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ABUNDANCE AND SIZE DISTRIBUTION DYNAMICS OF ABYSSAL EPIBENTHIC MEGAFAUNA IN THE NORTHEAST PACIFIC

HENRY A. RUHL[1]

Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, California 95039 USA, and
Marine Biology Research Division, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, California 92093-0202 USA

Abstract. The importance of interannual variation in deep-sea abundances is now becoming recognized. There is, however, relatively little known about what processes dominate the observed fluctuations. The abundance and size distribution of the megabenthos have been examined here using a towed camera system at a deep-sea station in the northeast Pacific (Station M) from 1989 to 2004. This 16-year study included 52 roughly seasonal transects averaging 1.2 km in length with over 35 600 photographic frames analyzed. Mobile epibenthic megafauna at 4100 m depth have exhibited interannual scale changes in abundance from one to three orders of magnitude. Increases in abundance have now been significantly linked to decreases in mean body size, suggesting that accruals in abundance probably result from the recruitment of young individuals. Examinations of size-frequency histograms indicate several possible recruitment events. Shifts in size-frequency distributions were also used to make basic estimations of individual growth rates from 1 to 6 mm/month, depending on the taxon. Regional intensification in reproduction followed by recruitment within the study area could explain the majority of observed accruals in abundance. Although some adult migration is certainly probable in accounting for local variation in abundances, the slow movements of benthic life stages restrict regional migrations for most taxa. Negative competitive interactions and survivorship may explain the precipitous declines of some taxa. This and other studies have shown that abundances from protozoans to large benthic invertebrates and fishes all have undergone significant fluctuations in abundance at Station M over periods of weeks to years.

Key words: California Current Ecosystem (CCE); climate; deep sea; echinoderm; echinoid; holothurian; holothuroid; long-term ecological research (LTER); megafauna; ophiuroid; pelagic–benthic coupling; time series.

INTRODUCTION

Fluctuations in the abundance of holothuroids, echinoids, ophiuroids, and other invertebrates have been observed in both the deep northeast Pacific and northeast Atlantic since 1989 (e.g., Billett et al. 2001, Ruhl and Smith 2004), but the underlying population dynamics that can lead to such changes remain difficult to quantify. The importance of describing deep-sea habitats is growing as anthropogenic ocean warming is becoming realized (Houghton et al. 2001, Barnett et al. 2005, Hansen et al. 2005, Karl et al. 2006) and natural resource industries are now operating at abyssal depths (Glover and Smith 2003, Thiel 2003). The deep-sea benthos is a key component of the carbon cycle and can affect long-term bioturbation, remineralization, and sequestration rates of carbon over the majority of the earth's surface. This study examines how mobile epibenthic megafauna vary in abundance and body size over a 16-year period.

Benthic surveys have been conducted to quantify megabenthic abundances at several slope and abyssal plain locations including examples from the northeast Pacific (Smith and Hamilton 1983, Lauerman et al. 1996, Lauerman and Kaufmann 1998, Nybakken et al. 1998), Clarion-Clipperton Fracture Zone (Foell and Pawson 1986, Tilot 1992), central North Pacific (Kaufmann et al. 1989, Smith 1992), Peru Basin (Bluhm and Gebruk 1999, Bluhm 2001), northeast Atlantic (Lampitt et al. 1986, Sibuet et al. 1989, Thurston et al. 1994, Billett et al. 2001), central Indian Basin (Sharma and Rao 1992, Rodrigues et al. 2001), Arctic Ocean (Bluhm et al. 2005), and the Weddell Sea (Gutt and Piepenburg 1991). Work in several regions has provided exploratory descriptions at a particular time and many were initiated to examine the effects of metallic nodule mining and energy industry activities. Benthic trawls and/or towed camera systems have typically been used to estimate megafaunal abundances. The usefulness of photogrammetric methods in deep-sea research has led to megafauna being defined as those organisms large enough (typically $\geq$1 cm) to be identified in photographs (Grassle et al. 1975). These studies have shown that

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[1] Present address: Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, California 95039 USA. E-mail: hruhl@mbari.org

echinoderms are an integral component of the abyssal benthos throughout the world ocean. Regional holothuroid densities in the Pacific seem to be related to the general productivity of the overlying surface waters with the California slope stations having higher-to-similar densities (Smith and Hamilton 1983, Nybakken et al. 1998), and the oligotrophic Peru Basin station having order-of-magnitude lower densities (Bluhm and Gebruk 1999), for instance. The short temporal span and logistical limitations of many deep-ocean studies, however, have limited their ability to observe if and how megafauna fluctuate in abundance over time.

Longer time-series measurements are necessary to evaluate population dynamics and the processes affecting larger deep-sea animals. In 1989, studies at Station M (34°50′ N, 123°00′ W, 4100 m depth) began adding temporal perspective to abyssal ecology in the northeast Pacific. Research at Station M has been designed to monitor variation in biogeochemical processes, physiology, and faunal dynamics at the abyssal benthic site (Smith and Druffel 1998). Analysis of portions of the data from the site have shown that several macro-infaunal taxa exhibit seasonal abundance trends and that foraminifera can respond to particulate organic carbon (POC) food fall inputs within weeks (Drazen et al. 1998). In eutrophic regions such as the northeast Pacific, echinoderms dominate the mobile megafauna on the abyssal seafloor in both abundance and biomass (Lauerman et al. 1996). Portions of the time series have also examined the abundance and distribution of many megafauna taxa both mobile and sessile (Lauerman et al. 1996) and how these variables may be related to food supply (Lauerman and Kaufmann 1998). This work provided baseline information on the abundance and distribution of several megafaunal taxa, but the need for longer time-series analysis became apparent from these two year-long examinations (Lauerman et al. 1996, Lauerman and Kaufmann 1998).

Further analysis revealed a long-term discrepancy in the POC food supply vs. the sediment community carbon demand from 1989 to 1996, which raised an important question: Could the community experience long-term variation in food supply without undergoing shifts in abundance (Smith and Kaufmann 1999)? An examination of data from 1989 to 2002 found that several echinoderms varied in abundance and those changes are likely the result of climatically driven variation in POC food supply (Ruhl and Smith 2004). Additional studies found recent fluctuations in the abundance of a hemichordate enteropneust (Smith et al. 2005) and fishes from 1989 to 2004 (Bailey et al. 2006).

Another time-series program has examined benthic communities in the Porcupine Abyssal Plain (PAP) in the northeast Atlantic (48°50′ N, 16°30′ W, 4850 m depth). The interdisciplinary analysis found a difference in benthic megafauna abundances between the periods 1989–1994 and 1996–1999 (Billett et al. 2001). Several taxa shifted in dominance, and several mobile epibenthic megafauna had decreased body-size distributions associated with increased abundances. Shifts in megafauna abundances were associated with variations in climate and subsequent changes in the POC food supply to the seafloor (Billett et al. 2001, Wigham et al. 2003*a*).

