RAFFLES BULLETIN OF ZOOLOGY **63**: 401–417
Date of publication: 2 October 2015
http://zoobank.org/urn:lsid:zoobank.org:pub:9648B3CD-ADE3-4F0B-8190-4F3A1CFB822A

Tropical polychaete community and reef dynamics: insights from a Malayan *Sabellaria* (Annelida: Sabellariidae) reef

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Abstract. The ecology of tropical sabellariid reefs is scarcely known, and only few records of such systems were reported from Southeast Asia. The present investigation describes the only documented polychaete reef of western Peninsular Malaysia, which has been previously reported on in two other studies. More recent surveys documented dramatic temporal changes of the reef's extension and polychaete community composition. This reef appears to experience different phases of growth and destruction, associated with sediment dynamics, possibly determined by monsoons. In the present study, the extent, temporal dynamics and polychaete species composition of the reef are documented from December 2010 to April 2013. Semi-quantitative sampling of the polychaete community in selected portions of the reef along the intertidal zone revealed drastic changes in the composition and geomorphic structure of the reef. The reef reached its largest extension in December 2010, when *Sabellaria* sp. 1 was the primary builder. The tubiculous *Polydora cavitensis* and *Loimia verrucosa* dominated the reef at different stages of reef development. A total of 26 polychaete species from 12 families were recorded, including errant and associated species. Eight un-described species were found, plus five new records for an area including the South China Sea, the Malacca Straits and the Andaman Sea, and five new records for the Malay Peninsula only. Hypotheses of the reef cycle, the synecological dynamics, and the abiotic factors triggering the ecological succession are also discussed.

Keywords. Sabellariidae, Polychaeta, biogenic reef, ecological succession, intertidal ecology, tidal flat

INTRODUCTION

Polychaete reefs are biogenic structures globally distributed in intertidal and subtidal marine benthic ecosystems (Kirtley, 1994). The reef framework is typically built by a single tube-building species, the primary frame-builder, forming aggregations with areal extensions from a few square metres up to several hectares (Dubois et al., 2002). This framework is also encrusted and strengthened by several secondary frame-builder polychaete species (Scoffin & Garrett, 1974). A polychaete reef affects bottom hydrodynamics, alters sedimentation processes, and has a stabilising effect on sediments (e.g., Van Hoey et al., 2008). Such three-dimensional structure offers a variety of habitats and trophic niches to diverse animal associations, including crustaceans, molluscs, echinoderms and other polychaetes (Cusson & Bourget, 1997). For these reasons, primary frame-builders are considered ecosystem engineers. Polychaete reefs also host more diversified communities than adjacent sand-flats, and associated species include fishes and shrimps of commercial importance (Vorberg, 2000).

All polychaete primary frame-builders belong to the families Sabellariidae and Serpulidae (Canalipalpata: Sabellida), which build their tubes by cementing sand grains and shell fragments, or by secreting calcium carbonate, respectively (Bosence, 1979; Naylor & Viles, 2000). Recently, the terebellid *Lanice conchilega* (Pallas, 1766) has also been discussed as a potential reef-building species, although its aggregations cannot fit the current definition of reef (Van Hoey et al., 2008; Callaway et al., 2010).

Sabellariids are filter-feeders usually occurring in the intertidal or shallow subtidal zone, although some species have been found at greater depths, in the mesopelagic (e.g., the genus *Bathysabellaria* Lechapt & Gruet, 1993; see Lechapt & Kirtley, 1996), bathyal and abyssal zones [e.g., *Phalacrostemma elegans*, sensu Kirtley, 1994 = *Gesaia elegans* (Fauvel, 1911)]. Several studies indicated that sabellariids have diverse life histories and ecological niches, and often are stenotopic, stenobathic and endemic (Pohler, 2004). However, although this family includes > 130 valid species (Barrios et al., 2009), ecological studies have been conducted on few representatives, such as *Sabellaria alveolata* (Linnaeus, 1767), *S. spinulosa* (Leuckart, 1849), *Phragmatopoma californica* (Fewkes, 1889), and *Idanthyrsus cretus* Chamberlin, 1919 (e.g., Pawlik et al., 1991; Holt et al., 1998; Barrios et al., 2009). In the western Pacific and Indian

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ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

oceans, some *Sabellaria*, *Neosabellaria* and *Idanthyrsus* species have been known to form miniature reefs or intertidal to subtidal belts (Badve, 1996; Pandolfi et al., 1998; Nishi & Kirtley, 1999; Bailey-Brock et al., 2007; Huang et al., 2008; Chen & Dai, 2009; Reuter et al., 2009; Nishi et al., 2010). In particular, ecological knowledge of tropical sabellariid polychaete reefs is considerably fragmentary (e.g., Pohler, 2004; McCarthy et al., 2008).

