

COMMUNITY CHANGE IN THE VARIABLE RESOURCE HABITAT OF THE ABYSSAL NORTHEAST PACIFIC

HENRY A. RUHL¹

Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, California 95039 USA

Abstract. Research capable of differentiating resource-related community-level change from random ecological drift in natural systems has been limited. Evidence for nonrandom, resource-driven change is presented here for an epibenthic megafauna community in the abyssal northeast Pacific Ocean from 1989 to 2004. The sinking particulate organic carbon food supply is linked not only to species-specific abundances, but also to species composition and equitability. Shifts in rank abundance distributions (RADs) and evenness, from more to less equitable, correlated to increased food supply during La Niña phases of the El Niño Southern Oscillation. The results suggest that each taxon exhibited a differential response to a sufficiently low dimension resource, which led to changes in community composition and equitability. Thus the shifts were not likely due to random ecological drift. Although the community can undergo population-level variations of one or more orders of magnitude, and the shape of the RADs was variable, the organization retained a significant consistency, providing evidence of limits for such changes. The growing evidence for limited resource-driven changes in RADs and evenness further emphasizes the potential importance of temporally variable disequilibria in understanding why communities have certain basic attributes.

Key words: *California Current Ecosystem (CCE); climate; deep sea; echinoderm; holothuroid; Long-Term Ecological Research (LTER); megafauna; niche hierarchy; ophiuroid; pelagic–benthic coupling; rank abundance; relative abundance.*

INTRODUCTION

The vast majority of research on the potential influences of either resources or dispersal and recruitment in community structuring explicitly examines or assumes steady-state conditions (e.g., Motomura 1932, Preston 1948, MacArthur 1957, Whittaker 1965, MacArthur and Wilson 1967, May 1975, Hubbell 1979, 2001, Sugihara 1980, Tokeshi 1990, 1999, Chase and Liebold 2003, Olding-Smee et al. 2003, Sugihara et al. 2003). Over interannual time scales, however, variations in climate clearly impact marine and terrestrial populations worldwide through pulsed and pressed forcing (e.g., Stenseth et al. 2002). Long-term studies in the California Current Ecosystem (CCE) region and greater northeast (NE) Pacific Ocean, for instance, have shown relationships between climatic and environmental conditions and shifts in productivity, zooplankton, and fish abundances (McGowan et al. 1998, Hare and Mantua 2000). Further research has continued to examine how environmental variation can lead to such changes and how shifts might be distinguished from random ecological drift (e.g., Mantua 2004, Hsieh et al. 2005).

Several mechanisms have been developed to explain how the pervasive trends in the relative abundance of species are shaped and maintained, including theories

based on niches, dispersal, and stochastic processes. Rank abundance distributions (RADs) and equitability are widely thought to be indicators of how a resource or resources are divided up by a particular guild or community (e.g., Motomura 1932, MacArthur 1957, Whittaker 1965, Sugihara 1980, Tokeshi 1990, 1999, Chase and Liebold 2003). Equitability has also been linked to differences in hierarchical resource partitioning (Sugihara et al. 2003). Neutral ecological theory (Hubbell 2001), a type of dispersal structuring, has provided a comprehensive null model for such niche-based theories.

Many recent studies have evaluated hypotheses based on niche and neutral theories of relative abundance in both the context of evolution and contemporary ecology (Gaston and Chown 2005, Pandolfi 2006). A number of complications commonly limit unequivocal interpretation as to whether one or the other is dominant (Willis and Whittaker 2002), including the covariation of species distributions, geographic range, and environmental gradients (Gilbert and Lechowicz 2004); the pooling of spatial or temporal variability (Thibault et al. 2004); and the notion that many factors can potentially affect individual-level to species-level success.

Interpreting temporal dynamics from natural systems, where environment and resource variation can significantly affect a species and vice versa, has also had limitations (e.g., Brown et al. 2001, Chase and Liebold 2003), but temporal concepts have emerged that are relevant here. Shifts in the abundance at the population

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² E-mail: hruhl@mbari.org

level of one taxon over time are often linked with either influencing or response variables (e.g., Ernest and Brown 2001), and variation can facilitate coexistence of similar species maintaining diversity (Connell 1978, Levins 1979). For example, local disturbance can reduce local diversity but provide greater habitat diversity at larger scales. Variation is also important in that a species can be risk averse, risk neutral, or risk taking with regard to environmental or resource variability (Chase and Liebold 2003, Chesson et al. 2004).

