mergence observed in several groups also suggests that the high southern latitude region was the source for some of the elements of the modern outer shelf and slope communities. The recognition of the importance of the high latitudes to the development of Cenozoic biotas suggests that the high latitudes may have played a more important role in the evolution of the earth's biota throughout the Phanerozoic than has previously been acknowledged.

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References and Notes

1. L. J. Hickey, R. N. West, M. R. Dawson, D. K. Choi, *Science* **221**, 1153 (1983).
2. A high latitudes region is considered in this report to be above 60° latitude.
3. P. J. Darlington, *Biogeography of the Southern End of the World* (Cambridge Univ. Press, Cambridge, 1965).
4. H. B. Fell, *Nature (London)* **193**, 759 (1962).
5. W. R. B. Oliver, *J. Linn. Soc. London Bot.* **47**, 99 (1925).
6. The only major expedition to the Seymour Island region was conducted by the Swedish South Polar Expedition led by Otto Nordenskjold in 1901 through 1903.
7. D. H. Elliot, C. Rinaldi, W. J. Zinsmeister, T. A. Trautman, W. A. Bryant, D. del Valle, *Antarct. J. U.S.* **10**, 183 (1975).
8. W. J. Zinsmeister, *ibid.* **17**, 63 (1982).
9. ———, *J. Geol. Soc. London* **139**, 770 (1982).The Upper Cretaceous–lower Tertiary sequence on Seymour Island has been divided into the Marambio Group consisting of the Lopez de Bertodano and Sobral formations [C. A. Rinaldi, in *Antarctic Geosciences*, C. Craddock, Ed. (International Union of Geological Sciences, Madison, Wis., 1982), series B, vol. 4, pp. 281–286] and the Paleocene Cross Valley and upper Eocene La Meseta formations of the Seymour Island Group (D. H. Elliot and T. A. Trautman, in *ibid.*, pp. 287–297].
10. W. J. Zinsmeister, *J. Paleontol.* **56**, 84 (1982).
11. D. B. Blake and W. J. Zinsmeister, *ibid.* **53**, 1145 (1979).
12. W. J. Zinsmeister and H. H. Camacho, *ibid.* **54**, 1 (1980).
13. R. M. Feldmann and W. J. Zinsmeister, *Geol. Soc. Am. Abstr. Program* **15**, 571 (1983).
14. ———, *J. Paleontol.*, in press.
15. The absence of these cool water groups elsewhere in the Southern Hemisphere is not believed to be an artifact of collecting on the southern continents. The Tertiary deposits of both Australia and New Zealand have been intensively studied for more than 100 years [C. A. Fleming, *N. Z. Dep. Sci. Ind. Res. Bull.* **173**, 1 (1966)]. Although the Tertiary deposits of southern South America have received little study since the turn of the century, it seems unlikely that the early workers [G. B. Sowerby, in C. Darwin, *Geological Observations* (Appleton, London, 1846), pp. 605–627; R. A. Philippi (*26*); H. von Ihering, *An. Mus. Nac. Buenos Aires* (1907); A. E. Ortmann, *Rep. Princeton Univ. Exped. Patagonia* **4**, 45 (1902)] would have overlooked them. During the last 10 years, W.J.Z. has conducted an extensive collecting program in southern South America. Except for the extension of the range of *Eurhomalia* back to the early Miocene, none of the cool water taxa which are abundant in the La Meseta Formation has been found in deposits of Paleogene age in South America.
16. C. A. Fleming, *Tuatara* **10**, 53 (1962).
17. N. J. Shackleton and J. P. Kennett, *Initial Rep. Deep Sea Drill. Project* **29**, 743 (1975).
18. W. J. Zinsmeister, in *Historical Biogeography, Plate Tectonics, and the Changing Environment*, J. Gray and A. J. Boucot, Eds. (Oregon State Univ. Press, Corvallis, 1979), pp. 349–355.
19. The movements have a general south to north component for Australia and New Zealand and an east to west component for South America. In contrast, Antarctica has remained nearly stationary through the Cenozoic.
20. N. Mulimian, H. H. Camacho, R. Gorrono, *Ameghiana* **15**, 265 (1978).
21. W. J. Zinsmeister, *Antarct. J. U.S.* **13**, 25 (1978).
22. H. W. Rasmussen, *Inst. Antart. Argent. Publ.* **4**, 79 (1979).
23. M. O. Woodburne and W. J. Zinsmeister, *Science* **218**, 284 (1983).
24. J. H. Lipps and C. S. Hickman, in *The Environment of the Deep Sea*, W. G. Ernst and J. G. Morin, Eds. (Prentice-Hall, Englewood Cliffs, N.J., 1981), vol. 2, p. 325.
25. W. J. Zinsmeister, *J. Paleontol.* **56**, 84 (1982).
26. R. E. Philippi, *Fosiles Terciarios y Cuatarios de Chile* (Universidad de Chile, Santiago, 1887).
27. M. J. Rathbun, *U.S. Natl. Mus. Bull. 97* (1918).
* Present address: Department of Geosciences, Purdue University, West Lafayette, Ind. 47907.

