

Size–frequency dynamics of NE Pacific abyssal ophiuroids (Echinodermata: Ophiuroidea)

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Abstract The 17-year time-series study at Station M in the NE Pacific has provided one of the longest datasets on deep-sea ophiuroids to date. Station M is an abyssal site characterized by low topographical relief and seasonal and interannual variation in surface-derived food inputs. From 1989 to 2005, over 31,000 ophiuroid specimens were collected. Size–frequency distributions of the four dominant species, *Ophiura bathybia*, *Amphilepis patens*, *Amphiura carchara* and *Ophiacantha cosmica*, were examined for recruitment and the role of surface-derived food supplies on

body size distributions. Juveniles were collected in sediment traps and used to investigate settlement patterns and seasonality. Trawl samples showed no indication of seasonal changes in recruitment to larger size classes; however, there was evidence of seasonal settling of juveniles. Interannual differences in median disk diameters and size distributions of trawl-collected adults are greater than those at the seasonal scale. Three of the four species, *O. bathybia*, *A. patens* and *O. cosmica*, had co-varying monthly median disk diameters, suggesting they may have a similar factor(s) controlling their growth and abundance. Interannual differences in monthly size distributions were generally greater than those between seasons. Cross-correlations between the particulate organic carbon (POC) flux (food supply) and size distribution indices for *O. bathybia*, *A. patens* and *O. cosmica* all were significant indicating that increases in food supply were followed by increases in the proportion of smaller size classes after approximately 17–22 months. These findings suggest that food inputs are indeed an important factor influencing deep-sea ophiuroid populations on interannual time scales, more generally supporting the long-hypothesized connection between food availability and population size structure in the deep sea.

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Introduction

Seasonal changes in the surface-derived particulate organic carbon (POC) flux to the deep sea have been suggested as a driver of reproduction, abundance and recruitment patterns of deep-sea fauna. Although the direct evidence is insufficient for many groups (Tyler 1988; Young 2003), animals feeding directly on sedimented material may show temporal correlations to POC flux (Tyler et al. 1982; Gooday 2002; Billett et al. 2001; Ruhl and Smith, 2004). Deep-sea

ophiuroid populations have long been thought to have a demographic connection to food supply (Schoener 1968; Lightfoot et al. 1979; Tyler et al. 1982). Shallow-water ophiuroids predominantly have annual spawning periods and juvenile settlement (Bowmer 1982; Turon et al. 2000; Sköld et al. 2001; Falkner and Byrne 2003). Lacking many cues found in shallow-water habitats (Young 1994), deep-sea ophiuroids are thought to follow one of three basic reproductive patterns: one in which gametogenesis is linked to seasonal peaks in POC flux (Schoener 1968; Tyler and Gage 1979, 1980; Gage and Tyler 1981a, 1982a; Sumida et al. 2000; Gage et al. 2004), one that is continuous throughout the year (Rokop 1974; Lauerman, 1998) or one that is asynchronous (Tyler and Gage 1979, 1982). Additionally, some species reproduce continuously but recruit seasonally (Gage and Tyler 1982b; Gage 1994).

Presented here are results from a 17-year study of ophiuroid size distribution dynamics in the abyssal NE Pacific and an evaluation of potential food supply influences on settlement and recruitment from seasonal to interannual timescales. The abyssal study site, Station M, lies beneath the California Current Ecosystem which experiences seasonal and interannual variability in the sinking POC flux (food supply) with peaks typically occurring in the summer and fall (Baldwin et al. 1998; Lauerman and Kaufmann 1998; Smith et al. 2006). Holothuroids, echinoids, and smaller organisms such as protozoans, foraminifera, and metazoan infauna have shown changes in abundance and community structure in response to fluctuations in food supply at Station M on both seasonal and interannual scales (Drazen et al. 1998; Ruhl and Smith 2004; Ruhl 2007).

Seven species of ophiuroid have been collected over the past 17 years at Station M. The four dominant species are discussed here: *Ophiura bathybia* H.L. Clark, 1911, *Ophiacantha cosmica* Lyman, 1882, *Amphilepis patens* Lyman, 1879, and *Amphiura carchara* H.L. Clark, 1911. Also found at the site are three rarer species: *Ophiosphalma glabrum* Luetken and Mortensen, 1899; *Amphioplus daleus* Lyman, 1879 and Ophiuroidea n. sp. All of these species reside on or just under the sediment surface, with the exception of *O. cosmica* that can also be found on hard substrates, such as rocks, pumice or polychaete tubes (Lauerman et al. 1996). Ophiuroid species visible at the sediment surface (principally *O. bathybia*, the most abundant) have been observed at densities of approximately $0.1\text{--}1\text{ m}^{-2}$ (Lauerman et al. 1996; Ruhl 2007). Previous investigations of *O. bathybia* have observed more individuals at the sediment surface during times of peak abundance of detrital aggregates on the seafloor. This species is normally associated with sediment depressions that outline their bodies (Lauerman et al. 1996; Lauerman and Kaufmann 1998). Protein, carbohydrate and lipid content data also suggest that *O. bathybia* feed on newly arrived particulate matter

