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Macrofaunal colonization across the Indian Margin oxygen minimum zone

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Abstract

There is a growing need to understand the ability of bathyal assemblages to recover from disturbance and oxygen stress, as human activities and expanding oxygen minimum zones increasingly affect deep continental margins. The effects of a pronounced oxygen minimum zone (OMZ) on slope benthic community structure have been studied in both the Western and Eastern Arabian Sea; however, little is known about the dynamics or resilience of these benthic populations. To examine the influence of oxygen and phytodetritus on short-term settlement patterns we conducted colonization experiments along two cross-OMZ transects on the West Indian continental margin. Four colonization trays were deployed at each depth for 4 days at 542 and 802 m (16°58′ N) and for 9 days at 817 m and 1147 m (17°31′ N). Oxygen concentrations ranged from 0.9 µM (0.02 mL L^{-1}) at 542 m to 22 µM (0.5 mL L^{-1}) at 1147 m. All trays contained local defaunated sediments; half of the trays at each depth also contained $^{13}C/^{15}N$-labeled phytodetritus mixed into the sediments. Sediment cores were collected between 535 m and 1140 m for analysis of background (source) macrofaunal (> 300 µm) densities and composition. Background densities ranged from 0 ind. m^{-2} (at 535–542 m) to 7400 ind. m^{-2}, with maximum values on both transects at 700–800 m. Macrofaunal colonizer densities ranged from 0 ind. m^{-2} at 542 m, where oxygen was lowest, to average values of 142 ind. m^{-2} at 800 m, and 3074 ind. m^{-2} at 1147 m, where oxygen concentration was highest. These were equal to 4.3 % and 151 % of the ambient background community at 800 m and 1147 m, respectively. Community structure of settlers showed no response to the presence of phytodetritus. Increasing depth and oxygen concentration, however, significantly influenced the community composition and abundance of colonizing macrofauna. Polychaetes constituted 92.4 % of the total colonizers, followed by crustaceans (4.2 %), mollusks (2.5 %), and echinoderms (0.8 %). The majority of colonizers were found at 1147 m; 88.5 % of these were *Capitella* sp., although they were rare in the background community. Colonists at 800 and 1147 m also included ampharetid, spionid, syllid, lumbrinerid, cirratulid, cossurid and sabellid polychaetes. Consumption of

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$\delta^{13}C/\delta^{15}N$-labeled phytodetritus was observed for macrofaunal foraminifera (too large to be colonizers) at the 542 and 802/817 m sites, and by metazoan macrofauna mainly at the deepest, better oxygenated site. Calcareous foraminifera (*Uvigerina, Hoeglundina* sp.), capitellid polychaetes and cumaceans were among the major consumers. These preliminary experiments suggest that bottom-water oxygen concentrations may strongly influence ecosystem services on continental margins, as reflected in rates of colonization by benthos and colonizer processing of carbon following disturbance.

1 Introduction

Oxygen minimum zones (OMZs), areas with O_2 concentrations $< 0.5\,mL\,L^{-1}$ (= 22 µM), blanket a significant fraction of the upper bathyal zone along the eastern Pacific, western Africa and north Indian Ocean continental margins, covering over 1 million square km of seafloor (Helly and Levin, 2004). Early studies of these regions revealed distinct macrofaunal assemblages characterized by reduced densities at the lowest oxygen levels and density maxima in the lower OMZ transition zone (reviewed in Levin, 2003). OMZs exhibit a high proportion of annelids and low representation of echinoderms (Levin, 2003) with strong diversity shifts linked to oxygen gradients (e.g., Levin et al., 2009). Within the Indian Ocean, these patterns have been observed on the Oman (Levin et al., 2000) and Pakistan (Hughes et al., 2009; Levin et al., 2009) margins, as well as on the W. Indian margin (Ingole et al., 2010; Hunter et al., 2011, 2012) and in the Bay of Bengal (Gooday et al., 2010; Raman, unpublished data). In most of these investigations oxygen has been shown to be an important factor limiting the density, body size and taxonomic groups of macrofauna found in OMZs. Macrofaunal species richness tends to exhibit a positive correlation with bottom-water oxygen concentration, although organic carbon content exerts strong control on evenness and dominance (Levin and Gage, 1998).

Most studies of OMZ macrobenthos are based on single (or sometimes two) cross-margin transects that provide a static picture of community structure. They do not pro-

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vide information about whether the structural attributes of OMZ assemblages described above are generated at settlement, or involve species interactions and differential mortality that occurs after settlement. Short-term colonization studies can be used to examine settlement potential and preferences as well as successional trends. This approach has been adopted frequently with fouling panels in shallow water (e.g., Pacheco et al., 2010), but is less common in the deep sea.

Information about community dynamics and resilience is taking on added importance as margin ecosystems are increasingly subject to human disturbance (Ramirez-Llodra et al., 2011). Physical disturbance from bottom trawling or proposed seabed mining (e.g., of phosphates) and chemical disturbance from hydrocarbon spills are examples relevant to bathyal margin ecosystems. Expansion and shoaling of oxygen minimum zones in upwelling regions also raises questions about the influence of declining oxygen on the dynamics of deep-water margin assemblages.

Deep-water colonization was originally shown to be a relatively slow process compared to shallow depths (Levin and Smith, 1984; Desbruyeres et al., 1985; Grassle and Morse-Porteous, 1987; Smith and Hessler, 1987). The stability of different patches in the deep sea was thought to allow for more specialization than in shallow water to and promote succession (Snelgrove et al., 1994). Longer-term (6 month to > 1 yr) colonization experiments in the deep sea have been performed to determine which taxa are the most efficient colonizers in a given area and to observe the effect of variable food type (Grassle and Morese-Porteous, 1987), organic matter quantity and quality (Snelgrove et al., 1992, 1994, 1996; Menot et al., 2009), hydrodynamics/current and terrain, (Levin and DiBacco, 1995), and sulfide present in sediments (Levin et al., 2006; Menot et al., 2009).

In contrast to the results of early studies, faunal colonization rates on productive margins or in the presence of enhanced organic matter can be rapid. In situ experiments involving deposition of ^{13}C-labeled phytodetritus demonstrated rapid utilization of organic matter on margins (Blair et al., 1996; Levin et al., 1997, 1999; Witte et al., 2003; Aberle and Witte, 2003; Hunter et al., 2012; Pozatto et al., 2013). In the Northwest

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Atlantic, enriched colonization trays exhibited higher densities than both background sediments and unenriched trays (Desbruyères et al., 1980). The type of food present also affected colonization. Trays containing the diatom *Thalassiosira* attracted significantly more colonists than those containing the seaweed *Sargassum* (Snelgrove et al., 1992, 1994). On the Pakistan margin consumers of phytodetritus varied as a function of oxygen regime (Woulds et al., 2007, 2009), with protists dominating phytodetritus consumption at O_2 concentrations below 0.1 mL L^{-1} (4 µM) and macrofauna dominating at slightly higher oxygen levels. Given the strong influence of oxygen on macrofaunal community structure and trophic functions, we hypothesized that oxygen availability should influence the rate of colonization and the effect of phytodetritus on colonization patterns.

Colonization in the deep sea can be increased by higher sulfide concentrations at cold seeps (Levin et al., 2006), increased time of deployment, increased rate of sediment transport on seamounts (Levin and DiBacco, 1995), increased organic matter (Levin and Smith, 1984), and preferred food types (Snelgrove et al., 1992). Six-month exposures of defaunated sediments in the Pacific have shown recovery rates of 50 to 75 % of background densities (Levin et al., 2006; Levin and DiBacco, 1995), whereas sediment trays collected after only 7 weeks yielded densities as low as 6 % of background levels in coarse-grained seamount sediments (Levin and DiBacco, 1995).

Early experiments in the Atlantic revealed abundant, opportunistic colonizers that were often rare in background (ambient) sediments (Desbruyères et al., 1980; Grassle and Morse-Porteous, 1987; Snelgrove et al., 1992). These included capitellids, hesionids, dorvilleids, spionids, sigalionids, cumaceans and leptostracans. However, colonization experiments in the Pacific Ocean, in the low-oxygen Santa Catalina Basin, yielded assemblages containing a significant proportion of background fauna (Levin and Smith, 1984). On a high-energy seamount in the east Pacific, Levin and DiBacco (1995) found that 95 % of individuals were taxa present in background cores. A six-month experiment on the California margin showed that nearly all of the abundant colonizers were com-

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mon in ambient sediments. However, polychaetes were less abundant in colonization trays than in ambient assemblages (Levin et al., 2006).

This study examines the effects of oxygen and water depth, as well as the presence of phytodetritus, on macrobenthos distributions and colonization patterns across the Indian Margin OMZ. It is unique in documenting the very first steps of recolonization. Trays were deployed on the sea floor for 4 and 9 days while most other deep-water experiments left trays out for 6 months or longer. In this experiment we tested the null hypotheses for macrofauna that (1) oxygen and depth are not correlated with colonizer abundance, composition, diversity and lifestyle and (2) the type and abundance of animals colonizing the trays is unaffected by the presence of phytodetritus. Our alternative hypotheses were that the abundance of organisms would increase with oxygen concentration and depth, there would be a significant difference in community composition between different depths and oxygen concentrations, and that trays containing phytodetritus would support more colonizers. We also examined the density and composition of macrofauna in background sediments along two cross-margin transects to better understand the source assemblage available to colonize the trays.

