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Harpacticoid copepod colonization of coral fragments in a tropical reef lagoon (Zanzibar, Tanzania)

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Introduction

Back-reef systems are tropical nearshore environments between the leeward side of the reef-crest and mean high tide along the shore. They consist of an interconnected mosaic of diverse habitat types such as mangroves, seagrass meadows, patch reefs and the hard- or soft-bottom seafloor (Adams *et al*., 2006). The East-African coast supports extensive intertidal lagoon flats composed mainly of carbonate sediments and in Zanzibar these account for approximately 90% of the total coastal area (Ndaro & Ólafsson, 1999). These carbonate sediments are commonly composed of coralline sediment, and the skeletal remains of dead corals and other carbonate-bearing organisms (Alongi, 1989). These skeletal remains progressively degrade into smaller pieces until it becomes coralline sediment, the term "coral degradation zone" has been coined by Raes *et al*. (2007) to indicate the dynamic character of these sediments in a tropical reef lagoon. This process of gradual degradation results in a large variety of substrates with different structural complexity, which provide a wide range of potential microhabitats for the benthic fauna (Gheerardyn *et al*., 2008).

Coastal ecosystems, such as intertidal lagoons, are more and more stressed because the coastal human population continues to increase (Adams *et al*., 2006). Human impacts, like overfishing, sediment and nutrient runoff, introduction of invasive species and hydrological alterations, cause severe damage to the ecosystem. Next to these direct disturbances, there is also an indirect impact caused by global warming (Hughes *et al*., 2003, Orth *et al*., 2006). Changes in ocean chemistry due to higher atmospheric carbon dioxide levels may cause weakening of coral skeletons, and coral bleaching events are strongly associated with elevated temperatures (Hughes *et al*., 2003). Habitat destruction and fragmentation are considered major causes of the increase in the rate of species extinction in recent decades (Henle *et al*., 2004).

An important ecosystem function of back-reef systems, of which carbonate sediments are an important component, is providing nursery grounds for (economically important) juvenile fish (Nagelkerken *et al*., 2000, Adams *et al*., 2006). The main reason for these high densities of juvenile fish is the availability of shelter from predation, because the area is separated from the main coral reef and its predators by a shallow reef terrace (Nagelkerken *et al*., 2000). Due to their structural complexity dead and living corals provide an ideal hiding space for juvenile fish. These juveniles subsequently make an ontogenetic shift to the adult populations on the coral reefs (Adams *et al*., 2006). Therefore, back-reef systems can be an important source of new adults for adjacent coral reefs (Dorenbosch *et al*., 2006).

Meiofauna play a prominent role in these ecosystems. They influence primary production through micro-grazing (Jackoby & Greenwood, 1988), participate in the breakdown of particulate organic

matter (Beesly *et al*., 2000), are an obligate food source for most juvenile fishes (Coull *et al*., 1995), have temporary membership of macrofauna larvae (Jackoby & Greenwood, 1988), and part of the meiofauna is an important component of the vertically migrating plankton that move up into the water column at night to disperse (Forward & Tankersley, 2001).

Harpacticoid copepods form an important group in the meiofaunal community, especially in carbonate sediments where they are often the dominant taxon (Alongi, 1989; Logan *et al*., 2008). They play a prominent trophic role in carbonate sediments because of their numerical abundance, capacity to recycle nitrogen and high bacterial ingestion rates (Gray 1985; Moriarty *et al*. 1985). Furthermore, they are an important food source for small, often juvenile demersal fish, carnivorous crustaceans and polychaetes (Giere, 2009) due to their epibenthic occurrence and high nutritional value (Coull, 1999). It is important to understand the dynamics of the harpacticoid community because they are fundamental to many processes that operate in back-reef systems. Colonization experiments are of particular interest in investigating these dynamics because they allow one to trace the process of community establishment from the very beginning, and to observe changes in its most important characteristics (Chertoprud *et al*. 2005).

There have been several studies which investigated the meiofauna communities associated with carbonate reef sediments (e.g. Alongi, 1989; Ndaro & Ólafsson 1999, Lagon *et al*., 2008, Raes *et al*., 2007, Gheerardyn *et al*., 2008). These studies focussed mainly on meiofauna assemblages living on or within soft sediments, whereas research on the epi-meiofauna associated with hard coral substrates is scarce. Only two studies (i.e. Raes *et al*., 2007, Gheerardyn *et al*., 2008) have investigated the epi-meiofauna living on hard coral substrates along the eastern African coast. Both for the nematode and the harpacticoid copepod fauna, coral fragments harboured a different community than the surrounding sediment. These differences were attributed to the more exposed nature of the coral microhabitat, differences in available surface area for epifaunal taxa and the presence of a microbial biofilm and algal cover on the dead coral's surface. In both studies, the differences between coral fragments and surrounding sediment were based in particular on different contributions of the taxa present. Gheerardyn *et al*. (2008) found that coral fragments support a specific harpacticoid assemblage composed of epibenthic or phytal taxa with an addition of sediment-dwelling species. Raes *et al*. (2007) showed an increased importance of typical coarse sand/coarse substrate taxa in the nematode communities of the coral fragments. The various microhabitats contribute to the overall meiofaunal species diversity in the reef lagoon because each harbours a specific meiofaunal assemblage. Other studies also revealed that meiofaunal assemblages on hard substrates (as e.g. rocky shores and piers) were taxonomically different from surrounding soft-sediment assemblages (Danovarro & Frashetti, 2002) and that these were often

dominated by phytal copepods (Atilla *et al*., 2003). A considerable amount of research has been conducted on epi-meiofauna assemblages on macroalgae and seagrass (e.g. Hicks, 1985; Ólafsson *et al.*, 2001; De Troch *et al*., 2001, 2003). These studies showed that species composition in phytal assemblages is usually quite distinct from other closely adjacent sedimentary habitats (Hicks, 1985), and even different within-plant subhabitats may be occupied by a different suite of species (Hicks, 1985; De Troch *et al*., 2001).

Experimental research on harpacticoid colonization has been conducted for a wide range of substrates such as sediment depressions (Sun & Fleeger, 1994), mesh pads (Atilla & Fleeger 2000; Atilla *et al*., 2003), floating seaweed (Ólafsson *et al*., 2001), sediments of different grain-size (Chertoprud *et al*., 2005) and seagrass mimics (De Troch *et al*., 2005). These studies all observed a fast colonization by harpacticoids reaching high abundances, even in less than a day, and sometimes exceeding the natural situation in less than a week. In a short time the community also reached a high species diversity which was generally similar to the background diversity, but with substantially different abundance patterns, especially in early colonization stages (Sun & Fleeger, 1994; Chertoprud *et al*., 2005; De Troch *et al*., 2005). Furthermore, taxa absent from the background community were also recorded during colonization, the total diversity of the colonization pool is thus broader than the actual observed local taxonomic diversity. This indicates the presence of a metacommunity, where a set of local communities are linked by migration flows and a common regional species pool (Chertoprud *et al*., 2005). Sun & Fleeger (1994) found that phytal and epibenthic species were generally fast colonizers while interstitial and burrowing species appeared later during colonization.

Little is know about which mode of colonization (i.e. along the substrate surface or through the water column) is decisive in the formation of the community structure during colonization. Previous studies found that there is a highly mobile and diverse pool of harpacticoid copepods in the water column which can rapidly colonize newly available, free biotopes (Atilla *et al*., 2003; Chertoprud *et al*., 2005). Swimming abilities and passive or active emergence in the water column are known to be species-specific among sediment-dwelling and phytal meiofauna (Walters & Bell, 1994) and these differences in behaviour may lead to variation in colonization abilities of different species (Atilla *et al*., 2003).

The purpose of this study was to investigate the temporal dynamics of the harpacticoid community during colonization of dead coral fragments. We also wanted to investigate the contributions of different colonization modes, through the sediment or the water column, to the formation of the community.

Aims

The general aim of the present study is to investigate the biodiversity and dynamics of colonization by harpacticoid copepods on dead coral fragments along the coast of Zanzibar (Tanzania). The colonization experiment of dead coral will examine whether these hard biogenic substrates are colonized from the sediment or through the water column, and how the associated communities change over time.

Materials and methods

Sampling location

Unguja Island (Tanzania) is one of the two main islands of the Zanzibar archipelago. The island is located in the Indian Ocean approximately 40 km off the coast of East-Africa, and is separated from mainland Tanzania by the Zanzibar Channel. The currents near the coast of Unguja are dominated by the East-African coastal currents, which have a net northward flow. Current speed varies between 0.25 and 2m/s, being fastest during the SE monsoon (May to September) and lowest during the NE monsoon (November to March)(Shaghude *et al*.).

Samples were taken in front of Fumba (6°19'S, 39°16'E)(Fig. 1), a village located on the south-western coast of the island at the tip of a small peninsula. This area is bordered by the Zanzibar Channel in the west and Menai Bay in the east. The sampling site was located in the WWF Menai Bay Marine Conservation Area. This conservation area aims to sustain biological resources of the Menai bay by reducing destructive forms of fishing such as dynamite fishing (Levine, 2006).