(Lauerman, 1998). *O. bathybia* are gonochoric and females have small oocytes (no larger than $78\text{ }\mu\text{m}$ diameter) suggesting planktotrophic larval development (Lauerman 1998). Lauerman (1998) found that *O. bathybia* showed no reproductive synchrony within individuals of the population but oocyte size–frequency plots suggested an underlying annual cycle in gametogenesis.

Little is known of the next two most common species, *O. cosmica* and *A. patens*. *O. cosmica* have different feeding habits than the three other ophiuroid species, which could make their link to POC flux more indirect. Species of *Ophiacantha* probably suspension feed on planktonic matter by filter feeding. However, prey organisms that reside on the sediment have also been found in their gut contents suggesting that they either spend some time on the sediment surface or capture resuspended particles disturbed by currents (Fell 1961; Dearborn 1977; Pearson and Gage 1984; Beaulieu 2001). The reproductive system of *O. cosmica* is unknown but may be similar to a deep-sea congener, *Ophiacantha bidentata*, which is a protandric hermaphrodite and broadcast spawner. Tyler and Gage (1982) suggest that *O. bidentata* may have lecithotrophic development indicated by a large egg size ($\sim 650\text{ }\mu\text{m}$).

Amphilepis patens are infaunal but it is unknown if they feed directly on settling detritus or prey on other infaunal organisms. Beyond the original description (Schoener 1967), the life history and reproduction of *A. patens* is unknown. An Atlantic deep-sea congener, *Amphilepis ingolfiana*, however, has an intermediate egg size ($250\text{--}300\text{ }\mu\text{m}$) and may have a direct or modified indirect development (Schoener 1972).

Amphiura carchara lives at or near the sediment surface. This species is gonochoric and the only ophiuroid species at Station M known to brood its young. Offspring are direct developing and may be matrotrophic (Hendler and Tran 2001).

The principal goal of our long-term study was to examine the variability in the biology of deep-sea ophiuroids in response to food supply over a 17-year period. Here we present data on the size distribution dynamics of *O. bathybia*, *O. cosmica*, *A. patens*, and *A. carchara* and seasonality of settling juveniles from 1989 to 2005.

Materials and methods

Study site

The long time-series station (Station M) is located 220 km west of Point Conception, California, USA ($34^{\circ}50'N$, $123^{\circ}00'W$) at a depth of approximately 4,100 m. The abyssal habitat is characterized by silty-clay sediments and low topographical relief ($<100\text{ m}$ over $1,600\text{ km}^2$) (Smith and Druffel 1998). Data on size–frequency distributions of ophiuroids were collected for 41 monthly time points on a roughly seasonal basis from October 1989 to June 2005

with gaps apparent in Fig. 1. During the 17-year collection period, eight complete annual cycles were sampled.