2 Methods

2.1 Field conditions

Studies were conducted on the Indian margin in October and November 2008 aboard the R/V *Yokosuka* with the submersible Shinkai 6500. Site characteristics are presented in Table 1 and reviewed in Hunter et al. (2011, 2012). Salinity and temperature data were obtained with a Seabird SBE 19 CTD. Temperature ranged from 7.03 to 12.06 °C and salinity ranged from 34.82 to 35.20. Oxygen concentrations were measured with an Aanderaa Optode 3830 mounted on the Shinkai 6500; calibration procedures are described in Hunter et al. (2011). Oxygen ranged from 0.35 µM at 530 m to 21.1 µM at 1147 m (Table 1). Sediments were coarsest (44.5 % sand) with lowest

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organic C content (3.24 %) at the 542 m (Transect 1) site and finest (9.6 % sand) with highest organic C content (5.71 %) at 802 m on Transect 1. The 817 and 1147 m sites on Transect 2 were intermediate (Table 1).

In the study region megafauna and macrofauna are rare at 500–600 m where oxygen concentration is lowest. Megafauna (animals visible in video imagery) exhibit maximum densities at 800 m and decline at greater depths; however mega-infauna and lebensspuren are common only below 1100 m on both transects (Hunter et al., 2011, 2012).

2.2 Colonization experiments

Two cross-margin transects were occupied at slightly different latitudes (Fig. 1). On Transect 1 four colonization trays were deployed for 4 days, from 7–11 October at a depth of 542 m and from 8–12 October at 802 m (Table 1). On Transect 2, four trays were deployed from 23 October to 1 November at a depth of 1147 m and from 24 October to 2 November at 817 m. The colonization trays consisted of an 11.1 cm diameter central cup (9 cm deep) lined with 20 µm mesh, surrounded by a flat delrin nylon collar 40 cm in diameter. The design of the colonization trays is described by Levin and DiBacco (1995) and is identical to those used by Snelgrove et al. (1992, 1994, 1996) in the Atlantic Ocean and Levin et al., (2006, 2013) in the Pacific Ocean. The broad collar is designed to reduce turbulent flow over the central cup and prevent scour. Trays were nestled into sediments such that the sediment surface of the cup and the collar were flush with the surrounding sediment. Trays were covered with water-tight lids during deployment and recovery to prevent loss of sediment.

Among the 4 colonization trays deployed at each depth, two each received additions of freeze-dried phytodetritus, made from the diatom *Thalassiosira weissflogii* labeled with ^{13}C and ^{15}N (see Hunter et al., 2012 for preparation details); the other two had no algae. In preparing the colonization trays, sediments were collected from the study sites by scoop and stored on board ship at −80 to −20 °C for 1–3 days. They were then thawed on deck at 30 °C and sonicated for 5 min to destroy foraminifera and metazoans.

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Algae was mixed in 50 cc tubes with ~50 cc of mud and spread on the tray surface immediately before deployment in a 0.25 mm-thick surface layer. The trays contained additions equivalent to ~500 mg C m^{-2}, roughly the C input for a single year at the 500 m site. These doses were similar to those used in experiments on the Pakistan margin (e.g., Woulds et al., 2007) and reflect the pulsed nature of natural organic matter delivery in the Arabian Sea. Sediment-filled trays were recovered and the cup contents were sectioned vertically at 0–1, 1–2, 2–3, and 3–5 cm. All samples were preserved in 8 % buffered formalin.

2.3 Background faunal collection

Background fauna were collected in October and November 2008 using 8.3 cm diameter tube cores deployed from the Shinkai submersible (Table 2). Samples from Transect 1 (16°58′ N, 71°55′ E) were collected roughly 100 km southeast of Transect 2 (17°31′ N, 71°10′ E) (Fig. 1). Pairs of cores were taken by the Shinkai 6500 at a range of depths between 500 and 1150 m. Tube core sediments were sectioned vertically on board ship at 0–1, 1–2, 2–3, 3–5, and 5–10 cm intervals and fauna were preserved in 8 % buffered formalin. All fractions were sieved in the laboratory on a 300-µm mesh and macrofauna were removed from retained sediments under a dissecting microscope. Animals were counted and identified to the lowest taxon possible.

2.4 Shipboard and laboratory analyses

The upper fractions were sieved in the lab through a 300-µm mesh to separate out macrofauna and through a 45-µm mesh to retain smaller organisms for later meiofaunal studies. Macrofauna were sorted under a binocular microscope, counted, and identified to the lowest taxon possible. Colonization tray samples were sorted to consecutive 1-cm depth fractions until no more animals were present. All trays from Transect 1 and the 800 m trays from Transect 2 were thus sorted to only 2 cm, as no animals were present below the 1st cm. The 1147 m trays from Transect 2 were sorted to 3 cm (2

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trays) and 5 cm (2 trays.) Isotope analysis was performed on the organisms found in trays to determine which taxa consumed phytodetritus.

2.5 Statistical testing

Multivariate community analysis was performed using Primer software V. 6. Bray–Curtis similarity indices were used to create similarity matrices from untransformed family abundance values. Differences in community composition are presented in MDS plots. ANOSIM and SIMPER were used to measure sources and statistical significance of the differences in community composition between depths, high and low oxygen concentration, transect, the presence of algae, and between colonizer and background communities. The differences between the proportion of polychaetes and between densities of colonizer and background fauna at a given depth were measured by performing one tailed *t* tests using JMP software.

2.6 Stable isotope analyses

Macrofauna from background sediments were sorted, identified and frozen on board ship, prior to stable isotope analyses. Foraminifera from the 0–1 cm fraction in 542 m and 802 m trays on Transect 1 were also sorted and frozen on board. Isotopic analyses of macrofaunal tray colonizers were performed after animals had been preserved in 8 % buffered formalin, as it was not possible to process them all at sea. Formalin introduces minimal alteration of isotope signatures, with shifts in δ^{13}C of −0.5 ‰, and δ^{15}N of +0.14 ‰ (Levin et al., 2006). In contrast, uptake of isotopically labeled algae (with δ^{13}C and δ^{15}N values greater than 50 000 ‰) creates a signature in consumers that is many orders of magnitude larger than the small formalin shift. Infauna were handled with methanol-dipped forceps, rinsed in Milli-Q water, and placed in preweighed tin boats. Multiple individuals were combined for small taxa. Specimens were dried, weighed on a Sartorius CP2250 and then, prior to δ^{13}C and δ^{15}N analysis, they were acidified with one drop of 1 % $PtCl_2$ to remove inorganic carbon. Samples were run on

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a Costech elemental analyzer interfaced with a continuous-flow Micromass Isoprime isotope ratio mass spectrometer at Washington State University (by R. Lee), Isotope ratios are expressed as δ^{13}C or δ^{15}N in units of per mil (‰). Standards were PeeDee Belemnite for δ^{13}C and nitrogen gas for δ^{15}N (atmospheric).

3 Results

3.1 Colonizer and background densities

Rates of macrofaunal colonization were greater where oxygen was higher on both transects. On Transect 1 after 4 days exposure, no metazoan macrofaunal individuals were found in trays at 542 m depth; this is consistent with the absence of metazoan macrofauna at a comparable depth in background sediments (Figs. 2, 3). Average colonizer density was 258.3 m^{-2} at 802 m on Transect 1 after 4 days and an order of magnitude lower (25.8 ind. m^{-2}) at 817 m on Transect 2 after 9 days (Table 2). The colonizer densities were 10.7 % and 0.62 % of background densities for Transects 1 and 2, respectively (Fig. 2), but significantly lower than background densities only on Transect 1 (P = 0.012) and not on Transect 2 (P = 0.110). Colonizer densities were considerably higher (3074.3 ind.m^{-2}) at 1147 m on Transect 2; they were approximately 151 % of background density but not significantly different (P = 0.39) (Fig. 2). Overall, colonization densities were over 20× higher at 1147 m than 802–817 m (t_{10} = 4.11, P = 0.002). Metazoan macrofaunal densities in background sediments were zero from 500–550 m, increased from 575 to 700 m to > 4000 ind. m^{-2}, then declined with fairly constant low levels from 900–1050 m (ind. m^{-2}) (Fig. 3). Background metazoan macrofaunal densities at the colonization tray depths were 2405 ± 506 ind. m^{-2} at 800–835 m Transect 1, 4163 ± 1572 ind. m^{-2} at 800–816 m on Transect 2 and 2035 ± 0 ind. m^{-2} at 1147 m on Transect 2. General density trends with depth across the two transects were similar (Fig. 3).

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3.2 Colonizer and background composition

Polychaetes were the dominant taxon in background sediments at all depths from 575 m to 1150 m (Table 3). They comprised 100 % of the fauna at 575 m and declined in proportion to only 50 % at 800–900 m, where Mollusca, Crustacea and Echinodermata became abundant (Fig. 4).

Polychaetes comprised the majority (93.8 %) of the 151 colonizers documented in this study (Table 4). The remaining colonizers were molluscs (2.3 %), crustaceans (3.1 %), echinoderms (0.8 %) and a single turbellarian and sipunculan (Table 3). Of the colonizing polychaetes, 85 % were in the family Capitellidae; all of these were found at 1147 m. This family of polychaetes was not collected from background sediments at 1147 m, but was present at low densities (103.3 ind. m^{-2}) in background sediments at 802 m on Transect 1 and at 930 m on Transect 2.

Calcareous foraminifera were present in trays at 542 m. However, they were not quantified because they were too large to have been colonizers and, in most cases, it was not possible to determine whether they were alive or dead in sediments at the time of tray deployment. However, those individuals that had taken up labeled ^{13}C and ^{15}N were presumably alive. No macrofauna were recovered in trays or background sediments at 542 m (Table 3).