Empirically tracking relative abundance over time has included the documentation of community changes during forest succession (Bazzaz 1975) and shifts in desert rodent communities (Thibault et al. 2004). Additionally, a study of a marine fish community noted that commonly occurring taxa had different relative abundance dynamics than rarer taxa, and those differences were founded in basic life history attributes (Magurran and Henderson 2003, Magurran 2007). In aquatic systems, increases in nutrients have been shown to lead to the dominance of certain algal taxa during blooms (e.g., Coale et al. 1996, Smayda 1997, Vitousek et al. 1997). Evenness has even been suggested to be an indicator of eutrophication (e.g., Cottingham and Carpenter 1998, Tsirtsis and Karydis 1998, Kitsiou and Karydis 2000). Coexistence in diatoms has been shown to be facilitated by fluctuating environmental factors (Descamps-Julien and Gonzalez 2005). Other results have shown that the nature of shifts in equitability in marine macrophytes can depend on whether the system is open or isolated (Nielsen 2003). As Magurran (2007) noted though, the empirical study of temporal dynamics in relative abundance warrants substantially greater attention.

The dynamics of an abyssal megafauna community were examined here within the context of niche and neutral theories of community structuring. Overall, the abyssal environment at the study site in the NE Pacific (Station M; 4100 m depth; 34°50' N, 123°00' W) has been relatively stable, with no sunlight, temperatures around 1.5°C, and relatively consistent prevailing currents and dissolved O₂ when compared to shallower marine habitats (Beaulieu and Baldwin 1998). The food supply, however, is now known to vary over seasonal and interannual scales (Baldwin et al. 1998, Smith et al. 2006), but there is no major feedback mechanism for abyssal consumers to affect surface productivity within the timescales examined here. The habitat at the scale of the mobile megabenthos at the abyssal site can thus be seen as less variable in environmental and resource parameters when compared to more dynamic sea surface habitats.

Studies at Station M have found climatically influenced seasonal and interannual variations in surface water productivity and subsequent sinking of particulate organic carbon (POC) food supply to the seafloor from 1989 to 2004 (Baldwin et al. 1998, Smith et al. 2006). Links from surface climate to POC flux and POC flux to

mobile epibenthic megafaunal abundances of several species have previously been made at the site (Ruhl and Smith 2004). On a species-specific basis, several holothuroids such as *Elpidia minutissima* had significant negative correlations with POC flux, and others such as *Abyssocucumis abyssorum* had positive correlations. Importantly, some taxa appeared to increase in abundance during higher food supply conditions, while others increase during lower food fluxes, suggesting that the utilization of the resource was not equal. Similar processes involving climate, pelagic–benthic coupling of food resources, and subsequent changes in abyssal benthic communities have been observed in the north-east Atlantic Ocean as well (Billett et al. 2001, Gooday 2002, Wigham et al. 2003a).

Greater than 99% of the mobile epibenthic megafauna observed during the 16-year period were from 10 echinoderm taxa: the holothuroids *E. minutissima*, *Peniagone diaphana*, *P. vitrea*, *A. abyssorum*, *Synallactes profundus*, *Scotoplanes globosa*, *Oneirophanta mutabilis*, and *Psychropotes longicauda*; the echinoid *Echinocrepis rostrata*; and the ophiuroids dominated by *Ophiura bathybia*. Deposit-feeding echinoderm megafauna like those here have been shown to selectively feed on fresh phytopigments (Billett et al. 1988, Lauerma et al. 1997, Ginger et al. 2001, Iken et al. 2001, Demopoulos et al. 2003) and to partition and differentially utilize the food source in terms of their organic contents (Hudson et al. 2003, Wigham et al. 2003a, b). Specific organic compounds have also been related to reproductive processes in deep-sea holothuroids (Hudson et al. 2003, Wigham et al. 2003b).

This study examined variations in the species composition, RADs, Pielou's evenness, and interspecific body size vs. abundance relationships of the top 10 most dominant mobile epibenthic megafauna at Station M from 1989 to 2004, a period of significant community change and food supply variability. Addressed here is the extent to which the community descriptors varied over the study period and whether the variations were essentially random or linked to the dominant resource variable, POC flux.

METHODS

The in situ setting, Station M, lies beneath the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and the California Current Ecosystem Long-term Ecological Research (CCE LTER) principal study areas, and is subject to seasonal and interannual scale variations in POC flux (Baldwin et al. 1998, Smith et al. 2006). These changes in flux are influenced, in part, by climatic shifts expressed in the Northern Oscillation Index (NOI; Schwing et al. 2002) and Bakun upwelling index (BUI; Bakun 1973).

Abundance and body size estimates for the study were collected using a camera sled system to conduct line transect photography (Lauerma et al. 1996, Ruhl and Smith 2004, Ruhl 2007). An otter trawl system was towed

behind the sled to collect photographed specimens for identification. Over the 16-year study, 52 transects averaging 1.2 km in length were conducted during 37 monthly time intervals on a roughly seasonal basis. A transect length weighted-abundance estimate was created if more than one transect was conducted during any particular month. Uneven temporal sampling and significant gaps in the time series exist due to logistical constraints. Further details on line transect data collection and analysis methods used here can be found in Wakefield and Genin (1987), Wakefield and Smithey (1989), Buckland et al. (1993), Laake et al. (1994), Lauerman et al. (1996), Ruhl and Smith (2004), and Ruhl (2007).

