



University
of Glasgow

Bailey, D.M. and Ruhl, H.A. and Snith, K.L. (2006) Long-term change in benthopelagic fish abundance in the abyssal northeast Pacific Ocean. *Ecology* 87(3):pp. 549-555.

<http://eprints.gla.ac.uk/4780/>

16 March 2009

1
2
3
4
5
6
7
8
9
10
11
12
13

Running head: Long-term change in abyssal fish abundance

**LONG-TERM CHANGE IN BENTHOPELAGIC FISH ABUNDANCE
IN THE ABYSSAL N.E. PACIFIC OCEAN**

D.M. Bailey^{1,2*}, H.A. Ruhl¹ and K.L. Smith Jr¹.

*¹Marine Biology Research Division, Scripps Institution of Oceanography, UCSD,
9500 Gilman Drive, La Jolla, CA 92130-0202, USA. ²Oceanlab, School of Biological
Sciences, University of Aberdeen, Newburgh, Aberdeenshire, AB41 6AA, UK.*

**Author for correspondence, d4bailey@ucsd.edu, Tel +1 858 534 4858, Fax +1 858
534-7313*

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

17

18 *Key Words: Pacific Ocean, deep water, marine fish, Coryphaenoides spp., benthic*
19 *megafauna, population dynamics.*

INTRODUCTION

1
2 The oceanic abyssal plains are the world's largest habitats, making deep-sea fish the
3 dominant carnivores and scavengers across most of the Earth's surface. Found in
4 distinct depth zones, and differing between oceans, the spatial distribution of deep-sea
5 fish has been extensively studied (Merrett and Haedrich 1997). In contrast, no studies
6 have been able to investigate long-term temporal patterns in abyssal fish distribution
7 or abundance. Indeed, there is little data available on the long-term population and
8 predator-prey dynamics of any large, and unexploited, marine fish population
9 (Jennings and Blanchard 2004). Studies in fished systems have reached no consensus
10 on how animal abundances and productivities are controlled in marine systems, with
11 apparent demonstrations of both top-down (Worm and Myers 2003, Frank et al. 2005)
12 and bottom-up controls (Ware and Thomson 2005). The controls of animal
13 abundances in abyssal systems remain poorly-understood.

14
15 Recent studies in the abyssal Pacific have demonstrated significant changes in benthic
16 invertebrate community structure at inter-annual timescales (Ruhl and Smith 2004).
17 These changes were linked to long-term patterns in the surface climate, and to food
18 supply in the form of particulate organic carbon flux from the surface (Ruhl and
19 Smith 2004). It is unknown whether similar changes in abundance also occur at
20 higher trophic levels, such as fish, and what effects any changes in fish abundance
21 have on the benthic invertebrates. Most benthopelagic deep-sea fish are predators and
22 scavengers, and do not feed directly on the sinking particulate organic matter that
23 comprises the majority of the flux from the surface (Merrett and Haedrich 1997,
24 Drazen et al. 2001). Fish may act as predators on primary consumers, such as the
25 echinoderms, and have their diet supplemented by carrion fall-out from the surface.

1 The availability of both resources might vary as a result of changing surface
2 productivity, as particulate fall-out affects echinoderm behavior (Lauerman and
3 Kaufmann 1998), and the abundance and position of shallow-water animals changes.

4
5 Evidence for the influence of surface productivity on abyssal fishes includes
6 observations that grenadier abundance, size structure, behavior, and swimming speed
7 can be linked to spatial and temporal variations in overlying productivity and
8 invertebrate abundance (Armstrong et al. 1991, Priede et al. 1994, Priede et al. 2003).

9 The precise mechanisms for the effects remain unclear, and studies of Pacific
10 grenadier biochemistry suggest inter-annual rather than seasonal changes in a range of
11 indicators of nutritional status in these fishes (Drazen 2002b).

12
13 In this study, we provide new information on both seasonal and inter-annual patterns
14 in the abundance of a predominant benthopelagic predator and its prey. By testing for
15 long-term temporal relationships between the abundance of the predator and climate,
16 particle flux, and abundance of potential prey taxa, we provide compelling evidence
17 for bottom-up influences in this system.