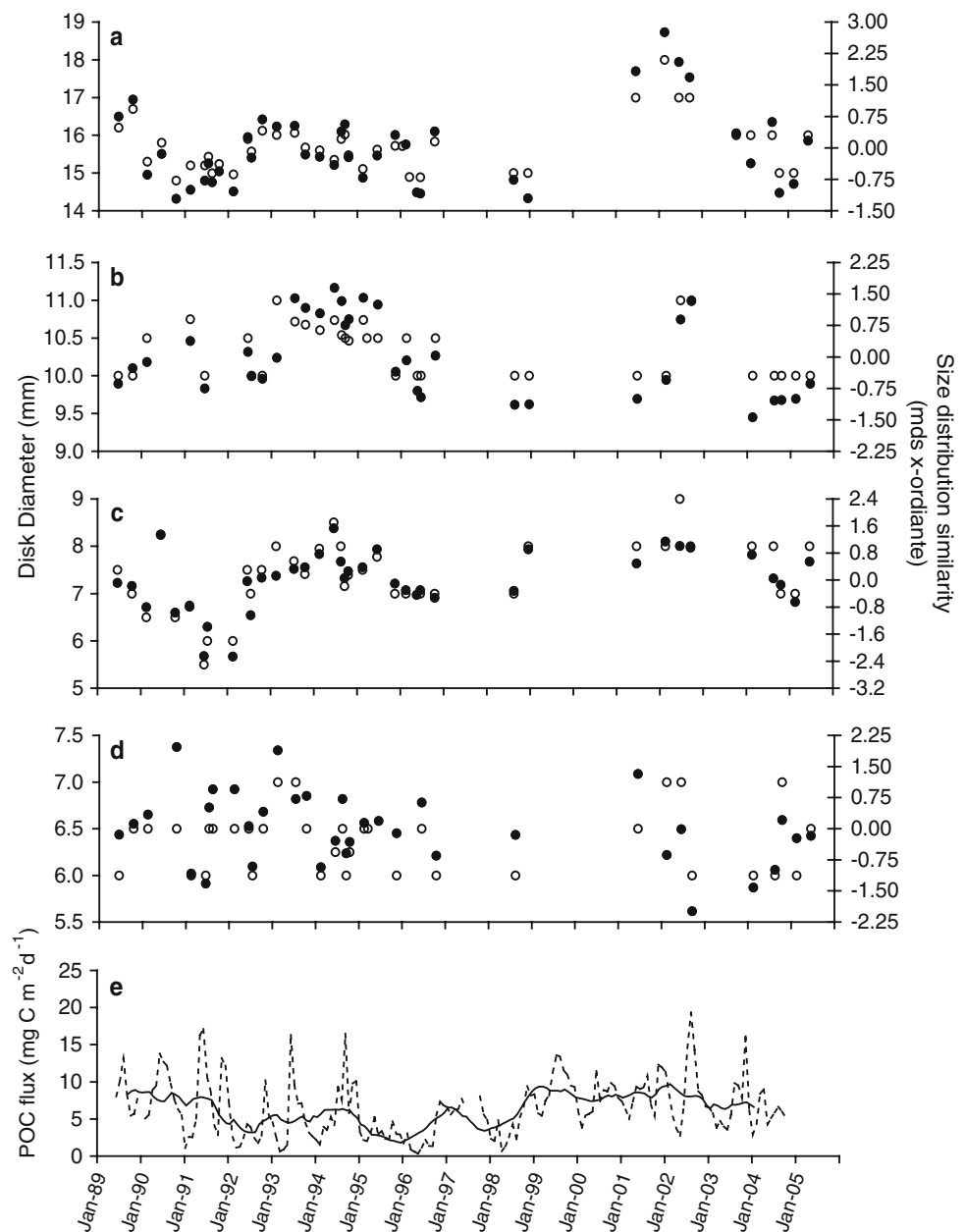
Trawl samples

Ophiuroids were collected principally by otter trawl, which was towed across the seafloor behind a benthic sled for an average of 1.2 km at a speed of approximately 1.5 knots. For a full description of the sled and otter trawl system and associated methods see Wakefield and Smithey (1989), Lauerman et al. (1996), and Lauerman and Kaufmann (1998). The trailing otter trawl had a 38 mm stretch mesh

net with 13 mm cod end liner. Ophiuroids collected by the otter trawl were sorted to major taxa on board ship and preserved in either 95% ethanol or 10% formalin.

Ophiuroid size was estimated in the laboratory by disk diameter, which was defined as the distance from the base of one arm to the opposite inter-radius (Lauerman 1998) and measured using a vernier caliper. Accurate measurement required three-fifths of the disk to be intact. Measurements were rounded to the nearest millimeter. All ophiuroid specimens measured are archived in either the Scripps Institution of Oceanography Benthic Invertebrate Collection or the Los Angeles County Museum of Natural

Fig. 1 Median disk diameters (open circles) and size distribution similarity index (solid circles) for **a** *Ophiura bathybia*, **b** *Amphilepis patens*, **c** *Ophiacantha cosmica*, and **d** *Amphiura carchara*. Also shown is the monthly POC flux composite (e, dotted line) for 50 mab representing food supply to the seafloor with a 13-month running mean (solid line)



History Echinoderm Collection. In cases where more than one trawl was conducted during any particular month the trawl samples were pooled.

The timing of any peaks in median disk diameter during each year was used to examine the effects of season on body size and size distribution similarity. Size–frequency histograms were used to identify potential recruitment events to adult size classes and distribution trends. An index of similarity for the monthly size distributions was created for each taxon by taking the multidimensional scaling (MDS) x -ordinate of the size frequency (%) distribution Bray–Curtis similarity matrix (Clarke and Warwick 2001). Spearman-rank correlations were used to evaluate links between median size and changes in the size distribution similarities. Spearman-rank correlations were also used to examine co-variation of size distributions between the four taxa. Quantitative analyses were performed using PRIMER 6 by PRIMER-E Ltd 2006 and Statistica 1999 by StatSoft®.