The monthly POC flux data used for this analysis were a composite of particle flux trap data collected at 50 m and 600 m above bottom (mab) at the site, as well as model estimated flux where trap data were unavailable. The POC flux data were collected using a sedimentation trap with a 0.25-m² opening with a 10-day sampling interval (Baldwin et al. 1998, Smith et al. 2006). The primary data for the composite were the 50-mab trap data. Where available, 600-mab trap data were used to fill in any gaps in the 50-mab POC flux data. An empirical model for estimating POC flux to 50 mab at the site was recently proposed that incorporates lagged influences from satellite-estimated sea surface temperature and net primary production (sensu Laws 2004), sea level air pressure anomalies (NOI), and regional upwelling (BUI) (Smith et al. 2006). The model-estimated flux could account for >50% of the observed variation in the monthly estimates (see Supplement). The model thus effectively differentiated between high and low flux periods. Any remaining gaps in the POC flux record were filled in using the model estimates. The resulting composite represents the best information available on the monthly POC flux to the study site, and use of the composite here avoided the complexities of cross-correlating two data sets with multiple gaps.

Rank abundance distributions (RADs) were created for each sampling time by ranking the abundances of the 10 most dominant taxa in descending order, with rank one being most abundant. Species composition is characterized here using species-specific densities. The Bray-Curtis similarity index was used to create similarity matrices for the RADs and species composition data with a $\log(x+1)$ transformation. These matrices then served as input for the similarity vs. time lag scatter plots (Fig. 1A, B), hierarchical similarity dendrograms using group average clustering (Fig. 1C, D), and nonmetric multidimensional scaling (MDS) x -ordinations (Fig. 2A–C).

An analysis of similarity (ANOSIM), with 999 permutations, was used to determine if deviations in either POC food supply or climate were related to either the RAD or species composition similarities. ANOSIM is a randomization test for differences between groups separated by specified factors and is similar to an analysis of variance (ANOVA). These nonparametric, multivar-

iate analyses were conducted using the PRIMER-5 software package (PRIMER-E, Lutton, Devon, UK).

Additionally, a Mantel randomization test was used to evaluate the significance of the RAD and species composition similarity shifts over time (Fig. 1A, B), since there are many more pairwise comparisons between sampling times than actual sample times. Cross-correlations between the RAD and species composition similarity MDS x -ordinates, evenness, and the POC flux composite were conducted using the nonparametric Spearman rank correlation. All correlations were conducted using monthly data with POC flux changes preceding megafauna sample shifts.

RESULTS

Directional changes in both the rank abundance distribution (RAD) and species composition were evident from 1989 to 2004, with samples taken at closer time intervals being more similar than samples taken with longer temporal lags between them ($P < 0.001$, Fig. 1A, B). A partial convergence, or a return direction to starting similarity, might have even begun in the longer lags of species composition similarity (Fig. 1B, Supplement). The significantly lower slope of the RAD plot, when compared to species composition, was at least partially due to the fact that some variability is lost when ranking the species abundance data. Further analysis was able to illustrate the degree to which the RADs had shifted.

Similarity dendrograms for the RAD and species composition illustrate that while similar RAD distributions were found at a variety of times, the species composition dendrogram had temporally oriented similarity clusters, including 1989–1998 and 2001–2004 (Fig. 1C, D). Other notable species composition clusters included observations from 1989 to August 1994 and September 1994 to 1998, but the two groups were not temporally exclusive, since June 1992 clusters into the otherwise September 1994–1998 group (Fig. 1D, Supplement). Also of note is that the principal change in species composition after the 1997–1999 El Niño/La Niña discussed in Ruhl and Smith (2004) has persisted through 2004.

Time series plots of the RAD and species composition similarity, as well as evenness over time illustrate changes that occurred over months to years, and each community descriptor had time-lagged links to particulate organic carbon (POC) flux (Fig. 2A–D). Significant correlations with the POC food supply existed, with peaks at 10–12 months for the RAD (Spearman rank correlation [r_s] = 0.38, $P < 0.05$), 12 months for evenness ($r_s = 0.33$, $P = 0.05$), and 10–13 months for species composition ($r_s = 0.48$, $P < 0.01$). A temporal lag of many months is sensible considering that while the community can respond with rapid changes in activity (Kaufmann and Smith 1997, Bett et al. 2001), it appears to take several months or more for a shift in resources to lead to observable changes in abundance resulting from

