UNIVERSITY OF CALIFORNIA, SAN DIEGO

Climate and Food Supply Influences on Mobile Epibenthic Megafauna Populations in the Abyssal NE Pacific from 1989 to 2004

A dissertation submitted in partial satisfaction of the
requirements for the degree of Doctor of Philosophy

in

Marine Biology

by

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The dissertation of Henry A. Ruhl is approved, and it is acceptable in quality and form for publication on microfilm:

Lisa A. Levin

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For my family, friends, and dearest love
&
For all those who have nurtured, supported, and inspired

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JOURNAL PUBLICATIONS

Bailey, D., **H. A. Ruhl**, and K. L. Smith, Jr. 2006. Long-Term Changes in Benthopelagic Fish Abundance in the Abyssal N.E. Pacific Ocean. Ecology 87: 549-555.

Beaulieu, S. E., K. L. Smith Jr., **H. A. Ruhl**, and R. J. Baldwin. in preparation. Megafauna at the abyssal seafloor underlying the North Pacific Subtropical Gyre: composition and abundance from photographic and video surveys. Deep-Sea Research I.

Cranmer, T. L., **H. A. Ruhl**, R. J. Baldwin, and R. S. Kaufmann. 2003. Spatial and Temporal Variation in the Abundance, Distribution and Population Structure of Epibenthic Megafauna in Port Foster, Deception Island. Deep-Sea Research II 50: 1821-1842.

Kendall, K. A., **H. A. Ruhl**, and R. C. Wilson. 2003. Distribution and Abundance of Marine Bird and Pinniped Populations Within Port Foster, Deception Island, Antarctica. Deep-Sea Research II 50: 1873-1888.

Ruhl, H. A., P. A. Hastings, L. A. Zarubick, R. M. Jensen, and K. Zdzitowiecki. 2003. Fish Populations of Port Foster, Deception Island, Antarctica and Vicinity. Deep-Sea Research II 50: 1843-1858.

Ruhl, H. A. and K. L. Smith Jr. 2004. Shifts in Deep-Sea Community Structure Linked to Climate and Food Supply. Science 305: 513-515.

Smith, Jr. K. L., R. J. Baldwin, R. C. Glatts, T. K. Chereskin, **H. A. Ruhl**, and V. Lagun. 2003. Weather, Ice, and Snow Conditions at Deception Island, Antarctica: Long Time-Series Photographic Monitoring. Deep-Sea Research II 50: 1649-1664.

Smith, Jr., K. L., R. J. Baldwin, **H. A. Ruhl**, M. Kahru, B. G. Mitchell, and R.S. Kaufmann. 2006. Climate effect on food supply to depths greater than 4000 m in the northeast Pacific. Limnology and Oceanography 51: 166-176.

Smith, Jr., K. L., Holland, N. D., **H. A. Ruhl**. 2005. Enteropneust Production of Spiral Fecal Trails on the Deep-Sea Floor Observed with Time-Lapse Photography. Deep-Sea Research I 52: 1228-1240.

Rybicki, N. B., D. McFarland, **H. A. Ruhl**, J. T. Reel, and J. W. Barko. 2001. Investigations of the Availability and Survivability of Submersed Aquatic Vegetation Propagules in the Tidal Potomac River, 1994–95. Estuaries 24: 407-424.

OTHER PUBLICATIONS

Carter, V., J. T. Reel, N. B. Rybicki, **H. A. Ruhl**, P. T. Gammon, and J. K. Lee. 1999. Vegetative Resistance to Flow in South Florida: A Summary of Vegetation Sampling at Sites NESRS3 and P33, Shark River Slough, November, 1996. US Geological Survey Open File Report-99-218, 73p.

Carter, V., **H. A. Ruhl**, N. B. Rybicki, J. T. Reel, and P. T. Gammon. 1999. Vegetative Resistance to Flow in South Florida: A Summary of Vegetation Sampling at Sites NESRS3 and P33, Shark River Slough, April, 1996. US Geological Survey Open File Report-99-187, 73p.

Carter, V., N. B. Rybicki, J. T. Reel, **H. A. Ruhl**, and J. K. Lee. 1999. Vegetative characterization for Everglades studies. U.S. Geological Survey Open-File Report 99-181, p. I0-II.

Carter, V., N. B. Rybicki, J. M. Landwehr, J. T. Reel, and **H. A. Ruhl**. 1998. Correlations Among Seasonal Water Quality, Discharge, Weather, and Coverage by Submersed Aquatic Vegetation in the Tidal Potomac River and Estuary, 1983-96. US Geological Survey Open File Report-99-657, 81p.

Interstate Commission on the Potomac River Basin (ICPRP). 1999. Tidal Potomac Integrative Project, ICPRB Report 99-4.

Ruhl, H. A., N. B. Rybicki, J. T. Reel, and V. Carter. 1999. Submersed Aquatic Vegetation and Hydrilla verticillata Distribution and Abundance for the Tidal Potomac River, Maryland, Virginia, and The District of Columbia, 1993-1998. US Geological Survey Open File Report-99-233, 37p.

Ruhl, H. A., N. B. Rybicki, V. Carter, and J. T. Reel. 1998. Epiphyte Growth, Water Quality, and Submersed Aquatic Plants in the Tidal Potomac River and Estuary. Poster Session, in: Ecological Society of America 1998 Annual Meeting Abstracts, p.211.

Ruhl, H. A., N. B. Rybicki, and J. T. Reel. 1997. Light Effects on Tuber Production. Poster Session, in: Bulletin of the Ecological Society of America Vol. 78 (4), p.305.

Ruhl, H. A., N. B. Rybicki, and J. T. Reel. 1997. The Effects of Light on Tuber Production of *Hydrilla verticillata* and *Vallisneria americana*. Poster Session, in: Fourteenth Biennial Estuarine Research Federation International Conference Abstracts, p.159.

Ruhl, H. A., and R. W. Schaffranek. 1999. The Southern Inland and Coastal System Project of the USGS South Florida Ecosystem Program. USGS Bulletin.

Schaffranek R. W., **H. A. Ruhl**, and M. E. Hansler. 1999. An Overview of the Southern Inland and Coastal System Project of the US Geological Survey South Florida Ecosystem Program, in: The Proceedings of the Third International Ecohydraulics Symposium, (http://sofia.usgs.gov/publications/papers/overview_sics/).

Rybicki, N. B., J. T. Reel, **H. A. Ruhl**, P. T. Gammon, V. Carter, and J. K. Lee. 1999. Biomass and Vegetative Characteristics of Sawgrass Grown in a Tilting Flume as Part of a Study of Vegetative Resistance to Flow. US Geological Survey Open File Report-99-230, 29p.

Rybicki, N. B., **H. A. Ruhl**, J. T. Reel and V. Carter. 1999. A Survey of Potential Dredge Disposal Sites for the Tidal Potomac River Between Washington, D.C. and the Route 301 Bridge. US Geological Survey Open File Report-99-234, 12p.

Rybicki, N. B., J. T. Reel, **H. A.**, **Ruhl,** P. T. Gammon, and V. Carter. 2001. Vegetative Resistance to Flow in South Florida: Summary of Vegetation Sampling in Taylor Sough, Everglades National Park, September 1997-July 1998. US Geological Survey Open File Report-01-102, 117p.

Rybicki, N. B., J. T. Reel, **H. A. Ruhl**, P. T. Gammon, V. Carter, and J. K. Lee. 2000. Sawgrass Density, Biomass, and Leaf Area Index: A Flume Study in Support of Research on Wind Sheltering Effects in the Florida Everglades. US Geological Survey Open File Report-00-172, 48p.

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ABSTRACT OF THE DISSERTATION

Climate and Food Supply Influences on Mobile Epibenthic Megafauna Populations in the Abyssal NE Pacific from 1989 to 2004

By

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Doctor of Philosophy in Marine Biology

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The effects of climate on abyssal megafaunal populations are largely unknown. Photo-transecting techniques have been used at a long-term abyssal study site in the NE Pacific to examine the population dynamics of mobile echinoderms on a roughly seasonal basis from 1989-2004. At 4,100 m depth, these animals live in a relatively stable environment with no light and relatively invariant temperatures. The primary habitat variables at the site are the quantity and quality of the particulate organic carbon (POC) that sinks from the surface waters above. Significant time-lagged correlations indicate that climatic variations related to the El Niño Southern Oscillation can influence surface ocean productivity and the amount of POC that is exported to the abyssal benthos.

All of the ten most dominant fauna at the site had order of magnitude or greater fluctuations in abundance with the most prominent differences occurring between 1989-1998 and 2001-2004. Increases in abundance were often linked to increases in smaller individuals suggesting that population fluctuations were the result of recruitment, biological interactions, and mortality. Significant correlations also exist between changes in the POC food supply and the abundance of several mobile megafauna with measurable changes in abundance lagging changes in food supply by 6 or more months. Some species, such as the holothuroid *Elpidia minutissima*, increased in abundance during periods of low food supply while other echinoderms thrived during periods of higher food flux.

One assumption of the line-transect methodology used here is that non-random aggregations are not present at scales or patterns that might bias density estimates. To help verify this assumption a three-term local quadrat variance technique was employed and found few aggregations that might bias the abundance estimates presented.

A significant shift in megafauna community structure occurred between the 1989-1998 and 2001-2004 periods. An analysis of the rank abundance distributions of megafauna indicated that the overall species dominance changed between the two periods. This shift in equitability was also linked to the POC flux further indicating that these animals have differential responses to the food supply. This and other long-term research have indicated that interannual-scale climatic fluctuations could be influencing abyssal populations thousands of meters beneath the ocean surface.

I

General Introduction

Beginning with the realization in the 1960's that deep-sea communities were highly diverse (e.g. Hessler and Sanders, 1967), research began to examine deep-sea life and how such diversity could be supported (e.g. Sanders, 1968, Dayton and Hessler, 1973, Abele and Walters, 1979). Since then, several temporal and spatial trends in diversity have been described providing insights into not only diversity but community structure as well. Most species are rare and potentially millions of species remain undescribed in the deep ocean (Grassle and Maciolek, 1992). Animals that occupy abyssal depths are also generally smaller than in other habitats, with an overall reduction in the physical scale of habitat heterogeneity (Snider et al., 1984; Etter and Grassle, 1992). There are now many descriptions of diversity gradients with depth, latitude, and environmental parameters (e.g. Rex et al., 1993, 2000, 2005, Flach and de Bruin, 1999, Levin et al., 2001, Stuart et al., 2003, Blankenship et al., 2006), as well as shifts in diversity over glacial time scales related to changing surface temperature (Cronin and Raymo, 1997, Cronin et al., 1999) and thermohaline circulation (Behl and Kennett, 1996).

Indications that the deep ocean may experience seasonality first appeared in 1980. Measurements from particle flux traps moored to the seafloor measured seasonal peaks in sinking particulate organic carbon (POC) that were in synchrony to both surface production and the abundance of foraminifera on the seafloor (Deuser and Ross, 1980, Deuser et al., 1981). Other studies soon found that seasonal pulses of particulate rain were occurring at several stations in the NE Atlantic (Billet, et al, 1983, Graf, 1982, Asper et al., 1992) and there were indications that in addition to foraminifera, ophiuroid echinoderms may also be responding to the pulsed food supply with seasonal reproduction (Tyler et al., 1982).

Examples of contemporary interannual studies of deep-sea communities include research in the Mediterranean (Danovaro et al., 2001, 2004), Nordic shelf (Tunberg and Nelson, 1998), and the North Atlantic (Billett and Rice, 2001). Throughout these studies, pelagic-benthic coupling has been integral in explaining the observations (Gooday, 2002). The abundances of megafauna have been most difficult to quantify (Lauerman et al., 1996), but interannual variation of megafauna abundances has been shown using trawl data from the abyssal NE Atlantic (Billett et al., 2001). Several studies have also shown that echinoderm megafauna select certain food sources differentially (Lauerman et al., 1997, Billett et al., 1988, Iken et al., 2001, Ginger et al., 2001, Demopoulos et al., 2003). It is now widely believed that deep-sea diversity is maintained by a mosaic of physical disturbances and variations in the sinking food supply (Grassle, 1989). This belief is similar to other marine and terrestrial theories that incorporate temporal variation in resources and the environment (Connell, 1978, Chesson and Huntly, 1997, Chesson, 2000).

In 1989 a deep-sea study site (Station M, 4100 m depth, 34°50’N, 123°00’W) was established approximately 220 km west of Pt. Conception California. This site was chosen partly because it is located beneath the seasonally productive waters of the California Current. Seasonal pulses of phytodetrius and other forms of organic matter were observed to begin in June or July and last until as late as December (Smith et al., 1994). Subsequent POC flux measurements found that this variation can also be interannually variable with the low in one year being higher then the high of another year (Baldwin et al., 1998). Examination of the biological response to the variable food supply at Sta. M has revealed seasonality in sediment community oxygen consumption (Smith and Kaufmann, 1999, Smith et al., 2001), sediment infauna abundance (Drazen, et al., 1998), and megafaunal behavior (Kaufmann and Smith, 1997).

A camera sled system (Wakefield and Smithey, 1989, Wakefield and Genin, 1987) has been the primary method for estimating the abundance and distribution of megafauna at Sta. M. An initial examination of photographic transects at Sta. M by Lauerman et al. (1996) from June 1990 to October 1991 found that echinoderms dominated the mobile epibenthic megafauna at the site, but could not detect a seasonal signal in abundance. An examination of ophiuroid reproduction from 1989-1996 also found no indication of seasonality (Lauerman, 1998). Another analysis of megafauna data from June 1994 and June 1995 from Sta. M gave no indication of any clear trends in abundance or distribution patterns (Lauerman and Kaufmann, 1998). However, aggregations greater than 100 m in scale and links between detrital aggregates and mobile megafauna distributions were occasionally observed (Lauerman and Kaufmann, 1998). A radiotracer analysis also determined that megafauna at the site were selectively feeding on recently deposited phytodetritus (Lauerman et al., 1997).

Since 1996 the NE Pacific has undergone pervasive ecological changes related to an intense El Niño Southern Oscillation (ENSO) event (Kahru and Mitchell, 2002a, 2002b, Brinton and Townsend, 2003, Bograd and Lynn, 2003, Chavez et al., 2003, Lavaniegos and Ohman, 2003). An examination of the sinking POC food supply at Sta. M versus the food demand for small (typically <1cm in size) benthic organisms from 1989-1998 found that a long-term deficit in food supply had occurred through 1998

(Smith et al., 2001). POC flux is thought to have then returned to surplus levels in 1999 (Smith et al., 2001, Smith et al., 2006). A central question resulted from these findings: If the food supply was interannually variable, could benthic megafauna populations also vary in response to such perturbations? Chapters II-V present research that examined the population dynamics of the mobile epibenthic megafauna at Sta. M and the potential factors controlling their abundance and distribution, with a focus on POC flux.

Chapter II documented the epibenthic megafaunal abundance variations from 1989-2002 and the possible influences of food supply and climate. Were there significant changes in the abundance of the dominant mobile epibenthic megafauna from 1989-2002? Were any changes related to the quantity of POC flux or climatic indicators such as the Northern Oscillation Index (Schwing et al., 2002), Southern Oscillation Index (Trenberth and Shea, 1987), or the Multivariate ENSO Index (Wolter and Timlin, 1998)? Were all potential responses similar?

Chapter III contains further analysis of the dominant megafauna abundances through 2004 and explortion whether increases in abundance were associated with the recruitment of younger/ smaller individuals. Abundance trends and size-frequency histograms were also used to evaluate individual and population-level growth rates. Were the shifts in abundance observed from 1989 to 2002 persistent through 2004? Were any observed changes in abundance related to body size distributions? What can be inferred about the relative importance of reproduction, recruitment, growth rates, migration, and disease from the observed dynamics?

Chapter IV addressed the importance of aggregation as a potential bias in the presented abundance estimates, as well as any ecologically important trends in non-random dispersions. Were there any persistent trends in the three-term local quadrat variance through time, over certain spatial scales, or within any taxon? Were observed uniform, random, or aggregated dispersions linked to either the POC food supply or megafauna density?

Chapter V contains a community level examination of the population shifts first described in Chapter II. Was there temporal variability in rank-abundance distributions or evenness? Were there any links between community structure and the climatically driven food supply? Do the results indicate an equivalent per capita response (*sensu* Hubbell, 2001) to resource availability or are responses non-random?

References

Abele, L. G., and K. Walters. 1979. Marine benthic diversity: a critique and alternative explanation. Journal of Biogeography 6: 115-126.

Asper, V. L., W. G. Deuser, G. A. Knauer, and S. E. Lorenz. 1992. Rapid coupling of sinking particle fluxes between surface and deep ocean waters. Nature 357: 670–672.

Baldwin, R. J., R. C. Glatts, and K. L. Smith, Jr. 1998. Particulate matter fluxes into the benthic boundary layer at a long time-series station in the abyssal NE Pacific: composition and fluxes. Deep-Sea Research II. 45: 643-666.

Behl, R. J., and J. P. Kennett. 1996. Brief interstadial events in the Santa Barbara Basin, NE Pacific, during the past 60 kyr. Nature 379: 243-246.

Blankenship, L. E., A. Yayanos, D. B. Cadien, and L. A. Levin. 2006. Vertical zonation patterns of scavenging amphipods from the Hadal zone of the Tonga and Kermadec Trenches. Deep-Sea Research I 53: 48-61.

Bograd, S. J., and R. J. Lynn. 2003 Long-term variability in the Southern California Current System. Deep-Sea Research II 50: 2355-2370.

Brinton, E., and A. Townsend. 2003. Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. Deep-Sea Research II 50: 2449-2472.

Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47: 103-145.

Billett, D. S. M., R. S. Lampitt, A. L. Rice and R. F. C. Mantoura. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature 302: 520-522.

Billett, D. S. M., C. Llewellyn, and J. Watson. 1988. Are deep-sea holothurians selective feeders? Pages 421-429 *in* R. D. Burke, P. V. Mladenov, P. Lambert, R. L. Parsley, and A. Balkema, editors. Echinoderm biology. Rotterdam.

Billett, D. S. M., B. J. Bett, A. L. Rice, M. H. Thurston, J. Galeron, M. Sibuet, and G. A. Wolff. 2001. Long-term changes in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). Progress in Oceanography 50: 325-348.

Billett, D. S. M., and A. L. Rice. 2001. The BENGAL programme: introduction and overview. Progress in Oceanography 50: 13-25.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Ecology and Systematics 2000 1:343-366.

Chesson P, and N. Huntly, 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. American Naturalist 150:519–553.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199:1302-1310.

Cronin, T. M., D. M. DeMartino, G. S. Dwyer, and J. Rodriguez-Lazaro. 1999. Deep-sea ostracod species diversity: response to late Quaternary climate change. Marine Micropaleontology 37: 231-249.

Cronin, T. M., and M. E. Raymo. 1997. Orbital forcing of deep-sea benthic species diversity. Nature 385: 624-627.

Dayton, P. K., and R. R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep sea. Deep-Sea Research 19:199-208.

Deuser, W. G., and E. H. Ross. 1980. Seasonal change in the flux of organic carbon to the deep Sargasso Sea. Nature 283: 364-365.

Deuser, W. G., E. H. Ross, and R. F. Anderson. 1981. Seasonality in the supply of sediment to the deep Sargasso Sea and implications for the rapid transfer of matter to the deep ocean. Deep-Sea Research 28A: 495-505.

Danovaro, R., A. Dell'Anno, M. Fabriano, A. Pusceddu, A. Tselepides. 2001. Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study. Trends in Ecology and Evolution 16: 505-510.

Danovaro, R., A. Dell’Anno, and A. Pusceddu. 2004. Biodiversity response to climate change in a warm deep sea. Ecology Letters 7: 821-828.

Demopoulos, A. W. J., C. R. Smith, D. J. DeMaster, and W. L. Fornes. 2003. Evaluation of excess 234Th activity in sediments as an indicator of food quality for deep-sea deposit feeders. Journal of Marine Research 61:276-284.

Drazen, J. C., R. J. Baldwin, and K. L. Smith, Jr. 1998. Sediment community response to a temporally varying food supply at an abyssal station in the NE Pacific. Deep-Sea Research II 45: 893-913.

Etter, R. J., and J. F. Grassle, 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. Nature 360: 576-578.

Flach, E., and W. de Bruin. 1999. Diversity patterns in macrobenthos across a continental slope in the NE Atlantic. Journal of Sea Research 42: 303-323.

Ginger, M. L., et al. 2001. Organic matter assimilation and selective feeding by holothurians in the deep sea: some observations and comments. Progress in Oceanography 50: 407–422.

Gooday, A. J. 2002. Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. Journal of Oceanography 58: 305–332.

Graf, G. 1989. Benthic-pelagic coupling in a deep-sea benthic community. Nature 341: 437–439

Grassle, J. F. 1989. Species diversity in deep-sea communities. Trends in Ecology and Evolution 4: 12-15.

Grassle, J. F., and N. J. Maciolek. 1992. Deep-sea species richness: regional and local diversity estimates form quantitative bottom samples. American Naturalist 139: 313-341.

Hare, S.R. and N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47: 103-145.

Hessler, R. R., and H. L. Sanders. 1967. Faunal diversity in the deep-sea. Deep-Sea Research 14: 65–78.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Iken, K., T. Brey, U. Wand, J. Voigt, and P. Junghans. 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Progress in Oceanography 50, 383-405

Kaufmann, R. S., and K. L. Smith, Jr. 1997. Activity patterns of mobile epibenthic megafauna at an abyssal site in the eastern North Pacific: Results from a 17-month time-lapse photographic study. Deep-Sea Research 44: 559-579.

Kahru, M., and B. G. Mitchell. 2002a. Influence of the El Niño-La Niña cycle on satellite-derived primary production in the California Current. Geophysical Research Letters 29: 1846.

Kahru, M., and B. G. Mitchell. 2002b. Seasonal and nonseasonal variability of satellite-derived chlorophyll and colored dissolved organic matter concentration in the California Current. Journal of Geophysical Research 106: 2517–2529.

Lauerman, L. M. L. 1998. Deep-sea epibenthic echinoderms and a temporally varying food supply: results from a long time-series study in the N.E. Pacific. PhD dissertation, University of California, San Diego, USA.

Lauerman, L. M. L., and R. S. Kaufmann. 1998. Deep-sea epibenthic echinoderms and a temporally varying food supply: Results from a one year time-series in the NE Pacific. Deep-Sea Research II. 45: 817-842.

Lauerman, L. M. L., R. S. Kaufmann, and K. L. Smith, Jr. 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. Deep-Sea Research I 43: 1075-1104.

Lauerman, L. M. L., J. M. Smoak, T. J. Shaw, W. S. Moore, and K. L. Smith, Jr. 1997. ^{234}Th and ^{210}Pb evidence for rapid ingestion of settling particles by mobile epibenthic megafauna in the abyssal NE Pacific. Limnology and Oceanography 42: 589-595.

Lavaniegos, B. E., and M. D. Ohman. 2003. Long-term changes in pelagic tunicates of the California Current. Deep-Sea Research II 50: 2473-2498.

Levin, L. A., et al. 2001. Environmental influences on regional deep-sea diversity. Annual Review of Ecology and Systematic 32: 51-93.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78: 1069-1079.

Rex, M. A., C. R. McClain, N. A. Johnson, R. J. Etter, and J. A. Allen. 2005. A Source-Sink Hypothesis for Abyssal Biodiversity. American Naturalist 165: 163-178.

Rex, M. A., C. T., Stuart, G. Coyne. 2000. Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. Proceedings of the National Academy of Sciences USA 97: 4082-4085.

Rex, M. A., C. T. Stuart, R. R. Hessler, J. A. Allen, H. L. Sanders, and G. D. F. Wilson. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. Nature 365, 636-639.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. American Naturalist 102: 243–82

Schwing, F. B., T. Murphree, and P. M. Green. 2002. The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. Progress in Oceanography 53: 115-139.

Smith, K. L., Jr., R. J. Baldwin, H. A. Ruhl, M. Kahru, B. G. Mitchell, and R. S. Kaufmann. 2006. Climate effect on food supply to depths greater than 4000 m in the northeast Pacific. Limnology and Oceanography 51: 166-167.

Smith, K. L., Jr., and R. S. Kaufmann. 1999. Long-term discrepancy between food supply and demand in the deep eastern North Pacific. Science 284: 1174-1177.

Smith, K. L., Jr., R. S. Kaufmann, and R.J. Baldwin. 1994. Coupling of near-bottom pelagic and benthic processes at abyssal depths in the eastern North Pacific Ocean. Limnology and Oceanography 39: 1101-1118.

Smith, K. L., Jr., R. S. Kaufmann, R. J. Baldwin, and A. F. Carlucci. 2001. Pelagic-benthic coupling in the abyssal eastern North Pacific: An eight-year time-series study of food supply and demand. Limnology and Oceanography 46: 543-556.

Snider, L. J., B. R. Burnett, and R. R. Hessler. 1984. The composition and distribution of meiofauna in the central North Pacific deep-sea area. Deep-Sea Research 31: 1225-1249.

Stuart, C. T., M. A., Rex and R. J. Etter 2003. Large-scale spatial and temporal patterns of deep-sea benthic species diversity. Pages 295-311. *in* P. A. Tyler, editor. Ecosystems of the deep oceans. Ecosystems of the world Vol. 28. Elsevier, Amsterdam.

Trenberth, K. E., and D. J. Shea. 1987. On the evolution of the Southern Oscillation. Monthly Weather Review 115: 3078-3096.

Tunberg, B.G. and W.G. Nelson. 1998. Do climatic oscillations influence cyclical patterns of soft bottom macrobenthic communities on the Swedish west coast? Marine Ecology Progress Series 170: 85-94.

Tyler, P. A., A. Grant, S. L. Pain, and J. D. Gage. 1982. Is annual reproduction in deep-sea echinoderms a response to variability in their environment? Nature 300: 747-750.

Wakefield, W. W., and A. Genin 1987. The use of a Canadian (perspective) grid in deep-sea photography. Deep-Sea Research 34: 469-478.

Wakefield, W. W., and W. Smithey. 1989. Two camera sleds for quantitative study of deep-sea megafauna. Scripps Institution of Oceanography Ref. Ser. No. 89-14, 25 pp.

Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO - how does 1997/98 rank? Weather 53: 315-324.

II

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

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 $\geq$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 $\sim$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*, *Synallactes* 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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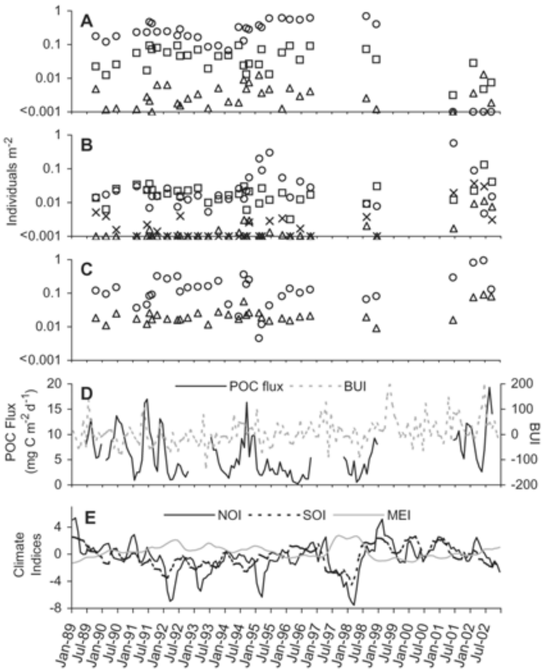

Fig. 1. (**A**) Abundance estimates for the holothuroids *E. minutissima* (circles) *P. vitrea* (squares), and *Synallactes* sp. (triangles). (**B**) Abundances of the holothuroids *P. diaphana* (circles), *A. abyssorum* (squares), *S. globosa* (crosses), and *Ps. longicauda* (triangles). (**C**) Abundances of *Ophiura* spp. (circles) and *Echinocrepis* spp. (triangles). (**D**) Monthly POC flux (mg of C per m^2 per day) at 50 m above bottom (4050-m depth) at Station M, representing food supply to the sea floor, and upwelling index (m^3 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.

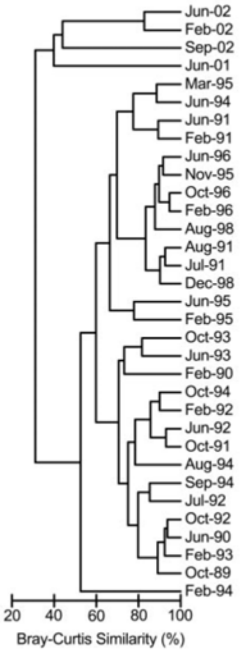

Fig. 2. A Bray-Curtis similarity dendrogram of dominant mobile epibenthic megafauna community similarity from 1989 through 2002. This analysis indicates a major difference in community structure between the 1989 to 1998 cluster and the 2001 to 2002 cluster. The taxa included in the analysis are *E. minutissima*,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

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 during 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 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
E. minutissima	31	33	−0.40	0.02	14	−0.40	0.02	17	0.35	0.05	15	29	−0.44	0.018	7
S. globosa	73	33	0.39	0.03	14	0.61	<0.001	18	−0.56	<0.001	16	29	0.35	0.067	8
P. vitrea	79	33	−0.33	0.06	14	−0.30	0.09	17	0.35	0.04	11	29	−0.37	0.045	6
A. abyssorum	91	33	0.33	0.06	15	0.46	0.01	22	−0.41	0.02	22	26	0.46	0.018	10
Synallactes 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 presumably 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.

References and Notes

1. W. S. Broecker, *Oceanography* **4**, 79 (1991).
2. D. S. M. Billett, R. S. Lampitt, A. L. Rice, R. F. C. Mantoura, *Nature* **302**, 520 (1983).
3. A. J. Gooday, *Nature* **332**, 70 (1988).
4. K. L Smith Jr., R. S. Kaufmann, *Science* **284**, 1174 (1999).
5. R. J. Baldwin, R. C. Glatts, K. L. Smith Jr., *Deep-Sea Res. II* **45**, 643 (1998).
6. S. E. Beaulieu, K. L. Smith Jr., *Deep-Sea Res. II* **45**, 781 (1998).
7. L. M. L. Lauerman, R. S. Kaufmann, K. L. Smith Jr., *Deep-Sea Res. I* **43**, 1075 (1996).
8. L. M. L. Lauerman, J. M. Smoak, T. J. Shaw, W. S. Moore, K. L. Smith Jr., *Limnol. Oceanogr.* **42**, 589 (1997).
9. L. M. L. Lauerman, R. S. Kaufmann, *Deep-Sea Res. II* **45**, 817 (1998).
10. Materials and methods are available as supporting material on *Science* Online.
11. E. Brinton, A. Townsend, *Deep-Sea Res. II* **50**, 2449 (2003).
12. M. Kahru, B. G. Mitchell, *Geophys. Res. Lett.* **29**, 1846 (2002).
13. B. E. Lavaniegos, M. D. Ohman, *Deep-Sea Res. II* **50**, 2473 (2003).
14. J. A. McGowan, D. R. Cayan, L. M. Dorman, *Science* **281**, 210 (1998).
15. F. P. Chavez, J. Ryan, S. E. Lluch-Cota, M. Ñiquen C., *Science* **299**, 217 (2003).
16. S. R. Hare, N. J. Mantua, *Prog. Oceanogr.* **47**, 103 (2000).
17. S. J. Bograd, R. J. Lynn, *Deep-Sea Res. II* **50**, 2355 (2003).
18. A. J. Miller, N. Schneider, *Prog. Oceanogr.* **47**, 355 (2000).
19. D. S. M. Billett *et al.*, *Prog. Oceanogr.* **50**, 325 (2001).
20. R. S. Lampitt *et al.*, *Prog. Oceanogr.* **50**, 27 (2001).
21. B. D. Wigham, P. A. Tyler, D. S. M. Billett, *J. Mar. Biol. Assoc. U.K.* **83**, 175 (2003).
22. I. R. Hudson, B. D. Wigham, D. S. M. Billett, P. A. Tyler, *Prog. Oceanogr.* **59**, 381 (2003).
23. B. J. Bett, M. G. Malzone, B. E. Narayanaswamy, B. D. Wigham, *Prog. Oceanogr.* **50**, 349 (2001).
24. K. L. Smith Jr., R. S. Kaufmann, W. W. Wakefield, *Deep-Sea Res. I* **40,** 2307 (1993).
25. C. R. Smith, L. A. Levin, D. J. Hoover, G. McMurtry, J. D. Gage, *Deep-Sea Res. II* **47**, 227 (2000).
26. B. J. Smallwood *et al.*, *Naturwissenschaften* **86**, 320 (1999).
27. D. S. M. Billett, C. Llewellyn, J. Watson, in *Echinoderm Biology*, R. D. Burke, P. V. Mladenov, P. Lambert, R. L. Parsley, Eds. (Balkema, Rotterdam, 1988), pp. 421–429.
28. K. Iken, T. Brey, U. Wand, J. Voigt, P. Junghans, *Prog. Oceanogr.* **50**, 383 (2001).
29. R. Witbaard, G. C. A. Duineveld, A. Kok, J. van der Weele, E. M. Berghuis, *Prog. Oceanogr.* **50**, 423 (2001).
30. D. Roberts, H. M. Moore, *Biodiv. Cons.* **6**, 1487 (1997).
31. D. Roberts *et al.*, *Prog. Oceanogr.* **50**, 443 (2001).
32. S. Uthicke, R. Karez, *J. Exp. Mar. Biol. Ecol.* **236**, 69 (1999).
33. O. Pfannkuche, K. Lochte, *Deep-Sea Res. I* **40**, 727 (1993).
34. G. B. West, J. H. Brown, B. J. Enquist, *Science* **276**, 122 (1997).
35. We thank R. J. Baldwin, R. S. Kaufmann, G. Sugihara, M. D. Ohman, D. R. Cayan, D. P. Phillips, D. Bailey, and J. H. Lowenstein for assistance in the preparation of this manuscript. This work is made possible by the efforts of countless individuals, including our laboratory colleagues R. J. Baldwin, R. C. Glatts, and F. Uhlman, the Scripps Institute of Oceanography (SIO) ship crews, shipboard technical support led by R. C. Wilson, and L. Lovell and the SIO Benthic Invertebrate Collection. Supported by the National Science Foundation (grant nos. OCE 89-22620, OCE92-17334, and OCE98-07103).

Supporting Online Material

www.sciencemag.org/cgi/content/full/305/5683/513/DC1
Materials and Methods
SOM Text
Fig. S1
References and Notes

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Supporting Material

Materials and Methods:

Forty-eight photographic line transects, typically 1.5 km in length, were conducted between October 1989 and September 2002. These transects were typically conducted seasonally, but this frequency was variable due to logistical constraints. Line-transect photography was conducted using a Benthos 372 35mm film camera and Benthos 382 strobe mounted on a towed benthic camera sled, at a height of 82 cm and 22.5° below horizontal (*S1*). The camera took photographs approximately every five s as the sled moved along the bottom at roughly 2.8 km h^{-1} creating a continuous image mosaic of the seafloor with overlapping frames. A semi-balloon otter trawl was towed behind the camera sled to non-quantitatively collect specimens from the line transect area. Collected specimens were then identified and used, in part, as a voucher collection to identify species in the line-transect photographs. The semi-balloon trawl had a 6.1 m opening and 3.8 cm stretch mesh net with a 1.3 cm mesh cod-end liner (*S1*).

The photographs were evaluated using a Canadian grid system (*S2*) and the computer program DISTANCE (*S3*), which was based on line-transect theory (*S4*). The relative location of each individual along each transect was digitized. DISTANCE estimated the visibility of an object at a distance perpendicular to the centerline of the transect and provided a probability density function and effective strip width (ESW) for each species. The sum of non-overlapping distances between frames along the transect axis provided the transect length. Overlap was estimated by measuring the relative positions of a distinct object in sequential frames. The ESW was multiplied by the transect length to provide an estimation of abundance. When the abundance of any given group was below 15 individuals transect^{-1}, an ESW from a species of similar visibility was used to estimate abundance. Detailed descriptions of the line-transect methods applied to the analysis of deep-sea camera sled photographs can be found in the supplemental reference materials (*S5, S6*). The Bray-Curtis dendrogram was created using log transformed (log(x+1)) monthly abundance estimates for each of the ten most dominant taxa with group average clustering.

POC flux to the seafloor was measured using a Teflon® coated parflux sediment trap with a 0.25m^2 opening moored at 50 m above bottom (4050m water depth) (*S7, S8*). Four climatic indices were also examined as part of the study, the Northern Oscillation Index (NOI; *S9*), Southern Oscillation Index (SOI; *S10*), the Multivariate ENSO Index (MEI; *S11*), and the North Atlantic Oscillation (NAO; *S12*). The NOI is based on the difference in sea level air pressure anomalies (SLPA) between the N Pacific high, located in the NE Pacific and a climatologically low-pressure region near Darwin, Australia. The SOI is similar to the NOI, but is based on two S Pacific locations, one near Darwin, and the other near Tahiti. Although the SOI and the NOI are highly correlated, the NOI is correlated more closely with ecological variables in the NE Pacific (*S9*). The MEI is a more integrated anomaly index incorporating parameters such as sea surface temperature, clouds, and wind. Correlations with NOI and SOI have the same sign and correlations with the MEI have the opposite sign of the NOI and SOI. The NAO is based on SLPA differences between NE Atlantic high and low-pressure regions. Positive values of the NAO are associated with increased westerly winds, and decreased sea surface temperature in the NE Atlantic.

All time-lagged correlations used the non-parametric Spearman-Rank correlation with monthly data and 1-month lag intervals. Pearson (parametric) correlations have several assumptions that are violated by the biological data in this study including normality and homoscedasticity. Nonparametric tests were used here since they do not make assumptions about the distribution of the data. Numerical analyses were done using Excel (Microsoft®) and Statistica (StatSoft®).

