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Shifts in Deep-Sea Community Structure Linked to Climate and Food Supply

Henry A. Ruhl* and Kenneth L. Smith Jr.

A major change in the community structure of the dominant epibenthic megafauna was observed at 4100 meters depth in the northeast Pacific and was synchronous to a major El Niño/La Niña event that occurred between 1997 and 1999. Photographic abundance estimates of epibenthic megafauna from 1989 to 2002 show that two taxa decreased in abundance after 1998 by 2 to 3 orders of magnitude, whereas several other species increased in abundance by 1 to 2 orders of magnitude. These faunal changes are correlated to climate fluctuations dominated by El Niño/La Niña. Megafauna even in remote marine areas appear to be affected by contemporary climatic fluctuations. Such faunal changes highlight the importance of an adequate temporal perspective in describing biodiversity, ecology, and anthropogenic impacts in deep-sea communities.

The deep sea occupies more than two-thirds of the Earth's surface. This vast area remains largely unexplored, especially in terms of its biota. Only a very small fraction of the deep sea has been sampled spatially, and few areas have been sampled temporally. The deep sea is isolated from ocean surface conditions in several ways, including the negligible penetration of light and millennial-scale vertical circulation of deep water masses (1). Time-series studies have shown, however, that the deep sea can experience rapid inputs of food supplies from overlying surface waters (2), as well as rapid responses by micro- and macrofaunal taxa such as foraminifera (3). It has since been hypothesized that climate fluctuations such as those related to El Niño/La Niña could be affecting deep-sea communities through long-term variations in the food supply (4). Here we examine variations in the abundance of mobile epibenthic megafauna at an abyssal location in the northeast Pacific over a 14-year study period. The influences of climate and food supply on megafaunal abundance and community structure are also assessed.

A long time-series station, Station M (34°50'N, 123°00'W) was established in the northeast Pacific at 4100-m depth to study benthic boundary-layer processes and deep-sea ecology from 1989 through 2002. This study site is influenced by seasonal pulses of particulate organic matter that reach the sea floor after sinking from overlying surface waters (5, 6). Echinoderms dominate the conspicuous mobile epibenthic megafauna on the sea floor at Station M (7), and they are known to rapidly ingest settling particles at the site (8). Short-term analysis over two 12-month periods before 1996 revealed no discernible temporal change in echinoderm abundance and no correlation with food supply (7, 9).

We analyzed 48 photographic line transects across the sea floor from 1989 to 2002 at Station M to determine the abundance of mobile epibenthic megafauna (animals conspicuous in photographs and typically ≥ 1 cm in size). These transects were typically conducted seasonally, but this frequency was variable because of logistical constraints (10). Results indicate that the holothuroid *Elpidia minutissima* increased in abundance from 1989 through 1996, peaking at ~ 1 individual per m^2 , but then decreased markedly during a hiatus in sampling from 1999 to 2000, as none were subsequently observed in 2001 to 2002 (Fig. 1A). Another

species of holothuroid, *Peniagone vitrea*, showed a similar overall trend in abundance, remaining relatively stable in numbers through 1998 but then declining sharply in 2001 and 2002 (Fig. 1A). In contrast, the holothuroids *P. diaphana*, *Abyssocucumis abyssorum*, *Scotoplanes globosa*, *Psychropotes longicauda* (Fig. 1B), the echnoid group *Echinocrepis* spp., and the ophiuroid group *Ophiura* spp. (Fig. 1C) occurred in lower abundances through most of the time series but increased substantially during 2001 and 2002. The abundance of *P. diaphana* also had a notable increase in 1995.

A Bray-Curtis similarity analysis was applied using the ten most dominant mobile epibenthic megafauna over the 14-year period and revealed a major dissimilarity in abundances between the 1989 to 1998 and 2001 to 2002 periods (10) (Fig. 2). When examined as separate species, the abundances of six taxa, *E. minutissima*, *P. vitrea*, *S. globosa*, *Ps. longicauda*, *Echinocrepis* spp., and *Ophiura* spp., were significantly different between the two periods (Mann Whitney U Test, $P < 0.05$).

