



First observations of Onuphidae (Polychaeta) patch ecology on the abyssal seafloor

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ABSTRACT

Abyssal plains are important systems within the global carbon cycle. Acquiring a basic knowledge of natural temporal variations of abyssal fauna and understanding the underlying processes driving these variations are required to predict how these systems will respond to climate change. In particular, changes in bio-engineer organisms, such as sessile epibenthic megafauna building hard-structures, may have complex consequences on the abyssal system functioning. This study examines changes of Onuphidae patches (tube-worm aggregations) in terms of density, spatial coverage and size from December 2006 to June 2013 using ROV videos from Station M in the North East Pacific. Associations between Onuphidae patches and other megafaunal organisms were also investigated. Onuphidae patch density and spatial coverage significantly decreased over the study period whereas the mean size of a patch did not change. Density changes were negatively correlated to temporal variation in climate processes 13 months before and particulate organic carbon flux 7 month before. But, the details of the underlying mechanisms remained elusive. Among the megafauna occurring with the patches, three organisms, two Porifera and Ophiuroidea, appeared to be non-obligate associates. The

community structure of Onuphidae patch assemblage over time was different inside and outside the patch suggesting that Onuphidae created micro-habitats within the abyssal seafloor. Therefore changes in Onuphidae patches over time may have cascading effect on diversity, nutrient-cycling and abyssal seafloor system functioning.

INTRODUCTION

Temporal changes in abyssal benthic communities have been evidenced in the North-East Pacific, in particular for mobile megafauna (Ruhl and Smith, 2004, Ruhl, 2008) while less is known about sessile megafaunal organisms forming hard-structures except for some plate sponges (Kahn et al., 2012, 2013). In a muddy seafloor environment, these sessile organisms have the potential to create micro-habitats and increase the system diversity. Patches of tube worms are a conspicuous feature found on abyssal seafloor (Grassle et al., 1975, Lauermaun et al., 1996). For the first time, temporal changes in tube worm patch density and size over time as well as megafaunal associations have been characterized to better understand processes shaping abyssal communities in time. Indeed, deep-sea systems are the most common environment on Earth and are major actors of carbon cycling (Witte and Pfannkuche, 2000, Bett et al., 2001, Smith K.L. et al., 2001, Ruhl et al., 2008, Smith K. L. et al., 2009). But, the carbon cycle is modifying under climate change, and assessing deep-sea community structures and characterizing their temporal variations is now critical (Glover and Smith C.R., 2003, Thiel, 2003, Smith et al., 2009). In particular, global warming modifies surface ocean conditions impacting primary and export production to the deep ocean (Bopp et al., 2005, Sarmiento and Gruber, 2006, Richardson, 2008, Steinarcher et al., 2010). Most deep-sea fauna relies on the sinking particulate organic carbon (POC) flux for food through pelagic-benthic coupling (Smith KL, 1987, Billett, 1991). In turn, deep-sea fauna mediates many long-term carbon processes such as bioturbation, remineralisation, and burial (Witte and Pfannkuche, 2000, Bett et al., 2001, Smith K.L. et al., 2001, Ruhl et al., 2008, Smith K. L. et al., 2009). Characterizing deep-sea system temporal variations is important to assess how carbon-related ecosystem processes respond to climatic variations (Smith KL et al., 2009, Glover et al., 2010).

Abyssal long-term time series has been conducted since 1989 at Station M (Sta. M) in the North East Pacific. Both intra- and inter-annual variations in POC flux quantity reaching the seafloor were measured (Baldwin et al., 1998, Smith K.L. et al., 2006, Smith et al., submitted) and related to climate processes, in particular the El Niño Southern Oscillation

(ENSO, Smith K.L. et al., 2006). Fauna has been shown to respond to POC flux temporal changes in various ways: some decreased in density during high food supply period whereas other increased in density as a result of recruitment/reproduction event (Ruhl and Smith K.L., 2004, Ruhl et al., 2008, Kahn et al., 2012, Laguionie-Marchais et al., 2013). Changes in mobile megafauna such as echinoderm species have been extensively studied over the time-series and correlated to POC variations (Ruhl and Smith 2004, Ruhl, 2008).

Studies of sessile megafauna building biogenic hard-structures have been scarcer. At Sta. M the sessile epibenthic megafauna is dominated by various sponges (Beaulieu, 2001a,b, Kahn et al., 2013) and Onuphidae polychaete patches (Lauerman et al., 1996). Using camera-sled data, Khan et al. (2012) have found that two Hexactinellida plate sponge species displayed inter-annual variations in density and average body size between 1989 and 2006. Density changes correlated with POC flux values 13 month before and with the North Oscillation Index (NOI, an ENSO indicator) values 15 month before. Hexactinellida spicules have been found to create habitat islands at Sta. M that persist after the death of the organism (Beaulieu, 2001a). Less is known for Onuphidae patches. Onuphidae density was only measured between June 1990 and October 1991. Lauerman et al. (1996) found that Onuphidae was the dominant epibenthic megafauna in all transects over this period representing 26 to 48% of the individuals. Both sponges and tube worms are considered as bio-engineering fauna in various environments (Bett and Rice, 1992, Kim, 1992, Beaulieu, 2001a). As deep-sea sponges, Onuphidae patches have the potential to create micro-habitats. So if these patches change over time, it may impact many more organisms. Therefore, understanding Onuphidae patch temporal variations could provide important insights not only on diversity but also on deep-sea carbon flow dynamics at Sta. M.

As far as the authors are aware, this is the first time than tube worm patch ecology is studied in sedimentary abyssal plain. Patches rather than individuals were used as biological entity to provide a first overview of their functional role. The main reason for using Onuphidae patch (OP) is that Sta. M data have been obtained from Remotely Operated Vehicle (ROV) high definition videos. Images, even high definition ones, do

not allow identifying Onuphidae to species level or assessing occupancy rate of tubes. Considering OP rather than individuals virtually cancelled these indetermination. Both the tube occupancy rate and Onuphidae species diversity within patches will be studied in future work. So far the only information on Onuphidae was collected between 1989 and 2006 using a semi-balloon trawl trailed to the camera sled (Lauerman et al., 1996). Epibenthic Onuphidae obtained from the trawls were two undescribed species of the *Diopatra* complex, with a majority of specimens in the *Paradiopatra* genus and a minority in the *Epidiopatra* genus (L. Harris, Natural History Museum of Los Angeles County, personal communication). Some deep-sea *Paradiopatra* and *Epidiopatra* species found in other locations have been morphologically described (Fauchald, 1982, Paxton, 1986, Budaeva and Fauchald, 2011). But, no species information on their life-history is available. Both genera are close in the way they build their tubes. The tubes are made of a relatively thick outer layer of mud particles without ornament and a thin parchment-like lining (Budaeva and Fauchald, 2011). Feeding and reproductive habits are known to the family level in general and has been described for a few shallow-water species (Paxton, 1986, Hsieh and Simon, 1990, Pires et al., 2012). Onuphidae are thought to be omnivore feeders (Fauchald and Jumars, 1979) whereas four reproductive modes have been recognized (Paxton, 1986). So, from a functional point of view and with the current knowledge on deep-sea species of the *Diopatra* complex, it is meaningful to used patches as biological entities. Another advantage of using patch rather than individuals is that patches remain more clearly visible whatever the particle sedimentation rate during the sampling. Food pulse levels have been found to be highly variable form one sampling period to another (Smith et al., submitted). The presence of phytodetritus or dead gelatinous organisms such as salp can greatly modify the visibility of details on the seafloor but are less likely to hide a whole patch.

This study examines temporal variations in Onuphidae patch density, spatial coverage and size at Sta. M from 2006 to 2013. Using the ROV long time-series videos, three main questions were addressed: (1) Did OP change in terms of density, spatial coverage and size over time? (2) Were OP temporal dynamics driven by environmental factors? (3)

Were there any megafauna associated with OP and if so, did the association change over time? (4) Did OP create micro-habitats?

2. MATERIALS AND METHODS

2.1. Sampling

From December 2006 to June 2013, ten research cruises were conducted at Sta. M (50°00 N, 123°00 W, 4100 m depth, see details in Smith K.L. and Druffel, 1998) in the North East Pacific. Overall, silty-clay particles dominate the sediments and little relief is found over large areas (< 60 m relief over 770 km², Smith et al., 1993). Seabed video footages were acquired using ROV Tiburon (December 2006-September 2007) and ROV Doc Ricketts (February 2009-June 2013). A total of 16 transects were filmed (Table 1) using a Ikegama high definition cameras fitted with HA10Xt.2 Fujinon lenses. Transect lengths varied according to cruise imperatives. However, the transect width was kept the closer to 1 m by using the ROV lasers as guide.

Videos were analyzed using the MBARI Video Annotation and Reference System (VARS) software. Each Onuphidae patch seen during a transect was recorded into the database with its position, depth, time of occurrence within the transect. Several patches had biogenic structures within them and these observations were also recorded. Patch annotation was conservative: only clear patches, defined as an aggregation of numerous intertwined Onuphidae tubes with sediment disturbance were used for data analysis. Observations of patch-like features, mainly sediment disturbance with fewer tubes, were separately recorded as sediment disturbance.

As a first approximation and as no sampling was done on the patches, the occupancy rate of tubes and Onuphidae species composition were considered to be similar for all patches.