18

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 non-cryptic demersal fishes and benthic invertebrates conducted at one site over a 15-year 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 N.E. Pacific ($34^{\circ} 50'N$, $123^{\circ} 00'W$, 4100 m depth). Sta. M is located about 220 km west of Point Conception, California, and has been extensively studied and described in detail elsewhere (Smith and Druffel 1998). Camera sled deployments took place within an approximately 25 x 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 $0.8 \text{ m} \cdot \text{s}^{-1}$, 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 travelled by the sled and the Effective Strip Width (ESW) based on the visibility of the targets. ESW varied between deployments due to differences in

1 illumination or film development, and was estimated for fish by incorporating ESW
2 values for benthic animals with the most similar size and colouration (the sea
3 cucumber *Abyssoicum abysorum*).

4

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

12 Grenadiers were recorded as *Coryphaenoides* spp. as it was impractical to
13 discriminate between species from the photographs. In particular *C. armatus* and *C.*
14 *yaquinae* are common at Sta. M. The variable position and orientation of the fishes
15 precluded estimation of fish size.

16

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

23

Data Analysis

1
2 The only fish that were sufficiently abundant to allow statistical analysis were the
3 grenadiers, *Coryphaenoides* spp. Data on the abundances of the dominant mobile
4 epibenthic megafauna (Lauerman et al. 1996, Lauerman and Kaufmann 1998, Ruhl
5 and Smith 2004), collected from the same series of tows were used to investigate
6 coupling between the benthos and the fish assemblage. The dominant megafaunal
7 taxa included here are potential prey of grenadiers (Pearcy and Ambler 1974) and
8 make up approximately 99% of mobile animals observed on the seafloor in terms of
9 abundance.

10

11 The possible affect of climate fluctuation, and Particulate Organic Carbon (POC) flux
12 to the seafloor on fish populations were also examined. The climate indices used are
13 indicative of El Niño/La Niña, (Northern and Southern Oscillation Indexes (NOI:
14 Schwing et al. 2002; SOI: Trenberth and Shea 1987) and Multivariate El Niño-
15 Southern Oscillation Index (MEI: Wolter and Timlin 1998) and regional upwelling
16 measured by the Bakun Upwelling Index (BUI: Bakun 1973). The flux of POC to the
17 seafloor (Baldwin et al. 1998, Smith et al. in press), was measured with a 50 meter
18 above bottom (mab) sediment trap. POC flux data used for the study includes
19 monthly data from June 1991-October 1992, July 1993-October 1996, November
20 1997-December 1998, and June 2001-September 2002. The 50 mab trap was chosen
21 for these comparisons since 600 mab trap data from 2001-2002 were not available.
22 Although the 50 mab trap can capture re-suspended mass flux, the 600 mab and 50
23 mab trap data are highly correlated and differences in POC flux were not significant
24 (Baldwin et al. 1998, Smith et al. in press). Cross correlations between POC flux at
25 50 mab and satellite estimated surface export flux were significant to at least a 100 km

1 radius around the study site and up to 300 km parallel to the coast (Smith et al. in
2 press).

3

4 Spearman rank cross correlations were conducted between the observed grenadier
5 abundances and mobile epibenthic megafaunal (MEM) taxa, as well as between
6 grenadier abundances and the climate and POC parameters. These correlations were
7 done using monthly values and temporal lags. Since the benthic invertebrate and fish
8 population data sets were discontinuous, 13 month centred running means were used
9 to conduct the monthly cross correlations. Lags of -24 to +24 months between the
10 fish and invertebrate data were introduced to investigate top- and bottom-down
11 predator-prey interactions. For comparison of the climate and POC flux data with fish
12 abundances, lags of 0 to 24 months were used. Climate and POC flux data were only
13 allowed to lead abundance and not *vice versa*. The modified Chelton method (Pyper
14 and Peterman 1998) was used to correct the resulting *P* values for serial
15 autocorrelation.