Colonizers at 802–817 m exhibited extremely low densities and diversities in this experiment. Of the 10 macrofaunal animals present in the 802 m colonization trays on Transect 1, five were polychaetes, one was a turbellarian, one a sipunculan and the other three were mollusks (Fig. 5b; Table 4). Two of the polychaetes in these four trays were cirratulids. The other five polychaetes at this site each represented a different family. Only a single polychaete specimen was present in the 817 m colonization trays on Transect 2 (Table 4). Thus, in total, seven polychaete families, most represented by a single individual, were represented in the eight 800 m trays; none of these were found in sediment trays at 1147 m (Fig. 6). In background sediments at 800–835 m, polychaetes, crustaceans, mollusks, and echinoderms were all well represented. Poly-

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chaetes accounted for 55.6 % of macrofauna, mollusks accounted for 22.2 %, crustaceans for 13.3 %, and echinoderms for 8.9 % in background sediments at 817 m Transect 2 (Fig. 5c).

Over 95 % of the 120 individuals colonizing sediment trays at 1147 m were polychaetes. Although the proportion of polychaetes was higher than in the background sediments (59 %), densities were not significantly greater ($P = 0.115$) (Fig. 4). Of the colonizing polychaetes at this depth, Capitellidae accounted for 90.4 % (Fig. 6). Also present were Spionidae (7 %), Ampharetidae (1.7 %), and Syllidae (0.9 %). Most of the polychaete families found in colonization trays were also present in background sediments at this depth; *Capitella* was a notable exception. Background sediments at 1147 m contained 36.4 % crustaceans, compared to only 3.33 % crustaceans in colonization trays (Fig. 5).

Multidimensional scaling analysis of tray colonizers revealed a significant difference in community composition between the 802/817 m and 1147 m sites ($R = 0.50$; $P = 0.024$); these sites also represent lower and higher oxygen availabilities, respectively (Fig. 7b). There was a significant difference in composition between colonization tray and background fauna ($R = 0.263$: $P = 0.002$; Fig. 7a) as well as between colonizers at all depths on the two transects ($R = 0.50$; $P = 0.024$; Fig. 7c).

Species richness of tray colonizers was higher at 1147 m (3.75 ± 0.78 spp./tray) than at 802–817 m (1.38±0.55 spp./tray) ($t_{10} = 2.47$; $P = 0.033$) (Table 4). Background cores (54 cm^2), roughly 2/3 the area of the colonization trays, exhibited average species richness per core of 0.0, 8.25 ± 1.25, and 7 ± 1.0 at 535–542 m, 800–817 m, and 1147 m, respectively (Table 3). Thus, the order of magnitude oxygen differences between 800 and 1150 m did not appear to affect local background richness, based on the limited number of cores examined.

3.3 Phytodetritus effects

The presence of ^{13}C-labeled phytodetritus did not appear to influence the density, composition, or species richness of macrofaunal colonizers (Table 4, Fig. 8a, b). At 802 m

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on Transect 1, faunal density in trays without labeled phytodetritus was double that of trays with labeled phytodetritus. At 817 m on Transect 2, the single colonizer entered a tray with no labeled phytodetritus, but at 1147 m on Transect 2 trays with labeled phytodetritus exhibited a density 1.3 times that of trays without phytodetritus (Fig. 8a). In all instances sample size ($n = 2$ per treatment at each depth) was too small to evaluate the significance of phytodetritus presence. Notably, *Capitella* sp. did not respond positively to the phytodetritus.

Two of the three animals found in trays with labeled phytodetritus at 802 m on Transect 1 were mollusks and one was a polychaete. These numbers compare with four polychaetes, one turbellarian, one sipunculan and one gastropod in the two trays without added algae. At 1147 m, polychaetes represented 94.1 % ($n = 68$) of the fauna in trays with labeled phytodetritus and 98.1 % ($n = 52$) in trays without labeled phytodetritus. Crustaceans comprised 4.4 and 1.9 % of colonizers in trays with and without labeled algae, respectively (Table 4, Fig. 8b). Trays with phytodetritus collected fewer species than trays without phytodetritus at 802–817 m (3 vs. 7 species) but had similar richness at 1147 m, (6 vs. 5 species) (Table 4). There were no significant differences in species richness between trays with and without phytodetritus but sample sizes were small. Notably, cumaceans and ophiuroids appeared only at the deepest station, in trays with phytodetritus.

3.4 Phytodetritus ingestion by colonizers

The stable isotopic signature of the phytodetritus added to colonization trays was $\delta^{13}C = 50\,626$ ‰ and $\delta^{15}N = 57\,190$ ‰. Although no metazoan macrofauna colonized trays with algae at 542 m, several species of calcareous foraminifera, which were too large to have been colonizers, appeared to have consumed labeled phytodetritus in colonization trays at this depth (Table 5). Greatest uptake at 542 m was by *Hoeglundina* sp. ($\delta^{13}C = -11.6$ ‰, $\delta^{15}N = 712$ ‰; $n = 1$) and *Uvigerina* sp. ($\delta^{13}C = -13.5$ ‰ and $\delta^{15}N = 368$; $n = 3$), with little evidence of phytodetritus uptake by *Lenticularia* sp. ($\delta^{13}C = -8.1$ ‰, $\delta^{15}N = -1.44$ ‰; $n = 2$). However, *Lenticularia* sp., and several other

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taxa including *Hoeglundina* sp., *Chilostomella,* and/or *Globobulimina* and an unidentified tubular form, appeared to ingest labeled phytodetritus at 802 m (Table 5, Fig. 9). No isotope data are available for the 817 m trays.

For metazoan macrofauna colonizing trays with labeled algae, the consumption of labeled phytodetritus and thus the departure from background isotopic signatures was greater at 1147 m than at the 802 m station (Table 5; Fig. 9b). The mean (±1 SE) isotopic signatures of background macrofauna at 802 m was $\delta^{13}C = -18.98 \pm 2.87$ ‰ and $\delta^{15}N = 7.1 \pm 4.1$ ‰. In 802 m trays without phytodetritus, the mean isotopic signature of colonizers was -23.4 ± 0.9 ‰ and 4.0 ± 1.3 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. In 802-m trays with phytodetritus the respective macrofaunal signatures were $\delta^{13}C = -21.0 \pm 4.2$ ‰ and $\delta^{15}N = 5.6 \pm 0.65$ ‰. The 802 m trays with algae only had a gastropod and sabellid polychaete; these did not appear to take up any algae (Table 5). The one specimen colonizing at 817 m was not assayed for stable isotopes. Of the colonizers examined from 1147 m trays, 89 % had $\delta^{15}N$ above background levels and 44 % had $\delta^{13}C$ above background levels (Table 5). Mean isotopic signatures of colonizers at 1147 m were $\delta^{13}C = 980.3 \pm 1845.5$ and $\delta^{15}N = 1439.4 \pm 3382.7$ for trays containing labeled phytodetritus and $\delta^{13}C = -22.4 \pm 1.3$ and $\delta^{15}N = 8.8 \pm 2.6$ for trays without phytodetritus. All of the colonizing capitellid polychaetes tested from trays with phytodetritus had $\delta^{13}C$ signatures above background levels. The highest label uptake was by a capitellid ($\delta^{13}C = 5384.5$ ‰) and a cumacean ($\delta^{13}C = 2530.4$ ‰). Two spionids and an amphipod did not take up labeled phytodetritus in trays at 1147 m.

4 Discussion

In this experiment we examined how colonizer density and composition differed at three water depths and oxygen levels, and explored the possible influence of phytodetritus on the type and abundance of colonizing invertebrates. We initially hypothesized that the abundance of organisms would increase with oxygen and depth, there would be a significant difference in community composition among stations, and that trays containing

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phytodetritus would support more colonizers. Our limited results suggest that oxygen exerts a strong effect on macrofaunal abundance and community composition, with core OMZ values of 0.7 µM O_2 at 542 m (Transect 1) inhibiting macrofaunal colonization completely. Colonizers were more abundant, with higher species richness at the better-oxygenated 1147 m station than at 802–817 m. While the labeling experiments indicate that many colonizers are capable of consuming phytodetritus, the presence of the algae did not unidirectionally affect density or composition of tray colonizers.

Sample sizes in this study were very small and experimental duration was very short. These were constrained by limited dive time and access to the sites. However, they provide a first glimpse into the dynamics of recolonization over very short periods in oxygen minimum zones. Such information is highly relevant to understanding consequences for benthic ecosystems of expanding oxygen minimum zones (Stramma et al., 2008, 2010) and the management of human-made disturbance such as might result from bottom trawling or phosphate mining, both of which occur on OMZ margins.

4.1 Density: background vs. colonizers

Density recovery rates in this study were fast at depths with higher oxygen, relative to other experiments with significantly longer duration. At 1147 m (this study) the density of animals in colonization trays on the Indian Margin (3074.3 m^{-2}) overshot ambient densities, reaching 150 % of background sediment after only 9 days. At methane seeps on the Northern California margin (525 m), densities returned to only 50 % (6827 ± 753 ind.m^{-2}) of background levels after 6 months in similar colonization trays (Levin et al., 2006). A similar result was found on Fieberling Guyot in the Eastern Pacific Ocean (585–635 m), where recovery was 50 % (~ 700 ind. m^{-2}) and 75 % (~ 1250 ind. m^{-2}) of background densities after 6 months (Levin and DiBacco, 1995).