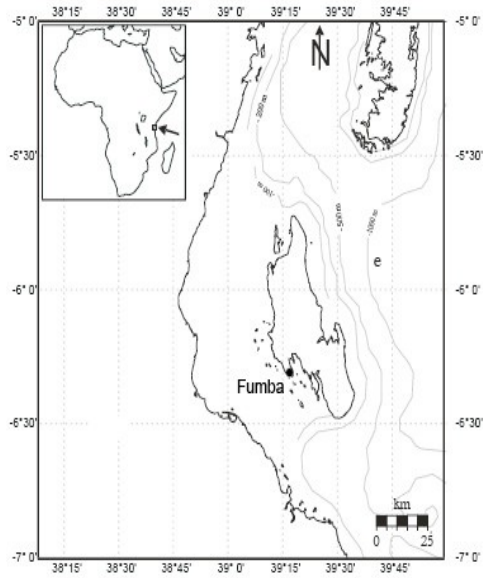


Fig. 1: *Map of the study area indicating the sampling site. The northmost island is Pemba, the southmost is Unguja.*

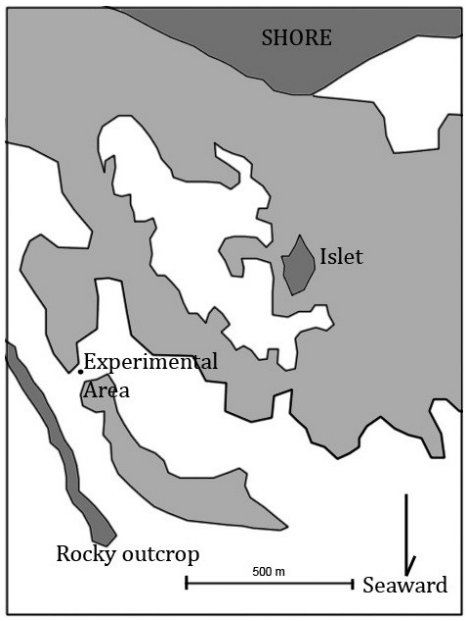


Fig. 2: *Schematic overview of the sampling area indicating the experimental area. Seagrass fields are light grey; the shoreline, islet and rocky outcrop are dark grey; carbonate sediment is white.*

Samples were collected in the subtidal zone, at a distance of approximately 1000m from the high-tide line (Fig. 2). The sampling area consisted of bare sediment with dead coral fragments and sparsely distributed colonies of living coral. The sediment was mainly composed of medium- (20.2% ±3.5%), coarse - (45% ±2.9%) and very coarse sand (25.3% ±5.5%) with low silt, clay and fine sand content. The surrounding area consisted of bare sediment and large seagrass fields, of the genera *Zostera*, *Halophila*, *Halodule* more closely to the beach and *Thalassia*, *Cymodocea*, *Thalassodendron* and *Syringodium* more seawardly. The experimental area was located at approximatly 10m from a seagrass field of *Thalassia*, and was protected by a rocky outcrop which was inundated only at high tide. Between this rocky outcrop and the island there was a channel which connected the area to the open sea.

Experimental set-up

For this field experiment, dead coral fragments of comparable complexity were collected in the experimental area. Meiofauna samples were collected from five coral fragments to characterize the natural communities. Afterward, all coral fragments were defaunated by rinsing thoroughly with tap water and drying for at least 24 hours. Coral fragments were then placed in one of two types of PVC-cores, according to treatment. The open-type core consisted of an open PVC-tube with a height of 10cm and a diameter of 20cm (Fig. 3a). The closed-type core differed from the open-type by a bottom that was present in the center of the tube (Fig. 3b). These cores were inserted about 5cm in the sediment and were anchored with 3 metal hooks. The cores and coral fragments remained inundated during low spring tide.

To investigate whether colonization of coral fragments occurs through the sediment or the water column, two different treatments were used: *open* and *closed*. The *open* treatment consisted of a coral fragment placed in an open-type PVC core in order to keep direct contact between the coral fragment and both the underlying sediment and the water column. In the *closed* treatment, a coral fragment was placed in a closed-type PVC core to prevent contact between coral fragment and the underlying sediment, while direct contact with the water column remained.To investigate the effect of time on colonization, meiofauna was sampled at five different colonization times, i.e. 2, 4, 6, 10 and 14 days after the start of the experiment. The same coral fragments were used to sample both days 2, 4 and 6. Here, after collecting the meiofauna, the coral fragments were defaunated by rinsing with tap water and drying for at least 24h before placing them back into the core. For both day 10 and 14 distinct coral fragments were used.



Fig. 3*: Illustration of PVC-cores; A: open-type PVC core; B: closed-type PVC core; C: in-situ photograph during the experiment of a coral fragment inside a PVC core.*

Both treatments were replicated three times (A, B, and C) and replicates were placed several meters apart from each other (Fig. 4). Each replicate consisted of three *open* and three *closed* cores which were placed 1m from each other.

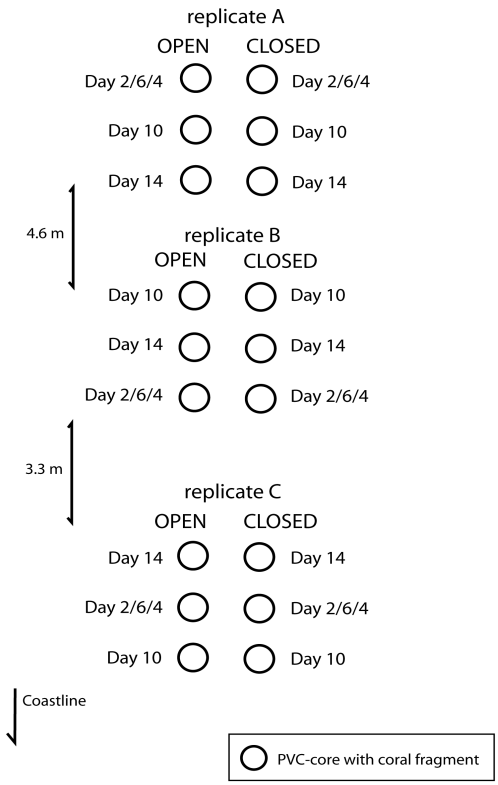


Fig. 4 *Field design of the experiment. PVC-cores are indicated with a circle, on the left is the* open *treatment and on the right the* closed *treatment. Days on with the corals inside the cores were sampled are indicated next to the core. Three replicates (indicated as A, B and C) are placed several meters apart from each other.*

To characterize the community in the surrounding sediment, samples were taken by inserting a 10cm^2 core as deeply as possible in the sediment. The core was then subdivided in three depth horizons (0-1cm, 1-3cm and 3-5cm).

Due to time limitations, only two replicates of days 2, 6 and 14, two replicates of the natural community and two replicates of the sediment (0-1cm) were analyzed.

Meiofauna collecting

Samples were taken during low tide. The coral fragment was gently placed in a plastic bag, with as little disturbance as possible, and sealed with rubber bands to transport to the shore for further treatment. $MgCl_2$ was added to the bag to stun the meiofauna. After adding the $MgCl_2$ and shaking for 15 minutes the bag and the coral fragment were rinsed thoroughly with filtered seawater over a 1mm and 32µm sieve. The contents of the 1mm sieve and 32µm sieve were collected and fixed in 4% buffered formalin.

Sample processing

The samples were filtered over a 1mm and a 32µm sieve. The contents of the 32µm sieve were put in Ludox HS40 floating medium with a specific density of 1.18 (Heip *et al*., 1985). This was centrifuged for 12 minutes at 3000 rpm. The supernatans, which contained the meiofauna, was poured onto a 32µm sieve and the Ludox was flushed away with water. This process was repeated three times to extract all meiofauna from the sample. Meiofauna was stained with rose Bengal and fixed in 4% buffered formalin.

From each sample, 200 copepods (or all the copepods in the sample if there were less than 200) were randomly picked out under an Wild M5 binocular microscope and mounted on glycerin slides.

Adult copepods were identified to genus level with Lang (1948, 1965), Huys *et al*. (1996) and Boxshall & Halsey (2004). Systematics and nomenclature follow Wells (2007) and Huys (2009). Genera were classified according to body shape following Coull (1977) (Fig. 5).

Statistics

A non-metric, multidimensional scaling, two dimensional plot (MDS) was produced, using the Bray-Curtis similarity index. Per sample data were standardized to relative abundance data and root transformed prior to analysis. The root-transform has the effect of down-weighting the importance of highly abundant species, so that similarities depend not only on their values but also those of less common mid-range species. The significance of the MDS was tested using a one-way ANOSIM and a two-way crossed ANOSIM. Similarity of percentages (SIMPER) was used to identify the taxa contributing to the differences found in the ordination analysis. All multivariate tests were performed using the PRIMER 6.1.12 software (Plymouth Marine Laboratory; Clarke & Gorley, 2009).

