### References and Notes

1. J. F. Evernden, D. E. Savage, G. H. Curtis, G. T. James, *Am. J. Sci.* **262**, 170 (1964).
2. L. G. Marshall, R. Pascual, G. H. Curtis, R. E. Drake, *Science* **195**, 1325 (1977); L. G. Marshall, R. F. Butler, R. E. Drake, G. H. Curtis, *ibid.* **212**, 43 (1981).
3. S. D. Webb, *Paleobiology* **2**, 220 (1976); L. G. Marshall, R. F. Butler, R. E. Drake, G. H. Curtis, R. H. Tedford, *Science* **204**, 272 (1979).
4. L. G. Marshall, S. D. Webb, J. J. Sepkoski, Jr., D. M. Raup, *Science* **215**, 1351 (1982).
5. These totals do not include cricetine rodent genera which may have arrived in South America as immigrants before final completion of the Panamanian land bridge and thus may have preceded the arrival of species that walked across the land bridge [L. G. Marshall, *Paleobiology* **5**, 126 (1979)]. North American genera recorded in the Chapadmalalan include *Conepatus* and *Argyrohyus* (*19*); those recorded, some provisionally, in the Uquian include *Dusicyon, Protocyon, Arctodus, Conepatus, Galictis, Stipanicicia, Felis (Puma), Smilodontidion, Cuvieronius, Hippidion, Onohippidium, Tapirus, Platygonus* (including *Mylohyus* of Rusconi), *Selenogonus, Hemiauchenia, Lama, Palaeolama, Blastocerus, Morenelaphus*, and *Ozotoceros* (*6*).
6. L. G. Marshall *et al.*, *Fieldiana Geol.*, in press.
7. Patterson and Pascual (*20*, p. 287) note that this marked increase of taxa of North American origin may reflect the real situation with some degree of accuracy, at least in the latitudes of these faunas. Montehermosan and Chapadmalalan faunas are rich and varied and include more than 72 mammalian genera each (*6*). Uquian faunas, which are not nearly as well known, include some 84 genera (*6*) and provide a good idea of South American faunal composition south of the tropical zone during Pliocene-Pleistocene time.
8. A. Castellanos, *Univ. Nac. Litoral Fac. Cienc. Mat. Fis. Quim. Nat. Ser. Tecnico-Cientifica Rosario No. 36* (1950), p. 1.
9. L. Kraglievich, *Physis (Florence)* **10**, 127 (1930).
10. ———, *Imprenta "El Siglo Ilustrado," Montevideo* (1934), p. 17.
11. G. G. Simpson, *Proc. Am. Philos. Soc.* **83**, 696 (1940).
12. C. Rusconi, *An. Mus. Nac. Hist. Nat. Bernardino Rivadavia* **36**, 121 (1930).
13. J. L. Kraglievich, *Rev. Mus. Munic. Cienc. Nat. Trad. Mar del Plata* **1**, 8 (1952); *Comun. Mus. Argent. Cienc. Nat. Bernardino Rivadavia* **1**, 1 (1959).
14. R. Pascual, E. J. Ortega Hinojosa, D. Gondar, E. Toni, *An. Com. Invest. Cient. Prov. Buenos Aires* **6**, 165 (1965).
15. R. Pascual, *Actas 4th Congr. Latinoamer. Zool.* **2**, 991 (1970).
16. Sampling techniques were similar to those of N. M. Johnson, N. D. Opdyke, and E. H. Lindsay [*Geol. Soc. Am. Bull.* **86**, 5 (1975)].
17. Natural remanent magnetization (NRM) was measured by R.F.B. on a cryogenic magnetometer at the U.S. Geological Survey, Menlo Park; alternating-field (AF) demagnetization was done with a single-axis demagnetizer. Intensities of NRM ranged from $8 \times 10^{-7}$ to $4 \times 10^{-4}$ gauss. Progressive demagnetization studies indicated that, in most cases, secondary components of NRM were erased by AF demagnetization at 200-Oe peak field. The remaining characteristic NRM is believed to be a depositional remanent magnetization. Isothermal remanent magnetization characteristics and Curie temperature determinations on magnetic separates indicate that the carrier of the remanence is detrital magnetite, which may have suffered a small degree of low-temperature oxidation to maghemite. After initial measurement of NRM, all samples were demagnetized at 200-Oe peak field and measured again. Site average directions were calculated by the technique of R. A. Fisher [*Proc. R. Soc. London Ser. A* **217**, 295 (1953)], and the site average directions were used to compute the virtual geomagnetic pole latitudes (Fig. 2). Any site yielding ambiguous polarity determination after AF demagnetization to 200-Oe peak field was subjected to further demagnetization at 100-Oe steps up to 500 Oe in order to clarify the polarity of the characteristic NRM. Clustering of the NRM vectors after alternating field demagnetization was tested by the statistical technique of G. S. Watson [*Mon. Not. R. Astron. Soc. Geophys. Suppl.* **1**, 160 (1956)] to determine whether the grouping was significant from selection from a random population at a 95 percent confidence level. Sites which yield NRM vectors that pass this test are judged more reliable than sites from which the NRM vectors show poorer grouping.
18. E. H. Lindsay, N. M. Johnson, N. D. Opdyke, *Univ. Mich. Pap. Paleontol. No. 12* (1976), p. 111, figure 8.
19. L. G. Marshall, R. Hoffstetter, R. Pascual, *Fieldiana Geol.*, in press.
20. B. Patterson and R. Pascual, in *Evolution, Mammals and Southern Continents*, A. Keast *et al.*, Eds. (State Univ. of New York Press, Albany, 1972).
21. Polarity zones in Fig. 2 are designated by the prefix "Uquía" after the nearby geographic location Uquía. The basal normal polarity zone is thus designated Uquía A+. This nomenclature is in keeping with recommendations regarding magnetostratigraphic nomenclature described in *Geology* **7**, 578 (1979). Time intervals of the magnetic polarity time scale are referred to by attaching the suffix chron.
22. E. A. Mankinen and G. B. Dalrymple, *J. Geophys. Res.* **84**, 615 (1979).
23. W. A. Berggren and J. A. Van Couvering, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **16** (1974), figure 1.