Three month centered running means were used for each of the climate anomaly indices. Centered monthly POC flux values were computed from the 10-day integrated POC flux measurements. Monthly abundance estimates represent the abundance estimates from one or more transects conducted during any particular month. In cases where more than one transect was carried out during a particular month a mean weighted by transect length was used giving 33 estimates for each taxa during the study period (see Fig. 1A-1C). No data were interpolated for the analysis. Cross correlations allow for the examination of significant relationships over a distribution of temporal lags (e.g. *S7*). The peaks in cross-correlation results were selected by the highest correlation coefficient and associated p-values are presented in Table 1 of the manuscript.

A modified Spearman-Rank test (*S13*) was used to account for serial autocorrelation by adjusting the effective sample sizes and *p* values for reported correlations. Due to the relatively infrequent and uneven sampling frequency in the abundance data serial autocorrelation is not considered in the significance of correlations using abundance data.

Time-lagged correlations between two time-series data sets with gaps such as the POC flux and abundance data can be biased by excluding data temporally close to gaps in sampling at different time steps. The results from the correlations of the continuous climate record and abundance data helped to validate the results for the POC flux and abundance correlations.

To analyze dispersion (see Supplemental Text) each photo transect was divided into 1m segments and the number of individuals in each 1m segment was assessed for each taxa. This information was used to create three-term local quadrat variances (*S14*) with quadrat sizes from 1m to 10% of the total transect length. A randomization test with 1000 iterations was used to evaluate whether the observed variances are greater than the randomization 95% confidence interval.

Adjustments for multiple comparisons are not used here. Multiple test adjustments to the *p* value, such as the Bonferroni correction, are often used to reduce Type I errors, but can also increase Type II errors and result in a loss of test power, especially for smaller sample sizes (*S15*). Subjective decisions about what constitutes a test, or group of tests, are also avoided by not using such corrections. Instead, conclusions were based, in part, on several factors. At Sta. M, taxa for which the following basic criteria were not met are not recognized as having probable links with climate or food supply.

- The relationships between abundance and all three climate indices were consistent having the appropriate relative sign. Correlations with NOI and SOI should have the same sign. Correlations with the MEI should be the opposite of the NOI and SOI.
- The sign of correlations between POC flux and climate are in agreement with described oceanographic processes in the NE Pacific (e.g. *S16, S17*). For instance, fluctuations reflected in the NOI do correlate earlier to abundance at Sta. M than the SOI.
- The sign of correlations between POC flux and abundance are in agreement with correlations between climate and abundance, when the POC flux to climate correlations are also considered.
- High correlations that fell within a haphazardly variable distribution of cross correlations were not considered significant.
- The temporal lag in the peak of cross correlations between climate indices and abundance is roughly consistent with the time lags found in the climate to POC flux and POC flux to abundance correlations (Fig. 3). Partial correlations between climate and abundance accounting for POC flux were insignificant in all cases. These partial correlations were examined using the temporal lags reported for peaks in climate to abundance, and POC flux to abundance cross correlations.
- An ancillary cross-correlation analysis indicated that during the study period (1989-2002), shifts in the climatic indices (NOI, SOI, and MEI) may precede shifts in

upwelling (BUI; *S18*) along the coast near Sta. M by 1-9 months or more. The nature of the connections between these climate indices and the California Current system has not been well determined though. This could be, in part, because the mechanism, intensity, and timing of such connections may vary with time (*S17*).

- Plausible mechanisms exist for changes in abundance over the timescales observed. A growth rate of 1 mm month^{-1} has been suggested for deep-sea holothuroids. An animal growing at only twice that rate, for example, could be visible in the photography (≥1cm in size) after about 5 months of growth. Growth rates are likely to vary significantly between taxa. Also animals with a larger average body size had longer temporal lags than those with smaller bodies. Body size has been shown to correlate to a number of physiological parameters in many taxa (*S19, S20*). Changes in abundance may also involve other mechanisms, such as long-term migration related to food supply.

Supporting Text

Global climatic variation affects, in part, regional and local air and sea surface temperature, wind, cloudiness, and ocean circulation (*S21*). Previous studies conducted along Nordic shelf waters (*S22*) and on the eastern Mediterranean slope (*S23*) have implicated climate in deep-water community changes. Geologic time-series data have shown that climate can influence deep-sea communities through changes in ocean chemistry, temperature, and circulation (*S24*, *S25*). It is difficult, though, to judge the shorter-term ecological responsiveness of deep-ocean communities to climate from such studies. This study provides compelling evidence that climate variation is correlated to megafauna community change in the Earth’s largest and most remote environment on time scales comparable to those in pelagic marine (*S16*) and terrestrial systems (*S26*).

Although the relationships in Fig. 1 suggest that climate might affect food supply to the deep sea, and food supply might influence the population dynamics of the observed epibenthic megafauna through relatively stable temporal lags, we believe that this has not been conclusively determined. Considerable unexplained variation remains in the significant correlations that form the basis of these time lags. Gaps in the time-series data set also make it difficult to determine the accurate timing of shifts in community structure. Given that the mechanism, intensity, and timing of climatic connections to overlying surface water processes may vary with time, it seems likely that the precise timing and intensity of climate to benthos correlations will also vary.

While spatial heterogeneity within the Sta. M site may account for some of the variability observed in the megafauna abundance estimates, there is no apparent spatial connection between the precise locations of the photo-transects within the study area and measured abundances of any particular taxa. An analysis of the dispersion of megafauna along each photo transect found that non-random distributions were infrequently observed and non-random dispersions were not consistent within any taxa. Dispersion, however, is difficult to assess reliably at quadrat scales near or beyond the size of the photo transects. Additionally many megafauna abundance estimates had inter-annual trends that are striking, compared to more random variation patterns expected due to high spatial heterogeneity alone. Animal behavior also might influence megafauna abundance estimates by changing the visibility of specific taxa.

Abyssocucumis abyssorum, for instance, is known to exhibit burrowing behavior (*S27*) that would decrease their visibility in photographs of the seafloor. Although possible, this type of behavior is not believed to be an overriding bias in the abundance estimates, especially given the observed relationships with climate and food supply.

The use of climatic indices, which are in essence principal components of climate (*S28*), for ecological analysis avoids the arbitrary choice of a climatic model whose parameters may not be well understood (*S29*). Little is known about reproduction, growth, migration, or mortality of deep-sea holothuroids. The examination of various models to explore deep-sea population dynamics will be useful as more basic knowledge of reproduction, growth rates, density dependence, and other parameters becomes available.

The continuation of time-series studies combined with process-oriented research will aid in determining the character of links between climate and deep-ocean life. New understanding may be further facilitated by the ongoing development of deep-sea observatories that can collect data autonomously with little servicing or ship time.

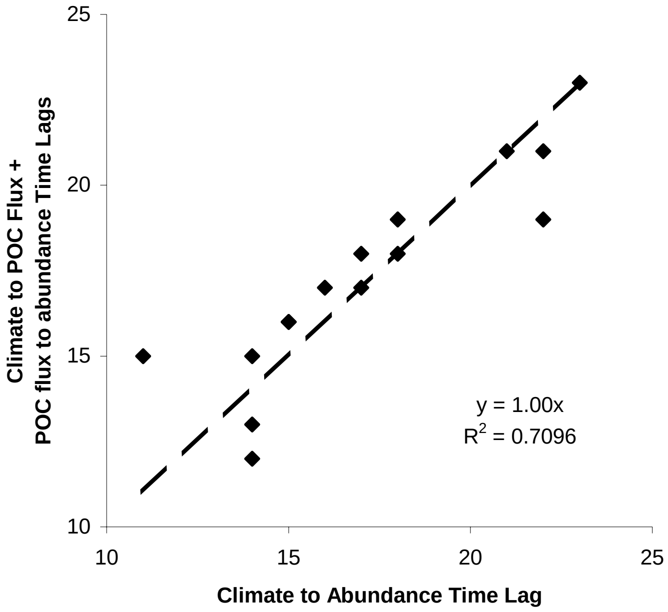


Fig. 3. Plot of the peaks in temporal lags in the climate to abundance vs. the climate to POC flux + POC flux to abundance correlations (see Table 1 in manuscript).

Supporting References

S1. W. W. Wakefield, W. Smithey, “*Two camera sleds for quantitative study of deep-sea megafauna*” (Scripps Inst. of Oceanogr. Ref. Ser. No. 89-14, 1989)

S2. W. W. Wakefield, A. Genin, *Deep-Sea Res. I* **34,** 469 (1987)

S3. Laake, J. L., S. T. Buckland, D. R. Anderson and K. P.Burnham. *Distance Users Guide V 2.1*. (Colorado Cooperative Fish and Wildlike Research Unit, Colorado State University, Fort Collins, CO, 1994) 84 pp.

S4. S. T., Buckland, D. R. Anderson, K. P. Burnham, J. L. Laake, *Distance Sampling: Estimating abundance of biological populations*, (Chapman and Hall, London, 1993) 446pp.

S5. L. M. L Lauerman, R. S. Kaufmann, K. L. Smith Jr., *Deep-Sea Res. I* **43,** 1075 (1996)

S6. L. M. L. Lauerman, R. S. Kaufmann, *Deep-Sea Res. II* **48**, 817 (1998)

S7. R. J. Baldwin, R. C. Glatts, K. L. Smith Jr., *Deep-Sea Res. II* **45,** 643 (1998)

S8. R. J. Baldwin, unpublished data

S9. F. B. Schwing, T. Murphree, P. M. Green, *Prog. Oceanogr*. **53,** 115 (2002)

S10. K. E. Trenberth, D. J. Shea, *Monthly Weather Rev.* **115,** 3078 (1987)

S11. K. Wolter, M. S. Timlin, *Weather* **53**, 315 (1998)

S12. J. C. Rogers, *Monthly Weather Rev*. **112**, 1999 (1984)

S13. P. Dutilleul, *Biometrics* **49**, 305 (1993)

S14. M. O. Hill, *J. Ecol.* **61**, 225 (1973)

S15. R. J. Feise, *BMC Med. Res. Meth.* **2.** 8 (2002)

S16. J. A. McGowan, D. R. Cayan, L. M. Dorman, *Science* **281**, 210 (1998)

S17. F. B. Schwing, T. Murphree, L. deWitt, P. M. Green, *Prog. Oceanog*. **54**, 459 (2002)

S18. A. Bakun, “Coastal upwelling indices, west coast of North America, 1946-1971” (NOAA Tech. Rep. NMFS SSRF-671, 1973)

S19. J. D. Gage, In: *Ecosystems of the World 28: Ecosystems of the deep oceans*, P. Tyler editor, Amsterdam, The Netherlands, 313 (2003)

S20. G. B. West, J. H. Brown, B. J. Enquist, *Science* **276**, 122 (1997)

S21. N. C. Stenseth, et al., *Science* **297**, 1292 (2002)

S22. B. G. Tunberg, W. G. Nelson, *Mar. Ecol. Prog. Ser*. **170**, 85 (1998)

S23. R. Danovaro, A. Dell'Anno, M. Fabriano, A. Pusceddu, A. Tselepides, *Trends Ecol. Evol*. **16**, 505 (2001)

S24. T. M. Cronin, M. E. Raymo, *Nature* **385**, 624 (1997)

S25. R. J. Behl, J. P. Kennett, *Nature* **379**, 243 (1996)

S26. M. Holmgren, M. Scheffer, E. Ezcurra, J. R. Gutierrez, G. M. J. Mohren, *Trends Ecol. Evol.* **16**, 89 (2001)

S27. K. L. Smith Jr., unpublished data.

S28. T. Hastie, R. Tibshirani, J. Friedman, *The Elements of Statistical Learning. Data Mining, Inference and Prediction*, (Springer, New York, 2001) 533pp.

S29. N. C. Stenseth, et al., *Proc. R. Soc. Lond. B* **270**, 2087 (2003)

III

Population Dynamics of Abyssal Epibenthic Megafauna in the NE Pacific from 1989-2004

Abstract

The importance of inter-annual variation in deep-sea populations has largely been unknown. Variations in abundance and size distribution of the megabenthos have been examined here using a towed camera system at a deep-sea station in the NE Pacific (Station M) from 1989-2004. This 16-year study included fifty-two roughly seasonal transects averaging 1.2 km in length with over 35,600 photographic frames analyzed. Mobile epibenthic megafauna populations at 4100 m depth have exhibited inter-annual scale changes in abundance from 1-3 orders of magnitude. Increases in abundance have now been significantly linked to decreases in mean body size suggesting accruals in abundance probably result from the recruitment of young individuals. Examinations of size-frequency histograms indicate several possible recruitment events. Shifts in the population-size distributions were also used to make basic estimations of individual growth rates from 1-6 mm month^{-1}, depending on the taxon. Regional intensification in reproduction followed by local recruitment could explain the majority of observed accruals in abundance. Although some adult migration is certainly probable in accounting for local variation in populations, 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 now shown that populations from protozoans to large benthic invertebrates and fishes all have undergone significant fluctuations in abundance at Sta. M over periods of weeks to years.

Introduction

Fluctuations in the abundance of holothuroids, echinoids, ophiuroids, and other invertebrates have been observed in both the deep NE Pacific and NE 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, 2001, Barnett et al., 2005, Hanson et al., 2005, Karl et al., 2006) and natural resource industries are now operating at abyssal depths (Glover and Smith, C. R., 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 populations of mobile epibenthic megafauna vary in abundance and body size over a 16-year period.

Benthic surveys have been conducted to quantify megabenthic populations at several slope and abyssal plain locations including examples from the NE Pacific (Smith, C.R., and Hamilton, 1983, Lauerman et al., 1996, Lauerman and Kaufmann, 1998, Nybakken et al., 1998), Murray-Molokai Fracture Zone (Beaulieu et al., in preparation), 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), NE 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, B. A., et al., 2005), and the Weddell Sea (Gutt and Piepenburg, 1991). Work in several regions has provided exploratory descriptions of populations 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 = 1cm) to be identified in photographs (Grassle *et al.*, 1975). These studies have shown that echinoderms are an integral component of the abyssal benthos throughout the world ocean. 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 NE Pacific. Research at Sta. M has been designed to monitor variation biogeochemical processes, physiology, and population dynamics at the abyssal benthic site (Smith and Druffel, 1998). Analysis of portions of the data from the site have shown that several macroinfaunal 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 NE Pacific, echinoderms dominate populations of 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 1989-1996, 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 1989-2002 found that several echinoderm populations shifted 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 1989-2004 (Bailey et al., 2006).

Another time-series program has examined benthic communities in the Porcupine Abyssal Plain (PAP) in the NE Atlantic (48°50’N, 16°30’W, 4800 m depth). The interdisciplinary analysis found a difference in benthic megafauna populations between the periods 1989-1994 and 1996-1999 (Billet et al., 2001). Several taxa shifted in dominance, and several mobile epibenthic megafauna populations 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 (Billet et al., 2001, Wigham et al., 2003a).

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 local 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 fifty-two photographic transects were conducted at Sta. M in the northeastern Pacific over a 16-year period from 1989-2004 to determine the population dynamics of mobile epibenthic megafauna over interannual time scales. Using this long-term data set several key questions were addressed: 1) Were the shifts in abundance observed from 1989-2002 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 NE Pacific and has little bathymetric relief, with less than a 100 m difference in elevation over 1600km^2 (Smith and Druffel, 1998). Surface waters above the site have seasonally and inter-annually variable phytoplankton blooms (Kahru and Mitchell, 2002a, 2002b), with subsequent peaks in sinking POC to the seafloor 4100 m below within weeks to months (Smith *et* *al.*, 1993, 1998, 2006, Baldwin et al., 1998, Drazen et al., 1998, Lauerman and Kaufmann, 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 to 3.6 cm s^{-1} with additional seasonal-scale variation in the mean flow and direction (Beaulieu and Baldwin, 1998). Stronger net flows were generally southerly and weakest flows were often northerly. The net flow was primarily to the south at less than 1 cm s^{-1} and potential temperatures were approximately 1° C.

The seasonal photographic line transects averaged more than 1.2 km in length and gaps in the data are apparent in Fig. 4. 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 approximately every 5 s as the sled moved along the bottom at roughly 0.3 m s^{-1} 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 Canadian grid system (Wakefield and Genin, 1987) and the computer program DISTANCE (Laake et al., 1994), which is based on line-transect theory (Buckland et al., 1993). The relative location and length of each relevant individual within the Canadian grid was digitized using a photoenlarger and acoustic digitizing system. Ophiuroid body sizes, which were generally the smallest of the dominant taxon, were calculated from trawl specimen measurements (Booth et al., in preparation). Such direct measurements were not possible with the other taxa due to deformation and damage to the specimens in the trawl net. 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 transect^{-1}) to use DISTANCE to evaluate the visibility of a group, an ESW from a more abundant and similarly visible species is used to estimate abundance. In cases were 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 non-parametric and randomization-based analyses. Yearly, as well as monthly groupings of cumulative body-size distribution data were examined where possible. All body-size distributions are available for reference in the supporting material. Relationships between monthly median body size and abundance were evaluated using Spearman-rank correlations (r(s)) and results with a *p*-value = 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 permits non-parametric evaluation of the similarity of body-size distributions over time and follows the methodology described in Thurston et al. (1994) and Billett et al. (2001). Supporting analyses included a randomization analysis of similarity (ANOSIM (R)) 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, as well as plotting by Julian day.

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 (supporting material). 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)/r was used to create these first approximations from yearly grouped data, where r is the observed percent difference in the population density from one year to the next and T is the estimated doubling time.

Results

The abundance of the holothuroid *Elpida 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. 4a-j). The above echinoderms comprised >99% of all mobile megafauna observed during the study period. The observations were dominated by inter-annual scale variations with no clear seasonality. True spectral analysis is not possible with the uneven temporal distribution of the data, but no other cyclical trends are yet evident.

The elasipod *Elpida minutissima* dominated the populations of mobile epibenthic megafauna during the 1989-1998 period with peaks in local abundance nearing 1 m^{-2} in 1998. Overall there was a gradual increase in abundance from 1989 through 1998 followed by a three order of magnitude reduction in population density in 2001 to 2004 (Fig. 4a). The density of *E. minutissima* was negatively correlated with the median size, and a relatively continuous change in body size from 1989-1998 was evident from the median densities through time (Fig. 4a, Table 2), and the annual size-frequency histograms (Fig. 5). The relationships between body size and density were unknown from 2001 to 2004 because so few individuals were observed during that period. Specific increases in small size classes were seen in annual size-frequency histograms in 1990 and 1994, as well as decreases in mean size from 1989-1996 with a slight upturn in 1998. Monthly size-frequency histograms reveal that the most notable increase in the proportion of smaller individuals was in June 1990 with more subtle peaks seen in, February 1994, and October 1994 (supporting material). ANOSIM results show that both monthly and yearly cumulative body-size frequency similarities were significantly different during times when the median body size was above or below the median (Table 3). Spearman-rank correlations between the median size and the body size index (Fig. 6a and 7a) were also significant (Table 3).

Peniagone diaphana and *P. vitrea* have also been dominant elasipod holothuroids at Sta. M, and although they are in the same genus they did not have co-varying abundances (r(s) 0.02; $p = 0.8$, Fig. 4b and 4c). *Peniagone diaphana* densities were roughly 0.01 m^{-2} for much of the time series with prominent spikes in abundance in 1995 and 2001 (Fig. 4b). The trend of *P. vitrea* over time was roughly similar to that of *E. minutissima* (r(s) 0.52; $p < 0.001$, Fig. 4a and 4c) with accumulating densities from 1989-1998 followed by an order of magnitude decline by 2001 then increasing in 2004.

Varying by more than two orders of magnitude, *S. globosa* was less abundant than the above taxa and decreased in abundance from 1989 through 1992, then increased through 1998, peaked in 2001-2002 and declined to its lowest levels by 2004 (Fig. 4d). Both remaining elasipods, *O. mutabilis* and *Ps. longicauda*, had relatively low stable abundances through 1998 but were higher during the 2001-2004 period (Fig. 4e and 4f) and had a significantly monotonic change over the entire study period (Table 2). The moderately abundant dendrochirotid, *A. abyssorum*, also had a slightly higher density from 1989 through 1990 then declined through 1998 with a subsequent order of magnitude increase to roughly 0.1 m^{-2} in 2002 and thereafter (Fig. 4g). The aspidochirotid, *Sy. profundi*, rose in density from 1990-1995 and then showed decreased values through 2001. The density subsequently increased to 0.01 m^{-2}, its highest values observed during the time series (Fig. 4h). The ophiuroid taxon, dominated by *O. bathybia* was highly dominant between 1989-1998 and became most prevalent in 2001-2004 with abundances approaching $1m^{-2}$ (Fig. 4i). *Echinocrepis rostrata* had a relatively constant density from 1989-1998 at approximately $0.01\text{-}0.02m^{-2}$ and increased monotonically to roughly $0.1m^{-2}$ by 2002 (Fig. 4j, Table 2).

Significant negative links between density and median body size were found for all but *P. vitrea*, *S. globosa*, and *O. bathybia* indicating that for most taxa, higher abundances were associated with increases in the proportion of smaller individuals (Table 3). In 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. 4c and 4i). Examination of remaining monthly and yearly size-frequency distributions revealed several other examples of peaks in smaller size classes that could indicate specific recruitment events. June 1990 had prominent peaks in smaller individuals of *E. minutissima*, *P. diaphana*, *P. vitrea*, *A. abyssorum*, and *Ec. rostrata* (Fig. 5, supporting material). Other notable increases in the abundance of smaller individuals were seen in June 1991, October 1994, and June 2004 for *P. diaphana*, October 1994 and August 1998 for *Peniagone vitrea*; February 2002 and June 1996 for *A. abyssorum*; August 1991, February 1994, February 1996, December 1998, and October 2003 for *Ec. Rostrata*. Several of the above peaks were also apparent in annual groupings of the size-frequency data (supporting material). Monthly histograms of each observed ophiuroid taxon revealed several minor increases in smaller size classes, but no clear cohorts were observed and recruitment to the level of juveniles and small adults was likely to be relatively continuous (supporting material, Booth et al., in preparation).

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 still highly variable, but did show a peak in the smaller sizes in 1990 and a reduction in the mean size was also evident in the 2001-2004 time period (supporting material). *Scotoplanes globosa* size distributions also indicated higher frequencies of smaller individuals in 1990 and 1995, two periods when abundance was moderately high (Fig. 4d, supporting material). No specific recruitment events of *O. mutabilis*, and *Ps. longicauda* were apparent.

The body-size distribution similarities were also significantly different when the body size was either higher or lower than the overall median for all but *S. globosa* and *Sy. profundi* (Fig. 7, Table 3). All taxa had significant links between the body size index and the median body size indicating that the median was a good descriptor of the overall distribution. One notably weak correlation occurred with the yearly body size similarities and median body size for *A. abyssorum*. All but *S. globosa*, *O. mutabilis*, *Ps. longicauda*, and *O. bathybia* had significant monotonic changes in the body size index over time (Fig. 6 and 7, Table 2).

Crude growth rate estimates were made for those taxa that had distinct peaks in size classes and were identifiable in sequential measurement periods. These analyses produced estimates that ranged from 1-4 mm month^{-1} for *E. minutissima*, 2-5 mm month^{-1} for *P. diaphana*, 2-6 mm month^{-1} for *P. vitrea*, 2-5 mm month^{-1} for *A. abyssorum*, and 2-5 mm month^{-1} for *Ec. rostrata*. Rough estimations of maximal, though un-sustained, 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 Sta. M have changed in density from one to three orders of magnitude over the 16-year period indicating, principally, that these populations were considerably dynamic over inter-annual time-scales. Several shifts in abundance observed in 2001-2002 (Ruhl and Smith, 2004) have persisted through 2004. The most dominant taxon from 1989-1998, *E. minutissima*, went from constituting more than 40% of the mobile megafauna individuals in the 1990’s 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 megafauna abundance could be related to aseasonal reproduction, as well as to the high inter-annual variability in food supply at Sta. 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 likely associated with the introduction of new smaller individuals to the population. In these cases reproduction and recruitment were likely important in explaining the observed population dynamics. This conclusion is also supported by the additional randomization and correlation tests presented in Table 3 and the specific peaks in smaller individuals observed in the size-frequency distributions (supporting material). Conversely if increases in median body size were linked to increases in abundance, there could be higher survivorship. Such prominent survivorship relationships were not seen here. 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 ten echinoderms examined here range from 5-65 cm h^{-1} at Sta. M and could lead to straight-line migrations of 0.4-5.7 km yr^{-1} (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 Sta. M.

Elpidia minutissima, *P. diaphana*, *O. mutabilis*, *Ps. longicauda*, *A. abyssorum*, *Sy. profundi*, and the echinoid *Ec. rostrata* all exhibit 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 including *S. globosa*, and *Ps. longicauda* could be a 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 inter-annual timescales.

Several of the species observed here were also common at the Porcupine Abyssal Plain in the NE Atlantic where the abundance of the megabenthos had significant ($p < 0.05$) variations from 1989-1999 (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 Sta. M, did not have any significant shifts in abundance at the PAP site. An order of magnitude increase in *O. mutabilis* was observed at Sta. M, but it was lesser in magnitude than most other taxa. *Amperima rosea* and *Ps. longicauda* at the PAP also had links between abundance and body size that were comparable with those at Sta. M (Billett et al., 2001).

Wigham et al. (2003b) suggest 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 elasipod with either a planktotrophic or brief lecithotrophic larval stage and may reach maturity as soon as one year after settlement (Billett et al., 2001, Wigham et al., 2003b). 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., 2003a, 2003b).

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 µm (Young, 2003). Cross-generational migrations of tens to hundreds of km seem reasonable given a pelagic phase of weeks to months. Pelagiclly dispersing juvenile *Ps. longicauda* for example have been taken from up to 3000 m above the seafloor (Gage and Tyler 1990). Several *Peniagone* species are also known to spend some portion of their adult life swimming off the seafloor (Barnes, et al., 1975, Bluhm and Gebruk, 1999). This behavior could increase the taxon's relative ability to migrate across the seafloor. At Sta. 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 Porcupine Abyssal Plain (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 Sta. M, but such behavior could make the taxon less likely to have cross-generational migrations at regional scales. If echinoderm populations at Sta. M are receiving recruits from the greater NE 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).

Rough estimations of growth were calculated from shifts in size distributions to further explore the plausibility of reproduction and recruitment driving increases in the megafaunal populations. Analyses of observed shifts in Sta. M megafaunal populations indicate that growth rates could be as high as 2-6 mm month^{-1}. Together with an estimate presented by Wigham et al. (2003) of 1 mm month^{-1} these represent the best approximations of growth rates available for deep-sea holothuroids and echinoids. A cultured holothuroid, *Holothuria scabra*, has been estimated to grow from 6-24mm month^{-1} for sub-adults (Battaglene et al., 1999). Comparisons between cultured or exploited holothuroid growth rates and those found at abyssal depths are problematic, but the ranges do overlap. The abundance measurements over time at Sta. M suggest that abyssal populations can experience multiple population doublings within one year. Such rapid increases in megafauna abundance indicate that with regional and local interaction the populations could respond to the factors affecting 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) may be influencing the responsiveness of populations below some threshold density and carrying capacities unquestionably limit the long-term extent of opportunistic reproductive responses.

Mobile megafauna have been previously observed to aggregate on scales from meters to km in deep-seafloor habitats both at Sta. M and other locations (Smith, C.R., and Hamilton, 1983, 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 Sta. M transects indicate that detectable non-random dispersion patterns do occur, but they were infrequent and no consistent aggregation behavior was found at the transect scales (Ruhl, in preparation). The synchronous abundance and body size trends observed are also unlikely if spatial heterogeneity was the primary source of the observed variation.

Other studies with repeated estimations of megafaunal abundance are relatively limited and were not designed to evaluate population dynamics *per se*. Regional holothuroid densities seem to be related to the general productivity of the overlying surface waters with the California slope stations having higher to similar densities (Smith, C.R., and Hamilton, 1983, Nybakken et al., 1998), the oligotrophic Peru Basin station having order of magnitude lower densities (Bluhm and Gebruk, 1999). The highly oligotrophic Murray-Molokai Fracture Zone site had some of the lowest observed abyssal mobile megafauna abundances (Beaulieu et al., in preparation). A more comprehensive examination of abyssal benthos surveys throughout the world is presented in Beaulieu et al. (in preparation).

Variation in climate and food supply have been linked to the population shifts observed at Sta. 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 (Lauerman et al., 1997, Billett et al., 1988, Iken et al., 2001, Ginger 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., 2003a, 2003b). 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 specific taxa can have variable responses to the food supply (Roberts et al., 1997, 2001, Billett et al., 2001, Hudson et al., 2003, Wigham et al., 2003a, 2003b, Ruhl and Smith, 2004, Ramirez-Llodra et al, 2005). Understanding how climate can affect POC quantity and quality, and how abyssal populations differentially utilize POC remain important areas of investigation.

The faunal density and activity changes observed at Sta. 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 Sta. M and the PAP clearly establish that inter-annual scale variability in megafaunal populations can occur at abyssal depths. Increases in abundance of echinoderm megafauna at Sta. M were typically linked to decreases in body size, which suggest that reproductive events on a local to regional scale are contributing young individuals. This study also provides some of the only estimates on individual and population growth rates for abyssal echinoderms. Basic population parameters such as reproduction, growth rates, generation times, longevity, and competitive interactions need further study since much of what is known is not measured directly. Abyssal populations 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 sea.

This chapter, in full, has been submitted to the journal Ecology (Ruhl, H. A., in review. Population dynamics of abyssal epibenthic megafauna in the NE Pacific from 1989-2004. Ecology). The dissertation author was the only investigator and author of this manuscript.

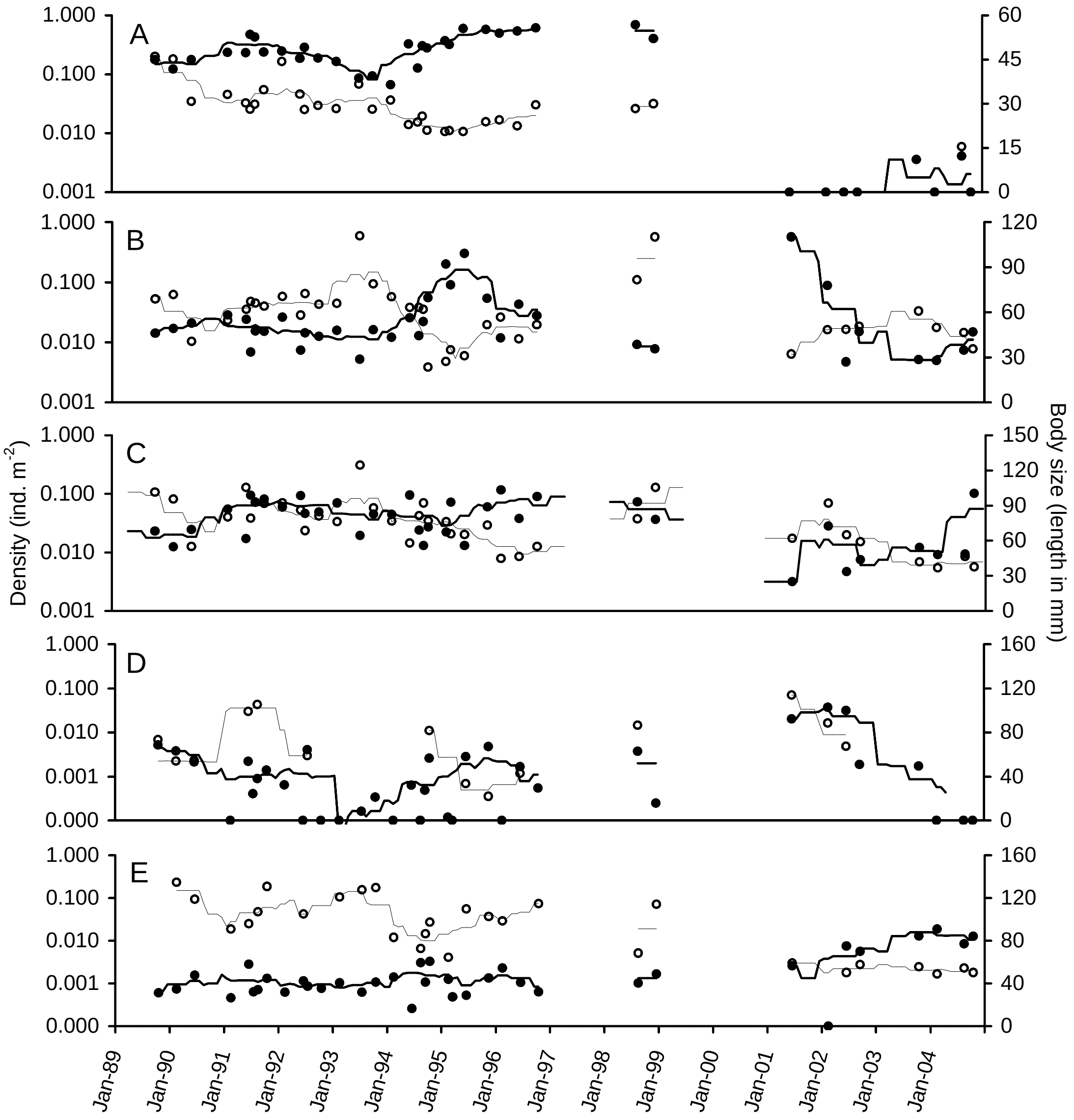


Fig. 4a-e. Abundance and body size of a) *E. minutissima*, b) *P. diaphana*, c) *P. vitrea*, d) *S. globosa*, e) *O. mutabilis*. Solid circles and lines are monthly abundance estimates and thirteen month running means and open circles and dashed lines are monthly median body sizes and thirteen month running means respectively. Note also that the scales on the various panels are different.

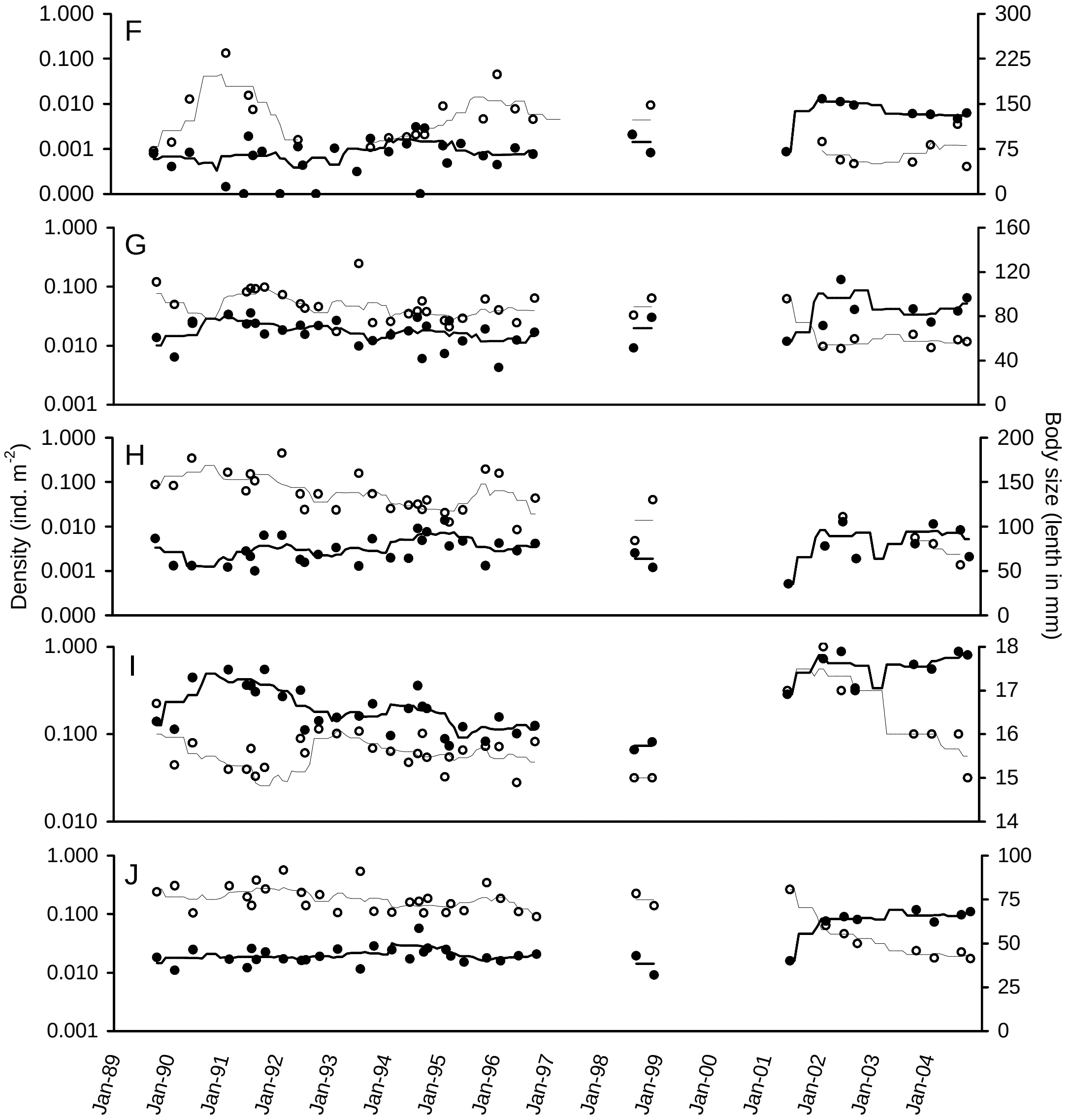


Fig. 4 (continued) f-j. Abundance and body size of f) *Ps. longicauda*, g) *A. abyssorum*, h) *Sy. profundi*, i) *O. bathybia*, j) *Ec. rostrata*. Solid circles and lines are monthly abundance estimates and thirteen month running means and open circles and dashed lines are monthly median body sizes and thirteen month running means respectively. Note also that the scales on the various panels are different.

