M B A R I

Effect of the pelagic food supply on benthic plate sponge abundance and size in the abyssal NE Pacific

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ABSTRACT

A long-term study was conducted to observe temporal changes in abundance and average size of plate sponges, *Bathydorus* sp. A (Rossellidae, Hexactinellidae, Porifera) and an undescribed sponge of the subfamily Euplectellinae (Euplectellidae, Hexactinellidae, Porifera). Benthic camera sled transects at Station M (4,100-m depth, 34º50'N, 123º0'W) were analyzed for sponge abundance and surface area over a seventeen-year time-series. *Bathydorus* sp. grows to larger sizes than Euplectellinae (385.6 ± 605.6 cm^2 and 114.1 ± 61.3 cm^2, respectively) but does not reach the same density (31.8 ± 30.4 sponges ha^{-1} and 59.4 ± 57.0 sponges ha^{-1}, respectively). The two sponge types had similar variations in density and average body size over time suggesting that the same factors may control the demographics of both species. Peaks in significant cross correlations between increases in particulate organic carbon flux and corresponding increases in sponge density occurred with a time lag of 13 months. When plate sponge abundance was higher, average sponge size was smaller suggesting new recruitment or regeneration of persistent sponge cells. The results also support previous suggestions that increased POC flux may induce recruitment or regeneration in deep-sea sponges. Ongoing research will use genetic markers to test these alternatives.

INTRODUCTION

Food webs in the deep ocean are not directly supported by primary production; instead, the main food supply is marine snow and detrital aggregates descending from surface waters in the form of particulate organic carbon (POC). Long-term observations have found that abyssal communities are affected by subtle fluctuations in this food supply (Priede et al. 1994, Ruhl & Smith 2004, Ruhl 2007).

Station M is a long-term study site in the northeast Pacific that has been monitored since 1989. Parameters measured include POC flux (Smith et al. 2006), megafaunal abundances and sizes (Ruhl & Smith 2004, Ruhl 2007), epibenthic megafaunal activity (Kaufmann & Smith 1997) and metabolic rates of infaunal communities (Smith et al. 1987, Smith and Kaufmann, 1999). Station M is ideal for

studies of fluctuations in food supply due to its location within the influence of the California Current, where upwelling and primary production vary on seasonal and interannual timescales (Smith 2006, Ruhl 2007).

This study focused on a distinct morphology of glass sponges at Station M, which we collectively called "plate sponges." *Bathydorus* sp. nov. is an opaque white sponge with a dense spicule tuft under a thin main body (Figure 1a). The other sponge is in subfamily Euplectellinae. It has not been described and does not match any genera in the family so far. This sponge is beige with visible oscula on the surface. The spicule tuft under the main body is much less dense than in *Bathydorus* but each individual spicule is thicker (Figure 1b).
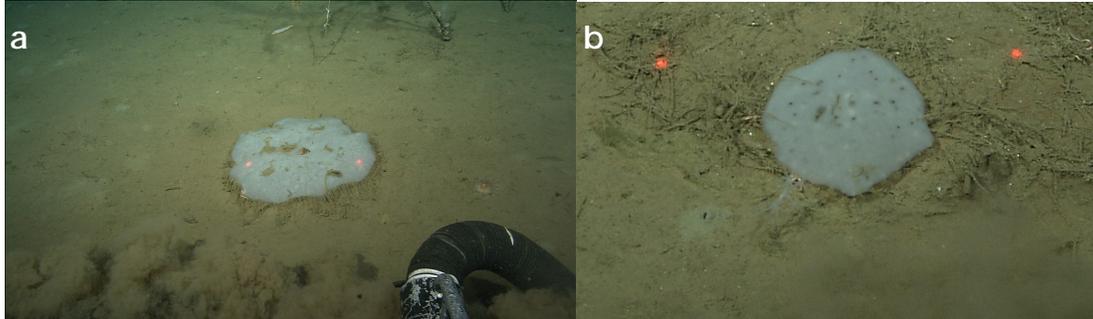

Figure 1. Plate sponges at Station M, an abyssal (4,100-m) study site off the California coast. *Bathydorus* sp. (a) has an opaque white surface and dense spicule tufts on the bottom. (b) Another plate sponge of subfamily Euplectellinae is more translucent with visible oscula and sparser spicule tufts on the bottom. The distance between laser points is 29 cm. Photos taken with ROV Tiburon.