POC that ultimately sinks to the seafloor can follow a multitude of pathways including reincorporation into animal tissues, partial digestion and excretion, dissolution and water column retention, or burial in sediments for eons. Deep-sea benthic megafauna can affect the sequestration of carbon through the continuous redistribution of organic material, oxygen, and other nutrients within the top few cm of the sediment surface. Activity patterns measured for abyssal megafauna indicate that they can rework the sediments on the seafloor within weeks (Bett et al. 2001) and activity has been shown to increase during higher food supply conditions (Smith et al. 1993, Kaufmann and Smith 1997). Understanding how megafaunal densities can vary will also be crucial in discerning the probable fate of carbon at the seafloor.

In this study, 52 photographic transects were conducted at Station M in the northeast Pacific over a 16-year period from 1989 to 2004 to determine the abundance dynamics of mobile epibenthic megafauna over interannual time scales. Using this long-term data set, several important questions were addressed: (1) Were the shifts in abundance observed from 1989 to 2002 persistent through 2004? (2) Were any observed changes in abundance related to potential recruitment events? (3) What can be inferred about the relative importance of reproduction, recruitment, growth rates, migration, and disease from the observed dynamics?

METHODS

Station M is located in an abyssal region of the northeast Pacific and has little bathymetric relief, with less than a 100 m difference in elevation over 1600 km^2 (Smith and Druffel 1998). The site is also in the vicinity of the California Cooperative Fisheries Investigations (CalCOFI) and the California Current Ecosystem Long-term Ecological Research (CCE-LTER) site which have provided critical supporting information to studies at Station M. Surface waters above the site have seasonally and interannually variable phytoplankton blooms (Kahru and Mitchell 2002*a, b*), with subsequent peaks in sinking POC to the seafloor 4100 m below within weeks to months (Smith et al. 1993, 2006, Baldwin et al. 1998, Drazen et al. 1998, Lauerman and Kaufmann 1998, Smith and Druffel 1998). Local current measurements, which could influence larval dispersal, were made within the benthic boundary layer at 2.5, 50, and 600 m above the seafloor. The principal flow forcing was found to be semidiurnal tidal with monthly flow speeds of 2.3–3.6 cm/s with additional seasonal-scale variation in the mean flow and direction (Beaulieu and Baldwin 1998). Stronger net flows were generally southerly and weakest

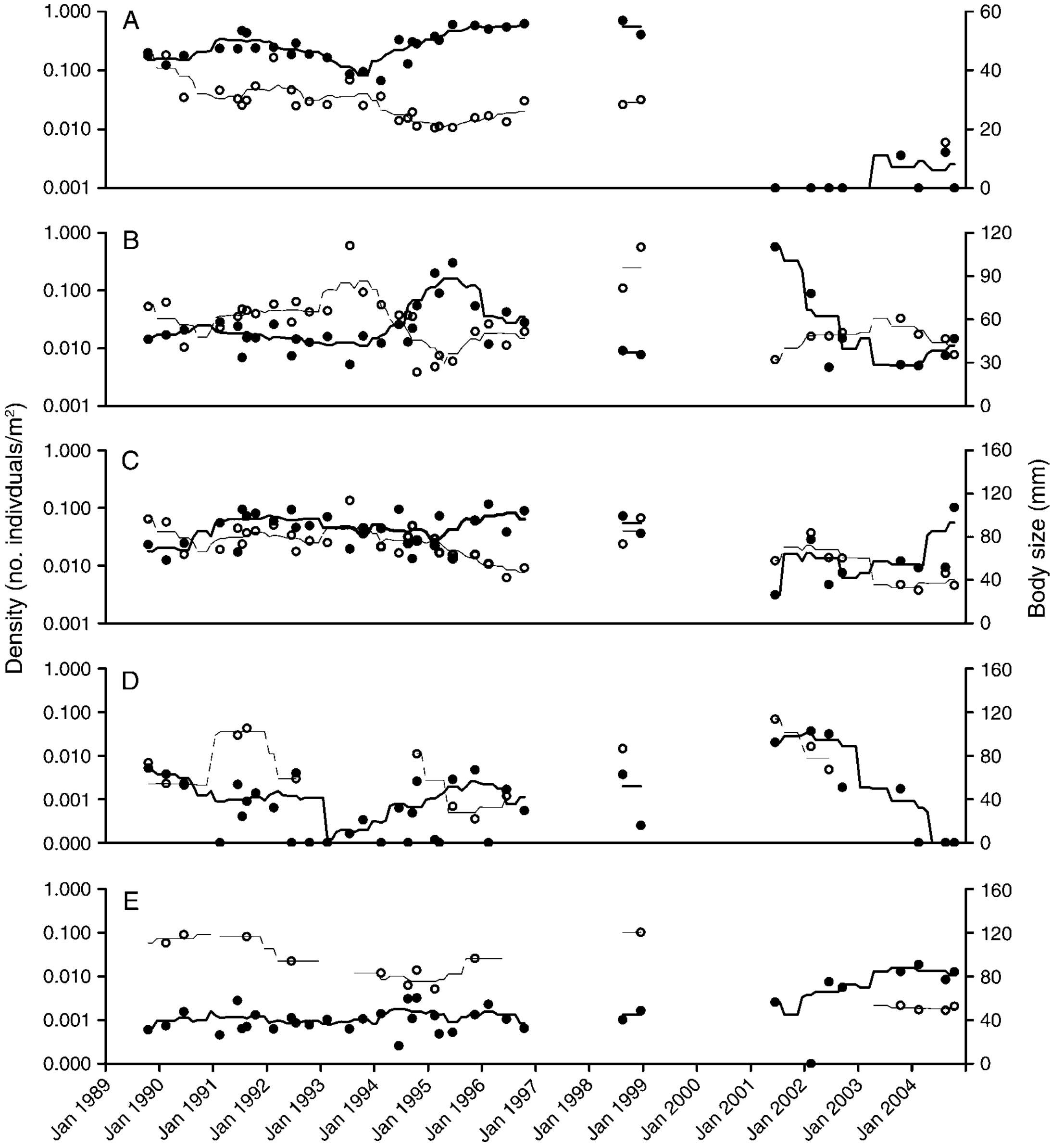

FIG. 1. Abundance (log scale) and body size of (A) *Elpidia minutissima*, (B) *Peniagone diaphana*, (C) *Peniagone vitrea*, (D) *Scotoplanes globosa*, (E) *Oneirophanta mutabilis*, (F) *Psychropotes longicauda*, (G) *Abyssocucurris abyssorum*, (H) *Synallactes profundi*, (I) *Oneirophanta bathybia*, and (J) *Echinocrepis rostrata*. Solid circles and thick solid lines are monthly abundance estimates and 13-month running means, and open circles and thin broken lines are monthly median body sizes and 13-month running means, respectively. Note also that the scales on the various panels are different.

flows were often northerly. The net flow was primarily to the south at <1 cm/s and potential temperatures were approximately 1°C.