However, other studies have recorded similar density overshoots. A 6 month study in the Bay of Biscay recorded colonizer densities 5 times higher than those in background sediment (Desbruyères et al., 1980, 1985). The background density on the Indian Margin was notably lower than in the Bay of Biscay experiments. Other relatively

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short-term colonization experiments using a similar tray apparatus have yielded a variety of results. In a 23 day experiment in the Northwest Atlantic, macrofaunal densities in *Thalassiosira* and *Sargassum*- enriched trays reached 66 450 ind. m^{-2} and 16 000 ind. m^{-2}, respectively, greatly exceeding background densities (Snelgrove et al., 1994, 1996). However, the unenriched controls did not exhibit the same background density overshoot seen in the enriched trays (Snelgrove, 1994, 1996). Macrofauna on the Indian Margin exhibited a density overshoot at 1147 m but it was not correlated with the presence of phytodetritus and the overshoot was not as extreme as that observed in the Snelgrove et al. and Desbruyeres et al. studies. Short-term experiments deployed on Fieberling Guyot for 7 weeks in the eastern Pacific Ocean showed recovery rates of 31 % (~ 700 ind.m^{-2}) and 6 % (~ 120 ind.m^{-2}) at two different sites with different energy regimes (Levin and DiBacco, 1995).

We observed slow recovery rates at the shallower, oxygen-deprived depths of 802 m (1.2 µM O_2) and 817 m (2.2 µM O_2). Densities were 10.7 % and 0.62 % of background densities, respectively. Trays left at 802 m were deployed for only 4 days, a duration much shorter than in other studies. With only one exception (Snelgrove et al., 1994, 1996) no other published study has tested colonization trays in the deep sea for less than a month. This short duration is one factor that could explain the low colonizer density relative to the background conditions. Low oxygen is another factor that may explain this. On the West African Margin, macrofaunal densities were positively correlated with organic enrichment except where anoxia imposed harmful conditions for colonists. Experiments left for 283–433 days on the lower slope acquired macrofaunal colonizers that never exceeded half the density of those in background sediments, and were an order of magnitude lower than at shallower depths (1300 m) (Menot et al., 2009).

4.2 Composition

Colonization trays yielded a different assemblage of taxa compared to that found in background cores at corresponding depths. Colonization trays at 802 m on Transect

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1 contained 1 bivalve and 2 gastropods; these accounted for 30 % of the 10 animals colonizing. However, no mollusks were collected in background sediment at that depth, although sampling was limited. The proportion of polychaetes was 92 % in background sediment and 70 % (7 individuals) in colonization trays. This resembles the trends obtained by Levin at al. (2006) at a methane seep on the Northern California margin, where polychaetes represented 57 % of ambient and only 27 % of colonization tray fauna. The background fauna obtained at 817 m on Transect 2 was among the most diverse and abundant of any depth (Table 3). In contrast, within all 4 colonization trays only a single adult lumbrinerid was found. At 1147 m, trays were strongly dominated by juvenile capitellid polychaetes.

Capitellids alone reached an average density of 2686 ind. m^{-2} in 1147 m trays, whereas macrofauna in background sediments at that depth were dominated by syllid and paraonid polychaetes, amphipods, and tanaids, and contained no Capitellidae. *Capitella* is an opportunistic genus and will rapidly colonize disturbed sediments (Grassle and Grassle, 1976). Off West Africa, Capitellidae appeared at 1300 m and 4000 m in enriched colonization trays, but were not exceptionally dominant (Menot et al., 2009). In an experiment in the Northwest Atlantic (900 m), capitellids accounted for half the animals in algae-enriched colonization trays after 23 days, but were absent in unenriched trays (Snelgrove et al., 1996). Capitellidae were also dominant in an experiment conducted south of New England at 1800 and 3600 m. They were among the three most consistent colonizers and proved to be the most responsive to organic enrichment after 2 months (Grassle and Morse-Porteous, 1987). On the West India margin we did not observe the same discrepancy between trays with phytodetritus and without. Capitellidae represented 83.8 % of the macrofauna in trays with algae and 90.4 % in trays without (Fig. 6b).

While most of the species in colonization trays did not match those found in background cores of the same depth, all of the polychaete taxa found in trays were present at some depths in India margin background sediments. These may have entered trays as planktonic larvae or resuspended individuals advected from other depths. It is also

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possible that we undersampled the background macrofaunal diversity, creating the appearance of a distinct disturbance colonizer fauna. The increasing incidence of large epifauna at greater depths and higher oxygen levels (Hunter et al., 2011) may have favored subsurface feeders like *Capitella* sp.

4.3 Phytodetritus consumption

Algae labeled with ^{13}C and ^{15}N was added to colonization trays to determine which animals consume phytodetritus. The greatest uptake occurred at 1147 m where oxygen was highest; capitellid and spionid polychaetes and a cumacean ingested labeled phytodetritus, with $\delta^{13}C$ values as high as +5384.5 ‰ observed after 9 days. But not all taxa took up the isotopic label; one spionid and an amphipod did not. Annelids exposed to labeled phytodetritus on the North Carolina slope at 850 m exhibited $\delta^{13}C = -10$ to +3870 ‰, values significantly higher than that of background sediments ($\delta^{13}C = -17.4$ to −23.5 ‰) (Blair et al., 1996), but non-annelid metazoans were slower to consume phytodetritus (Levin et al., 1999).

Our study, like others (Snelgrove et al., 1994, 1996), revealed large label uptake for cumaceans. In the NE Atlantic, Aberle and Witte (2003) found that the primary families to take up the labeled phytodetritus were Cirratulidae and Spionidae. The elevated role of these animals in the consumption of phytodetritus was attributed to their surface-deposit feeding lifestyle. The Capitellidae that were so abundant in our study are traditionally considered to be subsurface-deposit feeders. However, Levin et al. (2006) demonstrated that capitellid polychaetes can readily obtain carbon from labeled plant phytodetritus in shallow water. On the North Carolina slope (850 m), only 25 % of capitellids showed an increase in $\delta^{13}C$ after 14 months of exposure to ^{13}C labeled phytodetritus, while 100 % of cirratulids showed a response after the same amount of time (Levin et al., 1999). A similar result was also found in a Norwegian Fjord (688 m) where capitellid polychaetes showed little algal consumption after exposure to labeled algae for 2 to 14 days (Sweetman and Witte, 2008). While most of the capitellid individuals in our study exhibited an increased $^{13}C/^{12}C$ ratio, all Capitellidae had even more

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elevated $^{15}N/^{14}N$ ratios (Table 5). This suggests that ^{15}N might be a more sensitive and reliable tracer for phytodetritus use than ^{13}C; possibly it leaches from detritus into the dissolved organic matter pool and is quickly used by heterotrophic bacteria and then consumed by *Capitella* sp. Alternatively C may be respired more readily than N, which could be sequestered within tissues. At 1147 m one of the spionids had an elevated $^{15}N/^{14}N$ ratio but the other was not significantly different than those in background macrofauna or unlabeled trays. A high degree of variation in mean isotopic signatures between taxa and even families is typical for phytodetritus labeling experiments (Aberle and Witte, 2003; Levin et al., 1997, 1999, 2013).

During the same cruise, comparable replicated isotope tracing experiments ($n = 3$) using the same labeled phytodetrital material were carried out directly on sediment in order to investigate rates and pathways of OM processing by the established macrofaunal community (Hunter et al., 2012). In these experiments, macrofauna was absent at 540 m, and polychaetes were the most abundant taxon at the other three stations, with cirratulids and sabellids most abundant at 800 m on Transect 1, and oweniids and cirratulids most abundant at 800 m and 1100 m on Transect 2. In contrast to the colonizer community, C and N uptake by the established macrofauna community was dominated by cirratulids at both 800 m stations. At the 1100 m station, the majority of C and N uptake was spread more evenly among three polychaete families. In this study, only one individual of the genus *Capitella* was found in the mature community at 800 m on Transect 1 (Hunter et al., 2012), suggesting that patterns of OM processing are likely to differ significantly during the transition from a pioneering to mature community.

Research by Woulds et al. (2007, 2009) on the Pakistan margin has shown significant effects of oxygen on the taxa responsible for phytodetritus processing. Protists (foraminifera) dominate phytodetritus consumption at oxygen concentrations below 5 µM whereas metazoan macrofauna dominate at higher oxygen levels. Protists were not quantified in our experiments, but they were present in trays at 542 and 802 m and clearly took up labeled N and C, whereas metazoan phytodetritus uptake was significant only at higher oxygen levels. Where the foraminifera in the recolonization trays

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originated from is unclear. They are relatively large calcareous species that were retained on a 300-µm mesh sieve. Macrofauna-sized agglutinated foraminifera were reported from colonization trays by Kaminski et al. (1988), but these experiments were conducted over a 9-month time period. It would be impossible for individuals of this size to develop from colonizing propagules or juveniles within a period of days. There are several other possible explanations: the foraminifera may have crawled into the trays across the flat collar, been resuspended and wafted into the trays during submersible operations, or they survived freezing at −20 °C and sonication. Whatever their origin, the fact that they took up the label from phytodetritus demonstrates that they were alive during the experiment.

