

LONG-TERM CHANGE IN BENTHOPELAGIC FISH ABUNDANCE IN THE ABYSSAL NORTHEAST PACIFIC OCEAN

D. M. BAILEY,^{1,2,3} H. A. RUHL,¹ AND K. L. SMITH, JR.¹

¹Marine Biology Research Division, Scripps Institution of Oceanography, University of California-San Diego, 9500 Gilman Drive, La Jolla, California 92093-0202 USA

²Oceanlab, School of Biological Sciences, University of Aberdeen, Newburgh, Aberdeenshire AB41 6AA UK

Abstract. Food web structure, particularly the relative importance of bottom-up and top-down control of animal abundances, is poorly known for the Earth's largest habitats: the abyssal plains. A unique 15-yr time series of climate, productivity, particulate flux, and abundance of primary consumers (primarily echinoderms) and secondary consumers (fish) was examined to elucidate the response of trophic levels to temporal variation in one another. Towed camera sled deployments in the abyssal northeast Pacific (4100 m water depth) showed that annual mean numbers of the dominant fish genus (*Coryphaenoides* spp.) more than doubled over the period 1989–2004. *Coryphaenoides* spp. abundance was significantly correlated with total abundance of mobile epibenthic megafauna (echinoderms), with changes in fish abundance lagging behind changes in the echinoderms. Direct correlations between surface climate and fish abundances, and particulate organic carbon (POC) flux and fish abundances, were insignificant, which may be related to the varied response of the potential prey taxa to climate and POC flux. This study provides a rare opportunity to study the long-term dynamics of an unexploited marine fish population and suggests a dominant role for bottom-up control in this system.

Key words: benthic megafauna; *Coryphaenoides* spp.; deep water; marine fish; Pacific Ocean; population dynamics.

INTRODUCTION

The oceanic abyssal plains are the world's largest habitats, making deep-sea fish the dominant carnivores and scavengers across most of the Earth's surface. Found in distinct depth zones, and differing between oceans, the spatial distribution of deep-sea fish has been extensively studied (Merrett and Haedrich 1997). In contrast, no studies have been able to investigate long-term temporal patterns in abyssal fish distribution or abundance. Indeed, there is little data available on the long-term population and predator–prey dynamics of any large, and unexploited, marine fish population (Jennings and Blanchard 2004). Studies in fished systems have reached no consensus on how animal abundances and productivities are controlled in marine systems, with apparent demonstrations of both top-down (Worm and Myers 2003, Frank et al. 2005) and bottom-up controls (Ware and Thomson 2005). The controls of animal abundances in abyssal systems remain poorly understood.

Recent studies in the abyssal Pacific have demonstrated significant changes in benthic invertebrate community structure at inter-annual timescales (Ruhl and Smith 2004). These changes were linked to long-term patterns in the surface climate, and to food supply in the form of particulate organic carbon flux from the

surface (Ruhl and Smith 2004). It is unknown whether similar changes in abundance also occur at higher trophic levels, such as fish, and what effects any changes in fish abundance have on the benthic invertebrates. Most benthopelagic deep-sea fish are predators and scavengers, and do not feed directly on the sinking particulate organic matter that comprises the majority of the flux from the surface (Merrett and Haedrich 1997, Drazen et al. 2001). Fish may act as predators on primary consumers, such as the echinoderms, and have their diet supplemented by carrion fallout from the surface. The availability of both resources might vary as a result of changing surface productivity, as particulate fallout affects echinoderm behavior (Laurman and Kaufmann 1998), and the abundance and position of shallow-water animals' changes.

Evidence for the influence of surface productivity on abyssal fishes includes observations that grenadier abundance, size structure, behavior, and swimming speed can be linked to spatial and temporal variations in overlying productivity and invertebrate abundance (Armstrong et al. 1991, Priede et al. 1994, 2003). The precise mechanisms for the effects remain unclear, and studies of Pacific grenadier biochemistry suggest inter-annual, rather than seasonal, changes in a range of indicators of nutritional status in these fishes (Drazen 2002b).

In this study, we provide new information on both seasonal and interannual patterns in the abundance of a predominant benthopelagic predator and its prey. By

Manuscript received 5 December 2004; revised 21 July 2005; accepted 21 August 2005. Corresponding Editor: M. H. Carr.