Little is known about the life history and population dynamics of plate sponges. Other deep-sea glass sponges have been estimated to live for 35 to over 200 years (Leys & Lauzon 1998) and may have slow growth rates (1-3 cm yr^{-1}) (Leys & Lauzon 1998, DFO 2000, Leys et al. 2007). This study aimed to discern relationships in plate sponge demographics using comparisons of density, size, and live: dead sponge ratios. In addition, a lingering paradigm in the deep-sea is that long-lived denizens are not as affected by changes in surface conditions (Menzies & Imbrie 1958). To address this paradigm, this study compared sponge abundance to changes in POC flux.

MATERIALS AND METHODS

SITE CHARACTERISTICS

Station M (4,100-m depth) is part of the Monterey Deep Sea Fan, about 220 km west of the California coastline (34°50'N, 123°0'W)(Figure 2). There is little topographic relief over the silty-clay sediments (<100 m over 1,600 km^2). Station M is influenced by upwelling and the resultant seasonal changes in primary productivity. Currents of the California Current in the benthic boundary layer (BBL) at Station M vary between 2.3 to 3.6 cm s^{-1} (Beaulieu and Baldwin 1998). Monthly averages of particulate organic carbon (POC) flux into the BBL ranged from 0.22 mg C m^{-2} d^{-1} during low productivity years to 19.30 mg C m^{-2} d^{-1} over the 17 years of the time-series. High POC flux leads to seasonal detrital aggregates on the abyssal seafloor, with a primary peak in early summer and another in late fall (Baldwin et al. 1998). Sediment community oxygen consumption (SCOC), a measure of infaunal metabolic activity, varied from 1989 to 1999, with

interannual variability of 5 mg C m^{-2} d^{-1} in 1990 to 17 mg C m^{-2} d^{-1} in 1993, and seasonal variability with highs in the summer and fall and lows in the winter. The largest seasonal change in SCOC recorded was from 5 mg C m^{-2} d^{-1} in April 1991 to 16 mg C m^{-2} d^{-1} in July 1991 (Smith et al. 2001).
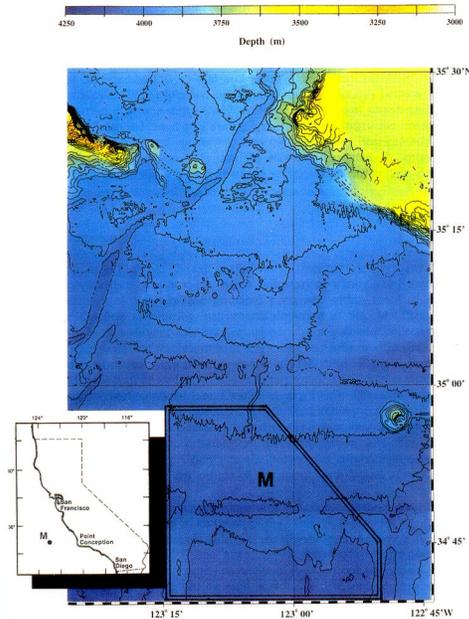

Figure 2. Plate sponges were located at Station M (4,100-m depth, 36º50'N, 123º0'W), a long-term study site (1989-2007) 220 km west of the California coastline.

SPONGE ABUNDANCE AND SIZE

Abundance and surface area of plate sponges were estimated using camera sled transects. Transects were roughly seasonal, with significant gaps due to logistical difficulties. A Benthos 372 film camera and 382 strobe were mounted obliquely on a benthic sled (Wakefield and Smithey 1989) and pulled across the seafloor at about 0.3 m s^{-1}. Photos were taken at five-second intervals, resulting in overlapping frames that together constituted a nearly continuous image mosaic of the seafloor (some skipping along the seafloor caused occasional gaps). Each photo was projected onto an acoustic digitizing system and analyzed using a perspective grid system (Wakefield and Genin 1987). Transect length was based on calculated frame overlap, not ship start/stop times. Transect width was corrected for each transect depending on image quality, color fidelity, and light. For a complete description of correcting to estimated strip widths (ESW), see Bailey, Ruhl, and Smith (2006) and Ruhl (2007).

Bathydorus and Euplectellinae abundance was determined by sponge counts in each transect. Counts were divided by ESW-corrected transect area. To determine sponge surface area, a series of points were digitized along the perimeter of a sponge, connected, and the area inside of those connected points was the approximate surface area of the sponge.