Dramatic changes in the areal extension of sabellariid reefs have been reported in several studies conducted in temperate regions (e.g., Holt et al., 1998; Frost et al., 2004; Vorberg, 2005). Gruet (1986) subdivided the typical ecological succession of a reef of *Sabellaria alveolata* into four different phases: absence or pre-settlement, settlement or growth, stagnation, and destruction. Each phase is characterised by specific geomorphic structures and ecological dynamics. Described factors driving such changes include temperature fluctuations, changes of sedimentological regimes, and anthropogenic impacts, such as bottom trawling and alterations of the hydrological regime (Hendrick & Foster-Smith, 2006).

Seilacher (1984) described a periodic fluctuation of a sabellariid intertidal reef on the Jeram shore, along the west coast of the Malay Peninsula. A preliminary study of this reef provided a qualitative description of the associated macrofauna (Ribero & Polgar, 2012). Seilacher (1984) observed rapid and sharp changes in the grain size of superficial sediments throughout the intertidal zone, occurring over a four-year period (1979–1983). In particular, the tidal flat was either covered by a layer of mud overlapping a shell bed, or by a shelly substrate, on top of which he recorded the presence of rapidly growing "*Sabellaria* reeflets" (Seilacher, 1984). According to his 'Jeram model', the Jeram shore is normally under positive sedimentary regime, dominated by mud sediments. The mudflat is colonised by infaunal communities, and the sessile epibenthos (e.g., barnacles) is restricted to other organisms or their remains (brachyuran crabs, gastropods and bivalves). Interviews with local fishermen suggested that in the 1920s, a catastrophic storm event established an extensive intertidal lag deposit of infaunal shell material (Seilacher, 1984). After the storm, a different and dominant epibenthos (sabellariid polychaetes, bryozoans, oysters, solitary corals, large barnacles) developed on top of the shell bed. As the mud gradually buried the shell bed and its encrusting community, the former dominant infaunal community was re-established. Since then, the mud layer has been repeatedly winnowed by storm events, and its infaunal shell content projected onto the previous shell lags, including the reference level of the 1920s. This model predicts that both epifaunal and infaunal communities are repeatedly mixed up in an increasingly thick shell lag by frequent and intense storm events, with no alternating layers of mud and shell beds.

In this study, the species composition of the Jeram polychaete community is presented, and observations of its spatial extent and temporal dynamics are provided, including measurements of the height, tube density, and tube diameter of the sabellariid clumps. Hypotheses on the reef's sedimentological and ecological processes are also discussed.

MATERIAL AND METHODS

Field and laboratory work. The Jeram beach [= Pantai Jeram], Selangor; 3°13'27"N, 101°18'13"E) is a tidal flat on the west coast of the Malay Peninsula (Fig. 1), 3.8 km north of the mouth of Sungai [= river] Sembilang and 3.3 km south of the mouth of Sungai Buluh. During spring low tides, the exposed tidal flat extends from sea to land for approximately 800 m (Fig. 1). The tidal flat is fringed by a mangrove stand of stunted *Avicennia alba* Blume and scattered trees of *Sonneratia* sp., and it is crossed by Sungai Jeram [= Jeram creek].

Five surveys were made on 7 December 2010, 19 January 2011, 7 August 2012, 30 November 2012 and 26 April 2013. Six sites were georeferenced during spring low tides when the *Sabellaria* reef was in place (December 2010); along the exposed intertidal zone, and along the northern margin of a large barrier south of Jeram creek (Fig. 1). Two sites (A, B) were positioned in the first and the last patch of the inner reef, one site (C) in the back reef, one (D) on the reef flat, one (E) along the northern exposed margin of the reef, and one (F) along its western exposed margin.

One qualitative sample of substrate or reef tubes (~ 1 L) was collected at each site during each survey. Large errant species were collected by digging and sorting ~ 75 L of substrate inside a quadrat (50×50 cm) dug to a depth of 30 cm (n = 1 per site). Measurements of the clumps' height relative to ground level were also conducted in August and November 2012.

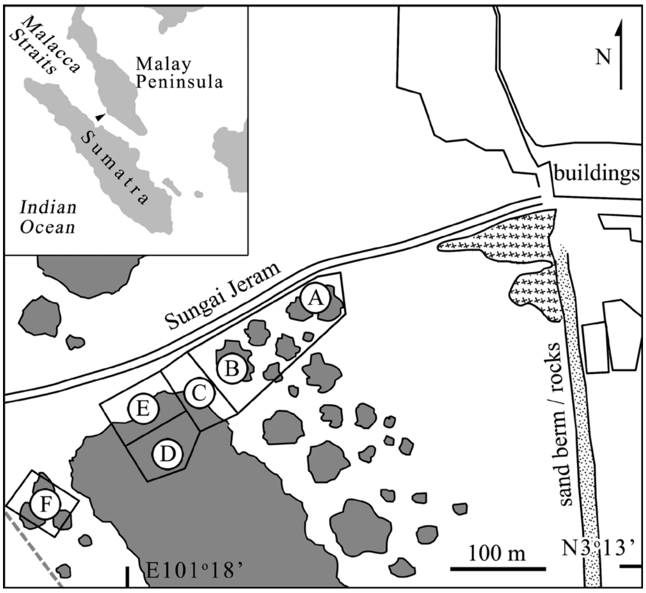

Fig. 1. Jeram Beach and sampling sites. Diagram of the polychaete reef as in December 2010. Sites: A, B (inner reef patches); C (back reef); D (reef flat); E (northern exposed margin); and F (western exposed margin). Hatched line = water's edge during spring low tide; crosses = trees of *Avicennia alba* and *Sonneratia* sp.; stippled area = sand berm; shaded areas with black contours = polychaete reefs. Map redrawn from a satellite image (Google Earth Plus, v. 7.0, 2012). Inset: black arrow = Jeram.