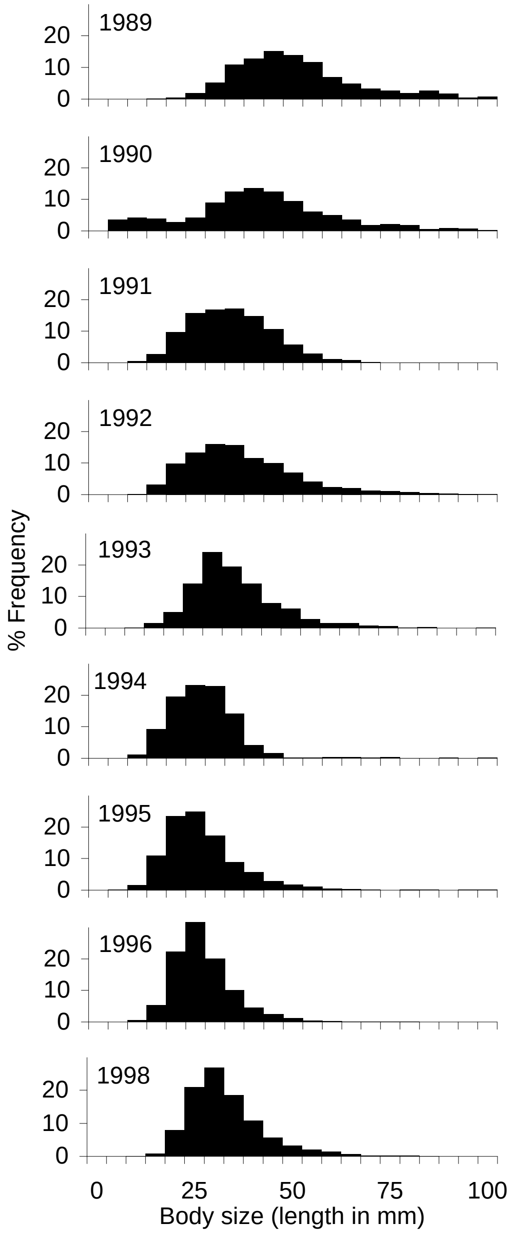


Fig. 5. Percent frequency histograms of body size for *E. minutissima*. Data from all transects grouped yearly for 1989-1996 and 1998. *Elpidia minutissima* was infrequently observed during 2001-2004 so no histograms were made for that period.

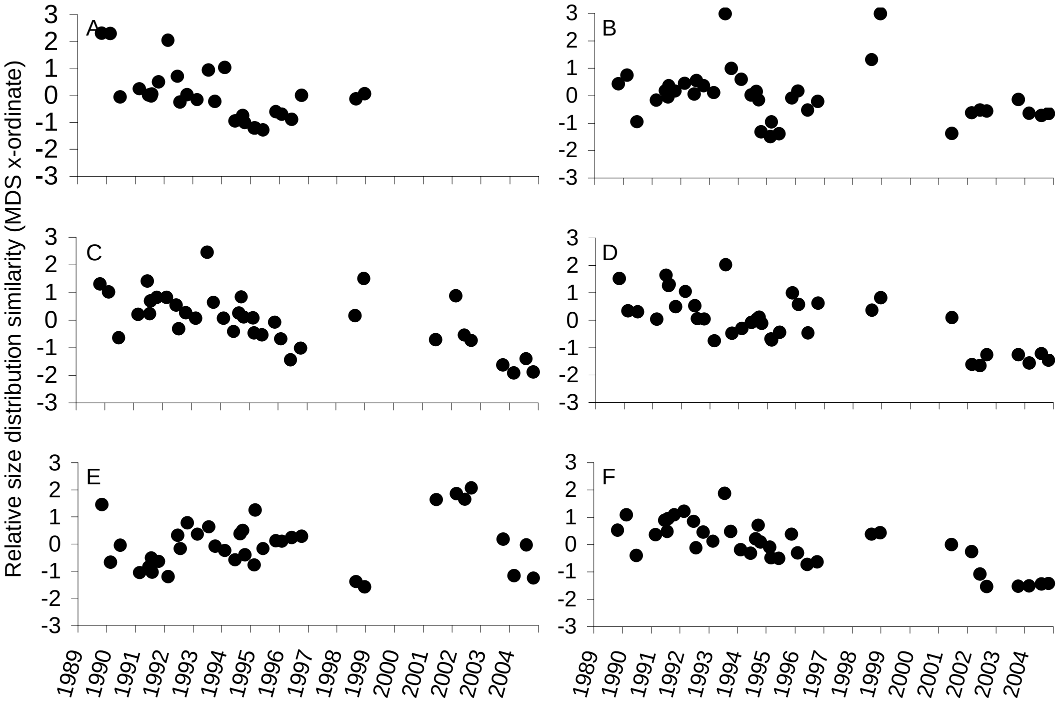


Fig. 6a-f. Relative similarity of monthly cumulative size distributions of a) *E. minutissima*, b) *P. diaphana*, c) *P. vitrea*, d) *A. abyssorum*, e) *O. bathybia*, and f) *Ec. rostrata*. Positive x-ordinate values are set to ordinate with distributions with a higher than average medians and negative values with lower than average medians.

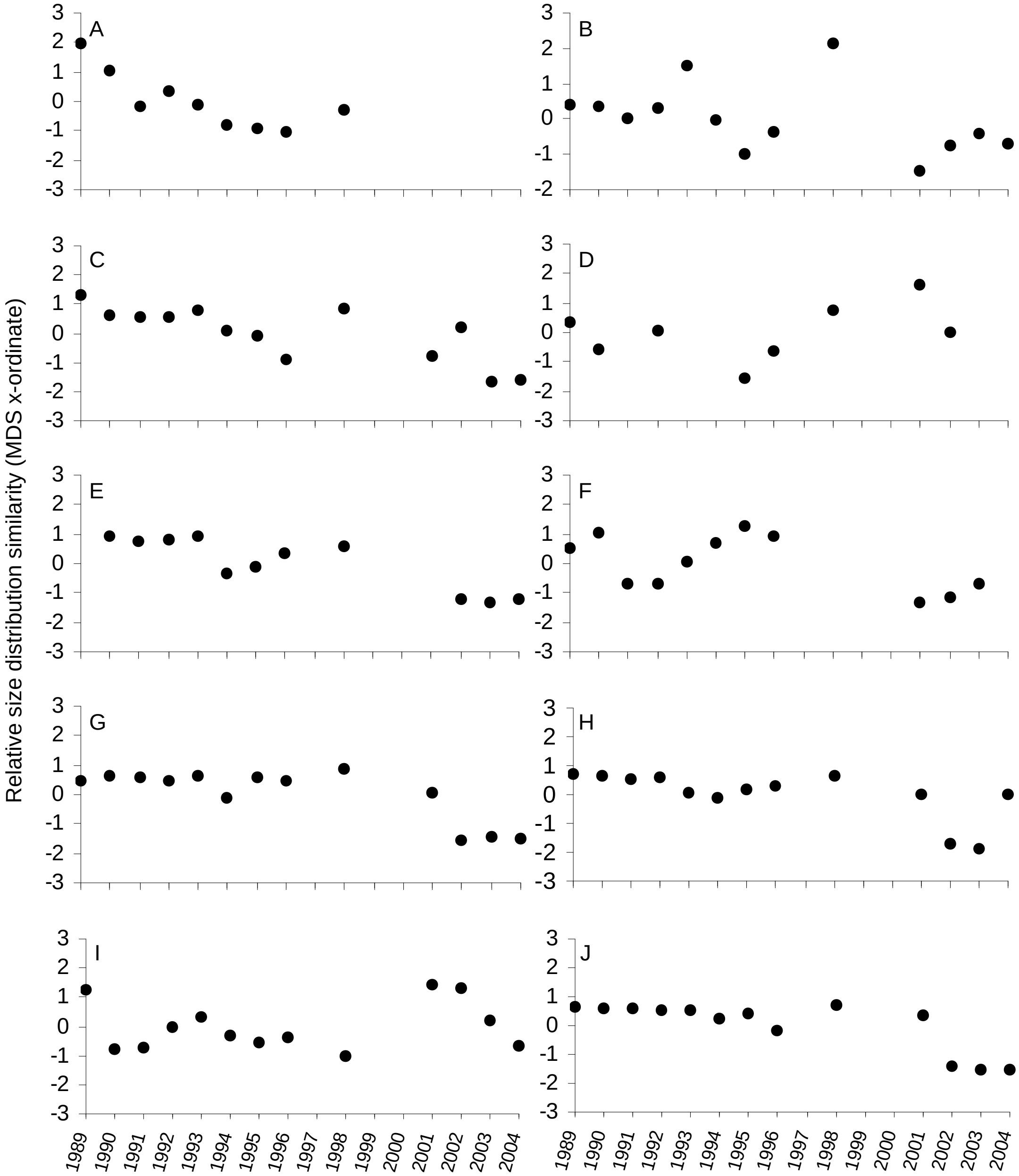


Fig. 7a-j. Relative similarity of yearly cumulative size distributions of a) *E. minutissima*, b) *P. diaphana*, c) *P. vitrea*, d) *S. globosa*, e) *O. mutabilis*, f) *Ps. longicauda*, g) *A. abyssorum*, h) *Sy. profundi*, i) *O. bathybia*, j) *Ec. rostrata*. Positive x-ordinate values are set to ordinate with distributions with a higher than average medians and negative values with lower than average medians.

Table 2. Spearman-rank correlations (r(s)) between abundance and time, as well as between cumulative body-size frequency distribution similarity MDS x-ordinates and time with monthly and yearly estimates.

Category	Medain Body Lenth (mm)	abundance vs. time						body size MDS x-ord. 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	37	-0.22	0.195	13	-0.39	0.184	29	-0.59	<0.001	9	-0.85	0.004
P. diaphana	61	37	-0.10	0.554	13	-0.07	0.817	37	-0.44	0.006	13	-0.60	0.03
P. vitrea	73	37	-0.25	0.143	13	-0.34	0.255	37	-0.63	<0.001	13	-0.72	0.01
S. globosa	70	37	-0.02	0.929	13	-0.05	0.859				8	0.21	0.61
O. matubilis	97	37	0.55	<0.001	13	0.86	<0.001				11	-0.19	0.57
Ps. longicauda	98	37	0.61	<0.001	13	0.75	0.003				11	-0.38	0.25
A. abyssorum	84	37	0.23	0.180	13	0.47	0.108	37	-0.61	<0.001	13	-0.58	0.04
Sy. profundi	130	37	0.24	0.150	13	0.33	0.271				13	-0.71	0.01
Echinoids													
Ec. 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	0.34	13	0.14	0.65

Table 3. Results form Spearman-rank correlations (r(s)) between median body size and abundance with monthly and yearly estimates, between median body size and cumulative body-size frequency similarity MDS x-ordinates, and ANOSIM comparisons (R) with cumulative body-size frequency distribution similarity MDS x-ordinates between higher and lower than overall median body size groups with monthly and yearly estimates. Shaded areas indicate tests with *p*-values > 0.05 or those were tests were not possible because distributions were not reliably estimated. Note that statistics with *E. minutissima* only include data from 1989-1998 since so few individuals were observed in 2001-2004 and size distributions were not discernable.

Category	Medain Body Lenth (mm)	median body size vs. density						median body size vs. body size MDS x-ord.					
		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	0.26	29	0.97	<0.001	9	0.90	<0.001
P. diaphana	61	37	-0.47	0.003	13	-0.65	0.02	37	0.96	<0.001	13	0.93	<0.001
P. vitrea	73	37	0.03	0.87	13	0.36	0.22	37	0.98	<0.001	13	0.98	<0.001
S. globosa	70	14	0.07	0.82	12	0.07	0.83				8	0.98	<0.001
O. matubilis	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	0.11				11	0.96	<0.001
A. abyssorum	84	37	-0.37	0.02	13	-0.52	0.07	37	0.94	<0.001	13	0.37	0.21
Sy. profundi	130	32	-0.46	0.01	13	-0.54	0.05				13	0.64	0.02
Echinoids													
Ec. rostrata	72	37	-0.73	<0.001	13	-0.74	0.004	37	0.79	<0.001	13	0.44	0.14
Ophiuroids													
Ophiura spp.	16	37	0.30	0.08	13	0.39	0.18	37	0.80	<0.001	13	0.92	<0.001

Table 3 (continued). Results form Spearman-rank correlations (r(s)) between median body size and abundance with monthly and yearly estimates, between median body size and cumulative body-size frequency similarity MDS x-ordinates, and ANOSIM comparisons (R) with cumulative body-size frequency distribution similarity MDS x-ordinates between higher and lower than overall median body size groups with monthly and yearly estimates. Shaded areas indicate tests with *p*-values > 0.05 or those were tests were not possible because distributions were not reliably estimated. Note that statistics with *E. minutissima* only include data from 1989-1998 since so few individuals were observed in 2001-2004 and size distributions were not discernable.

Category	Medain Body Lenth (mm)	+ or - size deviation vs. size MDS x-ord.					
		Monthly			Yearly		
		perm.	R	*p*	perm.	R	*p*
Holothuroids							
E. minutissima	28	999	0.44	<0.001	999	0.48	0.02
P. diaphana	61	999	0.43	<0.001	999	0.4	0.01
P. vitrea	73	999	0.62	<0.001	999	0.47	0.003
S. globosa	70				28	0.18	0.25
O. matubilis	97				330	0.37	0.03
Ps. longicauda	98				330	0.48	0.02
A. abyssorum	84	999	0.53	<0.001	999	0.29	0.04
Sy. profundi	130				462	0.2	0.07
Echinoids							
Ec. rostrata	72	999	0.2	<0.001	999	0.56	0.002
Ophiuroids							
Ophiura spp.	16	999	0.38	<0.001	999	0.68	0.002

Supporting Material

Presented here are the monthly and yearly percent frequency distributions for the top 6 mobile epibenthic megafauna found at Sta. M. Yearly plots are provided for the less abundant *Sy. profundi, S. globosa, O. mutabilis,* and *Ps. longicauda,* in part, to illustrate the limits of the distribution data.

In the monthly figures one can track the growth of putative cohorts over time. In examining both the shifts in these peaks and the rates of increase in abundance estimates we can make the best available estimates of growth, which are presented in the principal text. For instance, in Fig. S1a the peak in June 1991 can be tracked to February 1992 for a twenty mm increase over eight months giving a growth estimate of 2.5 mm month^{-1}. Thirty-nine growth estimates were made from the monthly distributions for the six most abundant taxa.

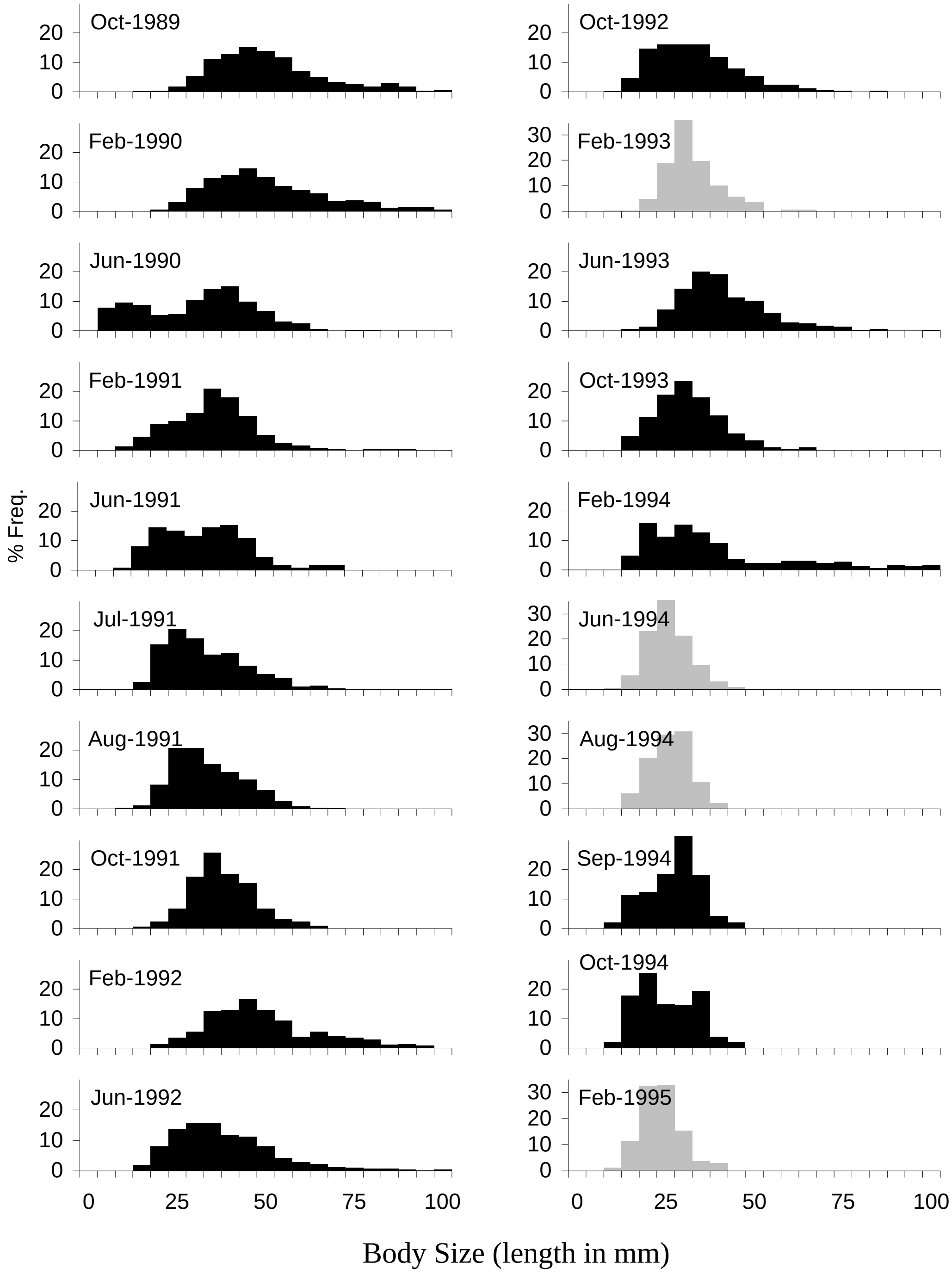


Figure 8. Monthly percent frequency distributions for *E. minutissima* for October 1989 to February 1995. Note that the gray bars filed bars have differing scales from black bars.

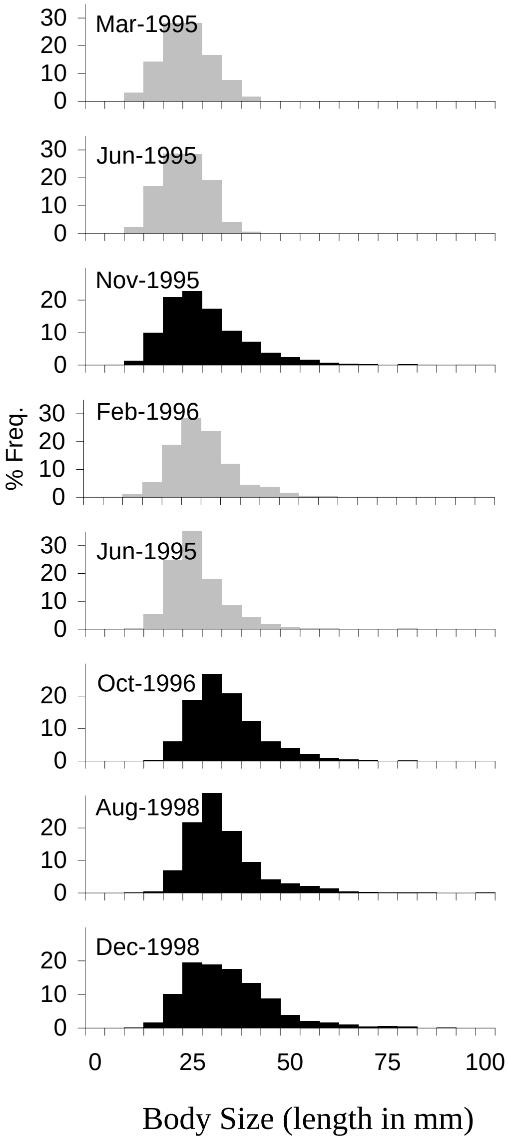
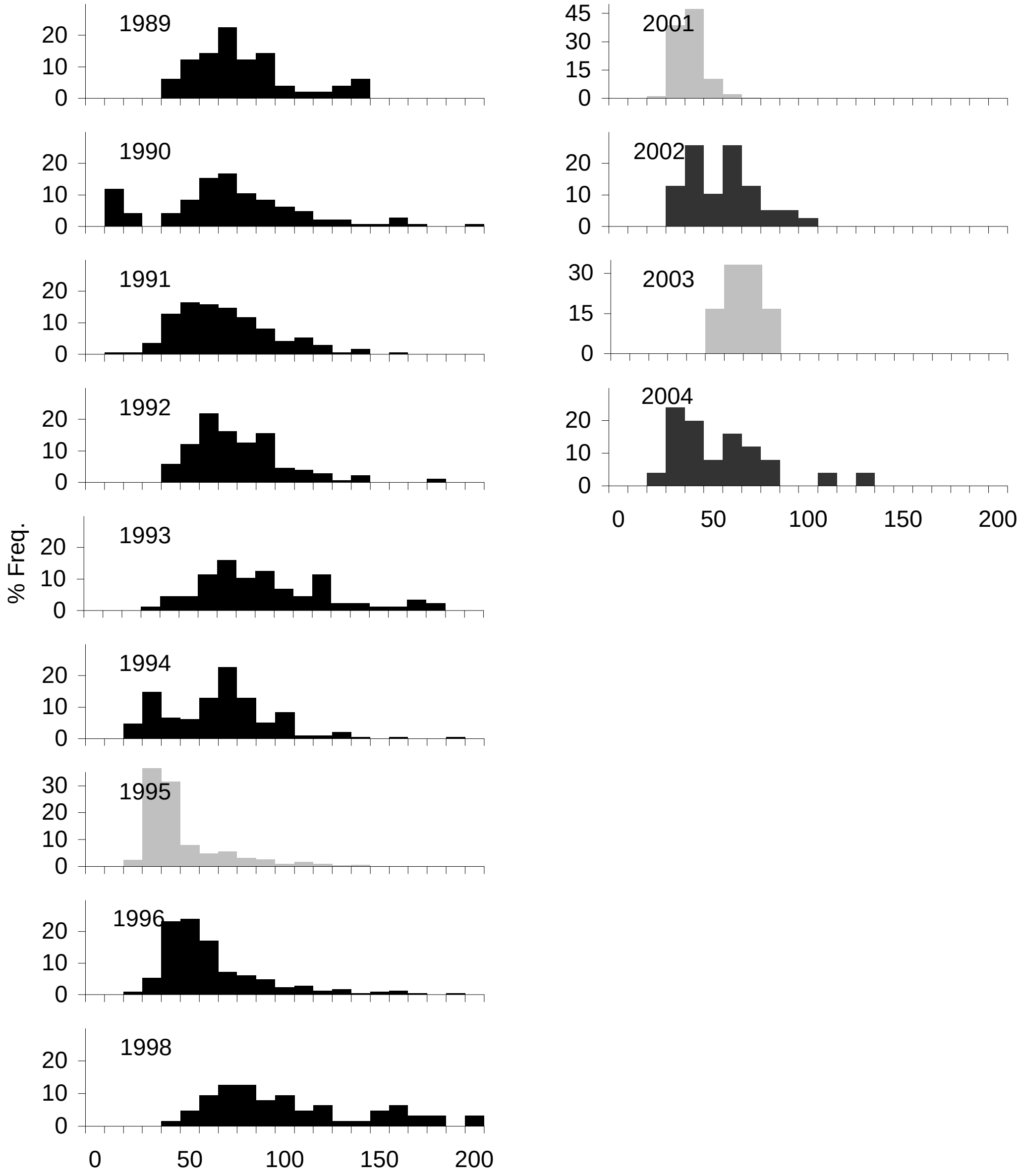
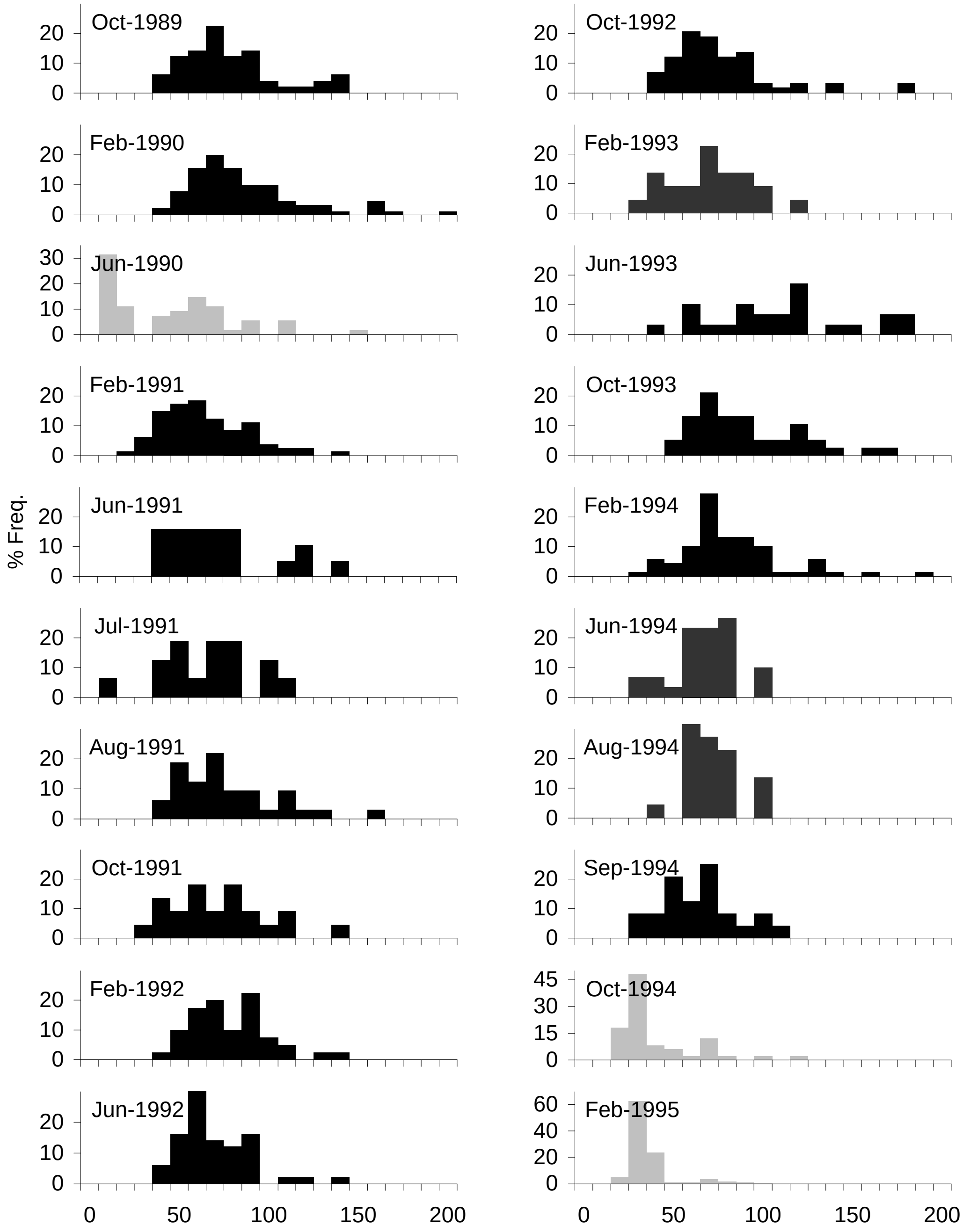


Figure 8 (continued). Monthly percent frequency distributions for *E. minutissima* for March 1995 to December 1998. Note that the gray bars filed bars have differing scales from black bars.



Body Size (length in mm)

Figure 9. Yearly percent frequency distributions for *P. diaphana* for 1989 to 1998. Note that the gray bars filed bars have differing scales from black bars.



Body Size (length in mm)

Figure 10. Monthly percent frequency distributions for *P. diaphana* for October 1989 to February 1995. Note that the gray bars filed bars have differing scales from black bars.

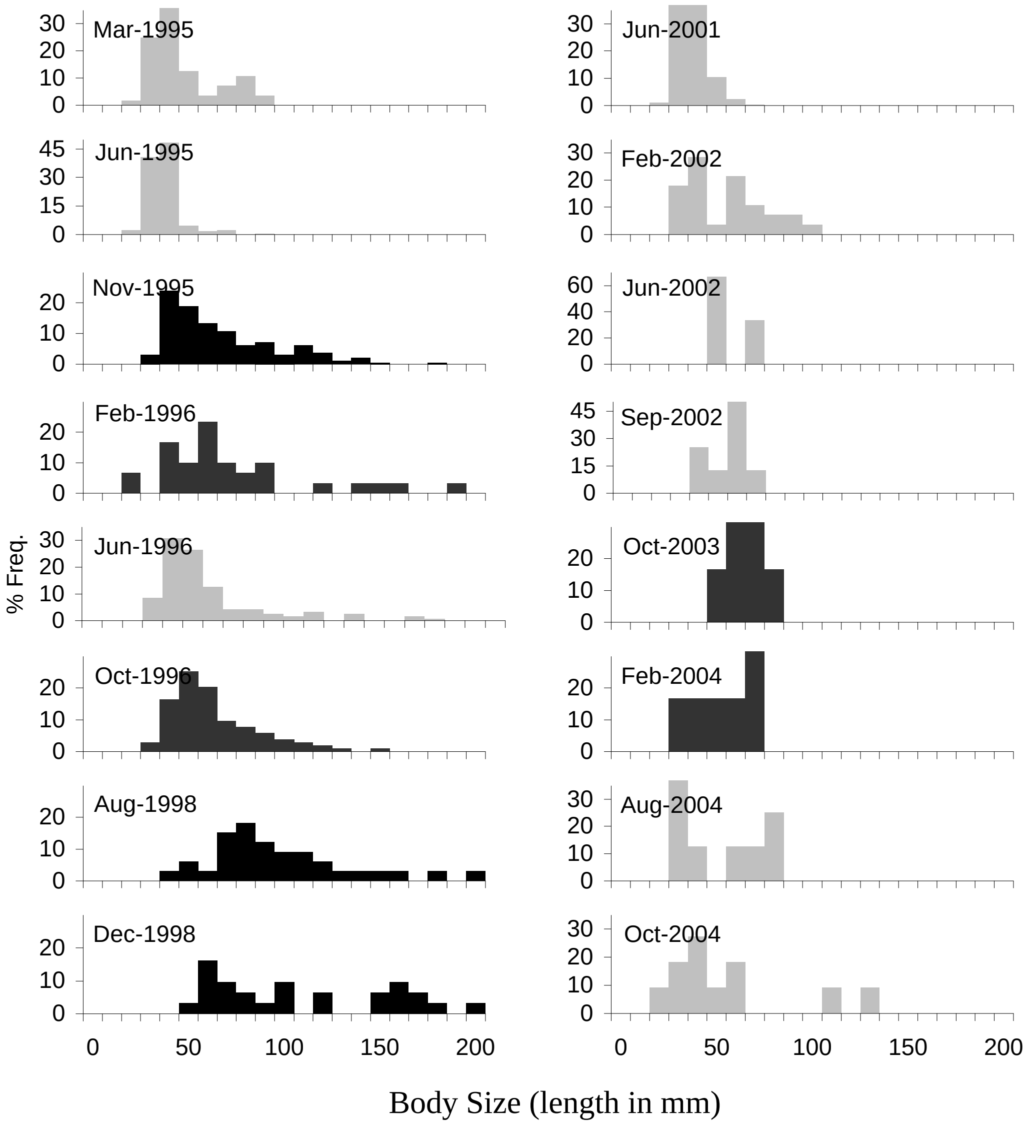
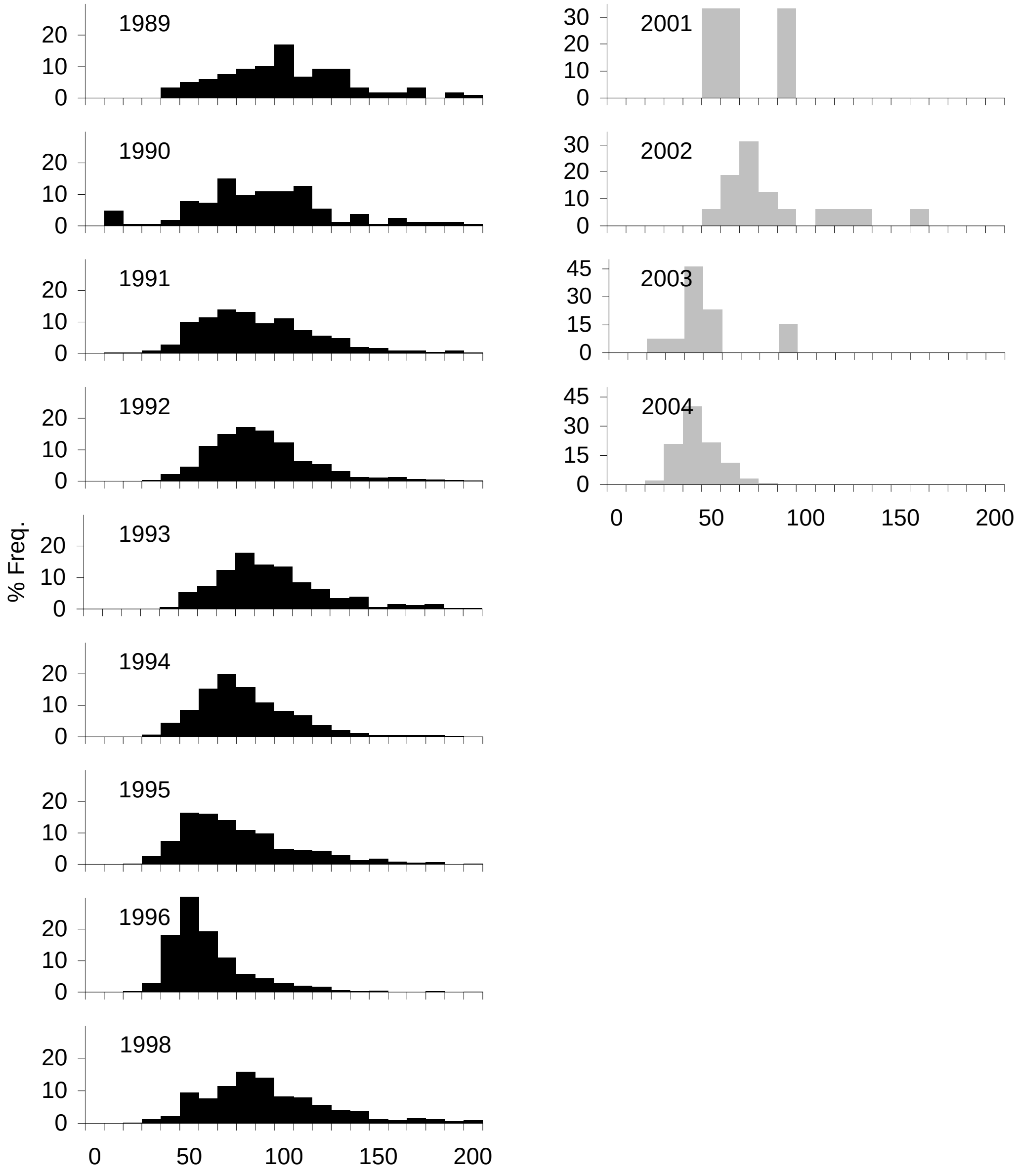


Figure 10 (continued). Monthly percent frequency distributions for *P. diaphana* for March 1995 to October 2004. Note that the gray bars filed bars have differing scales from black bars.



Body Size (length in mm)

Figure 11. Yearly percent frequency distributions for *P. vitrea* for 1989 to 2004. Note that the gray bars filed bars have differing scales from black bars.