24. We thank R. Pascual for help in all phases of this study. Fieldwork in Argentina and $^{40}K$-$^{40}Ar$ dating were supported by NSF grant EAR 7909515 to L.G.M.; processing of paleomagnetic samples was supported by NSF grant EAR 7919726 to R.F.B. and by the U.S. Geological Survey.

27 January 1982


# Catastrophic Decline of a Top Carnivore in the Gulf of California Rocky Intertidal Zone


Abstract. *The predatory sun star,* Heliaster kubiniji, *once the commonest rocky intertidal asteroid of the Gulf of California, has been rare throughout this region since summer 1978 when a devastating disease outbreak occurred. This unprecedented phenomenon and several other exceptional ecological events in marine communities of the northeastern Pacific appear to be linked to large-scale climatic changes that occurred during 1977 and 1978. Implications of the decline in* Heliaster kubiniji *are discussed.*


Extreme population fluctuations are likely to be important in the evolutionary history of a population (*1*). They may also have secondary effects on co-occurring species, a dramatic case in point being the recent crown-of-thorns starfish population explosion (*2*). We report here on a phenomenon of the opposite kind, the population crash of the predatory sun star, *Heliaster kubiniji* Xantus, throughout its principal range in the Gulf of California. The crash appears to be one of a series of events that were triggered by climate changes in the northeastern Pacific.

Prior to the summer of 1978, this large (up to 220 mm in diameter) multirayed asteroid was conspicuous in rocky intertidal habitats throughout the Gulf of California. In 1941, Steinbeck and Ricketts (*3*) characterized *H. kubiniji* as "the most common, obvious, and widely distributed shore starfish in the Gulf." At Puerto Peñasco, Sonora, Mexico, *H. kubiniji* was found regularly in abundance from 1946 to 1978 (*4*). This species was collected extensively in the northern Gulf by Paine in 1962–1964 (*5*), and found to be the commonest asteroid of rocky intertidal habitats of the Gulf in surveys during 1974–1975 (*6*). Brusca (*7*) also considered *Heliaster kubiniji* to be the commonest rocky-shore asteroid in the Gulf, found in greatest numbers in the northern and central Gulf, and ranging to Central America. This species occurred widely at densities of 0.1 to 1.0 per square meter in the northern and central Gulf prior to July 1978 (*6*, *8*).