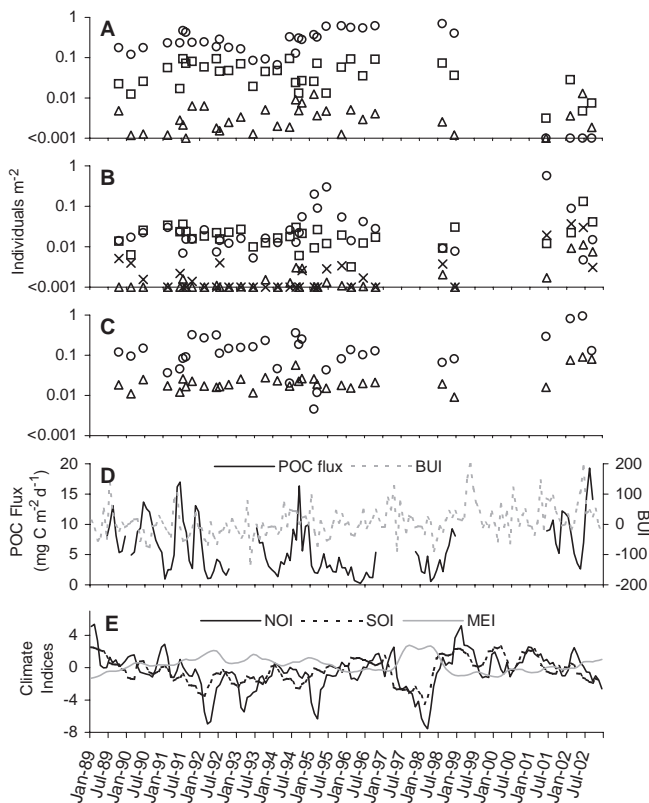
Climate has been implicated in the fluctuations of many Pacific pelagic communities ranging from plankton (11–14) to fishes (15, 16). There are also indications that a regime shift may have occurred in the north Pacific in 1998 to 1999 (15–18). Our studies have revealed that shifts in the abundance of epibenthic megafauna in the deep sea also correlate to three indices expressive of El Niño/La Niña (Table 1): the Northern Oscillation Index (NOI), the Southern Oscillation Index (SOI), and the Multivariate El Niño–Southern Oscillation Index (MEI) (10) (Fig. 1E). Cross-correlation coefficients between climate and abundance of the holothuroids *E. minutissima*, *P. vitrea*, *A. abyssorum*, *Synalactes* sp., and *S. globosa* peaked with abundance lagging climate by 11 to 22 months (Table 1). The relative temporal differences in correlations between climatic indices and megafauna abundance may be indicative of the connection between index parameters and pelagic-benthic processes at Station M, as well as the responsiveness of a particular taxon to any changes in climatic processes.

Further investigation explored whether climatic shifts were related to changes in food

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Fig. 1. (A) Abundance estimates for the holothuroids *E. minutissima* (circles), *P. vitrea* (squares), and *Synallactes* sp. (triangles). **(B)** Abundances of the holothuroids *P. diaphana* (circles), *A. abyssorum* (squares), *S. globosa* (crosses), and *Ps. longicauda* (triangles). **(C)** Abundances of *Ophiura* spp. (circles) and *Echinocrepis* spp. (triangles). **(D)** Monthly POC flux (mg of C per m² per day) at 50 m above bottom (4050-m depth) at Station M, representing food supply to the sea floor, and upwelling index (m³ per s per 100 m of shoreline) [monthly Bakun Upwelling Index (BUI) anomaly for 36°N 122°W]. **(E)** Three-month centered running means for the NOI, SOI, and MEI climate indices.



supply to the deep sea and how variations in food supply may influence megafauna abundance. In previous studies, the correlation of a regional upwelling index (Bakun Upwelling Index) to particulate organic carbon (POC; i.e., the food supply) flux at Station M indicated that upper ocean processes are likely affecting food supplies to the sea floor with a time lag of ~40 to 60 days (5) (Fig. 1D). Upwelling data suggest that POC flux may have been higher between 1998 and 2002 than at any other period in the time series (Fig. 1D). Studies using satellite data have also documented variation in phytoplankton, chlorophyll-*a*, and primary production during the strong El Niño/La Niña event from 1997 to 1999 near Station M (12). Current investigations have shown that the NOI, SOI, and MEI also have significant time-lagged correlations with POC flux to the sea floor at Station M (10) (Table 1). Significant correlations of climate indices and POC flux peaked with a time lag of 6 months for the NOI, 11 months for the SOI, and 9 months for the MEI. POC flux also had time-lagged correlations with the abundance of *E. minutissima*, *P. vitrea*, *A. abyssorum*, *Synallactes* sp., and *S. globosa* (Table 1). These correlations had roughly corroborative temporal patterns with the climate-to-abundance correlations (supporting online material).