³ E-mail: d4bailey@ucsd.edu

testing for long-term temporal relationships between the abundance of the predator and climate, particle flux, and abundance of potential prey taxa, we provide compelling evidence for bottom-up influences in this system.

METHODS

We used a two-part approach to test for long-term quantitative relationships between the abundance of predators, their benthic prey, surface productivity, and flux. First, we reviewed towed camera surveys of the density of noncryptic demersal fishes and benthic invertebrates conducted at one site over a 15-yr period. Then we used indices of ocean climate and estimates of POC flux to the benthos to test for relationships between these processes and predator dynamics.

Towed camera surveys

Forty-eight tow camera deployments were undertaken between October 1989 and February 2004 at Station M in the abyssal northeast Pacific (34°50' N, 123°00' W, 4100 m depth). Station M is located about 220 km west of Point Conception, California, USA and has been extensively studied and described in detail elsewhere (Smith and Druffel 1998). Camera sled deployments took place within an approximately 25 × 35 km area, 10–35 km from the sediment trap system. Full details of the camera system and survey procedure have been provided previously (Lauerma and Kaufmann 1998, Ruhl and Smith 2004). In summary, faunal abundance was estimated using photographs taken every 4–5 s as the camera sled moved along the seafloor at approximately 0.8 m/s, creating a continuous mosaic with a mean length of 1254 m.

As the fish were often photographed above the seafloor, the precise positions and visibility of the fish could not be determined by traditional line-transect theory (Buckland et al. 1993, Lauerma et al. 1996). The area viewed was calculated from the distance traveled by the sled and the effective strip width (ESW) based on the visibility of the targets. ESW varied between deployments due to differences in illumination or film development, and was estimated for fish by incorporating ESW values for benthic animals with the most similar size and coloration (the sea cucumber *Abyssoicum abyssorum*).

When more than one transect was done during any month, a transect length (sampling effort) weighted mean was used, providing 34 time-point estimates for the study period. Film transects were analyzed in random order, to avoid any training effect on the operator. Photographs were projected and viewed individually. One transect, previously used for invertebrate abundance estimates (from June 1991), was excluded here since the slow and erratic movement throughout the sled run may have affected the behavior of the fish. Fish were identified to genus or species where possible. Grenadiers were recorded as *Coryphaenoides* spp., as

it was impractical to discriminate between species from the photographs. In particular, *C. armatus* and *C. yaquinae* are common at Station M. The variable position and orientation of the fishes precluded estimation of fish size.

Only fish close to the seabed (<2 m above bottom) were visible to the camera. *Coryphaenoides armatus*, although a predominantly demersal species, does engage in excursions above the seafloor (Smith et al. 1989). The proportion of the time spent above the bottom by grenadiers during normal activity is not well known, but acoustic tracking studies at a nearby station indicated that grenadiers left the seafloor for less than 5% of the time (Priede et al. 1990).

Data analysis

The only fish that were sufficiently abundant to allow statistical analysis were the grenadiers, *Coryphaenoides* spp. Data on the abundances of the dominant mobile epibenthic megafauna (Lauerma et al. 1996, Lauerma and Kaufmann 1998, Ruhl and Smith 2004), collected from the same series of tows were used to investigate coupling between the benthos and the fish assemblage. The dominant megafaunal taxa included here are potential prey of grenadiers (Percy and Ambler 1974) and make up approximately 99% of mobile animals observed on the seafloor in terms of abundance.

The possible affect of climate fluctuation and particulate organic carbon (POC) flux to the seafloor on fish populations were also examined. The climate indices used are indicative of El Niño/La Niña, (northern and southern oscillation indexes [NOI, Schwing et al. 2002; SOI, Trenberth and Shea 1987]) and multivariate El Niño-southern oscillation index (MEI, Wolter and Timlin 1998) and regional upwelling measured by the Bakun upwelling index (BUI, Bakun 1973). The flux of POC to the seafloor (Baldwin et al. 1998, Smith et al., *in press*), was measured with a 50-m-above-bottom (mab) sediment trap. POC flux data used for the study includes monthly data from June 1991 through October 1992, July 1993 through October 1996, November 1997 through December 1998, and June 2001 through September 2002. The 50-mab trap was chosen for these comparisons since 600-mab trap data from 2001–2002 were not available. Although the 50-mab trap can capture resuspended mass flux, the 600-mab and 50-mab trap data are highly correlated and differences in POC flux were not significant (Baldwin et al. 1998, Smith et al., *in press*). Cross-correlations between POC flux at 50 mab and satellite estimated surface export flux were significant to at least a 100 km radius around the study site and up to 300 km parallel to the coast (Smith et al., *in press*).

