE increase with diminishing temperature, increasing inferred stratigraphic height, and increasing rock SiO_2 content (*1*). The material that erupted early is more differentiated than that erupted later, and this is interpreted to represent the inverse stratigraphy of the magma chamber. Criticisms of the liquid state–differentiation model have been based on reinterpretations of Hildreth's data (*6*) or on studies of granitoids (*7*). Important experimental studies of Soret diffusion in melts of Bishop Tuff compositions are now in progress but have not yet been published (*8*).

The data reported here are, to my knowledge, the first new geochemical analyses of the Bishop Tuff to be published since Hildreth's study, and these data are significantly more precise than his. In this study the differentiation of the Bishop Tuff is examined on the least equivocal scale, that of individual hand specimen–sized samples (about 1 kg). For such small-scale samples the differences in REE concentrations between porphyritic whole-rock specimens and their groundmass glasses must reflect crystal-melt processes such as crystal precipitation or accumulation, provided that the effects of alteration are minimal. These concentration differences cannot be the result of thermogravitational diffusion because no significant thermal or gravitational gradient existed on the scale of a hand specimen. Hildreth has detailed (*1*) several mineralogical arguments that establish that there was no significant crystal settling or accumulation in the Bishop Tuff magma chamber. These groundmass/whole-rock relations, therefore, clearly document the effects of crystal precipitation.

I discuss the samples in the context of Hildreth's (*1*) temperature stratigraphy. He found that the temperatures of the iron-titanium oxides ranged from 720°C in the early erupted air fall to 790°C in rocks that erupted late. Quartz, sanidine, oligoclase, biotite, ilmenite, titanomagnetite, zircon, and apatite are ubiquitous phenocrysts. Allanite, a light REE-rich mineral of the epidote family, appears at 763°C and is present in all samples of lower temperature.

For this study pumice blocks were collected from three of Hildreth's (*2*) sample localities that represent nearly