2.2. Density data analysis

Onuphidae patch density was defined as the number of patch per m². But, density is a function of the sampling area. As each sampled transect had a different length, the impact

of the transect length in the data was assessed prior to any temporal analysis. A linear regression was computed between the total number of patch per transect and the transect length to assess the correlation between these two parameters (SigmaPlot v.12). As a significant linear relationship was expected, the coefficient of dispersion (CD, variance:mean ratio) of patches was also determined for each sampling period. Indeed, data obtained over different sampling areas would only be meaningful in time if the patches were evenly distributed at the survey scale. By comparing the coefficient of dispersion of patches to the one of an equivalent even distribution (Poisson distribution, $CD = 1$), the evenness of patch spatial distribution was assessed.

To obtain the patch mean density and associated standard error for each time period, each transect was divided into 20 m² pseudo-replicates. Studies on holothurian at Sta. M have shown that 20 m² was the optimal-size for the pseudo-replicates (L. Kuhnz, personal communication). Holothurians are mobile organisms smaller than OP. Therefore the optimal pseudo-replicate area for the holothurian might not meet the one for tube worm patches. However, to compare the variability of patch density to those of other fauna at Sta. M, the same pseudo-replicate size was kept as a first approximation. Temporal changes were assessed using an Analysis of Variance (ANOVA, Kruskal-Wallis Rank Sum Test, SigmaPlot v.12).

2.3. Size data analysis

Patch size were estimated from framegrabs taken with VARS. Patch shape was approximated by a rectangle area (Fig. 1a). For each patch, the horizontal length could be accurately measured as the 2 ROV laser pointed gave an horizontal reference (19 cm distance between the pointers). On the contrary, the vertical length could only be estimated as the ROV camera direction was not exactly perpendicular to the seafloor. Based on the Canadian grid theory (Wakefield and Genin, 1987), centering the laser at mid vertical height allowed having the same percentage of distortion above and below the lasers. In this condition, the distance between the lasers can still be used as a measurement reference. As the camera filmed close from the seafloor and had a relatively

low tilt angle, the percentage distortion was found to be 30% in the worst case. Sizes should be more accurately assessed in near future as a new program based on Canadian grid will be added to VARS. Patch area estimates will then be reassessed based on this technique. For patches bigger than the camera frame, several pictures were taken with overlaps (Fig. 1b). Several small rectangle areas were estimated and added together to obtain the total patch area estimate.

Patch area estimates were used to analyze the mean spatial coverage of a patch over time defined as the percentage of area covered by all patch for a transect area. The mean patch area over time and frequency distributions of patch area over time were also computed. Patch density and means size were tested for correlation (Spearman-rank correlation, SigmaPlot v.12). Temporal changes were assessed using an ANOVA (Kruskal-Wallis Rank Sum Test, SigmaPlot v.12). The influence of biogenic features on patch size was also investigated. Regardless of the sampling period, areas of patch with and without biogenic structures were tested for significant differences (Mann-Whitney Rank t-test, SigmaPlot v.12).

2.4. Association data and statistical analysis

Living megafauna organisms seen within each patch (not its proximity) were recorded for each patch. To ensure the detection level of these organisms over different sampling periods, only high definition videos were used so February 2007 had to be excluded of the analysis (only standard definition videos were available for this sampling). Also only clearly visible and identifiable (at least to some taxonomic level) megafaunal specimens were counted giving a conservative estimate. To decipher which organisms were true associates, the density of organisms inside and outside the patch were computed and tested for differences (Mann-Whitney Rank t-test, SigmaPlot v.12). Organisms with a significantly higher density within the patch were considered as true associates. The densities of specimens outside the patch were deduced from the total density of organisms recorded for each transect.

The structures of communities formed by the whole assemblage and only true associates were analyzed inside and outside of patches using multivariate ordination techniques (Primer v.6, Clarke and Gorley, 2006). Compositions as Bray-Curtis Similarity of the square root-transformed density data inside and outside patches were computed over time. A group average cluster analysis was then applied to each similarity matrix. The correlation between the two community structures over time was assessed using a Mantel test (Relate routine, ρ , Primer v.6),

The influence of biogenic features within the patch on true associate densities was also investigated (Mann-Whitney Rank t-test, SigmaPlot v.12).

2.5. Statistical analysis of relationship with environmental factors

Spearman-rank correlations were used to investigate potential relationships between Onuphidae patch and environmental factors (SigmaPlot v.12). Several OP descriptors, mean density, spatial coverage, mean size, associate densities within and outside patches, were tested against two environmental factors. The first factor was the climate indicator NOI. The second factor was the POC flux to the seafloor. Sta. M is unique as it has a near-continuous monthly data record of POC flux. This data set was obtained by using a composite measure of POC flux integrated from sediment trap data at 50 and 600 mab and a model based on satellite data to fill in the gaps in the record (Ruhl et al., 2008). Monthly and yearly cross-correlations were used to test relationships over a distribution of monthly and yearly temporal lags between the environmental factors (climate and food supply) and OP descriptors. Because data sets were highly gapped, serial autocorrelation was not tested. Significance was assessed with several criteria regarding correlation sign, p-value and involved time lags. These tests were aimed to understand if climate processes, productivity and POC fluxes had a direct but lagged impact on the OP features at Sta. M.

RESULTS

3.1. Patch observations

Overall 101 observations were marked as Onuphidae patches (Fig. 2a, 2b) and 258 as sediment disturbances (fig. 2c, 2d, 2e). The so-called sediment disturbance structures had not enough tubes to be defined as a patch and were not included in the data analysis. Onuphidae tubes were all bended over the seafloor. The density of Onuphidae tubes within each patch varied but could not be objectively determined without sampling. Two main biogenic structures were frequently seen within patches. The first structures were mounds created by other megafaunal organisms. Mounds occurred on 18 % of the patches with the highest frequency observed in June 2007 when 50% of patches had mounds. No mound was observed in patches in June 2013. The second biogenic structures seen on patch were remains of dead sponges, particularly the plate sponges *Docosaccus maculates* and *Bathydorus laniger* and a vase-shaped Hexactinellida species. On average, 30 % of patches had sponge spicules with the maximum frequency 63% occurring in December 2006. No sponge spicule was observed within patches in February 2007.

3.2. Density data analysis

Onuphidae patch density changed between the sampling periods. As expected, the total number of patches observed was a linear function of the transect length ($R = 0.859$, Fig. 3). Also data obtained from shorter transects had a higher uncertainty, the patch coefficient of dispersion remained under 1 over the whole time series. The patches were evenly distributed in space at each sampling period. Therefore, all data were considered meaningful and retained for the temporal analyses. OP density varied over time (Fig. 4a). The highest density was found in February 2007 with $27 \pm 14 \cdot 10^{-3}$ patch per m^2 . The lowest density was approximately ten times less and was recorded in June 2012 with $2.5 \pm 2 \cdot 10^{-3}$ patch per m^2 . The decrease in patch density over time was statistically significant ($p = 0.024$).

3.3. Size data analysis

The patch spatial coverage but not the mean size of a patch changed over time (Fig. 4b, 4c). The lowest spatial coverage was measured in December 2006 when patches covered 0.02 ± 0.009 % of the transect area. The highest spatial coverage was found in June 2011 with 0.59 ± 0 %. Overall the temporal variations in patch spatial coverage were significantly different ($p < 0.001$).

In terms of patch mean size (Fig. 4c), the smallest patches occurred in May 2011 with an area of 0.191 ± 0.03 m² and the biggest patches were measured in June 2012 with a 0.480 m² area. However, these differences over time were not statistically significant ($p > 0.05$). OP density and mean size were not significantly correlated ($p > 0.05$). The patch size frequency distributions for each time period (Fig. 5) were not found to be significantly different either ($p > 0.05$). The most even distribution occurred in September 2007 whereas in June 2007, 2012, 2013 and November 2012 the distributions were more dominated by one size class. Except in June 2012, the dominant size classes were the smallest: $0-0.17$ m² and $0.18-0.35$ m².

The biogenic structures present within mounds did not have the same influence on the patch size. No difference was found between the mean size of a patch with or without mound ($p > 0.05$). On the contrary patches with dead sponge remains were significantly bigger ($p = 0.011$) with a median of 0.229 m² versus 0.154 m² for patch without dead sponge remains (Fig. 6).