Spearman rank cross correlations were conducted between the observed grenadier abundances and mobile epibenthic megafaunal (MEM) taxa, as well as between grenadier abundances and the climate and POC param-

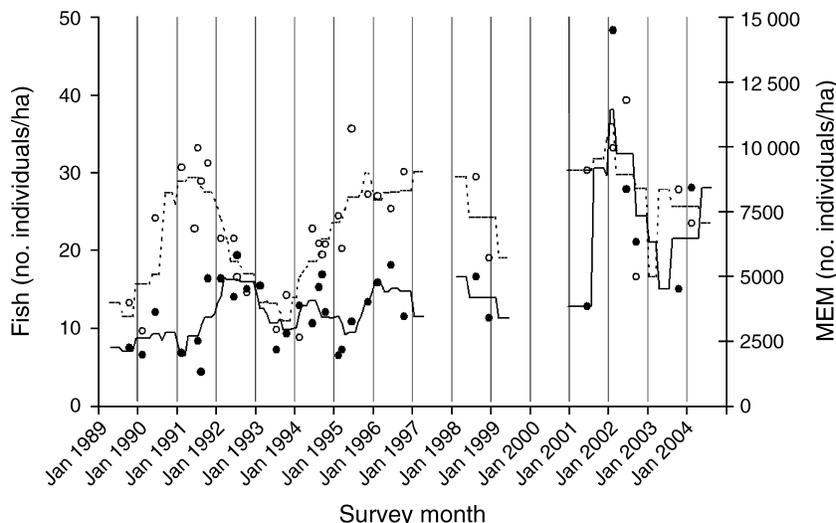


FIG. 1. Monthly abundances of mobile epibenthic megafauna (MEM, open circles) and grenadier fish, *Coryphaenoides* spp. (solid circles) recorded by towed camera at Station M in the northeast Pacific at 4100 m depth. MEM consisted of eight species of echinoderms. All data are monthly averages. Both series show large variations at annual and decadal time scales, with a general increase in abundances over time. Also shown are the 13-mo centered running means for the echinoderm MEM (dashed lines) and grenadier fish (solid lines).

eters. These correlations were done using monthly values and temporal lags. Since the benthic invertebrate and fish population data sets were discontinuous, 13-mo centered running means were used to conduct the monthly cross correlations. Lags of -24 to $+24$ months between the fish and invertebrate data were introduced to investigate top- and bottom-down predator-prey interactions. For comparison of the climate and POC flux data with fish abundances, lags of 0–24 mo were used. Climate and POC flux data were only allowed to lead abundance and not vice versa. The modified Chelton method (Pyper and Peterman 1998) was used to correct the resulting P values for serial autocorrelation.

Monthly average fish abundances were plotted against Julian date in order to examine the effects of season on these parameters. The timing of the annual highest and lowest observed abundances for each year was also examined. The same tests were also conducted after the effect of year was removed by subtracting the linear regression predicted value from each data point, and by deducting a five-point moving average from the raw data.

RESULTS

Fish abundances

Grenadiers (*Coryphaenoides* spp.) dominated the fish assemblage with abundances varying between 7.5 and 32.4 individuals/ha (Fig. 1). Grenadiers were unlikely to change their orientation or direction of travel until the sled was very close. Grenadiers remained within the field of view of the camera for an average of 8 s (where fish in only one frame = 0 s).

Abundances of other fish species were low with the most numerous other species (*Bathysaurus mollis*) ap-

pearing a maximum of twice per tow, and making up 3.0% of the observed assemblage. This is approximately an average of 0.7 individuals/ha over the entire data set. *Bathysaurus mollis* was always first observed lying horizontal on the seafloor and usually made a vigorous escape response (10 burst swims from 12 observations). The other fishes observed were *Spectrunculus grandis* (three individuals) and nine unidentified fishes.