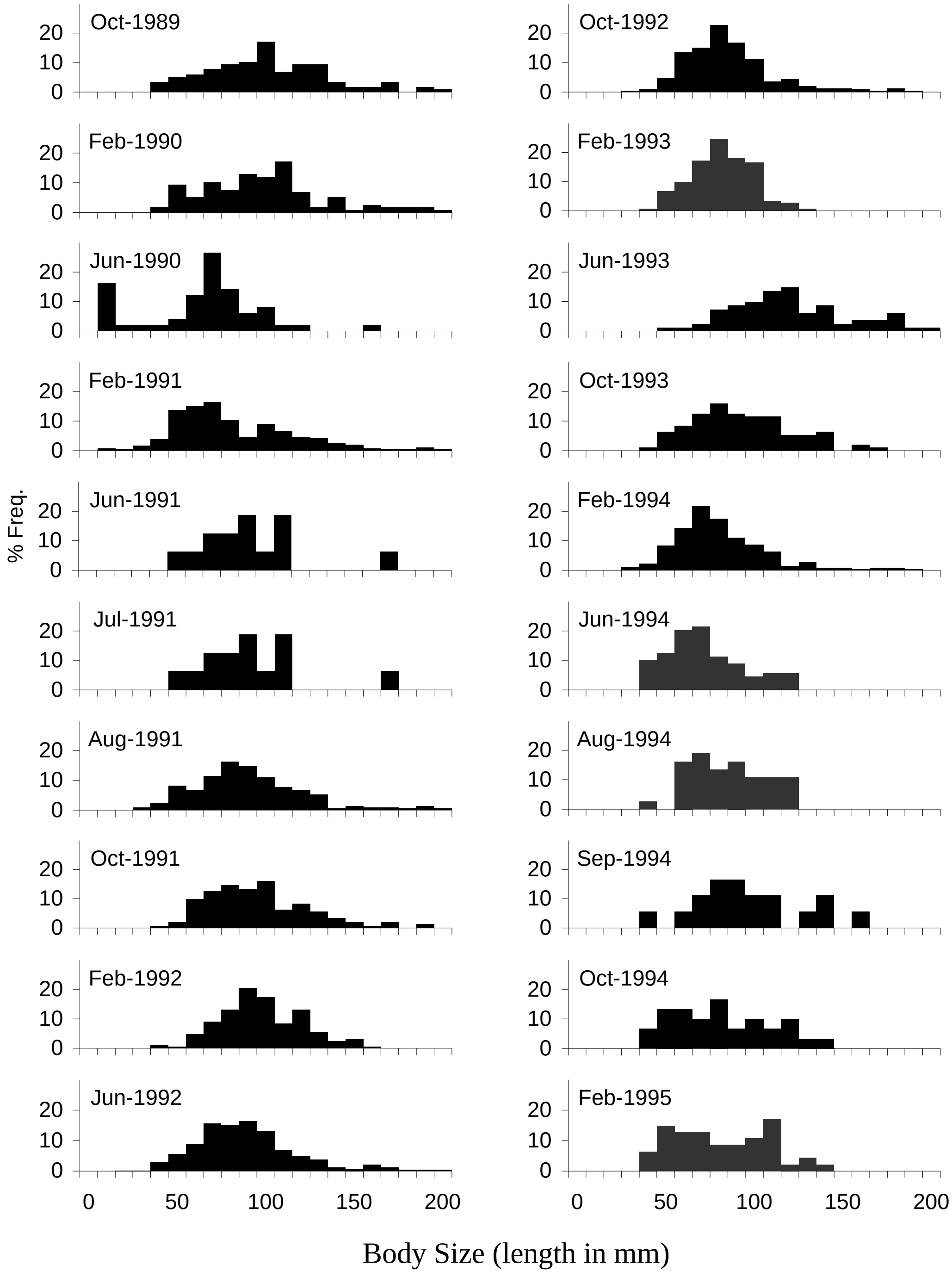
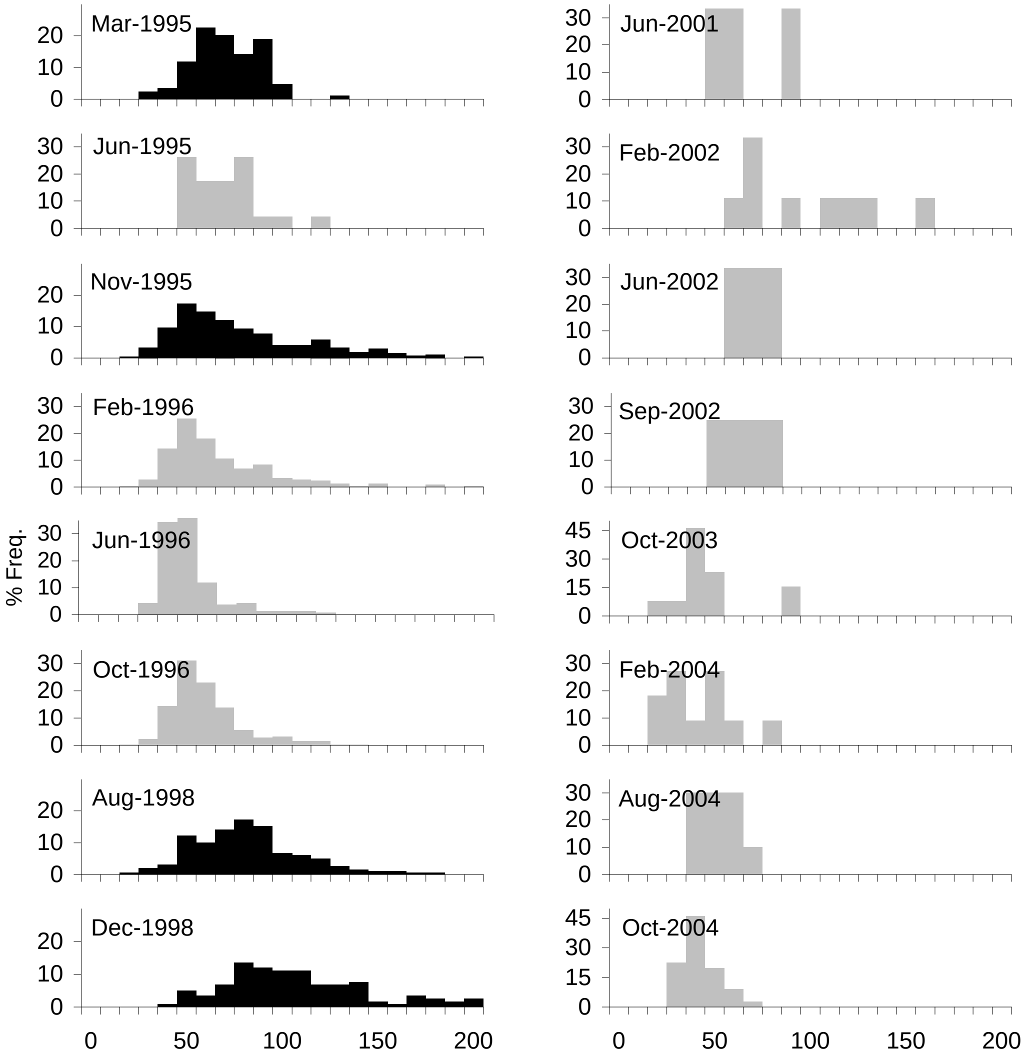


Figure 12. Monthly percent frequency distributions for *P. vitrea* for October 1989 to February 1995.



Body Size (length in mm)

Fig. 12 (continued). Monthly percent frequency distributions for *P. vitrea* for March 1995 to October 2004. Note that the gray bars filed bars have differing scales from black bars.

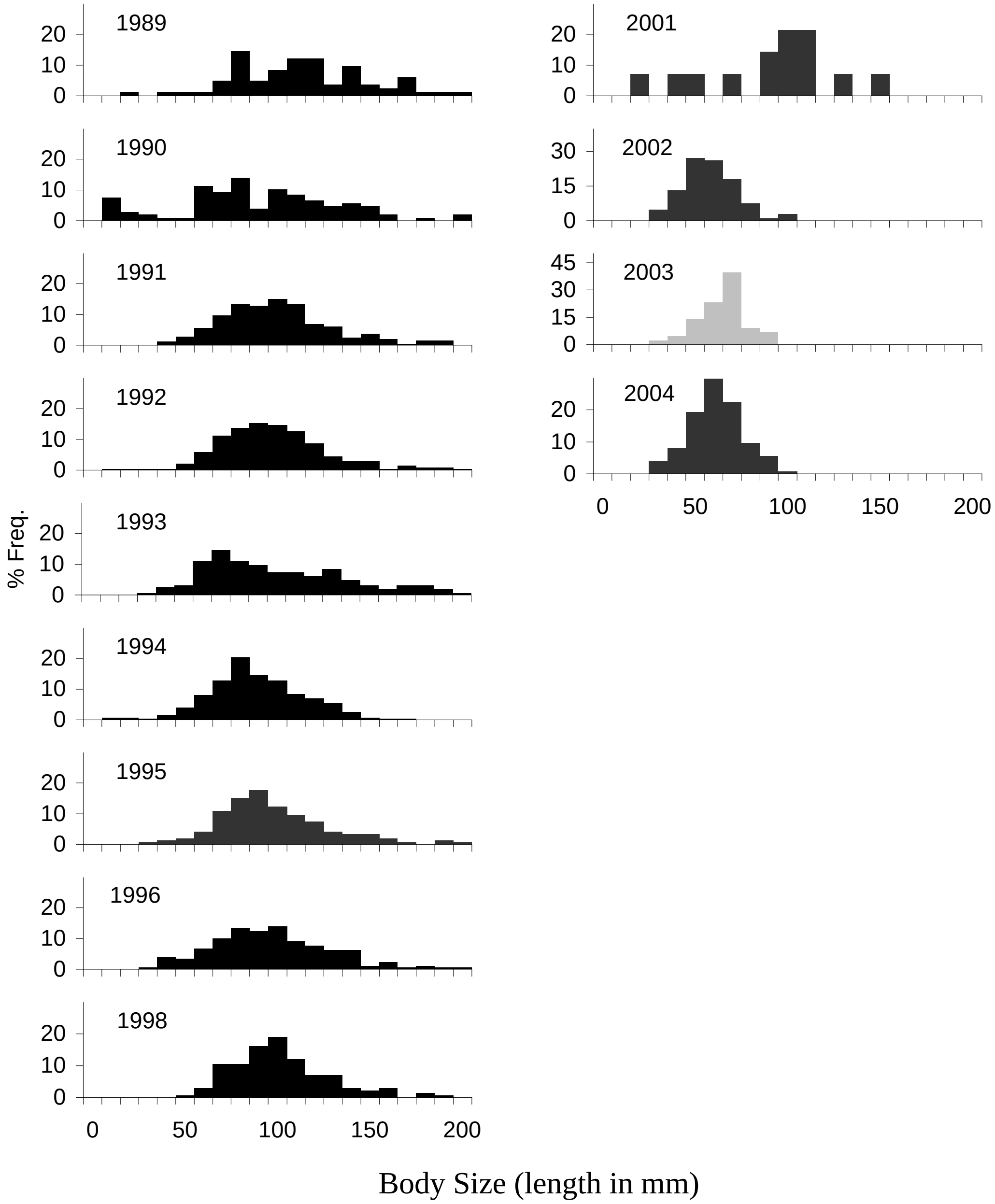
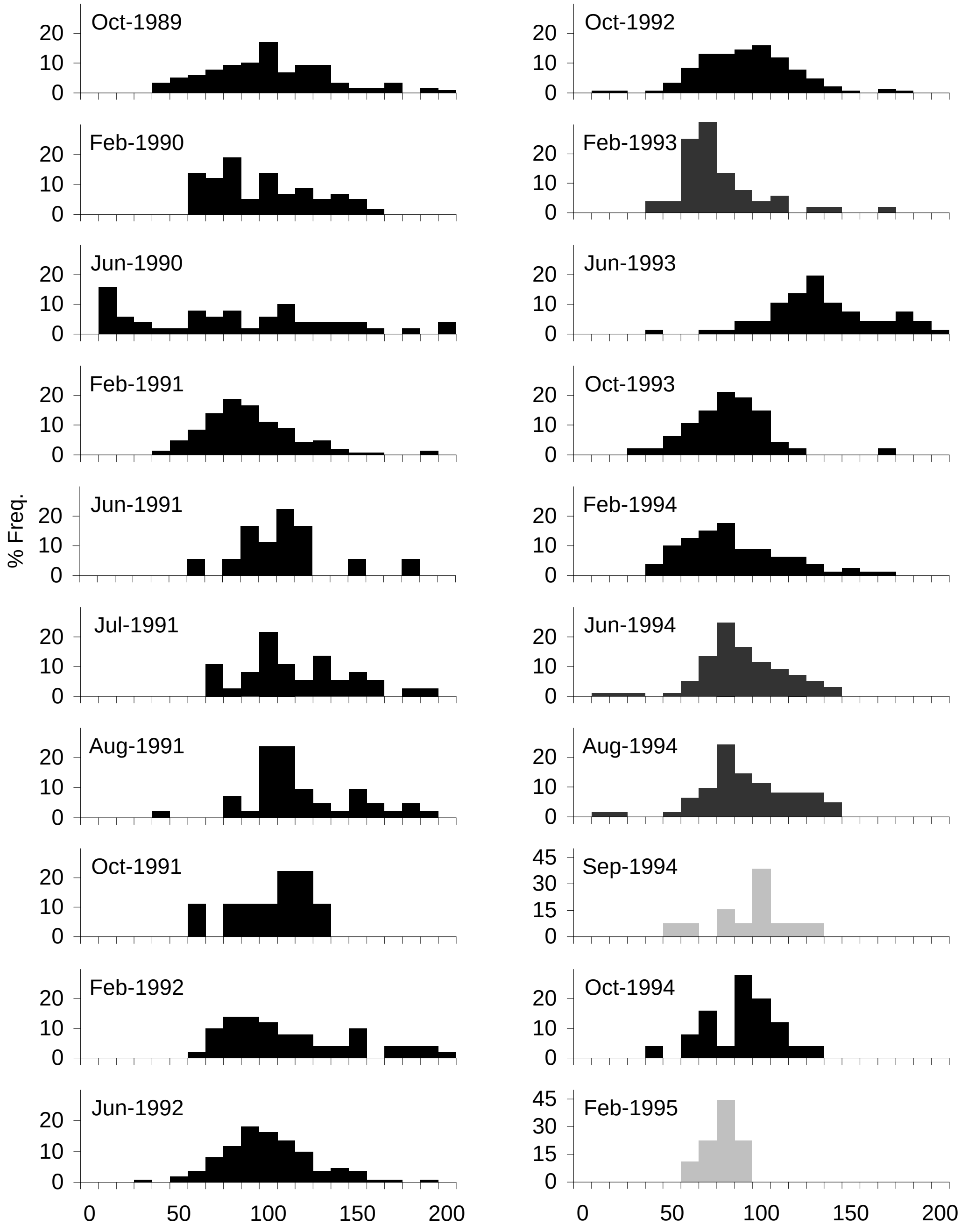


Figure 13. Yearly percent frequency distributions for *A. abyssorum* for 1989 to 2004. Note that the gray bars filed bars have differing scales from black bars.



Body Size (length in mm)

Figure 14. Monthly percent frequency distributions for *A. abyssorum* for October 1989 to February 1995. Note that the gray bars filed bars have differing scales from black bars.

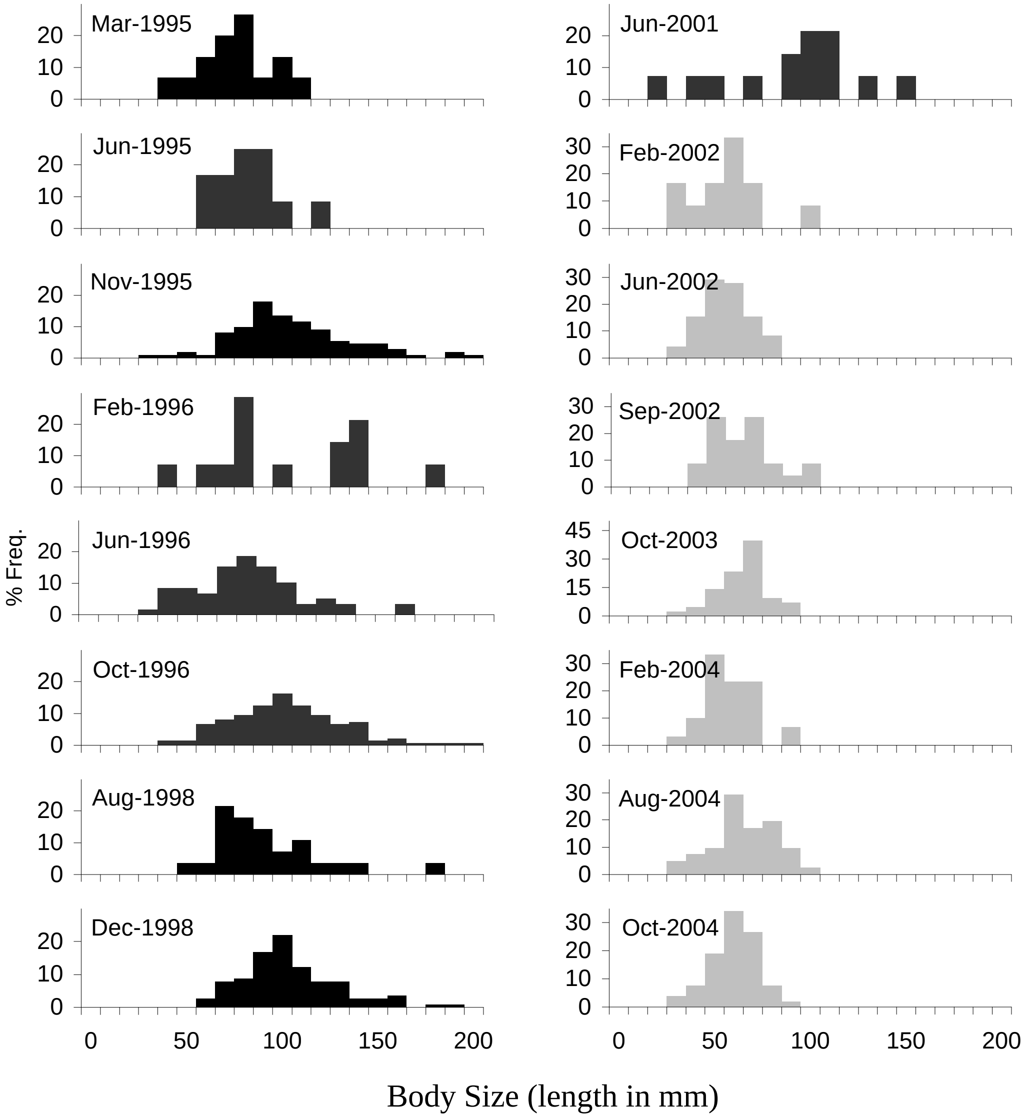


Figure 14 (continued). Monthly percent frequency distributions for *A. abyssorum* for March 1995 to October 2004. Note that the gray bars filed bars have differing scales from black bars.

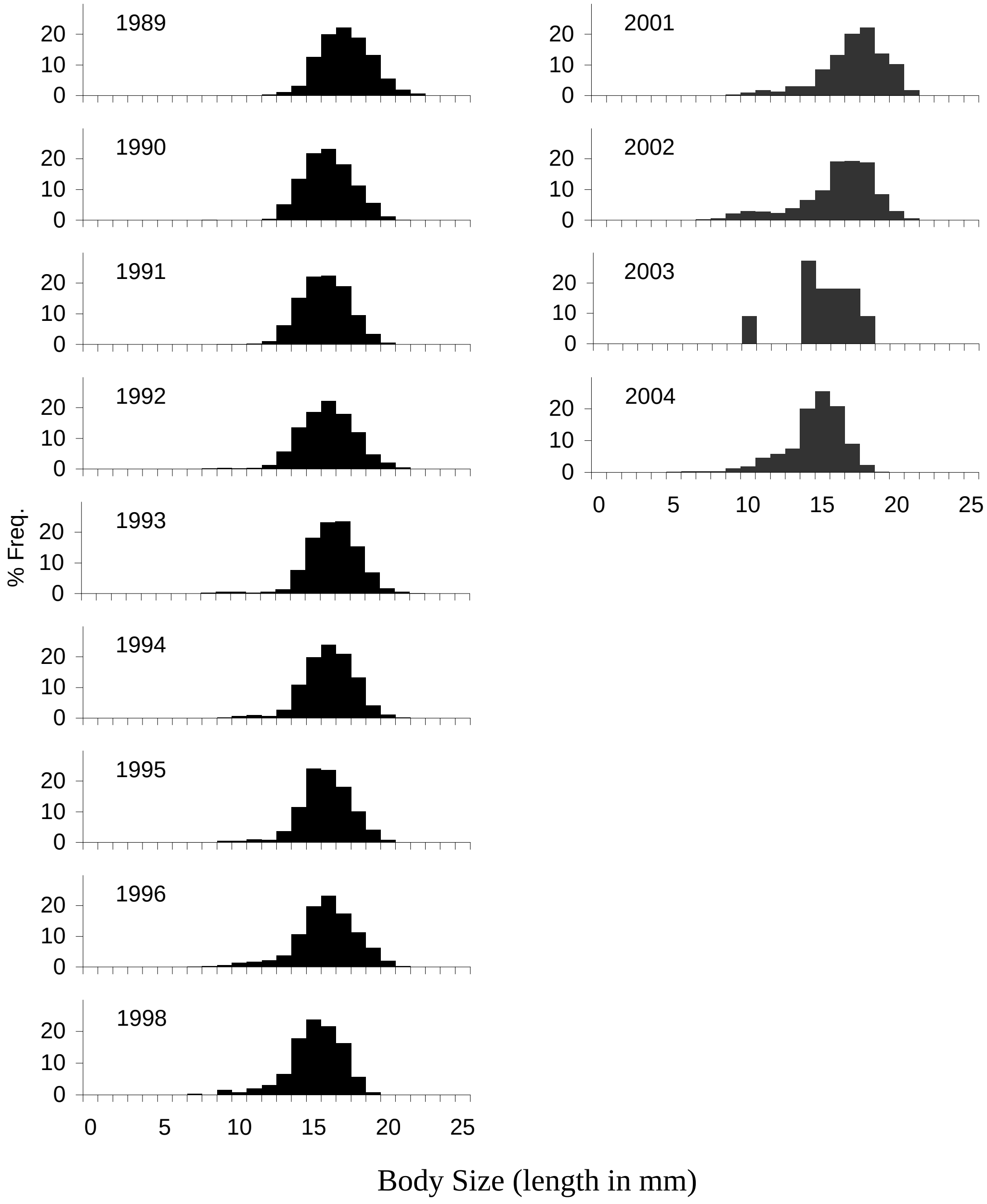


Figure 15. Yearly percent frequency distributions for *O. bathybia* for 1989 to 2004. Note that the gray bars filed bars have differing scales from black bars.

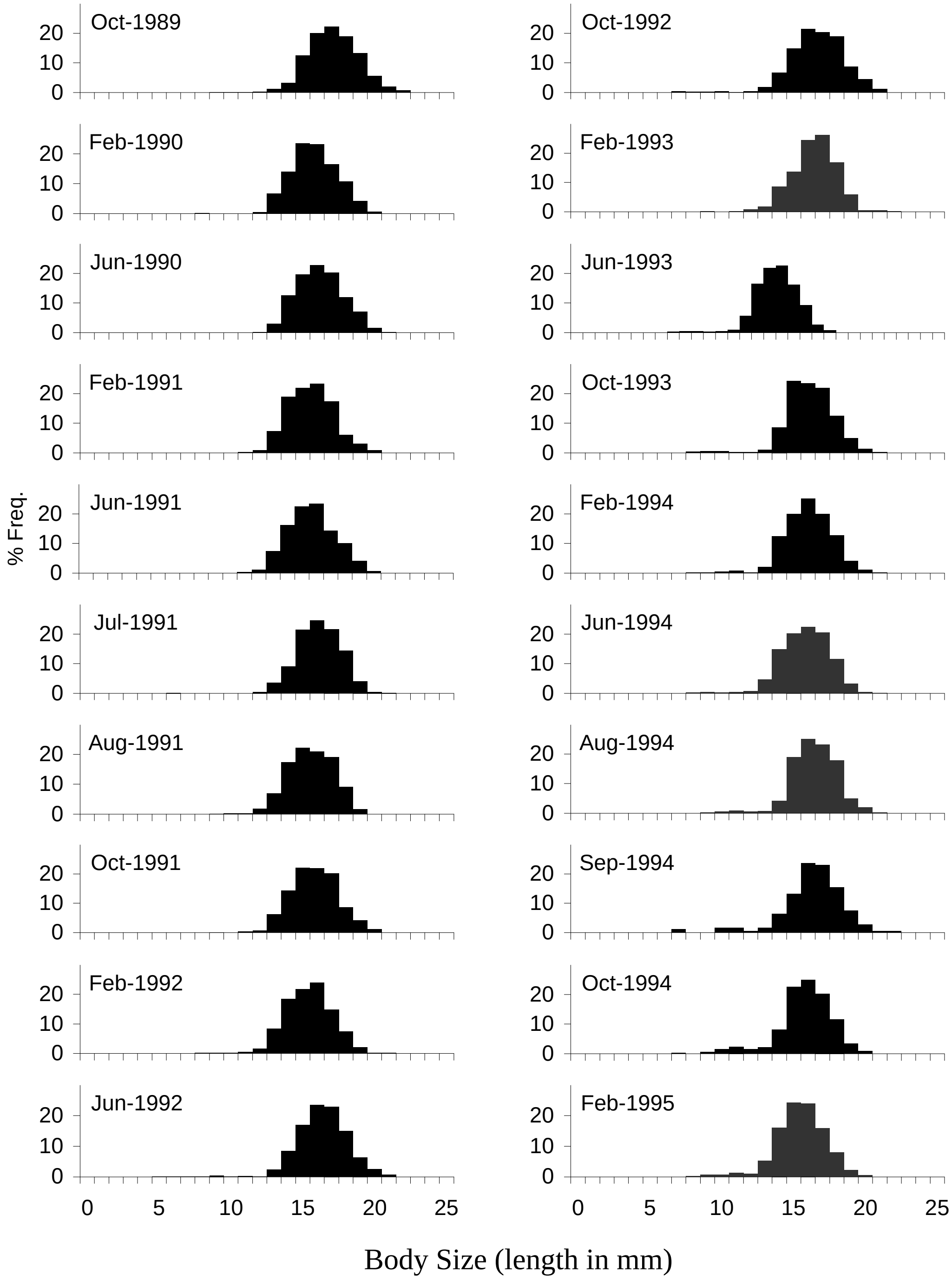


Figure 16. Monthly percent frequency distributions for *O. bathybia* for October 1989 to February 1995. Note that the gray bars filed bars have differing scales from black bars.

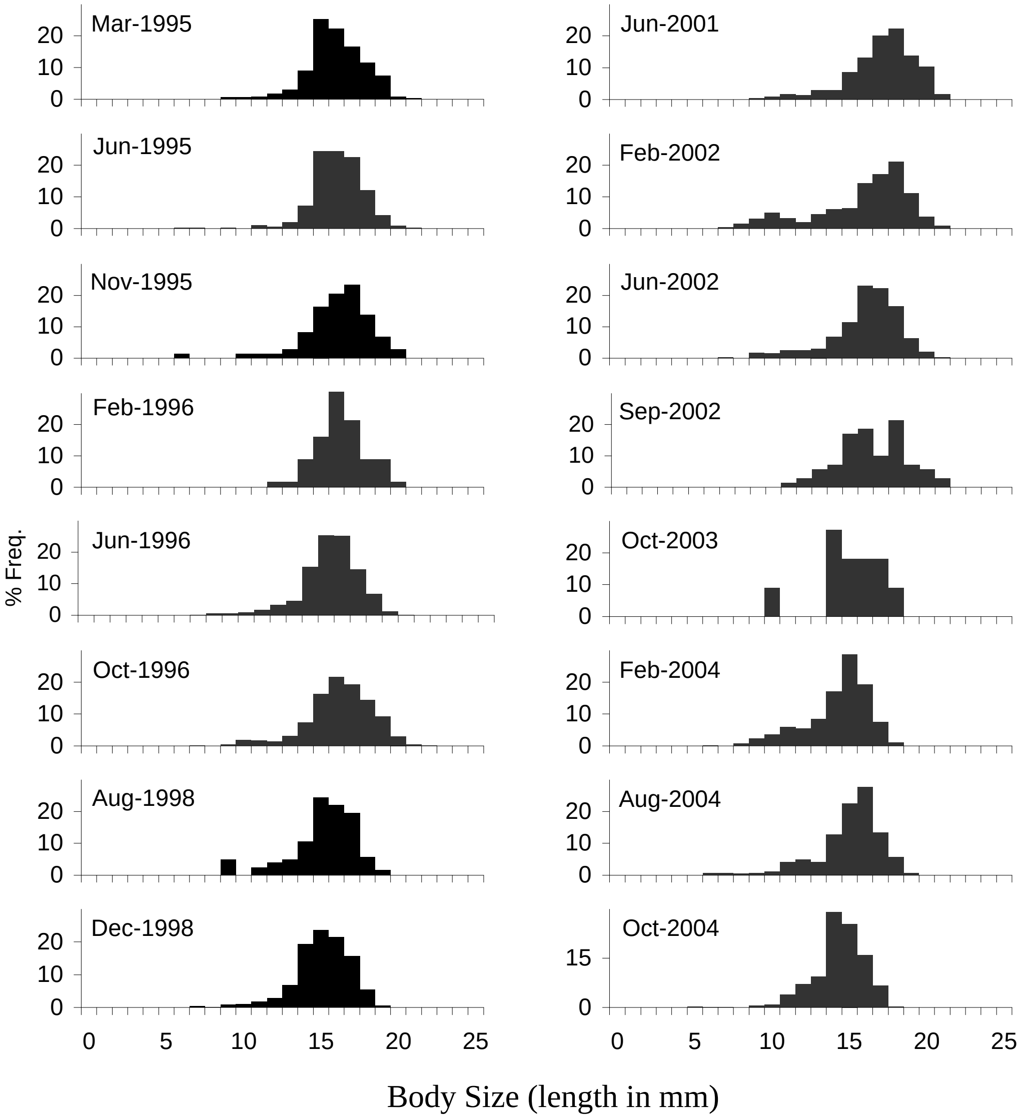


Figure 16 (continued). Monthly percent frequency distributions for *O. bathybia* for March 1995 to October 2004. Note that the gray bars filed bars have differing scales from black bars.

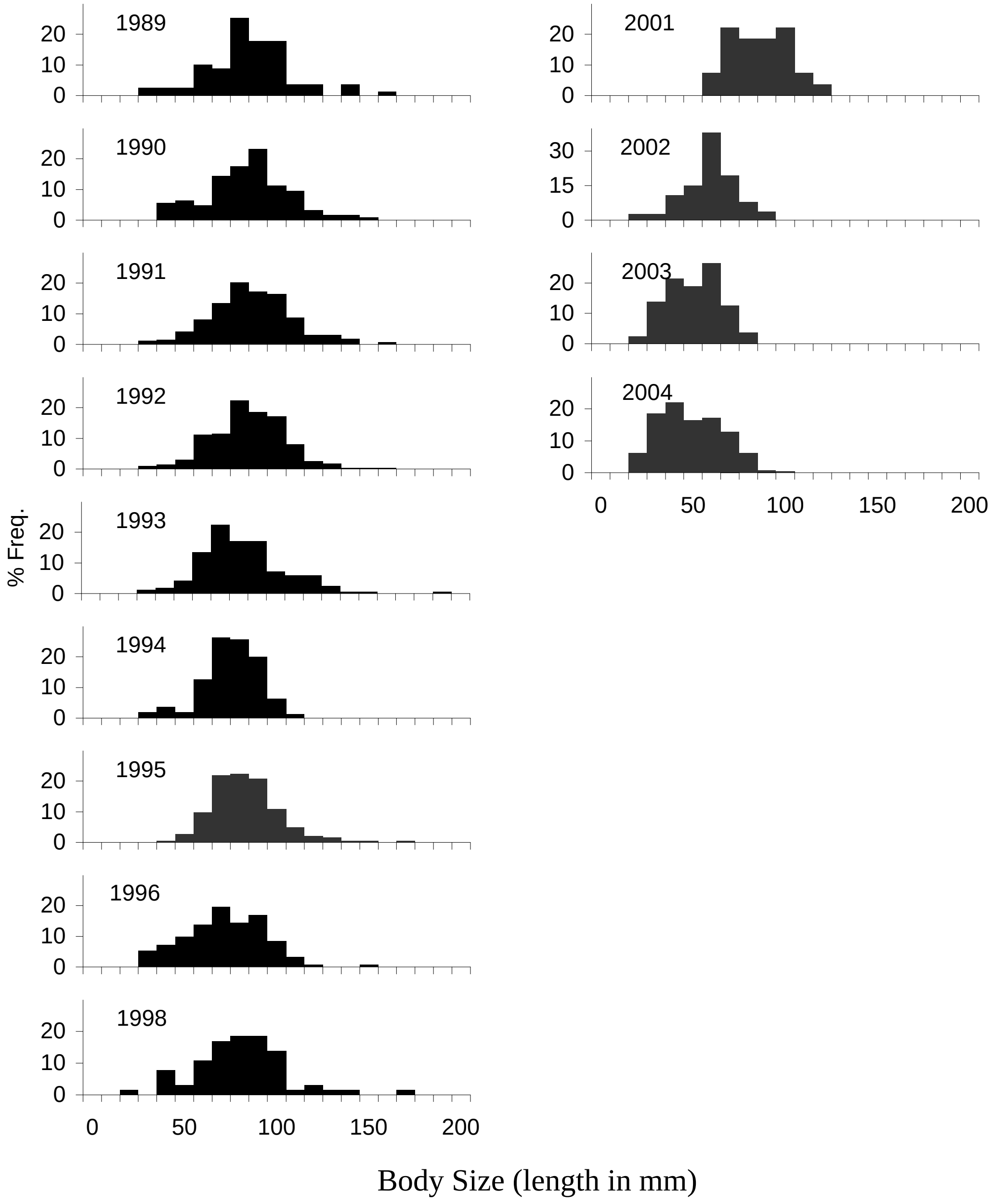


Figure 17. Yearly percent frequency distributions for *Ec. rostrata* for 1989 to 2004. Note that the gray bars filed bars have differing scales from black bars.

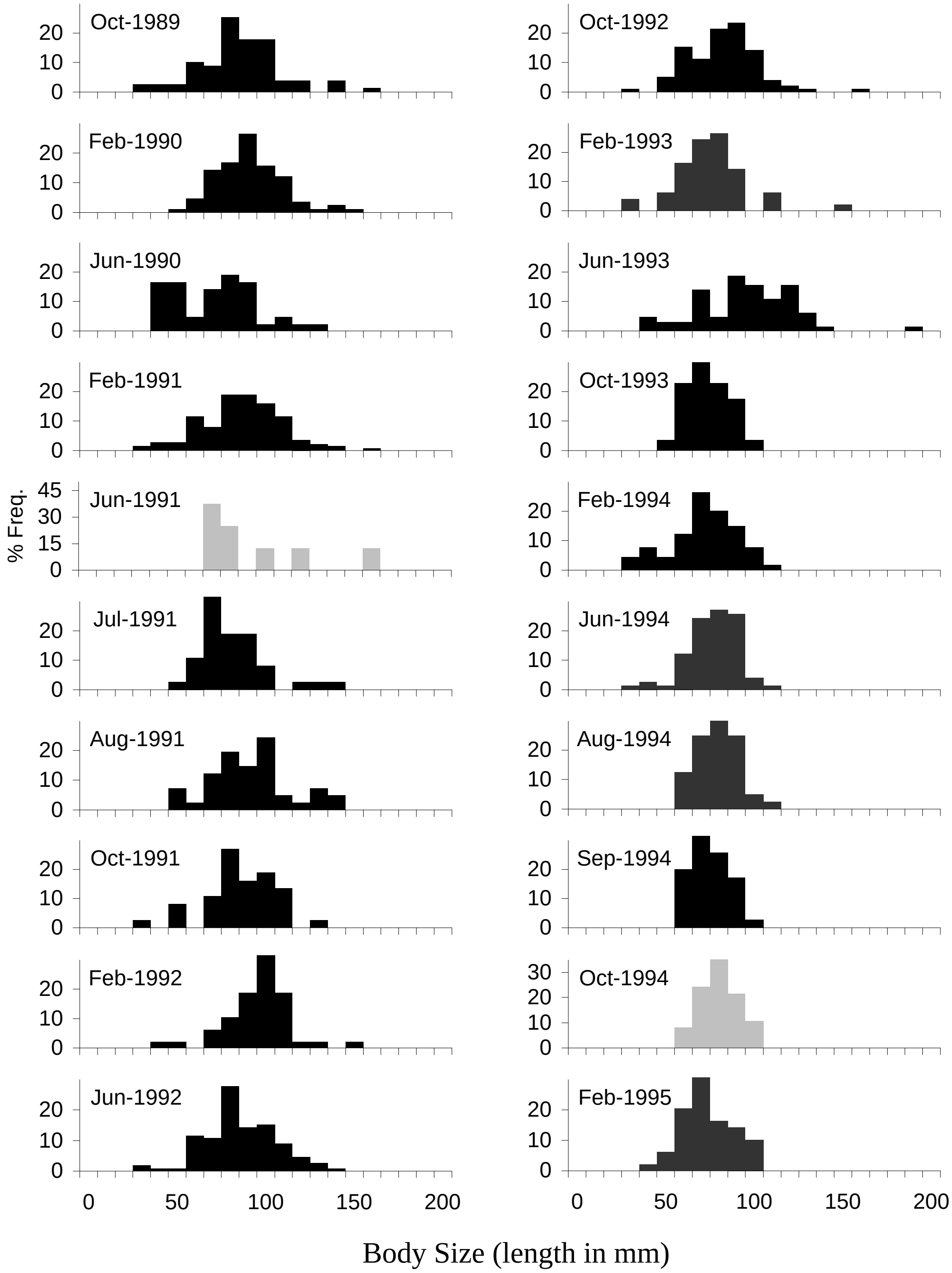


Figure 18. Monthly percent frequency distributions for *Ec. rostrata* for October 1989 to February 1995. Note that the gray bars filed bars have differing scales from black bars.

