CYCLICAL DEVELOPMENT AND COMMUNITY STRUCTURE OF THE INTERTIDAL POLYCHAETE REEFS IN THE JERAM MUDFLAT, PENINSULAR MALAYSIA

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CYCLICAL DEVELOPMENT AND COMMUNITY STRUCTURE OF THE INTERTIDAL POLYCHAETE REEFS IN THE JERAM MUDFLAT, PENINSULAR MALAYSIA

ABSTRACT

It is interesting but not clear how "hard" polychaete reefs can grow up on soft-bottom mudflats in tropical waters. Such polychaete reefs are also generally unknown in terms of their community structure and duration of existence. Ecological aspects of the polychaete reefs on Jeram intertidal mudflat were studied to 1) elucidate the faunal succession during the life cycle of the reef, in terms of species composition and spatio-temporal abundance; 2) examine the accompanying changes of the adjacent mudflat community structure; and 3) determine the relationship between the reef cycle and the hydrometeorological factors such as the wind field, current, erosion and sedimentation. Samplings on the polychaete reefs and mudflat were carried out from June 2012 to January 2014 to study the physical environment and the macrobenthic community. The macrobenthos were examined on both spatial (horizontal and vertical distribution) and temporal (monthly changes) scales. The Jeram polychaete reef cycled through four phases within a year: pre-settlement phase (March–May), growth phase comprising primary (May–November) and secondary (October–January) successional stages, stagnation phase (December–January) and destruction phase (January–March). At the onset of the southwest monsoon (May), strong erosive forces initiate the reef's primary succession of the growth phase where the dominant polychaete *Sabellaria jeramae* (>90 % of the reef macrobenthos density) colonise on the exposed lag deposits of shells. During the northeast monsoon (November–March), stronger depositional forces cover the developed reef with fine sediments. Subsequently, this reef is colonised by another polychaete, the spionid *Polydora cavitensis* during the reef's secondary succession of the growth phase. Polychaetes are the only inhabitants living inside the ephemeral Jeram reef clumps during

all successional phases of the reef cycle, with a total of 21 species. Overall, total polychaete abundance decreased from surface to deeper zones of the reef. *S. jeramae* dominated the entire reef depth during primary succession. A mixed *S. jeramae–P. cavitensis* community dominated the surface zone (depth= 0–5cm) during secondary succession, but no polychaetes except *P. cavitensis* were found at the surface zone during the stagnation phase. Five major taxa (Polychaeta, Anomura, Gastropoda, Caridea and Brachyura) dominated the immediate mudflat macrobenthos. However, the mudflat macrobenthos play no obvious or direct role in initiating the growth of the reef which is likely the result of settlement of dispersed polychaete larvae from unknown offshore reefs. Generally, the reef presence has a positive effect on the presence or abundance of surrounding mudflat macrobenthos such as mudflat polychaetes, shrimps, crabs and gastropods.

Keywords: Sabellariidae, Spionidae, polychaete reef, macrobenthos

KITARAN PEMBENTUKAN DAN STRUKTUR KOMUNITI TERUMBU POLYCHAETA DI KAWASAN PASANG SURUT LAPANGAN BERLUMPUR DI JERAM, SEMENANJUNG MALAYSIA

ABSTRAK

Adalah menarik tetapi tidak jelas bagaimana terumbu polychaeta yang berfizikal keras dapat terbentuk pada kawasan berlumpur di perairan tropika. Secara umumnya, pengetahuan mengenai terumbu polychaeta tersebut dari segi struktur komuniti serta kewujudannya adalah tidak diketahui. Dengan itu, aspek ekologi terumbu polychaeta di lapangan berlumpur Jeram telah diselidik bagi 1) memahami perubahan/perwarisan fauna dari segi komposisi spesies dan kelimpahan (bertempat dan bermasa) dalam kitaran hidup terumbu tersebut; 2) mengkaji perubahan serentak yang berlaku pada komuniti lapangan berlumpur disekitar terumbu; dan 3) menentukan hubungan antara kitaran hidup terumbu dengan faktor-faktor hidro-meteorologi seperti medan angin, arus, hakisan dan pemendapan. Persampelan pada terumbu polychaeta dan lapangan berlumpur telah dijalankan dari Jun 2012 hingga Januari 2014 untuk mengkaji persekitaran fizikal dan komuniti makrobentik. Makrobenthos telah diperiksa dari segi skala bertempat (sebaran mendatar dan menegak) dan bermasa (perubahan bulanan). Kitaran hidup terumbu polychaeta di Jeram merangkumi empat fasa dalam tempoh setahun: fasa pra-penempatan (Mac–Mei), fasa pertumbuhan termasuk peringkat pewarisan utama (Mei–November) dan peringkat pewarisan sekunder (Oktober–Januari), fasa genangan (Disember–Januari) dan fasa penghapusan (Januari–Mac). Semasa monsun barat daya (Mei), hakisan kuat memulakan peringkat pewarisan utama terumbu di mana spesies dominan iaitu *Sabellaria jeramae* (merangkumi >90 % daripada kelimpahan makrobenthos terumbu) bertapak di permukaan cangkerang yang terdedah. Semasa monsun timur laut (November–Mac), proses pemendapan yang lebih berpengaruh meliputkan terumbu yang telah dibentuk dengan sedimen halus, dan seterusnya diambil alih spesies polychaeta yang lain iaitu

spionid *Polydora cavitensis* semasa peringkat pewarisan sekunder dalam fasa pertumbuhan. Polychaeta merupakan satu-satunya kumpulan organisma yang menghuni terumbu tersebut dalam semua fasa pembentukan di sepanjang kitaran hidup terumbu, dengan sejumlah 21 spesies. Secara keseluruhan, jumlah kelimpahan polychaeta menurun dari permukaan terumbu hingga ke zon yang lebih mendalam. *S. jeramae* mendominasi keseluruhan terumbu semasa peringkat pewarisan utama. Komuniti majmuk yang terdiri daripada *S. jeramae* dan *P. cavitensis* mendominasi zon permukaan (kedalaman= 0–5 cm) semasa peringkat pewarisan sekunder, tetapi tiada polychaeta kecuali *P. cavitensis* ditemui di zon permukaan semasa fasa genangan. Lima taxa utama (Polychaeta, Anomura, Gastropoda, Caridea and Brachyura) mendominasi komuniti makrobenthos lumpur di sekitar terumbu. Walau bagaimanapun, makrobenthos tersebut tidak memainkan peranan yang jelas atau secara langsung dalam proses pembentukan/pertumbuhan terumbu yang berkemungkinan disebabkan oleh penyebaran larva polychaeta dari kawasan terumbu di luar perairan yang tidak diketahui. Sebaliknya, kehadiran terumbu mendatangkan kesan positif ke atas kelimpahan makrobenthos lumpur disekitarnya seperti polychaeta, udang, ketam dan gastropod yang berpenghuni di kawasan tersebut.

Kata kunci: Sabellariidae, Spionidae, terumbu polychaeta, makrobenthos

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LIST OF SYMBOLS AND ABBREVIATIONS

cm	centimeter
°C	Degree Celsius
E	east
S_{eff}	effective number of species
ECMWF	European Centre for Medium-Range Weather Forecast
g/l	gram per litre
GrADS	Grid Analysis and Display System
MMD	Malaysian Meteorological Department
MHWN	mean high water neaps
MHWS	mean high water springs
MLWN	mean low water neaps
MLWS	mean low water springs
µm	micrometer
N	north
NEM	north east monsoon
NW	northwest
n	number of observations
ppt	part per trillion
%	percentage
H'	Shannon-Wiener index
SWM	south west monsoon
S	species richness
SD	standard deviation
WSPD	surface wind speeds
×	times

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CHAPTER 1: INTRODUCTION

1.1   An overview of Sabellariidae

The polychaete family Sabellariidae Johnston, 1865 consists of 12 genera, with the genus *Sabellaria* Lamarck, 1818 being the most described taxon with 41 valid species (Nishi et al., 2015) distributed from temperate to tropical coasts (Posey et al., 1984; Dubois et al., 2002, 2006; Polgar et al., 2015). Sabellariids are sedentary polychaetes with a body consisting of three regions: the head, the parathorax, and the abdomen. The head of an individual is crowned with an operculum of golden paleae (spinous setae) which protects the worm from predators and prevents dessication. The slender caudal end of the worm is reflected forward under the abdomen so that the faecal pellets are excreted from the mouth of the tube. Sabellariids, which are also known as honeycomb worms, are capable of secreting mucoproteinaceous cement that mould sand and shell particles together to form tubes. These tubes can be solitary, or they could aggregate as colonies that eventually coalesce into biogenic masses or reefs. Their reefs typically develop in the intertidal or subtidal zone along exposed coasts that are subject to dynamic wave actions and tidal currents (Dubois et al., 2006). Such reefs also exist to depths of 100 m (Kirtley & Tanner, 1968). Under optimum environmental conditions (i.e. moderate hydrodynamics, availability of hard substrates), the reef framework may range from ball-shaped clumps adhering to rocks which are commonly found at the mid–level of the intertidal zone to large platform aggregations at the lower level of the intertidal zone (Dubois et al., 2002). In some places, the reefs cover large areas and contain structural stages that feature different infaunal assemblages. For example, the well-known *Sabellaria alveolata* reefs in the Mont Saint-Michel Bay, France, cover some 65 hectares (Noernberg et al., 2010).

The bioconstructions of sabellariids are significant both geologically and biologically. The tolerance of the worms to thrive under dynamic conditions and to extend

their tube masses upward and seaward by retention and agglutination of littoral drift particles make them critical vectors in coastline development. The crevices of the reefs also act as traps for sediment and shell fragments, thereby further facilitating sediment retention (Gram, 1968). Being wave resistant, the reefs display the role as a buffer zone which dissipates the high–energy waves and retard coastal erosion (Multer & Milliman, 1967).

In fact, the reefs are globally recognised as local hotspots of biodiversity by enhancing the topographic complexity (Escapa et al., 2004), and thereby increase the surface area to accommodate diverse invertebrate benthic species that inhabit the surf zone (Dubois et al., 2002). However, polychaete reefs constitute a highly dynamic habitat subject to various natural perturbations (e.g. cold winters or storms) and are frequently threatened by anthropogenic disturbances (Dubois et al., 2006). Besides the bioengineer species themselves, associated species could also be affected by the degradation of the reef.

1.2   The Jeram polychaete reef

In particular, ecological knowledge of tropical sabellariid polychaete reefs is relatively scarce (Nishi et al., 2010). The polychaete reef at Jeram shore in Klang Strait, Malaysia, was first documented by Seilacher (1984), who described its formation as the outcome of a sequence of alternating stormy (shell deposition) and calm (mud deposition) weather events that drove the cycle of reef formation and destruction. Specifically, he hypothesised that, amidst such events, the dead reefs that remained below the mud were revived and built over again by reef macrobenthos when environmental conditions became favourable. However, it is not clear how the "hard" polychaete reef could grow on soft-bottom mudflats such as in Jeram. Furthermore, it is also not clear whether these biogenic structures are short-lived or long-lasting ones.

Recently, Ribero and Polgar (2012) and Polgar et al. (2015) redescribed the Jeram polychaete reef in the light of new data from the reef faunal succession. The reef is now known to be dominated by *Sabellaria jeramae*, which was just recently described after the type locality (Nishi et al., 2015). Polgar et al. (2015) reported that the *S. jeramae* reef in the Jeram shore had four successional phases: pre-settlement, growth, stagnation, and destruction, which are similar to those of *S. alveolata* reefs in Mont Saint-Michel Bay, France (Gruet, 1986; Dubois et al., 2002, 2006). However, the reef cycle from the initial colonisation by *S. alveolata* to the final morphological development of the reef surface took more than ten years (Gruet, 1986). At present, the length of Jeram polychaete reef cycles in tropical waters is unknown.

1.3   Research aims and objectives

Given that the marine environment of the Malacca Strait is strongly influenced by the Asian monsoonal regime, i.e. the summer or southwest monsoon (SWM) from May to September and the winter or northeast monsoon (NEM) from November to March, it is hypothesised that the life cycle of the Jeram polychaete reef is annual, being influenced by the alternating SWM and NEM periods. Wave effects via the monsoon wind regime are expected to form part of the erosive and sedimentological forces modulated by the macro-tidal environment of the Klang Strait. The objectives of this study are thus to

1) elucidate the faunal succession during the life cycle of the reef, in terms of species composition and spatio-temporal abundance;

2) examine the accompanying changes of the adjacent mudflat community structure; and

3) determine the relationship between the reef cycle and four hydrometeorological factors: wind field, currents, erosion and sedimentation.