Particulate organic carbon and settling juvenile collection

Particulate organic carbon flux data were collected using sediment traps with a 0.25 m² opening (Baldwin et al., 1998). Ten-day samples were taken at 50 and 600 m above bottom (mab) with gaps evident in Fig. 1. The flux of settling juvenile ophiuroids was also estimated from sediment trap samples and included data from a sediment trap at 650 mab used primarily for ¹⁴C chemistry. Identification was only possible to the class level because the preservation process (mercuric chloride) dissolved the dentition.

Details of sediment trap data collection and analysis can be found in Baldwin et al. (1998) for 50 and 600 mab traps and Druffel et al. (1996) for the 650 mab trap. Because there are temporal gaps in POC flux measurements over the time series, a composite estimate of POC flux was used that incorporates available POC flux from 50 mab, then uses available data from the 600 mab sediment trap to fill in gaps where possible, and lastly an estimation of POC flux to 50 mab based on multiple regression analysis of empirical data. The empirical estimate of POC flux at 50 mab was generated using the Northern Oscillation Index, Bakun upwelling index, and satellite estimated export flux from surface waters overlying the study site (Smith et al. 2006). The export flux estimate utilized satellite-based NPP derived from the vertically generalized production model (VGPM, Behrenfeld and Falkowski, 1997) and sea surface temperature using the formulation of Laws (2004) for a 50 km radius around the site. The modeled POC flux data can explain about 50% of the sediment trap measured POC flux and can thus effectively determine if the flux is high or low. The VGPM based POC flux estimates were included from March 1997 until October 1997

because measured POC became available in November 1997. Beginning in January 1998 POC flux estimates to 50 mab, using the more appropriate carbon-based production model (CbPM; Behrenfeld et al. 2005), became available and was used to fill in POC flux time-series gaps beginning in January 1999 and thereafter. The CbPM model also can explain about 50% of the variation in measured POC flux. The composite of both measured values, where available, and model-estimated values provided a nearly continuous POC flux time series for cross-correlating with the size–frequency distribution data of trawled ophiuroids. Monthly cross-correlations, with temporal lags of up to 24 months, were used to evaluate if there were any time-lagged links between the size distributions and the POC flux composite at the site over monthly and yearly timescales.

Results

Trawl collections

The peaks in the disk diameters of the smallest average ophiuroid, *A. carchara*, were approximately 6 mm and suggest that size classes 6 mm or larger were reliably collected by the trawl net. Disk diameters as small as 2 mm were captured, although under sampling of specimens ≤ 5 mm disk diameter cannot be ruled out (Electronic supplementary material, ESM). The long arms and, in the case of *O. cosmica*, spines, cause the ophiuroids to become entangled in the net and with other caught specimens which allows for ophiuroids with disk diameters smaller than the largest possible trawl mesh opening to be regularly captured. The mesh size used here, however, was not fine enough to collect newly settled juveniles, which are typically 0.3–3.0 mm in disk diameter (Sumida et al. 1998). *O. bathybia* had the largest median disk size (16 mm; $n = 20,762$), ranging between 5 and 25 mm, of the four most prevalent species and was the only species to have a median disk diameter greater than the trawl mesh of 13 mm (Fig. 1a). *A. patens* had the second largest median disk size at 10 mm, with a range of 5–14 mm ($n = 4,468$; Fig. 1b). The median disk diameter of *O. cosmica* was 7 mm, ranging from 2 to 12 mm ($n = 4,742$; Fig. 1c). *A. carchara* disk diameters ranged from 3 to 12 mm, and had the smallest median disk diameter of all four species at 6 mm ($n = 1,104$; Fig. 1d). Yearly size–frequency histograms provided no indication of potential recruitment events to larger size classes (Fig. 2 for *O. bathybia*, ESM for other species) and monthly histograms showed gradual shifts in size distributions (Fig. 3 for *O. bathybia*, ESM for other species). There were no clear seasonal patterns in size distribution shifts in any of the four ophiuroid species.