Seasonal and interannual trends

When abundance was plotted against tow date (day of the year), there was no indication of seasonality in grenadier abundance, even when the effects of interannual variation were removed. There was no significant difference between the timing (day of the year) of the highest and lowest abundances of fish (ANOVA, $F_{1,18} = 0.13$, $P = 0.75$). Abundances were compared using ANOVA between months in which more than four tows took place (February, June, July, August, and October), using year as a covariate. There was no significant difference between months ($F_{4,40} = 0.27$, $P = 0.89$). Overall, there was a long-term increase in grenadier abundance (Fig. 1) from an annual mean abundance of 7.5 individuals/ha in 1989 to 28.1 individuals/ha in 2004, with the greatest increases occurring during the 1998–2001 sampling hiatus. There was, however, a period of notable decline in 1993–1994.

Correlations with climate, particle flux, and benthic invertebrates

Fish abundances did not correlate with any measure of surface climate or particle flux to the seafloor, regardless of the lag used. Echinoderms dominate the

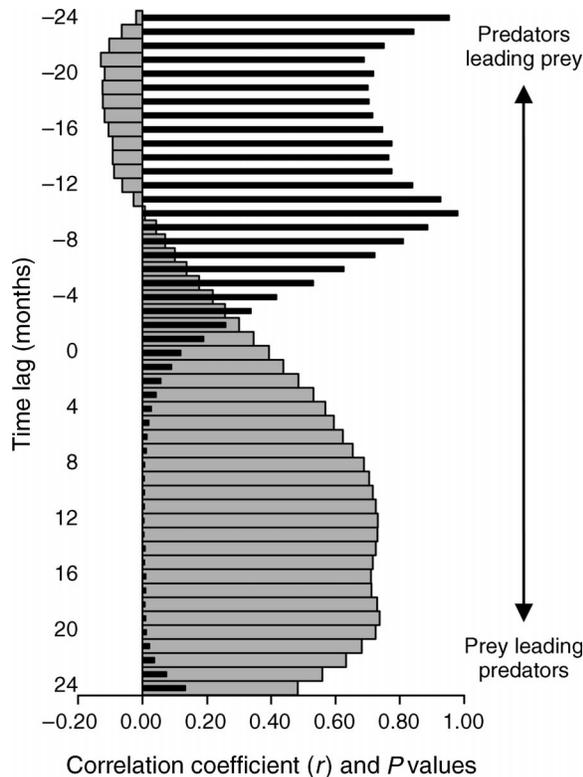


FIG. 2. Spearman rank cross correlations (r , gray histograms) and P values (black histograms) of correlations for +12 to -12 months time lag, showing the strength of links between fish and benthic echinoderm abundance at various time lags. The correlations peaked with fish lagging benthic fauna by approximately 9–20 mo.

mobile epibenthic megafauna at Station M (Lauerman et al. 1996), and taxa examined here are the holothuroids *Elpidia minutissima*, *Peniagone vitrea*, *P. diaphana*, *Abyssoecumis abyssorum*, *Synallactes* sp., *Scotoplanes globosa*, *Psychropotes longicauda*, *Oenirophanta mutabilis*; the echinoid, *Echinocrepis* spp.; and the ophiuroid, *Ophiura* spp. Significant interannual variation has been observed in all 10 benthic faunal categories examined, with some showing increases in abundance during periods of higher POC flux and others during lower fluxes (Ruhl and Smith 2004). Only weak links were found between grenadier numbers and numbers of any individual megafaunal invertebrate taxa. Fish abundance, however, was significantly positively correlated to total numbers of mobile epibenthic megafauna over the study period (Fig. 1). Monthly correlations were strongest when the fish abundances were lagged 9–20 mo behind these total invertebrate abundances (Fig. 2). Correlations were weaker (and always nonsignificant) when total invertebrate numbers were lagged behind fish numbers.

DISCUSSION

Numbers of grenadiers fluctuated over the study period, but showed an overall increase, more than dou-

bling in abundance between 1989 and 2004. No significant relationships were found between grenadier abundance and either POC flux or climate. The overall rise in fish numbers was, however, significantly correlated with the total abundances of epibenthic echinoderms, which may indicate an increase in food supply. It is possible that the apparent change in fish abundance during the second sampling hiatus is another example of the 1998–1999 northeast Pacific regime shift (Chavez et al. 2003).