The roughly seasonal photographic line transects averaged more than 1.2 km in length and gaps in the data are apparent in Fig. 1. The line-transect photographs were taken using a Benthos 372 camera and Benthos 382 strobe obliquely mounted to a benthic sled (Wakefield and Smithey 1989). The camera was set to take a photograph every 5 s as the sled moved along the bottom at about 0.3 m/s creating a continuous image of the seafloor with overlapping frames. A semi-balloon otter trawl was towed behind the camera sled to non-quantitatively collect specimens that appear in the line-transect images. These collected specimens were then used to identify the photographed animals. The semi-balloon trawl had a 6.1-m opening and 3.8-cm stretch mesh net with 1.3-cm mesh cod-end liner (Wakefield and Smithey 1989).

The photographic data were analyzed using a perspective grid system (Wakefield and Genin 1987) and the computer program DISTANCE (Laake et al.

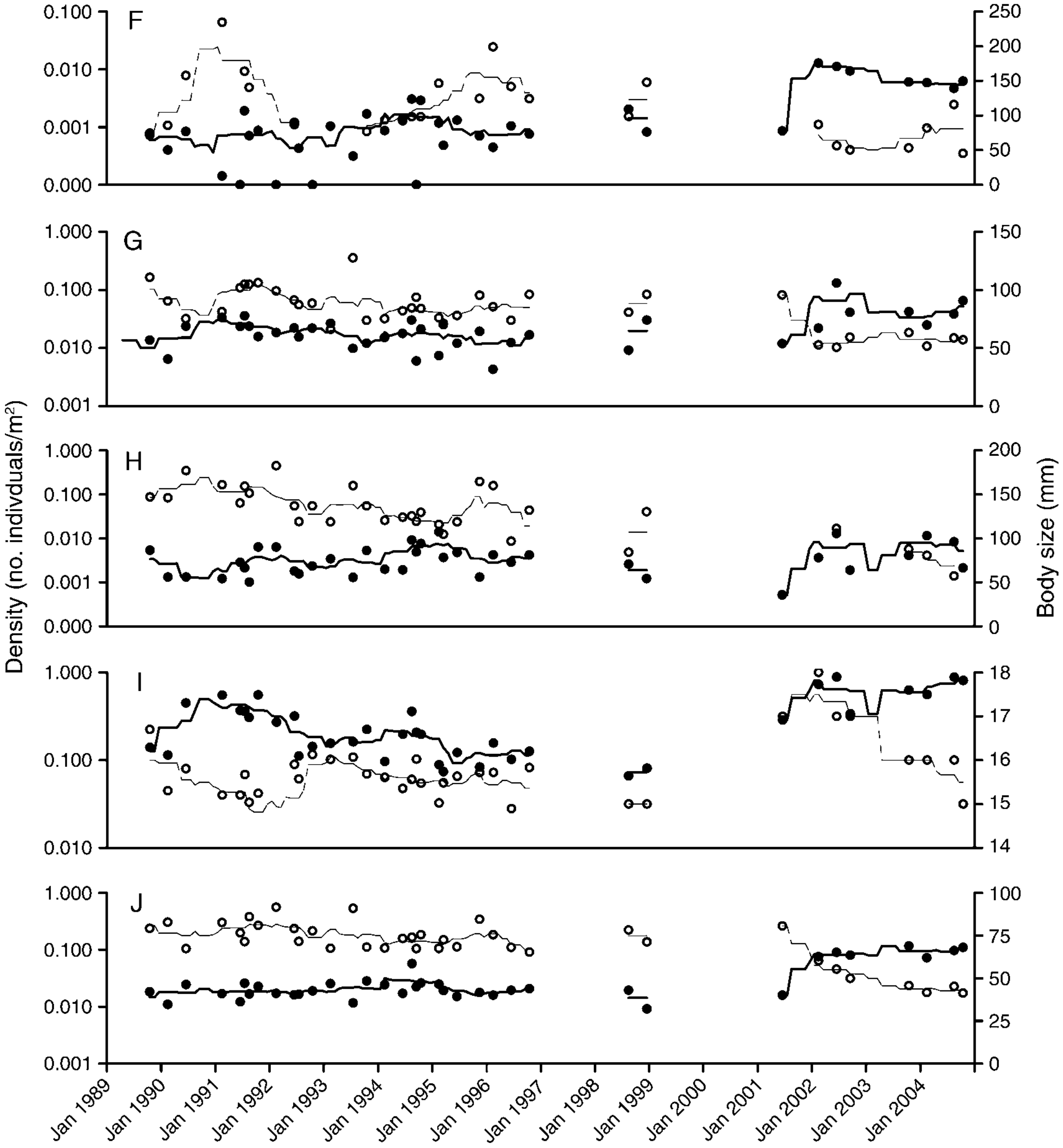

FIG. 1. Continued.

1994), which is based on line-transect theory (Buckland et al. 1993). The relative location and length of each relevant individual within the perspective grid was digitized using a photo enlarger and acoustic digitizing system. Ophiuroid body sizes were calculated from trawl specimen disk diameter measurements. Such direct measurements were not possible with the other taxa due to deformation and damage to the specimens in the trawl net. For the holothuroids, the body size was determined as the longest dimension from the anterior to the posterior excluding appendages. *Echinocrepis rostrata* body footprints approximate an isosceles triangle, and the body sizes were determined as the longer dimension of the triangle. The abundances of dominant epibenthic megafauna were then calculated using DISTANCE. To estimate the effective area viewed DISTANCE estimates visibility and provides an effective strip width (ESW) for each taxon on each transect. This can help account for differences in the visibility of each taxon, as well as water clarity, strobe intensity, and photo processing. When the abundance of any given group is not high enough (typically <15 individuals per transect) to use DISTANCE to evaluate visibility of a group, an ESW from a more abundant and similarly visible species is used to estimate abundance. In cases where more than one photo transect was conducted during a given month, transect length weighted means were calculated. For a more detailed description of line-transect photography methods, see Lauerman et al. (1996), Lauerman and Kaufmann (1998), and Ruhl and Smith (2004).

Body-size distribution and abundance trends for the dominant megafauna species were evaluated using several nonparametric and randomization-based analyses. Yearly, as well as monthly, groupings of cumulative body-size distribution data were examined where possible. Monthly distributions were not produced for *Synallactes profundi*, *Scotoplanes globosa*, *Oneirophanta mutabilis*, and *Psychropotes longicauda* because of their low average abundances during the study. All body-size distributions are available for reference in the Appendix. Relationships between monthly median body size and abundance were evaluated using Spearman-rank correlations (r_S) and results with a $P \leq 0.05$ are considered significant.