Scores of disintegrating sun stars were first observed during 18 to 20 June 1978 in the intertidal zone around Puerto Peñasco. Animals initially exhibited whitish lesions on the aboral surface. The lesions rapidly enlarged until the entire animal fragmented, and the decaying parts of the same individual were left in close proximity. High concentrations of bacteria were found in the lesions (*9*), but it is not known whether bacterial infection was the primary cause of death. Mortality of *H. kubiniji* approached 100 percent; within 2 weeks the sun star had virtually disappeared from this site.

Since the initial die-off was observed at Puerto Peñasco, we have surveyed many sites in the northern and central Gulf, and solicited information from colleagues who were familiar with *H. kubiniji* and who had worked in the Gulf in recent years in attempts to determine the present and former (pre-1978) status of the sun star. The decline of *H. kubiniji*, which to the best of our knowledge occurred throughout the Gulf during summer 1978, has been precipitous. Figure 1 shows the approximate locations of sites where *H. kibiniji* (i) was abundant and could be found at densities within the above range prior to 1978 and (ii) has either not been found at all, or at maximum local densities less than 0.05 per square meter in one or more surveys since summer 1978 (*10*). In more than 3 years, with several sites being monitored regularly, neither we nor our colleagues have found a single site where *H. kubiniji* has persisted at high densities, or where substantial recruitment of juveniles has occurred. Samples span the region

 0036-8075/82/0528-0989$01.00/0  

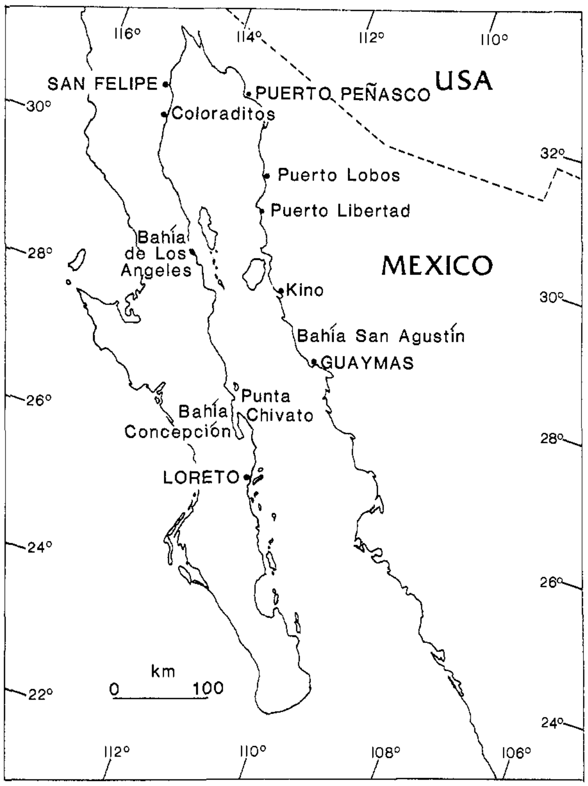


Fig. 1. The Gulf of California. All named locations designate (approximately) sites where *Heliaster kubiniji* was found at high densities prior to 1978 and has been found rarely or not at all since then (*10*).

where *H. kubiniji* was formerly most abundant (*7, 10*) (Fig. 1). We conclude that a population crash of major proportions has occurred.

This event appears to be unprecedented, at least within the last 40 years. There is no reason to suspect the operation of a long-term population cycle (*11*). The die-off of *H. kubiniji* was not preceded by a decrease in the abundance of its principal prey, the barnacle *Chthamalus anisopoma* (*12*).

Only one other species at Puerto Peñasco and other sites in Sonora (*13*) exhibited the symptoms and heavy mortality described above; this species is the small (to 90 mm in diameter) detritivorous sea star *Othilia tenuispina*. Unlike *H. kubiniji*, *O. tenuispina* occurs commonly in the subtidal (*7*) and persisted there while mortalities occurred in the intertidal zone. *Othilia tenuispina* has since again become locally common in the low intertidal zone at Puerto Peñasco. Less is known of the former distribution and abundance of this species than of *H. kubiniji*, and we cannot gauge the overall extent to which it has been affected. Other primarily subtidal asteroids appear to have been unaffected (*14*).