Studies suggest that change in food supply (amount and/or quality), is the most likely mechanism by which contemporary climatic variation affects deep-sea animals (Wigham et al. 2003, Ruhl and Smith 2004). At Station M, the majority of food arrives as seasonal pulses of particulates, with the amount of material in each pulse varying greatly between years, depending on phytoplankton productivity (Baldwin et al. 1998). Grenadiers do not feed directly on these particulates, but are otherwise catholic feeders, consuming carrion, fish, cephalopods, crustaceans, echinoderms, and other invertebrates (Percy and Ambler 1974). Of the known food items of grenadiers, the echinoderm megafauna were observed most frequently in the camera sled photographs, with observations of small fish, crustaceans, and cephalopods occurring in relatively very small numbers. Little quantitative data exists on the diets of abyssal grenadiers, as decompression (and swim bladder expansion) usually results in stomach regurgitation. Some studies at geographically or bathymetrically similar sites have been conducted (Percy and Ambler 1974, Martin and Christiansen 1997). For *C. armatus*, echinoderms comprised up to 7.6% of the stomach contents (by wet weight), with the largest proportions of the diet being mid-water cephalopods and fishes (Percy and Ambler 1974). The importance of mid-water prey to Station M grenadiers is unclear, especially given the rarity of vertical excursions in acoustically tracked grenadiers at similar depths in the northeast Pacific (Priede et al. 1990). The horizontal distributions and abundances of any grenadiers feeding in the mesopelagic may differ from those recorded here. Stomach content data for Station M grenadiers include echinoderms, though not in large quantities (J. Drazen, *personal communication*), probably because of the low nutritional value of these prey items (Drazen 2002a).

Grenadier abundance appeared to track the rises and falls in the abundance of the echinoderms. As the relative importance of echinoderms as prey is somewhat unclear for abyssal grenadiers, we cannot conclusively state that the correlation between the abundances of grenadiers and echinoderms represents a predator–prey relationship. While this would be the most parsimonious explanation for the observed relationship, it is possible that the grenadiers could be responding to other covarying taxa which were not visible to the camera sled. Billett et al. (2001) showed an increase in holothurian abundance in the abyssal northeast Atlantic

over the period 1989–1998, broadly mirrored by increases in the abundance of other prey taxa such as bivalves and annelids (Pearcy and Ambler 1974). The observed correlations between fish and echinoderm abundances likely represent some direct predator–prey interactions, and indications of changing levels of food availability to grenadiers through the abundances of other invertebrate prey.

Intra-annual, seasonal variation

In shallow-water and terrestrial systems, seasonal pulses of primary productivity often provide predictable sources of food for predators (especially items such as larvae and other young animals), and so predators may time their migrations and reproduction in response. At Station M, there was little evidence for seasonal invertebrate recruitment (Ruhl and Smith 2004), though seasonal changes in food supply appear to alter the behavior of benthic echinoderms, which could affect their vulnerability to fish (Lauerman and Kaufmann 1998). An alternative mechanism for rapid changes in food supply to fish is through the supply of the carrion. The distributions and abundances of fishes and marine mammals are highly variable, and related to oceanographic conditions and surface productivity (Dorn 1995, Keiper et al. 2005). Carrion falls in the deep ocean can cause significant local enrichment (Smith and Baco 2003), and attract large numbers of grenadiers (Jones et al. 1998). The proportion of the diet made up by carrion is unclear for most species, but in *Coryphaenoides acrolepis* it may reach 20% by wet mass in stomach contents (Drazen et al. 2001).

Any short-term changes in abyssal fish abundance resulting from such direct influences would require migrations from areas of lower food availability, which could closely track variations in surface production. Such changes were not seen here, and there was no evidence for seasonal changes in abundance. Possibly the scale at which seasonal spatial variation in relative food availability occurs (whole ocean basins), is too large for slow-swimming grenadiers (Priede et al. 1991) to migrate in response.