3.4. Associations

Only a subset of the megafauna known at Sta. M was seen on Onuphidae patches and only three organisms were found to be true associates. Overall, 32 different types of organisms were observed within patches (Table 2) mainly belonging to the Phyla Porifera (44%-86%) and Echinodermata (11%-55%, Fig. 7). Among these animals, three had density significantly higher within patch than outside patch. The strongest relationship was found for the group small Porifera ($p = 0.006$): 10.300 ind.m⁻² of patch versus 0.150

ind.m⁻² out of patch (Fig. 8a). This group was composed of small bulbous Porifera not readily identifiable on videos. Sampling will be needed to determine if they are new species or juveniles of Porifera such as *Bathydorus laevis spinosus*, Euplectella and/or Hexactinellida. Small Porifera highest density within patches was found in November 2012 with $29 \pm 11 \cdot 10^{-3}$ ind. m⁻². The lowest density was recorded in September 2007 with $1 \pm 1 \cdot 10^{-3}$ ind. m⁻². The second association involved another Porifera *Cladorhizidae* sp. 1 ($p = 0.015$) with a median of 0.894 ind.m⁻² of patch versus 0.019 ind.m⁻² out of patch (Fig. 8b). Within patches, *Cladorhizidae* sp. 1 highest density occurred in June 2007 with $22 \pm 1 \cdot 10^{-3}$ ind. m⁻² whereas the lowest density was found in December 2006 with $7 \pm 4 \cdot 10^{-3}$ ind. m⁻². The third associate was the Ophiuroidea ($p = 0.020$) with a median 0.609 ind.m⁻² of patch versus and 0.012 ind.m⁻² out of patch (Fig. 8c). Ophiuroidea density within patch varied from 0 ind. m⁻² in June 2012 to 33 ± 33 ind. m⁻² in June 2007. None of the associates had significant difference in terms of density in patches with and without mound ($p > 0.05$). However, small Porifera occurred in greater abundance on patches with dead sponge remains compared to those without spicules ($p = 0.044$, Fig. 9).

Overall, the community structure of the associates inside and outside patch were different over time (Relate test, $\rho = 0.048$, Fig. 10).

3.5. Relationships with environmental factors

A statistical relationship was found between Onuphidae density and environmental factors (Table 3). OP densities were negatively correlated to the POC flux with a 7 month-lag and to the NOI with a 13-month lag. In terms of OP associate density within patches, no correlation with compatible statistical and mechanistic rationale was found with POC flux or climate index. On the contrary, associate densities outside patches were significantly correlated with POC flux (Table 4).

DISCUSSION

4.1. Onuphidae patch temporal dynamics

Onuphidae patch significantly changed in terms of density and spatial coverage over the study period. OP density could not be compared with the previous study on epibenthic Onuphidae at Sta. M. Lauerman et al. (1996) estimated the density of individual Onuphidae tubes not of patches. But, OP density could be compared with the density of other sessile epibenthic megafauna inhabiting Sta. M. Plate sponges had an average density of 9.2×10^{-3} individual plate sponge per meter square (Kahn et al., 2012) and is consistent with the present OP data (2.5 to 27×10^{-3} ind.m⁻²). In terms of changes over time, Kahn et al. (2012) reported that plate-sponge density varied at inter-annual scale between 1989 and 2005. On the contrary, Lauerman et al. (1996) did not find significant differences in the individual Onuphidae density over a 16 month-period in 1990-1991. This finding suggested that there was no intra-annual variation in Onuphidae density. However, a longer time-period would have been required to correctly assess both intra- and inter-annual variations (Smith et al., submitted). This study showed that at least Onuphidae tube aggregations had intra- and inter-annual variations.

Onuphidae patches appeared to be evenly dispersed on the seafloor. Similar results were found for Sta. M plate sponge distribution: aggregation was scarce and occurred mostly on a few meters scale (Kahn et al., 2012). The random distribution of both plate-sponges and OP suggests that the soft-sediment habitat is homogeneous for both groups at Sta. M as evidenced for *Hyalonema* sp. at Sta. M (Beaulieu, 2001a) and epibenthic megafauna in the deep Atlantic (Grassle et al., 1975). However, the hypothesis that soft-sediment habitat is homogeneous for OP will need to be further investigated as biogenic structures such as mounds and dead sponge remains were frequently observed within patches. At Sta. M, biogenic structure spatial distribution has not been assessed yet. Biogenic structures may influence Onuphidae dispersion because they impact not only local concentrations of POC (Yager et al., 1993) but also hydrodynamics. Studies of shallower aggregated polychaetes have shown that as many colony forming invertebrates, juveniles

of tube worms tend to settle in the close vicinity of their adults (Callaway et al., 2010). In particular, the change in local hydrodynamics generated by the aggregated adults is an important cue to induce juvenile settlement (Callaway, 2003, Rabaut et al., 2009). Both mounds and dead sponge remains may induce a similar hydrodynamic disturbance to the one of an OP influencing Onuphidae juvenile settlement.

Two environmental factors potentially drove Onuphidae density temporal variations. Patch densities were negatively correlated to the POC flux with a 7 month-lag and to the NOI with a 13-month lag. The 6-month difference between the two correlations is consistent with the lag between POC and NOI at Sta. M (Smith et al., 2006). OP response to environmental factor was consistent with the time-lags of other mobile and sessile megafauna of Sta. M (Ruhl and Smith, 2004, Kahn et al., 2012). On the contrary to plate sponges, OP density was negatively linked to POC flux, which may result from several mechanisms. First, species of the Onuphidae family are considered omnivorous (Fauchald and Jumars, 1979). Analyses of lipids, sterols and fatty acid content of epibenthic Onuphidae (outside of patches) sampled in August 2006 at Sta. M confirmed omnivory. Onuphidae phytosterol levels revealed that phytodetritus was only one of their food source while Polyunsaturated Fatty Acid levels evidenced an important degree of carnivory (Drazen et al., 2008). So, higher level of POC flux may not have resulted in higher food level for Onuphidae. Drazen et al. (2008) found that Onuphidae storage lipid level were indicative of a sporadic diet. Being sessile, these organisms may store more energy for low food period. Second, POC flux may directly influence Onuphidae on a certain time-scale and indirectly affect their preys on another time-scale, further confusing the impact of POC flux on the Onuphidae population density. Third, higher particle sedimentation rates may have clogged Onuphidae tubes, disrupting their feeding and reproductive patterns. At Sta. M, Onuphidae tubes were bent over the sediment (J inverted structure, Myers, 1972) with their openings close to the seafloor. Tubes could have been buried under high POC flux. Overall the lack of information on abyssal Onuphidae life-history prevents a mechanistic understanding of POC flux variation effects on patches.

Onuphidae patch size did not significantly change over the study period while several mobile megafauna and plate sponge species displayed inter-annual variations in size (Ruhl, 2007, Kahn et al., 2012). Although the correlation between OP density and mean size was not significant in this study, it is worth noting that the lowest (highest) OP sizes occurred during February 2007 (June 2012) when OP density was the highest (lowest). These dynamics corresponds to the ones reported for some mobile megafauna by Ruhl (2007). During high period of POC flux, mobile megafauna with higher densities decreased in body size, suggesting increased reproduction followed by recruitment of young individuals (Ruhl, 2007). Several factors may explain the lack of significant correlation between OP density and mean size. First, patch growth may be slow and limited by density-dependent effects (Levin, 1982, Reise et al., 2001, Safarik et al., 2006). Such processes could de-correlate POC flux influence on patch density and size. Second, patches are 3-dimensional structures. Patch could have grown vertically rather than horizontally. Assessing the number of tubes within a patch will be necessary to resolve this issue. Third, some patches may have being partially or entirely dead. So, the active area of a patch may not correspond to its total area. Sampling patches for tube occupancy rate is now needed. Fourth, on the contrary to plate sponges or holothurians, OP are made of numerous polychaetes whose individual responses may confuse the overall patch response. Fifth, different Onuphidae species may compose different patches or co-exist within a same patch. Specific response in terms of growth and reproduction may confuse the relationship between patch size and density. Sixth, patch density and size could be driven by different factors or at least, not respond at the same rate to a same factor. Studying shallow-water *Diopatra ornata* patches, Kim (1992) reported that the food had an effect on the size of *D. ornata* after 6 month but not on patch density, at least not on the study scale. At last, patch may be evenly distributed in terms of abundance but not in terms of size. If so, the variable transect lengths would have brought noise into the size data. The few observations of patches made during each transect did not allow to test for this hypothesis but could explain the lack of significant correlation between patch density and mean size.

Overall, variations in surface conditions and subsequent food supply to the abyssal seafloor impacted Onuphidae patch density but the underlying mechanisms remained elusive.

4.2. Onuphidae patch assemblages

Onuphidae patch epibenthic megafaunal assemblages were composed of 32 types of different organisms from the 100 known at Sta. M and only 3 were associates. All 32 organisms were also observed outside of the patches. Therefore no obligatory relationship existed between the Onuphidae and its epibenthic megafauna. Indeed, assemblages of *Hyalonema* stalks and Onuphidae tubes had similar composition at St. M (Beaulieu, 2001a). OP composition seemed linked to the fauna composition at Sta. M rather than to Onuphidae polychaetes themselves. Similar results were found for polychaete tube aggregations in shallower ecosystems (Gherardi et al., 2001) or for deep-sea sponges (Buhl-Motensen et al., 2010). Specific obligate epibionts are considered as rare (Wahl and Mark, 1999). OP may expand the realized niche of several species otherwise living in sub-optimal conditions (Rabaut et al., 2007). And, secondary substrata provided by attached organisms will also influence the number of species found within this patch (Beaulieu, 2001a). The species richness of OP assemblages could not be obtained from ROV videos as many organisms were not identifiable to species level. Sampling patches is now necessary to determine if all megafaunal organisms of patches were seen, identify all epibenthic megafauna to species level and assess the macrofaunal and meiofaunal assemblages.