Nonparametric Spearman rank cross-correlations were used to elucidate relationships in sponge dynamics throughout the time-series. Abundance was also

compared to particulate organic carbon (POC) flux to study the relationship of food supply with sponge populations and results were considered significant with P≤0.05.

POC FLUX

Three sequencing conical sediment traps were deployed to measure POC flux, which was used as an analog for food supply. Traps with mouth openings of 0.25 m^2 were moored at 600 and 50 meters above the seafloor. POC measurements were taken in 10 d intervals, but were pooled to monthly timescales for this study. Particulate matter was collected into cups poisoned with 3.0 mmol $HgCl_2$, to eliminate any biological consumption of carbon during the traps' deployment. Samples were analyzed for total carbon and total inorganic carbon concentrations. The difference between the two was the POC, considered food supply, raining down to the abyssal plain (Baldwin et al. 1998). A model of POC export flux from surface waters was used to fill in gaps when abyssal POC data was not collected.

RESULTS

SPONGE ABUNDANCE AND SIZE

Bathydorus sp. density ranged from 4.8 to 148.4 sponges ha^{-1}, with an average of 31.8 ± 4.8 sponges ha^{-1} (mean ± SE). Density of Euplectellinae ranged from 11.3 to 288.3 sponges ha^{-1}, with an average of 59.4 ± 8.9 sponges ha^{-1}. The density of both species was positively correlated (r=0.52, p<0.001) meaning that *Bathydorus* and Euplectellinae density increased and decreased together.

Average plate sponge size was also highly variable among transects. *Bathydorus* size ranged from 25.2 cm^2 to 3,558 cm^2 with an average of 385.6 ± 94.6 cm^2. The average area of 385.6 cm^2 is equivalent to a circle with diameter 22 cm. Euplectellinae sponges were smaller, with size ranging from 5.2 to 244.7 cm^2 with an average surface area of 114.1 ± 9.6 cm^2 (equivalent to a 12.0 cm diameter circle). Like density, the average size of both species was positively correlated (r=0.64, p<0.001), meaning *Bathydorus* and Euplectellinae sizes fluctuated in sync with each other. A negative correlation existed between sponge abundance and average size (r=-0.34, p=0.032), meaning that as sponge density increased, average sponge size decreased.

Large mats of dead spicules, usually covered in detritus and coated in sediments, are also found on the seafloor. The mats are presumed to be derived from plate sponges, based on their shape and size. The size of these mats is difficult to quantify for two reasons: (1) the borders of the mats are not clearly defined, and (2) spicule mats were often much larger than the live sponges (on the order of twice the area), such that the total biomass often did not fit in a single photo frame. For these reasons, spicule mat sizes were not included in statistical analyses – only counts. There was a positive correlation between live plate sponge abundances and the abundance of spicule mats. This means that when sponge abundances increased, spicule mat abundances increased as well.

POC FLUX

POC flux over the 17-year time-series was highly variable, with seasonal and interannual fluctuations (Smith et al. 2006). Sponge densities were positively correlated with POC, with a time lag of 13 months (r=0.26, p=0.127) (Table 1). Though the p-value was not significant based on a generally accepted α=0.05, the correlation coefficient was highest with a time lag of 13 months, and this time lag was validated by a positive correlation between sponge density and the Northern Oscillation Index (NOI). Changes in the NOI are reflected in POC about six months after they occur (Table 1).

DISCUSSION

Little is known about the plate sponges that inhabit Station M. This study evaluated the density and size frequency of the two sponge types found at Station M. An ultimate goal will be to elucidate population dynamics of these sponges. This study also evaluated the paradigm that potentially long-lived deep-sea animals respond to changes in surface conditions on short timescales.

While *Bathydorus* sp. is generally larger than Euplectellinae, it is present at lower densities at Station M. *Bathydorus* density is positively correlated with Euplectellinae, a positive correlation also exists between the average size of the two sponge types. A possible explanation for this correlation is that population growth is controlled by the same factor or factors for both species.

Sponge abundance was negatively correlated with average sponge size. This means there when there was a high density of sponges, they were generally smaller. This could suggest recruitment (Witte 1996).