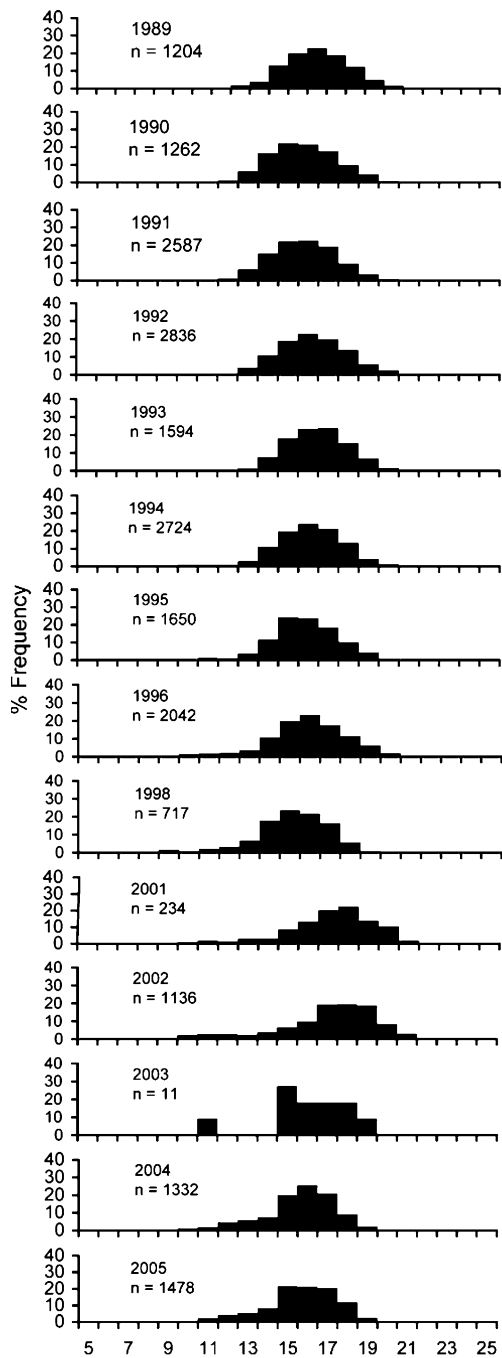


Fig. 2 Yearly size–frequency (%) distributions of *Ophiura bathybia* from 1989 to 2005. Yearly size–frequency distributions for all species are available in the ESM

The monthly median disk size was highly correlated to the size distribution similarity index for each of the four species (*O. bathybia*, $r_s = 0.97$, *O. cosmica*, $r_s = 0.93$, *A. patens*, $r_s = 0.85$, and *A. carchara*, $r_s = 0.71$, all with $P < 0.001$). *O. bathybia*, *A. patens*, and *O. cosmica* all had clear variations in the median and size distribution similarity over interannual timescales. For example, the

similarity ranges of certain yearlong periods had no overlap with the ranges of other such periods. Overall, these trends show indications of co-variation between species, with lower values around 1991, higher values again in 1994 and lower values by 1995 (Fig. 1). Significant covariations between the size distribution shifts over the whole time-series include those between *O. bathybia* and *O. cosmica* ($r_s = 0.45$, $P = 0.005$), as well as between *O. cosmica* and *A. patens* ($r_s = 0.36$, $P = 0.038$). Links between *O. bathybia* and *A. patens* were less clear ($r_s = 0.25$, $P = 0.15$), but correlations of both *O. bathybia* and *A. patens* with *O. cosmica* suggest some co-variation. All potential co-variations of *O. bathybia*, *A. patens*, and *O. cosmica* with *A. carchara* size distributions were not significant.

The size distribution similarity index, which is more sensitive to changes in specific parts of the distribution than the median disk diameter, was negatively correlated to the POC flux composite for three of the four taxa examined including *O. bathybia* ($r_s = -0.35$, $P = 0.040$, lag = 18 months, $n = 34$), *A. patens* ($r_s = -0.44$, $P = 0.015$, lag = 17 months, $n = 32$), and *O. cosmica* ($r_s = -0.39$, $P = 0.029$, lag = 22 months, $n = 31$). Because the median disk diameters and the size distribution indices all have significant positive correlations for each species, the negative cross-correlations between the POC flux and size distribution similarity indicate that increases in POC flux are followed by increases in smaller size classes after ~17–22 months.

Juveniles in sediment traps

The monthly abundances of settling juvenile ophiuroids that fell into sediment traps suggested a seasonal settlement trend with fewer juveniles present in March through June and in August (Fig. 4). Juveniles were captured in limited numbers. Over 17 years, only 6, 27, and 13 specimens were caught in the 50, 600, and 650 mab traps, respectively. The catch rate for juveniles was approximately on the order of $1 \text{ ind. m}^{-2} \text{ month}^{-1}$ ($0.02 \text{ ind. m}^{-2} \text{ day}^{-1}$, $n = 46$). Ophiuroids that settled in the traps averaged 1.5 mm in disk diameter with 6.5 arm segments. No more than four juveniles were caught in any given 10-day cup, suggesting that no obvious cohorts fell into the trap en masse, as was observed by Lampitt et al. (2002). More juveniles were caught in the 600 mab trap than the 50 mab trap, indicating that the samples were likely not resuspended organisms that had already settled to the bottom. Due to the identification limitations, some or all of the juveniles collected by the sediment traps could be species unrelated to the trawl specimens, further limiting the interpretation of the settling ophiuroid data.