Non-parametric analysis for comparing multiple independent sample groups was performed on untransformed data using a Kruskal-Wallis ANOVA. A Mann-Whitney U-test was employed for comparing two independent sample groups. All analyses were performed using STATISTICA7 software.

Expected number of genera was calculated by rarefaction method of Hurlbert (1971). This method uses counts of total genera (G) and individuals (N) to calculate how many genera EG(n) would have been expected had we observed a smaller number (n) of individuals. EG(n) was calculated for n = 25, this was the smallest number of individuals found in one sample.

$$EG_n = \Sigma_{i=1}^{G} [1 - \frac{(N - N_i)!(N - n)!}{(N - N_i - n)!N!}]$$

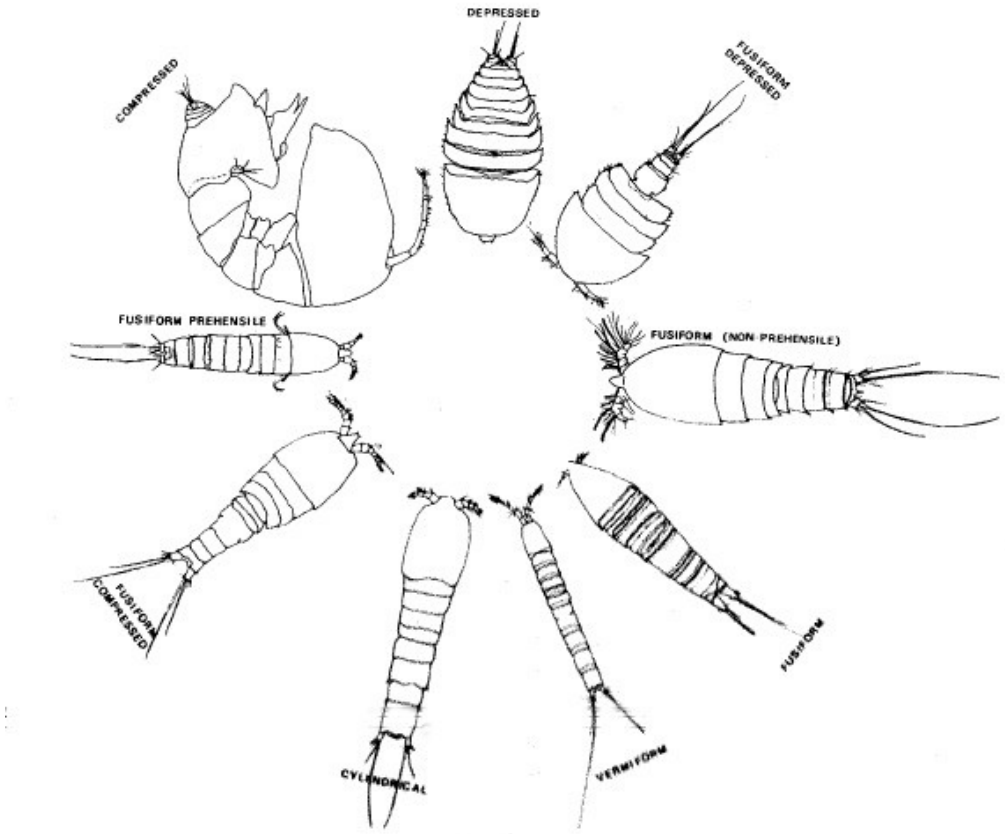


Fig. 5: *Various body shapes of harpacticoid copepods. Definitions of the body form are as follows:* ***vermiform*** *- narrow, wormlike;* ***cylindrical*** *- almost linear, squared off cephalothorax, non-articulated rostrum;* ***fusiform compressed*** *- broadened in prosome, narrow in urosome, thoracic somites compressed together from anterior to posterior;* ***fusiform prehensile*** *- just slightly broader in cephalon than thorax, almost linear in shape with prehensile (grasping) first leg;* ***compressed*** *- compressed laterally like amphipods;* ***depressed*** *- dorsoventrally flattened, very little tapering anterior to posterior;* ***fusiform depressed*** *- dorsoventrally flattened;* ***fusiform (nonprehensile)*** *- just slightly broader in cephalon than thorax, almost linear in shape, first leg not prehensile;* ***fusiform*** *- torpedo-shaped, cephalon narrowing to broad point anteriorly, anterior metasome wider than cephalon and/or urosome (restricted to family Ectinosomatidae) (From: Coull, 1977).*

Results

A total of 3030 copepods were identified of which 91.6% belonged to the order Harpacticoida, 8.5% to the order Cyclopoida and one individual to the order Siphonostomatoida.

Relative abundances of copepodids

In total, 69.5% of all harpacticoids were copepodids. A significant difference in copepodid abundance on coral fragments was found between different days (Kruskal-Wallis ANOVA, $p = 0.02$). The relative abundance of copepodids in the natural situation was 66.6% ±3.9% (Fig. 6). The highest percentages of copepodids were recorded on day 2 and day 6 of the colonization experiment. Here, abundances were comparable on both days, with no discernible differences between treatments (*open* day 2: 78.5% ±8.3%; *closed* day 2: 77.7% ±6.5%; *open* day 6: 78.9% ±1.8%; *closed* day 6: 79.7% ±3.2%). On day 14, both treatments had a slightly lower share of copepodids than the natural situation, with abundances of 62.8% ±0.4% in the *open*- and 56.5% ±1.9% in the *closed* treatment. The lowest abundance of copepodids was found in the sediment, where they only made up 34.1% ±1.7% of the harpacticoid community.

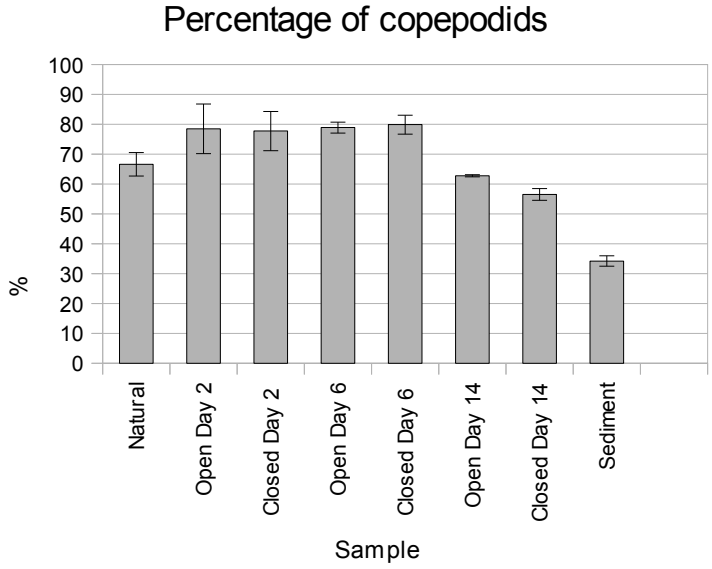


Fig. 6: *Relative abundance of copepodids over different sample times and treatments (error bar = SD).*

General characterization of the harpacticoid assemblages

Over the complete dataset, 30.5% of the 2776 harpacticoid individuals were adults. These belonged to 16 different families and 45 different genera (see Appendix). Overall, the families Ectinosomatidae (22.4%), Tisbidae (21.7%) and Ameiridae (15.6%) dominated. The most dominant genera were *Ectinosoma* (21.5%), *Tisbe* (19.4%) and *Ameira* (12.5%). The family Miraciidae showed the highest generic diversity, with a total of 8 different genera. An overview of the most abundant families and genera over different samples is given in Fig. 7 and Table 1.

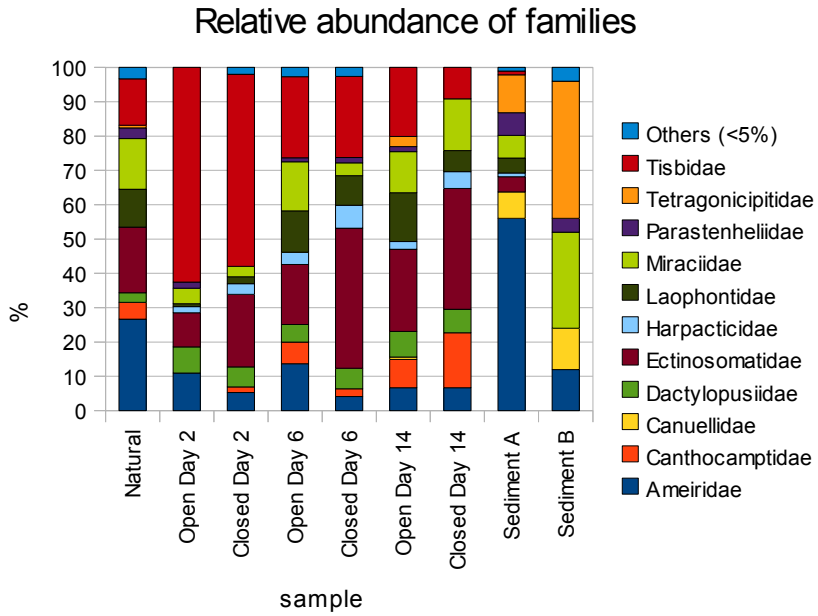


Fig. 7 *Relative abundances of the dominant harpacticoid families in: the natural community on coral fragments; day 2, 6 and 14 during the experiment for both the* open *and* closed *treatments; the two sediment replicates (A and B).*