CHAPTER 2: LITERATURE REVIEW

2.1   Life history

Sabellariids undergo a bentho-pelagic life cycle including a planktonic larval stage and two sedentary benthic juvenile and adult stages. Cazaux (1970) revealed that *S. alveolata* larvae on the French Atlantic coast exhibits a planktonic lifespan estimated to be about 12 weeks. However, the larvae are capable of delaying their metamorphosis if optimal habitat conditions for settlement are not encountered (Pawlik, 1988a). Upon settling onto some suitable substrate (e.g. shells, conspecific adult tubes), the larva develops into a juvenile, and eventually becomes an adult within a month (Eckelbarger, 1976). Sabellariids are dioecious and iteroparous breeders that attain sexual maturity after one year (Dubois et al., 2007). They have a mean lifespan of 4 to 5 years, but some individuals are known to survive up to 8-10 years (Gruet, 1986; Wilson, 1971). Literature reviews showed year-to-year variability in the spawning season of sabellariids depending on the locality; e.g. a short spawning period in July in North Cornwall, England (Wilson, 1971), two long spawning periods during March–April and June–September in Noirmoutier Island, France (Gruet & Lassus, 1983), and an extended reproductive period with semi-continuous spawning from April–October in Mont-Saint-Michel Bay, France (Dubois et al., 2007).

2.2   Ecological role

Mudflats are a relatively homogeneous environment which commonly occurs as part of the natural transition of habitat between the sublittoral zone and the mangrove. The living ecosystem "engineers" in the mudflats include bivalves (Crooks, 1998; Escapa et al., 2004), seagrass (Reusch, 1998) and polychaetes (Dubois et al., 2002, 2006) have the capability to construct biogenic structures that enhance the spatial heterogeneity of the intertidal flat, and consequently increase the surface area for the settlement of diverse benthic invertebrate species (Zühlke, 2001).

The polychaete reef complex on the intertidal shore is characterised by three-dimensional structures that provide food resources and critical nursery grounds for associated benthic communities composed principally of polychaetes (Dubois et al., 2002, 2006; La Porta & Nicoletti, 2009), decapod crustaceans (Gore et al., 1978; Almaça, 1990) and fishes (Palma & Ojeda, 2002). In addition, sabellariid reefs can facilitate sediment retention and protect the shores against erosion (Multer & Milliman, 1967; Gram, 1968).

In these reefs, the sabellariids live as suspension feeders, foraging primarily on planktonic diatoms, algae and other organisms encrusted on sand grains during high tide (Kirtley, 1966). They are in turn preyed upon by periodic visitors to the tidal flats during flood tide such as fish (Palma & Ojeda, 2002), as well as shore birds (Bruschetti et al., 2009). Because of this, sabellariids are an important component in the flow of energy through the food web of the coastal mudflat ecosystem.

2.3 Environmental requirements

Environmental factors (e.g. depth, availability of settlement site, sediment texture and oceanographic processes) exert an influence on the zonation of benthic marine fauna (Carvalho et al., 2005). Colonies of Sabellariidae often form complex reefs in the intertidal or shallow subtidal zone where there is sufficient wave energy to resuspend sand grains as a source material for reef lithification (McCarthy et al., 2003).

The survival of sabellariid larvae depends on their finding stable substrates for primary settlement. Shores comprising entirely of shifting sands or material subjected to constant rolling or burial offer no opportunity for settlement. There is a wide variety of natural and artificial substrates that can be colonised, such as shells of mollusks, coquina rock, sea walls and beach debris (Kirtley, 1966). However, existing living and dead worm reefs that can induce metamorphosis of larval worms are the preferred selection sites

(Eckelbarger, 1976). Studies have shown that the polychaete larvae are attracted to chemical stimuli found on conspecific tubes (Qian et al., 1999).

Despite the importance of stable substrates, the availability of similarly-sized sand grains in the vicinity of the colonisation site serves as a vital source for tube construction (Multer & Milliman, 1967). For this reason, habitats such as exposed rocky shorelines characterised by adequate wave action and stable substrates are less likely to be colonised by sabellariids due to a lack of suspended particles for tube construction (Zale & Merrifield, 1989). Ayata et al. (2009) emphasised the role of coastal eddies on the larval retention of *Sabellaria alveolata* within the Mont-Saint-Michel Bay, France. Furthermore, the settlement success of the *S. alveolata* larvae was greatly related to the wind direction and tidal conditions at spawning.

2.4   Natural and anthropogenic perturbations

The intertidal shore is a highly dynamic habitat subject to natural events. Several studies have reported that extreme temperature during severe frost and summer can cause the massive die-offs of sabellariid population in the temperate region (Wilson, 1971; Eckelbarger, 1976). In addition, sabellariid reefs are increasingly susceptible to direct and indirect anthropogenic disturbances including the space competition by colonisation of mussels and oysters from local aquaculture, the blooming of green algae in response to eutrophication and physical disintegration of the reef by human trampling (Dubois et al., 2002, 2006). Burial and siltation due to beach nourishment and dredging also exert a deleterious effect on the worm reefs (Nelson & Main, 1985).

CHAPTER 3: MATERIALS AND METHODS

3.1   Study area

The Jeram shore faces the Klang Strait and is located on the Selangor coast (3°13'27" N, 101°18'13" E) in Peninsular Malaysia (Figure 3.1a). The strait is characterised by a semi-diurnal macrotidal regime where tidal amplitudes range from 1.4 m (neap tide) to 4.2 m (spring tide), with annual mean tidal levels at Mean High Water Spring (MHWS), Mean Low Water Spring (MLWS), Mean High Water Neaps (MHWN) and Mean Low Water Neaps (MLWN) of 5.2, 1.0, 3.9 and 2.5 m above chart datum referenced at Port Klang (3° 2' N, 101° 21' E), respectively (National Hydrographic Centre, 2002). Maximum flood (to the southeast direction) and ebb (northwest direction) tidal stream velocities during spring tide are approximately equal at 1.3 ms^{-1}, while neap tidal velocities reach 0.35 ms^{-1} (Chong et al., 1996).

The Klang Strait, an approximately 45 km long waterway, is bounded by extensive mudflats to the east, and sand-mud shoals to the west. Its alignment along the northwest-southeast axis reflects the direction of the prevailing tidal currents. Despite being located in an area entirely surrounded by muddy sediments, the Jeram shore experiences strong tidal erosion due to its location which directly faces the strait's alignment (Figure 3.1a). Its eroding shoreline regularly exposes the bottom sandy-shelly substrate (Drainage and Irrigation Department, 2009).

At low spring tide, the intertidal zone of Jeram shore stretches over 900 metres. The backshore has a narrow strip of shelly-sand seafront (berm) fringed by mangroves (*Avicennia alba* and *Sonneratia alba*), and a rip-rap to protect settlement buildings behind it. A 4-metre wide creek, Sungai (=river) Jeram drains the shore to the north of the polychaete reefs. The reefs were observed during two successive annual reef cycles from June 2012 to January 2014. Two large polychaete reefs - the upper and the lower reef,

were located on the lower shore (Figure 3.1b). Their outer boundaries were drawn from GPS points.
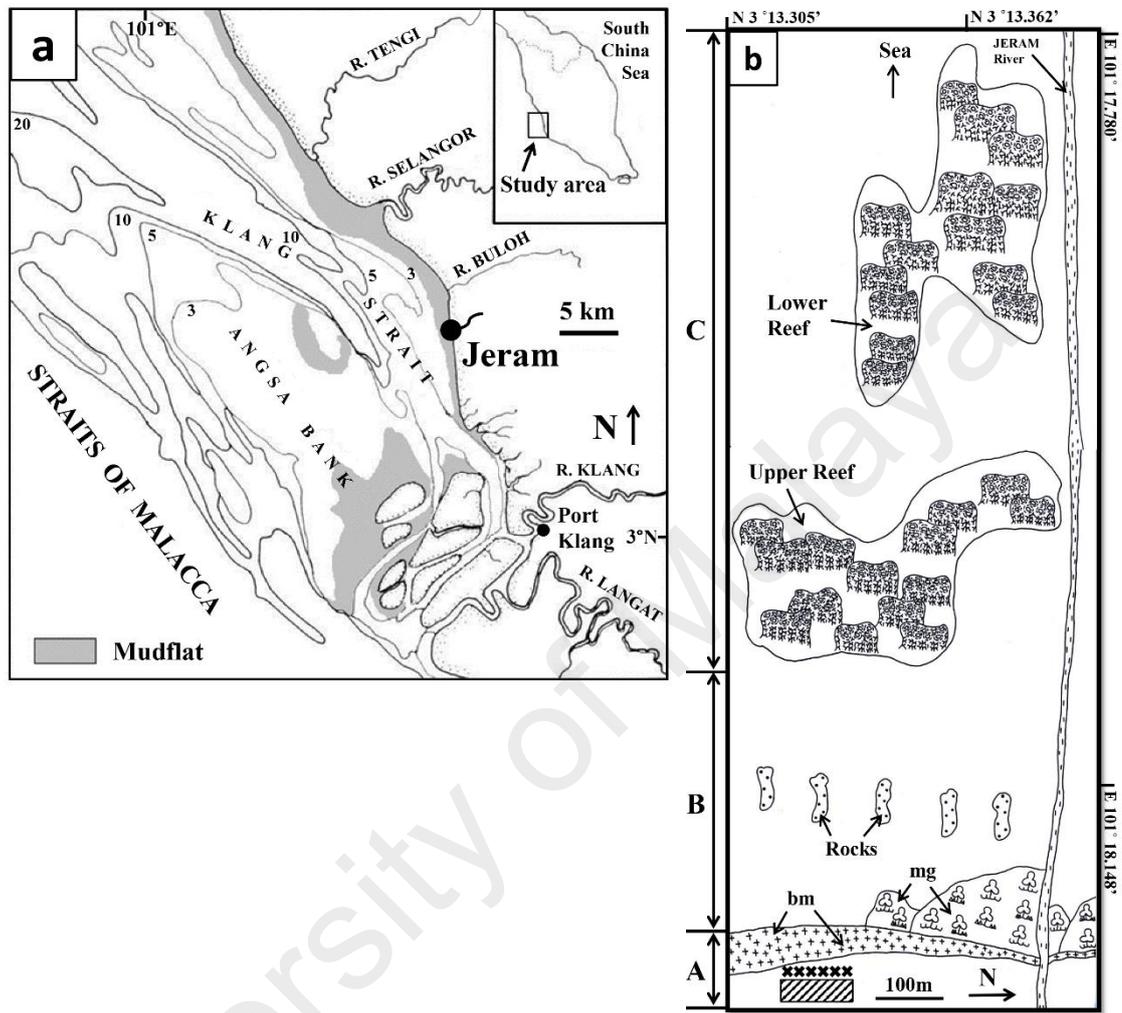
Figure 3.1: Map of Jeram study site in Klang Strait (Peninsular Malaysia). **(a)** Map of study site in Klang Strait which connects to the Straits of Malacca. Angsa Bank is an extensive sand-mud shoal exposed during low spring tides. Bathymetric contour lines in fathoms. **(b)** Aerial view of study site showing upper and lower polychaete reef contours on Jeram shore, Peninsular Malaysia, from February 2013 to January 2014. Stippled area=sandy backshore seafront (bm) fringed by mangroves (mg), XXX=rip-rap in front of settlement buildings (hatched box). A=backshore, B=upper to middle shore, C=lower shore.

The first reef cycle (June 2012–January 2013) was surveyed and preliminary samples were taken to understand the dynamics of reef building, before planned (qualitative and quantitative) samplings were carried out during the second reef cycle

(February 2013–January 2014). This study presents the data based on the second reef cycle.

3.1.1   Polychaete reef

Both the upper and lower reefs at the Jeram lower shore were selected as study sites. The reef area at the start of the reef cycle (June 2013) contained small reef clumps, which reached up to 5 cm above the ground level. Reef cores were taken from reef balls or clumps with height of >5 cm, using a cylindrical core sampler (5 cm height × 4 cm diameter). At the later phases of the reef cycle (July 2013–January 2014), when the reef clumps were larger, a longer customised split core sampler (21 cm height × 4 cm diameter) (see Appendix A) was used to sample the reef. One-half of the split cylinder was manually driven into the targeted reef, followed by the other half. The whole cylindrical core was then pulled out from the reef side after digging out the surrounding reef material. Each replicate of the cored reef material retained in the corer was cut into four sections according to depth: 0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm. The number of core samples taken monthly varied from 4–16 replicates as the reef clumps grew in height. In total, 67 cored reef samples were taken from the upper (38 cores) and lower reefs (29 cores) over the study period (see Appendix B), giving a total of 247 sections (upper reefs= 140 sections; lower reefs=107 sections).