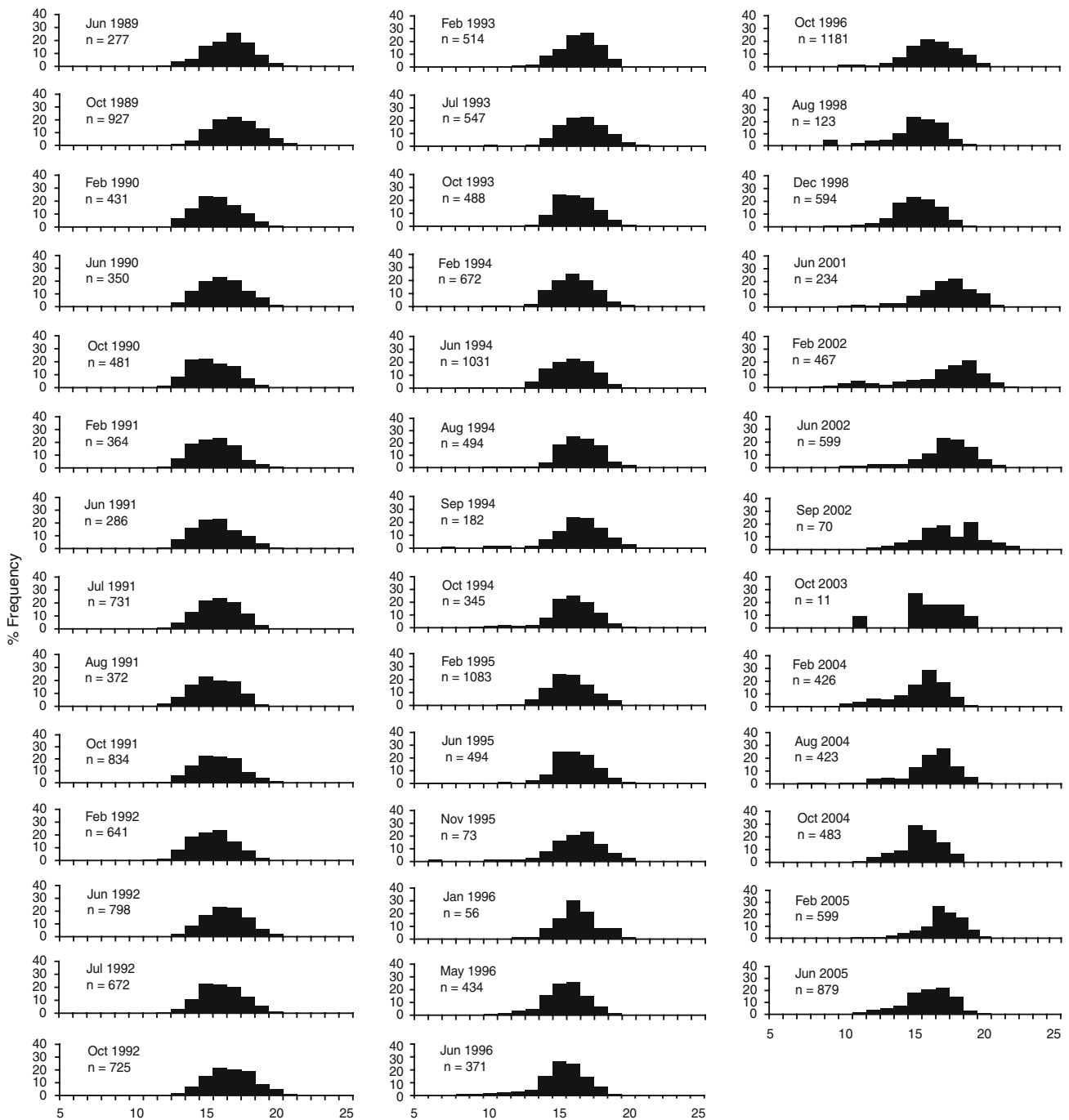


Fig. 3 Monthly size–frequency histograms for *Ophiura bathybia* from June 1989 to June 2005. Monthly size–frequency distributions for all species are available in the ESM