The relative similarity of the size distributions was also estimated by entering the absolute differences of each possible pair of distributions into a similarity matrix. This similarity matrix was then used to calculate a multidimensional scaling (MDS) *x*-ordinate of body size similarity. This body size index permitted nonparametric evaluation of the similarity of body-size distributions over time and followed the methodology described in Thurston et al. (1994) and Billett et al. (2001). Supporting analyses included a randomization analysis of similarity (ANOSIM, *R* statistic) to examine if a positive or negative deviation in overall median body size was significantly linked to the size distributions as a whole. The strength of any possible link between the body size index and the median body size was evaluated using the Spearman rank correlation. Spearman rank correlations were also conducted between the body size index and time to examine if changes in size distributions were continuous and generally monotonic over the whole time series. The existence of any significant monotonic trends was also evaluated for abundance over time. The presence of seasonal trends in abundance was evaluated by examining the timing of individual annual peaks in abundance.

Shifts in the body-size distributions over time were used to estimate individual growth rates since robust estimates of growth that include size at age information are not possible. Single size-class peaks in abundance that could be tracked over multiple time points were used to make individual estimates of growth in much the same way cohorts are tracked in fishery size distributions (sensu Hjort 1926). Thirty-nine such estimates were made from the monthly size-frequency distributions (Appendix). The estimates, however, are limited in their accuracy since age cannot be determined for the photographed specimens. Estimations of the maximal population growth rates and minimal population doubling time can also be made from rates of abundance increase over time. The relationship $T = (\ln 2)/d$ was used to create these first approximations from yearly grouped data, where d is the observed percent difference in density from one year to the next and T is the estimated doubling time.

RESULTS

The abundance of the holothuroids *Elpidia minutissima*, *Peniagone diaphana*, *P. vitrea*, *Abyssocucumis abyssorum*, *Synallactes profundi*, *Scotoplanes globosa*, *Oneirophanta mutabilis*, *Psychropotes longicauda*, the echinoid *Echinocrepis rostrata*, and the ophiuroids, dominated by *Ophiura bathybia*, varied by one to three orders of magnitude over the 16-year time series (Fig. 1). These echinoderms comprised >99% of all mobile megafauna observed during the study period. The observations were mainly characterized by interannual-scale variations with no clear seasonality. True spectral analysis is not possible with the uneven temporal distribution of the data, but no other cyclical abundance or size trends are yet evident.

Particularly notable was the shift in the abundance of the elasipodid *Elpidia minutissima*. After dominating the mobile epibenthic megafauna during the period 1989–1998 with a peak monthly abundance at 0.697 individuals/m^2, *E. minutissima* had a reduction in density of three orders of magnitude in 2001–2004 (Fig. 1A). *Peniagone diaphana* and *P. vitrea* have also been dominant elasipodid holothuroids at Station M, and although the two are in the same genus they did not have covarying abundances ($r_S = 0.02$, $P = 0.8$; Fig. 1B, C). *Peniagone diaphana* densities were roughly 0.01 individuals/m^2 for much of the time series with prominent spikes in abundance in 1995 and 2001 (Fig. 1B). The trend of *P. vitrea* over time was similar to that of *E. minutissima* ($r_S = 0.52$, $P < 0.001$; Fig. 1A, C) with accumulating densities from 1989 to 1998 followed by an order of magnitude decline by 2001 with a notably higher abundance observed in October 2004. Varying by more than two orders of magnitude, *S. globosa* was less abundant than the above taxa and showed lower abundances from 1989 to 1998, a peak in 2001–2002, and declined to its lowest levels by 2004 (Fig. 1D). Both remaining elasipodids, *O. mutabilis* and *Ps. longicauda*, had relatively low abundances through 1998 but were higher during the 2001–2004 period (Fig. 1E, F).

The moderately abundant dendrochirotid, *A. abyssorum,* also had a slightly higher density from 1989 to 1990, then declined through 1998 with a subsequent order of magnitude increase to about 0.1 individuals/m^2 in 2002 and thereafter (Fig. 1G). The aspidochirotid, *Sy. profundi*, rose in density from 1990 to 1995 and then showed decreased values through 2001. The density subsequently increased to 0.013 individuals/m^2, its highest values observed during the time series (Fig. 1H). The ophiuroid taxon, dominated by *O. bathybia*, was highly dominant between 1989 and 1998 and became most prevalent in 2001–2004 with abundances approaching 1 individual/m^2 (Fig. 1I). *Echinocrepis rostrata* had a relatively constant density from 1989 to 1998 at approximately 0.01–0.02 individuals/m^2

Table 1. Spearman rank correlations (r_S) between abundance and time, as well as between cumulative body-size frequency distribution similarity multidimensional scaling (MDS) x-ordinates and time, with monthly and yearly estimates.

		Abundance vs. time						Body size MDS x-ordinates vs. time					
		Monthly			Yearly			Monthly			Yearly		
Species	Median body length (mm)	n	r_S	P	n	r_S	P	n	r_S	P	n	r_S	P
Holothuroids													
Elpidia minutissima	28	37	−0.22	0.195	13	−0.39	0.184	29	**−0.59**	**<0.001**	9	**−0.85**	**0.004**
Peniagone diaphana	61	37	−0.10	0.554	13	−0.07	0.817	37	**−0.44**	**0.006**	13	**−0.60**	**0.030**
Peniagone vitrea	73	37	−0.25	0.143	13	−0.34	0.255	37	**−0.63**	**<0.001**	13	**−0.72**	**0.010**
Scotoplanes globosa	70	37	−0.02	0.929	13	−0.05	0.859				8	0.21	0.610
Oneirophanta mutabilis	97	37	**0.55**	**<0.001**	13	**0.86**	**<0.001**				11	−0.19	0.570
Psychropotes longicauda	98	37	**0.61**	**<0.001**	13	**0.75**	**0.003**				11	−0.38	0.250
Abyssocucumis abyssorum	84	37	0.23	0.180	13	0.47	0.108	37	**−0.61**	**<0.001**	13	**−0.58**	**0.040**
Synallactes profundi	130	37	0.24	0.150	13	0.33	0.271				13	**−0.71**	**0.010**
Echinoids													
Echinocrepis rostrata	72	37	**0.47**	**0.004**	13	0.44	0.133	37	**−0.73**	**<0.001**	13	**0.75**	**0.003**
Ophiuroids													
Ophiura spp.	16	37	0.13	0.439	13	0.41	0.168	37	0.16	0.340	13	0.14	0.650

Note: Body size statistics with *E. minutissima* only include data from 1989 to 1998 since so few individuals were observed in 2001–2004. Statictically significant. ($P < 0.05$) correlations and P values are highlighted by bold type.

and increased monotonically to 0.117 individuals/m^2 by 2003 (Fig. 1J, Table 1).