16

17 Monthly average fish abundances were plotted against Julian date in order to examine
18 the effects of season on these parameters. The timing of the annual highest and
19 lowest observed abundances for each year was also examined. The same tests were
20 also conducted after the effect of year was removed by subtracting the linear
21 regression predicted value from each data point, and by deducting a 5-point moving
22 average from the raw data.

23

RESULTS

Fish abundances

Grenadiers (*Coryphaenoides* spp.) dominated the fish assemblage with abundances varying between 7.5 and 32.4 ind · ha⁻¹ (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 = zero s).

Abundances of other fish species were low with the most numerous other species (*Bathysaurus ferox*) appearing a maximum of twice per tow, and making up 3.0 % of the observed assemblage. This approximated to an average of 0.7 ind · ha⁻¹ over the entire dataset. *Bathysaurus ferox* 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), a Halasaurid tentatively identified as *Aldovandia* sp., and eight unidentified fishes.

Seasonal and inter-annual trends

When abundance was plotted against tow date (Julian Day) there was no indication of seasonality in grenadier abundance, even when the effects of inter-annual variation were removed. There was no significant difference between the timing (Julian day) 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 4 tows took place (February, June, July, August, and October), using year as a covariate. There was no significant difference between months ($F_{4,40} = 0.27$, $P =$

1 0.89). Overall there was a long-term increase in grenadier abundance (Fig. 1) from an
2 annual mean abundance of 7.5 ind · ha⁻¹ in 1989 to 28.1 ind · ha⁻¹ in 2004, with the
3 greatest increases occurring during the 1998-2001 sampling hiatus. There was,
4 however, a period of notable decline in 1993-1994.

5

6 *Correlations with climate, particle flux, and benthic invertebrates*

7 Fish abundances did not correlate with any measure of surface climate or particle flux
8 to the seafloor, regardless of the lag used. Echinoderms dominate the mobile
9 epibenthic megafauna at Sta. M (Lauerman et al. 1996), and taxa examined here are
10 the holothuroids *Elpidia minutissima*, *Peniagone vitrea*, *P. diaphana*, *Abyssocucumis*
11 *abyssorum*, *Synallactes* sp., *Scotoplanes globosa*, *Psychropotes longicauda*,
12 *Oneirophanta mutabilis*; the echinoid, *Echinocrepis* spp.; and the ophiuroid, *Ophiura*
13 spp. Significant inter-annual variation has been observed in all 10 benthic faunal
14 categories examined with some showing increases in abundance during periods of
15 higher POC flux and others during lower fluxes (Ruhl and Smith 2004). Only weak
16 links were found between grenadier numbers and numbers of any individual
17 megafaunal invertebrate taxa. Fish abundance, however, was significantly positively
18 correlated to total numbers of mobile epibenthic megafauna over the study period
19 (Fig. 1). Monthly correlations were strongest when the fish abundances were lagged
20 9-20 months behind these total invertebrate abundances (Figure 2). Correlations were
21 weaker (and always non-significant) when total invertebrate numbers were lagged
22 behind fish numbers.

23

DISCUSSION

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

Numbers of grenadiers fluctuated over the study period, but showed an overall increase, more than doubling 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 1998-9 N.E. 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 Sta. 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 (Pearcy 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 (Pearcy and Ambler 1974, Martin and Christiansen 1997). For *C. armatus*, echinoderms comprised up to 7.6% of the stomach contents (by wet

1 weight), with the largest proportions of the diet being mid-water cephalopods and
2 fishes (Pearcy and Ambler 1974). The importance of mid-water prey to Sta. M
3 grenadiers is unclear, especially given the rarity of vertical excursions in acoustically
4 tracked grenadiers at similar depths in the N.E. Pacific (Priede et al. 1990). The
5 horizontal distributions and abundances of any grenadiers feeding in the mesopelagic
6 may differ from those recorded here. Stomach content data for Sta. M grenadiers
7 include echinoderms, though not in large quantities (J. Drazen, pers. comm.),
8 probably because of the low nutritional value of these prey items (Drazen 2002a).