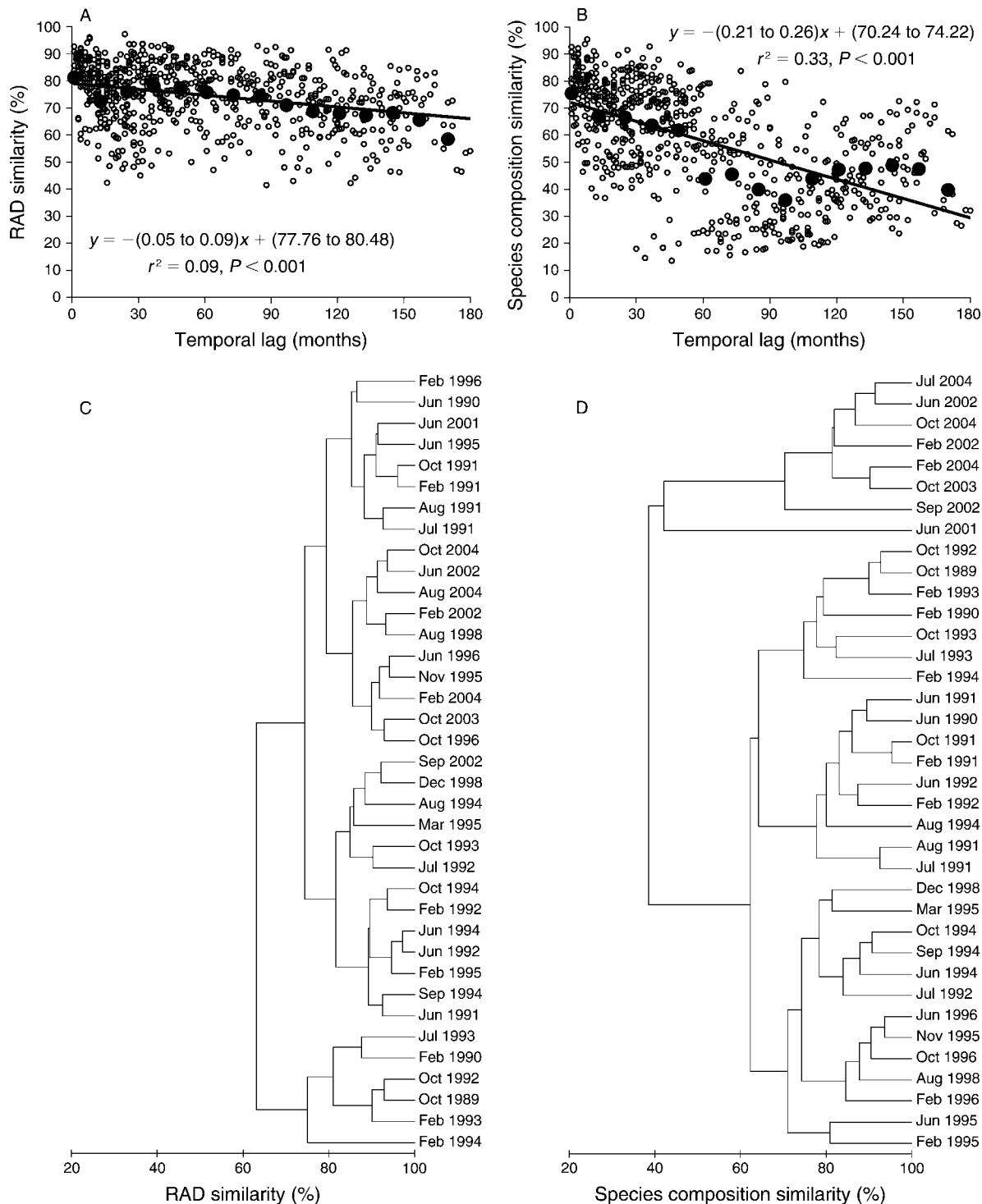


FIG. 1. Scatter plots (small open circles) of Bray-Curtis similarity for (A) all possible rank abundance distribution (RAD) pairs from 1989 to 2004 and (B) all possible monthly species composition pairs vs. the time (in months) between the compared samples. Also plotted on (A) and (B) (solid lines) are the best linear fits of the monthly data, with 95% confidence intervals in parentheses and randomization test *P* values. Discrete 12-month averages of similarity are also presented using large black circles. The reduced variation and slope in (A) relative to (B) are to some extent the result of ordering the compositional data by rank instead of taxon. Also shown are Bray-Curtis similarity dendrograms of (C) monthly RADs and (D) monthly species composition. All are based on monthly abundance estimates of the 10 most dominant epibenthic megafauna taxa observed from 1989 to 2004.