4.4 Effects of phytodetritus on density and composition

We observed no significant effect of phytodetritus additions on the density or composition of colonizers, which were similar in trays with and without phytodetritus additions. In earlier enrichment studies in the Northwest Atlantic (Snelgrove et al., 1992, 1994, 1996) and off southern California (Levin and Smith, 1984), unenriched trays never attained ambient densities and enriched trays greatly exceeded ambient densities. Opportunistic colonizers have been shown to respond more rapidly in situations with organic enrichment (Smith and Hessler, 1987). In our experiments, additions were designed to detect phytodetritus consumption rather than enhance organic matter availability. Thus the addition of phytodetritus represented a $< 1\,\%$ enrichment of carbon in the surface 1 cm of sediment. Nevertheless, similar organic matter additions have prompted benthic community responses in previous studies. This may have been partly due to the freshness or high "food quality" of added algal detritus compared to that which normally arrives at the deep-sea floor (e.g. Woulds et al., 2007). However, the lack of response observed in our colonization trays is consistent with a study done beneath the West African Margin OMZ, where macrofaunal densities were not positively correlated with organic enrichment when oxygen was limiting for colonists (Menot et al., 2009).

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4.5 Factors influencing colonization

As shown by Grassle and Morse-Porteous (1987), deployment time may be critical in determining the density and composition of the colonizers. Colonizers that respond rapidly to organic enrichment may be present after 2 months but could get outcompeted after 10 months. The time range of 4 to 9 days does not reveal the complete successional response.

Recolonization of natural sediment has been shown to occur more readily than in trays with prefrozen sediment and also to attract an assemblage of macrofauna more similar to background assemblages (Smith, 1985). The heavy colonization of the 1147 m trays by *Capitella* is consistent with past observations of *Capitella* as a disturbance opportunist (Grassle and Morse-Porteous, 1987; Snelgrove et al., 1994, 1996) that is rare in undisturbed background sediments in deep water. In a 6-month experiment, colonization of trays containing coastal sediment was 1/3 that of trays with sediment from the abyssal depths where the experiment took place, despite higher OM content in the coastal sediment (Desbruyères et al., 1980). Colonization trays have been posited to cause altered hydrodynamics and isolation, as well as having an arbitrary size (Smith, 1985). Although the trays used here are hydrodynamically unbiased and scour was limited, the tray design may exclude species that "crawl" within a limited area and preferentially select those settling or advected from the water column. This may contribute to differences between background fauna and colonizers.

5 Conclusions

This study was the first to examine the effects of reduced oxygen concentration on continental slope early colonization and to draw comparisons to background density and composition. Few colonization experiments have been conducted in the Indian Ocean; most experiments of this type have been conducted in the Pacific and Atlantic Oceans. This study was also unique in that deployment times were shorter than in any

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other reported deep-water colonization experiment. Results indicate the potential for rapid colonization by opportunists if oxygen is sufficient. As little as 9 days is enough time to overshoot background density by 150 %. Most colonizer taxa were present in background sediments.

Understanding of colonization dynamics and ensuing succession is important for management of areas subject to human disturbance. Trawling, oil spills, or submarine mining can all create scenarios in OMZs where colonization after disturbance occurs. Additional research is needed to address subsequent changes in colonizer assemblages over time, and to further explore spatial variation in colonization trends across hydrographic gradients, as well as the consequences for ecosystem services.

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Table 1. Depth, location, physical characteristics and colonization tray deployment information for experiments conducted on the W. India margin. Temperature, salinity and % POC data are taken from Hunter et al. (2012); these authors made measurements at identical study sites at the same time.

Depth (m)	Transect	Latitude	Longitude	Temperature °C	Salinity	Percent Sand	Percent Corg	Oxygen ($mL L^{-1}$)	Tray Numbers	Deployment Dates (2008)	Exposure Period (d)
540	1	16°58.82′ N	71°55.32′ E	12.06	35.20	44	3.24	< 0.01	A1, A2,A3, A10	7–11 Oct	4
802	1	16°58.73′ N	71°52.04′ E	9.99	35.09	9.6	5.57	0.025–0.055	C5, C6, C7, C	8–12 Oct	4
817	2	17°31.49′ N	71°10.4′ E	9.88	35.09	26.8	4.04	0.052	11b, 13b, 14, 15	23 Oct–1 Nov	9
1147	2	17°31.45′ N	71°5.04′ E	7.03	34.82	15.7	4.34	0.48	5b, 6b, 7b, 8b	24 Oct–2 Nov	9

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Table 2. Date, dive number, depth and location of background sediment cores collected for macrofaunal analysis. Each row reflects a single core.

Date	Dive No.	Depth (m)	Latitude	Longitude
TRANSECT 1			°N	°E
6 Oct 2008	1103	535	16°58.77′	71°55.41′
7 Oct 2008	1104	542	16°58.82′	71°55.32′
7 Oct 2008	1104	542	16°58.82′	71°55.32′
4 Oct 2008	1102	602	16°58.82′	71°54.63′
4 Oct 2008	1102	602	16°58.82′	71°54.63′
3 Oct 2008	1101	710	16°58.67′	71°53.24′
3 Oct 2008	1101	712	16°58.67′	71°53.24′
3 Oct 2008	1101	800	16°58.60′	71°52.06′
8 Oct 2008	1105	802	16°58.71′	71°52.04′
2 Oct 2008	1100	835	16°58.90′	71°51.96′
2 Oct 2008	1100	835	16°58.90′	71°51.96′
2 Oct 2008	1100	900	16°58.98′	71°51.13′
1 Oct 2008	1099	1000	16°58.97′	71°49.93′
1 Oct 2008	1099	1100	16°58.89′	71°48.58′
TRANSECT 2			°N	°E
8 Nov 2008	1123	575	17°33.33’	71°11.55’
8 Nov 2008	1123	575	17°33.33’	71°11.55’
8 Nov 2008	1123	650	N/A	N/A
28 Oct 2008	1117	693	17°32.19’	71°10.61’
28 Oct 2008	1117	746	17°31.99’	71°10.52’
28 Oct 2008	1117	746	17°31.99’	71°10.52’
26 Oct 2008	1115	813	17°31.49’	71°10.18’
23 Oct 2008	1112	816	17°31.50’	71°10.45’
16 Oct 2008	1110	930	17°32.58’	71°6.30’
16 Oct 2008	1110	930	17°32.58’	71°6.30’
27 Oct 2008	1116	1000	17°31.82’	71°6.01’
27 Oct 2008	1116	1000	17°31.82’	71°6.01’
27 Oct 2008	1116	1050	17°31.78’	71°5.62’
22 Oct 2008	1111	1147	17°31.46’	71°5.05’
22 Oct 2008	1111	1147	17°31.46’	71°5.05’

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Table 3a. Background macrofaunal densities (no. per 8.3 cm diameter core), Transect 1 (see Table 1 for locations).

TRANSECT 1	6 Oct 2008	7 Oct 2008	7 Oct 2008	4 Oct 2008	4 Oct 2008	3 Oct 2008	3 Oct 2008	3 Oct 2008	8 Oct 2008	2 Oct 2008	2 Oct 2008	2 Oct 2008	1 Oct 2008	1 Oct 2008
Depth (m)	535	542	542	602	602	710	712	800	802	835	835	900	1000	1100
Annelida														
Acrocirridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ampharetidae	0	0	0	0	0	6	4	1	0	0	1	0	0	0
Amphinomidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capitellidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Cirratullidae	0	0	0	0	0	0	5	2	9	2	3	1	0	0
Cossuridae	0	0	0	0	0	2	8	1	2	0	1	2	0	0
Fauveliopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesionidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Lumbrineridae	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Maldanidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtyidae	0	0	0	0	0	0	2	0	0	0	0	0	1	0
Nereididae	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Paraonidae	0	0	0	0	0	0	0	2	4	4	5	0	0	0
Pectinaridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllodocidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polynoidae	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Sabellidae	0	0	0	0	0	2	1	1	0	0	0	0	0	0
Scalibregmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigalionidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaerodoridae	0	0	0	0	0	0	0	0	0	0	0	3	0	0
Spionidae	0	0	0	12	0	3	0	2	1	0	1	0	0	0
Sternaspidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Syllidae	0	0	0	1	1	0	0	0	0	0	0	0	1	0
Trichobranchidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea														
Cumacean	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isopod	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda	0	0	0	0	0	3	1	0	0	3	0	0	0	0
Ampeliscid	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenothoidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanaidacia	0	0	0	0	0	0	0	0	0	0	0	0	0	12
Arachnida														
Mite	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mollusca														
Aplacophora	0	0	0	0	0	2	0	0	0	0	0	0	1	0
Bivalvia	0	0	0	0	0	11	5	0	0	0	0	0	0	0
Lucinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinodermata														
Ophiuroidea	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Nemertean	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown Metazoan	0	0	0	0	0	0	0	0	3	0	0	0	0	1

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Table 3b. Background macrofaunal densities (no. per 8.3 cm diameter core), Transect 2 (see Table 1 for locations).