Genus	Natural	Day 2 Open	Day 2 Closed	Day 6 Open	Day 6 Closed	Day 14 Open	Day14 Closed	Sediment A	Sediment B
Ameira	20.7	10.1	5.3	9.8		5.2	6.7	45.1	12.0
Ameiropsis	1.0	0.9		3.8	4.1	1.5		11.0	
Amphiascoides	1.8	0.9		1.1		4.5	2.5		
Amphiascus	10.3	0.9	3.1	7.8	2.2	6.0	9.5	3.3	12.0
Brianola								7.7	12.0
Dactylopusia	2.1	2.8	1.0	5.2	6.0	4.5	2.5		
Diagoniceps									32.0
Diarthrodes		4.7	4.8			1.5	1.9		
Ectinosoma	15.0	9.1	21.2	17.5	39.3	23.9	35.2	3.3	
Harpacticus		1.8	3.1	3.6	6.7	2.3	3.7		
Karllangia		0.9		1.1		0.7		3.3	
Emertonia									4.0
Laophonte	4.9			3.3		0.7	0.6	4.4	
Longipedia	2.3								
Mesochra	4.9		1.6	4.9	2.2	8.2	15.4		
Paradactylopodia	0.8					1.5	2.5		
Paralaophonte	5.2	0.9	2.0	7.6	7.2	13.5	5.6		
Parastenhelia	3.1	0.9			1.5	0.7		3.3	4.0
Phyllopodopsyllus	0.8					3.0		11.0	8.0
Psyllocamptus	4.1								
Robertgurneya	1.0	1.8		1.4		0.7	0.6	3.3	16.0
Schizopera		0.9		2.7	1.5				
Scutellidium	2.1	7.4	8.8	1.1		2.3			
Tegastes			2.0	1.4	2.6				
Tisbe	11.4	55.2	47.1	22.6	23.6	17.8	9.2	1.1	

Table 1: *Relative abundances (%) of harpacticoid genera after different colonization times and treatments. Only genera with a relative abundance >2% in at least one sample are given.*

Background communities

Assemblage on coral fragments

The natural assemblage on the coral fragments was dominated by the family Ameiridae (26.6% ±0.5%), followed by Ectinosomatidae (19.1% ±2.4%) and Miraciidae (14.7% ±2.2%). Together, these three families accounted for 60.4% ±4.2% of the natural harpacticoid community. Other abundant families were Tisbidae (13.5% ±7.3%), Laophontidae (11.1% ±2.8%) and Canthocamptidae (4.9% ±2.8%). In total, 11 different families were found on coral fragments in the natural situation.

On genus level, *Ameira (*20.7% ±2.2%) and *Ectinosoma* (15.0% ±0.4%) were the most abundant genera on coral fragments in the natural situation. *Tisbe* (11.4% ±5.3%) had a slightly higher abundance than *Amphiascus* (10.3% ±2.0%), and these were both the dominant genera in the families Tisbidae and Miraciidae, respectively. However, due to a higher number of individuals in other genera, the family Miraciidae comprised a larger percentage of the natural community than Tisbidae. Within the Laophontidae, the dominant genera were *Laophonte* and *Paralaophonte*, which had comparable relative abundances of 4.9% ±2.8% and 5.2% ±1.0%, respectively. The family Canthocamptidae was represented by only one genus, *Mesochra* (4.9% ±2.8%). A total of 25 genera

were recorded on coral fragments in the natural situation.

Assemblage in the sediment

The harpacticoid community in both sediment samples had a very different composition in comparison to the coral fragments. Furthermore, there was also a strong difference between the two sediment replicates, they are therefore treated separately here. Sediment replicate A was dominated by Ameiridae (56.0%), followed by Tetragonicipitidae (11.0%) and Canuellidae (7.8%). The families Miraciidae and Parastenheliidae made up an equal share of the community in this replicate, both having a relative abundance of 6.6%. In total, 10 different families were found in replicate A. Sediment replicate B was dominated by Tetragonicipitidae (40.0%). Miraciidae was the second most abundant family, with a relative abundance of 28.0%. Canuellidae and Ameiridae were both found at an equal abundance of 12.0%. The total number of families recorded in replicate B is six. Within the sediment samples, the families Ectinosomatidae, Harpacticidae, Laophontidae, Lourniidae and Tisbidae were only found in the A replicate, while the family Paramesochridae was unique for the B replicate.

In replicate A, the family Ameiridae was represented by the genera *Ameira* (45.1%) and *Ameiropsis* (11.0%), while in replicate B only *Ameira* (12.0%) was found. Within the Tetragonicipitidae, *Diagoniceps* was only recorded in the B replicate, where it was also the dominant genus. *Phyllopodopsyllus* was recorded in both replicates, with an abundance of 11.0% in replicate A and 8.0% in replicate B. In both replicate A and B, the family Canuellidae was represented by a single genus, *Brianola*, at abundances of 7.7% and 12.0%, respectively. In replicate A, the miraciid genera *Amphiascus* and *Robertgurneya* were found at an equal abundance of 3.3%, while in replicate B they made up 12.0% and 16.0% of the community, respectively. In total, 14 genera were recorded in replicate A, while in replicate B only 8 genera were found.

Colonization experiment

Day 2

On day 2 of the colonization experiment, Tisbidae dominated both the *open* and *closed* treatments. Here, this family made up 62.6% ±14.4% of the harpacticoid community in the *open* treatment and 55.9% ±15.1% in the *closed* treatment. Ameiridae was the second most abundant family in the *open* treatment (10.9% ±3.3%), followed by Ectinosomatidae which was present at only a slightly lower abundance (9.9% ±6.1%). In the *closed* treatment, Ameiridae (5.3% ±1.2%) had a much lower

abundance than Ectinosomatidae (21.1% ±11.5%), and was the second most abundant family. The family Dactylopusiidae was abundant in both the *open* (7.6% ±4.0%) and *closed* treatment (5.9% ±3.8%). After two days of colonization, the *open* and *closed* treatments had a total of 8 and 9 families, respectively. Here, the family Parastenheliidae was unique for the *open* treatment, while the families Canthocamptidae and Tegastidae were unique for the *closed* treatment.

Tisbe was the most abundant genus in both treatments (*open*: 55.2% ±14.1%, *closed*: 47.1% ±20.6%). Also within the Tisbidae, *Scutellidium* reached substantial abundances, making up 7.4% ±0.3% of the *open* treatment and 8.8% ±5.5% of the *closed* treatment. The families Ameiridae, Ectinosomatidae and Dactylopusiidae were mainly represented by the genera *Ameira* (*open*: 10.1% ±2.4%, *closed*: 5.3% ±1.2%), *Ectinosoma* (*open*: 9.1% ±5.2%, *closed*: 21.2% ±11.5%) and *Diarthrodes* (*open*: 4.7% ±2.9%, *closed*: 4.8% ±4.8%), respectively. After two days of colonization, the total number of genera was 16 in the *open* treatment, and 11 in the *closed* treatment.

Day 6

On day 6, Tisbidae (23.7% ±7.5%) was still the dominant family in the *open* treatment, but in the *closed* treatment this was Ectinosomatidae (40.8% ±1.4%). However, the share of Tisbidae in the *closed* treatment (23.6% ±3.6%) was comparable to the *open* treatment, while the percentage of Ectinosomatidae in the *open* treatment (17.5% ±4.1%) was substantially lower than in the *closed* treatment. In the *open* treatment, the families Ameiridae and Miraciidae made up a bigger share of the community, with relative abundances of respectively 13.7% ±2.6% and 14.3% ±3.5%, in comparison to the *closed* treatment where both Ameiridae and Miraciidae had a relative abundance of 4.1% ±1.9% and 3.7% ±0.7%, respectively. The family Laophontidae was abundant in both the *open* and *closed* treatment with the *open* treatment showing a slightly higher percentage (12.1% ±1.3%) than the *closed* treatment (8.7% ±6.5%). Other abundant families were Canthocamptidae, which represented 6.3% ±1.8% of the harpacticoid community in the *open* treatment, and Harpacticidae, with an abundance of 6.7% ±6.7% in the *closed* treatment. After six days of colonization, the total number of families found in the *open* treatment was 11, while in the *closed* treatment this was 10. Here, the same families were found in the *open* and *closed* treatment, except for the Paramesochridae which was unique for the *open* treatment.