Increases in abundance were often associated with increases in the proportion of smaller individuals (Fig. 1, Table 2). For example the density of *E. minutissima* was negatively correlated with the median size, and a relatively continuous change in body size from 1989 to 1998 was evident from the median body sizes over time (Fig. 1A, Table 2), and the annual size-frequency histograms (Fig. 2). The relationships between body size and density were unclear from 2001 to 2004 because so few individuals were observed during that period.

Similar analyses show that significant negative links between density and median body size were found for all but *P. vitrea*, *S. globosa*, and *O. bathybia* (Table 2). For both *P. vitrea* and *O. bathybia*, the mean body size was negatively correlated with abundance over much of the time series, but this otherwise significant relationship weakens in the 2001–2004 period (Fig. 1C, I). Notably, no clear cohorts of *O. bathybia* were observed during the entire study period either.

ANOSIM results show the body-size distribution similarity values were significantly different when a given monthly body size was either higher or lower than the overall median for all but *S. globosa* and *Sy. profundi* (Figs. 3 and 4, Table 2). Most taxa also had significant Spearman rank correlations between the body size index and the median body size for both monthly and yearly groupings. These results indicated that the median was a reasonable descriptor of the overall distribution (Figs. 3 and 4, Table 2). All but *S. globosa*, *O. mutabilis*, *Ps. longicauda*, and *O. bathybia* had significant monotonic changes in the body size index over time (Figs. 3 and 4, Table 1).

Prominent peaks in smaller individuals of *E. minutissima*, *P. diaphana*, *P. vitrea*, *A. abyssorum*, and *Ec. rostrata* were seen in the size-frequency histograms of June 1990 in particular (Fig. 2; Appendix). *Synallactes profundi*, *S. globosa, O. mutabilis,* and *Ps. longicauda*, had abundances that precluded monthly analyses of size-frequency distributions. Annual size-frequency histograms of *Sy. profundi* were highly variable, but showed a peak in the smaller sizes in 1990 and a reduction in the mean size was also evident in the 2001–2004 time period (Appendix). *Scotoplanes globosa* size distributions also indicated higher frequencies of smaller individuals in 1990 and 1995, two periods when abundance was moderately high (Fig. 1D, Appendix).

Crude growth rate estimates were made for those taxa that had distinct peaks in size classes that were identifiable in sequential measurement periods. These analyses produced estimates that ranged from 1 to 4 mm/month for *E. minutissima*, 2 to 5 mm/moth for *P. diaphana*, 2 to 6 mm/month for *P. vitrea*, 2 to 5 mm/month for *A. abyssorum*, and 2 to 5 mm/month for *Ec. rostrata*. Estimations of maximal, though unsustained, annual population growth rates ranged from around 100% to over 500% and minimal doubling times ranged from about 50 days to almost 1 year depending on the taxon.

Discussion

All of the dominant mobile epibenthic megafauna at Station M have changed in density from one to three orders of magnitude over the 16-year period indicating, principally, that these abundances were considerably dynamic over interannual time scales. Several shifts in abundance observed in 2001–2002 (Ruhl and Smith 2004) have persisted through 2004. The most dominant taxon from 1989 to 1998, *E. minutissima*, went from constituting more than 40% of the mobile megafauna individuals in the 1990s to virtually absent in 2001–2004. Changes in *E. minutissima* abundance were also accompanied by shifts in the size-frequency distributions over time. The apparent lack of seasonality in megafau-

TABLE 2. Spearman rank correlations (r_S) between median body size and abundance (with monthly and yearly estimates) and between median body size and cumulative body-size frequency similarity multidimensional scaling (MDS) x-ordinates. The table also presents ANOSIM comparisons (R) between cumulative body-size frequency distribution similarity MDS x-ordinates and deviation (positive or negative) from the overall median body size.

Species	Median body length (mm)	Median body size vs. abundance						Median body size vs. body size MDS x-ordinates vs. time					
		Monthly			Yearly			Monthly			Yearly		
		n	r_S	P	n	r_S	P	n	r_S	P	n	r_S	P
Holothuroids													
E. minutissima	28	29	**−0.52**	**0.004**	9	−0.42	0.265	29	**0.97**	**<0.001**	9	**0.90**	**<0.001**
P. diaphana	61	37	**−0.47**	**0.003**	13	**−0.65**	**0.017**	37	**0.96**	**<0.001**	13	**0.93**	**<0.001**
P. vitrea	73	37	0.03	0.868	13	0.36	0.223	37	**0.98**	**<0.001**	13	**0.98**	**<0.001**
S. globosa	70	14	0.07	0.817	12	0.07	0.829				8	**0.98**	**<0.001**
O. mutabilis	97	28	**−0.69**	**<0.001**	11	**−0.93**	**<0.001**				11	**0.90**	**<0.001**
Ps. longicauda	98	26	**−0.60**	**0.001**	13	−0.47	0.108				11	**0.96**	**<0.001**
A. abyssorum	84	37	**−0.37**	**0.023**	13	−0.52	0.071	37	**0.97**	**<0.001**	13	0.37	0.212
Sy. profundi	130	32	**−0.46**	**0.008**	13	−0.54	0.055				13	**0.64**	**0.019**
Echinoids													
Ec. rostrata	72	37	**−0.73**	**<0.001**	13	**−0.74**	**0.004**	37	**0.79**	**<0.001**	13	0.44	0.135
Ophiuroids													
O. spp.	16	37	0.30	0.076	13	0.39	0.183	37	**0.80**	**<0.001**	13	**0.92**	**<0.001**

Notes: Empty cells indicate instances where tests were not possible because distributions were not reliably estimated. Note that statistics with *E. minutissima* only include data from 1989 to 1998 since so few individuals were observed in 2001–2004. For full names of genera, see Table 1. Statistically significant (P <0.05) results are highlighted by bold type.

† Number of permutations.

na abundance could be related to aseasonal reproduction, as well as to the high interannual variability in food supply at Station M. Migration, reproduction, recruitment, and survivorship could all be influential factors in the observed dynamics. Direct measurement of all population parameters has not been logistically possible and migration potential, recruitment, growth rates, and life spans are still inadequately known. The detailed abundance and size distribution data provide the best information available to help elucidate the population dynamics of these megafauna.

Evaluating the importance of migration vs. recruitment can be done, in part, by examining size-frequency distributions. Median size and size-frequency distribution trends over time have indicated that increases in abundance were associated with decreases in body size in most cases, suggesting that density increases were associated with the introduction of new smaller individuals. In these cases, reproduction and recruitment were likely to be important in explaining the observed abundance dynamics. This conclusion is also supported by the additional randomization and correlation tests presented in Table 2 and the specific peaks in smaller individuals observed in the size–frequency distributions (Appendix). Conversely if increases in median body size were linked to increases in abundance, there could be higher survivorship. The observations even show a loss of larger individuals in some taxa, such as *E. minutissma* and *O. mutabilis*, when abundances were increasing. The reasons for decreased survivorship of the larger individuals are less clear and could include size specific competitive interactions, predation, or disease. Time-lagged correlations, though, suggest that predation by benthopelagic fishes at the site did not have a discernable impact on the invertebrate megafauna abundances studied here (Bailey et al. 2006).