TRANSECT 2	8 Nov 2008	8 Nov 2008	8 Nov 2008	28 Oct 2008	28 Oct 2008	28 Oct 2008	26 Oct 2008	23 Oct 2008	16 Oct 2008	16 Oct 2008	27 Oct 2008	27 Oct 2008	27 Oct 2008	22 Oct 2008	22 Oct 2008
Depth (m)	575	575	650	693	746	746	800	816	930	930	1000	1000	1050	1147	1147
Annelida															
Acrocirridae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ampharetidae	0	0	12	8	0	1	2	2	0	0	0	0	0	0	0
Amphinomidae	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Capitellidae	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Cirratulidae	0	0	1	1	2	4	5	3	0	0	0	0	0	0	0
Cossuridae	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1
Fauveliopsidae	0	0	0	3	0	0	2	0	1	0	0	0	0	0	0
Hesionidae	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Lumbrineridae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Maldanidae	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0
Nephtyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Nereididae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Paraonidae	0	0	0	0	0	0	2	3	0	0	0	1	0	0	3
Pectinaridae	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Phyllodocidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Polynoidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sabellidae	0	0	2	2	1	1	1	0	1	0	1	0	0	0	1
Scalibregmatidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sigalionidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sphaerodoridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spionidae	5	3	4	0	0	0	0	0	0	1	2	1	1	0	1
Sternaspidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syllidae	1	2	0	6	0	0	0	0	1	0	0	2	0	4	0
Trichobranchidae	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0
Crustacea															
Cumacean	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Isopod	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Amphipoda	0	0	0	1	0	0	2	2	0	0	0	0	1	2	0
Tanaid	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0
Ampeliscid	0	0	0	2	2	1	0	1	0	0	0	0	0	0	0
Stenothoidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Phoxocephalidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Arachnida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mite	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Mollusca															
Aplacophora	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Bivalvia	0	0	0	0	0	3	10	0	0	1	0	1	0	0	1
Lucinidae	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
Pectinidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Echinodermata															
Ophiuroidea	0	0	0	3	0	0	2	2	0	0	0	0	0	0	0
Nemertean	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Unknown Metazoan	0	0	0	0	0	1	0	0	0	0	2	0	0	1	0

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Table 4. Macrofauna colonizing sediment trays deployed on the W. Indian Margin.

Date	11 Oct 2008	11 Oct 2008	11 Oct 2008	11 Oct 2008	12 Oct 2008	12 Oct 2008	12 Oct 2008	12 Oct 2008	2 Nov 2008	2 Nov 2008	2 Nov 2008	2 Nov 2008	1 Nov 2008	1 Nov 2008	1 Nov 2008	1 Nov 2008
Depth (m)	542	542	542	542	802	802	802	802	817	817	817	817	1147	1147	1147	1147
Replicate	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Fraction	0–2	0–2	0–2	0–2	0–2	0–2	0–3	0–2	0–2	0–2	0–2	0–2	0–5	0–3	0–5	0–3
Algal Treatment	$^{13}C/^{15}N$ Label	$^{13}C/^{15}N$ Label	No algae	No algae	$^{13}C/^{15}N$ Label	$^{13}C/^{15}N$ Label	No algae	No algae	$^{13}C/^{15}N$ Label	$^{13}C/^{15}N$ Label	No algae	No algae	$^{13}C/^{15}N$ Label	$^{13}C/^{15}N$ Label	No algae	No algae
TAXON																
Annelida																
Ampharetida																2
Capitellida													9	48	36	11
Cirratulida							1	1								
Cossurida							1									
Lumbrineridae												1				
Sabellida						1										
Spionidae													2	4		1
Prionospio sp.								1								
Pygospio sp.																1
Syllida														1		
Turbellarian							1									
Sipunculan							1									
Mollusca																
Aplacophora																
Bivalvi					1											
Gastropod						1		1								
Crustacea																
Amphipoda													1	1	1	
Cumacea														1		
Echinodermat																
Ophiurode														1		

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Table 5. Carbon and nitrogen stable isotopic signatures for colonizers of trays with and without labeled phytodetritus added. Background data are also given for sediments and protistans. Background data for macrofauna are given in Hunter et al. (2012) (Fig. 4).

Depth (m)	Treatment	Major Taxo	Taxon ID	No. Individual	δ^{13}C (V-PDB)	δ^{15}N (AIR)
542	^{13}C/^{15}N Algae	Alga	Algae, labelled	N/A	50 625.6	57 190.12
542	^{13}C/^{15}N Algae	Protista	*Lenticularia* sp.	1	−4.29	1.59
542	^{13}C/^{15}N Algae	Protista	*Lenticularia* sp.	12	−11.9	−4.47
542	^{13}C/^{15}N Algae	Protista	*Uvigerina* sp.	34	−9.4	652.3
542	^{13}C/^{15}N Algae	Protista	*Hoeglundina* sp.	23	−11.6	711.86
542	^{13}C/^{15}N Algae	Protista	*Uvigerina* sp.	40	−12.74	415.76
542	^{13}C/^{15}N Algae	Protista	*Uvigerina* sp.	30	−18.31	36.02
802	No Algae	Polychaeta	Cirratulidae	1	−22.79	3.04
802	No Algae	Polychaeta	Cossuridae	1	−24.02	4.96
802	^{13}C/^{15}N Algae	Molluska	Gastropoda	1	−18.06	5.14
802	^{13}C/^{15}N Algae	Molluska	Sabellidae	1	−24.02	6.06
802	^{13}C/^{15}N Algae	Mollusca	Bivalve	1	−3.49	12.85
802	^{13}C/^{15}N Algae	Ascidiacea	Ascidian	1	235.3	2059.63
802	^{13}C/^{15}N Algae	Protista	*Lenticularia* sp.	10	15.61	1712
802	^{13}C/^{15}N Algae	Protista	*Hoeglundina* sp.	16	−17.36	271.28
802	^{13}C/^{15}N Algae	Tube	Protozoa		16.9	131.44
802	^{13}C/^{15}N Algae	Protista	*Chilostomella* sp., *Globobulimina sp.*	6	−18.13	255.43
802	^{13}C/^{15}N Algae	Tube	Polychaete	1	−10.72	7.48
1147	No Algae	Polychaeta	Ampharetidae	1	−23.14	11.48
1147	No Algae	Polychaeta	Capitellidae	2	−24.48	3.09
1147	No Algae	Crustacea	Amphipoda	1	−22.62	8.45
1147	No Algae	Polychaeta	Spionida	1	−24.32	8.98
1147	No Algae	Polychaeta	*Pygospio*	1	−22.47	7.88
1147	No Algae	Polychaeta	Capitellidae	2	−21.7	7.89
1147	No Algae	Polychaeta	Capitellidae	3	−20.55	12.2
1147	No Algae	Polychaeta	Capitellidae	3	−21.25	10.74
1147	No Algae	Polychaeta	Capitellidae	3	−21.8	7.62
1147	No Algae	Polychaeta	Capitellidae	2	−21.59	9.73
1147	^{13}C/^{15}N Alga	Polychaeta	Spionida	1	−11.62	14.46
1147	^{13}C/^{15}N Alga	Polychaeta	Spionida	2	−4.29	237.91
1147	^{13}C/^{15}N Alga	Polychaeta	Capitellidae	1	348.58	167.19
1147	^{13}C/^{15}N Alga	Polychaeta	Capitellidae	3	614.48	207.40
1147	^{13}C/^{15}N Alga	Polychaeta	Capitellidae	1	−22.21	111.37
1147	^{13}C/^{15}N Alga	Polychaeta	Capitellidae	3	5384.46	10 335.71
1147	^{13}C/^{15}N Alga	Polychaeta	Capitellidae	2	−15.14	67.34
1147	^{13}C/^{15}N Alga	Crustacea	Amphipoda	1	−2.04	20.56
1147	^{13}C/^{15}N Alga	Crustacea	Cumacea	1	2530.38	1792.31
835	Background	Protista	*Globobulimina* sp., *Chilostomella* sp.	15	−9.34	5.46
900	Background	Protista	*Reophax* sp.	3	−21.71	3.02
800	Background	Protista	Allogromid	1	−20.21	3.72
800	Background	Protista	*Nonionella* sp.	7	−22.01	3.59
540	Background		Sediment		−20.38	5.53
800	Background		Sediment		−20.41	6.20
814	Background		Sediment		−20.22	6.02
1145	Background		Sediment		−20.59	7.49

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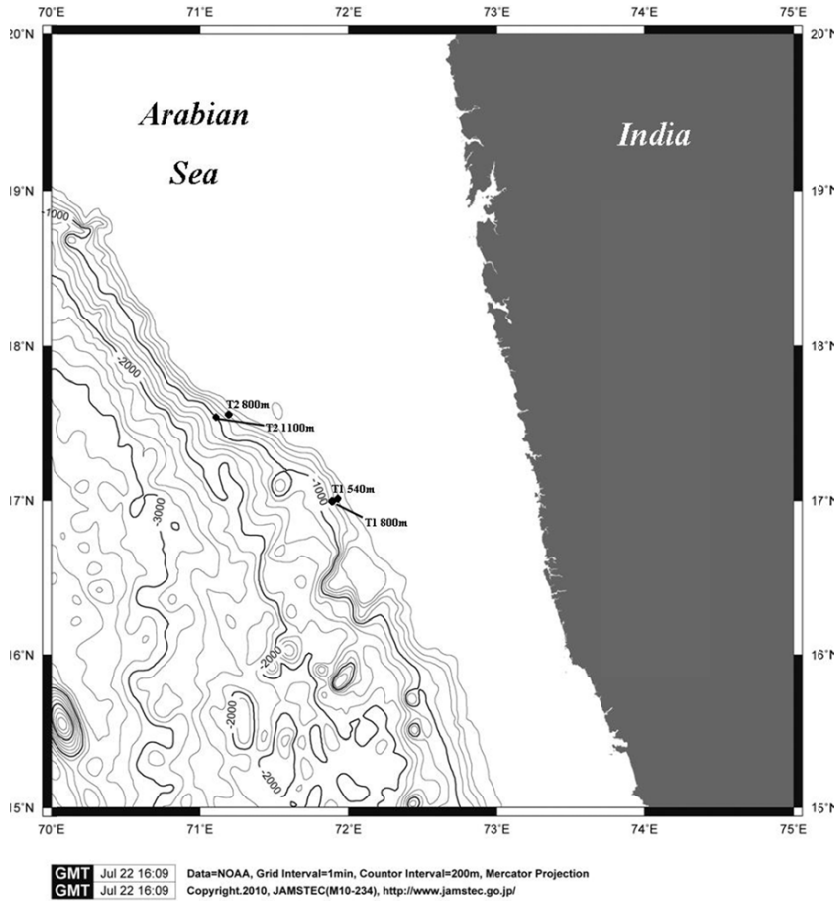

Fig. 1. Location of colonization study sites and Transects 1 (T1) and 2 (T2) on the W. Indian Margin.