A similar die-off of shallow water echinoderms involving the same symptoms in a greater number and variety of species occurred in southern California waters during summer 1978 and to a lesser extent during summer 1979 (*15*). Mortalities were sharply restricted to shallow waters, and have had persistent effects; several species continue to be atypically rare intertidally in many areas (*15*).

The occurrence of similar die-offs in geographically and oceanographically distinct regions argues for a common cause, and probably rules out most types of localized disturbance as potential explanations. Several lines of evidence implicate the influence of climatic changes. During winter 1977–1978, atmospheric conditions produced unusually strong southerly winds along the Pacific coast of North America and across the southern United States, enhancing the northward transport of warm surface water in

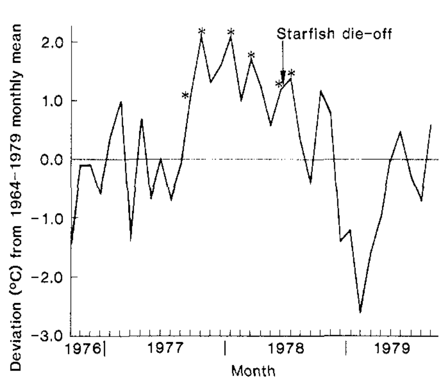


Fig. 2. Deviations from average monthly mean onshore sea surface temperatures at Puerto Peñasco, Sonora, Mexico, between September 1976 and September 1979. Mean values are based on data from June 1964 through December 1979 (*19*). Asterisks denote record high monthly means.

coastal areas (*16–18*). Sea surface temperatures increased substantially during this time along the Pacific coast (*16–18*). At Puerto Peñasco, a period of record warm onshore sea surface temperatures lasted from September 1977 to August 1978, with temperatures consistently averaging 1° to 2°C above long-term means (*19*) (Fig. 2). The greatest increase on the Pacific coast, of similar magnitude, was recorded offshore of southern California (*16*). Heavy rains occurred in California and in the deserts surrounding the northern Gulf of California during early 1978 (*20*), and extreme low salinities and downwelling were recorded along the California coast (*16*).

Numerous unusual ecological events along the Pacific coast during 1978 have been attributed to the aforementioned climatic changes (*16–18*). Recent data on seabird reproduction (*21, 22*) also point to changes in oceanographic conditions along the Pacific coast during 1978.

The restriction of the die-offs to shallow water, where the climatic changes were most strongly expressed is consistent with the hypothesized role of climate. Further, investigators in both the Gulf and southern California induced the disease symptoms in previously normal animals by moving them into shallower water (*23*). Finally, identical symptoms have since been observed in *H. kubiniji* in buckets and aquaria, coincident with increasing temperatures.

Some of the phenomena reported from the Pacific coast for 1978 (*16, 17, 21, 22*) represent typical effects of climatic variation on marine organisms, which are widely appreciated (*24*). The asteroid die-offs in southern California and the Gulf of California suggest an additional way in which climate may exert severe effects on marine populations.

We hypothesize that prolonged elevated temperatures, perhaps in conjunction with other factors, rendered the animals increasingly susceptible to infection by the as-yet-unidentified pathogen (or pathogens). Little is known about the susceptibility of asteroids to bacterial infection (*25*).

Localized disease outbreaks, although not related to unusual climatic conditions, have been documented at other locales (*26*). The climate changes discussed above were relatively slight in relation to the short-term variations to which intertidal organisms are regularly exposed. In this case, it appears that a large-scale shift in the climate regime of the Gulf and much of the Pacific coast produced a prolonged change sufficient to trigger the disease outbreaks and cause the near elimination of *H. kubiniji* from the region where it was formerly abundant.

The sun star is a top carnivore in the rocky intertidal zone and may play an important role in structuring intertidal communities in the Gulf (5). In other marine communities where top carnivores have been removed by various agents, dramatic changes have ensued (5, 27).