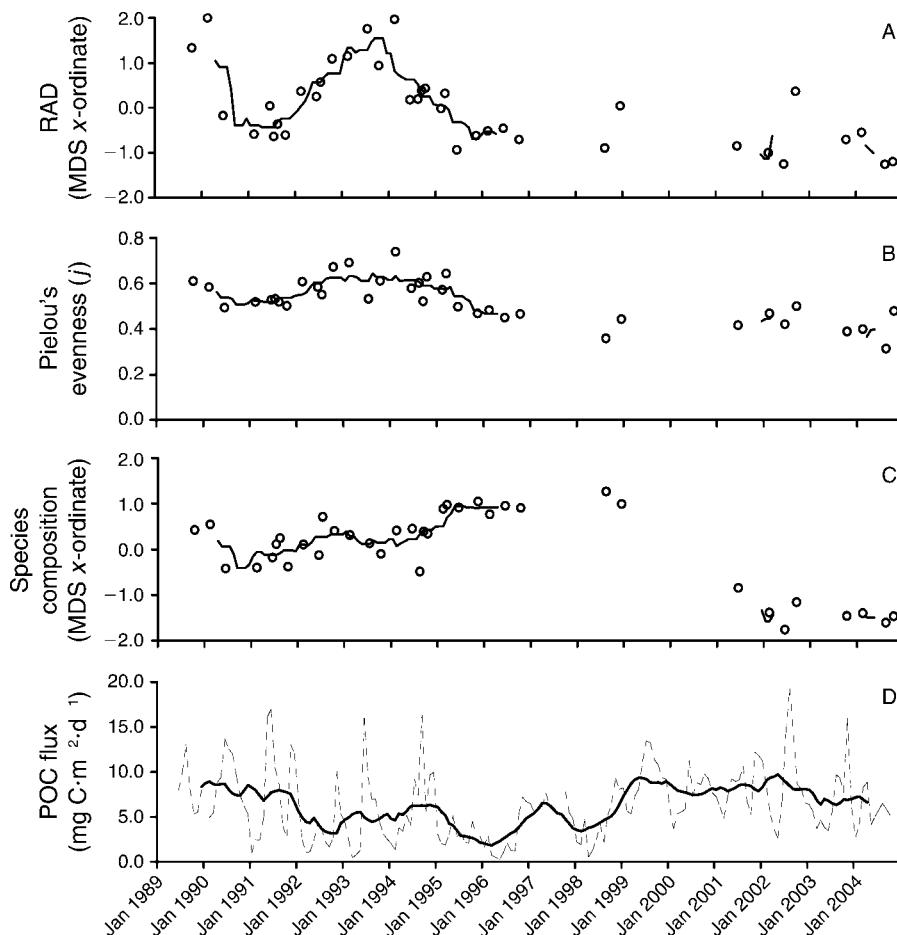


FIG. 2. Time series plots showing (A) the Bray-Curtis rank abundance distribution (RAD) relative similarity over time as measured by the multidimensional scaling (MDS) x -ordinate, as well as (B) Pielou's evenness, (C) species composition relative similarity MDS x -ordinate, and (D) particulate organic carbon (POC) flux ($\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) composite. The monthly data are plotted as open circles for the community descriptors and a dashed line for POC flux. All have a 13-month running mean shown as a solid black line. All correlations were conducted using monthly data. The 13-month centered running means are for display purposes only.

processes such as reproduction, recruitment, biotic interactions, and mortality (Ruhl and Smith 2004). The RADs and evenness exhibited significant covariation ($r_s = 0.82$, $P < 0.001$). Although both the RAD similarity and evenness were correlated to species composition during certain periods, the correlation was insignificant for the whole time series, providing evidence that equitability may have had some independence from species composition. The ANOSIM test results supported the cross-correlations and showed that the RAD and species composition distributions were significantly different ($P < 0.05$) during times when the annual POC flux was above and below the long-term average and when the Northern Oscillation Index (NOI) condition was above and below zero.

The monthly RADs throughout the time series from 1989 to 2004 had an approximately geometric distribution (Fig. 3A), with each rank switching between one and six times and the middle ranks experiencing the

most variability. When the monthly RADs were grouped by the principal communities outlined in Fig. 1D, they all had similar slopes (Fig. 3B–E). Even with observed directional changes that were linked with evenness and resource availability, the relative abundances in each lower-density rank were typically less abundant by roughly one-half. The continuity in RAD shape for the different species compositions suggests that shifts in RADs were limited. It is tempting here to try to discern what RAD model best fits the observations, be it geometric (Motomura 1932), sequential breakage (Sugihara 1980), or another. The implications here, however, do not rely on any particular distribution. There are often subtle differences between such distributions and subsequent models, especially for a small assemblage (Sugihara 1980, Tokeshi 1999).

Interspecific body size vs. abundance also had significantly ($P < 0.05$) consistent negative correlation slopes between the entire study period and the principal