At Sta. M, Onuphidae polychaetes forming patch act as bio-engineers as defined by Jones et al. (1994). Bio-engineer organisms have non assimilatory effects on their environments and influence benthic organisms either through direct interactions or through indirect sediment-mediated interactions (Rowe, 1996, Wright and Jones, 2006, Buhl-Mortensen et al., 2010). As Sta. M physical environment is calm (Beaulieu and Bladwin, 1998), biological interactions should prevail in determining OP assemblages (Nybakken, 1997, Beaulieu, 2001a). The 32 organisms composing OP assemblages had various life-

histories: mobile/sessile, deposit feeders/filter feeders/predators that may differently benefit of OP. First, OP provide a rare hard-substrate while modifying hydrodynamic conditions and sediment chemistry, all important factor for larval settlement in particular for sessile organisms (Eckman et al., 1981, Luckenbach, 1987, Woodin, 1991, Snelgrove and Butman, 1994, Qian, 1999, Beaulieu, 2001). Second, Onuphidae tube canopy may provide a localized refuge from large epibenthic and benthopelagic predators, such as Echinoidea or Asteroidea. OP would benefit many species juveniles and adult macrofauna and meiofauna (Thistle, 1979, Levin, 1991, Olafsson et al., 1994). Third, Onuphidae may enhance food availability for various feeding types. Onuphidae banded and intertwined tube network may retain more phytodetritus than surrounding sediment benefiting surface and sub-surface deposit feeders. In shallower systems, the current velocity is reduced in patches, increasing the residence time of particles within them (Friederichs et al., 2000). Also, filter feeders may use tubes to reach the near bottom boundary layer to catch more particles (Levin, 1991, Buhl-Mortensen, 2010). And mobile predators may benefit of enhanced prey abundance. Studying deep-sea sponge assemblages, Buhl-Mortensen et al. (2010) found that, sessile taxa and detritivores, tend to inhabit older and dead parts of the host organism, whereas mobile predators or filter feeders inhabit the upper and younger parts of the host. All the interactions within a patch will be highly dependent on the tube density and patch geometry (Eckman, 1983, Bolam and Fernandes, 2003).

Among the three associates, Ophiuroidea was the only mobile organism and displayed the weakest relationship with the OP. Ophiuroidea are conspicuous component of Sta. M megafauna either on hard substrate (*Ophiacantha* sp., Lauerman et al., 1996) or on sediment (Booth et al., 2008). Ophiuroidea have been shown to respond to variations in POC flux and surface climate conditions (Ruhl and Smith, 2004, Ruhl, 2007, Booth et al., 2008). When comparing Ophiuroidea density within and outside OP, visibility issues had to be considered. Indeed, Ophiuroidea live at the interface or just above the seafloor. Therefore, Ophiuroidea visibility varied over time depending on their activity and particle sedimentation rates (Lauerman et al., 1996). Lauerman et al. (1996) estimated that Ophiuroidea may be buried 67 to 85% of the time at Sta. M. By considering a buried time

of 85% throughout a year, Ophiuroidea density in sediment could be 7 times higher. Even with this scenario, Ophiuroidea density within patch would still be 10 times higher than outside patch confirming that Ophiuroidea were OP non-obligate associates. Ophiuroidea are known to associate to deep-sea hard structures to gain access to higher flux and enhance filter feeding (Levin, 1991, Buhl-Mortensen et al., 2010). However, OP did not appear high enough to allow such benefit. Rather, observations suggest that Ophiuroidea lived with their central disc protected within the tubes and their filter-feeding arms emerging out into the water as also reported in shallower systems (Haanes and Gulliksen, 2011).

The relationship between Onuphidae patches and its two Porifera non-obligate associates may be more mutualistic. Porifera are also bio-engineer species (Bett and Rice, 1992, Beaulieu, 2001, Buhl-Mortensen et al., 2010). Both Onuphidae and Porifera may benefit from the hard substrate build by the other that generates variations in hydrodynamic conditions, settlement, refuge and food enhancement (Eckman et al., 1981, Witte et al., 1997, Phillips and Lovell, 1999, Schlacher et al., 2007). Onuphidae could use sponge spicules to incrust in their tubes as Onuphidae are known to actively select for the particles they incorporate into their tubes (Fauchald, 1982). But, Sta. M Onuphidae had rather smooth tubes without spicule (L. Harris, personal communication and personal observations). Assessing the molecular composition of tubes may be necessary to determine if Onuphidae select small siliceous particles from degrading spicules over the regular sediment. Most likely, sponges increase food sources for Onuphidae by mediating the deposition of very fine grained material. In laboratory experiment, Witte et al. (1997) found that deep-sea sponges ingested small particles (up to 6 μm) which were ejected after digestion as pellets (50-100 μm) and thus become available to deposit feeding organisms. For Porifera, OP could first also enhance food supply: filter feeder sponges may benefit from microbial activity linked to tubes (Yahel et al., 2007) and the carnivorous *Cladorhizidae* sp. 1 (Vacelet, 2007) could benefit from small preys within the patch. OP could also provide a shelter for the sponges. The small Porifera group was constituted of small individuals may either be juveniles of some Hexactinellida species or one/several new small species. In both case, the small Porifera group may benefit from

the protection offered by the tube patch from large mobile megafauna predators such as Echinoidea and Asteroidea. Regarding *Cladorhizidae* sp. 1, many juveniles were observed within patches. However, the proportion of juveniles and adult specimen has not been yet recorded outside of the patch preventing further investigation. Other deep-sea bio-engineer species have been found to increase social interaction acting as a mate location and refuges for young (Levin, 1991).

To better understand associations and biological interaction within patches, more sampling is now required in particular determining the smaller size-class organisms present as epi- and in-fauna. Overall, as OP density changes over time, patch assemblages are spatially and temporally dynamic.

4.3. Onuphidae patch functional role at abyssal seafloor

Onuphidae patches created micro-habitats at Sta. M. Indeed, the community structures of the complete assemblage (32 organisms) and of the associates (3 organisms) were different over time within and outside patches. And no significant or different correlations were found between Ophiuroidea, *Cladorhizidae* sp. 1, small Porifera group density and NOI/POC flux within patches and outside patches. So, OP created both spatial heterogeneity in associate abundance and temporal heterogeneity in their responses to environmental factor. Both processes are known to increase diversity as proposed in the patch mosaic theory (Grassle and Sandler, 1973, Grassle and Morse-Porteous, 1987). Size and structural complexity of the patch are expected to be positively related to species diversity for both sessile and mobile species (Bell, 1985, Beaulieu, 2001b, Rabaut et al., 2007, Buhl-Mortensen et al., 2010). *Hyalonema* stalks were also found to be micro-habitats at Sta. M (Beaulieu, 2001a). Having similar assemblages as OP, their functional role is expected to be close. *Hyalonema* stalks generated a spatial and temporal mosaic of biological disturbances with different taxa colonizing new space at different rates (Beaulieu, 2001b). The stalk-colonization rates were similar to those reported for other deep-sea, hard substratum recruitment experiments (about 1.5×10^{-3} ind.cm⁻².d⁻¹) with frequent recruitment of a few common taxa and infrequent recruitment

of many rare taxa (Beaulieu, 2001b). Biogenic structures providing hard-substrate can act as habitat islands as evidenced by Beaulieu (2001b). Rosenzweig (1995) defined habitat islands as insular habitat surrounded by an environment that poses difficulties for dispersal. Because not all size-class associations were assessed during OP study, and not all epibenthic megafauna could be identified to species level, no species accumulation curve could be computed for OP. Therefore, there is no firm evidence of OP being habitat island but based on the similarity between sponge spicule mat and Onuphidae patch at Sta. M, sampling should be carried to test this hypothesis.

Onuphidae patches also play a role in nutrient cycles at abyssal seafloor. First, OP locally modify the current velocity and particle residence time (Friederichs et al., 2000, Rabaut et al., 2007). Second, tube-worms have been shown to modify the stability of local sediments. Tube aggregations may impact both sediment stabilization due to a skimming flow effect (Hall, 1994) and destabilization due to enhanced erosion (Eckman et al., 1981). OP size and tube density may be important for determining the outcome of stabilization/destabilization processes in the sediments (Luckenbach, 1986). Also, hydrodynamic stabilization is thought to be rare and stability may result from mucus binding (Eckman et al., 1981, Dyer, 1986). Third, polychaete tubes can enhance the diffusional fluxes within the sediment (Aller, 1980). Tube linings of macro-infaunal organisms may act as a highly hydrated porous membrane (Aller, 1983). Polychaetes actively transport material in their tube (Magnum et al., 1968, Levin et al., 1997). By allowing the diffusion of small molecules through the tube, both bacteria activity, meiofauna and macrofauna abundance can be supported at depth in the sediment (Reimers et al., 1992). Increased oxygen level and Onuphidae activity provide chemoclines (N, P, C) around the tube creating niches for microbial growth (Forster and Graf, 1995, Phillips and Lovell, 1999). Fourth, both tube building and microbial activity increase the mucus content of the sediment (Eckman et al., 1981). In turn, mucus secretions and tube lining may impact the transport of solute such as Dissolved Organic Carbon. Specific class of organic molecules may be differently impacted. Sediment viscosity may also increase with mucus (Hannides et al., 2005). Fifth, sediment grain size can be modified by tube-building polychaetes. Tubes can get buried and biodegraded

underneath the seafloor accumulating finer sediment after the inhabiting polychaete died (Carey, 1987). Therefore, Onuphidae patches play an important role in nutrient cycling and locally impact the pelagic-coupling.