Within the Tisbidae, both *Tisbe* and *Scutellidium* showed a strong decline in abundances in comparison to day 2. While *Tisbe* was still the dominant genus in the *open* treatment, it only reached a relative abundance of 22.6% ±6.3%. In the *closed* treatment *Tisbe* was no longer the dominant genus, although here it had a higher abundance (23.6% ±3.6%) than in the *open* treatment. *Scutellidium* had a relative abundance of only 1.1% ±1.1% in the *open* treatment, and

was not recorded at all in the *closed* treatment. In both treatments, *Ectinosoma* reached higher abundances on day 6 than on day 2. Here, it was the dominant genus in the *closed* treatment (39.3% ±2.9%) and the second most abundant genus in the *open* treatment (17.5% ±4.1%). Within the Ameiridae, *Ameira* was only found in the *open* treatment (9.9% ±1.0%), while *Ameiropsis* was recorded in both the *open* (3.8% ±1.6%) and *closed* (4.1% ±1.9%) treatment. The family Miraciidae was mainly represented by *Amphiascus* in both treatments (*open*: 7.8% ±7.8%; *closed*: 2.2% ±2.2%). *Paralaophonte* was the most abundant genus of the Laophontidae, making up 7.6% ±3.2% of the *open* treatment and 7.2% ±5.0% of the *closed* treatment. Other genera of this family recorded on day 6 were in *open* treatment *Heterolaophonte* and *Laophonte*, with abundances of respectively 1.1% ±1.1% and 3.3% ±3.3%, and in the *closed* treatment *Esola*, with an abundance of 1.5% ±1.5%. The genera *Mesochra* (*open*: 4.9% ±0.5%; *closed*: 2.2% ±2.2%) and *Harpacticus* (*open*: 3.6 ±0.8%; *closed*: 6.7% ±6.7%) also made up a substantial part of the community in the *open*- and *closed* treatment, respectively. In total, 20 genera were recorded in the *open* treatment after 6 days of colonization, while in the *closed* treatment only 13 different genera were found.

Day 14

On day 14, Ectinosomatidae had the highest relative abundance in both the *open* (23.9% ±0.4%) and *closed* treatment (35.2% ±0.3%). The family Tisbidae made up a larger part of the community in the *open* treatment (20.1% ±1.9%) than in the *closed* treatment (9.2% ±1.3%). The same was true for the Laophontidae, with an abundance of 9.2% ±1.3% in the *open* treatment and 6.2% ±0.4% in the *closed* treatment. The families Canthocamptidae and Miraciidae showed comparable abundances in the *closed* treatment (16.0% ±1.5% and 15.0% ±3.4%, respectively) and made up a larger share of the community than in the *open* treatment, where both families were represented by 8.2% ±0.9% and 12.0% ±1.7%, respectively. Dactylopusiidae and Ameiridae showed comparable abundances in both the *open* treatment (7.5% ±1.6% and 6.7% ±3.6%, respectively) and the *closed* treatment (6.9% ±1.0% and 6.7% ±1.4%, respectively). After 14 colonization days, more families were recorded in the *open* (11) than in the *closed* treatment (8). Here, the families Canuellidae, Parastenheliidae and Tetragonicipitidae were only found in the *open* treatment.

The dominant family, Ectinosomatidae, was in both treatments only represented by the genus *Ectinosoma*, so contributions on genus level are the same as on family level (see above). In comparison to day 6, abundances of *Ectinosoma* were slightly lower in the *closed* treatment, while the *open* treatment showed higher abundances of this genus. *Tisbe* made up the largest part of the Tisbidae (*open*: 17.9% ±4.2%; *closed*: 9.2% ±1.3%), while *Scutellidium* was only present in the *open* treatment, at a low abundance (2.3% ±2.3%). Within the Laophontidae, *Paralaophonte* was

the most abundant genus, making up 13.5% ±1.7% and 5.6% ±1.0% of the *open* and *closed* treatment, respectively. *Laophonte* had very low abundances (<1.0%) in both treatments. *Mesochra* was the largest contributor to the Canthocamptidae, with abundances of 8.2% ±0.9% in the *open* treatment and 15.4% ±0.9% in the *closed* treatment. *Amphiascoides* (*open*: 4.5% ±1.4%; *closed*: 2.5% ±0.2%) and *Amphiascus* (*open*: 6.0% ±3.1%; *closed*: 9.5% ±3.7%) had the highest abundances within the Miraciidae. In other genera from this family only *Diosaccus* had an abundance greater than 1% (i.e. 1.9% ±0.7% in *closed* treatment). Genera from the family Dactylopusiidae had rather low abundances, with *Dactylopusia* being the most abundant (*open*: 4.5% ±0.1%; *closed*: 2.5% ±0.2%), followed by *Paradactylopodia* (*open*: 1.5% ±1.5%; *closed*: 2.5% ±0.2%) and *Diarthrodes* (open: 1.5% ±0.0%; *closed*: 1.9% ±0.7%). In the *open* treatment the Ameiridae were represented by *Ameira* (5.2% ±3.7%) and *Ameiropsis* (1.5% ±0.0%), while in the *closed* treatment only *Ameira* (6.7% ±1.4%) was found. After 14 days of colonization, a total of 20 genera were recorded in the *open* treatment, and 17 in the *closed* treatment.

Composition of the different body types

Classification according to body type (following Coull, 1977) shows that the natural situation is dominated by the fusiform prehensile body type (61.4% ±5.0) (Fig. 8) followed by the fusiform- (19.1% ±2.4%) and the fusiform depressed body type (13.5% ±7.3%). On day 2 of the colonization the fusiform depressed body type (mainly due to the presence of *Tisbe)* is the most abundant in both treatments, with relative abundances for the open and closed treatments being 62.6% ±14.4% and 55.9% ±15.1%, respectively. Other abundant body types are fusiform and fusiform prehensile. On day 6, the fusiform prehensile body type is dominant in the *open* treatment (51.0% ±2.3%) while in the *closed* treatment the fusiform (mainly *Ectinosoma*) body type makes up the largest percentage (40.8% ±1.4%). The fusiform depressed body type makes up an equal share in both treatments (respectively 23.7% ±7.5% and 23.6% ±3.6%). On day 14, both treatments are dominated by the fusiform prehensile body type which had comparable abundances in both the *open* (47.0% ±0.0%) and *closed* treatment (46.9% ±0.8%). The fusiform compressed body type is present in all coral samples and the compressed body type is found in three coral samples, both these body types are absent from the sediment. The sediment is dominated by the fusiform prehensile body type (84.3% ±0.3%) followed by the fusiform (non-prehensile) (10.4% ±1.6%) and with low abundances of the vermiform, fusiform depressed and fusiform body types.

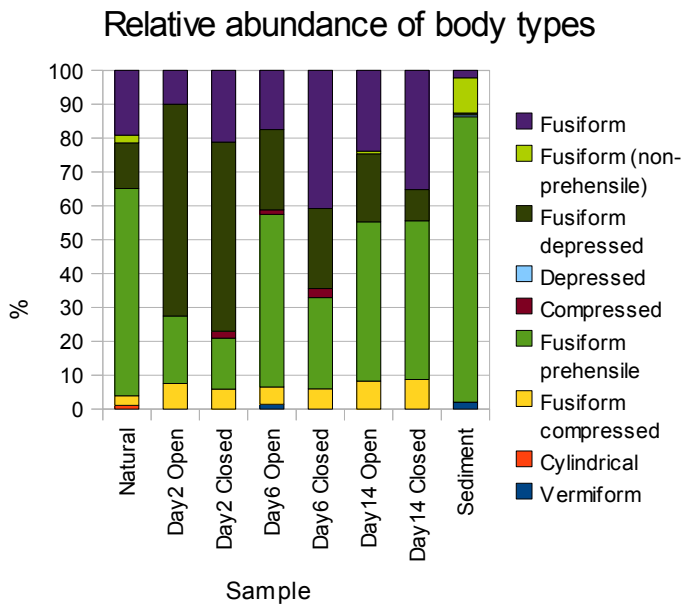


Fig. 8: *Relative abundances of different body types over different samples.*

Similarity analysis

MDS

The stress level of the 2-dimensional MDS is 0.09 which corresponds to a good ordination with no real prospect of a misleading interpretation. The ordination shows that the samples taken from the sediment are clearly separated from the coral samples. Within the coral samples it is hard to delineate clear groupings. Overall, samples taken on day 14 cluster closely together, and are also near samples of the natural situation. Samples taken on day 2 and day 6 show a high degree of scattering, with some close to the natural situation and some further away from it. MDS at the family level or of morphological types (not shown) produced the same overall plot with a clear separation of the sediment samples from the coral fragments, but no clear delineated groups within the coral samples.