Correlations between food supply and megafauna abundance over the 14-year time series suggest that some taxa increase in abundance during periods of high food supply, whereas others may be favored dur-

ing deficits. The relationship between POC flux and *E. minutissima* abundance was negative, suggesting that this species could undergo increases in abundance during periods of lower food supply, such as those observed from 1993 through 1998. Higher POC fluxes, conversely, were associated with the 1989 to 1992 and the 2001 to 2002 intervals (Fig. 1D), when *E. minutissima* abundances were lower (Fig. 1A). From 1989 through 1996, the food supply was found to be decreasing compared to the sediment community oxygen demand, which was interannually stable, over the 7-year time span (4). The increasing deficit in food supply occurred as *E. minutissima* increased in abundance through 1996, suggesting that *E. minutissima* may have a competitive advantage when food supply is low. *P. vitrea* and *Synallactes* sp. abundances also had negative relationships with food supply. Conversely, *A. abyssorum* and *S. globosa* had positive relationships with POC flux (Table 1).

A similar shift in benthic community structure was also observed on the Porcupine Abyssal Plain (PAP; 48°50'N, 16°30'W, at 4800-m water depth) in the northeast Atlantic between 1989 to 1994 and 1996 to 1998 (19). Changes in dominant taxa and increases in overall epibenthic megafauna abundance and activity in many of the benthic taxa were observed over the study period. Major increases in the abundance of the holothuroids *Amperima rosea* and *Ellipinion molle* were

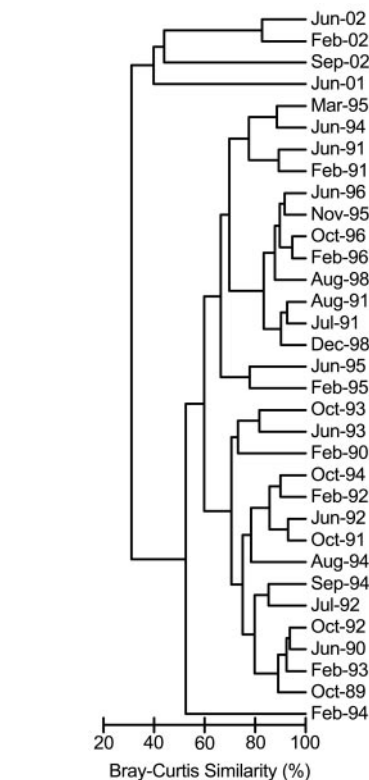


Fig. 2. A Bray-Curtis similarity dendrogram of dominant mobile epibenthic megafauna community similarity from 1989 through 2002. This analysis indicates a major difference in community structure between the 1989 to 1998 cluster and the 2001 to 2002 cluster. The taxa included in the analysis are *E. minutissima*, *P. vitrea*, *P. diaphana*, *A. abyssorum*, *Synallactes* sp., *S. globosa*, *Ps. longicauda*, *Oneriophanta mutabilis*, *Echinocrepis* spp., and *Ophiura* spp.

observed between 1989 to 1994 and 1996 to 1998 (19). The PAP site also experiences seasonal pulses of food supply (20), and phytopigments appear to be important in reproductive processes of benthic fauna (21, 22). Overall, community changes were attributed to variation in the quantity and quality of food supplied to the community, and climate was suggested to be influencing the benthos (19, 21–23).

We applied a cross-correlation analysis to POC flux data from the PAP site (20) and found links between an Atlantic climate index and food supply. The North Atlantic Oscillation (NAO) index has a significant positive relationship with POC flux with a peak in time-lagged correlations at 5 months (Spearman's $r = 0.62$, $P < 0.01$, POC flux data at 100 m above the sea floor). The NAO was primarily positive between 1989 and 1994 and primarily negative in the 1996 to 1998 period. The relationship between climate and food supply at the PAP further indicates that climate variation may have played a major role in megafaunal shifts observed in the northeast Atlantic.