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Catastrophic Storms, El Niño, and Patch Stability in a Southern California Kelp Community

Abstract. *Strong winter storms in southern California destroyed most of the canopy of the giant kelp* Macrocystis pyrifera *but not the patches of understory kelps in the Point Loma kelp forest near San Diego. Subsequent massive recruitment of* Macrocystis *juveniles and adults that survived the storms had low survival in the summer during the California El Niño of 1983. The combined disturbance may have long-lasting structural consequences for this community because, once established, the understory patches can resist invasion by* Macrocystis.

On 30 November 1982 the first of 11 unusually powerful storms struck the southern California coastline. For 15 days wave heights exceeding 3m were measured at the entrance to Mission Bay in San Diego; some of these waves were the largest measured in 8 years. Seven of the 11 storms had wave periods of more than 20 seconds, the first such occurrence in over a decade (*1*). The storms occurred during an El Niño event, which by many indications appears to be the most extreme yet measured (*2*). Technically, El Niños are periodic events characterized by anomalously warm sea surface temperatures along the coasts of Ecuador and Peru (*2*), but the strength of the California Current correlates to these eastern tropical Pacific Ocean phenomena. The California events were marked by a diminution of the California Current, anomalous poleward flow, and depression of the thermocline (*3*). We now describe the separate and combined effects of the catastrophic storms and the strong El Niño on the structure and stability of the kelp community off Point Loma near San Diego (*4*).

This community is characterized by the giant kelp *Macrocystis pyrifera*, the fronds of which float on the sea surface. There are three other perennial canopy types that occupy areas of various sizes on the sea floor: (i) *Pterygophora californica* and *Eisenia arborea*, whose fronds are held above the substratum by woody stipes and occupy often distinct patches up to several hectares in area; (ii) *Laminaria farlowii*, whose fronds lie prostrate on the substratum and form patches usually less than 100 m^2 in area; and (iii) two types of turf of articulated coralline algae (mostly *Calliarthron cheilosporioides*) or fleshy red algae (often dominated by *Gelidium* spp.), which form patches usually less than 30 m^2 in area. The resistance and resilience stability of these patches were characterized from 1970 to 1981 (*5*). At Point Loma, *Macrocystis* is the competitive dominant, but each of the other patch types has resistance to disturbance or invasion. The winter storms of 1982–1983, however, reduced the surface canopy area from over 600 to less than 40 ha (*6*), and there were periods with essentially no canopy. Our diving surveys covering 960 to 1440 m^2 of subsurface *Macrocystis* plants revealed that the damage was not uniform. Mortality, measured by densities of extant plants and recently killed holdfasts or fresh holdfast scars, was highest (66 percent) in the shallow (12-m) inner margin of the forest, lower (47 percent) at mid depths (15 m) of the central part of the forest, and lowest (13 percent) in the deeper (18-m) central outer margin. Mortality at the northern and southern ends of the forest, 40 and 41 percent, respectively, was higher than that at the central outer station even though these regions are all at the same depth (18 m). Two- and 3-year-old plants survived better than others at Point Loma (*5*). In the winter of 1975–1976, mortality of 2-year-old plants in a 400-m^2 area in the central part of the kelp forest was 6 percent ($N = 84$); during the following winter, mortality of 3-year-old plants was 21 percent ($N = 38$). In the winter of 1981–1982, mortality of 2-year-old plants in the same area was 7 percent ($N = 56$), but the 1982–1983 winter storms resulted in 44 percent ($N = 48$) mortality (*7*).