If rising densities were primarily caused by migrations of similarly sized individuals then the size distributions would be far less likely to shift in synchrony with changes in abundance. Known movement rates for seven of the 10 echinoderms examined here range from 5 to 65 cm/h at Station M and could lead to straight-line migrations of 0.4–5.7 km/yr (Kaufmann and Smith 1997). These echinoderms exhibit frequent stops, turns, and loop movement patterns on scales of hours to weeks, so one-way migrations of tens to hundreds of kilometers by benthic stages are unrealistic for most echinoderms at Station M.

Elpidia minutissima, *P. diaphana*, *O. mutabilis*, *Ps. longicauda*, *A. abyssorum*, *Sy. profundi*, and the echinoid *Ec. rostrata* all exhibited negative relationships between body size and abundance over time. Abundance and body size relationships with *P. vitrea* were less clear since although the links between the body size index and median body size were significant, direct correlations of abundance and median body size were insignificant. Inconsistencies in the results for *S. globosa*, and *Ps. longicauda* could be the result, at least in part, of the lower overall number of samples from which size distributions were derived. Nevertheless, the size distributions of all taxa examined show some indication of links between size distributions and abundances and evidence for recruitment of new small individuals to existing populations over interannual timescales.

The smaller size class increases in June 1990 are particularly interesting since it is the only time when

TABLE 2. Extended.

Positive or negative size deviation vs. size MDS x-ordinates					
Monthly			Yearly		
Perm.†	R	P	Perm.†	R	P
999	**0.44**	<0.001	999	**0.48**	**0.016**
999	**0.43**	<0.001	999	**0.40**	**0.012**
999	**0.62**	<0.001	999	**0.47**	**0.003**
			28	0.18	0.250
			330	**0.37**	**0.033**
			330	**0.48**	**0.015**
999	**0.53**	<0.001	999	**0.29**	**0.035**
			462	0.20	0.071
999	**0.20**	<0.001	999	**0.56**	**0.002**
999	**0.38**	<0.001	999	**0.68**	**0.002**

there is evidence for reproduction and/or recruitment across several taxa. Free of interspecific competition each taxa might increase in abundance with increased resources. In this food-limited abyssal setting, though, competition appears to be important and different taxa appear to have different responses to the food supply on average (Ruhl and Smith 2004). The period prior to June 1990 may have been a time when the food resource was less limiting, but as yet similar mass recruitments have not been seen since. The lack of evidence for seasonality also points to the importance of opportunistic reproduction and/or recruitment processes.

Several of the species observed here were also common at the PAP site in the northeast Atlantic where the abundance of the megabenthos had significant ($P <$ 0.05) variations from 1989 to 1999 (Billett et al. 2001). The abundance of the holothuroids *Amperima rosea*, *Ellipinion molle*, *Ps. longicauda*, *Pseudostichopus* sp., and *P. diaphana* all had significant changes in abundance. *Oneirophanta mutabilis*, which also occurs at Station M, did not have any significant shifts in abundance at the PAP site. An order of magnitude increase in *O. mutabilis* was observed at Station M, but it was lesser in magnitude than most other taxa. Several taxa, such as *Amperima rosea* and *Ps. longicauda*, at the PAP also had links between abundance and body size that were comparable with those at Station M, including the loss of larger individuals in some cases (Billett et al. 2001).

Wigham et al. (2003*b*) suggested that *Amperima rosea* is capable of opportunistic responses to ecological cues by withholding full vitellogenesis until ecological conditions are met. Examination of abundance and gonad development gave no clear indication of seasonal or other cyclical recruitment. *Amperima rosea*, which increased in abundance by three orders of magnitude at the PAP site, is a small elasipodid with either a planktotrophic or brief lecithotrophic larval stage reaching maturity as soon as one year after settlement (Billett et al. 2001, Wigham et al. 2003*b*). Particularly notable is that *A. rosea* was identified as selectively feeding on specific phytopigments and could metabolize a specific sterol that several other holothurioids at the PAP cannot (Wigham et al. 2003*a*, *b*).

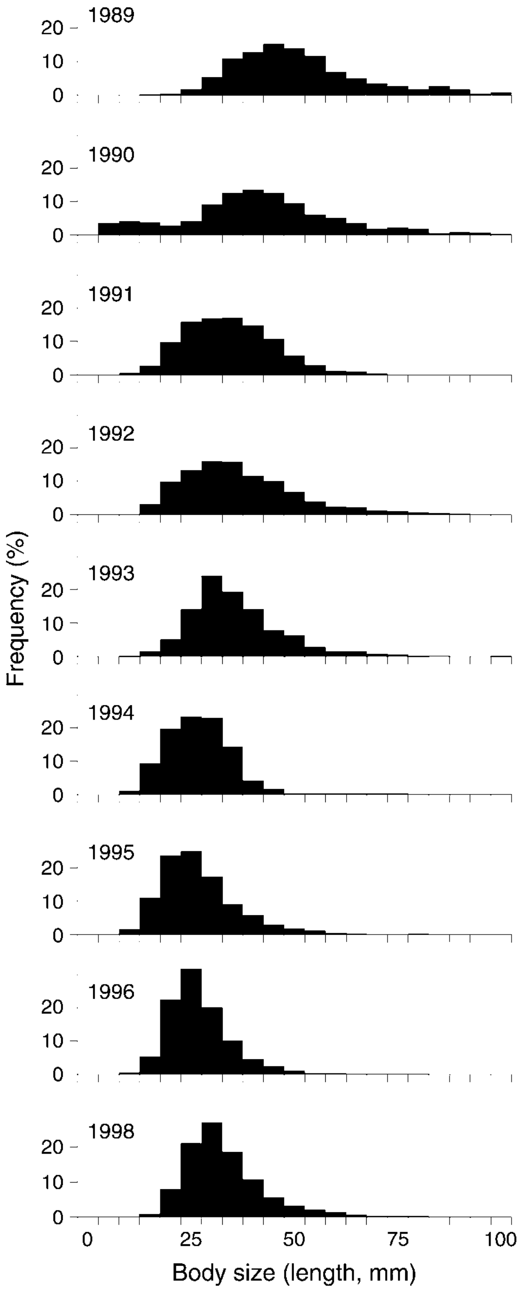

FIG. 2. Percentage frequency histograms of body size for *Elpidia minutissima*. Data from all transects are grouped yearly for 1989–1996 and 1998. *Elpidia minutissima* was infrequently observed during 2001–2004, so no histograms were made for that period.