*Chthalamus anisopoma*, the most frequent prey of *H. kubiniji*, has been shown to be capable of competitively excluding other species from emergent rock surfaces (28). *Chthalamus* abundance shows no significant changes between 1976 and 1981 at one site near Puerto Peñasco (29), but at another site *Chthalamus* has increased since 1978 and has remained significantly above 1978 levels (30). This increase in density is correlated with significant decreases in cohabiting encrusting algae and limpets (31). Considering the marked seasonality of northern Gulf of California populations and the difficulty of sorting out predator removal effects from impacts of other factors, it is premature to characterize these changes as responses to the removal of the top carnivore in this system.

MICHAEL L. DUNGAN
*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson 85721*
THOMAS E. MILLER
*W. K. Kellogg Biological Station, Michigan State University, Hickory Corners 49060*
DONALD A. THOMSON
*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson*

### References and Notes

1. M. Nei, T. Murayama, R. Chakraborty, *Evolution* **29**, 1 (1975).
2. A. M. Cameron, in *Proceedings of the Third International Coral Reef Symposium* (Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Fla., 1977), p. 193–199; R. H. Chesher, *Science* **165**, 280 (1969).
3. J. Steinbeck and E. F. Ricketts, *Sea of Cortez. A Leisurely Journal of Travel and Research* (Viking, New York, 1941).
4. Personal observations of P. Vreeland, resident of Cholla Bay since 1946; P. E. Pickens and D. A. Thomson, University of Arizona Marine Sciences Program.
5. R. T. Paine, *Am. Nat.* **100**, 65 (1966).
6. L. Y. Maluf, thesis, University of Arizona, in preparation.
7. R. C. Brusca, *Common Intertidal Invertebrates of the Gulf of California* (Univ. of Arizona Press, Tucson, 1980).
8. S. A. Mackie and E. H. Boyer, *BioScience* **148**, 120 (1977); P. K. Dayton and R. T. Paine, personal communication.
9. Bacteria noted but not identified by D. V. Lightner, Environmental Research Laboratory, University of Arizona.
10. Our assessment is based on quantitative surveys during 1974–1975 [see (6)], on both quantitative and qualitative surveys by M.L.D. and D.A.T. from 1978 to the present, personal communications from P. K. Dayton and T. Present for the San Felipe area, from P. K. Dayton for Bahía de Los Angeles and Bahía Concepcíon, from D. W. Anderson for Bahía de Los Angeles, and from L. T. Findley for Guaymas. Specific locations of sites and details of before and after abundance of *H. kubiniji* are available from the authors.
11. M. D. Burkenroad, *Science* **103**, 684 (1946).
12. Barnacle cover was monitored regularly by M.L.D. from June 1977 to July 1978 at one site near Puerto Peñasco.
13. M. L. Dugan and D. A. Thomson, unpublished observations during 1978 to 1979 at all the sites labeled on the mainland coast (Fig. 1).
14. Subtidal species include *Pharia pyrimidata*, *Phataria unifascialis*, *Oreaster occidentalis*, and *Nidorellia armata*, all of which we have found at several sites in abundance before and after the die-off of *H. kubiniji*.
15. M. J. Sherwood, J. Word, J. Engel, P. K. Dayton, R. C Brusca, personal communications. Species showing a high incidence of disease symptoms included asteroids of the genus *Pisaster* (carnivores), *Patiria miniata* (an omnivorous asteroid), and the holothurian *Stichopus parvimensis* (a deposit feeder).
16. E. D. Haynes, *Nat. Oceanic Atmos. Adm. Tech. Memo. NMFS-OF-5* (1980).
17. R. Lasker, *Coastal Oceanogr. Climatol. News* **1**, 3 (1978); R. H. Parrish and A. Bakun, *ibid.*, p. 13; H. J. Niebauer, *ibid.* **3**, 7 (1980).
18. D. O. Duggins, *Limnol. Oceanogr.* **26**, 391 (1981).
19. Daily onshore sea surface temperature data were taken and provided by the Environmental Research Laboratory, University of Arizona. Long-term means are based on data for 1964 to 1979. The warmest 12-month consecutive period recorded was between September 1977 and August 1978.
20. NOAA Environmental Data and Information Service, *Monthly Climatic Data for the World* (National Climatic Center, Asheville, N.C., 1948 to the present).
21. D. W. Anderson, F. Gress, K. F. Mais, *Oikos*, in press.
22. D. G. Ainley, unpublished data. The Pacific Seabird Group at Point Reyes, Calif., has monitored seabird populations in the Farallon Islands since 1971; the poorest year on record in terms of the reproductive success of nine species was 1978.
23. Similar experiments were conducted by R. Abugov of the University of Arizona and J. Engel of the Catalina Marine Science Center.
24. D. H. Cushing and R. R. Dickson, *Adv. Mar. Biol.* **14**, 2 (1975); E. F. Ricketts, J. Calvin, J. W. Hedgpeth, *Between Pacific Tides* (Stanford Univ. Press, Stanford, Calif., 1968).
25. F. B. Bang and A. Lemma, *J. Insect Pathol.* **4**, 410 (1962).
26. B. A. Menge, *Oecologia* **41**, 245 (1979); J. S. Pearse, D. P. Costa, M. B. Yellin, C. R. Agegian, *Fish. Bull.* **75**, 645 (1977).
27. For example, D. O. Duggins, *Ecology* **61**, 447 (1980); J. A. Estes, N. S. Smith, J. F. Palmisano, *ibid.* **59**, 822 (1978); R. T. Paine, *ibid.* **52**, 1096 (1971).
28. M. L. Dungan, *Bull. Ecol. Soc. Am.* **62**, 69 (1981).
29. E. H. Boyer and N. P. Yensen, in *Simposium Sobre Biologia Marina III* (Universidad Autonoma de Baja California Sur, La Paz, in press).
30. M. L. Dungan and D. A. Thomson, in *ibid.*
31. M. L. Dungan, thesis, University of Arizona, in preparation.
32. We thank D. Ainley, D. Anderson, J. Brown, R. Brusca, P. Dayton, P. Delaney, J. Engel, L. Findley, T. Gibson, R. Houston, K. Nealson, R. Paine, P. Pepe, P. Pickens, T. Present, M. Sherwood, P. Vreeland, N. Yensen, and members of the Marine Sciences Group at the University of Arizona for sharing information or making helpful suggestions.