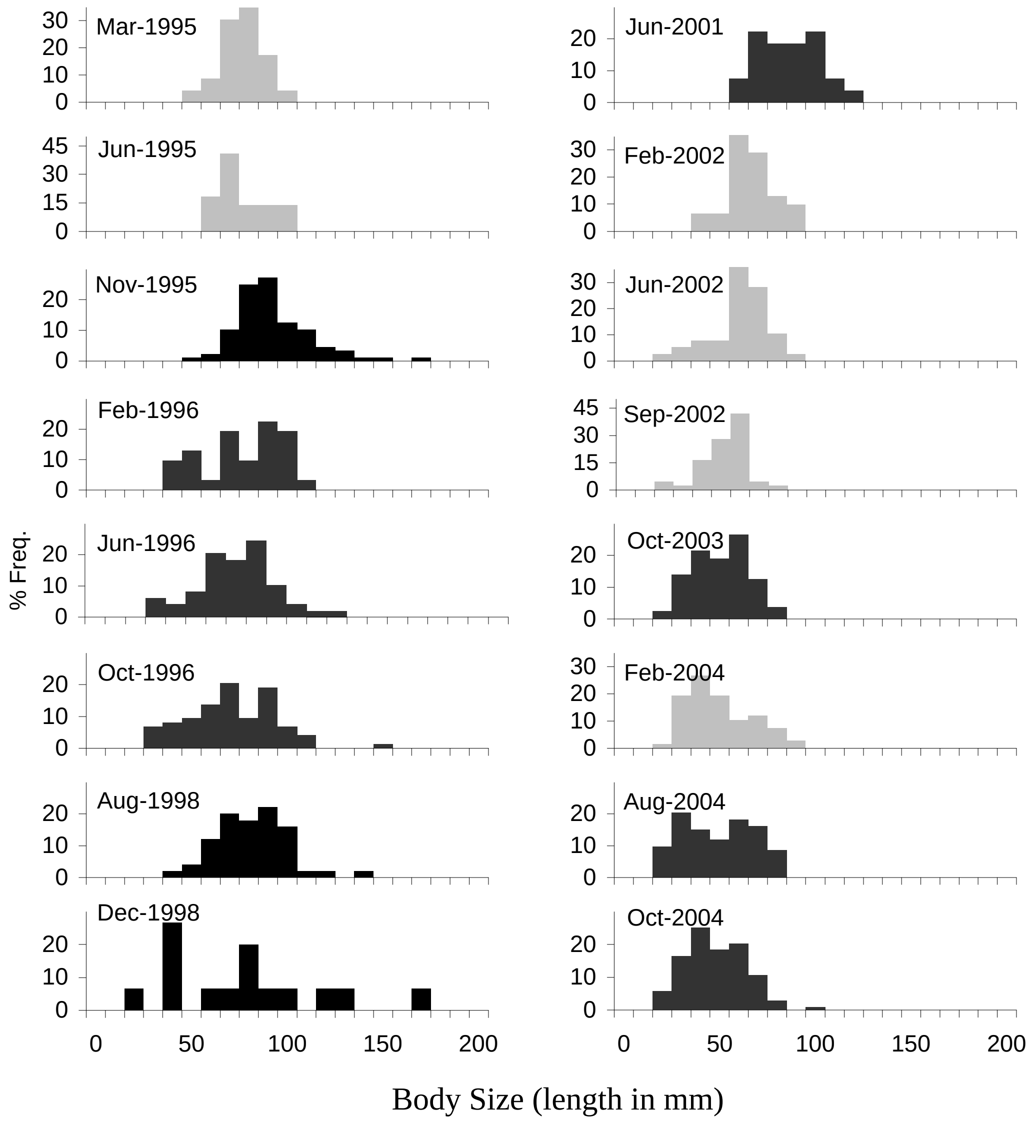
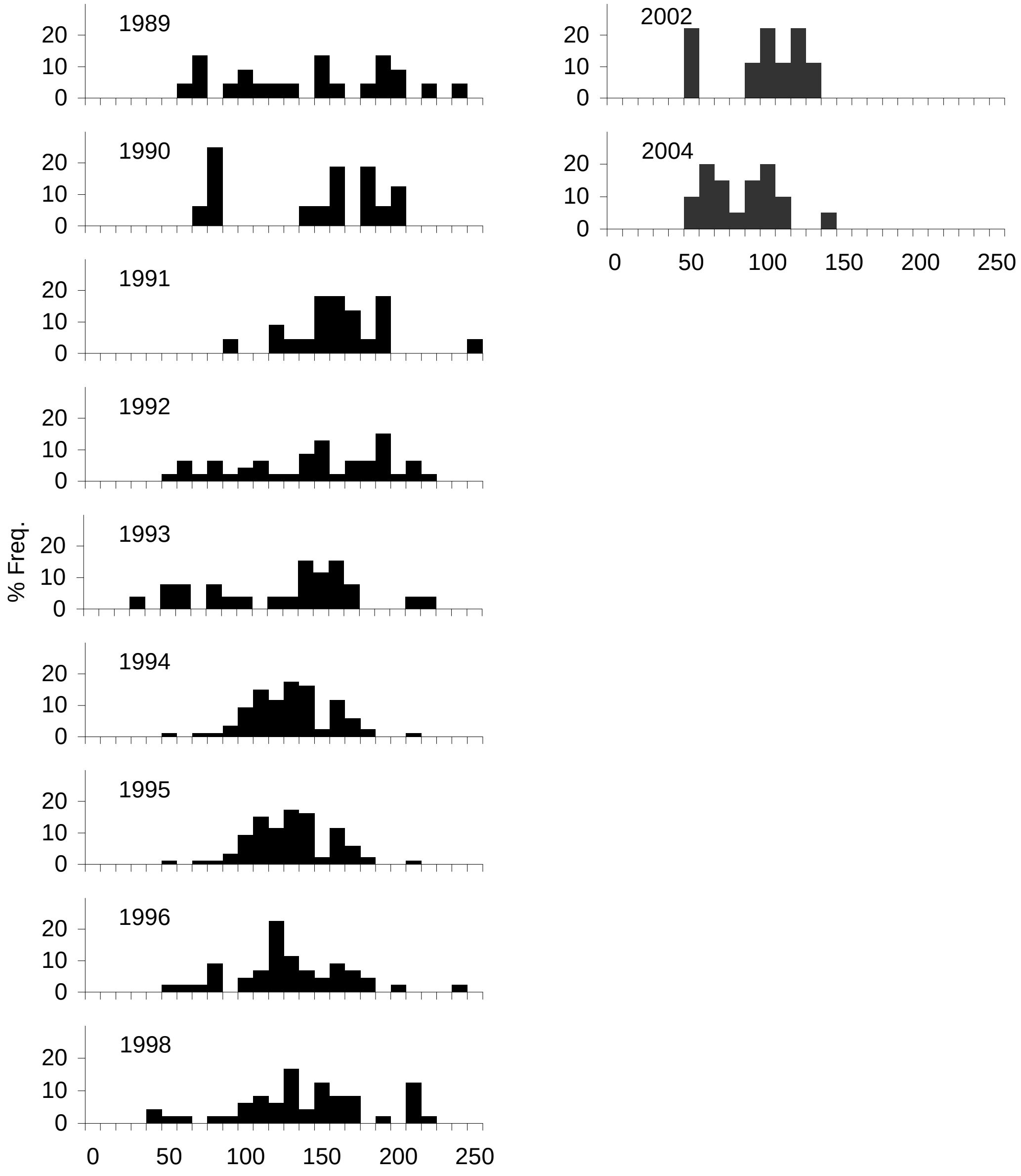


Figure 18 (continued). Monthly percent frequency distributions for *Ec. rostrata* for March 1995 to October 2004. Note that the gray bars filed bars have differing scales from black bars.



Body Size (length in mm)

Figure 19. Yearly percent frequency distributions for *Sy. profundi* from 1989-2004.

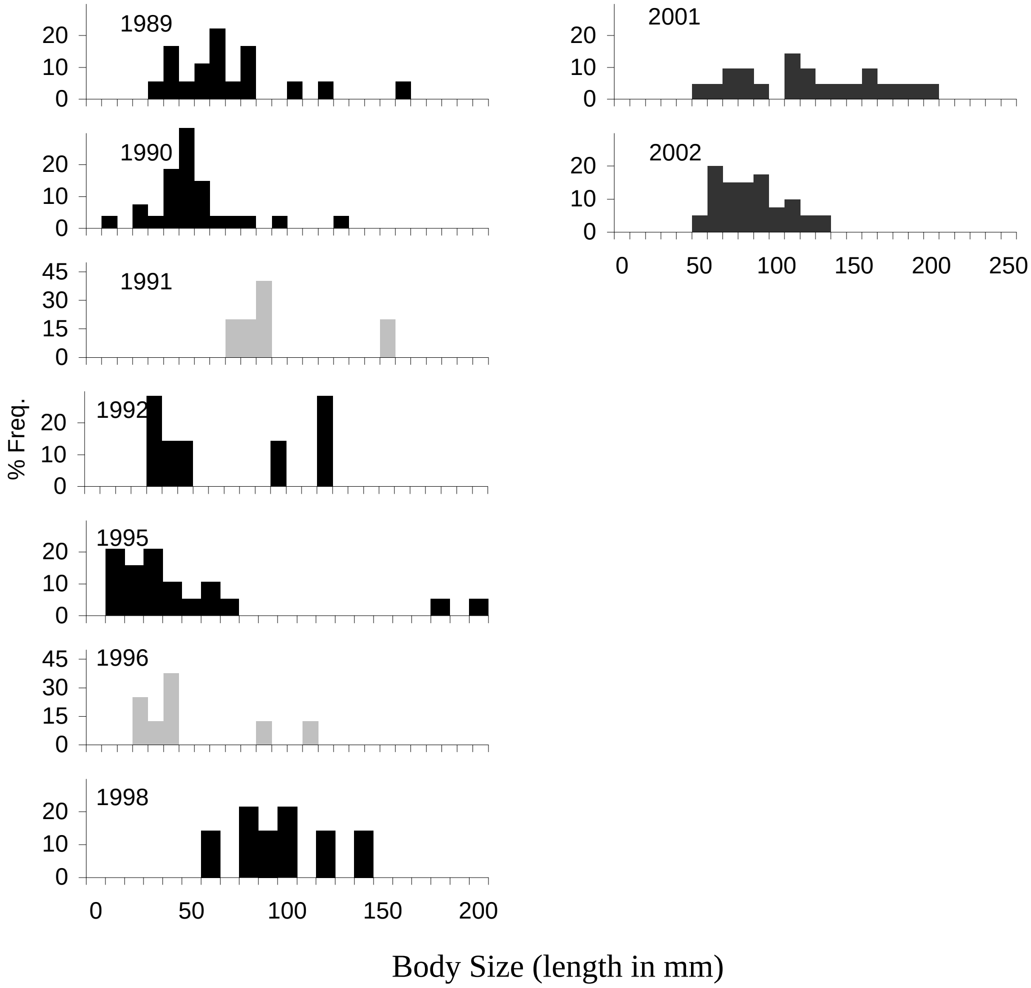


Figure 20. Yearly percent frequency distributions for *S. globosa* from 1989-2002.

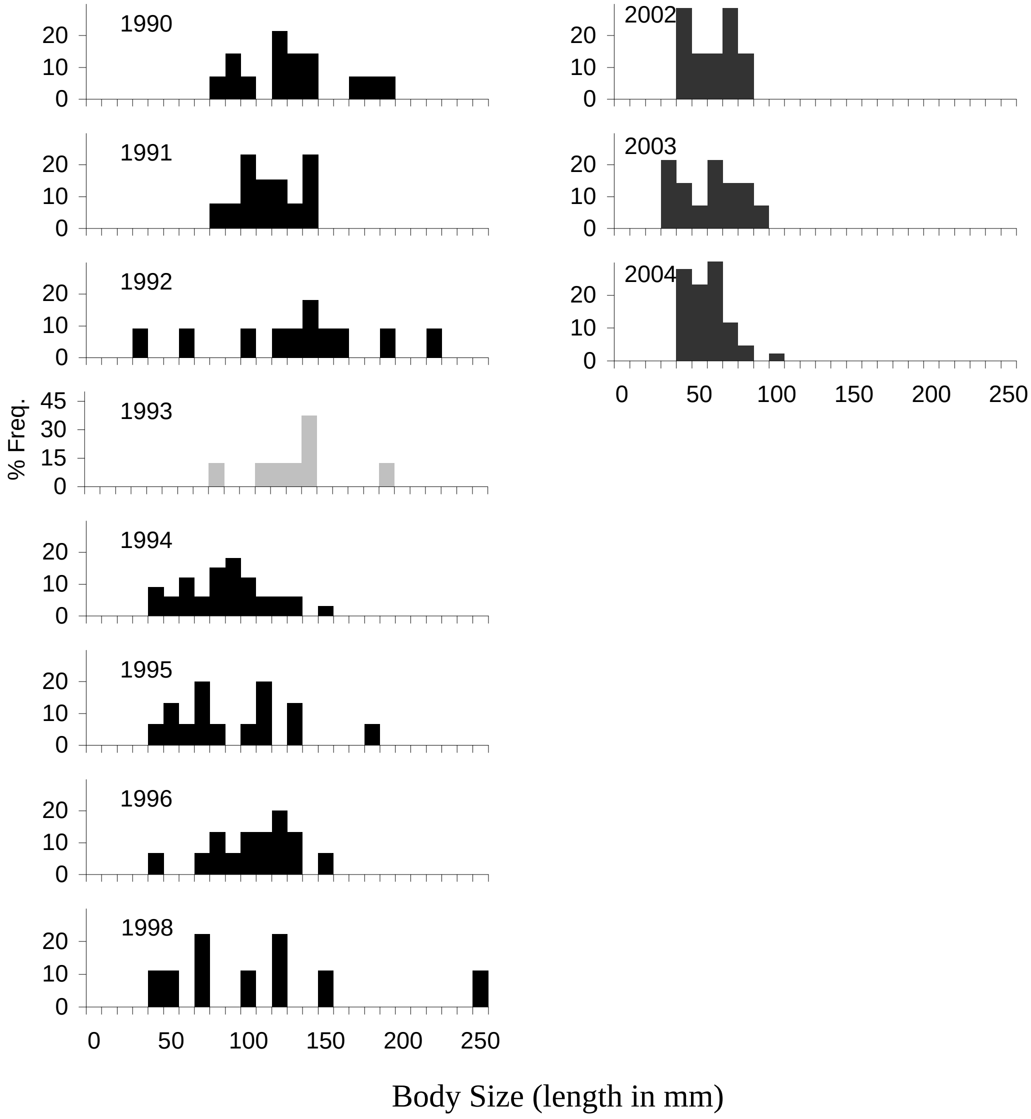


Figure 21. Yearly percent frequency distributions for *O. mutabilis* from 1990-2004.

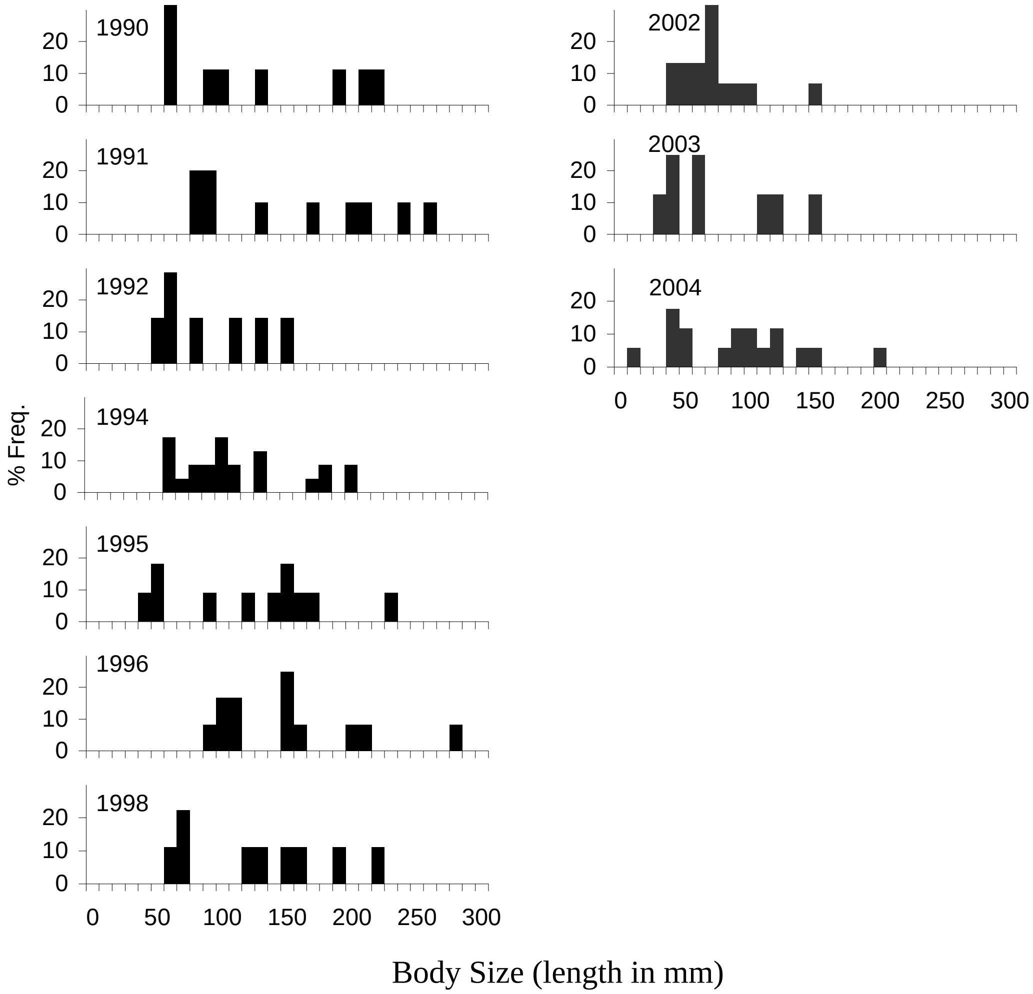


Figure 22. Yearly percent frequency distributions for *Ps. longicauda* from 1990-2004.

References

Allee, W. C. 1938. The social life of animals. Norton, New York, USA.

Bailey, D. M., H. A. Ruhl, K. L. Smith, Jr. 2006. Long-term changes in benthopelagic fish abundance in the abyssal northeast Pacific Ocean. Ecology 87: 549-555.

Baldwin, R. J., R. C. Glatts, and K. L. Smith, Jr. 1998. Particulate matter fluxes into the benthic boundary layer at a long time-series station in the abyssal NE Pacific: composition and fluxes. Deep-Sea Research II. 45: 643-666.

Barnett, T. P., D. W. Pierce, K. M. AchutaRoa., P. J. Gleckler, B. D. Santer, J. M. Gregory, and W. M. Washington. 2005. Penetration of human-induced warming into the world's oceans. Science 309: 284-287.

Battaglene, S.C., J.E. Seymour, and C., Ramofafia. 1999. Survival and growth of cultured juvenile sea cucumbers, *Holothuria scabra*. Aquaculture 178: 293-322.

Beaulieu, S., and R. Baldwin. 1998. Temporal variability in currents and the benthic boundary layer at an abyssal station off central California. Deep-Sea Research II. 45: 587-615.

Beaulieu, S. E., K. L. Smith, Jr., H. A. Ruhl, and R. J. Baldwin. (in preparation) Megafauna at the abyssal seafloor underlying the North Pacific Subtropical Gyre: composition and abundance from photographic and video surveys. Deep-Sea Research I.

Bett, B. J, M. G. Malzone, B. E. Narayanaswamy, and B. D. Wigham. 2001. Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. Progress in Oceanography 50: 349-368.

Billett, D. S. M., B. J. Bett, A. L. Rice, M. H. Thurston, J. Galeron, M. Sibuet and G. A. Wolff. 2001. Long-term changes in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). Progress in Oceanography 50: 325-348.

Billett, D. S. M., C. Llewellyn and J. Watson. 1988. Are deep-sea holothurians selective feeders? Pages 421-429 *in* R. D. Burke, P. V. Mladenov, P. Lambert, R. L. Parsley, and A. Balkema, editors. Echinoderm biology. Rotterdam.

Bluhm, B. A., I. A. MacDonald, C. Debenham, K. Iken. 2005. Macro- and megabenthic communities in the high Arctic Canada Basin: initial findings. Polar Biology 28: 218-231.

Bluhm, H. 2001. Re-establishment of an abyssal megabenthic community after experimental physical disturbance of the seafloor. Deep-Sea Research II 48:3841-3868.

Bluhm, H., A. Gebruk. 1999. Holothuroidea (Echinodermata) of the Peru Basin – ecological and taxonomic remarks based on underwater images. Marine Ecology, 20:167-195.

Boetius, A., T. Ferdelman, and K. Lochte. 2000. Bacterial activity in sediments of the deep Arabian Sea in relation to vertical flux. Deep-Sea Research II 47:2835-2875.

Booth, J. A. T., H. A. Ruhl, K. L. Smith, Jr., L. Lovell, and D. M. Bailey. (in preparation). Population dynamics of NE Pacific abyssal ophiuroids. Deep-Sea Research I.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance Sampling: Estimating abundance of biological populations. Chapman and Hall, London.

Campos-Creasey, L. S., P. A. Tyler, J. D. Gage, and A. W. G. John. 1994. Evidence for coupling the vertical flux of phytodetritus to the diet and seasonal life history of the deep-sea echinoid *Echinus affinis*. Deep-Sea Research 41: 369-388.

Cronin, T. M., D. M. DeMartino, G. S. Dwyer and J. Rodriguez-Lazaro. 1999. Deep-sea ostracod species diversity: response to late Quaternary climate change. Marine Micropaleontology 37: 231-249.

David, B., Magniez, F., Villier, L., and P. deWeaver. 2003. Conveying behavior of the deep sea pourtalesiid Cystocrepis setigera off Peru. Pages 253-257 *in* J.P. Féral, and B. David, editors. Echinoderm Research 2001. Swets & Zeitlinger, Rotterdam.

Demopoulos, A. W. J., C. R. Smith, D. J. DeMaster, and W. L. Fornes. 2003. Evaluation of excess 234Th activity in sediments as an indicator of food quality for deep-sea deposit feeders. Journal of Marine Research 61:276-284.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling 3: 481-538.

Drazen, J. C., R. J. Baldwin and K. L. Smith, Jr. 1998. Sediment community response to a temporally varying food supply at an abyssal station in the NE Pacific. Deep-Sea Research II. 45: 893-913.

Foell, E. J., and D. L. Pawson. 1986. Photographs of invertebrate megafauna from abyssal depths of the north-eastern equatorial Pacific Ocean. Ohio Journal of Science 86:61-68.

Gage J. D., and P. A. Tyler. 1991. Deep-sea biology. Cambridge University Press, New York, 504 pp.

Ginger, M. L., et al. 2001. Organic matter assimilation and selective feeding by holothurians in the deep sea: some observations and comments. Progress in Oceanography 50:407–422.

Glover, A. G., and C. R. Smith. 2003. The deep-sea floor ecosystem: current status and prospects of anthropogenic change by the year 2025. Environmental Conservation 30: 219-241.

Gooday, A. J. 1988. A response by benthic Foraminifera to the deposition of phytodetritus in the deep sea. Nature 332, 70-73.

Grassle, J. F., H. L. Sanders, R. R. Hessler, G. T. Rowe, and T. McLellan. 1975. Pattern and zonation: a study of the bathyal megafauna using the research submersible Alvin. Deep-Sea Research 22: 457-481.

Grassle, J. F. 1989. Species Diversity in Deep-Sea Communities. Trends in Ecology and Evolution 4: 12-15.

Gutt, J., and D. Piepenburg. 1991. Dense aggregations of three deep-sea holothurians in the southern Weddell Sea, Antarctica. Marine Ecology Progress Series 68:277-285.

Hansen, J., et al., 2005: Earth's Energy Imbalance: Confirmation and Implications. Science 308: 1431-1435.

Hjort, J. 1926. Fluctuations in the year classes of important food fishes. Journal du Conseil International Pour l'Exploration de la Mer 1:1-38.

Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, and D. Xiaosu, editors, IPCC. 2001. Climate Change 2001: The Scientific Basis. Cambridge University Press, Cambridge.

Hudson, I. R., D. W. Pond, D. S. M. Billett, P. A. Tyler, R. S. Lampitt and G. A. Wolff. 2004. Temporal variations in the fatty acid composition of deep-sea holothurians: evidence of bentho-pelagic coupling. Marine Ecology Progress Series 281: 109-120.

Hudson, I. R., B. D. Wigham, D. S. M. Billett, and P. A. Tyler. 2003. Seasonality and selectivity in the feeding ecology and reproductive biology of deep-sea bathyal holothurians. Progress in Oceanography 59: 381-407.

Iken, K., T. Brey, U. Wand, J. Voigt, and P. Junghans. 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Progress in Oceanography 50, 383-405

Kahru, M., and B. G. Mitchell. 2002a. Influence of the El Niño-La Niña cycle on satellite-derived primary production in the California Current. Geophysical Research Letters 29: 1846.

Kahru, M., and B. G. Mitchell. 2002b. Seasonal and nonseasonal variability of satellite-derived chlorophyll and colored dissolved organic matter concentration in the California Current. Journal of Geophysical Research 106: 2517–2529.

Karl, T. R., S. J. Hassol, C. D. Miller, and W. L. Murray, editors. 2006. Temperature Trends in the Lower Atmosphere: Steps for Understanding and Reconciling Differences. A Report by the Climate Change Science Program and the Subcommittee on Global Change Research, Washington, DC, USA.

Kaufmann, R. S., W. W. Wakefield, and A. Genin. 1989. Distribution of epibenthic megafauna and lebensspuren on two central North Pacific seamounts. Deep-Sea Research 36: 1863-1896.

Kaufmann, R. S., and K. L. Smith, Jr. 1997. Activity patterns of mobile epibenthic megafauna at an abyssal site in the eastern North Pacific: Results from a 17-month time-lapse photographic study. Deep-Sea Research I 44: 559-579.

Laake, J. L., S. T. Buckland, D. R. Anderson, and K. P.Burnham. 1994. Distance Users Guide V 2.1. Colorado Cooperative Fish and Wildlife Research Unit. Colorado State University, Fort Collins, Colorado, USA.

Lampitt, R. S., B. J. Bett, K. Kiriakoulakis, E. E. Popova, O. Ragueneau, A. Vangriesheim and G. A. Wolff. 2001. Material supply to the abyssal seafloor in the Northeast Atlantic. Progress in Oceanography 50: 27-63.

Lampitt, R. S., D. S. M. Billett, and A. L. Rice. 1986. Biomass of the invertebrate megabenthos from 500 to 4100 m in the northeast Atlantic Ocean. Marine Biology 93: 69-81.

Lauerman, L. M. L., and R. S. Kaufmann. 1998. Deep-sea epibenthic echinoderms and a temporally varying food supply: Results from a one year time-series in the NE Pacific. Deep-Sea Research II 45: 817-842.

Lauerman, L. M. L., R. S. Kaufmann, and K. L. Smith, Jr. 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. Deep-Sea Research I 43: 1075-1104.

Lauerman, L. M. L., J. M. Smoak, T. J. Shaw, W. S. Moore, and K. L. Smith, Jr. 1997. ^{234}Th and ^{210}Pb evidence for rapid ingestion of settling particles by mobile epibenthic megafauna in the abyssal NE Pacific. Limnology and Oceanography 42: 589-595.

Nybakken J., S. Craig, L. Smith-Beasley, G. Moreno, A. Summers, and L. Weetman. 1998. Distribution density and relative abundance of benthic invertebrate megafauna from three sites at the base of the continental slope off central California as determined by camera sled and beam trawl. Deep-Sea Research II 45: 1753-1780.

Ramirez-Llodra, E., W. D. K. Reid, and D. S. M. Billett. 2005. Long-term changes in reproductive patterns of the holothurian *Oneirophanta mutabilis* from the Porcupine Abyssal Plain. Marine Biology 146: 683-693.

Rodrigues, N., R. Sharma, and B. N. Nath. 2001. Impact of benthic disturbance on megafauna in Central Indian Basin. Deep-Sea Research II 48:3411-3426.

Ruhl, H. A. in preparation. Dispersion of mobile epibenthic megafauna on the abyssal seafloor in the northeast Pacific from 1989-2004. Deep-Sea Research I.

Ruhl, H. A., and K. L. Smith, Jr. 2004. Shifts in deep-sea community structure linked to climate and food supply. Science 305: 513-515.

Scheuring, I. 1999. Allee effect increases the dynamical stability of populations. Journal of Theoretical Biology 199: 407-414.

Sharma, R., and A. S. Rao. 1992. Geologic factors associated with megabenthic activity in the Central Indian Basin. Deep-Sea Research 39: 705-713.

Sibuet M., C. E. Lambert, R. Chesselet, and L. Laubier. 1989. Density of the major size groups of benthic fauna and trophic input in deep basins of the Atlantic Ocean. Journal of Marine Research 47: 851-867.

Smith, C. R., and S. C. Hamilton. 1983. Epibenthic megafauna of a bathyal basin off southern California: patterns of abundance, biomass, and dispersion. Deep-Sea Research 30: 907-928.

Smith, K. L., Jr. 1992. Benthic boundary layer communities and carbon cycling at Abyssal depths in the central North Pacific. Limnology and Oceanography 37:1034-1056.

Smith, K. L., Jr., R. J. Baldwin**,** H. A. Ruhl, M. Kahru, B. G. Mitchell, and R. S. Kaufmann. 2006. Climate effect on food supply to depths greater than 4000 m in the northeast Pacific. Limnology and Oceanography 51: 166-167.

Smith, K. L., Jr., and E. R. M. Druffel. 1998. Long time-series studies of the benthic boundary layer at an abyssal station in the NE Pacific. Deep-Sea Research II 45: 573-586.

Smith, Jr., K. L., N. D. Holland, and H. A. Ruhl. 2005. Enteropneust production of spiral fecal trails on the deep-sea floor observed with time-lapse photography. Deep-Sea Research I 52: 1228-1240.

Smith, K. L., Jr., R. S. Kaufmann and W. W. Wakefield. 1993. Mobile megafaunal activity monitored with a time-lapse camera in the abyssal North Pacific. Deep-Sea Research I 40: 2307-2324

Solan, M., B. D. Wigham, I. R. Hudson, R. Kennedy, C. H. Coulon, K. Norling, H. C. Nilsson, and R. Rosenberg. 2004. *In situ* quantification of bioturbation using time-lapse fluorescent sediment profile imaging (f-SPI), luminophore tracers and model simulation. Marine Ecology Progress Series 271: 1-12.

Summers, A. C., and J. Nybakken. 2000. Brittle star distribution patterns and population densities on the continental slope off central California (Echinodermata: Ophiuroidea). Deep-Sea Research II 47: 1107-1137.

Thiel, H. 2003. Anthropogenic impacts on the deep sea. Pages 427–471. *in* P. A. Tyler, editor. Ecosystems of the deep oceans. Ecosystems of the world Vol. 28. Elsevier, Amsterdam.

Thurston M. H., B. J. Bett, A. L. Rice, and P. A. B. Jackson. 1994. Variations in the invertebrate abyssal megafauna in the North Atlantic Ocean. Deep-Sea Research I 41: 3121-1348.

Tilot, V. 1992. La structure des assemblages megabenthiques d'une province à nodules polymétalliques de l'ocean Pacique tropical Est. Thése de Doctorat en Sciences de l'Université de Bretagne Occidentale. 380pp.

Tyler, P. A., J.D. Gage, and D. S. M. Billett. 1985. Life-history biology of Peniagone azorica and P. diaphana (Echinodermata: Holothuroidea) from the north-east Atlantic Ocean. Marine Biology, 89, 71-81.

Tyler, P. A., and D. S. M. Billett. 1987. The reproductive ecology of elasipodid holothurians from the N.E. Atlantic. Biological Oceanography 5:273-296.

Wakefield, W. W., and A. Genin. 1987. The use of a Canadian (perspective) grid in deep-sea photography. Deep-Sea Research 34: 469-478.

Wakefield, W. W., and W. Smithey. 1989. Two camera sleds for quantitative study of deep-sea megafauna. Scripps Institution of Oceanography Ref. Ser. No. 89-14, 25 pp.

Wigham, B. J., I. R. Hudson, D. S. M. Billett, and G. H. Wolff. 2003a. Is long-term change in the abyssal Northeast Atlantic driven by qualitative changes in export flux? Evidence from selective feeding in deep-sea holothurians. Progress in Oceanography 59:409-441.

Wigham, B. J., P. A. Tyler, and D. S. M. Billett. 2003b. Reproductive biology of the abyssal holothurian *Amperima rosea*: and opportunistic response to variable flux in surface derived organic matter? Journal of the Marine Biological Association of the United Kingdom 83: 175-188.

Young, C. M. 2003. Reproduction, development and life-history traits. Pages 381–426 *in* P. A. Tyler, editor. Ecosystems of the deep oceans. Ecosystems of the world Vol. 28. Elsevier, Amsterdam.

IV

Dispersion of Mobile Epibenthic Megafauna on the Abyssal Seafloor in the NE Pacific from 1989-2004

Abstract

The dispersion patterns for six mobile epibenthic megafauna were analyzed using forty-three photographic transects conducted from 1989-2004 at an abyssal NE Pacific station (Station M). Non-random dispersions occurred for all taxa analyzed, but aggregations occurred less than 25% of the time with no apparent trend in the timing or scale. Uniform dispersions also occurred at smaller scales of up to approximately 30 m about 25% of the time. Sporadic significant links between dispersion and density, as well as density and particulate organic carbon food flux also occurred. The holothuroid, *Peniagone diaphana*, tended to have higher densities and more aggregation during higher food flux conditions. The ophiuroids also had higher densities in transects with aggregation. The holothuroids *Elpidia minutissima*, *Peniagone vitrea*, *Abyssocucumis abyssorum*, and the echinoid *Echinocrepis rostrata*, did not have any detectable dispersion links with either density or food flux. The importance of density and food supply in determining dispersion remain inconclusive, but there are indications that higher densities can lead to increased aggregation at scales of tens of meters or more and higher food supply may lead to more uniformity at scales of 30 m or less.

Introduction

The nature of animal distributions on the seafloor can provide insights into factors controlling abundance and behavior patterns. Dispersion analysis can also help assess the assumption of line transect theory that populations are not heavily aggregated on scales that would strongly bias the results. Trawls and photographic transects have been used frequently to determine both baseline and longer-term dynamic information for deep-sea megafauna populations (animals typically = 1cm in size, Grassle et al., 1975) in the NE Pacific (e.g. Lauerman et al., 1996, Summers and Nybakken, 2000, Beaulieu et al., in preparation). The continuous photographic transects also provide detailed information on dispersion from scales of meters to over 100 m; information which is not recovered from trawl data. Uniform, random, and aggregated distributions are all possible within any given transect, with uniform distributions dominating at one scale and aggregation dominating at another. Ultimately all organisms have non-random distributions at some scale. Dispersion patterns of the six most dominant mobile epibenthic megafauna were examined here using data from a long-term abyssal study site (Station M, 4100 m depth, 34°50’N, 123°00’W) in the NE Pacific.

Several quantitative studies have examined echinoderm dispersions in the NE Pacific and found mixed results with aggregation occasionally observed at scales of 100 m or more (Smith, C.R., and Hamilton, 1983, Lauerman et al., 1996, Craig, 1997, Lauerman and Kaufmann, 1998, Summers and Nybakken, 2000). Localized food falls (Smith, C.R., 1985) and reproduction (Tyler et al., 1992, Young et al., 1992, Young, 2003) have been thought to be important megafauna aggregation factors in deep-sea habitats.

Dominant echinoderms at Sta. M have had order of magnitude shifts in abundance which have been linked to variation in surface climate and the sinking particulate organic carbon (POC) food supply (Ruhl and Smith, 2004). Correlations between population densities and community descriptors indicate that the abundance of several taxa have differential responses to food supply (Ruhl and Smith, 2004, Ruhl, in preparation). The differential responses could include influences on the quantity and quality of the food supply, the distribution of that resource on the seafloor, and the nature of any interactions within and between taxa. Dispersion analysis can help distinguish the degree to which spatially variable resources and animal interactions may be important. The mobile epibenthic megafauna also bioturbate marine sediments, affecting carbon sequestration processes. If the echinoderms at Sta. M are strongly aggregated then different areas of the seafloor may have different bioturbation and carbon sequestration properties.

Previous studies at Station M have examined the dispersion of the dominant fauna for two year-long periods from June 1990 to October 1991 and from June 1994 and June 1995 (Lauerman et al., 1996, Lauerman and Kaufmann, 1998). To examine dispersion these studies enumerated the number of individuals in discrete linear quadrats of 1, 2, 4, 8, 16, 32, 64, and 128 m in length. An index based on the variance to mean ratio was used to evaluate dispersion (e.g. Grassle et al., 1975; Kaufmann et al., 1989, Lauerman *et al.*, 1996). The significance of the variance to mean ratio was evaluated by comparing the result to a chi-squared distribution (Andrew and Mapstone, 1987, Lauerman et al., 1996). Combining quadrats into greater sizes by powers of two also limits the scales that can be tested. Influential portions of the transect data are lost in such analyses as sections that don’t fit into the fixed quadrats are discarded (Dale, 1999). Another common measure of aggregation, Morista’s *I,* is not able to reliably differentiate scales when more than one scale of dispersion is present (Dale, 1999). The results from discrete analyses of dispersion for Sta. M found significant aggregation at scales of up to 128 m but there was no consistent pattern within any taxon (Lauerman et al., 1996, Lauerman and Kaufmann, 1998).

Here a three-term local quadrat variance (3TLQV, Hill, 1973) technique was used to evaluate dispersion over a continuous range of scales. The results were then compared with randomized permutations to evaluate the significance of the observed dispersions. Using the 3TLQV method the dispersion patterns for forty-three continuous transects were examined for the period from 1989-1998. Uniform, random, and aggregated patterns were identified and used to evaluate any potential ecological importance. The potential for dispersion bias on density estimates made from line-transect images and any links between density or food supply and dispersion were evaluated.

Methods

Sta. M lies at the termination of the Monterey Fan and has very little relief over large areas of seafloor (< 100 m per 1600 km^2, Smith and Druffel 1998). Seafloor imagery suggests that low relief can also be found at smaller scales with changes in elevation typically less than 5 cm m^{-1}. The benthic environment experiences semidiurnal tidal currents with a slow principal southerly flow at 2.3 to 3.6 cm s^{-1} (Beaulieu and Baldwin, 1998). Variation in winds, sea surface temperatures, and upwelling in the California Current lead to changes in surface productivity and export flux at Sta. M (Smith et al., 2006). These interannual changes in surface conditions are related, in part, to variation in the El Niño Southern Oscillation (Kahru and Mitchell, 2002, Smith et al., 2006).

Information on the roughly seasonal abundance and distribution of the mobile epibenthic megafauna was collected using a camera sled and otter trawl system (Wakefield and Smithy, 1989). Abundance estimates are calculated using line-transect theory (Laake et al., 1994) and the computer program DISTANCE (Buckland et al., 1993), which accounts for the visibility of each taxon in each of the photographic transects. Further information on line-transect methods can be found in Wakefield and Genin (1987), Lauerman et al. (1996), Lauerman and Kaufmann (1998), and Ruhl and Smith (2004).