9
10 Grenadier abundance appeared to track the rises and falls in the abundance of the
11 echinoderms. As the relative importance of echinoderms as prey is somewhat unclear
12 for abyssal grenadiers, we cannot conclusively state that the correlation between the
13 abundances of grenadiers and echinoderms represents a predator-prey relationship.
14 While this would be the most parsimonious explanation for the observed relationship,
15 it is possible that the grenadiers could be responding to other co-varying taxa which
16 were not visible to the camera sled. Billett et al (2001) showed an increase in
17 holothurian abundance in the abyssal N.E. Atlantic over the period 1989-1998,
18 broadly mirrored by increases in the abundance of other prey taxa such as bivalves
19 and annelids (Pearcy and Ambler 1974). The observed correlations between fish and
20 echinoderm abundances likely represent some direct predator-prey interactions, and
21 indications of changing levels of food availability to grenadiers through the
22 abundances of other invertebrate prey.

23

24 *Intra-annual, seasonal variation*

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

16
17 Any short-term changes in abyssal fish abundance resulting from such direct
18 influences would require migrations from areas of lower food availability, which
19 could closely-track variations in surface production. Such changes were not seen
20 here, and there was no evidence for seasonal changes in abundance. Possibly the
21 scale at which seasonal spatial variation in relative food availability occurs (whole
22 ocean basins), is too large for slow-swimming grenadiers (Priede et al. 1991) to
23 migrate in response.

24

25 *Inter-annual, long-term change*

1 Although consistent seasonal variations in abundance were absent, there were
2 fluctuations in fish number during the study period, and a general increase over the
3 15-year duration. Over the whole time-series there was a positive relationship and
4 strong correlation between grenadier and echinoderm abundances. The apparent
5 response time of the fish population to changes in the total number of megafaunal
6 echinoderms (becoming significant after only a few months lag) is probably too rapid
7 to be caused entirely by fish recruitment and mortality. Grenadiers appear to be long-
8 lived (Andrews et al. (1999) estimated >50 years for *C. acrolepis*) and can probably
9 survive for long periods (>200 days) without food (Smith 1978). As a result they are
10 probably able to survive severe fluctuations in food supply. The reproductive ecology
11 of the predominant species at Sta. M (*C. armatus* and *C. yaquinae*) remains unknown,
12 and despite extensive sampling there is, as yet, no evidence for a reproductive
13 response to changes in resource availability. The strong correlations between
14 invertebrate and fish abundances at lags of over a year allow for the possibility of a
15 reproductive response to food availability. Ongoing studies, which will allow fish
16 sizes to be determined accurately, will likely elucidate the relative contributions of
17 recruitment and survivorship to long-term changes in this fish population.

18

19 Given the apparent response time, the observed rises and falls in fish numbers are
20 most likely caused by migration into, and out of, the survey area in response to spatial
21 variations in food availability at the seafloor. Station M is enriched by export from
22 the increased surface productivity of the California Current upwelling, and the quality
23 and quantity of the flux varies inter-annually according to the strength of the
24 upwelling (Baldwin et al. 1998). Inter-annual variation in productivity likely changes
25 the relative enrichment of Sta. M, compared to other areas of the seafloor which never

1 benefit from upwelling-enhanced surface productivity. Grenadiers appear not to
2 respond immediately to changes in export flux from the surface, as they do not feed
3 directly upon the material deposited. The invertebrate fauna responds over a range of
4 timescales (Ruhl and Smith 2004), and the grenadiers probably employ a nomadic
5 behaviour, with an inter-annually varying feeding aggregation beneath the area
6 influenced by the California Current System.

7

8 *Ecological consequences*

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

15

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

23

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

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

12

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

22

23 The abyss therefore does not act like other marine systems, because its primary
24 consumers do not have direct access to the producers (photic zone plankton) which
25 eventually provide their food. The long-term dynamics of primary and secondary

1 consumers in abyssal systems appear to be more like those of terrestrial systems
2 dependent on allochthonous food, or where prey availability is strongly driven by
3 external forces. Studies of desert islands, dependent on nutrients from guano, have
4 demonstrated the powerful bottom-up controls of animal abundance which variation
5 in allochthonous food from the euphotic zone can cause (Sánchez-Piñero and Polis
6 2000). Climatic variation strongly affects the abundances of wolves and insectivorous
7 birds, and these lagged changes are mediated through alterations in prey accessibility
8 (Vucetich and Peterson 2003) or abundance (Jones et al. 2003).