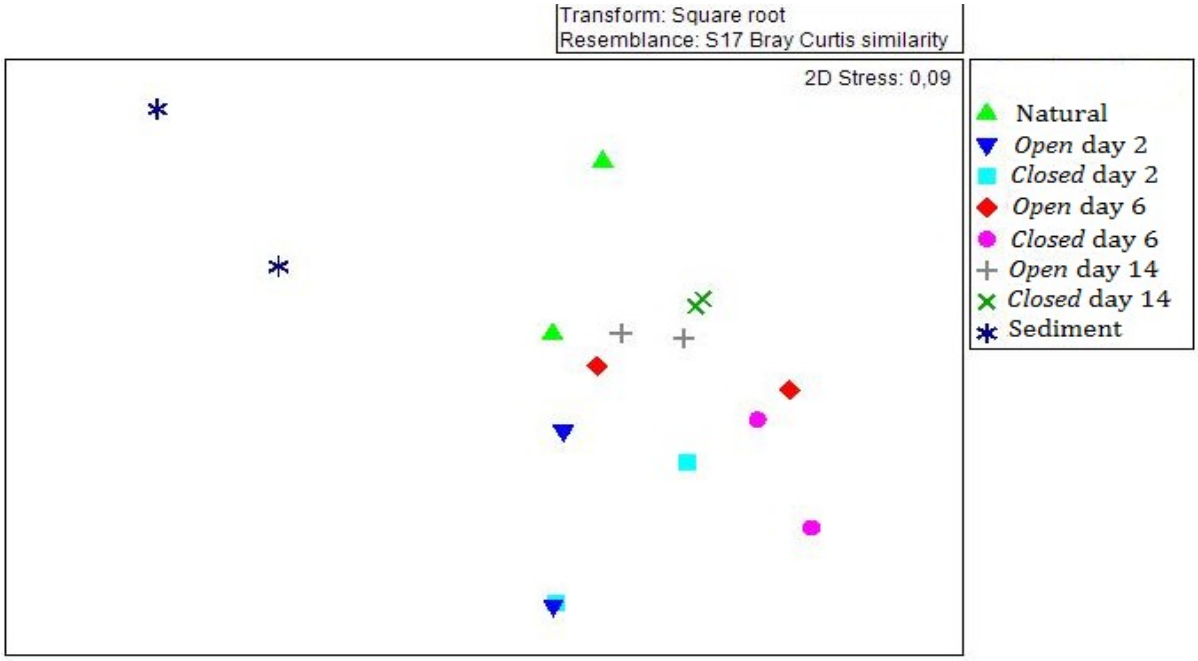


Fig. 9: *Multidimensional scaling two-dimensional ordination plot of all samples. Stress value is 0.09*

ANOSIM

A two-way crossed ANOSIM for the experimental coral samples indicated a significant difference in community composition between different days (global R = 0.389, p = 0.018), but absence of a significant difference between the *open*- and *closed* treatment (global R = -0.083, p = 0.63). A pairwise analysis did not indicate any significant differences between different days.

There was a significant difference in the harpacticoid community between the coral fragments and the sediment, as indicated by a one-way ANOSIM (global R = 0.929, p = 0.008).

A one-way ANOSIM for different days of the colonization experiment (without taking into account the different treatments) and the natural situation did not indicate any significant difference in community composition between them (global R = 0.545, p = 0.1).

SIMPER

A two-way SIMPER-analysis was conducted on the experimental coral samples (both *open*- and *closed* treatments for day 2, 6 and 14).

The similarity within the *open* treatment is 63.9% and within the *closed* treatment 65.1%. Dissimilarity between *open*- and *closed* treatment is 37.6%, which indicates only a small difference

between the two groups. Table 2 gives an overview of the five genera which contribute most to the differences between the two treatments. *Ectinosoma* has the greatest contribution to the dissimilarity between the two treatments (21.1%).

The similarity is 53.4% within day 2, 60.3% within day 6 and 79.9% within day 14. Dissimilarity between day 2 and day 6 is 49.3%. Here, the contribution of only three genera (*Tisbe*, *Ectinosoma* and *Scutellidium*) can explain half of the dissimilarity (Table 3). Dissimilarity between day 6 and day 14 is 39.5%, with *Tisbe* and *Mesochra* being the greatest contributors to dissimilarity. Dissimilarity between day 2 and day 14 is 55.2%, *Tisbe* is here also the main contributor to dissimilarity, followed by *Ectinosoma* and *Mesochra.*

A one-way SIMPER-analysis was conducted between the coral samples (both experimental and the natural) and the sediment samples. Similarity within the coral samples is 54.9% and within the sediment samples 49.7%. Dissimilarity between the coral- and sediment samples is 75.3%, which indicates a substantial difference between the two. The five genera which contribute most to this dissimilarity are listed in table 4.

Genus	Relative abundance		% Contribution	Cumulative %
	open	*closed*		
Ectinosoma	16.8	31.9	21.1	21.1
Tisbe	31.9	26.7	16.1	37.2
Ameira	8.4	4.0	8.1	45.3
Amphiascus	4.9	4.9	7.1	52.4
Paralaophonte	7.3	4.9	6.6	59.0

Table 2: *Results of the SIMPER-analysis for the open and closed treatments, only the five genera with the highest contribution to dissimilarity are given.*

Genus	Relative abundance		% Contribution	Cumulative %
	Day 2	Day 6		
Tisbe	51.1	23.1	28.7	28.7
Ectinosoma	15.1	28.4	13.7	42.4
Scutellidium	8.1	0.6	7.6	50
Paralaophonte	1.5	7.4	6.5	56.5
Amphiascus	2	5	5.5	62
	Day 6	Day 14		
Tisbe	23.1	13.5	14	14
Mesochra	3.6	11.8	10.4	24.4
Amphiascus	5	7.8	9.5	33.9
Ameira	4.9	5.9	7.2	41.2
Paralaophonte	7.4	9.5	6.8	48
	Day 2	Day 14		
Tisbe	51.1	13.5	34.1	34.1
Ectinosoma	15.1	29.55	13.1	47.2
Mesochra	0.8	11.8	10	57.1
Paralaophonte	1.5	9.5	7.3	64.4
Scutellidium	8.1	1.1	6.3	70.7

Table 3: *Results of the SIMPER-analysis for days 2, 6 and 14. Only the five genera with the highest contribution to dissimilarity are given.*

Genus	Relative abundance		% Contribution	Cumulative %
	Coral	Sediment		
Tisbe	4.9	0.5	10.0	10.0
Ectinosoma	4.6	0.9	8.3	18.3
Brianola	0.0	3.1	7.0	25.3
Diagoniceps	0.0	2.8	6.5	31.8
Phyllopodopsyllus	0.3	3.1	6.1	37.9

Table 4: *Results of the SIMPER-analysis for coral fragments (both natural and experimental) and sediment samples. Only the five genera with the highest contribution to dissimilarity are given.*

Diversity estimates

Estimation of expected number of genera for n=25 [EG(25)] are summarized in table 5. The background community on coral has the highest diversity (11.8). During the experiment diversity was lowest on day 2. Day 6 had the highest diversity in the open treatment, but diversity in the closed treatment was remarkably lower. On day 14 diversity was a little lower than the background diversity for both treatments. Diversity in the sediment was also lower than in the background community on coral fragments. There were no significant differences found in EG(25) between different days (Kruskal-Wallis ANOVA, $p = 0.12$) or different treatments (Mann-Whitney U-test, $p = 0.054$).

	EG(25)	SD
Natural	11.8	0.1
Day 2 *open*	7.8	1.9
Day 2 *closed*	6.6	1.0
Day 6 *open*	11.2	0.5
Day 6 *closed*	7.9	0.6
Day 14 *open*	10.4	0.2
Day 14 *closed*	9.4	0.4
Sediment	8.4	0.4

Table 5: *Expected number of genera for n = 25 [EG(25)] for different samples and standard deviation.*

Discussion

Characterization of the background community

The natural community on coral fragments was found to be an assemblage of both phytal (e.g. *Tisbe*, *Scutellidium*, *Dactylopusia*), eurytopic (e.g. *Ectinosoma*) and sediment-associated (e.g *Ameira*, *Amphiascus*) taxa [see Noodt (1971) for classification]. Eurytopic taxa can be found in a wide variety of habitats (e.g. mud, sand, phytal) (Gheerardyn *et al*., 2008) while phytal taxa are commonly associated with seagrasses and macroalgae (Noodt, 1971; Hicks, 1985) but have also been recorded on hard substrates (Atilla *et al*., 2003). Gheerardyn *et al*. (2008) explains the presence of both phytal and sediment-associated taxa by the structure of these coral fragments, where trapped sediment provides a suitable habitat for sediment-dwellers and the complex microtopography of the coral branches represents a suitable substratum for true epibenthic or even phytal harpacticoids. The natural assemblage on dead coral fragments at the experimental site (near Fumba) was quite comparable in composition to the assemblages described by Gheerardyn *et al*. (2008) on coral fragments along the eastern coast of Zanzibar. Although almost all recorded taxa were the same, a slightly different abundance pattern was found. Meiofaunal communities have been found to be variable both between and within reef zones (Ndaro & Ólafsson, 1999; Armenteros *et al*., 2010). These differences can be caused by several factors, such as food availability (algal biomass), predation pressure and substrate complexity (Klumpp *et al*., 1988)

Multivariate analysis showed that the harpacticoid community on coral fragments differed significantly from those in the surrounding sediment. This was also found in other studies where harpacticoid communities of hard substrates were compared to the surrounding sediment (e.g. Atilla *et al*., 2003; Gheerardyn *et al*., 2008). A SIMPER-analysis showed that differences in community composition between the coral fragments and the sediment were caused by a) high abundances of phytal (e.g. *Tisbe*) and eurytopic (e.g. *Ectinosoma)* taxa on the coral fragments and b) the presence of sediment-associated taxa in the sediment (e.g. *Brianola*, *Diagoniceps, Phyllopodopsyllus*) which were absent or occurred with very low abundances on the coral fragments. These results are similar to the studies by Atilla *et al*. (2003) and Gheerardyn *et al*. (2008), in which high abundances of typical phytal taxa were found on the hard substrates. These taxa were absent or rare in the sediment, while specific other taxa were restricted to the sediment.