Interannual, long-term change

Although consistent seasonal variations in abundance were absent, there were fluctuations in fish number during the study period, and a general increase over the 15-yr duration. Over the whole time-series, there was a positive relationship and strong correlation between grenadier and echinoderm abundances. The apparent response time of the fish population to changes in the total number of megafaunal echinoderms (becoming significant after only a few months lag) is probably too rapid to be caused entirely by fish recruitment and mortality. Grenadiers appear to be long lived (Andrews et al. [1999] estimated >50 yr for *C. acrolepis*) and can probably survive for long periods (>200 d) without food (Smith 1978). As a result, they are prob-

ably able to survive severe fluctuations in food supply. The reproductive ecology of the predominant species at Station M (*C. armatus* and *C. yaquinae*) remains unknown, and despite extensive sampling there is, as yet, no evidence for a reproductive response to changes in resource availability. The strong correlations between invertebrate and fish abundances at lags of over a year allow for the possibility of a reproductive response to food availability. Ongoing studies, which will allow fish sizes to be determined accurately, will likely elucidate the relative contributions of recruitment and survivorship to long-term changes in this fish population.

Given the apparent response time, the observed rises and falls in fish numbers are most likely caused by migration into, and out of, the survey area in response to spatial variations in food availability at the seafloor. Station M is enriched by export from the increased surface productivity of the California Current upwelling, and the quality and quantity of the flux varies interannually according to the strength of the upwelling (Baldwin et al. 1998). Interannual variation in productivity likely changes the relative enrichment of Station M, compared to other areas of the seafloor which never benefit from upwelling-enhanced surface productivity. Grenadiers appear not to respond immediately to changes in export flux from the surface, as they do not feed directly upon the material deposited. The invertebrate fauna responds over a range of time scales (Ruhl and Smith 2004), and the grenadiers probably employ a nomadic behavior, with an interannually varying feeding aggregation beneath the area influenced by the California Current System.

Ecological consequences

Ruhl and Smith (2004) showed that abyssal benthic echinoderm numbers likely respond to changes in food supply (bottom-up control), but the importance of predation (top-down control), was previously unknown. The long-term positive correlation between fish and invertebrate numbers, and the increase in the significance of the correlation when fish numbers lag behind invertebrate numbers, suggests that bottom-up controls predominate.

No consensus exists as to the dominant control of animal abundances in natural systems, and recent studies in gadiform fishes (the order which includes *Coryphaenoides*) provide apparently conflicting results (Worm and Myers 2003, Frank et al. 2005, Ware and Thomson 2005). Identifying natural ecological processes in systems, and fish populations, which are heavily modified by fishing, is not a trivial task (Jennings and Blanchard 2004, Rose 2004), which makes data for the unfished populations at Station M very valuable.

Benthic marine systems provide some of the best-known examples of top-down control (Strong 1992), and led to the development of the “keystone species”

concept (Paine 1969). In the present study, “bottom up” controls predominated, probably due to the dominant role of allochthonous food supply to the system. Variation in imported food is not influenced by the population dynamics of the abyssal fauna. Classical “trophic cascades” cannot form in such a system, as changes in the deep benthic fauna do not strongly influence primary production in the euphotic zone. The relative accessibility of vegetation to herbivores has been suggested as a reason why trophic cascades are most commonly observed in shallow-water marine systems (Strong 1992). In the abyss, all the photosynthetic producer biomass is completely inaccessible to the benthic fauna, due to their great vertical separation. The abyssal benthos subsists on biomass that has already died and left the euphotic zone, and therefore its consumption has no further effect on the surface fauna.

The apparent lack of top-down controls by grenadiers on the abundant echinoderms can be explained by modeling studies that indicate that northeast Pacific *C. armatus* take low numbers of prey, as a result of the low abundances and very low metabolic rates of these fishes (Drazen 2002a). The sizes of the fish populations are probably limited by the low productivity: biomass ratio of the benthic invertebrate fauna (Brey and Clarke 1993), and by large fluctuations in prey abundance which probably cause periodic restrictions on food supply for the fish. These fluctuations may be exacerbated by the lack of any stabilizing feedback between the dynamics of the benthic and pelagic communities.

The abyss, therefore, does not act like other marine systems, because its primary consumers do not have direct access to the producers (photic zone plankton) which eventually provide their food. The long-term dynamics of primary and secondary consumers in abyssal systems appear to be more like those of terrestrial systems dependent on allochthonous food, or where prey availability is strongly driven by external forces. Studies of desert islands, dependent on nutrients from guano, have demonstrated the powerful bottom-up controls of animal abundance that variation in allochthonous food from the euphotic zone can cause (Sánchez-Piñero and Polis 2000). Climatic variation strongly affects the abundances of wolves and insectivorous birds, and these lagged changes are mediated through alterations in prey accessibility (Vucetich and Peterson 2003) or abundance (Jones et al. 2003).