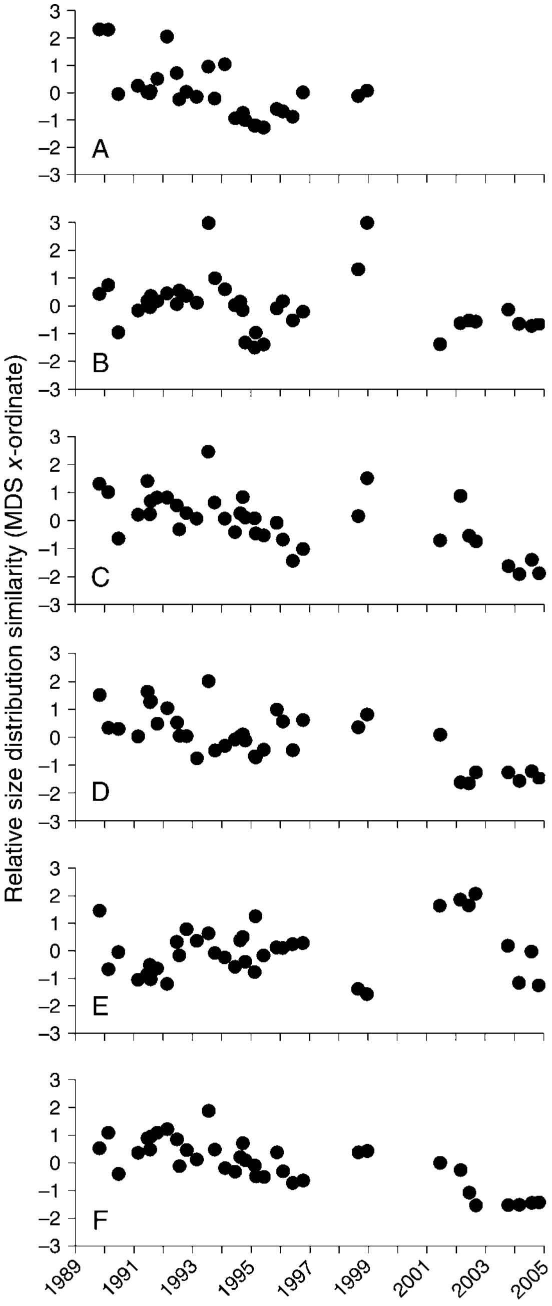

FIG. 3. Relative similarity of monthly cumulative size distributions of (A) *Elpidia minutissima*, (B) *Peniagone diaphana*, (C) *Peniagone vitrea*, (D) *Abyssocicurris abyssorum*, (E) *Oneirophanta bathybia*, and (F) *Echinocrepis rostrata*. Positive *x*-ordinate values are set to ordinate with distributions with higher than average medians and negative values with lower than average medians; MDS indicates multidirectional scaling.

Aseasonal patterns appear to dominate holothuroid fecundity and reproduction (Young 2003) including *P. diaphana* (Tyler et al. 1985), *O. mutabilis*, and *Ps. longicauda* (Tyler and Billett 1987), which were observed here. Most benthic echinoderms have pelagic dispersal and planktonic developmental stages with egg diameters from hundreds to thousands of micrometers (Young 2003). Cross-generational migrations of tens to hundreds of kilometers seem reasonable given a pelagic phase of weeks to months. Juvenile *Ps. longicauda*, for example, have been taken from thousands of meters above the seafloor (Billett et al. 1985, Gebruk et al. 1997). Several *Peniagone* species are also known to spend some portion of their adult life swimming off the seafloor (Barnes et al. 1976, Bluhm and Gebruk 1999). This behavior could increase a taxon's relative ability to migrate across the seafloor. At Station M, however, the *Peniagone* spp. swimming behavior was observed infrequently. *Oneirophanta mutabilis* has shown evidence of intra-ovarian brooding at the Panama Basin (Hansen 1968), but this brooding was not observed at the PAP site (Tyler and Billett 1987), and there also appear to be sustained unexplained sex ratio differences between the two sites (Ramirez-Llodra et al. 2005). It is unknown whether *O. mutabilis* exhibits brooding at Station M, but such behavior could make the taxon less likely to have cross-generational migrations at a regional scale. If echinoderm populations at Station M are receiving recruits from the greater northeast Pacific region, they could be more likely to originate from the north since water flows principally from the north and comparable habitat in terms of depth and food inputs are also aligned along the California Current system (Smith et al. 2006).

Estimations of growth were calculated from shifts in size distributions to further explore the plausibility of reproduction and recruitment driving increases in the megafaunal abundances. Analyses of observed shifts in Station M megafauna size-frequency distributions indicate that growth rates could be as high as 2–6 mm/month. Wigham et al. (2003*b*) estimated deep-sea holothuroid growth to be about 1 mm/month. Gage and Tyler (1985) also note that a congener echinoid, *Echinus affinis*, may reach reproductive size within five years. A cultured holothuroid, *Holothuria scabra*, has been estimated to grow from 6 to 24 mm/month for subadults (Battaglene et al. 1999). Estimates from cultured or exploited holothuroid populations are not directly comparable to natural growth rates, but the ranges of the shallow water and abyssal estimates do overlap.

The abundance measurements over time at Station M suggest that abyssal populations can experience multiple abundance doublings within one year. Such rapid increases in megafauna abundance indicate that with regional and local interaction the abundances at Station M could respond with changes in their reproduction and fitness. These estimates do not imply that measured growth rates or doubling times are sustainable over several years. Allee stability (Allee 1938, Dennis 1989, Scheuring 1999) can also influence the responsiveness of populations below some threshold density and carrying capacities unquestionably limit the long-term extent of opportunistic reproductive responses.