3.1.2   Mudflat macrobenthos on surrounding sediments

The purpose of investigating the type of macrobenthos in the reef vicinity (i.e. the mudflat) was to determine their relationship with the reef macrobenthos. The mudflat macrobenthos, unlike the reef macrobenthos, are non-reef building macrofauna living on the ground. They were sampled concurrently with the reef macrobenthos at different reef phases. A self-customised, stainless steel box corer (surface area of 20 cm × 20 cm, height 18 cm) featuring a removable drawer-like bottom piece was used to sample the mudflat

macrobenthos in the vicinity of the reef (Appendix C). The bottom piece was removed before the box corer was manually pushed into the mudflat sediments. A hole of about 20 cm depth was immediately dug besides the box corer before the bottom piece was inserted in and pushed underneath the corer through its side rails. The sediment was then sieved through a 0.2 mm stainless steel sieve using puddle water on the shore. The retained macrobenthos (>0.2 mm) on the sieve were carefully picked up and transferred into pre-labelled plastic bags. A total of 81 cored mud quadrats were sampled from the mud sediment surrounding the upper (40 samples) and lower reefs (41 samples) at the lower shore (Appendix B). At the middle shore of the mudflat where there was no reef (control site), an additional 36 cored mud quadrats were taken.

3.1.3   Environmental measurements and analysis

Ecological studies of the polychaete reef should also include the environmental parameters that characterise both the reef as well as the surrounding mudflat. These environmental parameters should include, commonly, the temperature and salinity of the sea water and interstitial water (sediment), and importantly, the grain size of the sediment which is known to profoundly influence the benthic community (Zale & Merrifield, 1989). In this study, tidal current and wind vector data were also studied to evaluate the water current, wave direction and longshore drift which affect the shoreline processes (coastal erosion and sedimentation) and hence, the dynamics of reef building and disintegration.

Monthly in-situ temperature (℃) and pH of the sediment were measured with a pH-temperature meter (EUTECH CyberScan Model 300, Thermo Fisher Scientific Inc., United States). Salinity (in ppt) of seawater in water puddles was measured using a temperature-compensated refractometer (Model MR100ATC, Milwaukee, United States). For grain size study, three polychaete reef samples were cored monthly (June

2013 to January 2014) from the upper and lower reef patches to a depth of 1–2 cm. Mudflat sediment surrounding the three polychaete reefs were also concurrently cored (3 cm depth) each month, including from February to May 2013 when the reefs broke up and disappeared.

Wind barb figures were obtained from the Malaysian Meteorological Department (MMD). The wind data presented in this study were surface wind speeds (WSPD) extracted from the European Centre for Medium-Range Weather Forecast (ECMWF). A Grid Analysis and Display System (GrADS) was used to download the WSPD (period: 2012–2014) at approximately 2am, 8am, 2pm and 8pm local time, and then run operationally at the Central Forecast Office of the MMD. The OpenGrADS Project was used to generate the site-specific wind barb figures. A fine grid mode (0.25° by 0.25° resolution) was used to run the model which covered the bounded region 0–10° N by 96–105° E.

3.2   Laboratory procedures

The sampled polychaete reef clumps and sediment macrobenthos were immersed in 6 % formalin for at least 24 hours, before being transferred to 70 % ethanol for long-term preservation (Day, 1967; Fauchald, 1977). Individuals of *S. jeramae* from the reef clumps were removed from their tubes by gently pulling out of the thorax to avoid breakage. Associated polychaete species were also carefully picked up from the crevices between the *S. jeramae* inhabited tubes. All reef and mudflat macrofauna were examined under a dissecting microscope (Leica M125 C, Leica Microsystems Inc., Germany). Polychaetes were identified with the aid of taxonomic references (Day, 1967; Fauchald, 1977) and by Chris Glasby (Museum and Art Gallery of the Northern Territory, Australia). Brachyurans, anomurans and carideans were identified by Peter Ng Kee Lin (National University of Singapore, Singapore).

Collected sediments from both the polychaete reef (after removal of worms) and mudflat were dried in an oven at 60 ℃ for a week before grain size analysis. Dried sediment was immersed in a solution of 6 % hydrogen peroxide overnight, and then in 500 ml of sodium hexametaphosphate aqueous solution (6.2 g/l) overnight (Holme & McIntyre, 1971). Grain size of the treated samples were analysed using a Coulter 230L Particle Size Analyzer, and results were categorised according to the Wentworth scale (Buchanan, 1984).

3.3   Computational analyses

3.3.1   Statistical analyses of faunal density

The density of reef fauna and bottom-sediment fauna is expressed as individuals per m^3 (ind. m^{-3}). Density estimates were calculated from the volume of sampled reef or sediment material. To test whether the median density of reef macrobenthos differred significantly between the four core sections (0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm), and different reef phases/stages (primary succession of the growth phase, secondary succession of the growth phase, stagnation phase), we used the robust non-parametric Mann-Whitney U and Kruskall-Wallis H tests (>2 groups). Reef phases were adopted or modified from Gruet's (1986) nomenclature. The total density of mudflat macrobenthos between upper and lower reefs, or among reef phases/stages, was also compared statistically using the same tests. All statistical tests were conducted using STATISTICA 8 software (StatSoft, Tulsa, USA).

3.3.2   Cluster analysis of mudflat macrobenthos data

Data processing and analysis packages in R (Version 3.2.1; R Core Team 2015) including monogeneaGM (Khang, 2015) and gplots (Warnes et al., 2014) were used to process the raw mudflat macrobenthos data. A data matrix with 117 rows (number of quadrats) and 46 columns (number of species) was obtained. Species abundance data was

normalised (Z-scores) and ranked in descending order based on the t-statistic. Next, a cluster heat map (Wilkinson & Friendly, 2008) was constructed. The cluster heat map graphically displays the normalised abundance value in each cell of the input data matrix, using different colours and tones to allow the visual detection of patterns of variation in the data. Then, a hierarchical clustering algorithm further groups the quadrats by similarity in a dendrogram. The Manhattan distance metric was used to calculate the distance between quadrats for hierarchical clustering. Heat map construction was done using the heatmap.2 function in the gplots package (Version 2.13.0; Warnes et al., 2014).

3.3.3 Diversity analysis

The Shannon-Wiener diversity index (H') (Shannon, 1948) is a commonly used index for quantifying the degree of diversity in a community of interest. It is the negative of the sum of the product of the relative proportion of each species in the community with the corresponding logarithm, with the maximum value attained at perfect evenness (i.e. uniform proportion for each species in the community). When there is only a single species in a community, H' takes the minimum value of 0. Species richness (S) and Shannon-Wiener index (H') were computed using the Plymouth Routines in Multivariate Ecological Research (PRIMER 6) software. Species diversity was estimated as the effective number of species (S_{eff}), which is the exponential of the Shannon-Wiener index H' (Jost, 2006), i.e. $\exp(-\sum_{i=1}^{S} p_i \ln p_i)$ where p_i is the proportion of the ith species, and S is species richness. S_{eff} is the number of equally-common species in a hypothetical community corresponding to the said H' value. Species accumulation curves for the upper (140 samples) and lower reef patches (107 samples) were derived by the observed species counts method in PRIMER 6 (Appendix D).

CHAPTER 4: RESULTS

4.1   Environmental variables

4.1.1   Salinity, pH and temperature

At the lower shore, the mean salinity was 30.9 ±2.5 ppt at the upper reef, and 29.9 ±2.7 ppt at the lower reef, over the study period of 12 months. The difference in mean salinity between the two sites was not statistically significant (p-value=0.21). The mean pH of the sediment water was not statistically significant (p-value=0.50) between upper 7.2 ±0.3 and lower reef 7.2 ±0.2. Likewise, the mean temperature of sediment water was also not statistically significant (p-value=0.54) between the upper (32.2 ±1.8 ℃) and lower reef sediment (32.5 ±1.6 ℃).

4.1.2   Wind field

The surface wind field over the study area and region is given in Figure 4.1, for both the SWM (in May) and NEM (in November) periods. During the SWM, the southwest wind over the Indian Ocean veers to a southeasterly direction in the study area in the Straits of Malacca (Figure 4.1a), and during the NEM, the northeast wind from the South China Sea veers to a northwesterly direction (Figure 4.1b). This change in direction is the result of the Coriolis effect. This is the force due to the earth's rotation which causes the wind to veer from a straight course. Jeram shore is thus exposed to two seasonal, alternating wind fields with their associated wave effects.
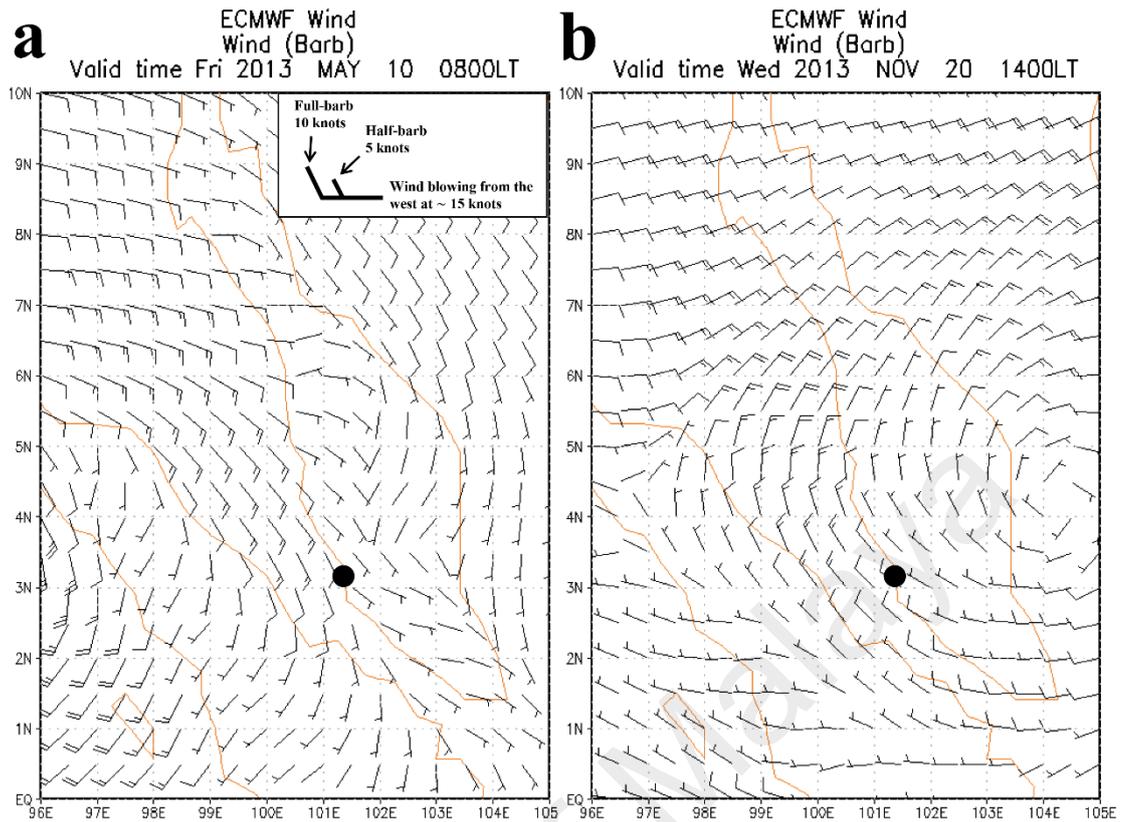
Figure 4.1: Map of the surface wind direction and speed (wind barb figures) over Jeram study site (black circle) in Peninsular Malaysia (red contour line) and Sumatra (left red contour line), during (a) Southwest (SW) Monsoon (May) and (b) Northeast (NE) Monsoon (November). Note veering of SW and NE winds as they cross the equator due to the Coriolis effect. Wind barb figures are each plotted within a grid size of 0.25° × 0.25°. Wind direction and approximate speed are explained in the inset.

4.1.3 Particle size distributions

The grain size analysis results showed that during the primary succession stage, very fine to medium sand (62–500 µm) was the major fraction in both studied reef (53.2 %) and mudflat sediment (86.9 %) with minimal variation between samples with each size class (Table 4.1). It was observed that the coarse sand component increased from reef base (4%) to the reef surface (17.3%), while the converse was true for the silt fraction, from 39.2 % to 25.6%. Upon the arrival of SWM, gradual deposition of finer sediments partially occluded the tube openings of the growing reef clumps, hence the composition

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of the reef's surface sediment (0–1 cm) was dominated by clay-coarse silt (0–62 µm). Concurrently, surrounding mudflat were also superficially covered. Continuous influx of finer sediment eventually clogged up the *S. jeramae* tubes. Results demonstrated a drastic change which clay–coarse silt has constituted the largest fraction throughout all the reef depth zones. Particularly, the surface of the stagnated reefs recorded the highest percentage of fine to coarse silt (68.7 %) and clay (16.1 %).