Discussion

Size–frequency and links to POC flux

The results indicated that body sizes of *O. bathybia*, *O. cosmica*, *A. patens* and *A. carchara* populations vary significantly. Changes in size distributions of *O. bathybia*, *O. cosmica*, and *A. patens* were linked to variations in POC

flux supporting the long-hypothesized connection between food availability and population size structure. Evidence for connections between variation in the ophiuroid size distributions and food supply at Station M suggests that such links can not only be on a seasonal scale (Tyler 1988), but also interannual. Despite not catching newly settled juveniles (generally 0.3–3.0 mm disk diameter; Sumida et al. 1998) on the sea floor over the length of the study, it is

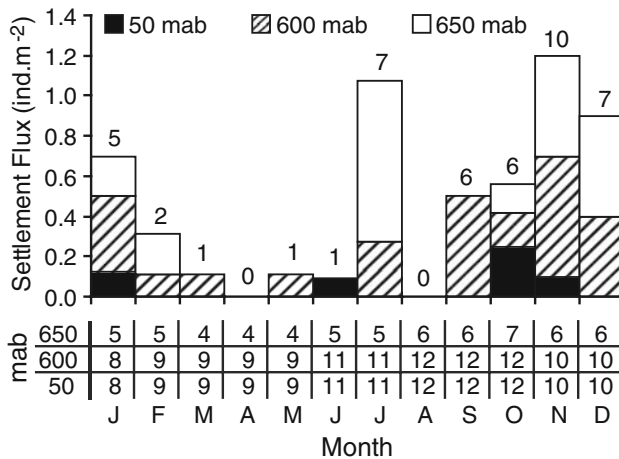


Fig. 4 Monthly abundance of juveniles found in sediment traps at 50, 600, and 650 m above bottom (mab) calculated per unit effort. Numbers above bars indicate cumulative number of juveniles caught per month over all depths and numbers below the histogram indicate total number of months sampled over the collection period for that respective month at each of the three depths

reasonable that major seasonal recruitment events would have been detected in higher size classes after growth occurred. *O. bathybia*, *O. cosmica* and *A. patens* the three larger species had similar size dynamics, which would not be expected if sampling bias were dominating the variation. It is, however, possible that settled juveniles grow at an exponential rate to adult sizes, rather than a constant rate which could mask seasonal trends as adult size relates less to age. Both juvenile growth strategies, linear and exponential, have been documented, as well as where growth rates change with season (Gage et al. 2004; Gage and Tyler 1981b). None of the four species from Station M showed a pattern in recruitment suggesting that either all species have exponential juvenile growth, or all have a continuous, aseasonal linear growth. The presence of an interannual, rather than seasonal, signal is probably related to the fact that interannual POC flux differences were at least as strong as seasonal differences at the site, which is largely related to variation in the El Niño Southern Oscillation (Smith et al. 2006). Considerable size distribution shifts to larger size classes were seen in all species between 1998 and 2001 samples after the strong El Niño/La Niña cycle around 1998. Nevertheless, the absence of a seasonal signal is still unexpected for deep-sea ophiuroids because if reproduction is by spawning, then synchrony might be necessary for successful fertilization rates when densities are low (Young 1994). The density of the most abundant species, *O. bathybia*, is only 0.1–1 ind. m⁻² based on photo estimations (Lauerma et al. 1996; Ruhl 2007), which is marginal for successful uncoordinated spawning (Young 1994). Yet, there were clear interannual scale variations observed in the size distributions of *O. bathybia*, *O. cosmica* and *A. patens*.

While variable, the median and size distribution similarity shifts for *A. carchara* were highly correlated indicating that some coherent population size distribution changes likely occurred in this species as well.

Strong positive covariation was observed between the median and size distribution similarity indices for all four of the examined taxa. The correlations between POC flux and the size distribution similarity indices for *O. bathybia*, *O. cosmica*, and *A. patens* suggest that smaller, and presumably younger, recruits made up a larger percentage of the population 17–22 months after peaks in POC flux. The increases in smaller individuals likely resulted from either increases in reproduction and/or recruitment rates in response to increased food availability either locally or over broader spatial scales. The correlation coefficients between the monthly size distribution similarities and POC flux were relatively low indicating that there was substantial unexplained variation. However, lag times were comparable between all species and were sensible considering that reproduction, recruitment and growth would presumably precede increases in smaller size classes. Photographically determined density of ophiuroids at Station M from 1989 to 2004, dominated by *O. bathybia*, were reported by Ruhl (2007). A time-lagged correlation found that the *O. bathybia* density reported by Ruhl (2007) lagged POC flux by 10–13 months ($r_s = 0.55–0.52$, $P < 0.05$). The time lags between changes in POC flux and density are not in exact agreement with temporal lags found here between POC flux and size distribution shifts of the four species of ophiuroids. This difference in timing may be because density was photographically determined and the size distributions were determined from trawl collected samples. Both density and size distributions of *O. bathybia* do have some significant link to POC flux after about a year or more. Size distribution shifts of *O. bathybia* correlated with density over major portions of the time-series, but such correlations were not significant for the time-series as a whole. Body size distributions, though, showed a greater proportion of smaller individuals when abundances were above average (Ruhl 2007).