As Onuphidae patches influence diversity and nutrient cycling, OP changes over time may have cascading effects on Sta. M system. In abyssal systems, where both food supply and physical disturbances are low, biological interactions within biogenic structures and associations are likely more complex than in shallow-environment (Levin et al., 2001; Carney 2005). Levin (1991) hypothesized that bio-engineered structures may have contributed to the origin and maintenance of metazoan diversity in the deep sea by providing distinct microenvironments in which species can specialize. Since December 2006, OP density has decreased with two main consequences. First, the reduced number of patches is expected to negatively impact OP assemblage abundance and diversity, making more complicated for new recruits or immigrant to settle within a patch. Second, the diminution of patch occurrence may reduce the overall rates of nutrient cycling at Sta. M by modifying nutrient diffusion and bacterial activities. The tube density within each patch will modulate these processes and its temporal dynamics should be assessed. As OP dynamics did not appear to results from an ecological drift but were linked to POC flux variations and climate processes on the surface (NOI), climate change is likely to impact OP density. Variations in OP and assemblages may modify the proportion of buried/remineralised carbon (Smith K.L. et al., 2009) and produce a positive feedback by increasing remineralisation rate (Vardaro et al., 2009). A better characterization of OP features (occupancy, Onuphidae species) and OP assemblage (all size-classes) is needed to better constrain carbon processes and rates at abyssal seafloor.

CONCLUSIONS/RECOMMENDATIONS

Sta. M Onuphidae patches varied intra- and inter-annual in terms of density and spatial coverage while keeping the same size in average. In particular, patch density decreased between December 2006 and June 2013 in relation to the POC flux and surface climatic condition, respectively 7 and 13 months before. However the underlying mechanisms linking food supply and patch density remained elusive. Onuphidae patches provide micro-habitats within the seafloor influencing local diversity and nutrient cycles and may potentially have cascading effect on abyssal system. A better mechanistic understanding of Onuphidae patch dynamics is now required. Future work will include: (1) using camera-sled data obtained at Sta. M between 1989 and 2006 to enhance the time-series and better characterize the influence of POC flux variations on abyssal Onuphidae patches; (2) samples OP to know if different species are found in different patches or compose a same patch; (3) sample OP to determine tube occupancy rates as well as tube density within patches; (4) samples macrofauna and smaller other epi- and in-faunal organisms found within OP to obtain a complete description of patch assemblages and associations; (5) samples patch-looking features to test if they are forming/dying patches; (6) samples patches to assess the importance of dead sponge remains within each patch (spicule:tube ratio); (7) samples the non-obligate associate small Porifera to determine if they are juvenile of known Hexactinellida species or new species.

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Table legends

Table 1: Sta. M ROV sampling details as year, month, dive reference and transect length. T and D in dive references indicates the ROV used for sampling (T = Tuberon, D = Doc Ricketts).

Table 2: List of organisms seen within all Onuphidae patches. Not all organisms could be identified to the same taxonomic level from the video data.

Table 3: Spearman rank correlation between Sta. M Onuphidae patch descriptors and various climate indexes at a particular time lag. R is the coefficient of correlation with its associate p-value (SigmaPlot v.12). NOI stands for North Oscillation Index, SOI stands for Southern Oscillation Index, m stands for month and y stands for year.

Table 4: Spearman rank correlation between the density inside and outside patches of organisms seen on patched and environmental factor for a particular time lag. R is the coefficient of correlation with its associate p-value (SigmaPlot v.12). NOI stands for North Oscillation Index, SOI stands for Southern Oscillation Index, BUI stands for Bakun Upwelling Index, POC stand for Particulate Organic Carbon flux and m stands for month.

Figure captions

Figure 1: Onuphidae measurement using VARS framegrabs. A) Patch smaller than the camera frame. Picture is taken with ROV laser pointers centered on the patch. The patch area estimate is defined by the white rectangle area. B) Patch bigger than the camera frame. Several pictures of the patch with overlaps are taken. The patch is decomposed in small rectangular areas, laser centered for each of them. Each rectangle is individually measured then summed together to obtain the total estimate area of the patch.

Figure 2: VARS framegrab showing A) Onuphidae patch, B) Onuphidae patch, C) sediment disturbance structure, D) sediment disturbance structure, E) sediment disturbance structure.

Figure 3: Total number of patch observed in 10^{-3} number of patch per m^2 as a function of the transect area travelled by the ROV during the 10 research cruises. The dotted line represent the linear relationship between both variables ($R = 0.859$, linear regression with $y = 2.38 + 0.005x$, SigmaPlot v.12).

Figure 4: Patch features over the 10 sampling periods. A) Mean density as 10^{-3} number of patch per m^2 with associated standard error. B) Patch mean spatial coverage as percentage of the transect area with associated standard error. C) Mean size of a patch with associated standard error.

Figure 5: Patch size frequency distribution (as percentage) for each sampling period. On the horizontal axis, the size class 1 represents sizes between 0 and $0.17 m^2$, the size class 2 represents $0.18-0.35 m^2$, the size class 3 represents $0.36-0.52 m^2$, the size class 4 represents $0.53-0.70 m^2$ and the size class 5 represents $0.71-0.86 m^2$.

Figure 6: Box plot representing the result of the Mann-Whitney Rank Sum t-test on mean patch size different with dead sponge remains (spicules) present within the patch and

without dead sponge remains (no spicules) within the patch. The difference in the median value between the two group was statistically significant ($p = 0.011$).

Figure 7: Onuphidae patch assemblage over time with percentage of Porifera (yellow), Echinodermata (pink), Bryozoa (black), Chordata (grey), Arthropoda (blue), Protista (brown) and Cnidaria (purple).

Figure 8: Mean densities of Onuphidae true associate per m^2 of patch (■) and per m^2 outside of patch (□) for each sampling period with associated standard error. A) Small Porifera group. B) *Cladorhizidae* sp. 1. C) Ophiuroidea.

Figure 9: Box plot representing the result of the Mann-Whitney Rank Sum t-test on mean small Porifera group densities per m^2 of patch with dead sponge remains (spicules) present within the patch and without dead sponge remains (no spicules) within the patch. The difference in the median value between the two group was statistically significant ($p = 0.044$).

Figure 10: Bray-Curtis dendrograms by group average of the structure of the community (A) comprising the three true Onuphidae patch associates: small Porifera group, *Cladorhizidae* sp. 1 and Ophiuroidea over time within patch, (B) outside of patch, (C) comprising all Onuphidae patch assemblage within patch, (D) outside of patch.

TABLE**Table 1**

Year	Month	Dive	Transect length (m)
2006	December	T1067	1120
2007	February	T1077,T1080	220
	June	T1094	80
	September	T1141, T1143	420
2009	February	D008	1560
2011	May	D230, D232	4500
	November	D321, D323, D324	2640
2012	June	D403	400
	November	D442, D443	2600
2013	June	D486	3000

Table 2

Phylum	Class	Order	Family	Genus	Species
Arthropoda	Malacostraca	Isopoda			
Arthropoda	Malacostraca	Decapoda	Munidopsidae	Munidopsis	
Arthropoda	Malacostraca	Isopoda	Munnopsidae	Munnopsis	
Arthropoda	Pycnogonida				
Bryozoa	Gymnolaemata	Cheilostomatida	Tessaradomidae	Striatodoma	dorothea
Chordata	Ascidiacea	Pleurogona	Pyuridae	Culeolus	
Chordata	Ascidiacea	Pleurogona	Pyuridae		
Chordata					
Cnidaria	Anthozoa	Actiniaria	Bathyphelellidae	Bathyphelellia	australis
Cnidaria	Anthozoa	Zoanthidea	Epizoanthidae	Epizoanthus	stellaris
Cnidaria		Anthomedusae	Hydractiniidae		
Echinodermata	Holothuroidea	Dendrochirotrida	Cucumariidae	Abyssocucumis	abyssorum
Echinodermata	Crinoidea	Bourgueticrinida	Bathycrinidae		
Echinodermata	Echinoidea	Cassiduloidea	Pourtalesidae	Cystechinus	loveni
Echinodermata	Echinoidea	Cassiduloidea	Pourtalesidae	Cystocrepis	setigera
Echinodermata	Holothuroidea	Elasipodida	Elpidiidae	Elpidia	sp. nov.
Echinodermata	Crinoidea	Comatulidina	Antedonidae	Fariometra	parvula
Echinodermata	Stelleroidea				
Echinodermata	Holothuroidea	Elasipodida	Elpidiidae	Peniagone	sp. nov.
Echiura					
Porifera	Hexactinellida	Lyssacinosida	Rossellidae	Bathydorus	
Porifera	Hexactinellida	Lyssacinosida	Rossellidae	Bathydorus	laniger
Porifera	Demospongiae	Poecilosclerida	Cladorhizidae		sp. 1
Porifera	Hexactinellida	Lyssacinosida	Euplectellidae	Docosaccus	maculatus
Porifera	Hexactinellida	Lyssacinosida	Euplectellidae		
Porifera	Hexactinellida				
Porifera	Hexactinellida				sp. 2
Porifera	Hexactinellida				sp. 3
Porifera	Hexactinellida	Amphidiscosida	Hyalonematidae	Hyalonema	bianchoratum
Porifera	Hexactinellida	Amphidiscosida	Hyalonematidae	Hyalonema	sp. A
Porifera					others
Sarcomastigophora	Xenophyophorea	Psamminida			