Table 4.1: Mean (±SD) sediment grain size of polychaete reef and adjacent mudflat during four reef phases. SD=standard deviation.

	Pre-settlement		Growth (Primary Succession)		Growth (Secondary Succession)		Stagnation		Destruction	
	March–May		May–November		October–January		December–January		January–March	
	Mudflat	Reef	Mudflat	Reef	Mudflat	Reef	Mudflat	Reef	Mudflat	Reef
Sample size	n=6	–	n=12	n=17	n=6	n=3	n=3	n=3	n=6	–
Clay (%) 0–3.9 µm	11.1 ±3.9	–	0.8 ±1.0	3.9 ±1.1	17.2 ±1.3	18.0 ±1.7	19.3 ±1.2	16.1 ±0.8	7.4 ±0.1	–
Fine to Coarse Silt (%) 3.9–62 µm	69.1 ±4.9	–	3.8 ±4.4	25.6 ±4.6	72.4 ±2.4	48.6 ±0.4	77.4 ±2.7	68.7 ±0.4	56.8 ±8.4	–
Very Fine to Medium Sand (%) 62–500 µm	19.8 ±8.2	–	86.9 ±11.6	53.2 ±8.3	10.4 ±2.3	33.4 ±1.8	3.4 ±3.0	15.1 ±0.6	35.7 ±8.3	–
Coarse Sand (%) 500–2000 µm	0.0	–	8.5 ±10.4	17.3 ±9.8	0.0	0.0	0.0	0.0	0.1 ±0.2	–

4.2   Life cycle of the polychaete reef

The Jeram reef cycle appeared to be annual, with two successive reef cycles observed from June 2012 to January 2014. Each cycle lasted approximately 10 months, each with four successive phases that passed through the life and death of the polychaete reef. The four phases of the reef cycle are as follows: the pre-settlement phase, the growth phase (comprising primary and secondary succession), stagnation phase and destruction (or dying) phase of the reef.

4.2.1   Pre–settlement phase (March–May)

When the survey began in March 2013, no polychaete reef was observed (Figure 4.2a). Parallel gullies and flat-top ridges (5 cm tall) of remnant mud aligning obliquely (NW-SE direction) to the shoreline soon appeared in April 2013 (Figure 4.2b, c) when tidal currents scoured the mudflat. These mud ridges were progressively eroded by waves and currents, revealing the sandy sediment (62–500 µm) and shell-lags of mainly *Tegillarca granosa* (blood cockle). No reef-forming polychaetes were observed on the shell-lags and old reef debris that remained, and on the rocks in the middle shore.

Figure 4.2: Cyclical development of the Jeram polychaete reef. **(a)** Jeram mudflat shore devoid of any polychaete reef during the pre-settlement phase (March–April 2013). **(b)** Low-tide landscape view of extensive mud ridges arranged like windrows on the lower shore of Jeram (late April 2013). **(c)** Narrow mud ridges standing out prominently as mudflat erosion by tidal currents further progressed; note the exposed fine sand (red arrows) and the shell-lag (late April 2013) after erosion. **(d)** Growth of sabellariid worms on a single dead shell of *Tegillarca granosa* (late May 2013). **(e)** Reef coalescence during the primary succession of the growth phase, two separate reef ball-shaped structures (25 June 2013). **(f)** Coalesced reef balls after one month of growth (25 July 2013). **(g)** Low-tide view of hummocky, coalesced polychaete reefs during primary succession of the growth phase (October 2012). **(h)** The highly eroded polychaete reef clump showing numerous fissures and holes (January 2014). **(i)** Vertical section of the upper polychaete reef site at the start of the growth phase showing surface layer of shell-lags (3–5 cm thick) and thick mud beneath it (upper 2 m); arrows indicate polychaete reef balls (RB), shell-lag layer (SL) and mud (MD).

4.2.2   Growth phase (May–January)

The growth phase could be divided into two successional stages distinguishable by the morphology of the reef surface and the polychaete species that colonised the reef.

4.2.2.1 Primary succession (May–November)

By the end of May 2013, young *S. jeramae* worms had settled on exposed shelly material at the lower shore (Figure 4.2d). Numerous clumps of worm tubes began to build up next to each other. Subsequently, they coalesced and covered the underlying shelly material. The initial conical clumps merged with neighbouring clumps, eventually growing into ball-shaped clumps. At the lower shore, the larger reef clumps measured 34–48 cm in length and 15–21 cm in height (*n*=15), before they coalesced as well. The process of coalescence was observed from August to October 2013. The coalescing process was studied in two reef balls (Figure 4.2e), that were 14 cm apart on 25 June 2013. In just 2 weeks, the inter-reef ball distance was reduced to 4 cm, and by 25 July 2013 the reef balls had merged (Figure 4.2f). Notably, young *S. jeramae* settled rapidly at the junction between the two reef balls, first forming a bridge that connected the two reef balls. The connected reef balls then progressed to become a two-hump reef clump. Newly settled worm tubes on the bridge eventually raised it to the level of the two side humps, which eventually merged. Contiguous reef clumps coalesced to form larger colonial patches (Figure 4.2g); the largest measured colonial reef patch had a maximum length of 19.8 m with a maximum height of 22 cm, recorded in November 2013.

The primary succession of the reef's growth phase was dominated by *S. jeramae*, which formed >90 % of the reef macrobenthos density (Appendix E). Externally, the growing reef, free of algal encrustations, took a black and white coloration from the black sand grains and white shell fragments that were newly cemented onto the rims of the worm tubes. Grain size data of the reef and surrounding sediment matched in terms of

relative composition of grain categories; very fine to medium sand (62–500 *µ*m) constituted the bulk of the reef material (Table 4.1). Growing *S. jeramae* porches often extended higher than the surrounding porch floor. *S. jeramae* tubes were densely arranged (Figure 4.3a). The different porch sizes indicated mixtures of old and young worms. The worm tubes were aligned parallel with one another, densely packed and vertically arranged, thus forming smooth curves across the reef's surface. Crevices between the vertical tubes of *S. jeramae* provided living spaces for other polychaetes from 11 different families.

4.2.2.2 Secondary succession (October–January)

The emergence of polychaete tubes of the spionid *Polydora cavitensis* marked the beginning of the secondary succession of the growth phase. During transition of the primary to secondary succession in October, 11 % of the upper reef clumps had emerged *P. cavitensis* tubes. By November, the presence of *P. cavitensis* had increased to 44 % of the reef clumps observed (*n*=16). Towards the end of November 2013, scattered mud clumps appeared on the surrounding sediment which consisted of mainly silt and clay (<62 *µ*m) (Table 4.1). The reef's surface experienced morphological changes as the *S. jeramae* tubes and porch floors became filled up by fine sediment (mainly silt and clay) (Table 4.1). The filled porch floors and covered porches formed a mud layer which facilitated the larval settlement of *P. cavitensis* (Figure 4.3b). The new coloniser immediately constructed numerous tiny tubes on the mud layer.

Characteristic features of the secondary succession stage include 1) the gradual occlusion of the honeycomb reef surface due to fine sediments (Figure 4.3b); 2) generally dull grey color of the reef surface; and 3) the emergence of numerous tiny *P. cavitensis* tubes that protrude from the mud-filled porches of *S. jeramae*. The *S. jeramae* population decreased (Appendix E), and the reef became co-dominated by *P. cavitensis* (Figure

4.3c). However, the latter was restricted to the reef's surface down to a depth of 3 cm, succeeding the upper region of the dilapidated tubes of *S. jeramae* which extend to the depth of 20 cm.

Despite the co-dominance of *S. jeramae* and *P. cavitensis*, the species composition of the other reef macrobenthos did not qualitatively change from the primary succession of the growth phase (Appendix E). Some rare species (*Neanthes willeyi*, *Lepidonotus* cf. *squamatus*, *Ophiodromus* sp.) continued to exist.

Towards the end of the secondary succession i.e. transition to the stagnation phase in December, 20 % of the reef clumps observed in the lower reef patch were without *S. jeramae*, and in January, this percentage increased to 60 % (*n*=10).

4.2.3 Stagnation phase (December–January)

All remaining or residual *S. jeramae* tubes were buried by fine sediments (Figure 4.3d) and the entire *S. jeramae* population eventually died out (Appendix E). The stagnation phase of the reef was characterised by a totally mud-covered layer on the reef surface with the tiny worm tubes of *P. cavitensis* protruding out (Figure 4.3e). In this phase, *P. cavitensis* was the dominant reef dweller constituting >90 % of the reef macrobenthos density (Appendix E). Domination of *P. cavitensis* in the reef community was associated with high percentage (85 %) of clay and silt (3.9–63 µm) sediments (Table 4.1), and the composition of the tubes of *P. cavitensis* is also mostly clay and silt.

4.2.4 Destruction phase (January–March)

During this phase, the reef structures progressively became eroded (Figure 4.2h), as the reef patches shattered and broke up into fragments. By March, the polychaete reefs were totally destroyed and the shore became a homogenous mudflat. Excavations at the reef sites showed no remaining hard or reef structures beneath the mud cover (see Figure 4.2i).
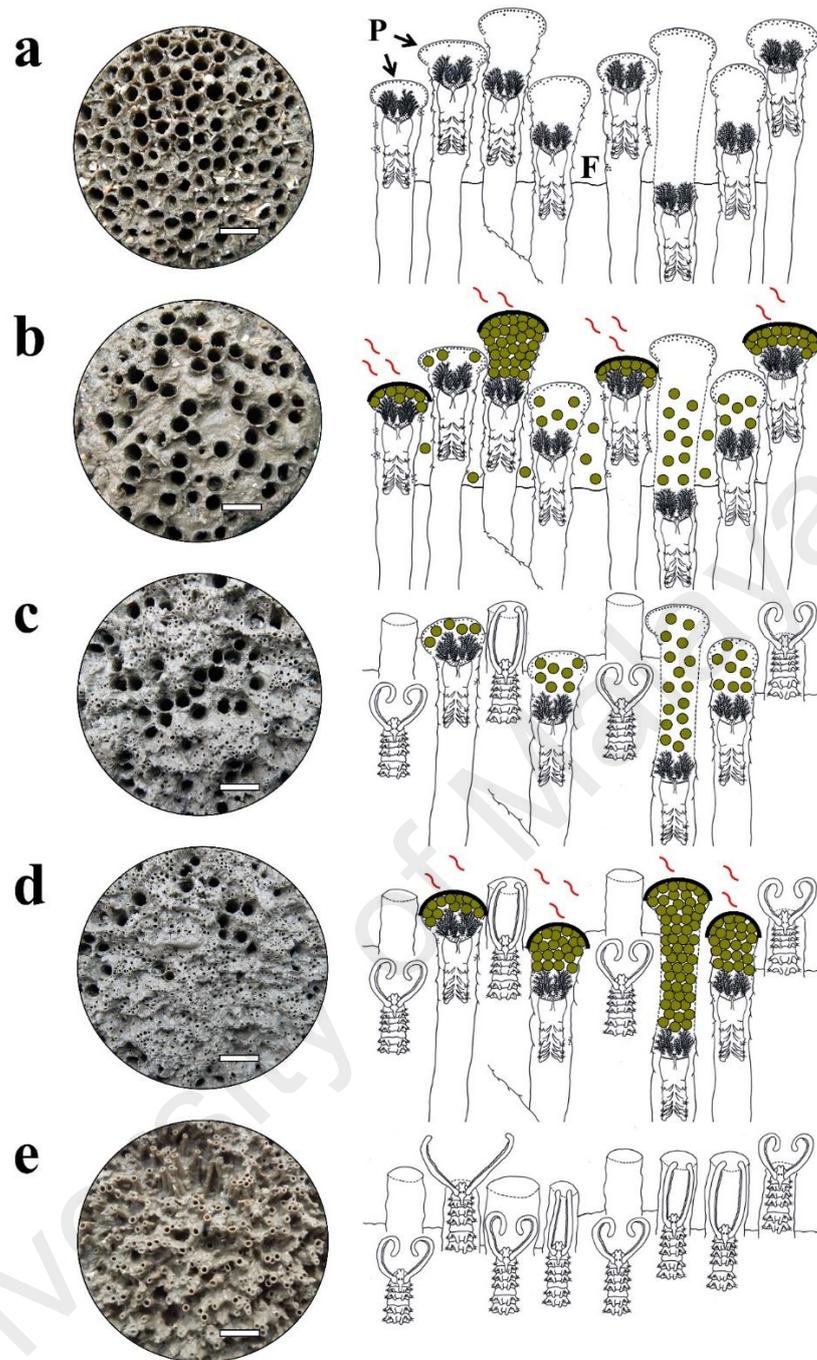
Figure 4.3: Enlarged view of polychaete reef's surface (scale bar=5mm, left) and schematic diagram of the dominant species of polychaetes (right), during: **(a)** primary succession of the growth phase as exemplified by the honeycomb pattern of densely packed tubes of *Sabellaria jeramae*, the primary reef builder, P=porches, F=porch floor; **(b)** early secondary succession of the growth phase, with tubes of *S. jeramae* now covered by fine sediments, which if not removed, are colonised by the larvae of *Polydora cavitensis*; **(c)** secondary succession of the growth phase, with further deposition of fine sediments which buries most of the *S. jeramae* tubes, and further settlement of *P. cavitensis*; **(d)** early stagnation phase, with increasingly heavier sedimentation rate of fine sediments; **(e)** stagnation phase, with the complete obliteration of honeycomb structure, elimination of *S. jeramae*, and colonisation by *P. cavitensis* in much smaller, protruding silt tubes on the reef surface. Olive green dots=fine sediments; red wiggly lines=larvae of *P. cavitensis*.