9
10 Direct abiotic influences, such as variation in winter temperatures, which are very
11 important in many terrestrial systems, are probably not nearly so powerful in the
12 physically stable abyss. Donor-control, through food supply changes, appears to be
13 the dominant source of inter-annual variation in abyssal animal abundances, due to the
14 overwhelming importance of allochthonous food to abyssal systems. This is likely to
15 be the root of any differences in the controls of shallow- and deep-water communities.

16

17 *Conclusions*

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

1 **ACKNOWLEDGEMENTS**

2 We would like to thank the many people involved in collecting the data used in this
3 study, in particular Rob Glatts, Fred Uhlman, Bob Wilson and Roberta Baldwin.
4 Mike Vardaro, Richard Rosenblatt, Phil Hastings, and Cindy Klepadlo scanned and
5 identified many of the unknown fishes. Thanks also to George Sugihara, Jeff Drazen,
6 Mark Carr, and the two anonymous reviewers for their useful comments. This
7 research was supported by NSF grants OCE89-22620, OCE92-17334, OCE98-07103,
8 and OCE0242472 to KLS as well as funding from UC and SIO. DMB was supported
9 by a Marie Curie Outgoing International Fellowship (MOIF-CT-2004-509286).

10
11 **LITERATURE CITED**

- 12 Andrews, A. H., G. M. Cailliet, and K. H. Coale. 1999. Age and growth of the Pacific
13 grenadier (*Coryphaenoides acrolepis*) with age estimate validation using an
14 improved radiometric ageing technique. Canadian Journal of Fisheries and
15 Aquatic Sciences **56**:1339-1350.
- 16 Armstrong, J. D., I. G. Priede, and K. L. Smith. 1991. Temporal change in foraging
17 behaviour of the fish *Coryphaenoides (Nematonurus) yaquinae* in the central
18 North Pacific. Marine Ecology Progress Series **76**:195-199.
- 19 Bakun, A. 1973. Coastal upwelling indeces, west coast of North America, 1946-1971.
20 NOAA Technical Report NMFS SSRF-671.
- 21 Baldwin, R. J., R. C. Glatts, and K. L. Smith. 1998. Particulate matter fluxes into the
22 benthic boundary layer at a long time-series station in the abyssal NE Pacific:
23 composition and fluxes. Deep-Sea Research Part II **45**:643-665.

- 1 Billett, D. S. M., B. J. Bett, A. L. Rice, M. H. Thurston, J. Galeron, M. Sibuet, and G.
2 A. Wolff. 2001. Long-term change in the megabenthos of the Porcupine
3 Abyssal Plain (NE Atlantic). *Progress in Oceanography* **50**:325-348.
- 4 Brey, T., and A. Clarke. 1993. Population dynamics of marine benthic invertebrates in
5 Antarctic and subantarctic environments: are there unique adaptations?
6 *Antarctic Science* **5**:253-266.
- 7 Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. *Distance*
8 *Sampling: Estimating abundance of biological populations*. Chapman and
9 Hall, London.
- 10 Chavez, F. P., J. Ryan, S. E. Lluch-Cota, and M. Niquen C. 2003. From anchovies to
11 sardines and back: multidecadal change in the Pacific Ocean. *Science*
12 **299**:217-221.
- 13 Dorn, M. W. 1995. The effects of age composition and oceanographic conditions on
14 the annual migration of Pacific whiting, *Merluccius productus*. *CalCOFI*
15 *Reports* **36**:97-105.
- 16 Drazen, J. C. 2002a. Energy budgets and feeding rates of *Coryphaenoides acrolepis*
17 and *C. armatus*. *Marine Biology* **140**:677-686.
- 18 Drazen, J. C. 2002b. A seasonal analysis of the nutritional condition of deep-sea
19 macrourid fishes in the north-east Pacific. *Journal of Fish Biology* **60**:1280-
20 1295.
- 21 Drazen, J. C., T. W. Buckley, and G. R. Hoff. 2001. The feeding habits of slope
22 dwelling macrourid fishes in the eastern North Pacific. *Deep-Sea Research I*
23 **48**:909-935.
- 24 Frank, T. K., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a
25 formerly cod-dominated ecosystem. *Science* **308**:1621-1623.