The observed effects of these storms and the El Niño, combined with the data accumulated over the past decade, allow consideration of the interactions of catastrophic scale events with the more common, smaller scale disturbances. Although the storms had a major effect on the *Macrocystis* patches, their effects on the other patches existing since 1971 were moderate to none. One large *Pterygophora* patch had been invaded slowly by *Macrocystis* after the 1979–1980 winter storms, but eight other *Macrocystis*-*Pterygophora* and *Eisenia* borders survived through the 1982–1983 storms, even though many of the *Macrocystis* did not. Four of four *Macrocystis*-*Laminaria* borders and ten of ten *Pterygophora* and *Eisenia*-*Laminaria* borders also survived. Five patches of *Gelidium* and of *Calliarthron* have yet to be invaded. In experiments where understory algae are removed and *Macrocystis* spores are introduced, each understory patch type can be invaded (*5*); however, the effects of the 1982–1983 storms show that the understory patches resist physical disturbance. In each case where an understory patch had bordered *Macrocystis*, the *Macrocystis* was gone or heavily disturbed, indicating that the understory species had successfully invaded the *Macrocystis*.

The resistance stability (*5*) of the understory is shown by the following observations. The only disturbances in six *Pterygophora* and *Eisenia* patches occurred in areas where *Macrocystis* had been introduced in the early 1970's by removing the *Pterygophora* and *Eisenia* and transplanting *Macrocystis* sporophylls; these isolated *Macrocystis* patches were in their second generation when they were detached by the storms. In many cases the drifting holdfast bundles of these plants disturbed the adjacent *Pterygophora* and *Eisenia* patches. Three other areas in which *Macrocystis* had been transplanted into *Laminaria* patches were also cleared by the storms, but there was no apparent damage to the adjacent *Laminaria* which lie prostrate on the substratum and are less susceptible to damage from drifting holdfasts. In both bases a mixture of several species recruited into the disturbed areas.

A California El Niño that lasted from 1957 to 1959 (*3*) severely affected southern California coastal kelp forests; the kelp beds along the mainland virtually disappeared and were replaced in many cases by sea urchin barrens (*4, 8*). The 1982–1983 California El Niño was larger than the 1957 to 1959 event. For example, the sea level anomaly (corresponding to poleward flow) off the Scripps Institution of Oceanography pier was 8.8 cm in January of 1958 and 23 cm in January of 1983. The 1982–1983 El Niño was associated with a deep mixed layer and negligible amounts of nutrients; the warm water anomaly, centered at 75- to 150-m depths in the nearshore, was as much as 11 standard deviations above the mean (*9*). These data, along with the occurrence of subtropical animals far north of their normal distribution, imply that subtropical waters intruded into California coastal waters.

Surface temperature readings taken from the Scripps pier were largely higher than the 63-year mean since July of 1982 and show two periods of unusually warm water in the winter and fall of 1983 (Fig. 1). There were indications of weak upwelling in the spring but none in the summer. Major upwelling events, defined as lasting more than 6 days with a maximum surface temperature reduction of more than 3°C from the long-term mean, usually occur twice a summer (*10*); no such events occurred in 1983. Bottom temperature records indicated that the water column was well mixed during the anomalously warm winter months. Apparent upwelling events resulted in cooler bottom temperatures during the spring, but in midsummer bottom temperatures were above 16°C from August through October and went as high as 21.4°C. The normal thermocline was depressed to depths below the kelp forests.