The 3TLQV method, originally designed for terrestrial plant studies (Hill, 1973), was used here to determine whether detectable non-random dispersions exist and at what scale do any observed patterns occur. The 3TLQV is less sensitive to peak drift and trends in transect data than the two-term variant (TTLQV, Dale, 1999) and is widely recommended for spatial pattern analysis (Ludwig and Goodall 1978; Lepš 1990; Dale, 1999). The 3TLQV method also allows for a broader range of discrete quadrat sizes to be examined based on the minimum unit in the analysis, which is 1 m in this case. To analyze the transect data for the 3TLQV, each transect was divided into 1-m units and the number of individuals of each taxon in each 1-m unit was assessed. The counts m^{-1} information provided input into the computer program PASSAGE (Rosenberg, 2001), which provided the 3TLQV with a 95% confidence interval over scales of up to 10% of the total transect length. The 10% threshold helped retain the power of the analysis (Ludwig and Reynolds, 1988). The 95% confidence intervals were estimated by Monte Carlo randomizations with 999 iterations. Forty-three continuous transect segments have been analyzed for thirty-one different times from

1989-2004. Transects were conducted on a roughly seasonal basis, but significant temporal gaps in the long-term record do exist. Taxa with fifteen or fewer individuals in a given transect were excluded from the analysis. For context, results from three example transects where the density and dispersion are known are also presented. Example simulations using 1000-m transects with overall densities of 0.2 m^{-1} illustrate 5-m scale uniform, random, and ~95-m scale aggregation with more random megafauna dispersion at smaller scales (Fig. 23a-f).

To examine whether composite POC flux influenced dispersion, the presence or absence of non-random dispersion was determined for large aggregation (> 100 m) scales, for all detectable scales, as well as for uniform dispersion. The non-parametric Mann-Whitney U test was then performed to determine if the POC flux was significantly different during times when a given taxon exhibited aggregation. Further details on the collection of POC flux data can be found in Baldwin et al. (1998), Smith et al. (2006) and methods for the preparation of the POC composite can be found in Ruhl (in preparation).

Results

Application of the 3TLQV method to the six most dominant taxa revealed the existence of non-random dispersion for all taxa during the study period (Table 4). However, the results were variable and consistent trends within any taxon were not found. Transects conducted synoptically had similar dispersion results 40-70% of the time and similar aggregation 50-80% of the time, depending on the taxon (Table 4).

The most dominant holothuroid, *Elpidia minutissima*, had uniform, random, and aggregated dispersion (Table 4, Fig. 24a-f). Uniform dispersion occurred at smaller scales in twenty transects with or without the presence of larger-scale aggregation. Twenty-six transects were long enough to detect aggregations = 100 m in scale, but of those only five transects had aggregation larger than 100 m. Five other transects had *E. minutissima* aggregations at scales of 66 to 100 m. There were no significant links between the observed dispersion patterns and POC flux or the density of *E. minutissima* (Table 4).

Abyssocucumis abyssorum also illustrates random dispersion (Fig. 25a and 25b, Table 4) and aggregation greater than 100 m in scale (Fig. 25c and 25d, Table 4). Uniform dispersions were not detected for *A. abyssorum*. The departure of the 3TLQV above the 95% confidence interval was only about 0.01, however, for the 107-m scale aggregation (Fig. 25d). The minimal departure is indicative of the other aggregations detected for *A. abyssorum* indicating that dispersions for *A. abyssorum* are still useful for detecting more intense aggregations, but interpretations for more subtle ecological or behavioral influences are speculative (Table 4).

Aggregations are most prominent for the ophiuroid group with 11 transects having greater than 100-m scale clumping out of 26 capable of detecting aggregation at the larger scale. The ophiuroid group, dominated by *Ophiura bathybia*, also had the most intense aggregation (Table 4, Fig. 25e and 25f). The intensity of the aggregation of the first June 1992 transect was rare, though, and most observed aggregations were much less intense (Table 4). Although no difference in the median POC flux was found for various dispersion conditions, ophiuroid transects with detectable aggregation had higher densities (Table 4).

The other holothuroids, *Peniagone diaphana* and *Peniagone vitrea*, had relatively few aggregations or uniform dispersions. Uniform distributions of *P. diaphana* had higher POC fluxes and aggregations had higher densities. *Peniagone vitrea*, on the other hand, had no significant links with POC flux or density. The echinoid *Ec. rostrata* had two aggregations at scales greater than 100 m, with seven instances of aggregation and six of smaller-scale uniform distribution. No significant links between non-random dispersions and POC flux or density were found for *Ec. rostrata* either. Overall, less than 25% of dispersion analyses exhibited aggregation and links between non-random dispersions and POC flux or density were not pervasive.

Discussion

The analysis of dispersion has revealed that abundance estimates using line transect data are not likely to be strongly biased by spatial heterogeneity at scales of up to approximately 100 m at Sta. M. Non-random patterns at scales larger than those examined here may still exist and be important in the overall distribution of epibenthic megafauna at Sta. M. Results for *P. diaphana* and the ophiuroid group suggest that higher POC food supply might lead to small-scale uniform dispersion and higher densities may lead to aggregation at larger scales. POC flux or density for most taxa, are not linked to dispersion at scales observable with line-transect photography.

The results here confirm the variance to mean ratio results of Lauerman et al. (1996) and Lauerman and Kaufmann (1998), where large-scale aggregations were relatively infrequent and did not have any clear patterns. The principal difference between the previous examinations of dispersion and the study here is that small-scale patterns of uniform dispersion were frequently observed using the 3TQLV method. Lauerman and Kaufmann (1998) also examined the importance of conspicuous phytodetrital aggregates from June 1994-June 1995 and found aggregate distributions were correlated to dominant mobile megafaunal distributions. Significant positive links between the distributions of *P. vitrea*, *E. minutissima*, *A. abyssorum*, *O. bathybia*, and *Ec. rostrata* and detrital aggregates were found for several transects during the year-long study (Lauerman and Kaufmann, 1998). Detrital aggregate patches were relatively rare, though, covering 0-1% of the seabed and correlations with animal dispersion were sporadic (Lauerman and Kaufmann, 1998). Photographically quantified aggregates can help discern the dispersion of a clumped food resource, but POC flux measured with sediment traps provide the best estimation of the amount of food reaching the site. The overall importance of aggregates at times of dense aggregate formation remains equivocal.

Most of the topographic relief visible in photographs of the seafloor at the site occurs at scales of meters or less with cm-scale megafaunal tracks, burrows, and mounds. Stalks, however, provide a substrate for a variety of mobile animals including the megafaunal ophiuroids (Beaulieu, 2001). A preliminary examination of transects from 2001-2004 found that roughly 10-20% of the polychaete *Paradiopatra* sp. tubes had an ophiuroid attached. The density and distribution of such tubes and stalks may influence ophiuroid populations and further study of covariance behavior is warranted.

Aggregations have also been associated with echinoderm reproduction. Most echinoderm fertilization is thought to be external and holothuroid clumping has been thought of as an efficient way to maximize contact of gametes (Young, 2003). Most aggregations observed at Sta. M are subtle and relatively intense aggregations like the one depicted in Figures 2e and f and 3e and f are rare, with no direct observation of reproduction.

Uniformity appears to occur at the scale of individuals indicating that there might be either some minimal avoidance behavior, or perhaps even spacing related to the utilization of a uniformly distributed resource. The existence of aggregations of epibenthic megafauna may still exist at scales larger than the photo transects, and results from linear transects may have some unknown directional dependence, or anisotropy. Mobile megafauna may change overall activity during increases in food supply or change position to feed on higher quality food aggregates. Analyses of spatial covariation between taxa, shorter time periods between sampling, and increase spatial scale may help yield a better understanding of megafauna interactions with the food supply and individuals from other megafauna taxa.

Other studies looking at deep-sea echinoderm distributions have also found aggregations over similar scales. A study in the Santa Catalina Basin (Smith, C R., and Hamilton, 1983, 33.25°N, 119.6W, 1300 m depth) observed aggregations of the holothuroid, *Scotoplanes globosa*, in 25-96 m clumps, and the ophiuroid, *Ophiophthalmus normani* in smaller 1-4 m patches. The megafaunal densities at the Basin site are higher than Sta. M and may have greater food inputs and habitat heterogeneity, all of which could contribute to the observed aggregation. *Scotoplanes* *globosa* was found at densities of 0.065 m^{-2} in the Basin, which is twice as high as the highest density found at Sta. M in 2002. The ophiuroid *Op. normani* reached densities ten times higher in the Santa Catalina Basin than the ophiuroids at Sta. M.

Summers and Nybakken (2000) found that ophiuroids had patchy distributions from less than cm to km scales using towed cameras, trawls, and box core measures along the central Californian slope from 550-3085 m. Large-scale aggregation was again found for *S. globosa* (Craig, 1997) and patchiness in phytodetrital aggregates was hypothesized to lead to such aggregations. A strong inverse relationship was also observed between the distributions of the holothuroids *S. globosa*, *Peniagone* sp., and *Elpidia* sp., and the ophiuroids. It was suggested that the holothuroids could dominate in low-energy areas where suspended particles would selectively settle and some ophiuroids could not filter feed effectively (Craig, 1997, Summers and Nybakken, 2000). Such inverse dispersions were not evident at Sta. M, possibly due to differences in habitat heterogeneity. A detailed examination of covariation among the dominant Sta. M taxa could reveal if subtle, but significant inverse dispersions may have occurred.

Several holothuroids have also been shown to have behaviors linked to currents including the use of a 'sail' by *Psychropotes* spp. (Gebruk, 1995) to orient with the direction of currents over interannual time scales (Foell et al., 1989). Non-random orientations have been observed for *Peniagone* sp. (Bluhm and Gebruk, 1999), *Scotoplanes* sp. (Barham et al., 1967, Pawson, 1976) *Phormosoma placenta* (Grassle et al., 1975), and *Kolga hyalina* (Billett and Hansen, 1982) as well. The reason for such behaviors remains speculative but may be linked to food patch selection, or reproduction.

The results here indicate that aggregations on the order of 100 m do not introduce a major bias to megafauna density estimates made from camera-sled transects. The tendency towards randomness in dispersion also indicates that the spatial distribution of bioturbation intensity over interannual timescales also may be essentially random. The importance of larger-scale or linear aggregations is yet to be evaluated, but these are not considered to influence the order of magnitude shifts in abundance observed for the top 10 most dominant taxa during the 1989-2004 study period (Ruhl and Smith, 2004, Ruhl, in preparation). The subtle covariation of dominant taxa at Sta. M, as well as possible links with sessile benthic features, may help elucidate dispersion patterns as well as animal interactions, resource selection, and factors leading to species coexistence.

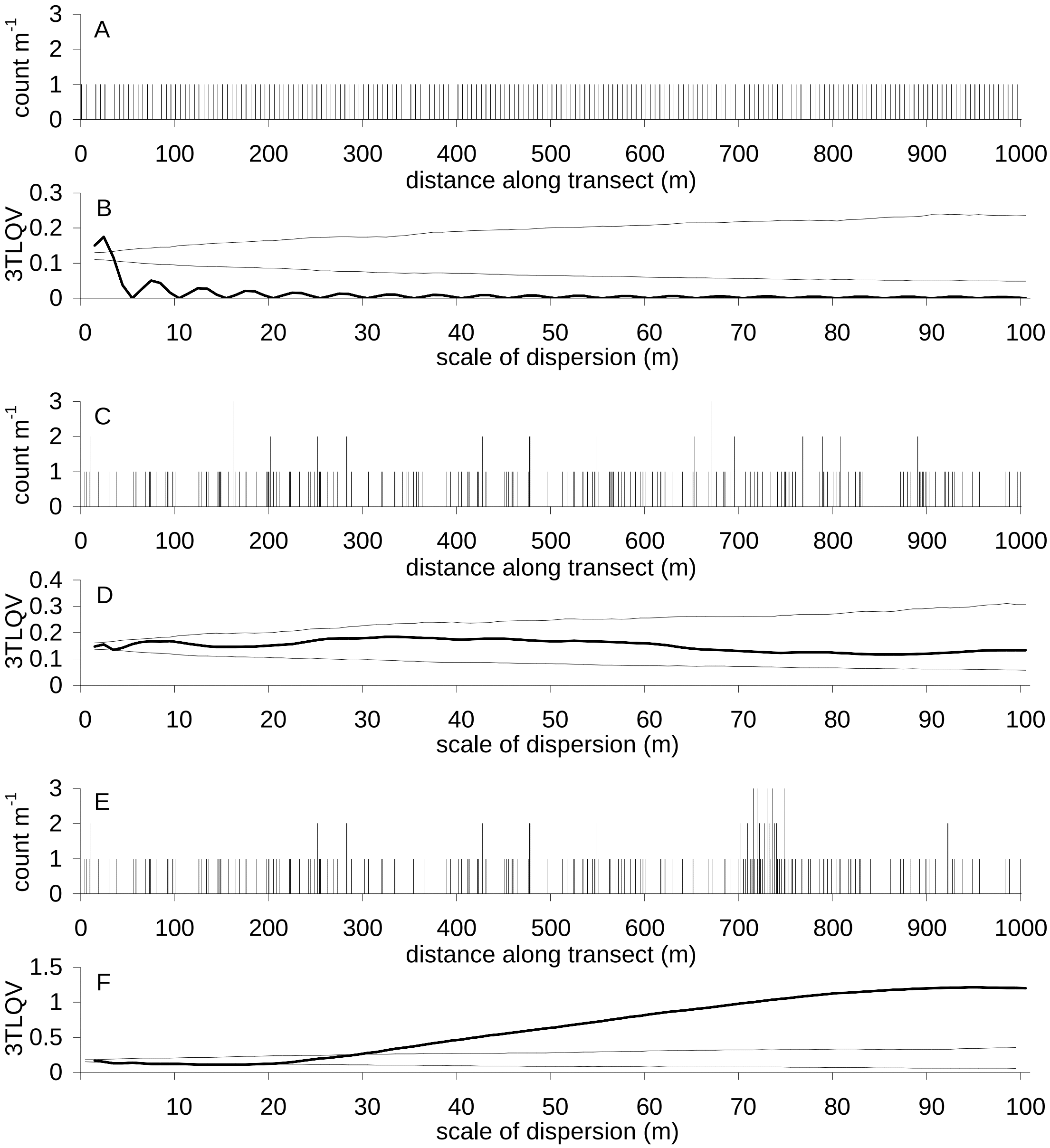


Fig. 23 Example count m^{-1} along the transect and resulting 3TLQV's with 95% confidence intervals in dashed lines. All examples have a transect length of 1000m and have a total density of 0.2 ind. m^{-1} of transect. Note that a and b illustrates totally uniform 5m scale, c and d random, and e and f an aggregation at roughly 95m scale with random dispersions at approximately 20-30 m and uniform at smaller scales.

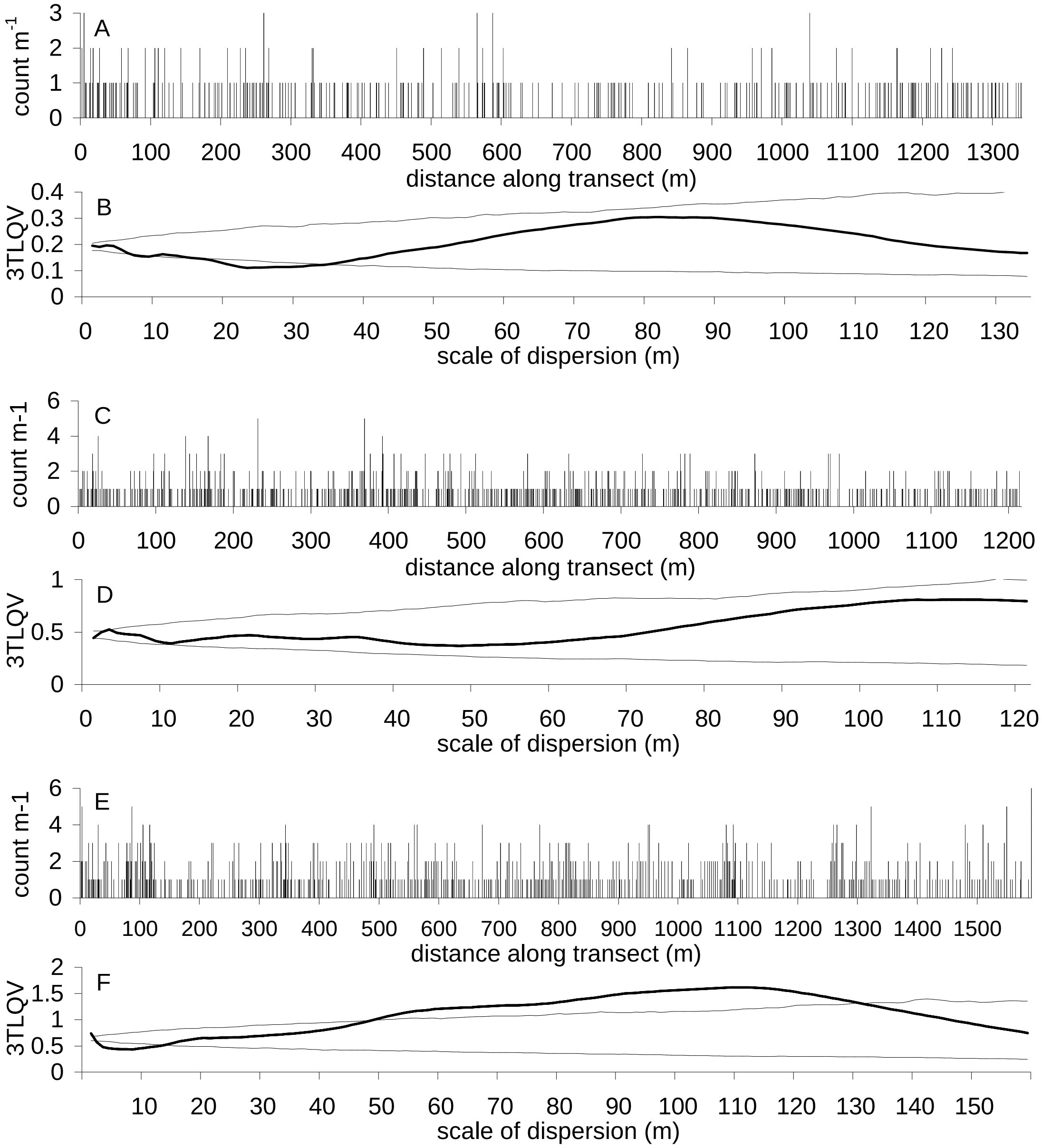


Figure 24. Example counts per meter along the transect and resulting 3TLQV's for *E. minutissima* with 95% confidence intervals in dashed lines for uniform (a, b), random (c, d), and small scale uniformity and larger scale aggregation (e, f).

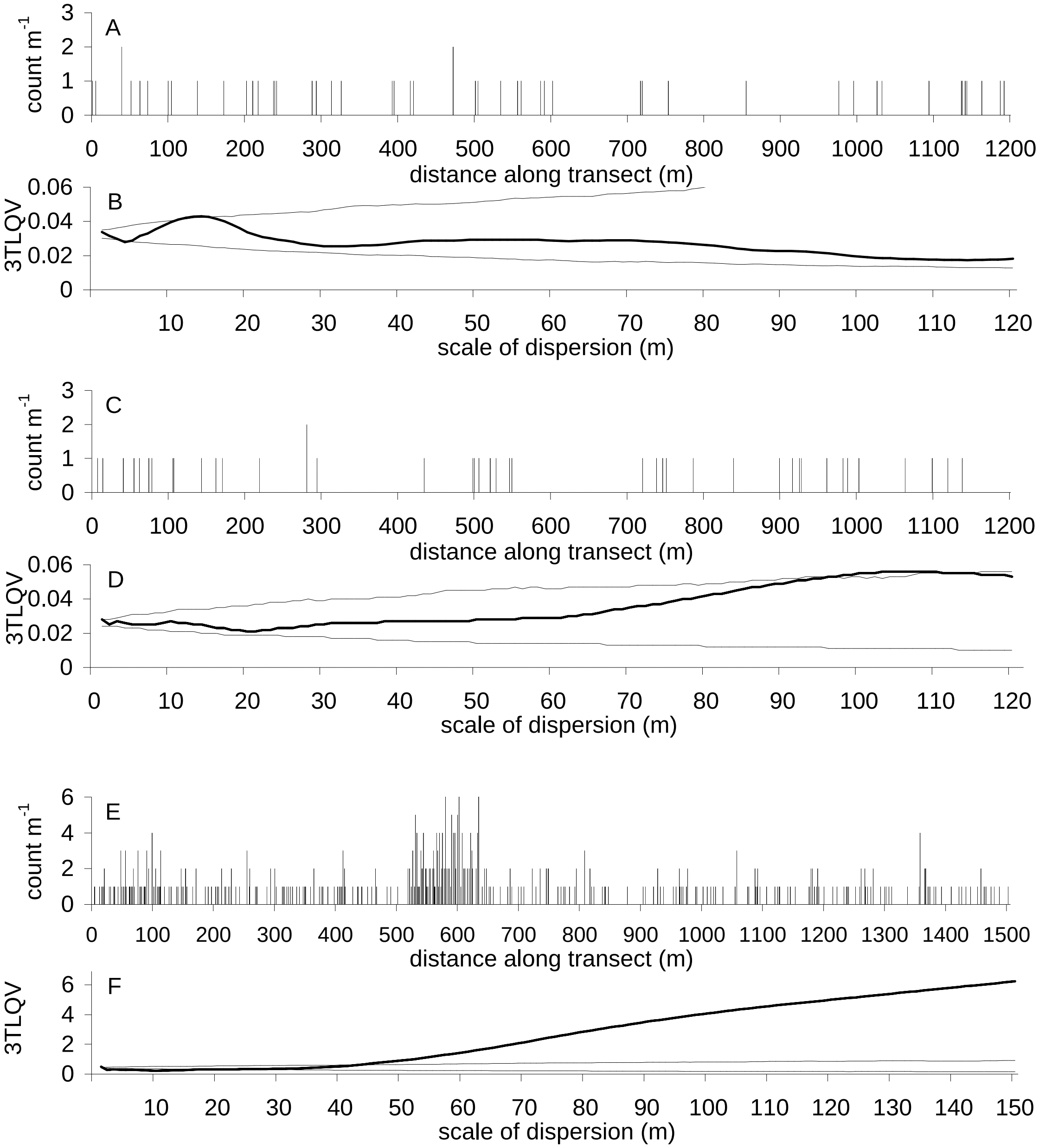


Figure 25. Example counts per meter along a transect and resulting 3TLQV's for *A. abyssorum* with 95% confidence intervals in dashed lines for random (a, b), and larger-scale low intensity aggregation (c, d). Also shown is an ophiuroid group plot of the highest intensity aggregation observed throughout the study (e, f).

Table 4. Dispersion analysis results for *E. minutissima*, *P. diaphana*, *P. vitrea*, *A. abyssorum*, *O. bathybia*, and *Ec. rostrata*. The departures from random dispersion are in parenthesis for uniform dispersion with any aggregation dispersion following for both the scale of dispersion (m), and the intensity given by the 3TLQV. An R indicates random dispersions. Results without shading indicate significant aggregation; gray random to uniform, and charcoal have no results. Also given are Mann-Whitney U test results to determine if the median POC or density was different for the presence/ absence (y/n) of the given non-random dispersions.

		E. minutissima					*P. diaphana*				
Date	Max scale	scale (m) (unif.), agg.	3TLQV (unif.), agg.	Unif. any	Agg. any	Agg. >100m	scale (m) (unif.), agg.	3TLQV (unif.), agg.	Unif. any	Agg. any	Agg. >100m
Oct-89	148	(25)	(0.16)	y	n	n	R		n	n	n
Oct-89	134	(24)	(0.238)	y	n	n	(5), 83	(0.009), 0.024	y	y	n
Feb-90	179	(32)	(0.094)	y	n	n	R		n	n	n
Feb-90	207	(23)	(0.158)	y	n	n	R		n	n	n
Jun-90	67	(16.5)	(0.16)	y	n		R		n	n	
Jun-90	46	(15)	(0.15)	y	n		R		n	n	
Feb-91	81	R		n	n		R		n	n	
Feb-91	30	R		n	n		R		n	n	
Jul-91	109	73	1.686	n	y	n					
Aug-91	42	R		n	n						
Aug-91	93	R		n	n		(14)	(0.03)	y	n	
Feb-92	127	(13.5)	(0.23)	y	n	n	R		n	n	n
Jun-92	151	R		n	n	n	R		n	n	n
Jun-92	146	R		n	n	n	R		n	n	n
Jul-92	130	(5), **113**	(0.35), 0.91	y	y	y	R		n	n	n
Oct-92	134	R		n	n	n	R		n	n	n
Oct-92	176	(25)	(0.23)	y	n	n	R		n	n	n
Feb-93	126	(5)	(0.21)	y	n	n	R		n	n	n
Jul-93	126	R		n	n	n	R		n	n	n
Jul-93	93	66	0.43	n	y						
Oct-93	91	84	0.12	n	y		R		n	n	
Oct-93	72	R		n	n	n	R		n	n	n
Feb-94	116	(3), **115**	(0.05), 0.12	y	y	y	**115**	0.04	n	y	y
Feb-94	156	**156**	0.28	n	y	y	R		n	n	n
Jun-94	122	R		n	n	n	R		n	n	n
Aug-94	134	(23)	(0.11)	y	n	n	R		n	n	n
Nov-95	121	(13), **120**	(1.30), 4.63	y	y	y	**120**	0.33	n	y	y
Nov-95	120	(23)	(0.45)	y	n	n	(12)	(0.03)	y	n	n
Feb-96	132	66.5	3.10	n	y	n	27.5	0.03	n	y	n
May-96	152	(9), 70	(0.68), 1.83	y	y	n	**152**	.10	n	y	y
Jun-96	131	(4)	(0.86)	y	n	n	**131**	0.07	n	y	y
Oct-96	166	(4)	(0.80)	y	n	n	R		n	n	n
Oct-96	148	(23)	(0.67)	y	n	n	R		n	n	n
Aug-98	175	(4)	(0.96)	y	n	n	R		n	n	n
Dec-98	159	(8), **111**	(0.43), 1.61	y	y	y	R		n	n	n
Jun-01	98						(5), 67	(0.65), 1.67	y	y	
Feb-02	34						26	2.67	n	y	
Jun-02	40										
Sep-02	34										
Oct-03	50										
Feb-04	60										
Aug-04	72										
Oct-04	64										

Mann-Whitney U test factors	Unif. any	Agg. any	Agg. >100m	Unif. any	Agg. any	Agg. >100m
POC (mg C $m^{-2}d^{-1}$)	ns	ns	ns	*p=0.03*	ns	ns
Density (ind. m^{-2})	ns	ns	ns	ns	*p* =0.04	*p* =0.01

Table 4 (continued).

		P. vitrea					*A. abyssorum*				
Date	Max scale	scale (m) (unif.), agg.	3TLQV (unif.), agg.	Unif. any	Agg. any	Agg. >100m	scale (m) (unif.), agg.	3TLQV (unif.), agg.	Unif. any	Agg. any	Agg. >100m
Oct-89	148	(20)	(0.036)	y	n	n	R		n	n	n
Oct-89	134	(11)	(0.021)	y	n	n	51.5	0.03	n	y	n
Feb-90	179	R		n	n	n	R		n	n	n
Feb-90	207	(4)	(0.024)	y	n	n	R		n	n	n
Jun-90	67	R		n	n		7.5	0.08	n	y	
Jun-90	46	R		n	n		R		n	n	
Feb-91	81	R		n	n		R		n	n	
Feb-91	30						R		n	n	
Jul-91	109	R		n	n	n	R		n	n	n
Aug-91	42	R		n	n		R		n	n	
Aug-91	93	(5)	(0.12)	y	n		R		n	n	
Feb-92	127	R		n	n	n	55	0.07	n	y	n
Jun-92	151	R		n	n	n	R		n	n	n
Jun-92	146	R		n	n	n	R		n	n	n
Jul-92	130	R		n	n	n	R		n	n	n
Oct-92	134	R		n	n	n	R		n	n	n
Oct-92	176	R		n	n	n	R		n	n	n
Feb-93	126	(6)	(0.09)	y	n	n	R		n	n	n
Jul-93	126	R		n	n	n	R		n	n	n
Jul-93	93	31	0.08	n	y		R		n	n	
Oct-93	91	R		n	n		18	0.02	n	y	
Oct-93	72	R		n	n	n	R		n	n	n
Feb-94	116	R		n	n	n	R		n	n	n
Feb-94	156	34	0.06	n	y	n	52	0.03	n	y	n
Jun-94	122	R		n	n	n	R		n	n	n
Aug-94	134	R		n	n	n	R		n	n	n
Nov-95	121	R		n	n	n	R		n	n	n
Nov-95	120	(17)	(0.09)	y	n	n	**107**	0.06	n	y	y
Feb-96	132	45	0.38	n	y	n					
May-96	152	R		n	n	n	R		n	n	n
Jun-96	131	R		n	n	n	R		n	n	n
Oct-96	166	R		n	n	n	R		n	n	n
Oct-96	148	(11), 97	(0.10), 0.25	y	y	n	R		n	n	n
Aug-98	175	R		n	n	n	R		n	n	n
Dec-98	159	R		n	n	n	R		n	n	n
Jun-01	98										
Feb-02	34										
Jun-02	40						R		n	n	
Sep-02	34						R		n	n	
Oct-03	50						R		n	n	
Feb-04	60						R		n	n	
Aug-04	72						R		n	n	
Oct-04	64	R		n	n		R		n	n	

Mann-Whitney U test factors	Unif. any	Agg. any	Agg. >100m	Unif. any	Agg. any	Agg. >100m
POC (mg C $m^{-2}d^{-1}$)	ns	ns	ns		ns	ns
Density (ind. m^{-2})	ns	ns	ns		ns	ns

Table 4 (continued).

Date	Max scale	*Ophiura sp.* scale (m) (unif.), agg.	3TLQV (unif.), agg.	Unif. any	Agg. any	Agg. >100m	*Ec . rostrata* scale (m) (unif.), agg.	3TLQV (unif.), agg.	Unif. any	Agg. any	Agg. >100m
Oct-89	148	(9), **148**	(0.15), 1.13	y	y	y	R		n	n	n
Oct-89	134	(7.5), **133**	(0.10), 0.43	y	y	y	R		n	n	n
Feb-90	179	R		n	n	n	R		n	n	n
Feb-90	207	(14)	(0.08)	y	n	n	(5)	(0.012)	y	n	n
Jun-90	67	(3)	(0.41)	y	n		R		n	n	
Jun-90	46	(2)	(0.23)	y	n		R		n	n	
Feb-91	81	R		n	n		80	0.100	n	y	
Feb-91	30	R		n	n		R		n	n	
Jul-91	109	(4)	(0.39)	y	n	n	(21)	(0.029)	y	n	n
Aug-91	42	R		n	n		R		n	n	
Aug-91	93	(8)	(0.28)	y	n		R		n	n	
Feb-92	127	**105.5**	1.09	n	y	y	(24), **127**	(0.24), 0.10	y	y	y
Jun-92	151	(10), **150**	(0.24), 6.24	y	y	y	R		n	n	n
Jun-92	146	R		n	n	n	72	0.04	n	y	n
Jul-92	130	(8), **111**	(0.09), 0.28	y	y	y	(8), 57	(0.02), 0.06	y	y	n
Oct-92	134	(5), **134**	(0.14), 1.45	y	y	y	R		n	n	n
Oct-92	176	(4), 27	(0.09), 0.15	y	y	n	R		n	n	n
Feb-93	126	(25)	(0.10)	y	n	n	R		n	n	n
Jul-93	126	(4), **103**	(0.24), 0.84	y	y	n	R		n	n	n
Jul-93	93	66	0.67	n	y		15	0.04	n	y	
Oct-93	91	(4), 46	(0.15), 0.37	y	y		(20)	(0.02)	y	n	
Oct-93	72	R		n	n	n	R		n	n	n
Feb-94	116	(12), **104**	(0.07), 0.26	y	y	y	R		n	n	n
Feb-94	156	**156**	0.21	n	y	y	**156**	0.11	n	y	y
Jun-94	122	R		n	n	n	R		n	n	n
Aug-94	134	**134**	1.02	n	y	y	R		n	n	n
Nov-95	121	(6)	(0.13)	y	n	n	R		n	n	n
Nov-95	120	**120**	0.05	n	y	y	(3)	(0.03)	y	n	n
Feb-96	132	74.5	0.38	n	y	n	R		n	n	n
May-96	152	R		n	n	n	R		n	n	n
Jun-96	131	86	0.49	n	y	n	R		n	n	n
Oct-96	166	(4), **166**	(0.07), 0.31	y	y	y	R		n	n	n
Oct-96	148	(4), **102**	(0.13), 0.43	y	y	y	R		n	n	n
Aug-98	175	R		n	n	n	R		n	n	n
Dec-98	159	R		n	n	n	R		n	n	n
Jun-01	98	(4)	(0.27)	y	n		R		n	n	
Feb-02	34	R		n	n		R		n	n	
Jun-02	40	R		n	n		R		n	n	
Sep-02	34	R		n	n		23	0.22	n	y	
Oct-03	50	(4), 32	(0.64), 2.16	y	y		R		n	n	
Feb-04	60	R		n	n		R		n	n	
Aug-04	72	R		n	n		R		n	n	
Oct-04	64	R		n	n		R		n	n	

Mann-Whitney U test factors	Unif. any	Agg. any	Agg. >100m	Unif. any	Agg. any	Agg. >100m
POC (mg C $m^{-2}d^{-1}$)	ns	ns	ns	ns	ns	ns
Density (ind. m^{-2})	ns	p =0.03	ns	ns	ns	ns

References

Andrew, N. L., and B. D. Mapstone. 1987. Sampling and the description of spatial pattern in marine ecology. Oceanography and Marine Biology Annual Review 25: 39-90.

Billett, D. S. M., and B. Hansen. 1982. Abyssal aggregations of *Kolga hyalina* Danielssen and Koren (Echinodermata: Holothurioidea) in the northeast Atlantic Ocean: a preliminary report. Deep-Sea Research 29A, 799-818.

Baldwin, R. J., R. C. Glatts, and K.L. Smith, Jr. 1998. Particulate matter fluxes into the benthic boundary layer at a long time-series station in the abyssal NE Pacific: composition and fluxes. Deep-Sea Research II 45: 643-666.

Barham, E. G., N. J. Ayer Jr., and R. E. Boyce. 1967. Macrobenthos of the San Diego Trough: photographic census and observations from the bathyscaphe, Trieste. Deep-Sea Research 14, 773-784.

Beaulieu, S. E. 2001. Life on glass houses: sponge stalk communities in the deep sea. Marine Biology 138, 803-817.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance Sampling: Estimating abundance of biological populations. Chapman and Hall, London 446pp.

Craig, S. 1997. Distribution of deep-sea invertebrate megafauna off central California. Masters Thesis, Moss Landing Marine Laboratories, San Jose State University, California, 133pp.

Dale, M. R. T., 1999. Spatial Pattern Analysis in Plant Ecology. Cambridge: Cambridge University Press.

Gebruk, A. V. 1995 Locomotory organs in the elasipod holothurians: functional-morphological and evolutionary approaches. In R. Emson, A. Smith, and A. Campwell Eds. Echinoderm Research. Balkema Rotterdam, 95-102pp.

Grassle J. F., H. L. Sanders, R. R. Hessler, G. T. Rowe, and T. McLellan. 1975. Pattern and zonation: a study of the bathyal megafauna using the research submersible Alvin. Deep-Sea Research 22, 457-481.

Hill, M. O. 1973. The intensity of spatial pattern in plant communities. Journal of Ecology 61:225-235.

Hurlbert, S. H. 1990. Spatial distribution of the montane unicorn. Oikos 58:257-271.

Kahru, M., and B. G. Mitchell. 2002. Seasonal and nonseasonal variability of satellite-derived chlorophyll and colored dissolved organic matter concentration in the California Current. Journal of Geophysical Research 106: 2517–2529.

Kaufmann, R. S. and K. L. Smith, Jr. 1997. Activity patterns of mobile epibenthic megafauna at an abyssal site in the eastern North Pacific: Results from a 17-month time-lapse photographic study. Deep-Sea Research I 44: 559-579.

Kaufmann, R. S.; W. W. Wakefield, A. Genin. 1989. Distribution of epibenthic megafauna and lebensspuren on two central north Pacific seamounts. Deep-Sea Research 36: 1863–1896.

Lauerman, L. M. L., and R. S. Kaufmann. 1998. Deep-sea epibenthic echinoderms and a temporally varying food supply: Results from a one year time-series in the NE Pacific. Deep-Sea Research Part II 45: 817-842.

Lauerman, L. M. L., R. S. Kaufmann, and K. L. Smith, Jr. 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. Deep-Sea Research I 43: 1075-1104.

Laake, J. L., S. T. Buckland, D. R. Anderson, and K. P.Burnham. 1994. Distance Users Guide V 2.1. Colorado Cooperative Fish and Wildlife Research Unit. Colorado State University, Fort Collins, CO. 84 pp.

Lepš, J. 1990. Comparison of transect methods for the analysis of spatial pattern. Pages 71-82. *in* F. E. Krahulec, A. D. Q. Agnew, S.Agnew and J. H. Willem, editors. Spatial Processes in Plant Communities. Academia Press, Prague.

Ludwig, J. A., and D. W. Goodall. 1978. A comparison of paired- with blocked-quadrat variance methods for the analysis of spatial pattern. Vegetatio 38:49-59.

Ludwig, J. A., and J. F. Reynolds. 1988. Statistical Ecology. John Wiley, New York, USA.