- 1 Jennings, S., and J. L. Blanchard. 2004. Fish abundance with no fishing: predictions
2 based on macroecological theory. *Journal of Animal Ecology* **73**:632-664.
- 3 Jones, E. G., M. A. Collins, P. M. Bagley, S. Addison, and I. G. Priede. 1998. The
4 fate of cetacean carcasses in the deep-sea: observations on consumption rates
5 and succession of scavenging species in the abyssal north-east Atlantic.
6 *Proceedings of the Royal Society London B* **265**:1119-1127.
- 7 Jones, J., P. J. Doran, and R. T. Holmes. 2003. Climate and food synchronize regional
8 forest bird abundances. *Ecology* **84**:3024-3032.
- 9 Keiper, C. A., D. G. Ainley, S. G. Allen, and J. T. Harvey. 2005. Marine mammal
10 occurrence and ocean climate off central California, 1986 to 1994 and 1997 to
11 1999. *Marine Ecology Progress Series* **289**:285-306.
- 12 Lauerma, L. M. L., and R. S. Kaufmann. 1998. Deep-sea epibenthic echinoderms
13 and a temporally varying food supply: results from a one-year time series in
14 the N.E. Pacific. *Deep-Sea Research II* **45**:569-913.
- 15 Lauerma, L. M. L., R. S. Kaufmann, and K. L. Smith. 1996. Distribution and
16 abundance of epibenthic megafauna at a long time-series station in the abyssal
17 northeast Pacific. *Deep-Sea Research I* **43**:1075-1103.
- 18 Martin, B., and B. Christiansen. 1997. Diets and standing stocks of benthopelagic
19 fishes at two bathymetrically different midoceanic localities in the northeast
20 Atlantic. *Deep-Sea Research I* **44**:541-558.
- 21 Merrett, N. R., and R. L. Haedrich. 1997. *Deep-Sea Demersal Fish and Fisheries*.
22 Chapman & Hall, London.
- 23 Paine, R. T. 1969. A note on trophic complexity and community stability. *American*
24 *Naturalist* **103**:91-93.

- 1 Pearcy, W. G., and J. W. Ambler. 1974. Food habits of deep-sea macrourid fishes off
2 the Oregon coast. *Deep-Sea Research* **21**:745-759.
- 3 Priede, I. G., P. M. Bagley, J. D. Armstrong, K. L. Smith, and N. R. Merrett. 1991.
4 Direct measurement of active dispersal of food-falls by deep-sea demersal
5 fishes. *Nature* **351**:647-649.
- 6 Priede, I. G., P. M. Bagley, and K. L. Smith. 1994. Seasonal change in activity of
7 abyssal demersal scavenging grenadiers *Coryphaenoides (Nematonurus)*
8 *armatus* in the eastern Pacific Ocean. *Limnology and Oceanography* **39**:279-
9 285.
- 10 Priede, I. G., A. R. Deary, D. M. Bailey, and K. L. Smith. 2003. Low activity and
11 seasonal change in population size structure of grenadiers in the oligotrophic
12 abyssal Central North Pacific Ocean. *Journal of Fish Biology* **63**:187-196.
- 13 Priede, I. G., K. L. Smith, and J. D. Armstrong. 1990. Foraging behaviour of abyssal
14 grenadier fish: inferences from acoustic tagging and tracking in the North
15 Pacific Ocean. *Deep-Sea Research* **37**:81-101.
- 16 Pyper, B. J., and R. M. Peterman. 1998. Comparison of methods to account for
17 autocorrelation analyses of fish data. *Canadian Journal of Fisheries and*
18 *Aquatic Science* **55**:2127-2140.
- 19 Rose, G. A. 2004. Reconciling overfishing and climate change with stock dynamics of
20 Atlantic cod (*Gadus morhua*) over 500 years. *Canadian Journal of Fisheries*
21 *and Aquatic Science* **61**:1533-1557.
- 22 Ruhl, H. A., and K. L. Smith. 2004. Shifts in deep-sea community structure linked to
23 climate and food supply. *Science* **305**:513-515.
- 24 Sánchez-Piñero, F., and G. A. Polis. 2000. Bottom-up dynamics of allochthonous
25 input: direct and indirect effects of seabirds on islands. *Ecology* **81**:3117-3132.