28 October 1981; revised 12 February 1982

# Bismuth Vanadate: A High-Pressure, High-Temperature Crystallographic Study of the Ferroelastic-Paraelastic Transition

Abstract. *Lattice dimensions of bismuth vanadate have been determined under 37 different high-pressure or high-temperature conditions or a combination of these conditions. New high-pressure, high-temperature, single-crystal x-ray techniques were used to bracket the reversible monoclinic (ferroelastic) to tetragonal (paraelastic) transition.*

Combined high-pressure, high-temperature (*P-T*) crystallography is a powerful new technique for measuring crystal structures and stabilities at nonambient conditions. In this report we describe the application of *P-T* crystallography to the determination of a reversible phase transition.

Bismuth vanadate, $BiVO_4$, has received considerable attention since the discovery of a ferroelastic-paraelastic phase transition at 250°C by Bierlein and Sleight in 1975 (1). Subsequent studies of crystal structure variation with temperature (2, 3), Raman spectroscopy at high temperature (4) and high pressure (5), transmission electron microscopy of the domain structure (6), birefringence at combined high temperature and pressure (7), and Brillouin spectroscopy (8) have provided a consistent set of descriptive parameters for the transition. The high-temperature paraelastic phase has the scheelite structure (space group, $I4_1/a$; multiplicity, $Z = 4$), in which vanadium atoms are in isolated tetrahedra and bismuth atoms are coordinated by eight oxygens. This high-symmetry, undistorted form was observed above 250°C at room pressure and above 15 kbar at room temperature; thus a negative $dP/dT$ for the transition is indicated. The low-temperature, low-pressure, ferroelastic phase is a slight distortion of the tetragonal structure to monoclinic symmetry ($I2/a$, $Z = 4$), with Bi and O atoms shifted by approximately 0.1 Å from their ideal tetragonal positions (2). There are two permissible orientations of the ferroelastic state, and twinning in the low-symmetry form is thus almost universal.

The transition in $BiVO_4$ is a pure displacive, reversible transformation [a "proper ferroelastic transition" in the terminology of Aizu (9)]. The monoclinic $\gamma$ angle, therefore, gradually changes to 90° as the temperature or pressure of the second-order transition is approached. The deviation of $\gamma$ from 90° is a sensitive measure of atomic displacements from their ideal tetragonal positions and is related to the order parameter of mean