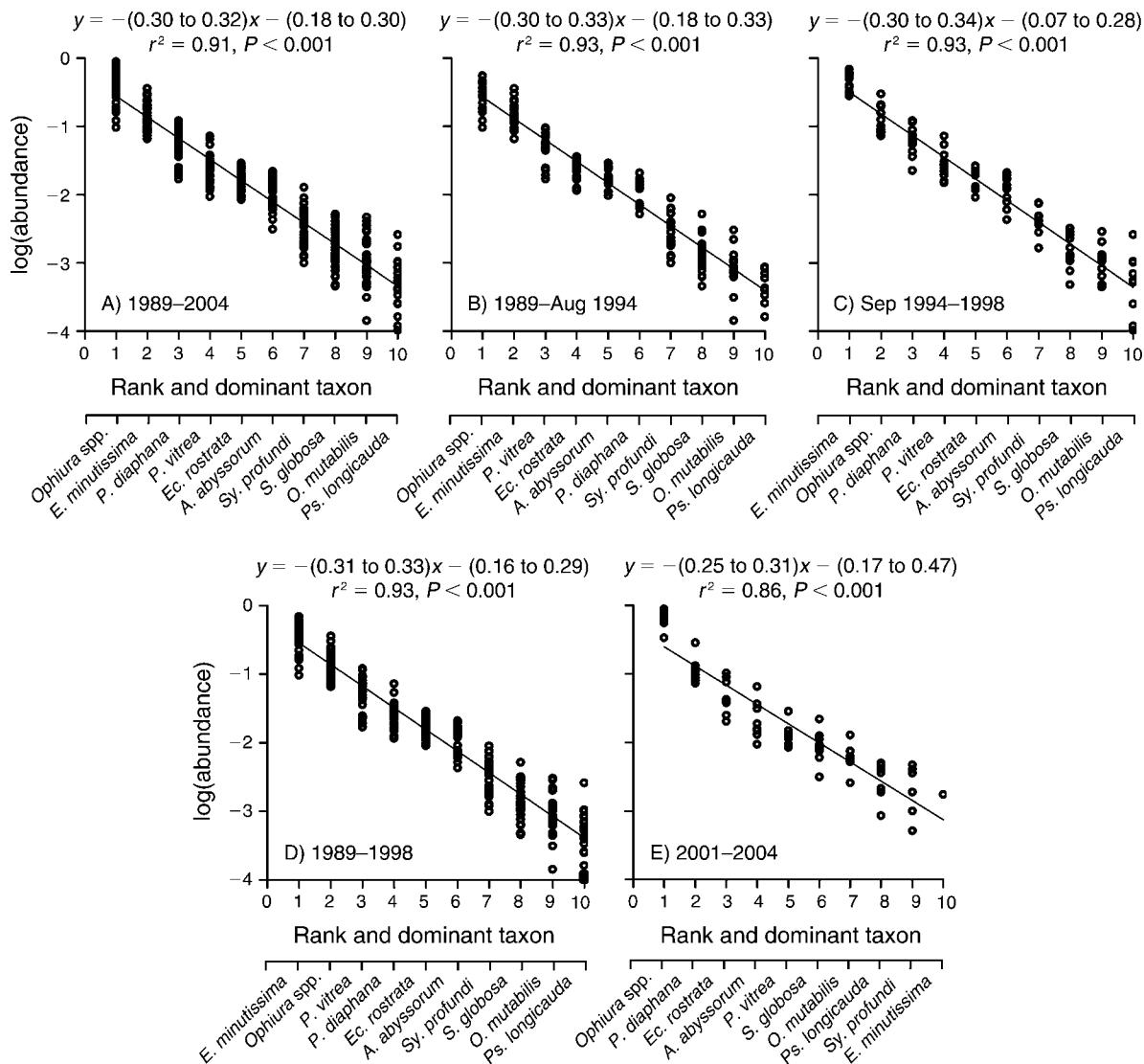


FIG. 3. The five panels show ranked monthly log-transformed abundances (originally measured as individuals/m²) for (A) 1989–2004, (B) 1989–August 1994, (C) September 1994–1998, (D) 1989–1998, and (E) 2001–2004. Below each abundance rank (1–10) is the taxon that dominated that rank during each principal species composition time. Above each panel are the 95% confidence intervals for the slope and intercept of the linear descriptions, as well as the r^2 and P value. Each point represents a species-specific monthly estimate for all size classes. It is important to note that the values are ranked, and thus significant correlations are not remarkable in each separate panel. The most relevant aspect of the statistics is the similarity of the linear descriptions among the panels. Species are *Ophiura* spp., *Elpidia minutissima*, *Peniagone diaphana*, *Peniagone vitrea*, *Echinocrepis rostrata*, *Abyssocucumis abyssorum*, *Synallactes profundus*, *Scotoplanes globosa*, *Oneirophanta mutabilis*, and *Psychropotes longicauda*.

temporal clusters (Fig. 4A–E). The abundances of several taxa changed by one or more orders of magnitude between the different temporal groupings, but the slopes were similar for each of the periods with different species compositions (Fig. 4A–E).

DISCUSSION

Niche theory envisions that the abundance of a species is a result of the availability of a multidimensional mix of resources, such as energy and space (e.g., Hutchinson 1957, Chase and Leibold 2003). Differential

responses to resource variability are thought to be one way competitive exclusion can be prevented. The broken-stick analogy (MacArthur 1957) and its modifications have led to a niche hierarchy model in which the total resource, or stick, is sequentially broken, with the length of each piece representing the relative abundance of each species utilizing the common resource. Furthermore, the overall equitability in the size of the pieces, and thus relative abundances, has been linked to resource type, with more evenness being representative of a more even utilization of a high-