The positive correlation seen between live sponge and spicule mat abundance could be explained if spicule mats do not remain intact for very long. It makes sense that having a higher number of live sponges would result in a higher number of dead sponges; however, conditions that cause live sponge densities to fluctuate should not also affect densities in the already-dead spicule mats. Instead, these mats may exist on short timescales and the structures disintegrate rapidly such that spicule mat abundances are closely coupled to live sponge abundance.

Finally, the results do not support the paradigm that long-lived deep-sea animals may not respond to changes in surface conditions. POC fluctuates on seasonal and interannual timescales. If the paradigm was true, then these long-lived sponge populations should not be able to reflect changes on such short timescales. Instead, this study found that

Table 1. Spearman rank correlations for densities of live and dead sponges compared to food supply (POC) and the Northern Oscillation Index (NOI). Time lags indicate the amount of time from when POC would change to the effect seen on sponge densities. A slightly lower correlation coefficient (r) was found at 13 months for Euplectellinae in addition to the 17 month lag.

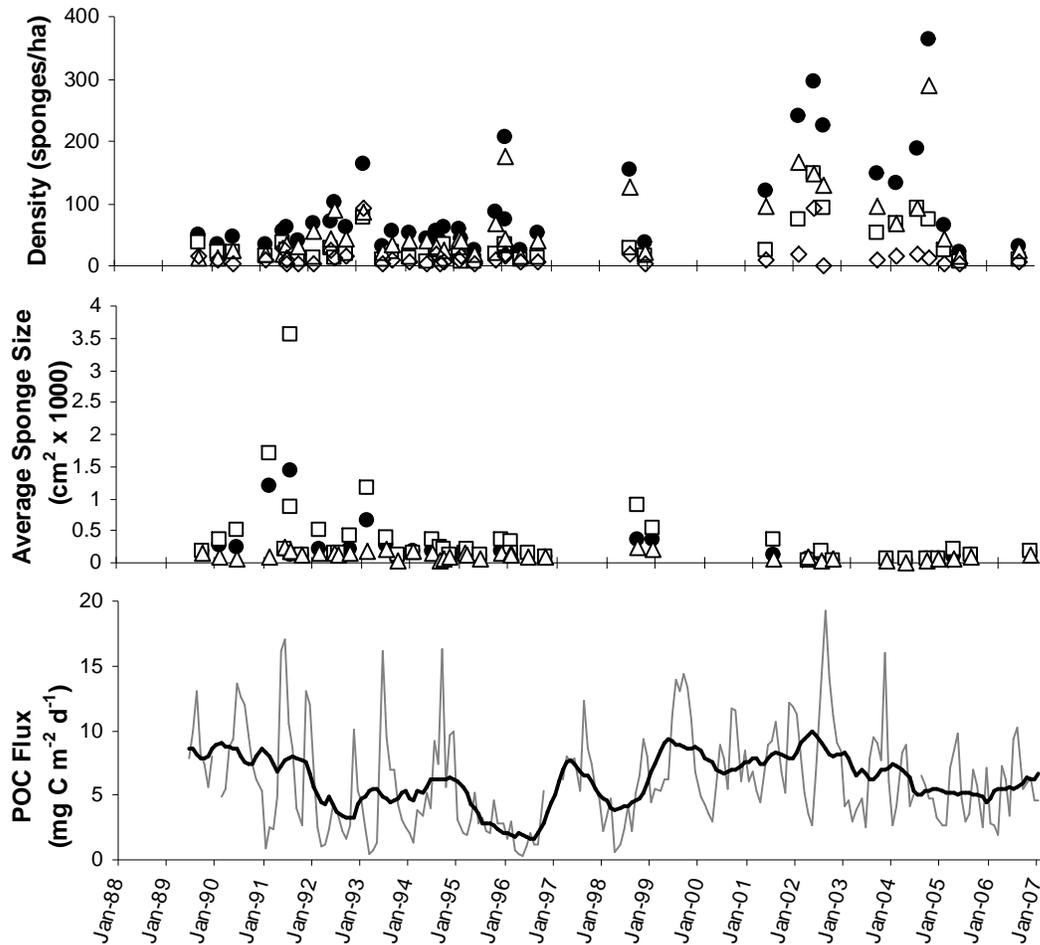| Density	POC flux				NOI			
	n	r	p	Time lag	n	r	p	Time Lag
Total sponge	37	**0.33**	**0.049**	13	41	**0.32**	**0.040**	18
Bathydorus sp.	37	**0.46**	**0.040**	13	41	0.23	0.154	17
Euplectellinae	37	0.27	0.107	17	41	**0.36**	**0.023**	18
Spicule mats	37	0.26	0.127	13	41	0.16	0.308	20