4.3   Polychaete reef community

A total of 21 species and morphospecies of polychaetes belonging to 13 families were recorded (Appendix E). In the upper reef, 15 polychaete taxa were recorded during the primary succession of the growth phase, 13 taxa during the secondary succession of the growth phase, and 2 taxa during the stagnation phase. In the lower reef, 10 taxa were recorded during both the primary and secondary successions of the growth phase, and 4 taxa in the stagnation phase.

Species richness, total mean abundance, and effective number species of polychaetes with respect to reef phase and depth zone are given in Table 4.2. Overall, polychaete abundance in the reef decreased from surface to deeper zones. During the primary succession of the growth phase, the mean density of polychaetes in the uppermost 0–5 cm zone was significantly higher ($\sim$ 1 million $\pm$0.3 million ind per m^3) than in the 15–20 cm zone (0.05 million $\pm$0.02 million ind per m^3) in the upper reef (Kruskal-Wallis test: $H_{3,72}$=29.86; p<0.01). Similarly, for the lower reef ($H_{3,59}$=30.14; p<0.01), the mean density of polychaete in the uppermost 0–5 cm zone was much higher ($\sim$ 1 million $\pm$0.3 million ind per m^3) compared to the 15–20 cm zone (0.04 million $\pm$0.008 million ind per m^3). During this phase, *S. jeramae* was the only species found throughout the sampled four depth zones both in the upper and lower reef and dominated the polychaete reef community (Appendix E).

In the secondary succession of the growth phase, the highest mean faunal density was also observed in the 0–5 cm zone (0.9 million $\pm$0.2 million ind per m^3), which was significantly higher than in the 15–20 cm zone (0.03 million $\pm$0.008 million ind per m^3) at the upper reef (Kruskal-Wallis test: $H_{3,64}$=47.26; p<0.01). Similarly, for the lower reef ($H_{3,24}$=12.17; p<0.01), the mean density of polychaete in the uppermost 0–5 cm zone was much higher (1.5 million $\pm$0.4 million ind per m^3) compared to the 15–20 cm zone (0.03

million $\pm$0.02 million ind per m^3). During this phase, the 0–5 cm zone in both the upper and lower reefs was inhabited by the two equally-common species, *S. jeramae* and *P. cavitensis* (Table 4.2). The 5–10 cm and 10–15 cm depth zones were dominated by *S. jeramae*. *Marphysa* cf. *mossambica* and *Cabira* sp. 1 were observed to be equally-common in the 15–20 cm depth zone of the upper reef.

A distinct vertical distribution pattern was observed during the stagnation phase, with highest mean abundance in the 0–5 cm depth zone which was dominated by *P. cavitensis* (>90 % of the reef macrobenthos density) (Table 4.2; Appendix E). No polychaetes were found in the deeper zones of 5–10 cm, 10–15 cm and 15–20 cm.

Table 4.2: Mean density and effective number of species (S_{eff}) of polychaetes recorded from the upper and lower reef of Jeram with respect to spatial (0–5, 5–10, 10–15, 15–20 cm reef depth) and temporal (primary succession, secondary succession, stagnation phase) factors. S=species richness, S_u=total richness (calculated on pooled samples), D=mean density (ind. m^{-3}), SD=standard deviation, n=sample size, S_{eff} =effective number of species rounded to integer, with superscript letter denoting species of higher numerical rank (arranged in descending order of abundance) up to the effective number of species. Abbreviations for polychaete species: *J=Sabellaria jeramae*; *P=Polydora cavitensis*; *C=Cabira* sp. 1; *M=Marphysa* cf. *mossambica*. Statistically significant difference in density distribution was tested using Mann-Whitney U tests or Kruskall-Wallis H tests (>2 groups); similar subscript numerals indicate densities not significantly different (p>0.05) among the depth zones.

Depth		Upper Reef				Lower Reef			
		Primary Succession	Secondary Succession	Stagnation		Primary Succession	Secondary Succession	Stagnation	
0–5 cm	S	7	6	2	S_u=10	5	7	4	S_u=9
	D	1,055,759 $_i$	962,916 $_i$	652,555	U=125	1,042,028 $_i$	1,472,227 $_i$	1,209,613	H= 3.14
	SD	1,479,982	824,400	–	p=0.19	1,335,497	1,013,773	629,677	p= 0.21
	n	21	16	1		17	6	6	
	S_{eff}	1 ^{J}	2 ^{J,P}	1 ^{P}		1 ^{J}	2 ^{J,P}	1 ^{P}	
5–10 cm	S	2	3	0	S_u=3	4	6	0	S_u=9
	D	416,624 $_i$	348,162 $_i$	0	U=127	633,228 $_i$	114,064 $_{i,ii}$	0	U=7
	SD	351,921	185,052	–	p=0.76	394,341	159,292	–	p<0.01
	n	17	16	1		14	6	6	
	S_{eff}	1 ^{J}	1 ^{J}	–		1 ^{J}	1 ^{J}	–	
10–15 cm	S	10	6	0	S_u=11	3	3	0	S_u=5
	D	178,821 $_{i,ii}$	57,695 $_{ii}$	0	U=62	312,635 $_{i,ii}$	151,202 $_{i,ii}$	0	U=28
	SD	150,312	97,400	–	p<0.01	370,833	152,578	–	p=0.25
	n	17	16	1		14	6	6	
	S_{eff}	1 ^{J}	1 ^{J}	–		1 ^{J}	1 ^{J}	–	
15–20 cm	S	11	9	0	S_u=13	6	6	0	S_u=7
	D	55,238 $_{ii}$	30,837 $_{ii}$	0	U=112	37,516 $_{ii}$	31,832 $_{ii}$	0	U=34
	SD	64,680	31,009	–	p=0.40	29,682	50,331	–	p=0.51
	n	17	16	1		14	6	6	
	S_{eff}	1 ^{J}	2 ^{C,M}	–		1 ^{J}	1 ^{J}	–	
		S_u=15	S_u=13	S_u=2		S_u=10	S_u=10	S_u=4	
		H=29.86	H=47.26			H=30.14	H=12.17		
		p<0.01	p<0.01			p<0.01	p<0.01		

4.4   Mudflat macrobenthos around the reef

A total of 46 species of mudflat macrobenthos were recorded from the middle shore sediments, and the sediments around the upper and lower reef patches at the lower shore (see Appendix F). Throughout the entire study, the highest number of identified species was recorded around the upper reef patch (35 species) and lower reef patch (30 species) at the lower shore (Table 4.3), followed by the middle shore sediment (22 species) where there was no reef (Appendix F). Five major taxa dominated the mudflat macrobenthos. For each taxon, the most abundant species were: *Loimia verrucosa* (Polychaeta), *Raphidopus johnsoni* (Anomura), *Nassarius jacksonianus* (Gastropoda), *Alpheus euphrosyne* (Caridea) and *Xenophthalmus pinnotheroides* (Brachyura).

All major faunal groups were present in the soft sediment throughout the year irrespective of the presence of the polychaete reef (Figure 4.4). The only exception is *A. euphrosyne*, which colonised the mudflat only in the presence of polychaete reefs (Figure 4.4). The highest mean sediment faunal density at both the upper (17060 ± 6295 ind m^{-3}) and lower reef vicinity (15528 ± 8963 ind m^{-3}) was recorded during the secondary succession of the reef's growth phase. The difference in mean density was significantly different between the upper and the lower reef ($p<0.05$; Table 4.3). Sediment faunal density was slightly reduced at both the upper (15833 ± 2332 ind m^{-3}) and lower reef vicinity (13528 ± 6077 ind m^{-3}) during the stagnation phase of the reef, and further reduced at both the upper (8234 ± 2692 ind m^{-3}) and lower reef vicinity (12934 ± 4885 ind m^{-3}) during the destruction phase. In the absence of the reef (pre-settlement phase), all faunal groups living in the soft sediment were present in about equal density (Figure 4.4). However, as the nearby reef re-established during the primary succession of the growth phase, the sediment macrobenthic community became dominated by mudflat polychaetes and anomurans (Table 4.3); this trend continued particularly during the secondary succession and the stagnation phase. For instance, during these latter phases of the cycle,

there were 2 or 3 equally-common species near to the upper and lower reef and the community was numerically dominated by *L. verrucosa* and *R. johnsoni* (Table 4.3). Also, there was generally an increase in abundance of brachyurans, caridean shrimps and gastropods (Figure 4.4), as compared to the macrobenthos present during the pre-settlement phase (no reef).

Table 4.3: Mean density and effective number of species (S_{eff}) of mudflat macrobenthos recorded from the sediments surrounding the upper and lower reefs during the reef's pre-settlement phase, growth phase (primary succession and secondary succession), stagnation phase and destruction phase. S=species richness, S_u=total richness (calculated on pooled samples), D=mean density (ind. m^{-3}), SD=standard deviation, n=sample size, S_{eff}=effective number of species rounded to integer, with superscript letter denoting species of higher numerical rank (arranged in descending order of abundance) up to the effective number of species. Abbreviations for equally common taxa: *L=Loimia verrucosa*, *M=Marphysa* cf. *mossambica*, *P=Parahalosydnopsis tubicola* (Polychaeta); *D=Diogenes moosai*, *R=Raphidopus johnsoni*, *Po=Polyonyx* aff. *loimicola* (Anomura); *N=Nassarius jacksonianus* (Gastropoda); *A=Alpheus euphrosyne* (Caridea); *X=Xenophthalmus pinnotheroides* (Brachyura). Statistically significant difference in density distribution was tested using Mann-Whitney U tests or Kruskall-Wallis H tests (>2 groups); similar subscript numerals indicate densities not significantly different ($p>0.05$) among the phases.