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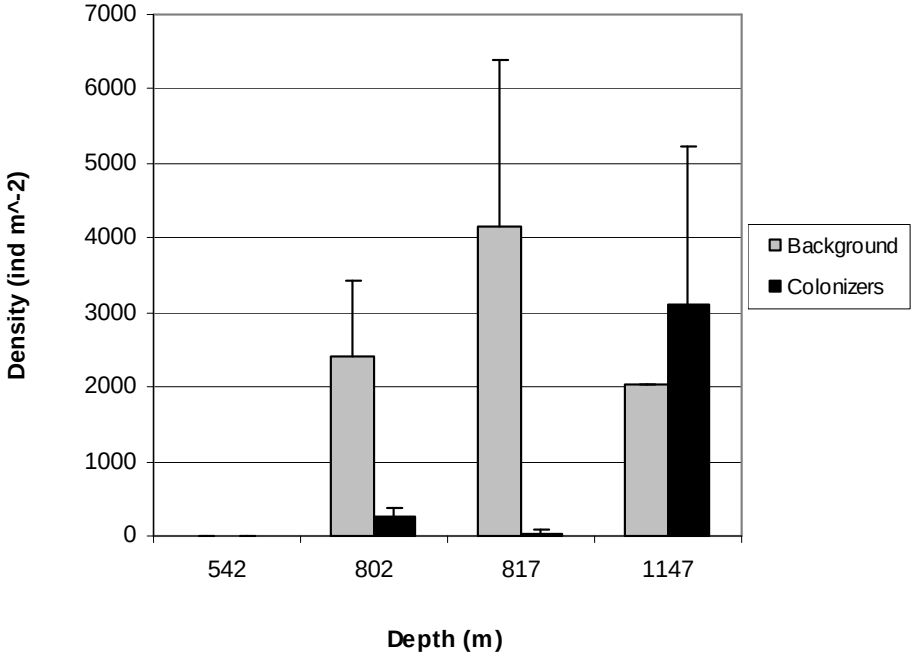

Fig. 2. Comparison of metazoan macrofaunal background and colonizer average density (±1 SD) at each depth studied on the W. India margin. See Table 1 for tray deployment periods and locations.

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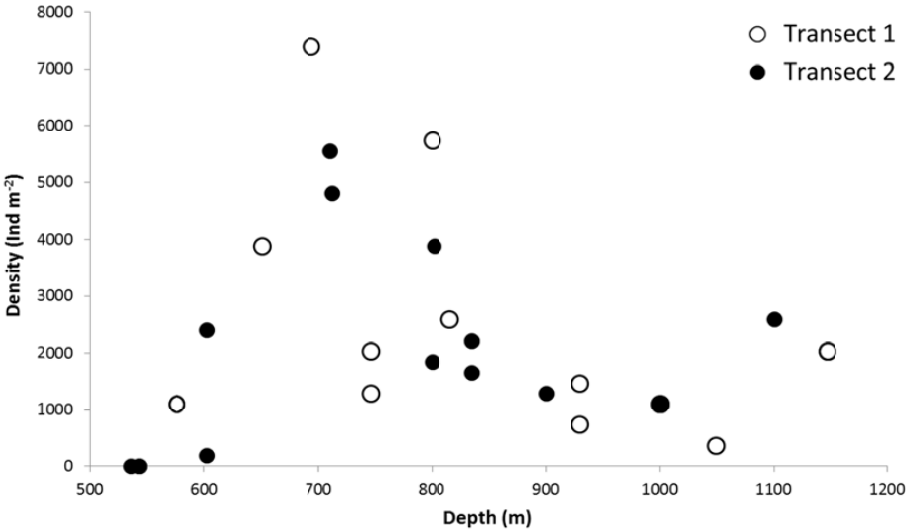

Fig. 3. Metazoan macrofaunal densities in background core samples (54 cm^2 × 10 cm deep) along two transects across the W. India margin.

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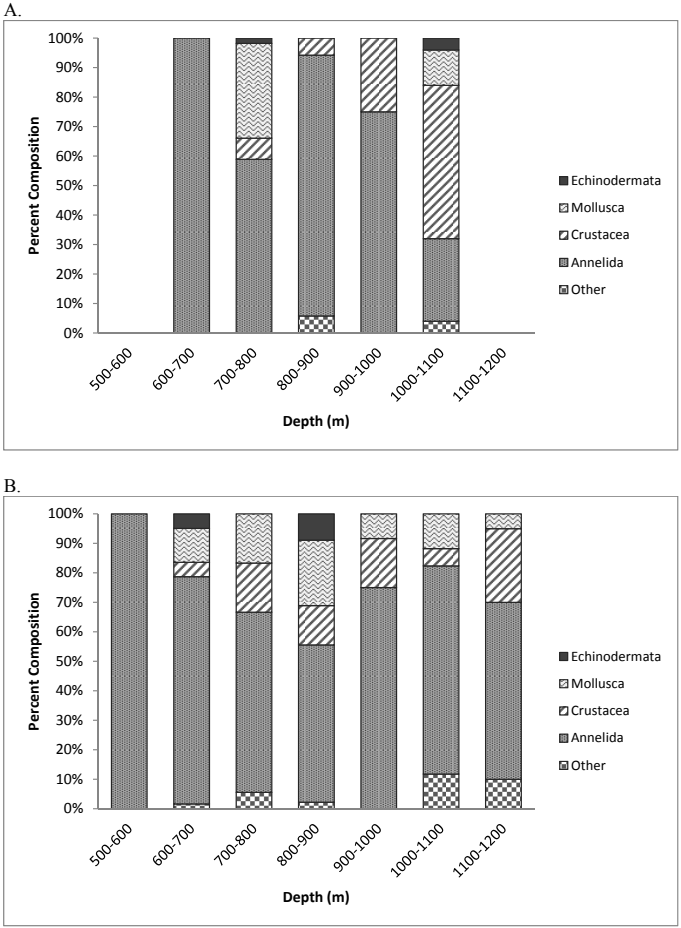

Fig. 4. Metazoan macrofaunal composition in background sediments sampled across the W. India margin along Transect 1 **(A)** and Transect 2 **(B)**.

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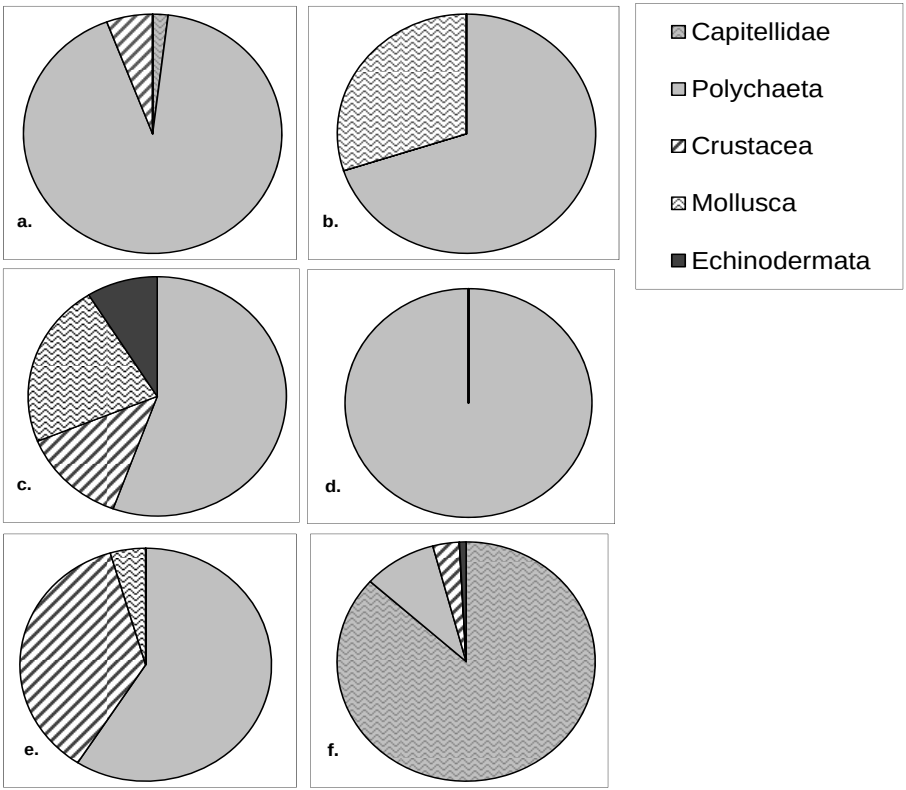

Fig. 5. Composition of higher macrofaunal taxa in background and colonization trays on the W. India margin. **(a)** Background at 800 to 835 m on Transect 1 **(b)** Colonizers at 802 m on Transect 1 **(c)** Background at 800 to 814 m on Transect 2 **(d)** Colonizers at 817 m on Transect 2 **(e)** Background at 1148 m on Transect 2 **(f)** Colonizers at 1147 m on Transect 2.