Figure 3. Sponge density and average size from 1989 to 2006 for total plate sponges (*Bathydorus* sp. and Euplectellinae combined)(●), *Bathydorus* (□), and Euplectellinae (Δ), and spicule mats (◊). Values of average sponge size were larger for *Bathydorus* than for all sponges combined because *Bathydorus* was much larger than Euplectellinae. Particulate organic carbon (POC) was measured from sediment traps at 50- and 600-m above bottom at 4,100-m depth. Gaps in the data were extrapolated based on satellite imagery and export flux. The pale line is the actual POC values for each month, the dark line is the 13-month running average for POC flux.

plate sponge density did fluctuate with changes in POC. These results say little regarding sponge lifespan; it is still unclear if deep-sea sponges are indeed long-lived or not. A follow-up experiment using sponge growth to estimate age would be appropriate to ensure that the paradigm was accurately addressed. Sponge growth is a difficult parameter to measure and has only been attempted for hexactinellid sponges in two studies (Dayton 1979, Leys & Lauzon 1998). Recent studies have proposed models for spicule development involving concentric rings of silica deposition around the axial filament (Müller et al. 2007). A method of ageing using these spicule rings may be developed to determine age and growth rates for the plate sponges in this study.

Higher POC flux was correlated with higher sponge densities, and higher sponge densities were correlated with smaller sponge sizes. This supports the results of Witte's study (1996), which found that increased POC flux induced reproduction in three deep-

sea demosponge species. The sponges appeared to respond to changes in POC on seasonal and annual timescales, which suggests generation times on similar timescales.

CONCLUSIONS/RECOMMENDATIONS

Bathydorus sp. grows to a larger size than Euplectellinae but does not reach the same density. Abundances were positively correlated between the two species, as was average size, which may suggest that the same factor or factors are controlling the demographics of both sponge types. When plate sponge density was higher, average size was smaller which may suggest recruitment. Coupled with the positive correlation between food supply (POC) and sponge density, the results presented here support the hypothesis that higher POC may induce recruitment in deep-sea sponges (Witte 1996). Finally, the time lag between an increase in food supply and an increase in sponge density is 13 months; this correlation is validated by a similar correlation to NOI that is offset by about 6 months, as suggested by Smith et al. (2001). The time lag means that it takes 13 months for sponge abundance to reflect a change in POC.

There are numerous directions for future work. Some deep-sea sponges acquire carbon primarily from dissolved organic carbon (DOC) instead of POC (Yahel et al. 2003, Pile & Young 2006), while others do not utilize DOC at all (Yahel et al. 2007). If these plate sponges convert DOC into a form of carbon useable by other organisms, they may greatly affect the surrounding benthic communities – especially during periods of low food supply (Druffel & Robison 1999, Smith & Kaufmann 1999). It is thus important to study the contribution of DOC to the overall carbon budget of these sponges. In addition, the impact of these sponges in their communities could be evaluated using sediment community oxygen consumption (*sensu* Smith & Kaufmann 1999), species richness, and abundances of other benthic species (i.e. Bett & Rice 1992, Beaulieu 2001).

The results of this study suggest that spicule mats are ephemeral, on a timescale short enough to convey a correlation with live sponge densities. Spicule mats are potentially important as microhabitat structures, habitat islands, larval settlement sites, and nutrient sources. Spicule mats were much larger than any live plate sponges in this study. A possible explanation is tissue sloughing, a process described by Barthel and Wolfrath (1989) in which sponges shed the outer layer of spicules to rid themselves of debris and fouling organisms. In this way, live sponges may contribute to the size of spicule mats on seasonal timescales corresponding to tissue sloughing.

Finally, the methods of reproduction in the two plate sponges are unknown. Budding and fragmentation may explain the higher densities of smaller sponges just as easily as sexual reproduction and recruitment. Some spicule mats contained two or three small live plate sponges growing within them. These sponges could have been a result of larval recruitment to the spicule mat or from fragmentation of the original sponge that produced the mat. A molecular method such as inter-simple sequence repeat PCR (ISSR-PCR) or analysis of microsatellite regions could be used to compare the genetic diversity of those sponges (Bornet & Branchard 2001).

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