- 1 Schwing, F. B., T. Murphree, and P. M. Green. 2002. The Northern Oscillation Index
2 (NOI): a new climate index for the northeast Pacific. *Progress in*
3 *Oceanography* **53**:115-139.
- 4 Smith, C. R., and A. R. Baco. 2003. Ecology of whale falls at the deep-sea floor.
5 *Oceanography and marine Biology Annual Review* **41**:311-354.
- 6 Smith, K. L. 1978. Metabolism of the abyssopelagic rattail *Coryphanoides armatus*,
7 measured *in situ*. *Nature* **274**:362-364.
- 8 Smith, K. L., D. Alexandrou, and J. R. Edelman. 1989. Acoustic detection and
9 tracking of abyssopelagic animals: description of an autonomous split-beam
10 acoustic array. *Deep-Sea Research* **36**:1427-1441.
- 11 Smith, K. L., R. J. Baldwin, H. A. Ruhl, M. Kahru, B. G. Mitchell, and R. S.
12 Kaufmann. in press. Climatic impact on food supply to depths > 4000 meters
13 in the northeast Pacific. *Limnology and Oceanography*.
- 14 Smith, K. L., and E. R. M. Druffel. 1998. Long time-series monitoring of an abyssal
15 site in the NE Pacific: an introduction. *Deep-Sea Research II* **45**:573-586.
- 16 Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in
17 speciose ecosystems. *Ecology* **73**:747-754.
- 18 Trenberth, K. E., and D. J. Shea. 1987. On the evolution of the southern oscillation.
19 *Monthly Weather Review* **115**:3078-3096.
- 20 Vucetich, J. A., and R. O. Peterson. 2003. The influence of top-down, bottom-up and
21 abiotic factors on the moose (*Alces alces*) population of Isle Royale.
22 *Proceedings of the Royal Society London B* **271**:183-189.
- 23 Ware, D. M., and R. E. Thomson. 2005. Bottom-up ecosystem trophic dynamics
24 determine fish production in the Northeast Pacific. *Science* **308**:1280-1284.

- 1 Wigham, B. J., I. R. Hudson, D. S. M. Billett, and G. H. Wolff. 2003. Is long-term
2 change in the abyssal Northeast Atlantic driven by qualitative changes in
3 export flux? Evidence from selective feeding in deep-sea holothurians.
4 *Progress in Oceanography* **59**:409-441.
- 5 Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO - how does
6 1997/98 rank? *Weather* **53**:315-324.
- 7 Worm, B., and R. A. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals
8 top-down control in oceanic food webs. *Ecology* **84**:162-173.