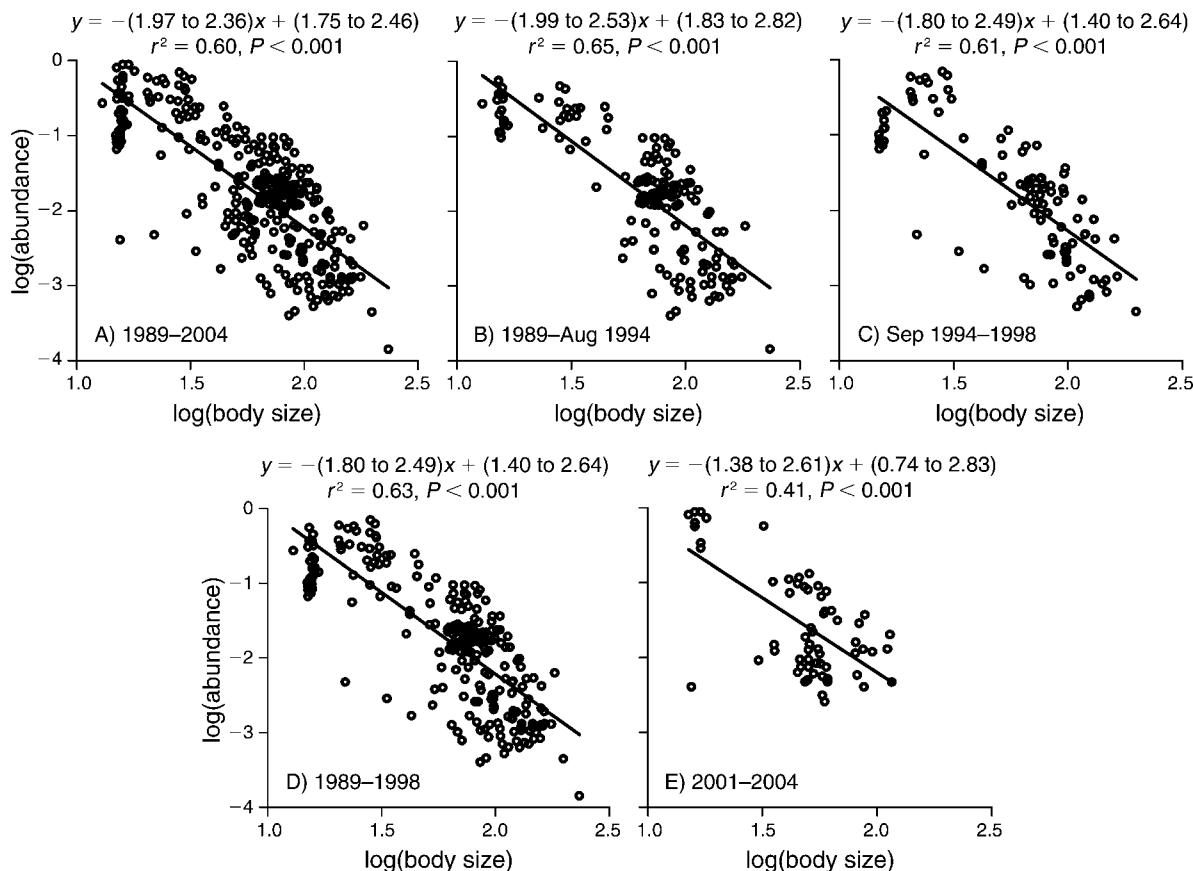


FIG. 4. The five panels show monthly log-transformed abundance (individuals/m²) vs. mean body size (length in mm) for all 10 taxa for (A) 1989–2004, (B) 1989–August 1994, (C) September 1994–1998, (D) 1989–1998, and (E) 2001–2004. Above each panel are the 95% confidence intervals for the slope and intercept of the linear descriptions, as well as the r^2 and P value. Each point represents a species-specific monthly estimate for all size classes. The most relevant aspect of the statistics is the similarity of the linear descriptions among the panels.

dimension resource and less equitable with a more basic, low-dimension resource (Sugihara et al. 2003). Neutral theory, conversely, can produce some pervasive patterns in ecology, such as species–area and rank–abundance distributions, with no requirements for the differential utilization of resources (Hubbell 2001).

At Station M there is now compelling evidence for seasonal and interannual variation in food supply resulting in interannual resource disequilibria (Smith and Kaufmann 1999, Smith et al. 2006). Predictions of niche theory were reevaluated here within the context of the fluctuating resource environment of the northeast (NE) Pacific abyssal seafloor. If each taxon had an equivalent per capita response to a variable resource, then any measured shift in rank abundance distributions (RADs), evenness, and species composition would be due to random ecological drift, and links between food supply and the relative community descriptors should be insignificant, regardless of any overall change in abundance or biomass. Alternatively, if each taxon exhibited a unique response to a sufficiently low-dimension resource, then nonrandom links between community shifts and food supply could be detectable,

and potentially include rank switching and local extinctions and recolonizations (Brown et al. 2001).