Pawson, D. L. 1976. Some aspects of the biology of deep-sea echinoderms. Thalassia Jugoslavia 12: 287-293.

Rosenberg, M. S. 2001. PASSAGE. Pattern Analysis, Spatial Statistics, and Geographic Exegesis. Version 1.0. Department of Biology, Arizona State University, Tempe, AZ.

Rowe, G. T. 1971. The exploration of submarine canyons and their benthic faunal assemblages. Proceedings of the Royal Society of Edinburgh B73: 159-169.

Ruhl, H. A. in preparation. Community stability in the variable resource habitat of the abyssal NE Pacific. Science.

Ruhl, H. A., and K. L. Smith, Jr. 2004. Shifts in deep-sea community structure linked to climate and food supply. Science 305: 513-515.

Smith, C. R., and S. C. Hamilton. 1983. Epibenthic megafauna of a bathyal basin off southern California: patterns of abundance, biomass, and dispersion. Deep-Sea Research 30: 907-928.

Smith, K. L., Jr., R. J. Baldwin, H. A. Ruhl, M. Kahru, B. G. Mitchell, and R. S. Kaufmann. 2006. Climate effect on food supply to depths greater than 4000 m in the northeast Pacific. Limnology and Oceanography 51: 166-167.

Smith, K. L., Jr., and E. R. M. Druffel. 1998. Long time-series studies of the benthic boundary layer at an abyssal station in the NE Pacific. Deep-Sea Research Part II 45: 573-586.

Summers, A. C., and J. Nybakken. 2000. Brittle star distribution patterns and population densities on the continental slope off central California (Echinodermata: Ophiuroidea). Deep-Sea Research II 47: 1107-1137.

Tyler, P.A., C. M. Young, D. S. M. Billett, and L. A. Giles, 1992. Pairing behavior, reproduction and diet in the deep-sea holothurian genus Parozia (Holothuroidea: Synallactidae). Journal of the Marine Biological Association of the United Kingdom 72: 447-462.

Wakefield, W. W., and A. Genin. 1987. The use of a Canadian (perspective) grid in deep-sea photography. Deep-Sea Research 34: 469-478.

Wakefield, W. W., and W. Smithey. 1989. Two camera sleds for quantitative study of deep-sea megafauna. Scripps Institution of Oceanography Reference Series 89-14, 25 pp.

Young, C. M. 2003. Reproduction, development and life-history traits. Pages 381–426 In P. A. Tyler, ed. Ecosystems of the deep oceans. Vol. 28. Ecosystems of the world. Elsevier, Amsterdam.

Young, C. M., P. A. Tyler, J. L. Cameron, S. G. and Rumrill. 1992. Seasonal breeding aggregations in low-density populations of the bathyal echinoid *Stylocidaris lineata*. Marine Biology 113: 603-612.

V

Community Stability in the Variable Resource Habitat of the Abyssal NE Pacific

Abstract

New evidence from an abyssal megafauna community in the NE Pacific has suggested that even with changes in species composition, shifts in megafaunal community organization relationships were limited and likely related to differential responses to resource variability. The mobile epibenthic megafauna community has undergone changes in rank abundance distributions (RADs), evenness, and species composition from 1989-2004. Shifts in the RADs and evenness from more to less equitable were correlated to increased food supply during La Niña phases of the El Niño Southern Oscillation. Even with the potentially enrichment-driven variation in the RADs over time, the shape of the RADs had a consistent slope and the interspecific relationship between body size and abundance did not vary significantly. The relationships imply that although the community can undergo population-level variations of one or more orders of magnitude, the organizing mechanisms of the community may be relatively stable. The results agree with several temporally oriented predictions and assumptions of niche theory involving resource apportionment and the regulation of diversity. Straightforward links between populations and interannual-scale climatic forcing have been made in many habitats further stressing the potential importance of disequilibria in understanding why communities have certain basal attributes.

Main Text

The majority of community assembly and resource partitioning research explicitly examines or assumes steady state conditions and has recently been focused on the potential influences of life history and dispersal (e.g. Motomura, 1932, MacArthur, 1957, Whittaker, 1965, MacArthur and Wilson, 1967, May, 1975, Hubbell, 1979. 2001, Sugihara, 1980, Tokeshi, 1990, 1999, Brown, 1995, Chase and Liebold, 2003, Olding-Smee et al., 2003, Sugihara et al., 2003). Rank abundance distributions (RADs) and equitability are widely thought to be indicators of how a resource(s) are divided up by a particular guild or community (Motomura, 1932, MacArthur, 1957, Whittaker, 1965, Sugihara, 1980, Tokeshi, 1990, 1999, Chase and Liebold, 2003, Olding-Smee et al., 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 assembly, has provided a comprehensive null model for niche-based partitioning theories. This study provided a first look at the stability of an abyssal megafauna community within the context of niche and neutral theories of community assembly. More specifically, RADs, evenness (Pielou, 1966), and interspecific body size vs. abundance relationships were examined using photographic transect data from 1989-2004; a period of significant species composition change and food supply variability.

The deep-sea study site in the NE Pacific (Station M; 4100 m depth; 34°50’N, 123°00’W) has experienced climatically influenced seasonal and interannual variations in surface water productivity and subsequent sinking of particulate organic carbon (POC) food supply to the seafloor from 1989-2004 (POC measured with sedimentation traps moored at 3,500 m and 4,050 m depth Baldwin et al., 1998, Smith and Druffel, 1998, Smith et al., 2006). Links from surface conditions to POC flux (Smith et al., 2006) and POC flux to specific mobile epibenthic megafaunal populations have also been made at the site (Ruhl and Smith, 2004). Similar processes involving climate, pelagic benthic coupling of food resources and subsequent changes in abyssal benthic communities have also been observed in the NE Atlantic (Billett et al., 2001, Gooday, 2002, Wigham et al., 2003a). There is also evidence that benthic megafauna significantly bioturbate local sediments and may influence the proportion of sinking POC that remains in the contemporary carbon cycle or is geologically sequestered (Reimers et al., 1992, Smith et al., 1993, Kaufmann and Smith, 1997, Bett et al., 2001, Solan et al., 2004).

Overall the abyssal environment at Sta. M has been relatively stable with no sunlight, temperatures around 1.5°C, and relatively consistent prevailing currents and dissolved O_2 when compared to other marine habitats (Beaulieu and Baldwin, 1998). The food supply, however, is now known to vary over seasonal and interannual scales in both quality and quantity (Baldwin et al., 1998, Smith et al., 2006), but there is no known feedback mechanism for abyssal consumers to affect surface productivity within the timescales examined here. The habitat at the scale of the mobile megabenthos at abyssal depths can thus be seen to have less variability in environmental and resource parameters when compared to more dynamic sea-surface habitats.

Greater than 99% of the mobile epibenthic megafauna observed during the 16-year period were from ten echinoderm taxa; 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*. The deposit-feeding echinoderm megafauna have been shown to selectively feed on fresh phytopigments (Billett et al., 1988, Lauerman 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, 2003b). Organic nutrient compounds have also been linked to reproductive processes in deep-sea holothuroids (Hudson et al., 2003, Wigham et al., 2003b). Increases in megafauna abundance were significantly ($p < 0.05$) linked with increases in smaller size classes, indicating that reproduction and recruitment likely influenced local increases in abundance (Ruhl, in preparation, supporting material). All available evidence suggests that epibenthic megafauna populations at Sta. M reflect regional reproduction and local recruitment, biotic interactions, and mortality.

Directional changes in both the RAD and species composition were evident from 1989-2004 with samples taken at closer time intervals being more similar than samples taken with longer temporal lags between them (Fig. 26a and b). It is possible that a partial convergence, or a return direction to starting similarity, might have occurred in the longer lags of species composition similarity (Fig. 1b; supporting material). The RADs and species compositions exhibited significant covariation (Spearman-rank correlation [r] = 0.42; $p < 0.001$). Further analysis, however, has bounded the degree to which the RADs have 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 26c and d). Other notable clusters included observations from 1989- Aug 1994 and Sep 1994-1998, but the two groups were not temporally exclusive since June 1992 clusters into the otherwise 1994-1998 group (Fig. 26d; supporting material). Also of note is that the principal change in species composition after the 1997-1999 El Niño/ La Niña event (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 POC flux (Fig. 27a-d, see also Baldwin et al., 1998, Smith et al., 2006). Significant correlations with the POC food supply existed with peaks at 10-12 months for the RAD ($r = 0.38$; $p < 0.05$), 12 months for evenness ($r = 0.33$; $p = 0.05$), and 10-13 months for species composition ($r = 0.48$; $p < 0.01$). A temporal lag of many months is sensible considering that while the community can respond with rapid changes in activity (Bett et al., 2001, Kaufmann and Smith, 1997, Smith et al., 1993), it appears to take several months or more for a shift in resources to lead to observable changes in abundance resulting from processes such as reproduction, recruitment, migration, and mortality (Ruhl and Smith, 2004). The RAD similarity was also highly correlated to evenness ($r = 0.82$; $p < 0.001$). Although both the RAD similarity and evenness were correlated to species composition during certain periods, no species-specific links were apparent for the whole time series, providing further evidence that equitability may have had some independence from species composition.

The monthly RADs throughout the time-series from 1989-2004 had an approximately geometric distribution (Fig. 28a), with each rank having between 2-7 taxa and the middle ranks experiencing more variability. When the monthly RADs were grouped by the principal communities outlined in Fig. 1d, they all had similar slopes (Fig. 28b-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 further demonstrates that shifts in RADs were limited and may have been only weakly dependant on species composition, if at all. It is tempting here to try to discern what theory and model best fit the observations, be it geometric (Motomura, 1932), sequential breakage (Sugihara, 1980), or others. 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 (Preston, 1948, Sugihara, 1980, Nee et al., 1991, Tokeshi, 1999).

Interspecific body size vs. abundance also had significant ($p < 0.05$) consistent negative correlations during the entire study period and the clusters outlined in Fig. 1d. Although the abundances of several taxa changed by one or more orders of magnitude between the different temporal groupings, the slopes were similar for each of the periods with different relative abundances (Fig. 28f-j). The photogrammetric methods preclude accurate biomass estimates, but there is no evidence that the observed slopes are likely to be different from the pervasive abundance = mass$^{-3/4}$relationship (Damuth, 1981, Nee et al., 1991, Blackburn and Gaston, 1997, supporting material).

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. Hutchison, 1957, Chase and Leibold, 2003). Niche-based precepts have been proposed to explain observed continuities in ecology including a constant or universal division rule regulating the utilization of resources (Brown, 1984, Brown et al., 2001). Differential responses to resource variability are thought to be one way competitive exclusion can be prevented (Chase and Leibold, 2003). 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 (Sugihara, 1980, Tokeshi, 1990, Sugihara et al., 2003). 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 higher-dimension resource and less equitable with a more basic, low-dimension resource (Sugihara et al., 2003). Neutral theory, conversely, can produce many pervasive trends in ecology, such as species-area and rank-abundance distributions, with no requirements for the differential utilization of resources (Hubbell, 2001).

At Sta. M there is now compelling evidence for seasonal and inter-annual variation in food supply resulting in inter-annual resource disequilibria (Smith and Kaufmann, 1999, Smith et al., 2006). Several predictions of niche theory were reevaluated here within the context of the fluctuating resource environment of the NE Pacific abyssal seafloor. If each taxon had an equivalent per capita response to a variable resource, then any measured shift in RADs, evenness, and species composition would solely 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 non-random links between community shifts and food supply might be detectable and potentially include rank switching, and local extinctions and recolonizations (Brown et al., 2001, Chesson and Huntly, 1997, Chesson, 2000).

Shifts in the RADs, evenness, and species composition were significantly linked to the POC food supply at Sta. M. suggesting a deterministic role for life-history processes in community assembly at some level. 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 lead to more asymmetrical RADs and lower evenness, which is an expected result of a niche hierarchy system.

The division of resources, and thus RADs, have generally been evaluated in steady state and only recently has research specifically addressed variation in RADs in a contemporary terrestrial community (e.g. Thibault et al., 2004). If species richness remains stable during times of resource change and a common principal governing the division of resources is in operation, then RADs should not vary (Brown et al., 2001). A long-term study of desert rodents found directional shifts in RADs similar to that illustrated in Fig. 26a without major changes in species richness (Thibault et al., 2004). The ideas that species richness and RADs may not be tightly coupled and that RADs are not static bring a constant division rule into question. In both the rodent and abyssal megafaunal analyses, the RADs have shifted within the context of resource change (Thibault et al., 2004). When examined for the principal species composition clusters, however, there is no persuasive evidence for fundamental changes between the slopes of the ranked abundances. The limited variation seems sensible within the context of a constant division rule that acknowledges shifts in relative abundance and equitability related to changes in resource dimensions.

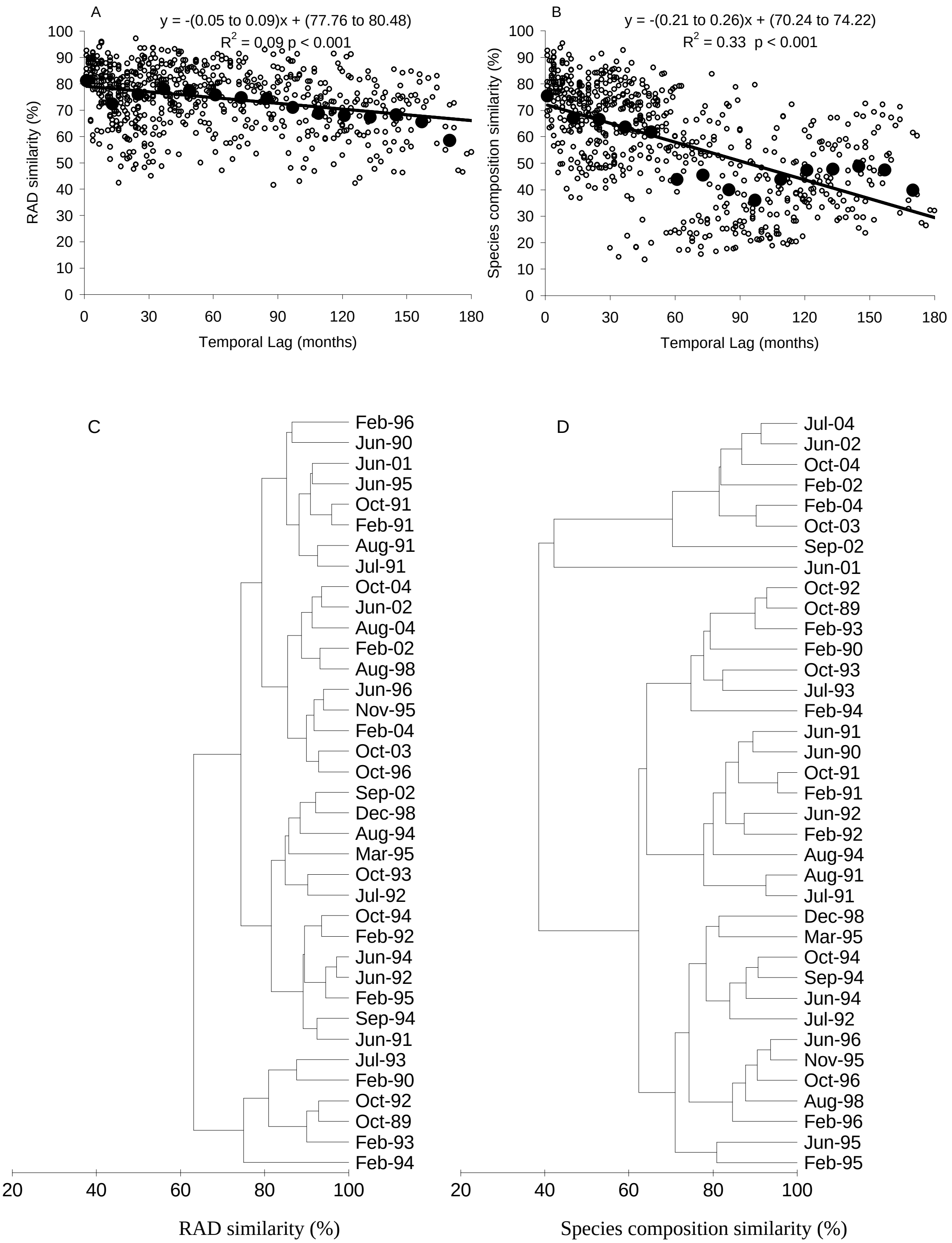
If constant mechanisms controlling abundance extend to the relative abundances of smaller and larger animals, then interspecific relationships between body size and abundance should also remain stable, even during shifts in species composition. The relationships between body size and abundance also appear to be relatively stable for the different community compositions, providing further evidence of the ubiquity of stability in whatever mechanisms govern the relationships.

Results from megafauna at Sta. M suggest that both individual populations and community descriptors like the RAD and evenness were linked to resource availability. The overall relative megafauna abundances found at Sta. M were similar to distributions expected when a single or few factors, such as POC flux quantity and quality, are controlling community structure (Fig. 28). 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 also been observed in smaller protist and metazoan taxa (Gooday, 2002, Drazen et al., 1998), invertebrate megafauna (Billett et al., 2001, Ruhl and Smith, 2004), as well as higher trophic level fishes (Bailey et al, 2006). Multi-year disparities between food supply and demand for smaller sediment-based organisms (Smith and Kaufmann, 1999) suggest that such processes could extend to other guilds and trophic levels at the site.

Climate variations such as the El Niño Southern Oscillation, the North Atlantic Oscillation, and the Antarctic Circumpolar Wave have cycles that often direct systems away from equilibrium over interannual scales for most of the world biome. Treatment of climate oscillations as discrete historical events belies their pervasive and ever-present ecological effects. The growing evidence for limited resource-driven changes in RADs and evenness further emphasize the need for further formalization of temporally variable resources in contemporary theories of ecology.

This chapter, in full, will be submitted to the journal Science (Ruhl, H. A. Community Stability in the Variable Resource Habitat of the Abyssal NE Pacific. Science). The dissertation author was the only investigator and author of this manuscript.

Figure 26. Scatter plots of Bray-Curtis similarity for A) all possible RAD pairs from 1989-2004 and B) the similarity of all possible monthly species composition pairs vs. the time in months between the compared samples. Also plotted on A and B is the best linear fit of the monthly data with Mantel randomization test *p*-values. Discrete twelve-month averages of similarity are also presented using heavy 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. Bray-Curtis similarity dendrograms of C) monthly RADs and D) monthly species composition. All are based on monthly abundance estimates of the ten most dominant epibenthic megafauna taxa observed from 1989-2004.


A
y = -(0.05 to 0.09)x + (77.76 to 80.48)
R^2 = 0.09 p < 0.001
RAD similarity (%)
100
90
80
70
60
50
40
30
20
10
0
0
30
60
90
120
150
180
Temporal Lag (months)
B
y = -(0.21 to 0.26)x + (70.24 to 74.22)
R^2 = 0.33 p < 0.001
Species composition similarity (%)
Temporal Lag (months)
C
Feb-96
Jun-90
Jun-01
Jun-95
Oct-91
Feb-91
Aug-91
Jul-91
Oct-04
Jun-02
Aug-04
Feb-02
Aug-98
Jun-96
Nov-95
Feb-04
Oct-03
Oct-96
Sep-02
Dec-98
Aug-94
Mar-95
Oct-93
Jul-92
Oct-94
Feb-92
Jun-94
Jun-92
Feb-95
Sep-94
Jun-91
Jul-93
Feb-90
Oct-92
Oct-89
Feb-93
Feb-94
20
40
60
80
100
RAD similarity (%)
D
Jul-04
Jun-02
Oct-04
Feb-02
Feb-04
Oct-03
Sep-02
Jun-01
Oct-92
Oct-89
Feb-93
Feb-90
Oct-93
Jul-93
Feb-94
Jun-91
Jun-90
Oct-91
Feb-91
Jun-92
Feb-92
Aug-94
Aug-91
Jul-91
Dec-98
Mar-95
Oct-94
Sep-94
Jun-94
Jul-92
Jun-96
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Oct-96
Aug-98
Feb-96
Jun-95
Feb-95
20
40
60
80
100
Species composition similarity (%)

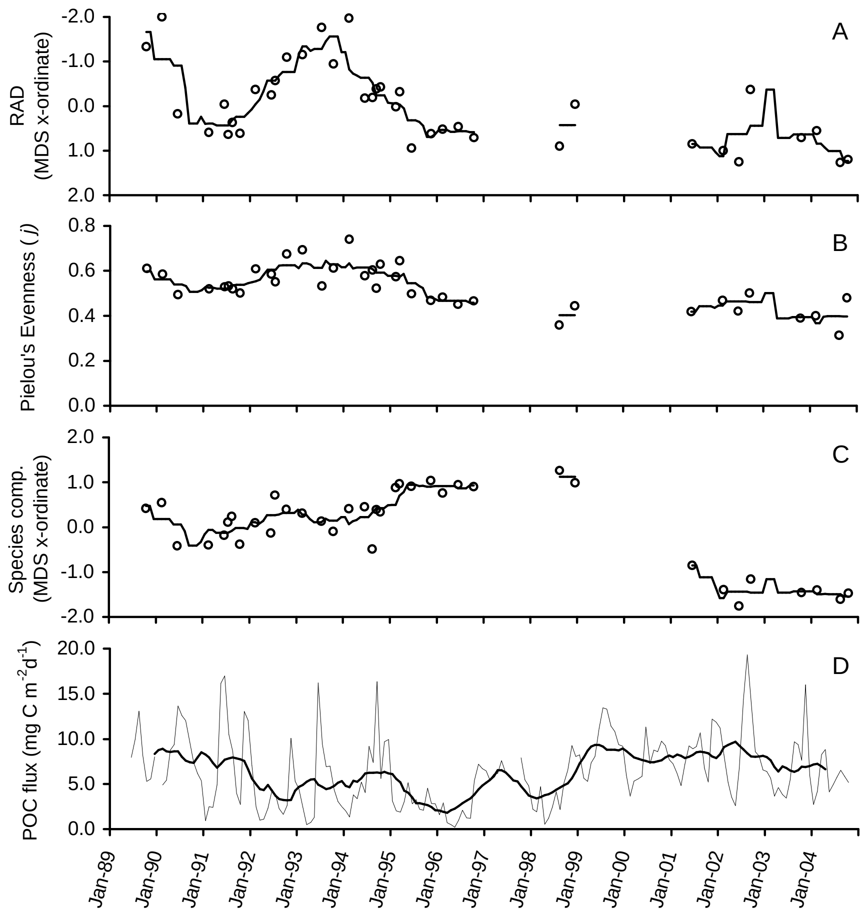

Figure 27. Time-series plots showing A) the Bray-Curtis RAD relative similarity over time as measured by the multi-dimensional scaling (MDS) x-ordinate, as well as D) Pielou's evenness, B) species composition relative similarity MDS x-ordinate, and D) POC flux (mg C m^{-2}d^{-1}) composite. The monthly data are plotted as open circles for the community descriptors and a dashed line for POC flux, all have a thirteen-month running mean in a solid black line. All correlations were conducted using monthly data and the thirteen-month running means are for display purposes only.

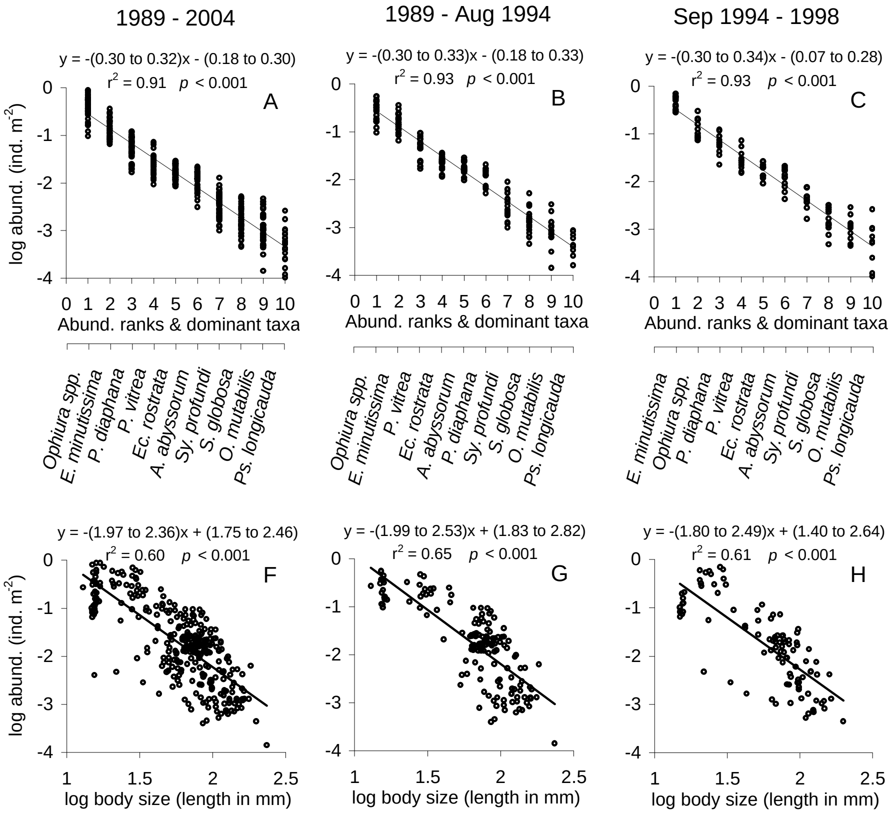

Figure 28. The top five panes show ranked monthly abundances for A) 1989-2004, B) 1989-Aug. 1994, C) Sep. 1994-1998, D) 1989-1998, E) 2001-2004. Also shown below the ranks are the taxon that dominated each rank during the principal species composition times. The bottom five panes show monthly mean body size vs. abundance for all ten taxa for F) 1989-2004, G) 1989-Aug 1994, H) Sep 1994-1998, I) 1989-1998, J) 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. It is important to note that for panels A – E, the values are ranked and thus significant correlations are not remarkable in each separate panel. The most relevant aspect of the statistics is the overlapping linear descriptions among the panels.

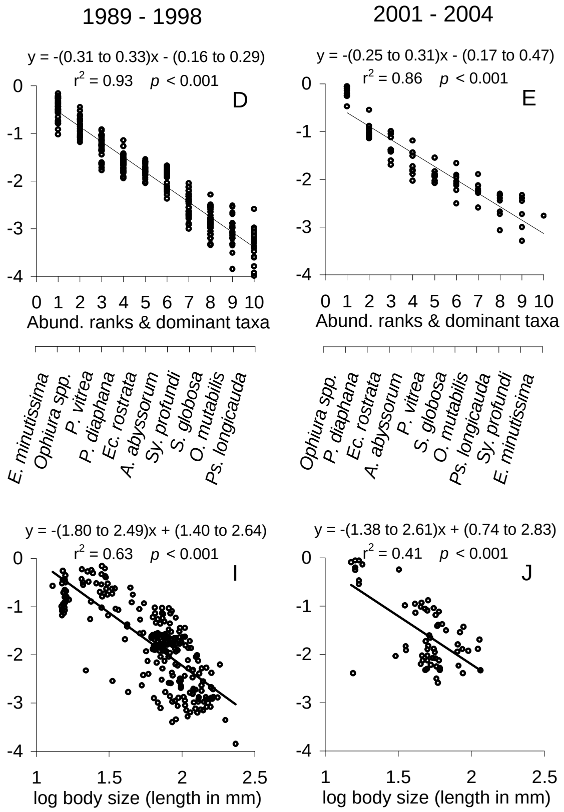

Figure 28 (continued). The top five panes show ranked monthly abundances for A) 1989-2004, B) 1989-Aug. 1994, C) Sep. 1994-1998, D) 1989-1998, E) 2001-2004. Also shown below the ranks are the taxon that dominated each rank during the principal species composition times. The bottom five panes show monthly mean body size vs. abundance for all ten taxa for F) 1989-2004, G) 1989-Aug 1994, H) Sep 1994-1998, I) 1989-1998, J) 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. It is important to note that for panels A – E, the values are ranked and thus significant correlations are not remarkable in each separate panel. The most relevant aspect of the statistics is the overlapping linear descriptions among the panels.

References

Bailey, D. M., H. A. Ruhl, and K. L. Smith Jr. 2006. Long-term changes in benthopelagic fish abundance in the abyssal northeast Pacific ocean. Ecology 87: 549-555.

Baldwin, R. J., R. C. Glatts, and K. L. Smith Jr. 1998. Particulate matter fluxes into the benthic boundary layer at a long time-series station in the abyssal NE Pacific: composition and fluxes. Deep-Sea Research II. 45: 643-666.

Beaulieu, S. and R. Baldwin. 1998. Temporal variability in currents and the benthic boundary layer at an abyssal station off central California. Deep-Sea Research II. 45: 587-615.

Bett, B. J, M. G. Malzone, B. E. Narayanaswamy, and B. D. Wigham. 2001. Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. Progress in Oceanography 50: 349-368.

Billett, D. S. M., B. J. Bett, A. L. Rice, M. H. Thurston, J. Galeron, M. Sibuet, and G. A. Wolff. 2001. Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). Progress in Oceanography 50: 325-348.

Billett, D. S. M., C. Llewellyn, and J. Watson. 1988. Are deep-sea holothurians selective feeders? In: Echinoderm biology, eds. R. D. Burke, P. V. Mladenov, P. Lambert and R. L. Parsley, pp. 421-429. A. Balkema, Rotterdam.

Beaulieu, S. E. 2001. Life on glass houses: sponge stalk communities in the deep sea. Marine Biology 138: 803-817.

Blackburn, T. M., and K. J. Gaston, 1997. A critical assessment of the form of the interspecific relationship between abundance and body size in animals. Journal of Animal Ecology 66: 233-249.

Brown, J. H. 1984. On the relationship between the abundance and distribution of species. American Naturalist 124: 255–279.

Brown, J. H., 1995. Macroecology. University of Chicago Press, Chicago, Illinois, USA.

Brown, J. H., and B. A. Maurer. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the American avifauna. American Naturalist 130: 1-17.

Brown, J. H., S. K. M. Ernest, J. M. Parody, and J. P. Haskell. 2001. Regulation of diversity: maintenance of species richness in changing environments. Oecologia 126: 321–332.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. Chicago: University of Chicago Press.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 2000 31:343-366.

Chesson P, and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. American Naturalist 150:519–553.

Demopoulos, A. W. J., C. R. Smith, D. J. DeMaster, and W. L. Fornes. 2003. Evaluation of excess 234Th activity in sediments as an indicator of food quality for deep-sea deposit feeders. Journal of Marine Research 61:276-284.

Drazen, J. C., R. J. Baldwin, and K. L. Smith Jr. 1998. Sediment community response to a temporally varying food supply at an abyssal station in the NE Pacific. Deep-Sea Research II. 45: 893-913.

Damuth, J. 1981. Population and body size in mammals. Nature 290: 699-700.

Ginger, M. L., D. S. M. Billett, K. L. Mackenzie, K. Kiriakoulakis, R. R. Neto, D. K., Boardman, V. L. C. S., Santos, I. M. Horsfall, and G.A. Wolff. 2001. Organic matter assimilation and selective feeding by holothurians in the deep sea: some observations and comments. Progress in Oceanography 50: 407-421.

Gooday, A. J. 2002. Biological Responses to Seasonally Varying Fluxes of Organic Matter to the Ocean Floor: A Review. Journal of Oceanography 58: 305-332.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203:1299–1309.

Hudson, I. R., B. D. Wigham, D. S. M. Billett, and P. A. Tyler. 2003. Seasonality and selectivity in the feeding ecology and reproductive biology of deep-sea bathyal holothurians. Progress in Oceanography 59: 381-407.

Hutchinson, R.E. 1957. Concluding remarks. Cold Spring Harbor Symposium. Quantitative Biology 22: 415-427.

Iken, K., T. Brey, U. Wand, J. Voigt, and P. Junghans. 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Progress in Oceanography 50: 383-405

Kaufmann, R. S., and K. L. Smith Jr. 1997. Activity patterns of mobile epibenthic megafauna at an abyssal site in the eastern North Pacific: Results from a 17-month time-lapse photographic study. Deep-Sea Research I 44: 559-579.

Lauerman, L. M. L., R. S. Kaufmann, and K. L. Smith Jr. 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. Deep-Sea Research I 43: 1075-1104.

MacArthur, R. H. 1957. On the relative abundance of bird species. Proceedings of the National Academy of Sciences USA 43:293–295.

MacArthur R. H., and E.O. Wilson, 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

May, R. M. 1975. Patterns of species abundance and diversity. Pages 81–120 *in* M. Cody and J. Diamond, editors. Ecology of species and communities. Harvard University Press, Cambridge, Massachusetts, USA.

Motomura, I., 1932. On the statistical treatment of communities. Zoological Magazine, Tokyo 44: 379–383.

Nee, S., P. H. Harvey, and R. M. May. 1991. Lifting the veil on abundance patterns. Proceedings of the Royal Society of London B 243: 161-163.

Nee, S., A. F. Read, J. J. D. Greenwood, and P. H. Harvey. 1991. The relationship between abundance and body size in British birds. Nature 351: 312-313.

Neto, R. R., G. A. Wolff, D. S. M. Billett, K. L. Mackenzie, and A. Thompson. 2006. The influence of changing food supply on the lipid biochemistry of deep-sea holothurians. Deep-Sea Research I 53: 516-527.

Olding-Smee, F. J, K. N. Laland, and M. W. Feldmann. 2003. Niche construction: neglected processes in evolution. Princeton University Press, Princeton, New Jersey, USA.

Pielou, E. C., 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13: 131-144.

Preston, F. W., 1948. The commonness, and rarity, of species. Ecology 29: 254-283.

Reimers, C. E., R. A. Jahnke, and D. C. McCorkle. 1992. Carbon fluxes and burial rates over the continental slope and rise off central California with implications for the global carbon cycle. Global Biogeochemical Cycles 6:199-224.

Ruhl, H. A., in preparation. Population dynamics of abyssal epibenthic megafauna in the northeast Pacific from 1989-2004. Ecology.

Ruhl, H. A., and K. L. Smith Jr. 2004. Shifts in deep-sea community structure linked to climate and food supply. Science 305: 513-515.

Smith, K. L., Jr., and E. R. M. Druffel. 1998. Long time-series studies of the benthic boundary layer at an abyssal station in the NE Pacific. Deep-Sea Research II. 45: 573-586.

Smith, K. L., Jr., and R. S. Kaufmann. 1999. Long-term discrepancy between food supply and demand in the deep eastern North Pacific. Science 284: 1174-1177.

Smith, K. L., Jr., R. J. Baldwin**,** H. A. Ruhl, M. Kahru, B. G. Mitchell, and R. S. Kaufmann 2006. Climate effect on food supply to depths greater than 4000 m in the northeast Pacific. Limnology and Oceanography 51: 166-167.

Smith, K. L., Jr., R. S. Kaufmann, and W. W. Wakefield. 1993. Mobile megafaunal activity monitored with a time-lapse camera in the abyssal North Pacific. Deep-Sea Research I 40: 2307-2324

Solan, M., B. D. Wigham, I. R. Hudson, R. Kennedy, C. H. Coulon, K. Norling, H. C. Nilsson, and R. Rosenberg. 2004. *In situ* quantification of bioturbation using time-lapse fluorescent sediment profile imaging (f-SPI), luminophore tracers and model simulation. Marine Ecology Progress Series 271: 1-12.

Sugihara, G., 1980. Minimal community structure: an explanation of species abundance patterns. American Naturalist 116: 770-87.

Sugihara, G., Bersier, L-F., Southwood, T. R., Pimm, S. L., and R. M. May. 2003. Predicted correspondence between species abundances and dendrograms of niche similarities. Proceedings of the National Academy of Sciences USA 100: 5246-5251.

Tokeshi, M., 1990. Niche apportionment or random assortment: species abundance patterns revisited. Journal of Animal Ecology 59:1129–1146.

Tokeshi, M., 1999. Species coexistence: ecological and evolutionary perspectives. Blackwell Science, Oxford, United Kingdom.

Thibault, K. M., E. P. White, and S. K. M. Ernest. 2004. Temporal dynamics in the structure and composition of a desert rodent community. Ecology 85: 2649-2655.

Whittaker, R. H., 1965. Dominance and diversity in land plant communities. Science 147: 250–260.

Wigham, B. J., I. R. Hudson, D. S. M. Billett, and G. H. Wolff. 2003. Is long-term change in the abyssal Northeast Atlantic driven by qualitative changes in export flux? Evidence from selective feeding in deep-sea holothurians. Progress in Oceanography 59:409-441.

Wigham, B. J., P. A. Tyler, and D. S. M. Billett. 2003. Reproductive biology of the abyssal holothurian *Amperima rosea*: and opportunistic response to variable flux in surface derived organic matter? Journal of the Marine Biological Association of the United Kingdom 83: 175-188.

Supporting Material

Methods

Community assembly of the dominant epibenthic megafauna was examined at an abyssal site in the NE Pacific as part of a long-term research program. Analyses of abundance and body size data collected from 1989-2004 were used to address variation in rank abundance distributions (RADs), Pielou's evenness (Pielou, 1966; also known as Shannon's evenness), species composition, and interspecific body size vs. abundance relationships. The community descriptors were then related to the habitat's primary fluctuating resource, particulate organic carbon (POC) flux to the seafloor. Few contemporary ecological studies examine temporal variations in rank abundance distributions and to the authors knowledge no such long-term studies have been conducted for the vast abyssal benthos.

Abundance and body size data for the study were collected using a camera sled system to conduct line-transect photography. An otter trawl system was also towed behind the sled to collect photographed specimens for identification. Over the 16-year study, 52 transects averaging 1.2 km were conducted during 37 monthly time intervals on a roughly seasonal basis. Significant gaps in the time-series exist due to logistical constraints and are apparent in Figure 27a-c. A transect length weighted abundance estimate was created if more than one transect was conducted during any particular month. Details on line-transect data collection and analysis methods used here are provided in Wakefield and Smithy (1989), Wakefield and Genin (1987), Laake et al. (1994), Buckland et al. (1993), Lauerman et al. (1996), Lauerman and Kaufmann (1998), and Ruhl and Smith (2004).