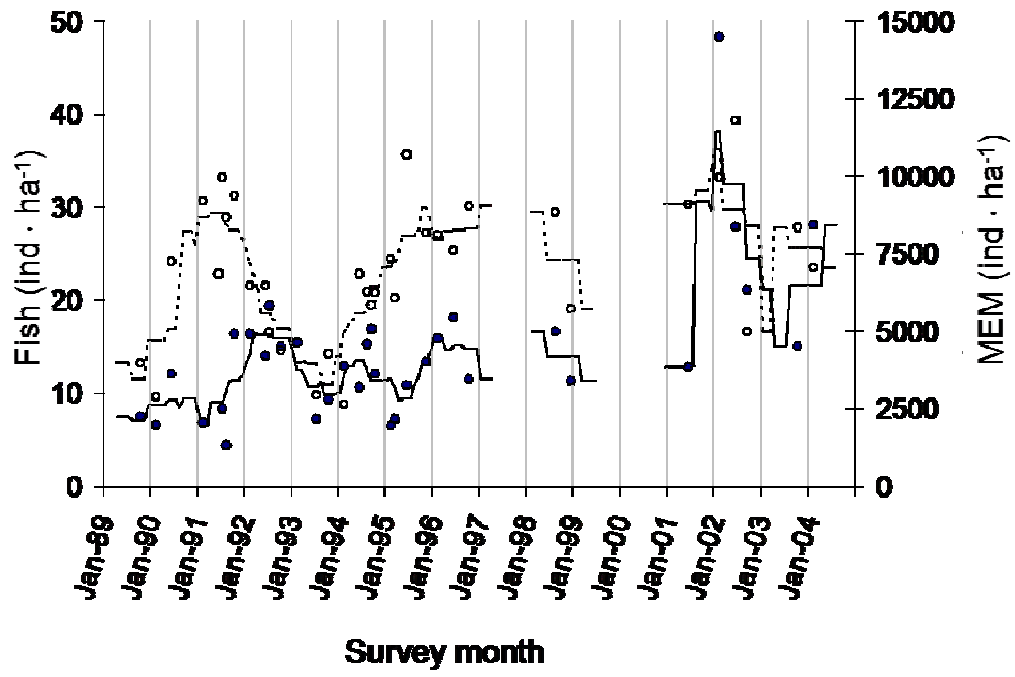
1 **Figure Legends**

2 Figure 1. Monthly Abundances of mobile epibenthic megafauna (M.E.M., open
3 points) and grenadier fish, *Coryphaenoides* spp. (solid points) recorded by towed
4 camera at Sta. M, N.E. Pacific, 4100 m depth. MEM consisted of 8 species of
5 echinoderm. All point data are monthly averages. Both series show large variations
6 at annual and decadal timescales, with a general increase in abundances over time.
7 Also shown are the 13 month centered running means for the echinoderm MEM
8 (dashed) and grenadier fish (solid line).

9

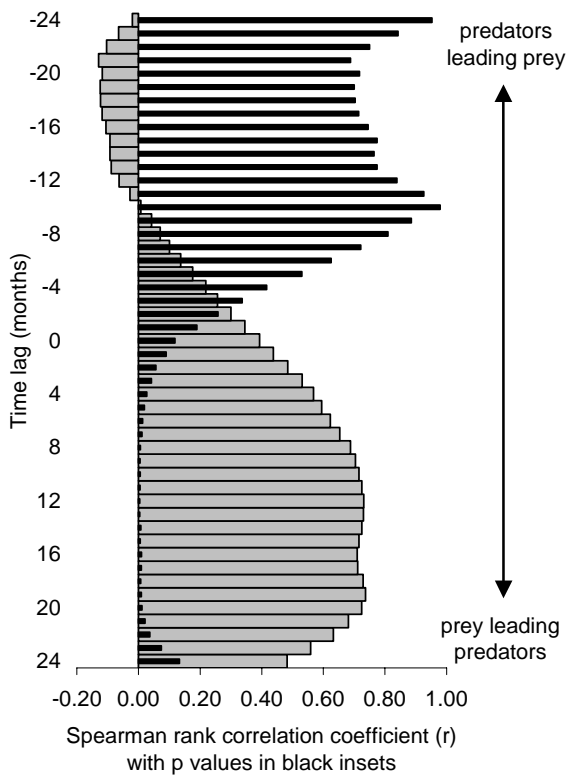
10 Figure 2. Spearman rank cross correlations for +12 to -12 months showing the
11 strength of links between fish and benthic echinoderm abundance at various time lags.
12 The correlations peaked with fish lagging benthic fauna by approximately 5-9 months.

1 Figure 1



2

1 **Figure 2**



2