Within the sediment samples, there was a great difference in composition between the two replicates. This was mainly due to the dominance of *Diagoniceps* in one replicate, while this genus was absent from the other. Hicks & Coull (1983) found that carbonate sediment assemblages can be

extremely localized. They found a coarse shell- gravel patch to be dominated by *Phyllopodopsyllus* (a member of the same family as *Diagoniceps*) while 200m further they only found two specimens of this genus over a period of 10 years in a site that was monthly sampled. A similar pattern was found in Gheerardyn *et al*. (2008), where *Diagoniceps* dominated the sediment at one location, while it occurred only with low abundances in another site. The sediment in which *Diagoniceps* dominated contained a large coarse sand fraction. Although there are no data available on the specific granulometry of the two replicates which were used to characterize the community in the sediment, it could be hypothesized that differences between both replicates are caused by a different granulometric composition of the sediment. A coarser sediment in replicate B would then explain the high abundance of *Diagoniceps*.

Temporal dynamics of the harpacticoid community during colonization

A two-way crossed ANOSIM between different days gave a low global R-value (global R = 0.389), this indicates that the different day were barely separable from each other. However, some abundance- and diversity patterns could be observed over the course of the colonization experiment.

After two days of colonization, there was already a substantial diversity of harpacticoid genera on the coral fragments. Copepods are generally fast colonizers due to their high motility and ability to actively emerge from the substrate, and are mostly the first to colonize a newly available habitat (Palmer, 1988). Most studies observe a rapid colonization by meiofauna, with total abundances reaching, and even exceeding, the natural situation early during colonization (e.g. Chertoprud *et al*., 2005; De Troch *et al*., 2005). Next to high abundances, these studies also found the establishment of a highly diverse community, even within a few hours. However, De Troch *et al*. (2005) found that nematodes were the dominant group during early colonization stages on artificial seagrasses and hypothesized that arrival of copepods was dependent on the development of a biofilm on the substrate.

The ability to rapidly colonize free space seems to be species-specific, with the sequence of colonization succession related to the life style and motility of the different harpacticoid species. Sun & Fleeger (1994) found that phytal and epibenthic species (e.g. *Coullana* sp., *Halicyclops coulli*) were generally fast colonizers while interstitial and burrowing species (e.g. *Nannopus palustris*) appeared later during colonization. In the present experiment, phytal taxa were found to be dominant on day 2 of the colonization experiment. Members of the genus *Tisbe* were the fastest colonizers, making up approximately half of the community after two days of colonization. Several behavioral and morphological aspects are related with their ability to quickly colonize newly

available habitats. Members of this genus live near the surface of the sediment or on macroalgae (Huys *et al*., 1996), which makes them more susceptible to suspension in the water column because of the more exposed nature of these habitats (Hicks, 1992). Walters & Bell (1994) also observed *Tisbe furcata* actively entering the water column through emergence. The combination of both passive erosion and active emergence will enable a high number of individuals to enter the water column, which will increase the availability of recruits for colonization via the water column. They are also known to be good swimmers, which is reflected by their cyclopoidean appearance (Noodt, 1971), and several studies already suggested that phytal meiofauna have good dispersing capabilities with the ability to travel trough the water column for relatively long distances (Palmer & Gust, 1985; Kurdizel & Bell, 1992). Palmer (1988) assumes that active habitat selection can be expected in these strong swimmers and this could give them the ability to rapidly colonize free space. Next to *Tisbe*, two other phytal genera, *Scutellidium* and *Diarthrodes,* were abundant on day 2 of the colonization. Most phytal taxa found on these coral fragments (i.e. *Dactylopusia*, *Harpacticus*, *Tisbe*, *Scutellidium*, *Diarthrodes*) have richly setose legs which are well adapted to swimming (Giere, 2009) and a prehensile first pair of pereiopods for clinging to the substrate. These morphological adaptations probably allow them to quickly colonize a new habitat and attach to it, as the rough surface of coral skeletons may favour copepods with strongly prehensile maxillipeds and first legs for efficient clinging (Gheerardyn *et al*., 2008). The overall relative abundance of phytal genera decreased over the course of the colonization experiment and they were no longer dominant after six days of colonization. However, certain families classified as phytal (i.e. Harpacticidae, Dactylopusiidae) were found in higher abundances on later days. This may reflect their inferior colonization capabilities in comparison to, for example, Tisbidae.

Eurytopic genera, of which Ectinosoma was the most abundant representative, occur in most marine habitats (sand, mud, phytal) and appear to be 'jacks-of-all-habitats' (De Troch et al., 2005). On day 2, they were already found in high abundances. Furthermore, on day 6 of the colonization experiment Ectinosoma had the highest relative abundance in the closed treatment, and there was a substantial increase in the open treatment. After 14 days of colonization Ectinosoma was the dominant genus in both treatments. Ectinosomatids are known to be good swimmers (Noodt, 1971) and active emergence from the sediment has also been recorded for this group (Walters & Bell, 1994; Thistle & Sedlacek, 2004). Furthermore, they are found in a wide array of benthic habitats (e.g. muddy and sandy sediments, macroalgae) (Huys et al., 1996). Their ability to make use of a wide range of habitats can explain why they were found to be the dominant group on coral fragments during later colonization stages. As the coral fragments were cleaned before the colonization experiment, all the sediment was removed from between the coral branches. During

the experiment, more sediment was retained between the coral branches as time progressed, creating different microhabitats on the coral fragments. In addition to coral branches, which might be a suitable substratum for true epibenthic or phytal harpacticoids, the accumulation of sediment can provide a microhabitat for sediment-dwellers. As ectinosomatids are found in both sandy sediments and in phytal habitats (Huys et al., 1996), they are likely to be found in both microhabitats provided by these coral fragments. This can explain why ectinosomatids were found at greater abundances during later colonization stages than groups who can only make use of one specific microhabitat on these coral fragments.

Of the sediment-associated harpacticoids, mostly fusiform prehensile forms (e.g. Ameira, Amphiascus, Mesochra, Paralaophonte) were found. These are good swimmers that live on sand and soft bottoms (Noodt, 1971). Other body types such as vermiform or cylindrical, which are mostly associated with an interstitial and burrowing lifestyle, were rarely found on coral fragments. The relative abundance of sediment-associated harpacticoids increased during the colonization experiment. Although none of the genera of this group becomes dominant, the group as a whole (represented mainly by fusiform prehensile forms) dominates the harpacticoid community after 14 days of colonization. Ameira is the fastest sediment-associated colonizer, this genus was also found to be dominant in the natural situation and in one sediment replicate. The high abundance of Ameira in the surrounding environment can be an explanation for the fast colonization by this genus. On day 2 of the colonization experiment, the relative abundance of the families Miraciidae, Canthocamptidae and Laophontidae was low, while on day 6 and day 14 they already made up a substantial part of the harpacticoid community. There are two possible factors which can explain the relatively low abundances of these families on day 2 of the colonization experiment, while they make up a substantial part of the community on day 6 and 14. First, these sediment-associated taxa may have slower dispersal rates, which causes them to arrive later during colonization. Second, the amount of sediment retained between the coral branches increases with time, which causes an increase in potential habitats for sediment- associated taxa. Both the colonization capabilities and the amount of suitable habitats on the coral fragments can be factors which influence the relative abundances of these taxa during colonization.

There was a significant difference in copepodid abundance between different days. Abundances of copepodids where highest on day 2 and day 6 and lowest on day 14. Hicks (1992) found that copepodids are more easier suspended in the water column through passive erosion than adults. This could increase the amount of potential copepodid recruits in the water column, which could give them the ability to colonize coral fragments faster than adults. This could explain the higher abundances of copepodids on earlier days during colonization. Sun & Fleeger (1994) also found a

demographic colonization pattern for an epibenthic species (*Coullana* sp.), where significantly more males and copepodids colonized defaunated sediment than females. The results of the present study can indicate that there are differences in dispersal between different age classes, with copepodids showing on average higher dispersal rates than adults.

Colonization mode

No significant differences between the *open* and *closed* treatments were found. Almost all genera found in the *open* treatment were also recorded in the *closed* treatment. However, some differences in relative abundance of certain taxa were found between the two treatments.