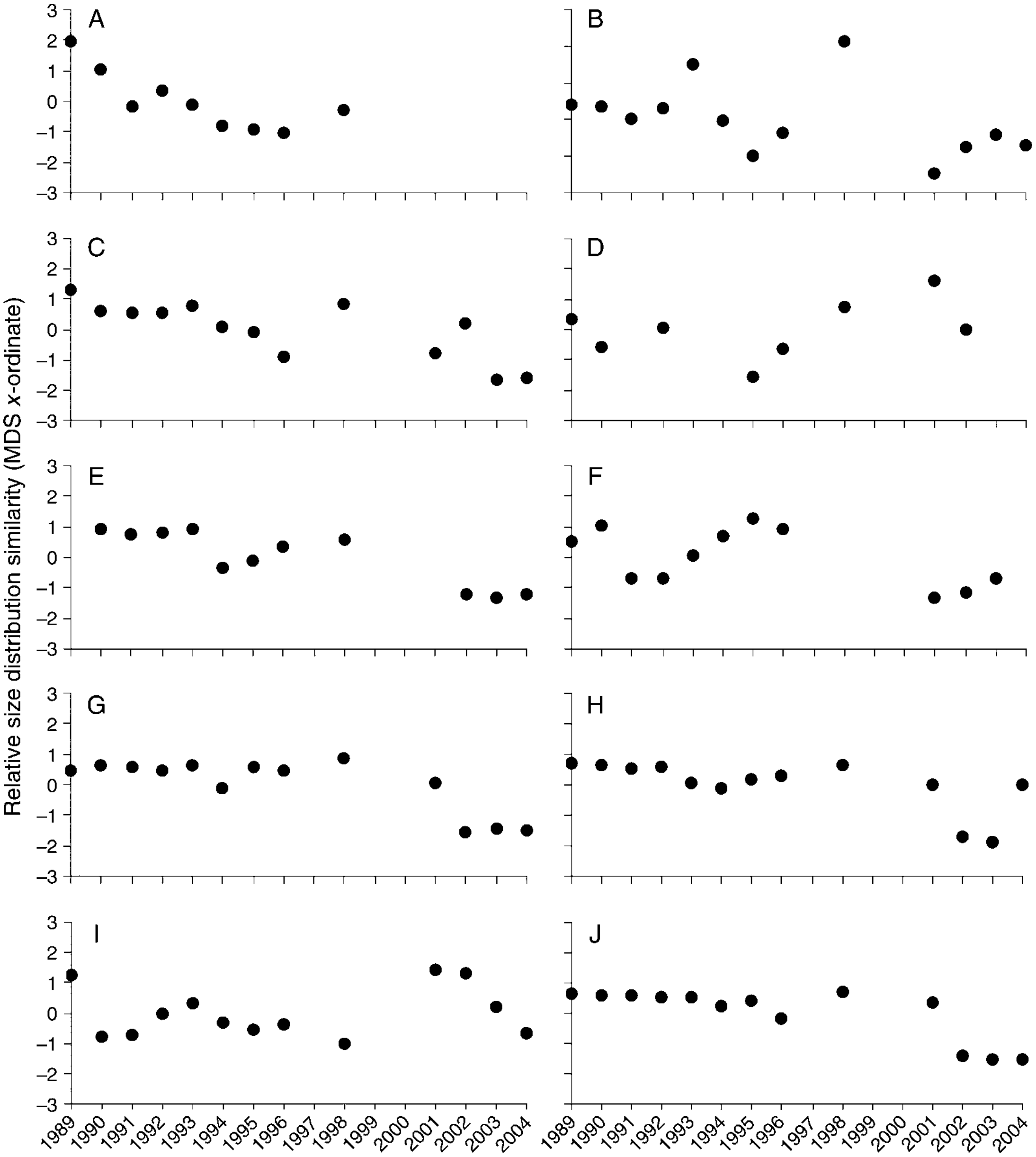

FIG. 4. Relative similarity of yearly cumulative size distributions of (A) *Elpidia minutissima*, (B) *Peniagone diaphana*, (C) *Peniagone vitrea*, (D) *Scotoplanes globosa*, (E) *Oneirophanta mutabilis*, (F) *Psychropotes longicauda*, (G) *Abyssocucurris abyssorum*, (H) *Synallactes profundi*, (I) *Oneirophanta bathybia*, and (J) *Echinocrepis rostrata*. Positive *x*-ordinate values are set to ordinate with distributions with higher than average medians, and negative values with lower than average medians; MDS indicates multidimensional scaling.

Mobile megafauna have been previously observed to aggregate on scales from meters to kilometers in deep-seafloor habitats both at Station M and other locations (Smith and Hamilton 1983, Billett 1991, Lauerman et al. 1996, Lauerman and Kaufmann 1998, Summers and Nybakken 2000). Such aggregations surely explain some of the variation seen in the density estimates. Detailed examinations of dispersion along the Station M transects indicate that detectable nonrandom dispersion patterns do occur, but they were infrequent and no consistent aggregation behavior was found at the transect scales. In the northeast Atlantic, synoptic samples have shown signs of spatial variability in recruitment (Tyler et al. 1985, Billett 1991). The scales at which spatial processes may be operating remain speculative, but the synchronous abundance and body size trends observed are unlikely if spatial heterogeneity was the primary source of the observed variation.

Climate and food supply have been linked to the shifts observed at Station M and PAP (Bett et al. 2001, Billett et al. 2001, Ruhl and Smith 2004, Smith et al. 2006). Benthic echinoderms appear to discriminate between specific phytodetrital food patches (Billett et al. 1988, Lauerman et al. 1997, Ginger et al. 2001, Iken et al. 2001, Demopoulos et al. 2003) and specific POC nutrients may be important in the development of reproductive tissues (Hudson et al. 2003, 2004, Wigham et al. 2003*a*, *b*). Competitive advantages in selecting and utilizing the fluctuating quality and quantity of the POC food supply are widely believed to be the principal way in which each specific taxon can have variable responses to the food supply (Roberts and Moore 1997, Billett et al. 2001, Roberts et al. 2001, Hudson et al. 2003, Wigham et al. 2003*a*, *b*, Ruhl and Smith 2004, Ramirez-Llodra et al. 2005, Neto et al. 2006). Ramirez-Llodra et al. (2005) noted that increased densities of *A. rosea* in recent samples may have reduced the fecundity of the congener *O. mutabilis* at the PAP site. Similar processes are likely to be occurring at Station M. As reported in Ruhl and Smith (2004) some taxa at Station M seemed to be favored during higher food supply conditions while others thrived during lower food fluxes. These differential responses to food supply are indicative of competitive interactions for a common resource. Understanding how climate can affect POC quantity and quality, and how abyssal taxa differentially utilize POC remain important areas of investigation.

The faunal density and activity changes observed at Station M and the PAP are likely affecting levels of activity and bioturbation. Understanding how much carbon is transported into deep-ocean waters for millennial scale recirculation to the surface or geologic sequestration in marine sediments will be critical to understanding the future carbon cycle. The dominance of echinoderms in the mobile megafauna and their apparent responses to the POC food supply support the use of megafaunal echinoderms as an indicator group for understanding the effects of climate variation on the abyssal benthos and the long-term sequestration of carbon.

Observations at Station M and the PAP clearly establish that interannual scale variability in megafauna abundances can occur at abyssal depths. Increases in abundance of echinoderm megafauna at Station M were typically linked to decreases in body size, which suggest that reproductive events on a local to regional scale are contributing young individuals. Basic population parameters such as reproduction, growth rates, generation times, longevity, and competitive interactions need further study, though, since much of what is known is not measured directly. Abyssal abundances have been observed to vary from interglacial (Cronin et al. 1999) to contemporary time scales of days to years in organisms from bacteria to megafauna (e.g., Gooday 1988, Drazen et al. 1998, Boetius et al. 2000, Billett et al. 2001, Ruhl and Smith 2004, Bailey et al. 2006), punctuating the importance of having a temporal perspective when describing life in the deep ocean.

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APPENDIX

Supplementary size frequency distributions (*Ecological Archives* E088-078-A1).