The deterioration of *Macrocystis* in warm water has been observed for about 25 years (*4*), but it is now clear that temperatures of 20° to 25°C do not damage kelps and that summer die-offs may be caused by nutrient depletion (*11, 12*). A strong negative correlation between temperature and nutrient concentrations has been established for the southern California Bight (*13*) and holds for kelp forests as well (*14, 15*); nitrate concentrations are negligible at temperatures of 16°C and above. In view of the existence of internal nitrogen reserves, other data (*15, 16*) suggest that *Macrocystis* can maintain rapid growth for up to a month in a nutrient-limited environment before its growth slows. Extreme nitrogen deprivation appears to cause weakening or sloughing of frond tissues resulting in canopy decline (*11*).

The El Niño may have exerted an effect along with the winter storms because the temperature averaged 16°C, suggesting limited amounts of nutrients available to the plants for repair of mechanical damage. However, the most important effects of the El Niño were exerted during the summer and fall. In

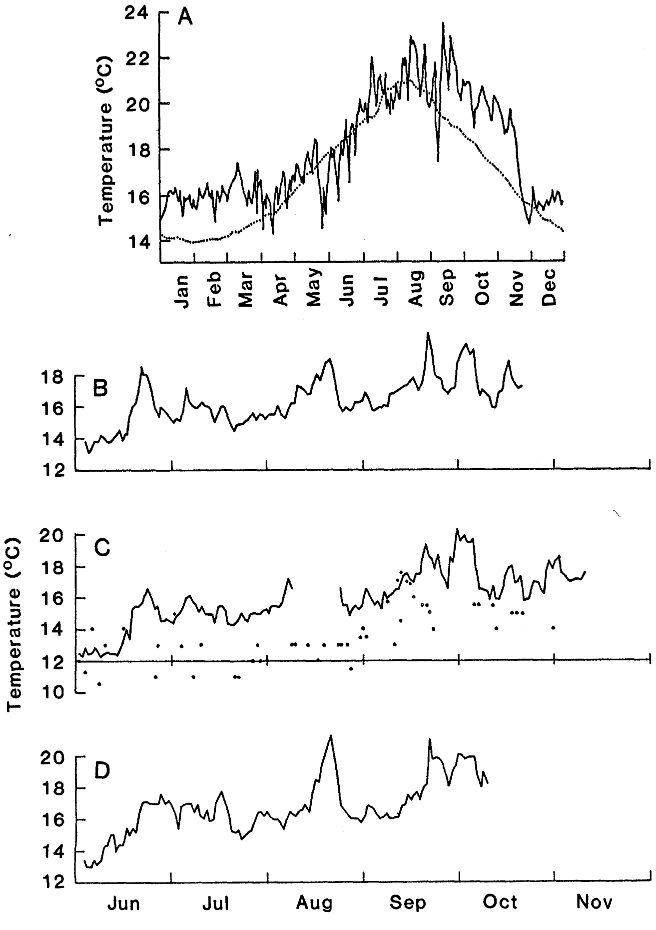

Fig. 1. (A) Daily surface temperature readings taken from the Scripps Institution of Oceanography pier for 1983. The dotted line represents the 63-year mean. Bottom temperatures in the Point Loma kelp forest during 1983 measured with recording thermographs at the southern end of the forest (18 m depth) (B): at the outer edge of the middle of the forest (18 m depth) (C); and at the inner edge of the middle of the forest (12 m depth) (D). The dots in (C) represent temperatures recorded from hand-held thermometers from 1978 to 1981. All temperatures above 16°C were from 1978, a minor El Niño year (*3*).