		Upper Mudflat	Lower Mudflat	Total
Pre-settlement	S	20	18	S_u=23
	D	1,698 $_i$	5,389	U=12
	SD	2,874	4,822	$p<0.01$
	n	9	10	
	S_{eff}	3 $^{L, M, N}$	5 $^{L, N, R, X, D}$	
Primary Succession	S	29	25	S_u=34
	D	3,383 $_i$	10,064	U=21
	SD	3,278	5,476	$p<0.01$
	n	14	13	
	S_{eff}	3 $^{N, L, D/R}$	4 $^{R, L, N, D}$	
Secondary Succession	S	24	15	S_u=26
	D	17,060 $_{ii}$	15,528	U=11
	SD	6,295	8,963	$p=0.47$
	n	6	5	
	S_{eff}	3 $^{L, R, Po}$	2 $^{L, R}$	
Stagnation	S	14	14	S_u=18
	D	15,833 $_{ii}$	13,528	U=10
	SD	2,332	6,077	$p=1.00$
	n	4	5	
	S_{eff}	3 $^{L, R, A}$	3 $^{L, A, R}$	
Destruction	S	15	21	S_u=21
	D	8,234$_{i, ii}$	12,934	U=8
	SD	2,692	4,885	$p<0.05$
	n	7	8	
	S_{eff}	3 $^{L, P, N}$	4 $^{L, R, N, D}$	
	Total	S_u=35	S_u=30	
		H=29.37	H=11.10	
		$p<0.05$	$p=0.08$	
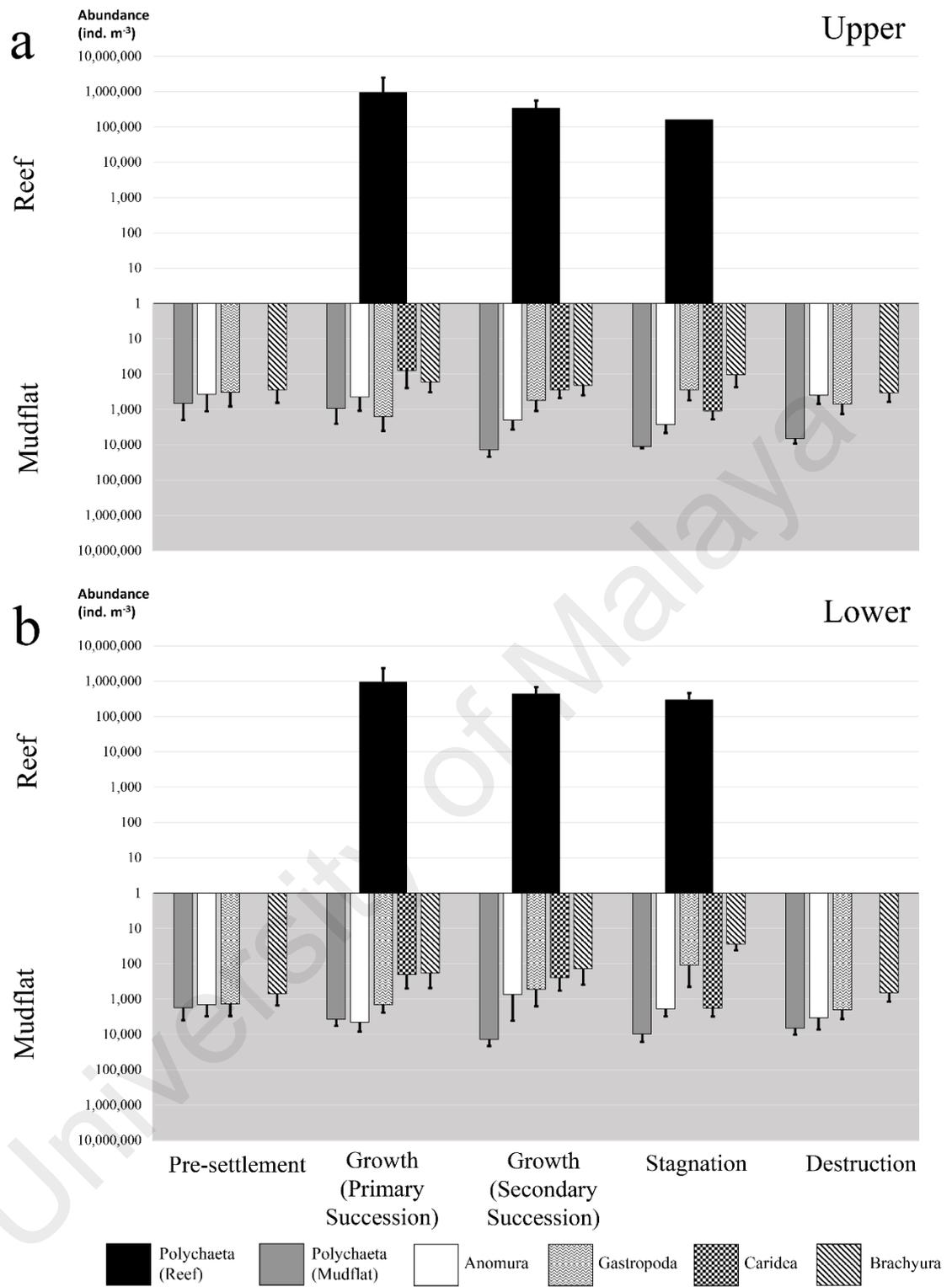
Figure 4.4: Mean density (ind. m^{-3}) of the major faunal groups of reef and mudflat macrobenthos, at the upper reef (a) and lower reef (b) sites on Jeram shore during the pre-settlement, growth (primary succession, secondary succession), stagnation and destruction phases. Mean density plotted on logarithmic scale. Vertical whiskers=SD.

4.4.1 Cluster analysis of adjacent mudflat macrobenthos

Figure 4.5 shows a cluster heat map of 117 mudflat quadrats featuring three spatial (site) and temporal (phase, month) variables based on the 46 species of the mudflat macrobenthos. The dendrogram hierarchy was divided into two major clusters. These clusters are strongly associated with site and reef phase factors. All quadrats based on the macrobenthos taxa sampled from the middle shore (control site: no reef) are clustered within cluster 1. Meanwhile, cluster 1 also consists of quadrats collected from the mud sediment adjacent to the upper and lower reefs (lower shore), predominantly during the reef's pre-settlement and early growth phase (primary succession). Members in cluster 2 are quadrats sampled during the remaining reef phases: late growth phase (secondary succession), stagnation and destruction.

The mudflat macrobenthos species are represented as rows of the heat map. The top 23 and bottom 13 species revealed strong between-cluster variation relative to within-cluster variation. Cluster 2 has relatively higher abundance (i.e. larger Z-score) for the top 23 species, which belong to the Polychaeta, Malacostraca (Anomura, Caridea) and Gastropoda. The high abundance of *Parahalosydnopsis tubicola*, *R. johnsoni* and *P*. aff. *loimicola* can be explained by its co-association within the *L. verrucosa* tubes. For the bottom 13 species, the converse was observed for Cluster 1, which was dominated by Malacostraca (Brachyura).
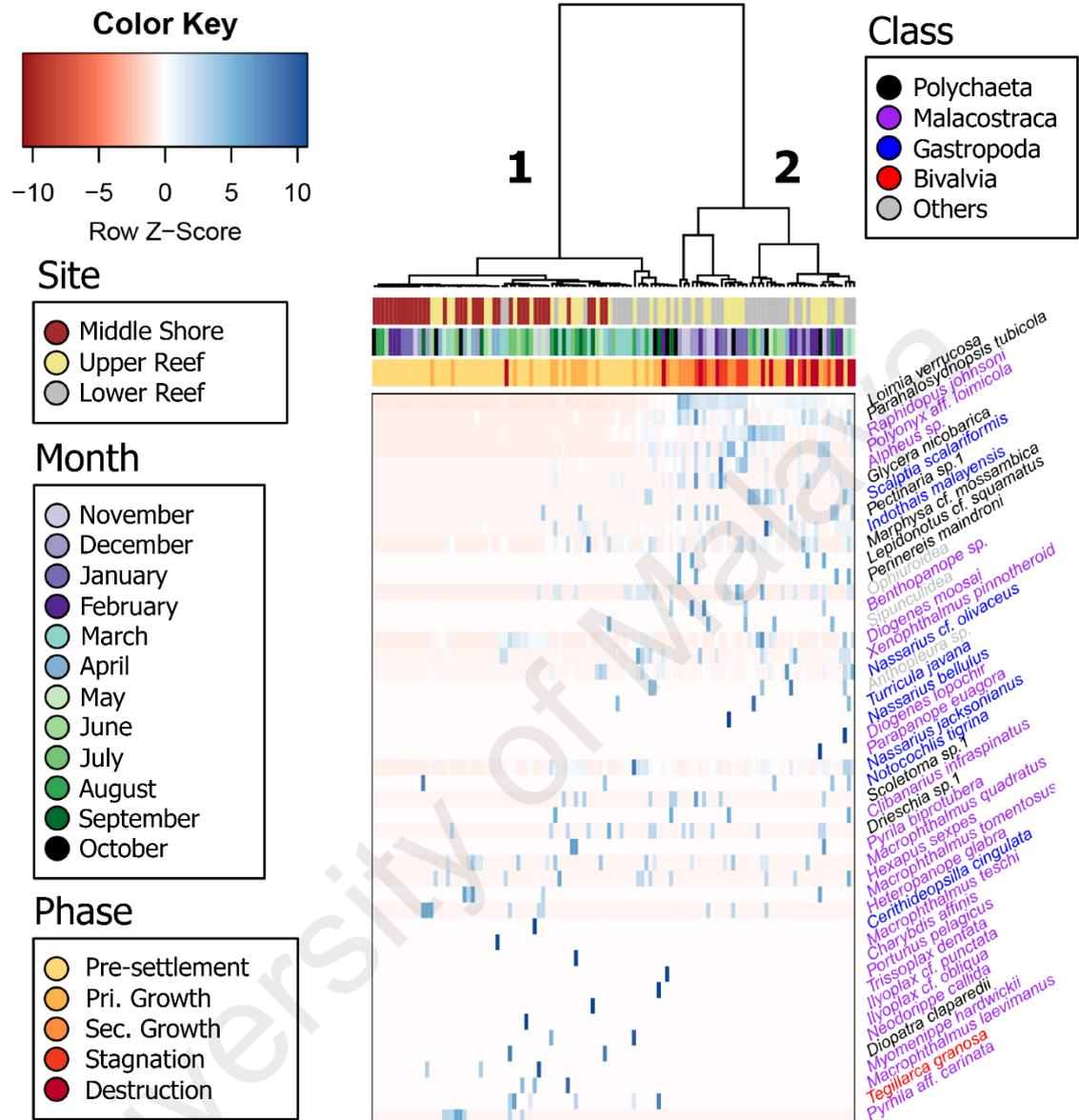
Figure 4.5: Heat map of hierarchical cluster analysis of 46 species based on Z-scores of mudflat macrobenthos data from 117 quadrats. 1=Cluster 1, 2=Cluster 2. Each quadrat consists of three studied factors: top horizontal strip represents site (middle shore, lower shore: upper reef and lower shore: lower reef); second horizontal strip represents month (NEM: November–February; Inter: March–April; SWM: May–September; Inter: October); bottom horizontal strip represents phase (pre-settlement phase, growth phase: primary succession and secondary succession, stagnation phase and destruction phase). Heat plots of species represents relative abundance as indicated by the top left color key (Z-scores).

CHAPTER 5: DISCUSSION

5.1 Effects of wave action and tidal dynamics

Among the taxa considered, only polychaetes were consistently found to inhabit the ephemeral Jeram reef clumps during all successional phases of the reef cycle, with a total of 21 species. Although Polgar et al. (2015) reported 26 species, the species accumulation curve shows that further samples are unlikely to increase the number of species significantly (Appendix D). In contrast, similar reefs in other regions are much richer in terms of species richness, e.g. the *S. alveolata* reefs in Mont Saint-Michel Bay, France, with 66 species (*n*=30; sieve size=0.5 mm) including polychaetes, sipunculids, nemerteans and insects (Dubois et al., 2006); and the *S. alveolata* reefs in Tyrrhenian coast, Italy, with 39 species (*n*=9; sieve size=0.5 mm) of polychaetes (La Porta & Nicoletti, 2009). The relatively low species richness of the Jeram polychaete reef likely results from the short life span of the polychaete reef.

The present study shows that the polychaete reef is eventually smothered by sedimentation, then strong tidal currents and breaking waves progressively induce erosion, before the reef completely disintegrates after 8 months of growth. The interaction between the sedimentological sequence and faunal changes was first described by Seilacher (1984) as the Jeram model. Seilacher's model is however based on the hypothesis of storm events that erode only the top mud layer while the shell bed beneath amalgamates progressively over the years from winnowed shell deposits. Seilacher further suggested that the base of large reeflets resists hydrodynamic reworking, thus remaining and acting as a firm surface for regrowth upon exhumation.

Our observations revealed no consolidated or remaining reef bases (Figure 4.2i), consistent with Polgar et al. (2015)'s observations. This confirms that the reef totally disintegrates at the end of the destruction phase. In the pre-settlement phase, during

erosive stripping of the top mud layer that results in the characteristic windrows, the shell-lag is initially revealed at the bottom of the troughs (gullies). Polgar et al. (2015) also reported the presence of shell-lag 15–30 cm deep in the mud during the pre-settlement phase (as well as all other phases). With the complete removal of the mud ridges, the shell-lag becomes exposed occurring in large to small patches. The shell-lag deposits are composed of both old (broken up) and new shells. However, the shell-lag layer we observed under a formerly large reef measured only 5 cm thick at the most, indicating no significant net accumulation of the shell deposits over the years. These observations suggest that the shell-lag deposits particularly the old, broken up pieces are also continuously removed just as new shells replenish them by the hydrodynamic forces (e.g. Watson, 1971; Hayward & Stilwell, 1995). This hypothesis of shell replenishment is not without support since on the updrift end, extensive semicultured and natural beds of *Tegillarca granosa* occur on the mudflats from north of the Selangor River to Buloh River (see Figure 3.1).