Table 1. Peaks in time-lagged Spearman rank cross-correlations (r) between climate indices and abundances, between climate indices and POC flux, and between POC flux and abundance. The correlations and associated time lags

(in months) shown in the table are the peaks in cross correlations (those with the highest r) and are not intended to represent fixed temporal lags. n , number of monthly estimates for each correlation.

Category	Average body length (mm)	n	NOI			SOI			MEI			n	POC flux		
			r	P	Time lag	r	P	Time lag	r	P	Time lag		r	P	Time lag
<i>E. minutissima</i>	31	33	-0.40	0.02	14	-0.40	0.02	17	0.35	0.05	15	29	-0.44	0.018	7
<i>S. globosa</i>	73	33	0.39	0.03	14	0.61	<0.001	18	-0.56	<0.001	16	29	0.35	0.067	8
<i>P. vitrea</i>	79	33	-0.33	0.06	14	-0.30	0.09	17	0.35	0.04	11	29	-0.37	0.045	6
<i>A. abyssorum</i>	91	33	0.33	0.06	15	0.46	0.01	22	-0.41	0.02	22	26	0.46	0.018	10
<i>Synallactes</i> sp.	131	33	-0.40	0.02	18	-0.58	<0.001	23	0.53	<0.01	21	26	-0.42	0.032	12
POC Flux		110	0.60	0.01	6	0.45	0.05	11	-0.45	0.05	9				

Changes in megafauna recruitment, immigration, emigration, and mortality related to climate-induced variations in food supply could explain the results found. The abyssal echinoderm assemblage can influence the benthos considerably, through rapid bioturbation and remineralization of organic material (24–26), suggesting that the assemblage may respond to changes in the quality and quantity of food supply. Feeding selectivity among deposit-feeding echinoderms (8, 27–29) may occur through differences in tentacle morphology (30), digestion (31), and patch selection (32). Differential selectivity and use of organic material by each taxon may provide a mechanism for a particular taxon to gain competitive advantage (22, 31, 32).

Organic material originating from surface waters above Station M has been shown to vary in quantity and composition (5, 6). Changes in the pigment content, polyunsaturated fatty acids, and other nutrients may have important implications in reproduction and growth for holothuroids (21, 22). Salp fecal pellets sink relatively rapidly and are a mechanism of pelagic-benthic coupling, having been observed in the gut contents of holothuroids (33). Salp abundance increased in the waters above Station M around 1998, after several years of decreased abundances (13). Such variations in overlying pelagic communities (11–16) probably contribute to fluctuations in abyssal food supply and nutrient content.

Long-term increases in food supply might induce reproduction, recruitment, and/or immigration to Station M of species such as *S. globosa*, which may be favored when food supply is higher. Likewise, species possibly favored when food supply is lower could have increased mortality and/or emigration from Station M after 1998. Because Station M is close to productive coastal upwelling areas to the east and more oligotrophic waters to the west, such long-term migration patterns seem plausible. If variability in reproduction or recruitment at Station M is the primary cause of abundance increases, then changes in megafauna recruitment presum-

ably precede shifts in abundance that are observed in the line transect photographs. Given a proposed growth rate of 1 mm per month for deep-sea holothuroids (21), reproductive events leading to increases in abundance of photographically detectable animals within the time lags observed appear plausible (supporting online text). Body size has been shown to scale with a variety of ecologically important parameters, including reproduction, growth rates, and behavior (34). Taxa with larger mean body lengths generally had longer temporal lags between both climate to abundance and POC flux to abundance events (Table 1). Spatial heterogeneity, animal behavior such as burrowing, and disease also may explain the variation in the population estimates at Station M, but little information is available for these parameters. Although possible, there have been no indications that these parameters may have an overriding bias in abundance estimates at Station M (supporting online text).

Abyssal time-series studies of mobile epibenthic megafauna have provided evidence of major megafaunal community changes that are correlated to modern climate variation, as well as to food supply. Longer time-series studies will be necessary to discern if contemporary changes in community structure are interannual, decadal, or longer in scale. More importantly, the underlying mechanisms linking climate to deep ocean population dynamics are yet to be conclusively determined.

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