The interannual connection to POC flux is supported by the results of Lauerma (1998) and Hendler and Tran (2001) who found *O. bathybia* and *A. carchara* females, respectively, produce a near continuous flow of ripe oocytes. Although *O. bathybia* did not show seasonal gametogenesis, the average oocyte size was found to be greatest after peaks in POC flux (Lauerma 1998). Such continuous or asynchronous investment might be especially advantageous in energy-limited habitats where food supplies are irregular (Tyler and Gage 1982; Lauerma 1998), allowing for ripe gametes and juveniles to be present when food becomes available. Thus, recruitment will more likely be successful during increases in the magnitude and duration

of POC pulses (Lauerman 1998). The results suggest, at least for *O. bathybia*, that gametogenesis and spawning are continuous and changes in that pattern may be a result of opportunistic feeding. However, the energy acquired by opportunistic feeding may not immediately go into gamete production. Pearson and Gage (1984) found that feeding ceased when ripe gonads compressed or ruptured the stomach, seemingly during peak POC flux, in a seasonally breeding, deep-sea species. Energy reserves could be stored before breeding, leading to a less obvious connection between food availability and reproduction. *O. bathybia*, for instance, is known to convert food into tissue in 20–90 days (Lauerman 1998).

Regardless of seasonal or continuous reproduction, the larvae may subsequently face other limitations in the water column affecting survival rates and links to POC fluxes. The correlation to POC flux does not explain all the variation in size distribution over monthly and yearly scales. *O. bathybia*, *O. cosmica* and *A. patens* showed similarities on an interannual scale and these species likely have other common factors influencing their growth and/or reproduction, such as food quality. They may also share a similar reproductive strategy or unseen resource limitation.

Settling juveniles and recruitment

Settling juvenile ophiuroids collected in our sediment traps are suggestive of seasonal settlement, but the limited data are not conclusive. Sediment trap samples showed peak settlement of ophiuroids in autumn and winter compared to peak POC flux in summer and autumn (Baldwin et al. 1998; Lauerman and Kaufmann 1998). Deep-sea NE Atlantic ophiuroids, however, show settlement peaks in summer (Lightfoot et al. 1979; Tyler and Gage 1979; Sumida et al. 2000; Gage et al. 2004) after spawning in early winter and pelagic development in spring. The observed pattern could arise from seasonally released larvae, or limiting conditions in the water column. *Ophiomusium lymani*, for instance, in the Rockall Trough have annual peaks in recruitment even though gametogenesis is not seasonal (Gage 1994). The juvenile settlement results are nonetheless speculative since it could not be determined if the observed specimens originated from the local benthos.

Variability in *A. carchara*

The smaller *A. carchara* had high temporal variability and no correlation with POC flux. This pattern was not initially expected for a brooding species. More variability would have been expected in a dispersal spawner whose offspring are exposed to unstable pelagic conditions. The mean disk diameter (6 mm) was the same as the apparent limit of capturing efficiency with the net, so *A. carchara* was more

prone to sampling error than the other species. This variability may then be related to greater sampling error of small individuals, but the biology of this species also has some notable differences. *A. carchara* is thought to reproduce year round and have direct-developing matrotrophic larvae (Hendler and Tran 2001). Because of its viviparous reproduction strategy, *A. carchara* may not follow a similar pattern in disk size variation as the other three species.

Conclusions

The 17-year data set of ophiuroids at Station M showed interannual trends in recruitment into adult stages to be more prominent than seasonal fluctuation. Variation in limited food supplies were linked to population processes of dominant ophiuroids at the study site. Although the individual species size distributions were linked to POC flux for *O. bathybia*, *O. cosmica*, and *A. patens*, other population regulators could be influential here. The link to POC may be related to opportunistic feeding rather than an organized reproductive strategy. Discerning what processes and development stages are limiting will continue to be essential in evaluating connections between the deep-sea benthos and its surface-derived food supply.

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