Shifts in the RADs, evenness, and species composition were significantly linked to the particulate organic carbon (POC) food supply at Station M, suggesting at least a partially deterministic role for life history processes in community dynamics at the site. Several taxa appeared to have opposing responses to long-term food supplies (Ruhl and Smith 2004), and resource utilization trade-offs have been demonstrated for several congeneric taxa (Hudson et al. 2003, Neto et al. 2006). Links between the RADs and evenness also indicated that more eutrophic conditions led to more asymmetric RADs and lower evenness, which is expected under niche hierarchy (Sugihara et al. 2003). Changes in surface conditions above Station M (e.g., Kahru and Mitchell 2002, Lavaniegos and Ohman 2003) inextricably lead to variation in the composition of POC flux material. If hierarchical partitioning of resources is occurring at Station M, such resource division would expectedly include the species-level preferences for specific pigments, and lipids observed in congeneric

taxa in the NE Atlantic (Hudson et al. 2003, Wigham et al. 2003a, b).

The degree to which a population can track a dominant forcing variable has been suggested to depend on whether the timescales of the dominant forcing and organism generation time are similar (Hsieh and Ohman 2006). The apparent interannual scale of the variation in the taxon-specific densities and community changes here suggest that generation times are roughly interannual as well. Increases in megafauna abundance at Station M were significantly correlated with increases in smaller size classes, indicating that reproduction and/or recruitment influenced local increases in abundance (Ruhl 2007). Decreases in density, on the other hand, likely resulted from inferior biotic interactions, decreased fitness, and mortality. Even though *Peniagone* spp. are known to exhibit swimming behavior, the mass migration of adult stages over thousands of meters is not reasonable for most taxa in the study (Ruhl 2007).

A long-term study of desert rodents also found directional shifts in RADs similar to that illustrated in Fig. 1A without major changes in species richness (Thibault et al. 2004). In both the rodent and abyssal megafaunal analyses, the RADs have shifted within the context of resource change. When the Station M RADs are examined for the principal species composition clusters, however, there is no persuasive evidence for fundamental changes between the slopes of the ranked abundances. This limit to variation is sensible within the context of a hierarchical system that allows for shifts in relative abundance and equitability related to changes in resource dimensions.

The relationships between body size and abundance were also relatively stable for the different community compositions, providing additional context for the limits of the community-level shifts at the site. Larger holothuroids, such as *P. longicauda* and *O. mutabilis*, varied in abundance by an order of magnitude but did not become more abundant than the smaller *Peniagone* spp. Smaller animals have been seen to be more abundant, in part because they require less resource per unit area (West et al. 1997), and body size has been linked to energy use and community structure (Ernest 2005). Southwood et al. (2006) recently illustrated how body size vs. abundance, body size vs. area, and species-area relationships are all interrelated in vertebrates, suggesting that a formal niche space exists. Further research could also unite such relationships in invertebrate groups. The importance of internal resource distribution and other mechanisms regulating body size and abundance relationships continues to be debated (Brown et al. 2005), but the results here are indicative of some stability in such a relationship, even with significant species composition and resource change. The limits to the changes observed in this study were probably a reflection of the limits of ecological plasticity in processes such as resource utilization, dispersal, and recruitment.

Results from megafauna at Station M indicate that both individual populations and community descriptors like the RADs and evenness were linked to resource availability. The overall relative megafauna abundances found at Station M were similar to distributions expected when a single or few factors, such as POC flux quantity and quality, control community structure (Figs. 3, 4). The asymmetric shape of the RADs and their link to POC flux provide further evidence that food supply from overlying surface waters is a key variable in the deep sea. Fluctuations in abyssal abundances have now been observed in smaller protist and metazoan taxa (Drzen et al. 1998, Gooday 2002) and invertebrate megafauna (Billett et al. 2001, Ruhl and Smith 2004), as well as in higher trophic-level fishes (Bailey et al. 2006). Multiyear disparities between food supply and demand for smaller sediment-based organisms (Smith and Kaufmann 1999) suggest that imbalances are forcing community processes at other guilds and trophic levels at the site. Benthic fauna mediate carbon cycle dynamics through the bioturbation of surface sediments (Reimers et al. 1992, Kaufmann and Smith 1997, Bett et al. 2001, Solan et al. 2004). Community changes like the one described here could be influencing the proportion of sinking POC that remains in the contemporary carbon cycle or is geologically sequestered.

The results here support theories that include disequilibria in modulating community diversity and relative abundance (Connell 1978, Levins 1979, Grassle 1989, Chesson and Huntly 1997, Chesson 2000, Chesson et al. 2004). Climate variations such as the El Niño Southern Oscillation and the North Atlantic Oscillation have cycles that direct systems away from equilibrium over interannual scales for much of the world biome. Interannual scale variations occur within the context of decadal and greater scale fluctuations, and treatment of climate oscillations as discrete historical events belies their pervasive and ever-present ecological effects. Testing of community structuring theories within a temporal as well as spatial context should continue to highlight the salient aspects of current structuring theories.

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APPENDIX

Supplemental methods (*Ecological Archives* E089-059-A1).