The cycle of life and death of Jeram's ephemeral reef appears to be strongly dictated by predictable events involving the regional monsoon climate and local tidal dynamics. Two different wind fields associated with the alternating SWM (May–September) and NEM (November–March) seasons are consistent with the cyclical events experienced by the Jeram reef. During the SWM period, the wave effect appears weak since the southeasterly winds blow mainly from land to sea, or if the winds become southerly, the wind fetch is small due to the Klang Islands in the south (see Figure 4.1a). Hence, the erosive power of the flood stream that flows towards the southeast along the Klang Strait exerts a greater effect on the mudflat at Jeram (Drainage and Irrigation Department, 2009). Tidal streams erode the mudflat in small jets creating parallel gullies and ridges (windrows) that appear on the mudflat in April–May when the southeasterly winds set in. During the NEM period, the prevailing northwesterly wind has a large wind

fetch thus forming larger waves that converge on the Selangor shore (Fitri et al., 2015). The breaking waves erode and transport fine sediment along the shore. The resulting cross-shore and longshore currents during NEM (Fitri et al., 2015) thus transport sediments from the updrift side towards the shore in the direction of the longshore drift (southwards). The measured shift in sediment grain size from fine sand to silt and clay is consistent with the described erosive and depositional forces at Jeram shore, as a result of the hydrological and wind conditions. In dense reef assemblages, the velocity of the near-bottom flow is reduced and near bottom laminar flow is deflected around and across the assemblages (Heuers, 1998). The reduced current velocity at the reef patches increases the residence time of particles (Friedrichs et al., 2000) and thus facilitates the deposition of finer silt in the surrounding sediment as observed in this study. Hence, during the NEM, sedimentation prevails over erosion and this marks the beginning of the reef demise.

5.2   Reef builders and colonisation

Literature survey suggests there are very few true reef or frame builders on the same polychaete reef. The present study shows that after a brief pre-settlement phase of about a month following the reef destruction, *S. jeramae* larvae begin to settle on the exposed shelly-fine sand substrate, following shore mud removal by tidal currents. Dense aggregations of *S. jeramae* reef mounds soon cover the lower shore. The other true reef builder on Jeram reef is *P. cavitensis*, during the secondary succession of the growth phase. Posey et al. (1984) reported the occurrence of three different sand-tube building species (*S. cementarium*, *Idanthyrsus ornamentatus* and *Schistocomus hiltoni*) in a mixed polychaete reef community in Oregon coast. In addition, Lomônaco et al. (2011) described reefs with the association of *S. wilsoni* and *S. nanella* in Brazil. However, monospecific reef builders are mostly reported; e.g. *S. alveolata* (Wilson, 1971; Dubois et al., 2002, 2006; La Porta & Nicoletti, 2009), *S. vulgaris* (Wells, 1970; Curtis, 1978), *S.*

nanella (Bremec et al., 2012), *P. lapidosa* (Gore et al., 1978) and *Lanice conchilega* (Rabaut et al., 2007, 2009; De Smet et al., 2013).

The polychaete reefs in Jeram appear similar to those observed along the French coast, where *S. alveolata* also builds two different types of intertidal reef structures: small sheet-like reefs adhering to rocks on the middle shore, and extensive reef formations of several hectares on the lower sand flats (Gruet, 1982; Dubois et al., 2002). *Sabellaria* worms are known to be highly competitive and rapid colonisers. They are characterised by a long life-span, with high fecundity and dispersal capability (Giangrande, 1997). Their larvae are gregarious with a high degree of specificity and tend to settle on the sand tubes of the adult worms (Pawlik, 1988a, b). This is consistent with the observed small colonies of polychaetes growing on single dead shells during the early primary succession, that eventually coalesce into a large mass of conspecific organisms. The grain size analysis showed that *S. jeramae* is capable of utilizing very fine to medium sand (62–500 μm) resuspended from the surrounding mudflat to provide for reef lithification (Table 4.1). In contrast, the Spionidae contains opportunistic polychaetes tolerant of disturbance, sediment load, high organic matter (Pearson & Rosenberg, 1978) and pollution (Bellan et al., 1988). *Polydora* species live in diverse habitats, from soft clay or mud to hard calcareous substrates (Blake, 1996). They have been reported to be either borers or non-borers that construct tubes in soft clay and mud (Blake & Evans, 1973; Martin & Britayev, 1998; Sato-Okoshi, 2000). The emergence of the tubiculous polychaete *P. cavitensis* is in tandem with the deposition of mainly silt and clay (<62 µm), which corresponds to the slowing down of reef-building by *S. jeramae*.

5.2.1   Particle selection of Sabellariidae

The suspended particles in the water column are ecologically important for sedentary sabellariids as a food source and as building material for their dwelling tubes

(Kirtley & Tanner, 1968). Dubois et al. (2006) characterised *S. alveolata* as an active suspension feeder that uses both its grouped lateral cilia and grouped frontal cilia to modify the current patterns around the tentacular filaments thereby capturing suspended particles.

Particle size selection in sabellariids is significantly correlated to the height of their building organ (Vovelle, 1965; Gruet, 1984). In the present study, the particle size distribution of reefal sand grains for each successive 5 cm tube segment suggests that *S. jeramae* uses coarser grain size with time. However, it has been reported that the selection of coarser or finer grains varies depending on the age proportion of the reef community and the particle size distribution of the surrounding sediment (Naylor & Viles, 2000). Our results showed that the largest proportion of the measured grain categories of the mudflat sediment consists of very fine to medium sand (62–500 µm), which is also the predominant component of the reef material (Table 4.1). Previous studies also demonstrated a similar tendency for the Sabellariidae to preferentially select sand-sized grains (and shell fragments) for tube construction (Multer & Milliman, 1967; Gram, 1968; Naylor & Viles, 2000). Fager (1964) also mentioned another selection criterion that the selected particles have at least one flattened surface to enable attachment to the tube. Particles collected are embedded with a biomineralised cement secreted from a building organ connected to specialized glands (Fournier et al., 2010).

Our results (Table 4.1) showed that the fine or clay-silt fraction (i.e. < 62 µm) differed considerably between *S. jeramae* reef and mudflat sediment during the primary succession of the growth phase (Mann–Whitney test: $Z=4.52$; $p<0.01$), with substantially finer materials found in the reef samples. This difference can be explained as due to the complexity of the reef structures which passively trapped the fine particles within the reef

crevices; the fine particles are however not cemented as part of the active matrix of individual worm tubes (Vovelle, 1965; Multer & Milliman, 1967; Naylor & Viles, 2000).

5.2.2   Particle selection of Spionidae

Spionids are sediment–water interface feeders, capable of either suspension feeding or deposit feeding in response to hydrodynamic conditions (Taghon et al., 1980; Dauer et al., 1981). Studies described several morphological features which may affect the worm during particle size selection: 1) since the secreted mucus possesses limited adhesive strength, particle loss at the initial encounter between palp and particle or during particle handling along the palp may result (Jumars et al., 1982; Taghon, 1982); 2) particle retention is size–selectively correlated with the palp width (Williams & McDermott, 1997); 3) the diameter of the worm's pharynx acts as the crucial determinant of the size of particles that can be ingested.

Preferential selection for fine-sized particles has often been demonstrated in spionids (Jumars et al., 1982; Taghon, 1982). This is because fine-sized particles are characterised by a larger surface area to volume ratio with proportionally with higher amount of bacteria (Dale, 1974; Hargrave, 1972). Dauer (1980) reported that the gut contents of spionids comprised 70–80 % of silt and clay-sized particles which is an indication of the type of particles available in their habitats. In addition, Mortensen and Galtsoff (1944) explained that the constant presence of finer grains in the gut of these worms suggests that grain size is prioritized as food and the material for tube building. Our results demonstrated a gradual increase of clay/silt (0–62 µm) during secondary succession, which eventually became the predominant component of the reef material during stagnation phase (Table 4.1).

5.3 Tolerance of sabellariids to sediment burial

Given the dynamic sedimentary environment of the intertidal mudflat, the degree of sensitivity of polychaete worms in response to sediment burial will decide their growth or decline with repercussion on the reef structure. Wilson (1971) reported that colonies of *S. alveolata* were able to withstand burial of >1 m of sediment for several weeks. On the other hand, *Phragmatopoma* could tolerate sand burial for only several days before dying off (Taylor & Littler, 1982; Sloan & Irlandi, 2008).

Polychaete species generally exhibit a high intolerance to low oxygen conditions and are generally sensitive to sulfides (Theede et al., 1969). The mortality of *Phragmatopoma lapidosa* is directly correlated with hydrogen sulfide (H_2S) concentration (Nelson & Main, 1985; Main & Nelson, 1988). Thus, sabellariid worms are equipped with a pair of opercular lobes that function to generate flowing sea water as a source of food and tube building particles, as well as flushing out faecal pellets. This function is apparently disrupted by the drastic influx of fine sediments (silt and clay) in November. As a result, the clogged *S. jeramae* tubes with impeded water flow and trapped organic matters could lead to asphyxiation and accumulation of hydrogen sulfide (J.J.Eeo, personal observation) thereby killing the worms. Subsequently, the decaying mass of dead worm bodies exacerbates anoxic conditions in the death zone (5–20 cm zone) during the stagnation phase (Table 4.2).

5.4 Relationship between reef and mudflat fauna

Other polychaetes in the reef are non-reef builders. Their presence in the reef may indicate co-habitation, refuge, foraging activity, symbiotic association, opportunistic species, etc. *Sabellaria* reefs featured numerous crevices and holes in between the tubes thereby increasing habitat heterogeneity and providing refugia space for associated benthic fauna (Woodin, 1978). The aggregations of associated benthic fauna also

facilitate secure conspecific sites allowing settlement of their larvae and post-larvae (Qian et al., 1999).

As reef building progresses, other rare species such as *Paleaequor breve*, *Alitta multignatha* and *Perinereis singaporiensis* also entered the reef, ultimately contributing to higher species richness (Appendix E). On the other hand, as reef development stagnates, a dead reef zone is formed below (5–20 cm) (J.J.Eeo, personal observation), thus reducing the space available for other species to colonise or inhabit. Nevertheless, errant carnivorous species (*Perinereis maindroni*, *Nereiphylla* sp. 1 and *Marphysa* cf. *mossambica*) found in the reef during the stagnation phase may be attracted to their prey. Other errant polychaetes (*Drieschia* sp. 1, *Scoletoma* sp. 1), and sedentary polychaetes (*Pectinaria* sp. 1, *Diopatra claparedii*) were sampled only from the surrounding sediment (mudflat) (Appendix F).

The present study indicates an all year-round occurrence of *Loimia verrucosa* at Jeram lower shore. During the pre-settlement phase, no *L. verrucosa* was found in the mud although they persisted under the remnant debris of the destroyed polychaete reef of the previous cycle (Appendix F). The remnant *Loimia* population constituted 6.8% of the total mudflat polychaete population. Although fine sand is known to be a suitable substrate for Terebellidae (Rabaut et al., 2007), we did not find *L. verrucosa* on the fine sand exposed by progressive washing of the surface mud layer during the start of the primary growth phase. *Loimia*, however, began to colonise the sediment around and below the growing reef clumps after colonisation by *S. jeramae*. Polgar et al. (2015), however, suggested that terebellid structures may facilitate sabellariid reef building on them but their observations were based on terebellids that occupied the bed patches at the lowest spring tide level (below our study sites) where stronger wave action had already removed the mud sediment.

The reef colonies enhance topographical complexity on the lower mudflat shore, thereby increasing the amounts of sheltered niches and hence facilitate the development of the secondary diversity (Dubois et al., 2006). At Jeram shore, *L. verrucosa* was observed to colonise only the sediment beneath the growing reef clumps at the lower shore. Such site–specific aggregations are possibly attributed to the hydrodynamic regime modified by the dense aggregations of sabellariid reef mounds (Heuers, 1998) that act as secure anchorages that induce the settlement of larval and postlarval benthic organisms (Qian et al., 1999). It has also been reported that dense aggregations of other terebellid beds (*L. conchilega*), are particularly distributed at the lee side of bedforms such as seabed ridges and sheltered sites (Hertweck, 1995; Degraer et al., 2008). Furthermore, the juveniles of *L. conchilega* are less likely to settle directly on the sediment of exposed sites which are subject to high risk of passive dislodgment (Callaway, 2003).

The distribution pattern of *L. verrucosa* at Jeram shore resembles that of previous studies such as from the Wadden Sea. There, the highly abundant *L. conchilega* were restricted to areas closest to the low tide line which gradually decreased in the landward direction (Reise, 1985; Carey, 1987; Strasser & Pieloth, 2001). Feasible factors that may explain why *L. verrucosa* was absent in the Jeram upper and middle shore include 1) lack of epibenthic substratum (e.g. reef and shell fragments) for settlement; and 2) deprivation of size-preferential particles for tube-building because the surrounding sediment are primarily of silt and clay (< 62 µm). For example, *L. conchilega* optimally occurs in fine to medium sands (Van Hoey et al., 2006; Willems et al., 2005) and actively selects larger sized particles (> 400 µm) for tube construction (Féral, 1989; Callaway, 2003).