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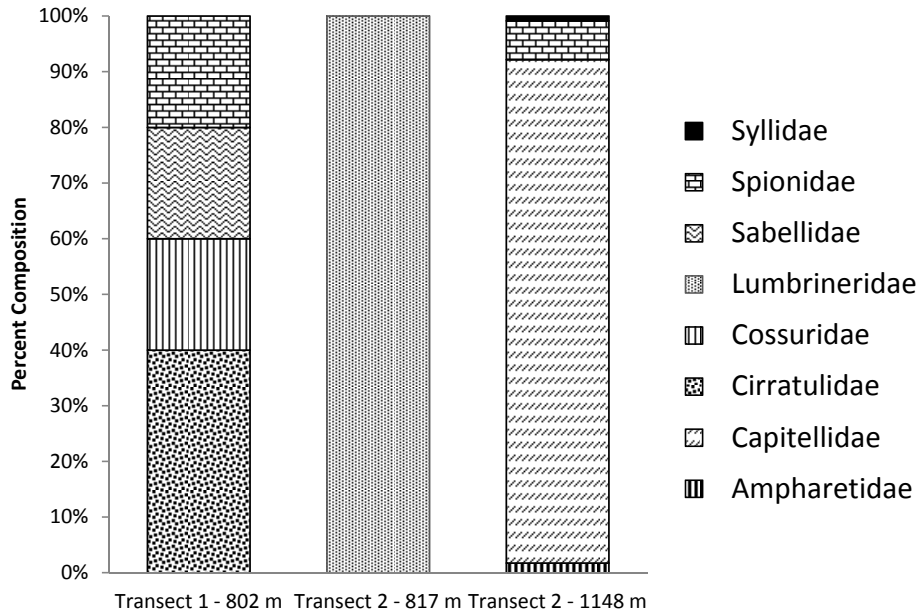

Fig. 6. Annelid family composition in colonization trays on the W. India margin. See Table 1 for tray deployment periods and locations.

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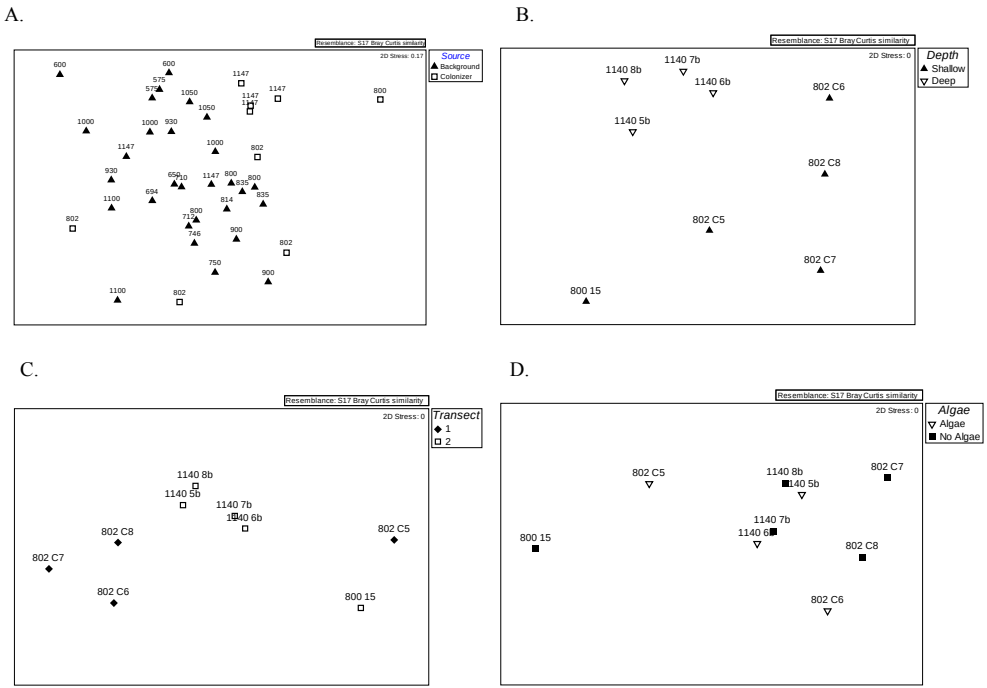

Fig. 7. Multidimensional scaling plot for metazoan macrofaunal community composition comparing: **(A)** background (closed symbols) and colonizers (open symbols) ANOSIM: $R = 0.263$; $p = 0.002$; **(B)** deep (high oxygen – open symbols) and shallow (low oxygen – closed symbols) depths; ANOSIM: $R = 0.5$; $p = 0.024$; **(C)** Trays on Transect 1 (closed symbols) and Transect 2 (open symbols); ANOSIM: $R = 0.5$; $p = 0.024$; and **(D)** Trays with labeled phytodetritus (open symbols) and without phytodetritus (closed symbols); ANOSIM: $R = -0.084$; $p = 0.81$.

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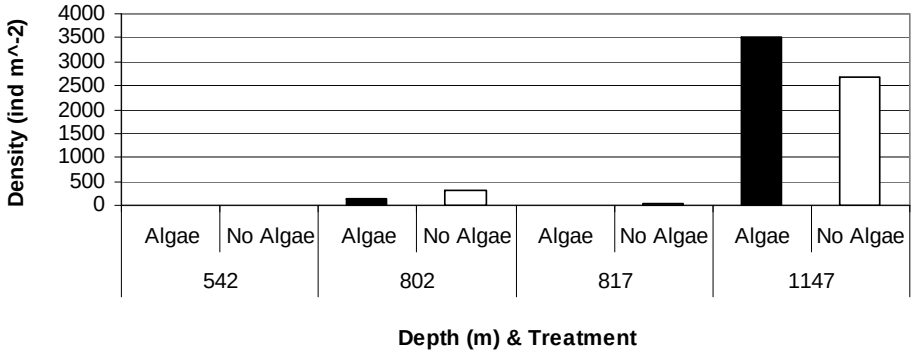

Fig. 8a. (A) Comparison of average metazoan macrofaunal density in colonization trays with and without $^{13}C/^{15}N$ – labeled phytodetritus on the W. India margin.

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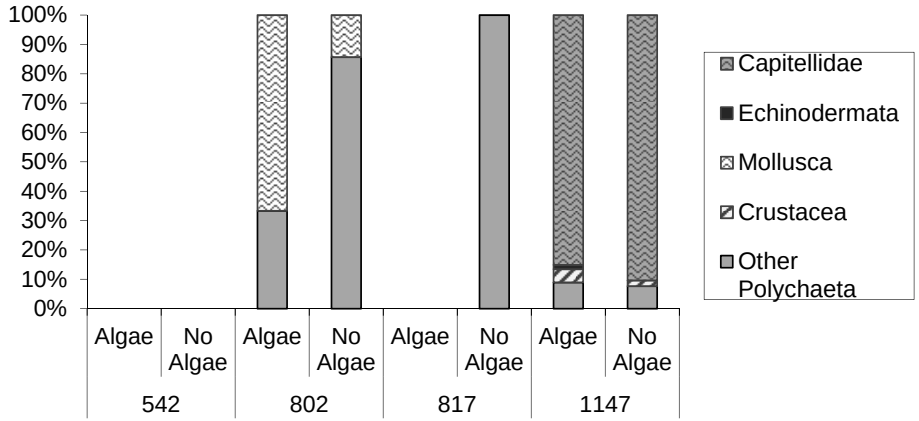

Fig. 8b. Comparison of metazoan macrofaunal composition in colonization trays with and without phytodetritus on the W. India margin. Each bar reflects data combined for 2 trays. See Table 1 for tray deployment periods and locations.

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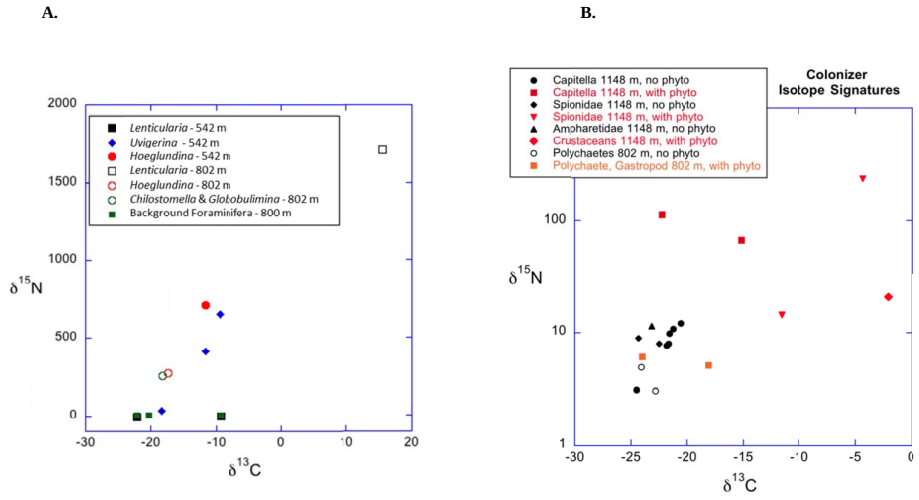

Fig. 9. (A) Stable isotopic composition of foraminifera in colonization trays with labeled phytodetritus and in background sediments. **(B)** Dual isotope plot of metazoan macrofaunal colonizers in colonization trays with $^{13}C/^{15}N$-labeled phytodetritus added (with phyto; red and orange symbols) and those without (no phyto, black symbols) from 802 m on Transect 1 and 1147 m on Transect 2.

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