These results indicate that most genera are able to colonize the coral fragments via the water-column. As coral fragments in the *closed* treatment were separated from the sediment by the walls and bottom of the core, colonizers had to enter the water column and disperse at least 5cm above the seafloor to be able to reach the coral fragments. However, the possibility that some individuals reached the coral fragments by crawling over the cores should not be excluded. Hicks & Coull (1983) suggested already that our traditional concept of benthic copepods as bound to the sediment must be re-assessed. A number of studies have convincingly shown that both adult and juvenile harpacticoid copepods are regularly found in the water column (e.g. Palmer, 1988; Sun & Fleeger, 1994; Atilla *et al*., 2003; Thistle & Sedlacek, 2004). Harpacticoids can enter the water column either through passive erosion from the sediment or active entry into the water column (emergence) (Palmer, 1988). Results from this study are unable to asses whether colonizers entered the water column due to active or passive processes.

Although no significant difference between both treatments was found, there was a noticeable difference in relative abundances of certain genera. On day 6, sediment-associated genera (i.e. *Ameira*, *Amphiascus*, *Mesochra*) had a higher relative abundance in the *open* treatment than the *closed* treatment. While in the *closed* treatment, eurytopic genera (mainly *Ectinosoma)* had a higher relative abundance than in the *open* treatment. This could be caused by a difference in recruitment to the water column between these different groups. A SIMPER-analyses showed that *Ectinosoma* had the greatest contribution to differences between both treatments, with higher abundances in the *closed* treatment than in the *open* treatment. This indicates that *Ectinosoma* can easily colonize coral fragments through the water column. The sediment-associated genera on the other hand had lower abundances in the *closed* treatment, which indicates that they colonize coral fragments mainly through the sediment and show slower colonization via the water column. Although these genera do disperse via the water column, they can probably better resist to passive erosion and/or show less emergence behavior than eurytopic species.

The genera Karllangia and Phyllopodopsyllus were only recorded in the open treatments, while they were completely absent from the closed treatments. Phyllopodopsyllus was only found on day 14 in the open treatment, while Karllangia was found at all days during the colonization experiment. This indicates that these genera only colonized the coral fragments through the sediment, and that there was no dispersal via the water column. Taxa that do not disperse via the water column must have the ability to resist passive erosion and must lack emerging behavior. Thistle & Sedlacek (2004) attempted to distinguish emerging- from non-emerging copepods using a set of morphological characteristics. They hypothesized that morphological characters associated with swimming should be characteristic for emerging copepods. Therefore, they used the morphology of pereiopods 2-4, which are the primary locomotor appendages in copepods, to predict whether a species was an emerger or a non-emerger. Emerging species were characterized by pereiopods 2-4 with 3 endopodal segments and 5 or more setae and spines on the distal exopodal segments. Non-emerging species were characterized by only 2 endopodal segments and 4 or fewer setae and spines on the distal exopodal segement on these appendages. In this study, Phyllopodopsyllus sp. was classified as non-emerger based on these morphological characteristics, and the results support the finding of Thistle & Sedlacek (2004) that members of this genus do not show emerging behavior. The absence of Karllangia in the closed treatments also indicates that this is a non-emerging taxon. However, the pereiopods 2-4 of Parastenheliidae typically have 3 endopodal segments and more than 5 spines and setae on the distal segments of the exopods (Huys et al., 1996). This finding indicates that the morphology-based classification of Thisle & Sedlacek (2004) is probably not generally applicable. Therefore, experiments are needed to specifically asses the emerging behavior of single species before any decisive conclusions can be drawn.

Conclusions

Temporal succession patterns on dead coral fragments depend on the life-style and morphology of the colonizers. Phytal taxa show a fast colonization rate and high abundances during the initial colonization phase. Eurytopic and sediment-associated taxa have higher colonization rates during later stages of the colonization process in which they dominate the harpacticoid community. Most taxa seem to have the ability to colonize coral fragments via the water column. However, colonization along the substrate surface can also be important, and this seems especially true for sediment-associated taxa, which showed lower colonization rates when migration through the sediment was hindered.

The coral fragments were mainly colonized by taxa also found in the natural community on coral fragments. After two days the five most abundant and almost half of the other genera found in the reference community are also found in the experimental community. Furthermore, genera absent in the reference community were also found (albeit in low abundances) in the experimental community. These included mainly phytal genera (i.e. Diarthrodes, Diosaccus, Harpacticus and Tegastes), but also some sediment-associated genera (i.e. Karllangia and Schizopera). This fast colonization and initial high diversity is consistent with other studies (Chertoprud et al., 2005; De Troch et al., 2005) in which, during the first phases of the recolonization process, there was a rapid increase in diversity followed by a slowing down of this process. Chertoprud et al. (2005) define a colonization process in which two stages are distinguished during the formation of the harpacticoid communities. A first stage, which lasts a few days, is characterized by active colonization of free space with rapidly increasing species diversity and abundance due to a significant extent to the species which are rare in the reference community. Subsequently (approximately after one week), the colonization process decelerates to result in a relatively uniform and stable dominant structure close to that in the reference community (the smoothing stage). This two-stage scenario of primary succession seems to apply to the present study in which similar trends have been found.

Coral fragments were also found to harbour a different community than the surrounding sediment. These coral fragments thus contribute to the overall diversity in lagoonal carbonate sediments.

Samenvatting

Een groot deel van het intertidaal in tropische lagunes bestaat vooral uit onbedekt koraalzand en degraderende kalkskeletten van marine organismen. Deze dergaderende kalkskeletten, zoals stukken dood koraal, bieden een grote verscheidenheid aan microhabitats voor benthische meiofauna. Harpacticoide copepoden spelen een belangrijke trofische rol in deze sedimenten en zijn er meestal het dominante taxon. Daarom is het belangrijk om de dynamiek van de copepoden gemeenschap te begrijpen, want deze zijn van fundamenteel belang voor veel ecosysteemprocessen.

Langs de kust van Zanzibar, Tanzania zijn kolonisatie-experimenten op stukken dood koraal uitgevoerd. Tijdens deze experimenten werd nagegaan of biogene substraten gekoloniseerd werden vanuit het onderliggend sediment of via de waterkolom door harpacticoide copepoden en hoe de gemeenschap van veranderde in de tijd.

De stukken dood koraal werden snel gekoloniseerd en na twee dagen was er al een hoge diversiteit aanwezig. De kolonisatie snelheid bleek vooral afhankelijk te zijn van de morfologie en levenswijze van de soorten. Epifytische soorten waren snelle kolonisatoren, met hoge abundanties in het initiële kolonisatie stadium. Sediment-geassocieerde en eurytopische soorten vertoonden een tragere kolonisatie snelheid en waren abundanter in het latere kolonisatie stadium. De meeste soorten konden de koraalfragmenten koloniseren via de waterkolom, hoewel niet alle taxa met dezelfde snelheid via de waterkolom konden disperseren.

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Appendix

List of identified families and genera

Ameiridae Boeck, 1865

Ameira, Boeck, 1865

Ameiropsis Sars, 1907

Psyllocamptus T. Scott, 1899

Sarsameira Wilson, 1924

Canthocamptidae Brady, 1880

Mesochra Boeck, 1865

Nannomesochra Gurney, 1932

Canuellidae Lang, 1944

Brianola Monard, 1927

Canuella Scott & Scott, 1893

Cletodidae T. Scott, 1905

Genus 1

Dactylopusiidae Lang, 1963

Dactylopusia Norman, 1903

Diarthrodes Thomson, 1883

Paradactylopodia Lang, 1944

Ectinosomatidae Sars, 1903

Ectinosoma Boeck, 1865

Halectinosoma Vervoort, 1962

Halophytophilus Brian, 1919

Microsetella Brady & Robertson, 1873

Pseudobradya Sars, 1904

Sigmatidium Giesbrecht, 1881

Harpacticidae Dana, 1846

Harpacticus Milne-Edwards, 1840

Perissocope Brady, 1910

Zausodes Wilson, 1932

Laophontidae T. Scott, 1905

Esola Edwards, 1891

Heterolaophonte Lang, 1948

Laophonte Philippi, 1840

Paralaophonte Lang, 1948

Apistophonte Gheerardyn & Fiers, 2006

Longipediidae Boeck, 1865

Longipedia Claus, 1862

Louriniidae Monard, 1927

Lournia Wilson, 1924

Miraciidae Dana, 1846

Amphiascoides Nicholls, 1941

Amphiascus Sars, 1905

Bulbamphiascus Lang, 1944

Diosaccus Boeck, 1873

Robertgurneya Lang, 1948

Robertsonia Brady, 1880

Schizopera Sars, 1905

Stenhelia Boeck, 1865

Paramesochridae Lang, 1944

Apodopsyllus Huys, 2009

Emertonia Wilson, 1932

Parastenheliidae Lang, 1936

Karllangia Noodt, 1964

Parastenhelia Thompson & Scott, 1903

Tegastidae Sars, 1904

Tegastes Norman, 1903

Tetragonicipitidae Lang, 1944

Diagoniceps Willey, 1930

Phyllopodopsyllus T. Scott, 1906

Tisbidae Stebbing, 1910

Scutellidium Claus, 1866

Tisbe Lilljeborg, 1853