The habitat structuring capacity of *L. conchilega* beds exerts positive implications on the density and species richness of the benthos (Rabaut et al., 2007). The scale worm *Parahalosydnopsis tubicola* was reported to co-occur inside the tubes of *L. verrucosa*

(Polgar et al., 2015). *P. tubicola* is also known to be mutually associated with *Loimia medusa* (Martin & Britayev, 1998). While the gaps and crevices between the *S. jeramae* reefs and bottom *L. verrucosa* beds serve as refuge for benthos from epibenthic predators and environmental stress (Woodin, 1978; Bolam & Fernandes, 2002), infaunal predators are certainly not restricted. On the contrary, predators are attracted to the species rich microbenthic assemblages. Previous studies documented a high number of predatory polychaete species positively associated with *L. conchilega* (Callaway, 2006; Rabaut et al., 2007).

Gore et al. (1978) indicated that the sabellariid bioherm allows decapods to inhabit the surf zone habitat in an area where they are less likely to be sighted. The decapod community inhabiting sabellariid reefs include those of *S. nanella*, Brazil (Fausto-Filho & Furtado, 1970); *S. alveolata*, Italy (Rivosecchi, 1961); *S. alveolata*, France (Gruet, 1970, 1971) ; *P. lapidosa*, North America (Gore et al., 1978). They show remarkably common or parallel association involving a suspension feeder (porcellanid crab), a carnivore (xanthid crab) and an omnivore (grapsid or pagurid hermit crab). We did not observe this association in Jeram's sabellariid reef. However, in the surrounding mud sediment, we found two species of porcellanid crab, *Raphidopus johnsoni* and *Polyonyx* aff. *loimicola* co-occurring with the solitary tube-dwelling polychaete *L. verrucosa*, while a diogenid hermit crab and xenophthalmid crab were observed to be the most common species living peripherally with the reefs (J.J.Eeo, personal observation). The association between tube-building polychaetes and *Polyonyx* species is well known, e.g. *Chaetopterus* sp. with *P. utinomii*, *P. macrocheles* and *P. sinensis* (Miyake, 1943; Johnson, 1958); *Chaetopterus* sp. with *P. quadriungulatus* (Haig, 1960) and *P. vermicola* (Ng & Sasekumar, 1993), and *Loimia medusa* with *P. loimicola* (Sankolli & Shenoy, 1965).

The high density of mudflat macrobenthos observed during the reef's destruction phase is likely attributed to habitat fragmentation (Table 4.3; Figure 4.4). Such alteration in reef topography exposes new settlement spaces and microhabitats which allow new recruitments (Dubois et al., 2002).

The appearance of the polychaete reef in Jeram seems unrelated to the mudflat macrobenthos of its immediate surroundings in the mudflat, suggesting an offshore origin for the larvae of *S. jeramae* and *P. cavitensis*. On the other hand, the reef presence has a positive effect on the surrounding mudflat macrobenthos including mudflat polychaetes, shrimps, crabs and gastropods (Figure 4.4; Appendix F). An ichthyofaunal study in the Jeram reef area sampled 70 species of fish using enclosure trap and gill nets over a year; 65 species of fish examined for their stomach contents showed a wide range of taxa including polychaetes, crustaceans, molluscs, echinoderms, fish, cnidarians, sipunculids and nematodes (V.C.Chong, unpublished data). Fifteen species of Ariidae, Cynoglossidae, Drepanidae, Scatophagidae, Sciaenidae and Triacanthidae had their stomachs filled with polychaetes, and 10 species fed almost exclusively on the sabellariids.

5.5   Comparisons with previous studies

Our study differs from that of Seilacher (1984) and Polgar et al. (2015) in several details of the cycling phases and their period of occurrence (Table 5.1). These differences are attributed to the timing and duration of the studies.

Table 5.1: Comparisons between Seilacher (1984), Polgar et al. (2015) and present study in terms of the reef cycling phases and their period of occurrence.

	Seilacher 1984	Polgar et al. 2015	Present study	Notes
Month Observed:	–	April 2013	March–May 2013	Similar descriptions among authors. Jeram shore covered by mud, no polychaete reefs observed. Seilacher suggested the presence of dead *Sabellaria* reeflets beneath the mud. Polgar et al. and present study found no *Sabellaria* reeflets, old reef totally disintegrated during the destruction phase. All studies reported permanent shell-lag below thin layer of surface mud. Seilacher suggested amalgamation of shell-lags over the years. Present study observed no amalgamation of shell-lags and postulated shell removal balanced by shell replenishment. Polgar et al. made no mention of shell-lag integrity.
Phase:	–	Absence or Pre-settlement	Pre-settlement	
Dominant Species:	–	–	–	

	Seilacher 1984	Polgar et al. 2015	Present study	Notes
Month Observed:	June 1979; July 1981	August 2012	May–November 2013	All studies reported erosional features of narrow mud ridges aligned perpendiculary (Seilacher, Polgar et al.) or obliquely (present study) to shore.
Phase:	–	Destruction	Growth (Primary Succession)	Seilacher reported the re-exposure of *Sabellaria* reeflets provided settlement surface for the larvae. It is not clear why Seilacher reported mud erosion on his subsequent visit to Jeram in February 1982. Omitting any typo error, it is possible an unusual extreme storm or early erosional event had occurred. Polgar et al. reported reef destruction but probably missed the early larval settlement period. The present study revealed the primary succession of this phase. The upper layer of the mudflat was eroded by waves and currents, revealing sandy sediment (62–500 µm) and shell-lags, the latter acting as the primary settlement surface for larvae of *S. jeramae*.
Dominant Species:	*Sabellaria* sp.	*Sabellaria jeramae*	*Sabellaria jeramae*	

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Table 5.1, continued

	Seilacher 1984	Polgar et al. 2015	Present study	Notes
Month Observed:	–	November 2012	October–January 2012, 2013	Polgar et al. reported an expansion of the reef due to the growth of the colonies of *S. jeramae*.
Phase:	–	Growth	Growth (Secondary Succession)	The present study emphasised the secondary succession of this phase by *P. cavitensis* after *S. jeramae*, and co-existence of the 2 species; reef continued to expand only because of remaining pioneer reef builder (*S. jeramae*) populations;
Dominant Species:	–	*Sabellaria jeramae* *Polydora cavitensis*	*Sabellaria jeramae* *Polydora cavitensis*	however, rate of reef expansion substantially reduced. Seilacher made no mention of this probably because this phase was out of his study period.

	Seilacher 1984	Polgar et al. 2015	Present study	Notes
Month Observed:	–	December 2010	December–January 2012, 2013	Polgar et al. reported that the reef reached its largest extension due to the prolonged absence of destructive storm events.
Phase:	–	Stagnation	Stagnation	The present study reports the smothering of the polychaete reef by mud and replacement of *S. jeramae* by *P. cavitensis*
Dominant Species:	–	*Sabellaria jeramae* *Polydora cavitensis*	*Polydora cavitensis*	as reef dwellers.

	Seilacher 1984	Polgar et al. 2015	Present study	Notes
Month Observed:	–	–	January–March 2013, 2014	No mention of the reef characteristics in this period by Seilacher and Polgar et al.
Phase:	–	–	Destruction	The present study reported signs of reef destruction (fissures, holes) due to death of *S. jeramae*. *P. cavitensis* could not maintain reef integrity, eventually the reef was destroyed by
Dominant Species:	–	–	–	strong tidal currents and breaking waves.

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5.6   Limitations in this study and future work

In this study, we investigated the reef faunal succession and the accompanying structural changes of the adjacent mudflat community in Jeram, in relation to the local hydrometeorological factors. The latter included the wind field, tidal currents, and the erosive and sedimentation forces. Within the scope of this study, there are still limitations that give rise to some uncertainties. These limitations serve to provide suggestions and ideas for further studies on the polychaete reef at Jeram.

1) The limitations in the current sampling regime: often, the sampled reef clump would be destroyed or much disturbed during coring. A more efficient sample corer could be designed to minimize the damage towards the sampled reef while more reef cores were allowed to be extracted from the same individual reef clump.

2) More studies could be conducted in the future to determine the relationship between the Jeram mudflat's topography to SWM–driven erosion (i.e. tilt degree that are prone to erosion). From the present two–year study, the mud ridges (aligning obliquely to NW–SE direction) resulted from erosion that occurs at the same place or at the reef areas. Since the shell lag patches are distributed randomly across the Jeram mudflat beneath the superficial mud layer, the SWM–driven erosion seems to be the prerequisite factor in the exposure of shell lag for primary settlement.

3) Mechanical properties of the biomineralised cement from the *S. jeramae* are poorly known. Mechanical tests can be performed through lab experiments to understand the nature of the cement. Such information could potentially lead to better understanding of the scale and magnitude that allow the tubes to dissipate the mechanical energy from the waves.

4) As the recolonisation of the sabellariid reefs at Jeram strongly depends on the external larval supply, understanding the connections between spatially discrete populations is a major challenge for the current study. It is thus vital for future studies to identify

where the offshore spawning areas (larval source) are, and to obtain data concerning larval abundance in order to determine both the spawning season and recruitment pattern. Assessments of the role of the local hydrodynamics on the presence of larval sources and sinks, and the scale of the spatio-temporal variability of larval dispersal and settlement, are also vital studies in conservation biology. In addition, laboratory experiments could be carried out to elucidate the worms' planktonic lifetime (i.e. fertilisation to metamorphosis period) in relation to the availability of suitable settlement substrata and quantity of food.

5) In the present study, no quantitative information regarding the sedimentation rates driven by NEM and at what scale and magnitude they are detrimental to sabellariids was obtained. Future field and laboratory experiments could be conducted to verify the threshold duration and depth of burial that can be tolerated by *S. jeramae* without death. Similar studies on *P. cavitensis* could also be done. Quantifying the natural sedimentation rates and the resilience capacity of these animals and other macrobenthos are important to predict the effects of anthropogenic activities on the polychaete reef and mudflat ecosystem. Future work should also investigate whether ephemeral polychaete reef can only occur in mudflats that are subject to significant erosive and sedimentary forces, with exposed shell lags or hard substrate.

6) Dietary studies of fish sampled from and around the Jeram reef area could be studied to investigate whether the polychaete reefs ecologically support coastal fisheries. A trophic study was independently carried out by other researchers in University of Malaya (Y.P.Ng, personal communication), some of the results of which has been discussed in the present study. In future, it would be interesting to know to what extent the polychaete reefs influence the diversity and ecology of the surrounding microbenthic, macrobenthic and fish community on a spatial and temporal basis.

7) The assumption of uniform spatial distribution of individuals is a prerequisite for the calculation of the mean density using sample density data. If this assumption was not met, density estimates obtained will thus be severely biased. Unfortunately, uniform distribution is the only computationally tractable option here because determining the existence of a clumped distribution requires additional work that could not covered in the present thesis.

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CHAPTER 6: CONCLUSION

The Jeram polychaete reef cycles through four consistent successional phases within a year: pre-settlement phase, growth phase (primary and secondary succession), stagnation phase and destruction phase. The reef dynamics appears to be linked to the regional monsoon climate and local hydrological conditions. Firstly, the reef's primary succession is initiated by strong erosional forces during the SW Monsoon; then, the secondary succession follows as a result of stronger depositional forces during the NE Monsoon. The "hard" polychaete reef can only establish itself on hard substrate comprising of exposed lag deposits of shells due to erosion of the surface mud layer. Polychaetes are the only reef-building macrobenthos in the Jeram mudflat. Initially, the reefs are built by *S. jeramae* from resuspended fine sand (primary succession). Subsequently, the reefs are augmented by *P. cavitensis* when more silt and clay are deposited onto the reef (secondary succession). Overall, total polychaete abundance decreased from surface to deeper zones of the reef. *S. jeramae* dominated the entire reef depth during primary succession. A mixed *S. jeramae–P. cavitensis* community dominated the 0–5cm or surface zone during secondary succession, but no polychaetes except *P. cavitensis* were found at the surface zone during the stagnation phase. On the surrounding mud-bottom (mudflat), mudflat polychaetes were also the most abundant macrobenthos, but the presence of the reefs appear to attract more anomurans, gastropods, carideans and brachyurans. The sediment macrobenthos on the mudflat do not appear to play a direct role in initiating the growth of the reef. It is suggested that the source of larval polychaetes comes from unknown offshore reefs. The polychaete reef of Jeram likely benefits the surrounding mudflat fauna including fish as a source of food and through trophic links.

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LIST OF PUBLICATIONS AND PAPERS PRESENTED

Eeo, J. J., Chong, V. C., & Sasekumar, A. (2017). Cyclical Events in the Life and Death of an Ephemeral Polychaete Reef on a Tropical Mudflat. *Estuaries and Coasts, 40*(5), 1418-1436.