Table 3

Patch feature	Index	R	Time lag	p
Patch total density	NOI	-0.678	13 m	0.038
Patch coverage	SOI	-0.833	6 m	0.002
Patch mean density	SOI	-1	1 y	0.017
Patch mean size	SOI	-1	1 y	0.017

Table 4

Associate	Index	R	Time lag	p
Cladorhizidae sp. 1 in density	NOI	0.905	2 m	<0.001
Cladorhizidae sp. 1 in density	SOI	0.786	2 m	0.019
Cladorhizidae sp. 1 out density	NOI	0.714	1 m	0.037
Cladorhizidae sp. 1 out density	POC	-0.905	10 m	<0.001
Porifera out density	NOI	0.857	9 m	0.002
Porifera out density	POC	0.762	7 m	0.021
Ophiuroidea out density	POC	0.690	15 m	0.047

Figure 1

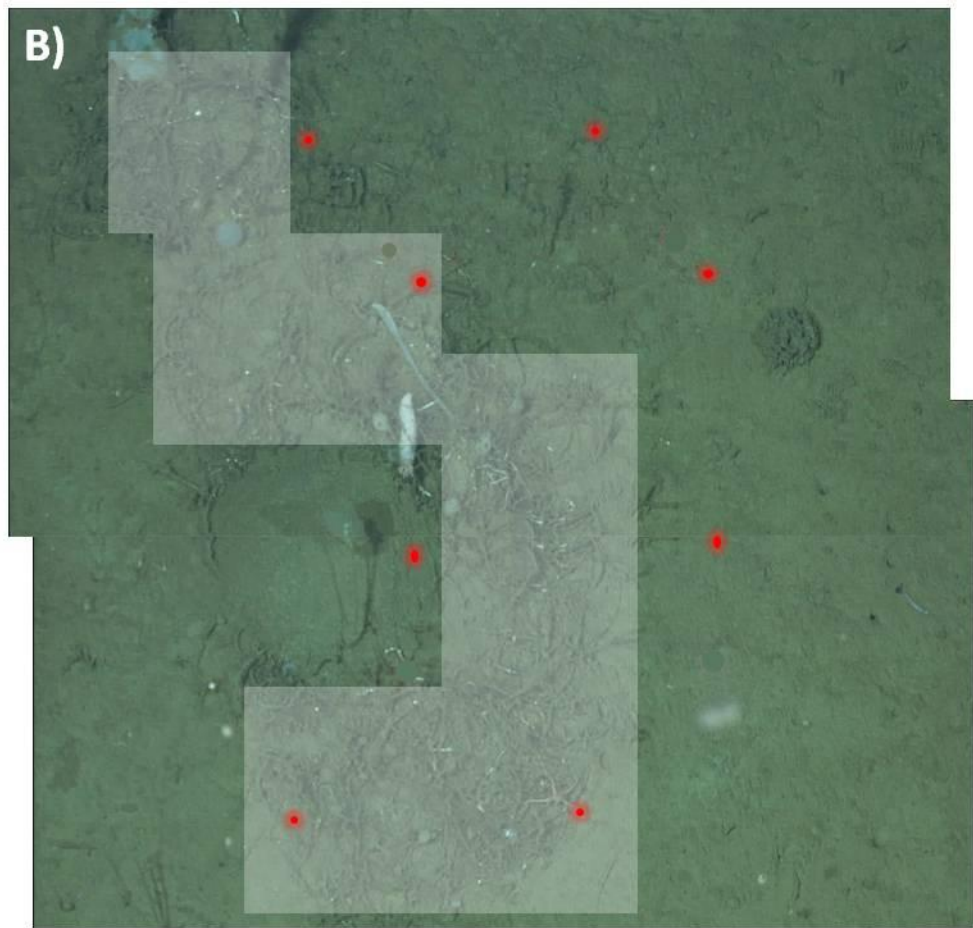
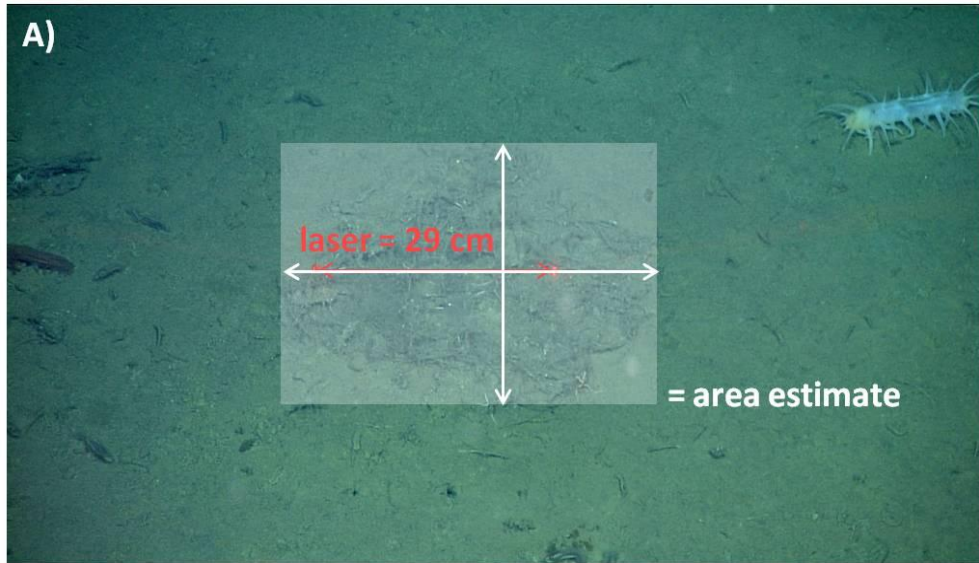


Figure 2

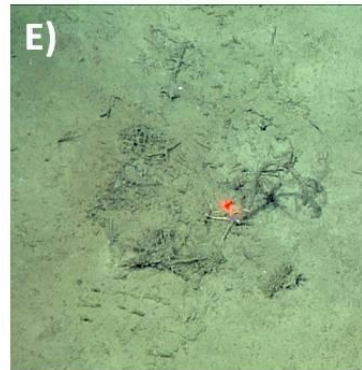
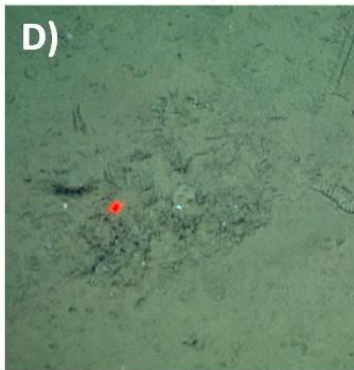
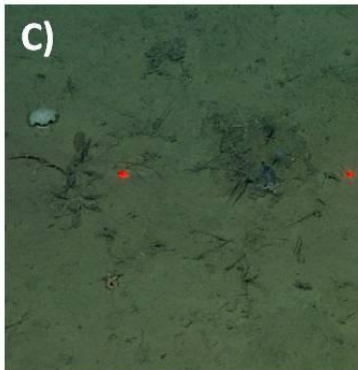
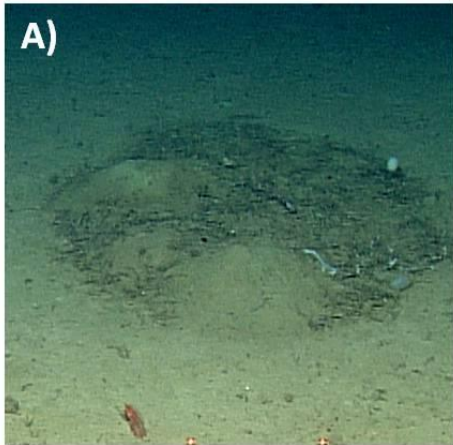


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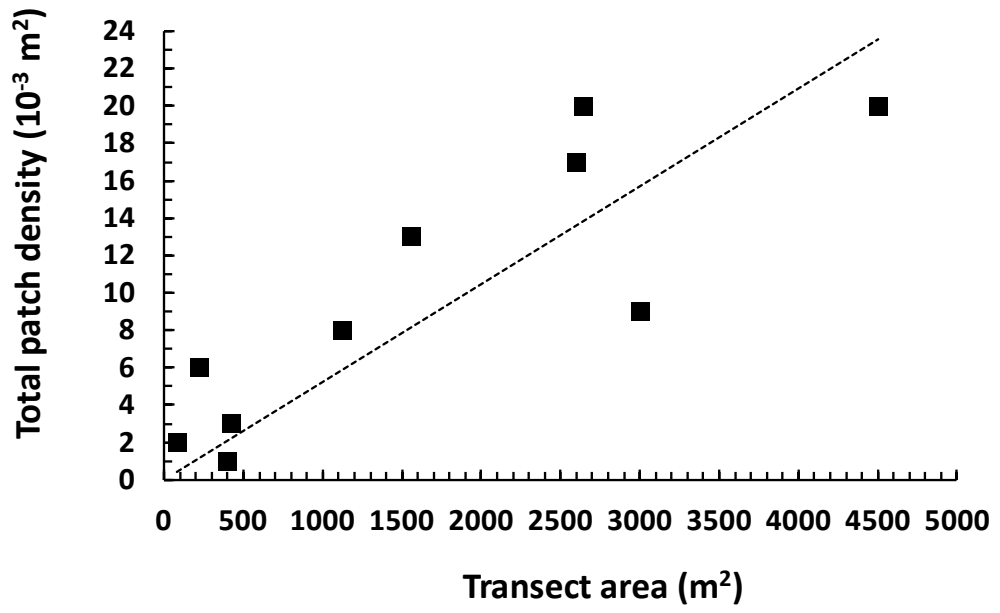