1975 the summer mortality of similarly age-structured 2- and 3-year-old *Macrocystis* plants located at the main study site in the center of the forest (*5*) was 14 percent (N = 128) and 9 percent (N = 45), respectively. In 1982, summer mortality of the 2-year-old plants was 2 percent (N = 52); and during the El Niño of 1983, summer mortality of the normally robust 3-year-old plants was 59 percent (N = 27) (*7*). In other areas of the kelp forest, mortality of adult plants in 400-m^2 transects between April and November 1983 ranged from 22 percent at the northern edge, 20 percent at the southern edge, and 58 percent in the central part of the forest to 61 percent at the outer and 67 percent at the inner edge of the forest. The northern and southern edges of the forest face into long shore currents, where they may be exposed to water which has not been scrubbed of nutrients by other plants. By late summer, few plants had healthy upper fronds and most plants had lost their fronds altogether. Immediately after the winter storms there was a strong recruitment of *Macrocystis* in all but the south portion of the Point Loma kelp forest. By May 1983 we observed hundreds of *Macrocystis* per square meter in patches along the transect lines not already dominated by understory algae. However, there was also a heavy recruitment of understory algae, especially *Pterygophora* and *Laminaria*, in most areas and unusually large areas of 100 percent cover of two annuals, *Dictyopteris undulata* in deeper water and *Desmarestia ligulata* in shallow water. Thus there was a scramble competition during the spring and early summer which, under "normal" conditions of light and nutrients, *Macrocystis* would have won easily (*5*).

The massive spring recruitment of *Macrocystis* during the El Niño summer had virtually no survivors, partly because of the heavy understory canopies which are known to interfere with giant kelp recruitment in this area (*5*). Those *Macrocystis* that had escaped the understory invasion grew slowly and were discolored and often diseased, and by September the fronds in many areas had died 2 to 3 m above the bottom; this was especially pronounced in the shallow area. Recruitment was first observed in April at this site, but by September the mean plant size was only 137 cm (standard deviation = 61 cm; N = 60), poor growth for a species that can grow as much as 5 to 15 cm/day under optimal conditions (*17*).

Wind and minor storms in November 1983 accompanying the slow deterioration of the El Niño have resulted in a drop in water temperature (Fig. 1). At this point there were scattered young *Macrocystis* plants ranging from 1 to 10 m in height; these plants may survive, but dense canopies of understories were also present. Isolated *Macrocystis* plants do not survive well because they are subject to relatively heavy encrustation by invertebrates that settle on the fronds and to fish grazing (*4, 18*). If most survive to reproduce, they are sufficiently dominant to slowly displace the understory algae which have become entrenched; but the resistance of these understory patches of perennial algae (*5*) can make this a long process. However, two sites were dominated by understories of annual algae which also could have inhibited successful recruitment of perennial understories. These canopies are now breaking up, and if the few remaining young *Macrocystis* survive, these areas may yet have scramble competition favoring *Macrocystis*.