The *in situ* setting, Station M (4100 m depth; 34°50’N, 123°00’W), lies beneath the western side of the California Current system and is subject to seasonal and interannual scale changes 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). Surface export flux in the waters above Sta. M has been estimated to be similar for areas extending hundreds of km north and south of the site along the California coast (Smith et al., 2006). The regional species pool for echinoderm megafauna is likely to be large considering the relatively contiguous abyssal seafloor habitat structure and the planktonic dispersal and cosmopolitan ranges of several taxa (Young, 2003).

The monthly POC flux data used for this analysis are a composite of particle flux trap data collected at 50 and 600 meters 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 m^{-2} opening with 10-day integrated samples (Baldwin et al., 1998). The primary data for the composite were the 50 mab trap data since they can potentially account for sinking, resuspended, and laterally advected POC (Smith et al., 2001). Where available, 600 mab trap data was used to fill in any gaps in the 50 mab POC flux data. It should be noted that although the 50 mab trap typically has a higher mass flux from resuspension and/ or lateral transport, the POC flux values have not been shown to be significantly different (Baldwin et al., 1998), possibly due to the relatively old and refractory nature of resuspended carbon (Bianchi et al., 1998, Druffel et al., 1998, Smith et al., 2001). An empirical model for estimating POC flux to 50 mab at the site was recently proposed (Smith et al., 2006) that incorporates lagged influences from satellite-estimated sea surface temperature and net primary production (Laws, 2004), sea level air pressure anomalies (NOI), and regional upwelling (BUI). The model-estimated flux could account for greater than 50% of the observed variation in the monthly estimates. The model effectively differentiated between high and low flux periods and the explanatory power of the model improves over larger time scales. The resulting composite (Fig. 29) represents the best information available on the monthly POC flux to the study site and avoids the complexities of cross-correlating two gapped data sets.

RADs were created by ranking the abundances of all dominant taxa in descending order with rank one being most abundant. Species composition is represented here by the species-specific abundances. The Bray-Curtis similarity index was used to create similarity matrices for the RADs and species composition data with a log(x+1) transformation. Bray-Curtis similarity has been shown to be superior to Euclidean distance in estimating the similarity of biological communities (Bloom, 1981). These matrices then served as input for the similarity vs. time lag scatter plots in Fig. 1a and b, hierarchical similarity dendrograms using group average clustering, and a non-metric multi-dimensional scaling (MDS) x-ordination. These multivariate analyses were conducted using the PRIMER-5 software package. A Mantel randomization test (Legendre and Legendre, 1998) was used to evaluate the significance of the RAD and species composition similarity shifts over time (Figs. 26a and b) since there are many more pairwise comparisons than actual samples.

A similar method of comparing similarity between samples as a function of the temporal lag has been used previously (e.g. Collins et al., 2000, Thibault et al., 2004, Venrick, 1990). Empirical data and simulations have determined the technique was rigorous over a range of scales (Collins et al., 2000). This method can be used to examine relative rates of change in a community and can detect basic non-linear trends as well (Fig. 30). Caution should still be used when interpreting such plots, however, since coherent cycles of divergence and convergence can happen at smaller scales than might be resolved. This is clear when the more cyclic MDS x-ordinate of RAD similarity (Fig. 26a) and the time lag plot (Fig. 26a) are compared. Records of sufficient time averaging or with several cyclical shifts present may, for example, show no apparent overall change.

Cross-correlations between the RAD and species composition similarity MDS x-ordinates, evenness, and the POC flux composite were conducted using the non-parametric Spearman-Rank correlation. This was done using only the monthly data with POC flux changes preceding megafauna sample shifts. Serial autocorrelation corrections were not used due to the uneven and relatively infrequent timing of the megafauna sampling. A supplementary investigation of similarity (ANOSIM) with 999 permutations was used to determine if particular observed differences in community structure (Fig. 26d) were significant and 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 and is similar to an analysis of variance (ANOVA).

Comparisons between the RADs during the principal species compositions of 1989-Aug 1994, Sep 1994-1998, 1989-1998, 2001-2004, and the time series as a whole were done by fitting a geometric line to the monthly RADs during each period. Linear descriptions using the Pearson correlations and 95% confidence intervals were used to help evaluate the similarity of the RADs during the different species compositions. This is similar to a method described by Fattorini (2005), but without attempts to assert what distribution best fits the data.

The interspecific relationship between abundance and body size was also examined for the time series as a whole and for the principal species-composition groups outlined in Figure 26d. Reliable biomass estimates are not yet available. An exploratory analysis has shown that if a crude conversion of length to body mass is done by taking 1/5 of the length as the diameter of a cylinder and converting its volume to mass using the density of water, a slope of approximately -0.24 for the length data translates to –3/4 for mass. This is the rudimentary shape of several of the holothuroid taxa present in the study. This explicitly ignores differences in body shapes and densities but provides provisional information that the mass corrected slope may not be greatly different from the common –3/4 rule (Damuth, 1981, Blackburn and Gaston, 1997, Nee et al., 1991). Further exploration of length to body mass relationships may help elucidate the body size vs. abundance power relation for this community. The results presented in the paper simply show that there was likely to be a consistent relationship that could have been approximately abundance = $\text{mass}^{-3/4}$. Neither here nor in any other part of the study do the implications rely on arbitrary delineations, definitions, or weakly discernable differences among distributions.

Supporting results

This study documents shifts in diversity that occurred over interannual scales that were linked with disequilibria in productivity. Supplementary ANOSIM results show that the 1989-1998 and 2001-2002 periods had significantly different ($p < 0.001$) megafaunal compositions and that 1989-Aug 1994 and Sep 1994-1998 periods were also significantly different ($p < 0.001$), but more similar to each other than to 2001-2004. RADs also were significantly different for the principal species compositions 1989-Aug1994 and 2001-2004 ($p < 0.001$), and 1989-1998 and 2001-2004 ($p < 0.05$), indicating that the directional changes may be linked at some level. The RAD and species composition distributions were also significantly different ($p < 0.05$) during times when the annual POC flux was above or below the long-term average and when the NOI condition was above or below zero.

The differential responses to food supply occurred within the context of a community setting and each taxon appeared to have differing responses to food supply variability, Allee effects (Allee, 1938, Dennis, 1989, Scheuring, 1999), as well as biotic interactions with other taxa. Small or incomplete communities such as the one examined here often have a geometric distribution and with more exhaustive sampling the overall shape could become more lognormal (Preston, 1948, Sugihara, 1980, Nee et al., 1991, Tokeshi, 1999). The residuals of the linear equations in Fig. 28a-e could be reflective of a combination of variation in any niche apportionment rule and sampling error.

Background on the Relative Abundance of Species

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, metabolism, body size, dispersal, and stochastic processes (e.g. Motomura, 1932, MacArthur, 1957, Whittaker, 1965, MacArthur and Wilson, 1967, May, 1975, Hubbell, 1979. 2001, Sugihara, 1980, Tokeshi, 1990, 1999, Brown, 1995, Chase and Liebold, 2003, Olding-Smee et al., 2003, Sugihara et al., 2003). There is a large and rapidly growing body of literature addressing relative abundance, species coexistence, and related areas and a sampling of the available references are addressed below to provide further context. Many recent studies have evaluated hypotheses based on niche and neutral theories of relative abundance in both the context of evolution, as well as paleo and contemporary ecology (Gaston and Chown, 2005, Pandolfi, 2006). Several complications commonly prohibit unequivocal interpretation of results (Willis and Whittaker, 2002) including the co-variation of species distributions, geographic range, and environmental gradients (Gilbert and Lechowicz, 2004), pooling of spatial or temporal variability (Thibault et al., 2004), and the notion that many factors can potentially affect success. In forests, for instance, although at one location many species could be rare, most of those rare species were abundant elsewhere (Murray et al., 1999).

Neutral theory can lead to species coexistence, species area, RADs, and other trends under certain assumptions (Hubbell, 2001, Hubbell and Borda-de-Água, 2004, Volkov et al., 2004). However, there do appear to be circumstances under which neutral theory may not be able to best explain certain observations (Brown et al., 2002, Gilbert and Lechowicz, 2004, Svenning et al., 2004, Arrington et al., 2005, McGill et al., 2005, Wootton, 2005, Dornelas et al., 2006).

Linking environmental and resource variables to the success of individuals and populations has provided a wealth of information, but evidence for differential responses to a common resource has been limited. Interpreting results from systems where environment and resources can significantly affect a species and vice versa have also been challenging (e.g. Brown, 2001B, Chase and Liebold, 2003). In aquatic systems, increases in nutrients have been shown to lead to the dominance of certain algal taxa during blooms (e.g. Cole et al., 1996, Smayda, 1997, Vitousek, 1997). Evenness has even been suggested to be an indicator of eutophication (e.g. Cottingham and Carpenter, 1998, Tsirtisi and Karydis, 1998, Kitsiou and Karydis, 2000). Coexistence in diatoms has been shown to be facilitated by fluctuating environmental factors (Descamps-Julien and Gonzales, 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 (Nielson, 2003). Temporal examination of central N Pacific copepod equitability has found little temporal variation during periods of environmental change (McGowan and Walker, 1985), but evidence for environmental and resource-driven differences in copepod equitability have been demonstrated between ocean provinces (Woodd-Walker et al., 2002) described by Longhurst (1998).

Several ideas about how to address temporal and spatial variation in population and community ecology have already been proposed (e.g. Chase and Leibold, 2003, Chesson and Huntly, 1997, Chesson, 2000, DeWoody et al., 2005). Shifts in the abundance of one taxon over time are often linked with another compensatory response(s) (e.g. Ernest and Brown, 2001) and disturbance can play an important roll in maintaining diversity (e.g. Connell, 1978). Local disturbance for instance can reduce local diversity, but provide greater habitat diversity at greater scales. Evenness has also been shown to be scale dependent in plant communities (Wilson et al., 1999). Temporally, a species can be risk averse, risk neutral, or risk prone with regard to environment or resource variability (Chase and Liebold, 2003, Chesson et al., 2004). Species can also respond to the mean or the variation of resources over time (Levins, 1979). The role of stochastic processes may still be important and require further consideration in the absence of deterministic certainty, especially since the parameterization of all relevant resource dimensions is unrealistic. Exploration into ideas that can unify such important aspects of prevailing theories could still prove useful (Gilbert and Lechowicz, 2005). The results here support theories that include disequilibria in the maintenance of diversity relationships such as relative abundance.

The relative relationship between body size and abundance has also been a relatively conservative feature of communities (Blackburn and Gaston, 1997), but this negative linear trend is not absolute and non-linear distributions have been observed in some bird populations for instance (Brown and Maurer, 1997). Furthermore, body size vs. abundance, body size vs. area, and species-area relationships are all interrelated in vertebrates suggesting that a formal niche space may exist (Southwood et al., in review). Smaller animals might be more abundant because they require less resource per unit area, have smaller internal resource distribution networks and higher metabolisms (West et al., 1997), and body size has been linked to energy use and community structure (Ernest, 2005). In the ocean, metabolism has also been shown to be related to vision and mobility, and metabolic enzyme activity (Childress, 1995, Somero, 1979, 1992). 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 describe stability in such a relationship even with significant composition and resource change.

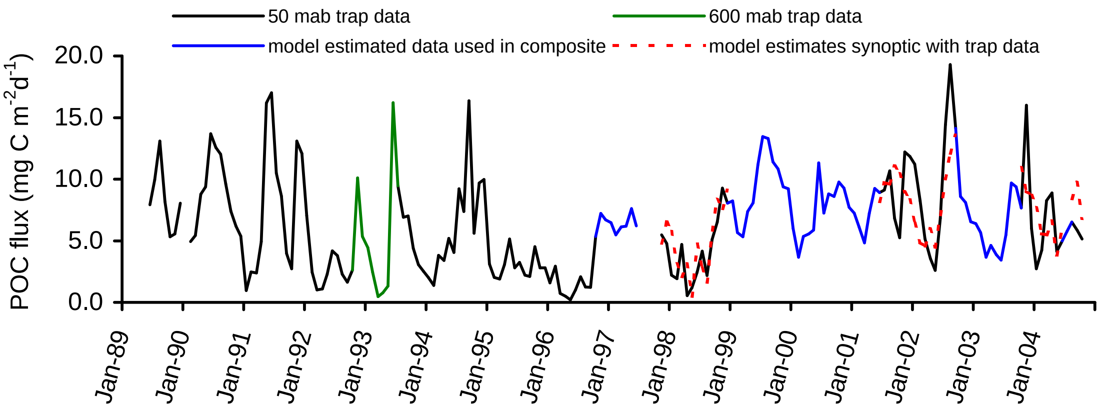

Fig. 29. The composite presented in Fig. 2 is a composite of POC flux estimates from 50 mab (black) and 600 mab (green) sediment traps and model-estimated flux (blue). The red dashed line is unincorporated model data. The difference between red dashed lined and the black line indicates how well the model estimates correspond to measured 50 mab POC flux values.

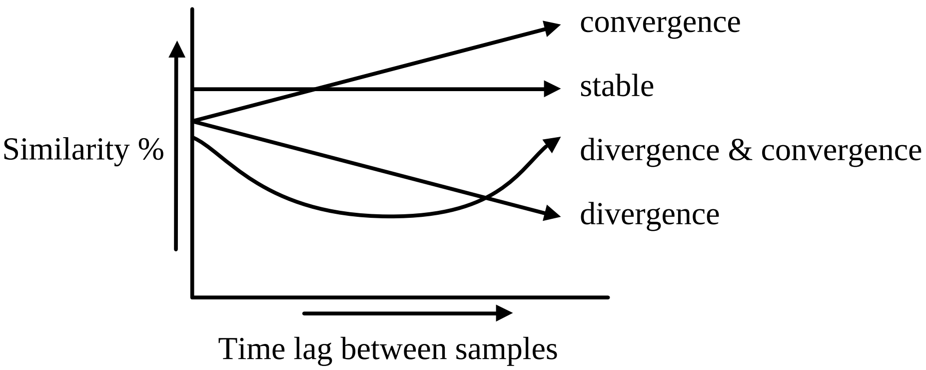

Fig. 30. Several potential outcomes of examining the similarity of two temporally different samples as was done in Figure 1a and b. This is similar to a figure that appeared in Collins et al. (2000).

Supporting References

Allee, W. C. 1938. The social life of animals. Norton, New York.

Arrington, D. A., Winemiller, K. O., and C. A. Layman. 2005. Community assembly at the patch scale in a species rich tropical river. Oecologia 144: 157–167

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-1971. NOAA Tech. Rep. NMFS SSRF-671. 103 pp.

Baldwin, R. J., R. C. Glatts, and K. L. Smith Jr. 1998. Particulate matter fluxes into the benthic boundary layer at a long time-series station in the abyssal NE Pacific: composition and fluxes. Deep-Sea Research II. 45: 643-666.

Bianchi, T. S., J. E. Bauer, E. R. M. Druffel, and C. D. Lambert. 1998. Pyrophaeophorbide-a as a tracer of suspended particulate organic matter from the NE Pacific continental margin. Deep-Sea Research II 45: 715-731.

Blackburn, T. M., and K. J. Gaston. 1997. A critical assessment of the form of the interspecific relationship between abundance and body size in animals. J. Animal Ecology 66: 233-249.

Bloom, S. A., 1981. Similarity indices in community studies: potential pitfalls. Marine Ecology Progress Series 5: 125-128.

Brown, J. H., 1995. Macroecology. University of Chicago Press, Chicago, Illinois, USA.

Brown, J. H., D. A. Kelt, and B.J. Fox. 2002. Assembly Rules and Competition in Desert Rodents. American Naturalist 160: 815-818.

Brown, J. H., and B. A. Maurer. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the American avifauna. American Naturalist 130: 1-17.

Brown, J. H., S. K. M. Ernest, J. M. Parody, and J. P. Haskell. 2001a. Regulation of diversity: maintenance of species richness in changing environments. Oecologia 126: 321–332.

Brown, J. H., G. B. West, and B. J. Enquist. 2005. Yes, West, Brown and Enquist’s model of allometric scaling is both mathematically correct and biologically relevant. Functional Ecology 19: 735 –738

Brown, J. H., T. G. Whitham, S. K. M. Ernest, and C. A. Gehring. 2001b. Complex Species Interactions and the Dynamics of Ecological Systems: Long-Term Experiments. Science 293: 643-650.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance Sampling: Estimating abundance of biological populations. Chapman and Hall, London 446pp.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. Chicago: University of Chicago Press.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Ecology and Systematics 1:343-366.

Chesson, P., R. L. E. Gebauer, S. Schwinning, N, Huntly, K, Wiegand, M. S. K. Ernest, A Sher, A. Novoplansky, and J. F. Weltzin. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141: 236-253.

Chesson, P., and N. Huntly, 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. American Naturalist 150:519–553.

Childress, J. J. 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals? TREE 10, 30–36.

Cole, K. H., et al. 1996. A massive phytoplankton bloom induced by and ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean. Nature 383: 495-501.

Collins, S. L., F. Micheli, and L. Hartt. 2000. A method to determine rates and patterns of variability in ecological communities. Oikos 91:285–293.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199:1302 –1310

Cottingham, K. L., and S. R. Carpenter. 1998. Population, community, and ecosystem variates as ecological indicators: phytoplankton responses to whole-lake enrichment. Ecological Applications 8: 508-530.

Damuth, J. 1981. Population-density and body size in mammals. Nature 290:699–700.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling 3: 481-538.

Descamps-Julien, B., and A. Gonzalez. 2005. Stable coexistence in a fluctuating environment: an experimental demonstration. Ecology 86: 2815–2824.

DeWoody, Y. D., R. K. Swihart, B. A. Craig, and J. R. Goheen, 2003. Diversity and Stability in Communities Structured by Asymmetric Resource Allocation. American Naturalist 162: 514-527.

Dornelas, M., S. R. Connolly, and T. P. Hughes. 2006. Coral reef diversity refutes the neutral theory of biodiversity. Nature 440:80-82.

Druffel, E. R. M., S. Griffin, J. E. Bauer, D. M. Wolgast, and X-C. Wang. 1998. Distribution of particulate organic carbon and radiocarbon in the water column from the upper slope to the abyssal NE Pacific Ocean. Deep-Sea Research II 45: 667-687.

Ernest, S. K. M. 2005. Energy flow, body size, and community structure in small mammal communities. Ecology 86: 1407-1413.

Ernest, S. K. M., and J. H. Brown. 2001. Homeostasis and compensation: the role of species and resources in ecosystem stability. Ecology 82:2118–2132.

Fattorini, S. 2005. A simple method to fit geometric series and broken stick models in community ecology and island biogeography. Acta Oecologica 28:199-205.

Gaston, K. J., and S. L. Chown. 2005. Neutrality and the niche. Functional Ecology 19: 1-6.

Gilbert, B., and M. J. Lechowicz. 2004. Neutrality, niches, and dispersal in a temperate forest understory. Proceedings of the National Academy of Sciences of the USA 101: 7651–7656.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203:1299–1309.

Hubbell, S. P., and L. Borda-de-Águal. 2004. The unified neutral theory of biodiversity and biogeography: reply. Ecology 85: 3175–3178.

Kitsiou, D., and M. Karydis. 2000. Categorical mapping of marine eutrophication based on ecological indices. The Science of the Total Environment 255: 113-127.

Laake, J. L., S. T. Buckland, D. R. Anderson, and K. P. Burnham. 1994. Distance Users Guide V 2.1. Colorado Cooperative Fish and Wildlife Research Unit. Colorado State University, Fort Collins, CO. 84 pp.

Laws, E. A. 2004. Export flux and stability as regulators of community composition in pelagic marine biological communities: Implications for regime shifts. Progress in Oceanography 60: 343–354.

Lauerman, L. M. L., and R. S. Kaufmann. 1998. Deep-sea epibenthic echinoderms and a temporally varying food supply: Results from a one year time-series in the NE Pacific. Deep-Sea Research II 45: 817-842.

Lauerman, L. M. L., R. S. Kaufmann, and K. L. Smith Jr. 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. Deep-Sea Research I 43: 1075-1104.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Elsevier Science, Amsterdam, The Netherlands.

Levins, R. 1979. Coexistence in a variable environment. American Naturalist 114: 765-783.

Longhurst, A. 1998. Ecological geography of the sea. Academic Press, London.

MacArthur, R. H. 1957. Proceedings of the National Academy of Sciences USA 43: 293-295.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

May, R. M. 1975. Patterns of species abundance and diversity. Pages 81–120 *in* M. Cody and J. Diamond, editors. Ecology of species and communities. Harvard University Press, Cambridge, Massachusetts, USA.

McGill, B. J., E. A. Hadly, and B. A. Maurer. 2005. Community inertia of Quaternary small mammal assemblages in North America. Proceedings of the National Academy of Sciences USA 102: 16701–16706.

McGowan, J. A., and P. W. Walker. 1985. Dominance and diversity maintenance in an oceanic ecosystem. Ecological Monographs 55:103–118.

Motomura, I. 1932. On the statistical treatment of communities. Zoological Magazine, Tokyo 44: 379–383.

Murray, B. R., B. L., Rice, D. A. Keith, P. J. Myerscough, J. Howell, A. G. Floyd, K. Mills, and M. Westoby. 1999. Species in the tail of rank-abundance curves. Ecology 80: 1806-1816.

Nee, S., P. H. Harvey, and R. M. May. 1991. Lifting the veil on abundance patterns. Proceedings of the Royal Society of London B 243: 161-163.

Nielsen, K. J. 2003. Nutrient loading and consumers: Agents of change in open-coast macrophyte assemblages. Proceedings of the National Academy of Sciences USA 100: 7660-7665.

Olding-Smee, F. J, K. N. Laland, and M. W. Feldmann. 2003. Niche construction: neglected processes in evolution. Princeton University Press, Princeton, New Jersey, USA.

Pandolfi, J. M. 2006. Corals fail a test of neutrality. Nature 440: 35-36.

Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13: 131-144.

Preston, F. W. 1948. The commonness, and rarity, of species. Ecology 29: 254-283.

Rex, M. A., C. R. McClain, N. A. Johnson, R. J. Etter, and J. A. Allen. 2005. A Source-Sink Hypothesis for Abyssal Biodiversity. American Naturalist 165: 163-178.

Ruhl, H. A., and K. L. Smith Jr. 2004. Shifts in deep-sea community structure linked to climate and food supply. Science 305: 513-515.

Schwing, F. B., T. Murphree, and P. M. Green. 2002. The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. Progress in Oceanography 53: 115-139.

Smith, K. L., Jr., R. J. Baldwin, H. A. Ruhl, M. Kahru, B. G. Mitchell, and R. S. Kaufmann. 2006. Climate effect on food supply to depths greater than 4000 m in the northeast Pacific. Limnology and Oceanography 51: 166-167.

Smith, K. L., Jr., and R. S. Kaufmann. 1999. Long-term discrepancy between food supply and demand in the deep eastern North Pacific. Science 284: 1174-1177.

Smith, K. L., Jr., R. S. Kaufmann, R. J. Baldwin, and A. F. Carlucci. 2001. Pelagic-benthic coupling in the abyssal eastern North Pacific: An eight-year time-series study of food supply and demand. Limnology and Oceanography 46: 543-556.

Smith, K. L., Jr., R. S. Kaufmann, and W. W. Wakefield. 1993. Mobile megafaunal activity monitored with a time-lapse camera in the abyssal North Pacific. Deep-Sea Res. 40: 2307-2324.

Savage, A. A. 2000. Community structure during a 27-year study of the macroinvertebrate fauna of a chemically unstable lake. Hydrobiologia 421: 115–127.

Scheuring, I. N. 1999. Allee Effect Increases the Dynamical Stability of Populations. Journal of Theoretical Biology 199: 407-414.

Somero, G. N. 1992. Biochemical ecology of deep-sea animals. Experientia 48: 537–543.

Somero, G. N., and J. F. Siebenaller. 1979. Inefficient lactate dehydrogenases of deep-sea fishes. Nature 282:100-102.

Southwood, T. R. E., R. M. May, and G. Sugihara. in review. Observations on related ecological exponents. Proceedings of the National Academy of Sciences USA. 103: 6931 (2006)

Sugihara, G., 1980. Minimal community structure: an explanation of species abundance patterns. American Naturalist 116: 770-87.

Sugihara, G., Bersier, L-F., Southwood, T. R., Pimm, S. L., and R. M. May. 2003. Predicted correspondence between species abundances and dendrograms of niche similarities. Proceedings of the National Academy of Sciences USA 100: 5246-5251.

Svenning, J.-C., D. A. Kinner, R. F. Stallard, B. M. J. Engelbrecht, and S .J. Wright. 2004. Ecological determinism in plant community structure across a tropical forest landscape. Ecology 85: 2526-2538.

Thibault, K. M., E. P. White, and S. K. M. Ernest. 2004. Temporal dynamics in the structure and composition of a desert rodent community. Ecology 85: 2649-2655.

Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patterns revisited. Journal of Animal Ecology 59:1129–1146.

Tokeshi, M. 1999. Species coexistence: ecological and evolutionary perspectives. Blackwell Science, Oxford, UK.

Tsirtsis, G., and M. Karydis. 1998. Evaluation of phytoplankton community indices for detecting atrophic trends in the marine environment. Environmental Monitoring and Assessment 50: 255–269.

Venrick, E. L. 1990. Phytoplankton in an oligotrophic ocean: species structure and interannual variability. Ecology 71: 1547–1563.

Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. Nature 424: 1035- 1037.

Wakefield, W. W., and A. Genin. 1987. The use of a Canadian (perspective) grid in deep-sea photography. Deep-Sea Research 34: 469-478.

Wakefield, W. W., and W. Smithey. 1989. Two camera sleds for quantitative study of deep-sea megafauna. Scripps Institution of Oceanography Ref. Ser. No. 89-14, 25 pp.

West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. Science 276: 372–373.

Whittaker, R. H. 1965. Dominance and diversity in land plant communities. Science 147: 250–260.

Willis, K. J., and R. J. Whittaker. 2002. Species Diversity-Scale Matters. Science 295: 1245-1248.

Wilson, J. B., J. B. Steel, W. M. King, and H. Gitay. 1999. The effect of spatial scale on evenness. Journal of Vegetation Science 10: 463-468.

Woodd-Walker, R. S., P. Ward, and A. Clarke. 2002. Large-scale patterns in diversity and community structure of surface water copepods from the Atlantic Ocean. Marine Ecology Progress Series 236: 189–203.

Wootton, J. T. 2005. Field parameterization and experimental test of the neutral theory of biodiversity. Nature 433: 309-312.

Young, C. M. 2003. Reproduction, development and life-history traits. Pages 381–426 In P. A. Tyler, ed. Ecosystems of the deep oceans. Vol. 28. Ecosystems of the world. Elsevier, Amsterdam.

VI

Conclusions

Conclusions

The seasonally and interannually variable NE Pacific had order of magnitude or greater fluctuations in abyssal megafauna populations from 1989-2004. Increases in mobile megafauna abundance were linked with decreases in smaller size classes; a result expected if new recruits are being added to the putative populations. Estimates presented here suggest that individual growth rates could be 1-6 mm month^{-1} and some echinoderm populations can more than double in size within one year. Megafaunal aggregations do occur at Sta. M but there was no indication that non-random dispersion biases the photographic transect results. The observed differential responses to food supply indicate that the mechanisms controlling the abundance and distribution of the mobile megafauna examined have non-neutral properties (*sensu* Hubbell, 2001). The greatest difference in echinoderm community composition centered on the 1998/99 El Niño/ La Niña event. Climatically driven pelagic-benthic coupling also may have influenced other communities at Sta. M from foraminifera (Drazen, 1998), and enteropneusts (Smith et al., 2005), to fishes (Bailey et al., 2006). The findings at Sta. M are consistent with observed shifts in an abyssal echinoderm assemblage in the NE Atlantic on the Porcupine Abyssal Plain (Billet et al., 2001).

A recent study by Smith et al. (2006) further described links between climate variations represented in the Northern Oscillation Index (NOI, Schwing, 2002) for Sta. M and the North Atlantic Oscillation (NAO, Visbeck, 1998) for the NE Atlantic. Time-lagged correlations exist between these climatic indicators and POC flux to the seafloor in both regions. Shorter time-lagged correlations also exist between POC flux and satellite estimated export flux (Smith et al., 2006). Supporting correlations between

POC flux at Sta. M and sea-level air pressure anomalies (SLPA's) across the entire Pacific indicate that the strongest positive and negative correlations roughly correspond to the locations that provide sea-level air pressure data for the NOI (North Pacific high (35°N, 130°W) and a location near Darwin, Australia (10°S, 130°E)). POC flux values at Sta. M also correlate to southerly winds and sea-surface temperatures along the California coast. The mechanisms that ultimately control climate variation related to El Niño and La Niña remain poorly understood, but it does appear that SLPA's influence winds, coastal upwelling (Bakun, 1973), SST's, pelagic productivity, and the proportion of that productivity that sinks to the abyssal seafloor (Smith et al., 2006).

Broader Ecological Implications

Although the logistical limitations of deep-sea research are many, research from deep-sea time-series studies has provided fundamental information about a realm that occupies most of the earth's surface. The changes in food supply and abyssal populations observed at Sta M provide strong evidence that climatic variations can influence abyssal fauna on timescales as short as months. At Sta. M, climatic influence also seems to have fundamentally altered the community composition of the mobile epibenthic megafaunal guild. The interannual timescales for community change are comparable to those in pelagic marine (e.g. McGowan et al., 1998, Brinton and Townsend, 2003, Lavangelos and Ohman, 2003) and terrestrial guilds (e.g. Holmgren et al., Thibault et al., 2004).

There is now strong evidence that anthropogenic global warming is occurring (Hanson et al., 2005, Houghton, 2001, Karl et al., 2006) and includes increasing ocean temperatures (Barnett et al., 2005, Knutson, 2006). Shifts in communities of planktonic formaminfera (Field et al., 2006) and intertidal invertebrates (Barry et al., 1995, Sagarin et al., 1999) have also been linked to secular warming in the California Current region. Long-term changes in ocean temperature could reduce upwelling and nutrient delivery through increased stratification. Increased temperatures may also reduce the proportion of surface production that is exported from surface waters (Laws, 2004). Current global climate models coupled with oceanic models of productivity already predict a long-term, 10-20% reduction in phytoplankton concentration in the subpolar N Pacific (Pierce, 2004). Considering our current understanding of pelagic-benthic coupling, it is very plausible that if surface climate conditions continue to change, deep-sea communities could be affected without any significant buffer. Even though vertical mixing of the ocean occurs on the order of 1000 yr or more (Broecker, 1991), the sinking particulate flux transcends the slow mixing and provides a physical link from the surface to the abyss within weeks to months.

Any changes in benthic community composition or distribution could be altering the nature and intensity of marine sediment bioturbation. Such faunal driven mixing, utilization, and modification of POC has essentially unknown impacts on the long-term carbon cycle. If long-term anthropogenic effects extend to the abyssal seafloor, then the millennial-scale carbon cycle could be affected.

A test of physical and biological variables over a fifty-year period in the NE Pacific has shown that environmental descriptors are essentially linear in nature, but that biological time series consistently were best described by non-linear models (Hsieh, et al., 2005). Non-linear biological trends could arise through the influence of multiple linear trends to form a non-linear response. As the nature of past ecological shifts in the NE Pacific are more thoroughly examined and longer-term deep-sea data sets become available, more informed forecasts about the climatic impacts will be possible.

Future Directions

Future megafaunal research should include more detailed time-series estimates of abundance and distribution patterns utilizing advances in automated underwater vehicle (AUV) technology. Photo transects of the deep sea have provided useful estimates of the abundance and distribution of many benthic fauna, but current methods are not as able to reliably determine shorter time scale fluctuations in abundance (e.g. Lauerman et al., 1996). Existing sled systems are not capable of estimating spatial patterns beyond 200 m in scale and linear transects themselves cannot reliably discern linear distribution patterns. The estimation of population dynamics of taxa that are currently considered relatively rare species is also difficult using such transects. An AUV system could reliably determine shorter time scale fluctuations in abundance and more subtle distribution patterns by conducting photo surveys of large areas of the seafloor with transects several km or greater in length. Such a system could be set up with a fixed navigation grid to ensure the same area is surveyed with an accuracy of a few meters on repeated surveys over time. A lattice-sampling grid could also elucidate whether linear aggregations are common at the site.

Long-term studies that can effectively evaluate population dynamics and the processes affecting deep-sea fauna have been relatively scarce due to numerous logistical limitations. Thus the development of a vehicle with the capability to biologically survey large areas of the vast abyssal benthos could provide massive amounts of new information about the deep-sea. Improved analytical techniques, such as digital image capture, image recognition, and streamlined processing, will help facilitate the timely analysis of new data. Increases in the amount and quality of photographic data of abyssal habitats will be critical in characterizing trends in population dynamics and discerning the underlying causes of such variations. It is possible that interannual variation in POC flux could be affecting abyssal communities throughout the world ocean with more oligotrophic regions experiencing lower-magnitude variations. A more effective platform for addressing such variation should prove useful in determining the extent of climatic influences in the deep ocean.

References

Bailey, D. M., H. A. Ruhl, K. L. Smith Jr. 2006. Long-term changes in benthopelagic fish abundance in the abyssal northeast Pacific ocean. Ecology 87: 549-555.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-1971. NOAA Tech. Rep. NMFS SSRF-671. 103 pp.

Barnett, T. P., D. W. Pierce, K. M. AchutaRoa., P. J. Gleckler, B. D. Santer, J. M. Gregory, and W. M. Washington. 2005. Penetration of human-induced warming into the world's oceans. Science 309: 284-287.

Barry, J. P., C. H. Baxter, R. D. Sagarin, and S. E. Gilman. 1995. Climate-realted, long-term faunal changes in a California rock intertidal community. Science 267: 672-675.

Billett, D. S. M., B. J. Bett, A. L. Rice, M. H. Thurston, J. Galeron, M. Sibuet and G. A. Wolff. 2001. Long-term changes in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). Progress in Oceanography 50: 325-348.

Bograd, S. J., and R. J. Lynn. 2003 Long-term variability in the Southern California Current System. Deep-Sea Research II 50: 2355-2370.

Brinton, E., and A. Townsend. 2003. Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. Deep-Sea Research II 50: 2449-2472.

Broecker, W. S. 1991. The great ocean conveyor. Oceanography 4: 79-89.

Drazen, J. C., R. J. Baldwin and K. L. Smith, Jr. 1998. Sediment community response to a temporally varying food supply at an abyssal station in the NE Pacific. Deep-Sea Research II. 45: 893-913.

Field, D. B., T. R. Baumgartner, C. D. Charles, V. Ferreira-Bartrina, and M. D. Ohman. 2006. Planktonic Foraminifera of the California Current Reflect 20th-Century Warming. Science 311: 63-66.

Hansen, J., et al., 2005: Earth's Energy Imbalance: Confirmation and Implications. Science 308: 1431-1435.

Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutierrez, and G. M. J. Mohren. 2001. El Niño effects on the dynamics of terrestrial ecosystems. Trends in Ecology and Evolution 16: 89-94.

Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, and D. Xiaosu, editors, IPCC. 2001. Climate Change 2001: The Scientific Basis. Cambridge University Press, Cambridge.

Hsieh, C., S. M. Glaser, A. J. Lucas, and G. Sugihara. 2005. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. Nature 435: 336-340.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Karl, T. R., S. J. Hassol, C. D. Miller, and W. L. Murray, editors. 2006. Temperature Trends in the Lower Atmosphere: Steps for Understanding and Reconciling Differences. A Report by the Climate Change Science Program and the Subcommittee on Global Change Research, Washington, DC, USA.

Knutson, T. R., et al., 2006. Assessment of twentieth-century regional surface temperature trends using the GFDL CM2 coupled models. Journal of Climate 19.

Lauerman, L. M. L., R. S. Kaufmann, and K. L. Smith, Jr. 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. Deep-Sea Research I 43: 1075-1104.

Lavaniegos, B. E., and M. D. Ohman. 2003. Long-term changes in pelagic tunicates of the California Current. Deep-Sea Research II 50: 2473-2498.

Laws, E. A. 2004. Export flux and stability as regulators of community composition in pelagic marine biological communities: Implications for regime shifts. Progress in Oceanography 60: 343–354.

McGowan, J.A., D.R. Cayan, and L.M. Dorman. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science 281: 210-217.

Pierce, D. W. 2004. Future changes in biological activity in the North Pacific due to anthropogenic forcing of the physical environment. Climate Change 62: 389–418.

Sagarin, R.D., J.P. Barry, S.E. Gilman and C.H. Baxter. 1999. Climate-related changes in an intertidal community over short and long time scales. Ecological Monographs 69: 465-490.

Schwing, F. B., T. Murphree, and P. M. Green. 2002. The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. Progress in Oceanography 53: 115-139.

Smith, K. L., Jr., R. J. Baldwin**,** H. A. Ruhl, M. Kahru, B. G. Mitchell, and R. S. Kaufmann. 2006. Climate effect on food supply to depths greater than 4000 m in the northeast Pacific. Limnology and Oceanography 51: 166-167.

Smith, Jr., K. L., N. D. Holland, and H. A. Ruhl. 2005. Enteropneust production of spiral fecal trails on the deep-sea floor observed with time-lapse photography. Deep-Sea Research I 52: 1228-1240.

Thibault, K. M., E. P. White, and S. K. M. Ernest. 2004. Temporal dynamics in the structure and composition of a desert rodent community. Ecology 85: 2649-2655.

Visbeck, M., H. Cullen, G. Krahmann, and N. Naik. 1998. An ocean model’s response to North Atlantic Oscillation–like wind forcing. Geophysical Research Letters 25: 4521–4524.