Direct abiotic influences, such as variation in winter temperatures, which are very important in many terrestrial systems, are probably not nearly so powerful in the physically stable abyss. Donor-control, through food supply changes, appears to be the dominant source of inter-annual variation in abyssal animal abundances, due to the overwhelming importance of allochthonous food to abyssal systems. This is likely to be the root of any differences in the controls of shallow- and deep-water communities.

Conclusions

There has been a major change in fish abundance at this northeast Pacific station over the period 1989 to 2004. Changes in grenadier abundance, and an overall increase over the study period, appears to follow changes in the abundance of benthic invertebrate prey. Seasonal patterns in fish abundance were not detected, with interannual variation driven by fish migration being the predominant pattern. This study provides some of the only data available on the natural interactions of benthopelagic fishes and the invertebrate megafauna, indicating both bottom-up control on animal abundances, and the dominant influence of food-limitation on the ecology of the deep ocean.

ACKNOWLEDGMENTS

We would like to thank the many people involved in collecting the data used in this study, in particular Rob Glatts, Fred Uhlman, Bob Wilson, and Roberta Baldwin. Mike Vardaro, Ray Wilson, Richard Rosenblatt, Phil Hastings, and Cindy Klepadlo scanned and identified many of the unknown fishes. Thanks also to George Sugihara, Jeff Drazen, Mark Carr, and the two anonymous reviewers for their useful comments. This research was supported by NSF grants OCE89-22620, OCE92-17334, OCE98-07103, and OCE0242472 to K. L. Smith as well as funding from University of California and Scripps Institution of Oceanography. D. M. Bailey was supported by a Marie Curie Outgoing International Fellowship (MOIF-CT-2004-509286).

LITERATURE CITED

- Andrews, A. H., G. M. Cailliet, and K. H. Coale. 1999. Age and growth of the Pacific grenadier (*Coryphaenoides acrolepis*) with age estimate validation using an improved radiometric ageing technique. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1339–1350.
- Armstrong, J. D., I. G. Priede, and K. L. Smith. 1991. Temporal change in foraging behaviour of the fish *Coryphaenoides (Nematonurus) yaquinae* in the central North Pacific. *Marine Ecology Progress Series* **76**:195–199.
- Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–1971. NOAA Technical Report NMFS SSRF-671. Pacific Fisheries Environmental Laboratory, Pacific Grove, California, USA.
- Baldwin, R. J., R. C. Glatts, and K. L. Smith. 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 Part II* **45**:643–665.
- 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.
- Brey, T., and A. Clarke. 1993. Population dynamics of marine benthic invertebrates in Antarctic and subantarctic environments: are there unique adaptations? *Antarctic Science* **5**:253–266.
- 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, UK.
- Chavez, F. P., J. Ryan, S. E. Lluch-Cota, and M. Niquen C. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* **299**:217–221.
- Dorn, M. W. 1995. The effects of age composition and oceanographic conditions on the annual migration of Pacific whiting, *Merluccius productus*. *CalCOFI Reports* **36**:97–105.