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References and Notes

1. Coastal Data Information Program, Nearshore Research Group, Institute of Marine Resources, *Monthly Summary Reports 85–89* (Scripps Institution of Oceanography, La Jolla, Calif., 1982–1983); R. J. Seymour and C. J. Sonv, *Jpn. J. Coastal Eng.*, in press.
2. M. A. Cane, *Science* **222**, 1189 (1983); E. M. Rasmusson and J. M. Wallace, *ibid.*, p. 1195; R. T. Barber and F. P. Chavez, *ibid.*, p. 1203; J. J. Simpson, *Geophys. Res. Lett.* **10**, 937 (1983); ———, *ibid.*, in press.
3. D. B. Chelton, P. A. Bernal, J. A. McGowan, *J. Mar. Res.* **40**, 1095 (1982).
4. W. J. North, *The Biology of Giant Kelp Beds in California* (Cramer, Lehre, Germany, 1971).
5. P. K. Dayton, V. Currie, T. Gerrodette, B. D. Keller, R. Rosenthal, D. Ven Tresca, *Ecol. Monogr.*, in press.
6. The Point Loma bed area decreased from over 1500 acres to less than 100 acres after the storms (R. McPeak, personal communication).
7. The N values for the age-specific mortalities refer to summer and winter periods only; spring and fall data are not included.
8. *Univ. Calif. Inst. Mar. Resources, IMR Ref. 63-6* (1963).
9. J. J. Simpson, *Geophys. Res. Lett.*, in press; J. A. McGowan, personal communication.
10. C. E. Dorman and D. P. Palmer, in *Coastal Upwelling*, F. A. Francis, Ed. (American Geophysical Union, Washington, D.C., 1981), pp. 44–56.
11. W. North, V. Gerard, J. Kuwabara, in *Synthetic and Degradative Processes in Marine Macrophytes*, L. M. Srivastava, Ed. (de Gruyter, Berlin, 1982), pp. 247–262.
12. W. J. North, in *Symposium on the Effects of Waste Disposal on Kelp Communities*, in press.
13. R. W. Eppley, E. H. Renger, W. G. Harrison, *Limnol. Oceanogr.* **24**, 483 (1979).
14. G. A. Jackson, *ibid.* **22**, 979 (1977).
15. R. C. Zimmerman, thesis, University of Southern California, Los Angeles (1983).
16. V. A. Gerard, *Mar. Biol.* **66**, 27 (1982).
17. M. Neushul, thesis, University of California, Los Angeles (1959).
18. B. B. Bernstein and N. Jung, *Ecol. Monogr.* **49**, 335 (1979).
19. We thank R. Butler and K. Plummer for technical assistance, E. Stewart for the pier temperature data, and J. Barry, A. Ebeling, W. North, and G. Jackson for comments on the manuscript. Supported in part by the National Science Foundation and the National Oceanic and Atmospheric Administration, National Sea Grant College Program, Department of Commerce grant NA80AA-D-00120.

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Primary Structure of v-*raf*: Relatedness to the *src* Family of Oncogenes

Abstract. *A replication-defective, acute transforming retrovirus (murine sarcoma virus 3611) was isolated from mouse and molecularly cloned. The nucleotide sequence of 1.5 kilobases encompassing the transforming gene (v-*raf*) was determined. This sequence, which predicts the amino acid sequence of a* gag-raf *fusion protein, terminates 180 nucleotides from the 3′ end of the acquired cellular sequence. Comparison of the predicted amino acid sequence of v-*raf *with the predicted amino acid sequences of other oncogenes reveals significant homologies to the* src *family of oncogenes. There is a lack of homology within the sequence of the tyrosine acceptor domain described for the phosphotyrosine kinase members of the* src *family of transforming proteins. Phylogenetic arrangement of this family of oncogenes suggests that tyrosine-specific phosphorylation may be a recently acquired activity.*

Viral oncogenes are derived from cellular genes (proto-oncogenes) (*1*) that endow the virus with the capacity to transform cells in vitro and induce rapid tumors in vivo. The proto-oncogenes are generally single-copy sequences and are highly conserved in evolution. Viral oncogenes may be functionally grouped into those that code for a tyrosine-specific protein kinase and those that are negative for this activity. The protein kinase–negative oncogenes fall into several functional categories: v-*sis* (*2*) is derived from a growth factor; v-*myc* (*3*) and v-*myb* (*4*) encode DNA-binding proteins; v-*mil* (*4*) encodes an RNA-binding protein; and Ha-*ras* (*5*) and Ki-*ras* encode guanosine nucleotide–binding proteins. Although their physiological significance is still unclear, proto-oncogenes have been directly implicated in the development of certain human tumors because their positions are adjacent to breakpoints in tumor-specific chromosomal translocations (*6*).

We have isolated and molecularly