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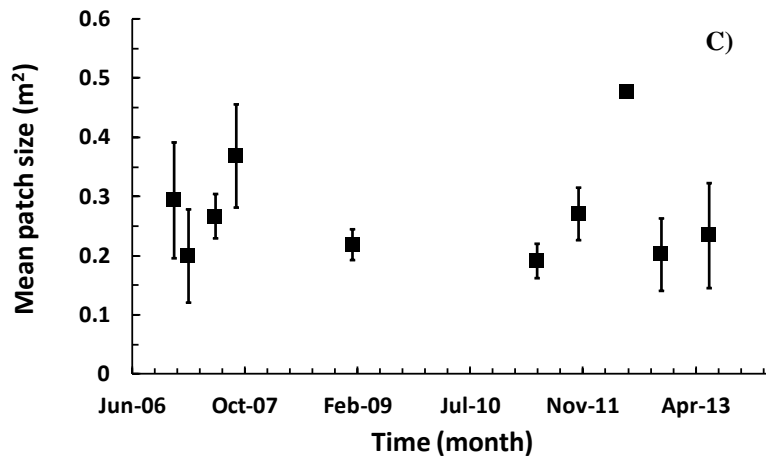
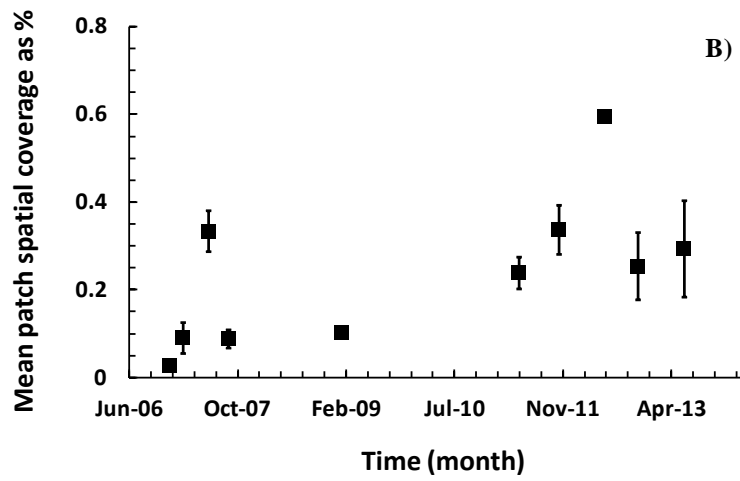
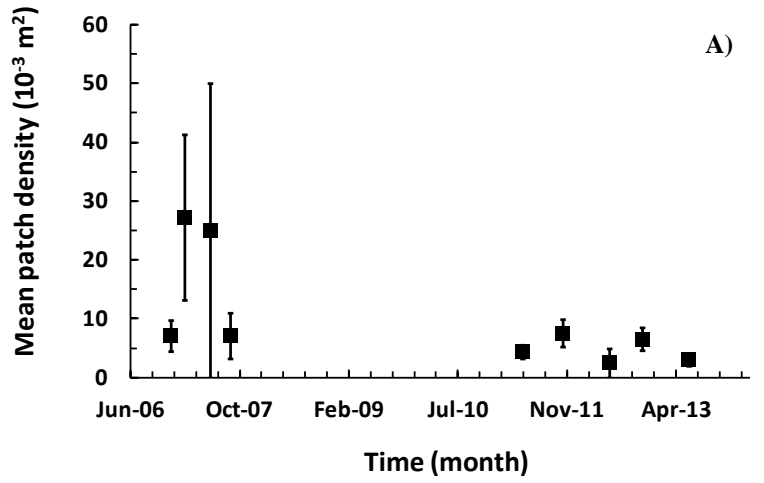


Figure 5

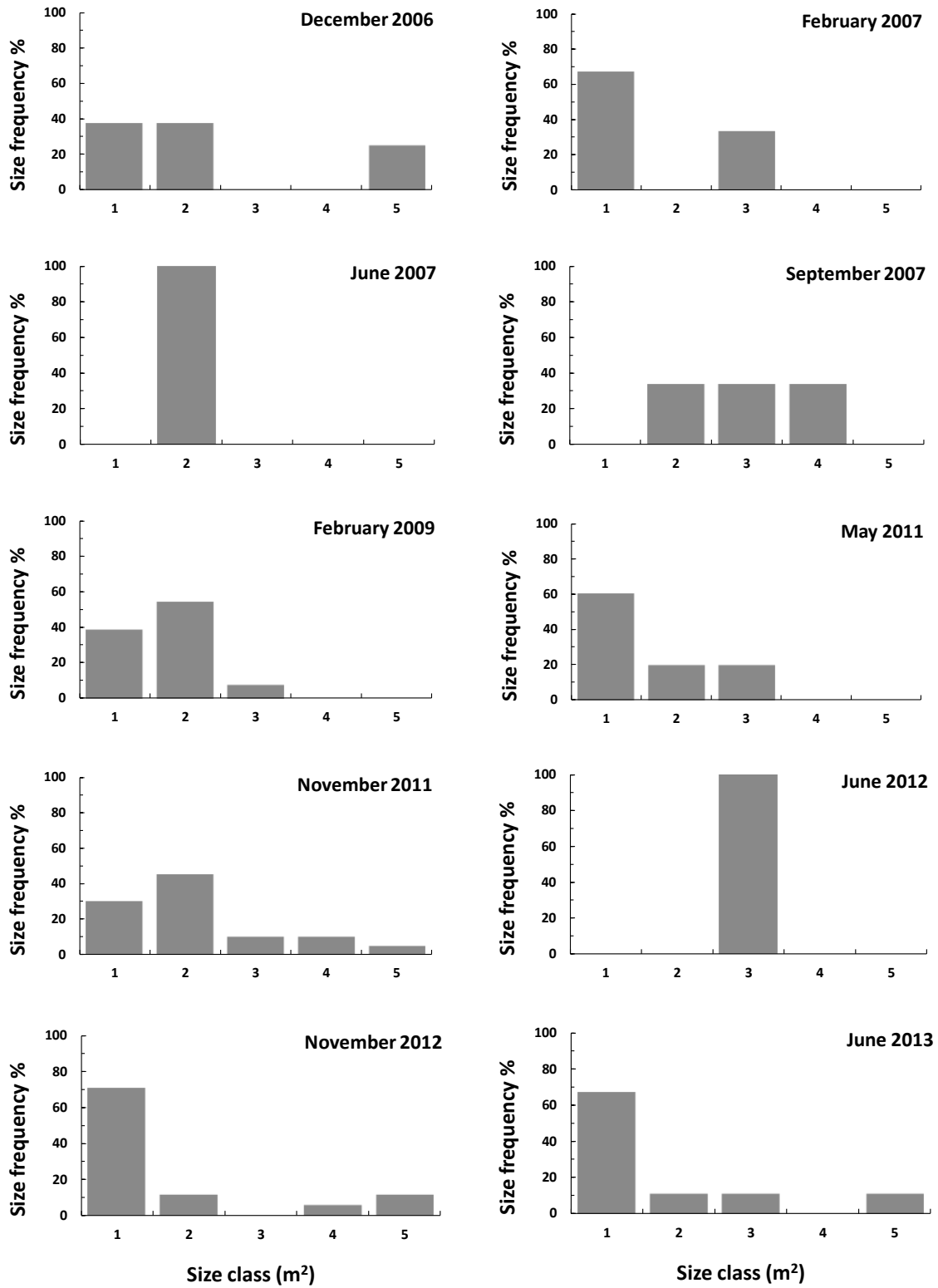


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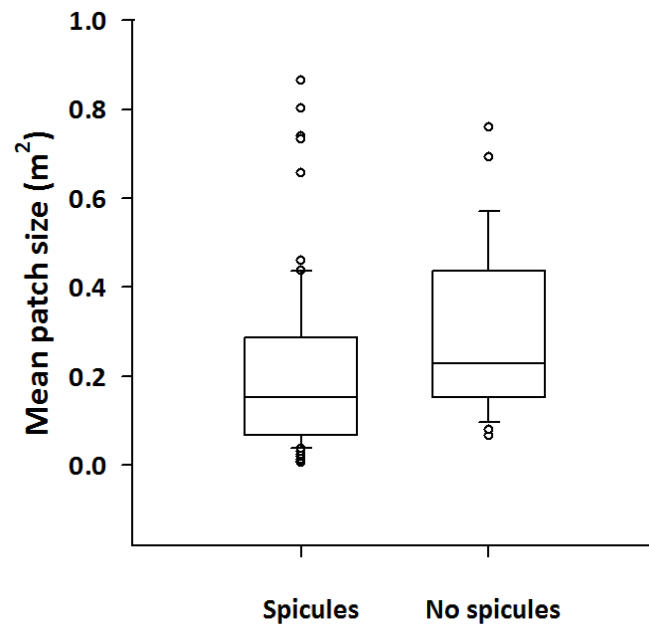