- Drazen, J. C. 2002a. Energy budgets and feeding rates of *Coryphaenoides acrolepis* and *C. armatus*. *Marine Biology* **140**:677–686.
- Drazen, J. C. 2002b. A seasonal analysis of the nutritional condition of deep-sea macrourid fishes in the north-east Pacific. *Journal of Fish Biology* **60**:1280–1295.
- Drazen, J. C., T. W. Buckley, and G. R. Hoff. 2001. The feeding habits of slope dwelling macrourid fishes in the eastern North Pacific. *Deep-Sea Research I* **48**:909–935.
- Frank, T. K., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**:1621–1623.
- Jennings, S., and J. L. Blanchard. 2004. Fish abundance with no fishing: predictions based on macroecological theory. *Journal of Animal Ecology* **73**:632–664.
- Jones, E. G., M. A. Collins, P. M. Bagley, S. Addison, and I. G. Priede. 1998. The fate of cetacean carcasses in the deep-sea: observations on consumption rates and succession of scavenging species in the abyssal north-east Atlantic. *Proceedings of the Royal Society London B* **265**:1119–1127.
- Jones, J., P. J. Doran, and R. T. Holmes. 2003. Climate and food synchronize regional forest bird abundances. *Ecology* **84**:3024–3032.
- Keiper, C. A., D. G. Ainley, S. G. Allen, and J. T. Harvey. 2005. Marine mammal occurrence in a docean climate off central California, 1986 to 1994 and 1997 to 1999. *Marine Ecology Progress Series* **289**:285–306.
- 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 N.E. Pacific. *Deep-Sea Research II* **45**:569–913.
- Lauerman, L. M. L., R. S. Kaufmann, and K. L. Smith. 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. *Deep-Sea Research I* **43**:1075–1103.
- Martin, B., and B. Christiansen. 1997. Diets and standing stocks of benthopelagic fishes at two bathymetrically different midoceanic localities in the northeast Atlantic. *Deep-Sea Research I* **44**:541–558.
- Merrett, N. R., and R. L. Haedrich. 1997. *Deep-sea demersal fish and fisheries*. Chapman and Hall, London, UK.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *American Naturalist* **103**:91–93.
- Pearcy, W. G., and J. W. Ambler. 1974. Food habits of deep-sea macrourid fishes off the Oregon coast. *Deep-Sea Research* **21**:745–759.
- Priede, I. G., P. M. Bagley, J. D. Armstrong, K. L. Smith, and N. R. Merrett. 1991. Direct measurement of active dispersal of food-falls by deep-sea demersal fishes. *Nature* **351**:647–649.
- Priede, I. G., P. M. Bagley, and K. L. Smith. 1994. Seasonal change in activity of abyssal demersal scavenging grenadiers *Coryphaenoides (Nematonurus) armatus* in the eastern Pacific Ocean. *Limnology and Oceanography* **39**:279–285.
- Priede, I. G., A. R. Deary, D. M. Bailey, and K. L. Smith. 2003. Low activity and seasonal change in population size structure of grenadiers in the oligotrophic abyssal Central North Pacific Ocean. *Journal of Fish Biology* **63**:187–196.
- Priede, I. G., K. L. Smith, and J. D. Armstrong. 1990. Foraging behaviour of abyssal grenadier fish: inferences from acoustic tagging and tracking in the North Pacific Ocean. *Deep-Sea Research* **37**:81–101.
- Pyper, B. J., and R. M. Peterman. 1998. Comparison of methods to account for autocorrelation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Science* **55**:2127–2140.
- Rose, G. A. 2004. Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. *Canadian Journal of Fisheries and Aquatic Science* **61**:1533–1557.
- Ruhl, H. A., and K. L. Smith. 2004. Shifts in deep-sea community structure linked to climate and food supply. *Science* **305**:513–515.
- Sánchez-Piñero, F., and G. A. Polis. 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology* **81**:3117–3132.
- 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, C. R., and A. R. Baco. 2003. Ecology of whale falls at the deep-sea floor. *Oceanography and marine Biology Annual Review* **41**:311–354.
- Smith, K. L. 1978. Metabolism of the abyssopelagic rattail *Coryphanoides armatus*, measured *in situ*. *Nature* **274**:362–364.
- Smith, K. L., D. Alexandrou, and J. R. Edelman. 1989. Acoustic detection and tracking of abyssopelagic animals: description of an autonomous split-beam acoustic array. *Deep-Sea Research* **36**:1427–1441.
- Smith, K. L., R. J. Baldwin, H. A. Ruhl, M. Kahru, B. G. Mitchell, and R. S. Kaufmann. *In press*. Climatic impact on food supply to depths > 4000 meters in the northeast Pacific. *Limnology and Oceanography*.
- Smith, K. L., and E. R. M. Druffel. 1998. Long time-series monitoring of an abyssal site in the NE Pacific: an introduction. *Deep-Sea Research II* **45**:573–586.
- Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* **73**:747–754.
- Trenberth, K. E., and D. J. Shea. 1987. On the evolution of the southern oscillation. *Monthly Weather Review* **115**:3078–3096.
- Vucetich, J. A., and R. O. Peterson. 2003. The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. *Proceedings of the Royal Society London B* **271**:183–189.
- Ware, D. M., and R. E. Thomson. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. *Science* **308**:1280–1284.
- 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.
- Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO—how does 1997/98 rank? *Weather* **53**:315–324.
- Worm, B., and R. A. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* **84**:162–173.