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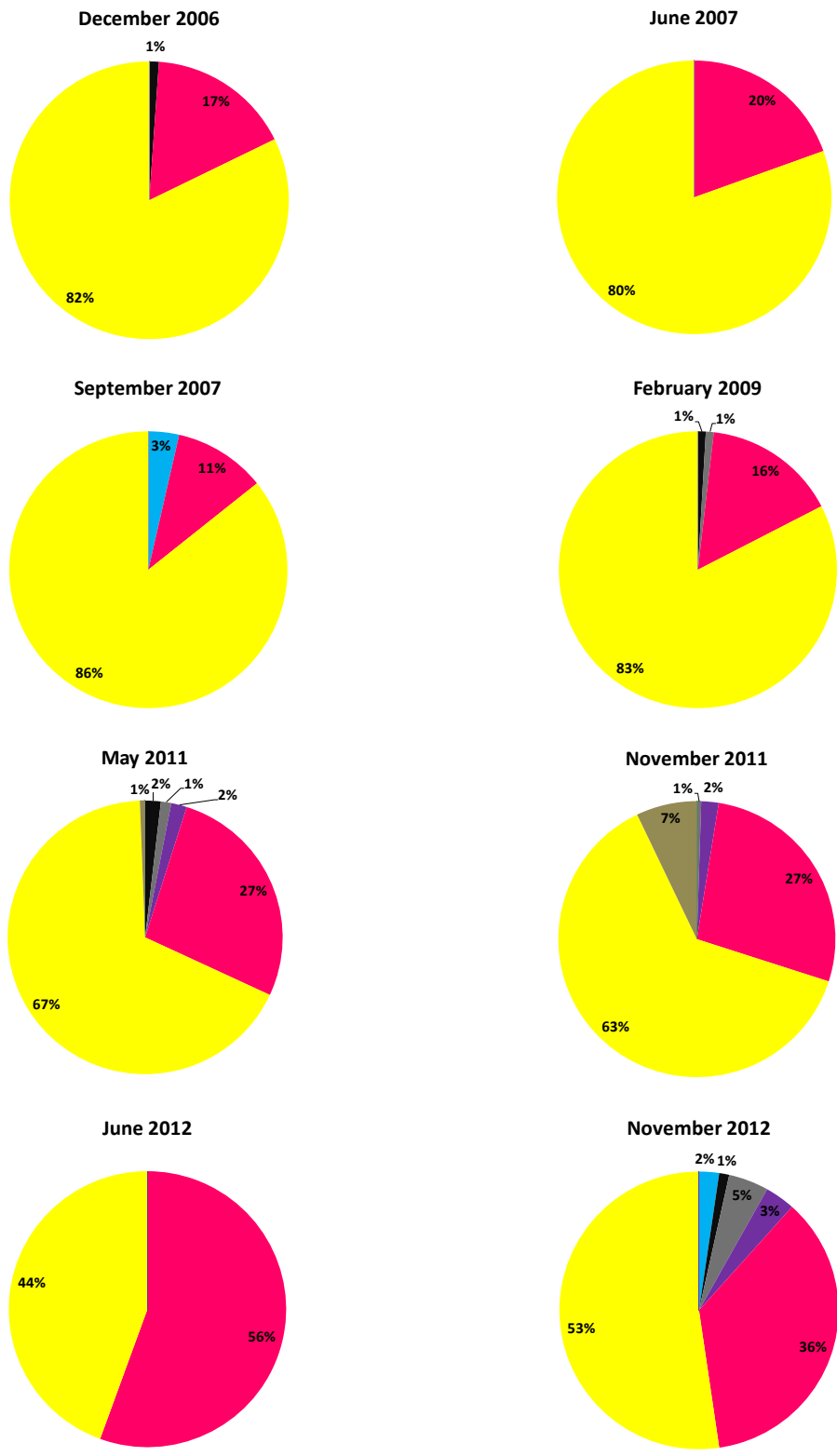


Figure 8

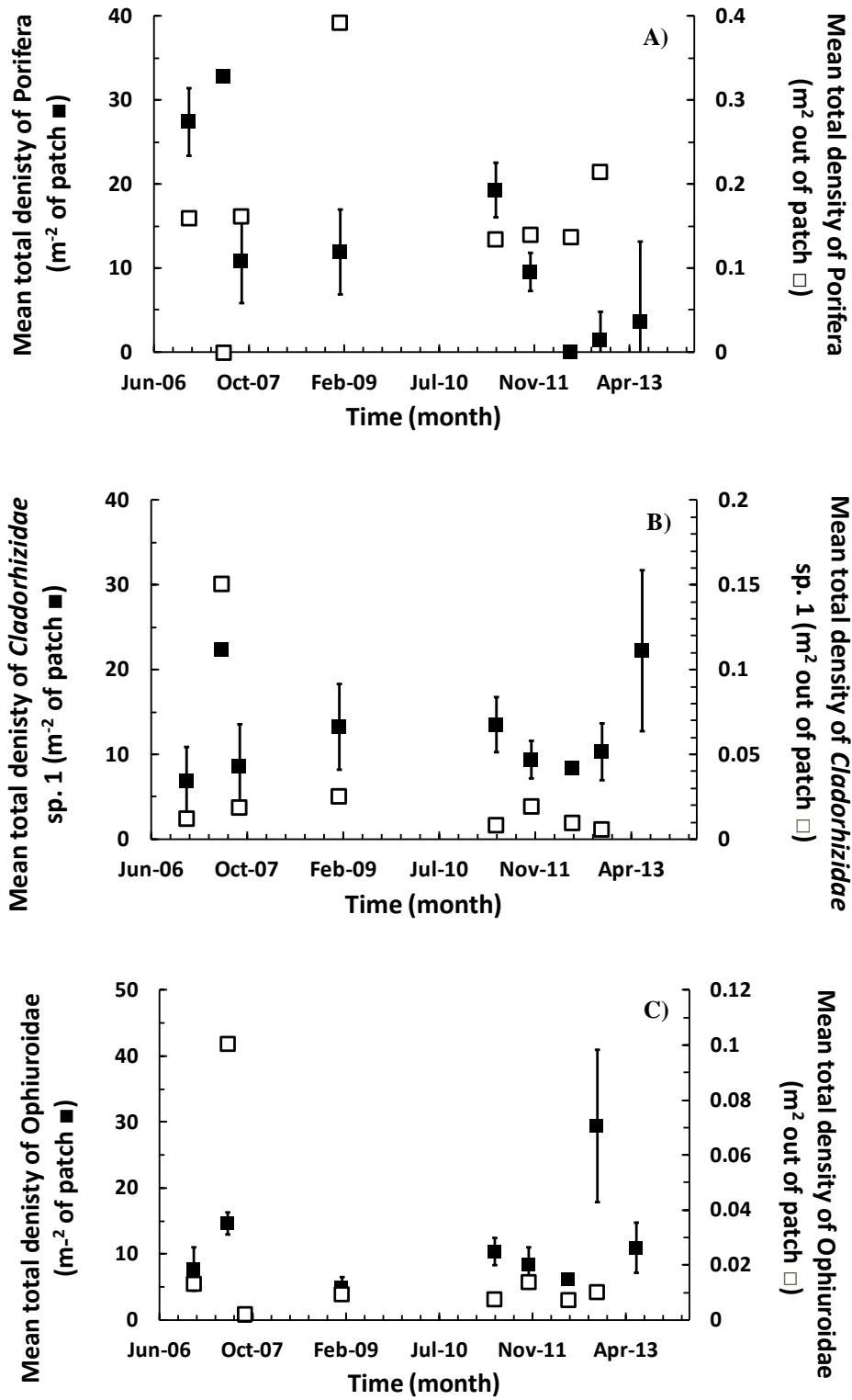


Figure 9

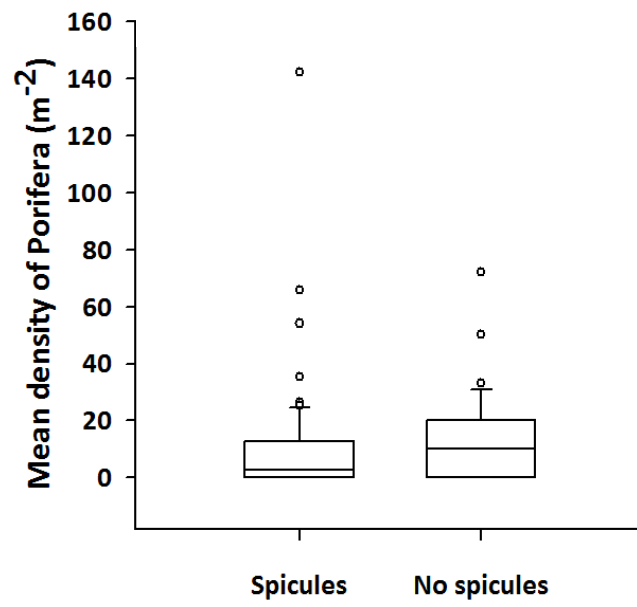


Figure 10