Table 1. Polychaete species and morphospecies collected in the Jeram Reef. First records: SA = new record for the South China Sea, Malacca Straits (including the Malay Peninsula) and Andaman Sea (Hylleberg et al., 1986; Tan & Chou, 1993; Paxton & Chou, 2000; Aungtonya et al., 2002; Chan, 2009; Rajasekaran & Fernando, 2012; Idris & Arshad, 2013); MP = new record only for the Malay Peninsula (Tan & Chou, 1993; Chan, 2009; Idris & Arshad, 2013).

Family, species	**First records**
Chrysopetalidae	
Paleaequor breve (Gallardo, 1968)	MP
Eunicidae	
Lysidice sp. 1	
Lysidice sp. 2	
Marphysa sp. 1	
Glyceridae	
Glycera nicobarica Grube, 1868	MP
Lumbrineridae	
Lumbrineris sp. 1	
Nereididae	
Ceratonereis (*Composetia*) *burmensis* (Monro, 1937)	
Laevispinereis sp. 1	
Leonnates crinitus Hutchings & Reid, 1991	SA
Neanthes willeyi (Day, 1934)	MP
Nectoneanthes oxypoda (Marenzeller, 1879)	
Nicon sp. 1	
Perinereis maindroni Fauvel, 1943	SA
Perinereis singaporiensis (Grube, 1878)	
Onuphidae	
Diopatra claparedii Grube, 1878	
Pilargidae	
Cabira sp. 1	
Sigambra sp. 1	MP
Polynoidae	
Lepidonotus sp. 1	
Lepidonotus sp. 2	
Lepidonotus sp. 3	
Lepidonotus cf. *sublevis* Verrill, 1873	SA
Parahalosydnopsis tubicola (Day, 1973)	SA
Phyllodocidae	
Eulalia sp. 1	
Sabellariidae	
Sabellaria sp. 1	
Spionidae	
Polydora cavitensis Pillai, 1965	MP
Terebellidae	
Loimia verrucosa Caullery, 1944	SA

Samples were haphazardly selected within each site, transported to the lab, sorted, and specimens were euthanised by chilling at 2–4°C or freezing at -25°C, then fixed in 10% formalin or 70% ethanol, and preserved in 70% ethanol. In the absence of phylogenies for most of the taxa considered in this study, the definition of species adopted here is the morphospecies concept as defined by Cronquist (1978), i.e., species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means. Where these taxonomic groups matched existing described species we have applied the appropriate Linnean binomial, otherwise we have used morphospecies units (sp. 1, sp. 2, etc.). Our proposed species are therefore hypotheses which are falsifiable when independent data, for example morphological synapomorphies and DNA sequences, become available. Genus group determinations were made using Wilson et al. (2003) and species identifications were made using regional checklists and revisionary studies, including Hylleberg et al. (1986), Tan & Chou (1993), Paxton & Chou (2000), Aungtonya et al. (2002), Chan (2009), Rajasekaran & Fernando (2012) and Idris & Arshad (2013).

When the reef was dominated by aggregations of sabellariids (December 2010), the density (tubes m^{-2}) and the diameter (mm) of tube openings were also measured. Tube density was measured counting all the tubes contained in digital photos containing 2–4 quadrats of 5×5 cm each (n = 30 quadrats, i.e. 1–2 photos per site, or 4-8 quadrats per site; Photoshop CS2 v. 9.0 ©Adobe). Tube diameters were measured in each collected sample (1 L), on haphazardly selected clusters of 30 adjacent tubes (n = 180 tubes, i.e. one cluster of 30 tubes per site). Measurements were taken with a digital calliper to the nearest 0.1 mm.

Statistical analyses. To explore the degree of association between polychaete species and morphospecies relative to space (sampling sites) and time (surveys), we performed hierarchical cluster analyses, utilising the Jaccard similarity index and the strong linkage aggregation method (Johnson & Wichern, 1992). Groups of taxa were considered, which corresponded to an arbitrary similarity cut-off value of 0.65. Distances from missing values were calculated by pairwise deletion (Hammer & Harper, 2005). All analyses

Fig. 2. Some of the species found in this study. a = *Lumbrineris* sp. 1 (scale bar = 1 mm); b = *Perinereis maindroni* (scale bar = 1 mm); c = *Parahalosydnopsis tubicola* (scale bar = 5 mm); d = *Eulalia* sp. 1 (scale bar = 3 mm); e = *Polydora cavitensis* (scale bar = 1 mm); f = *Loimia verrucosa* (scale bar = 5 mm).

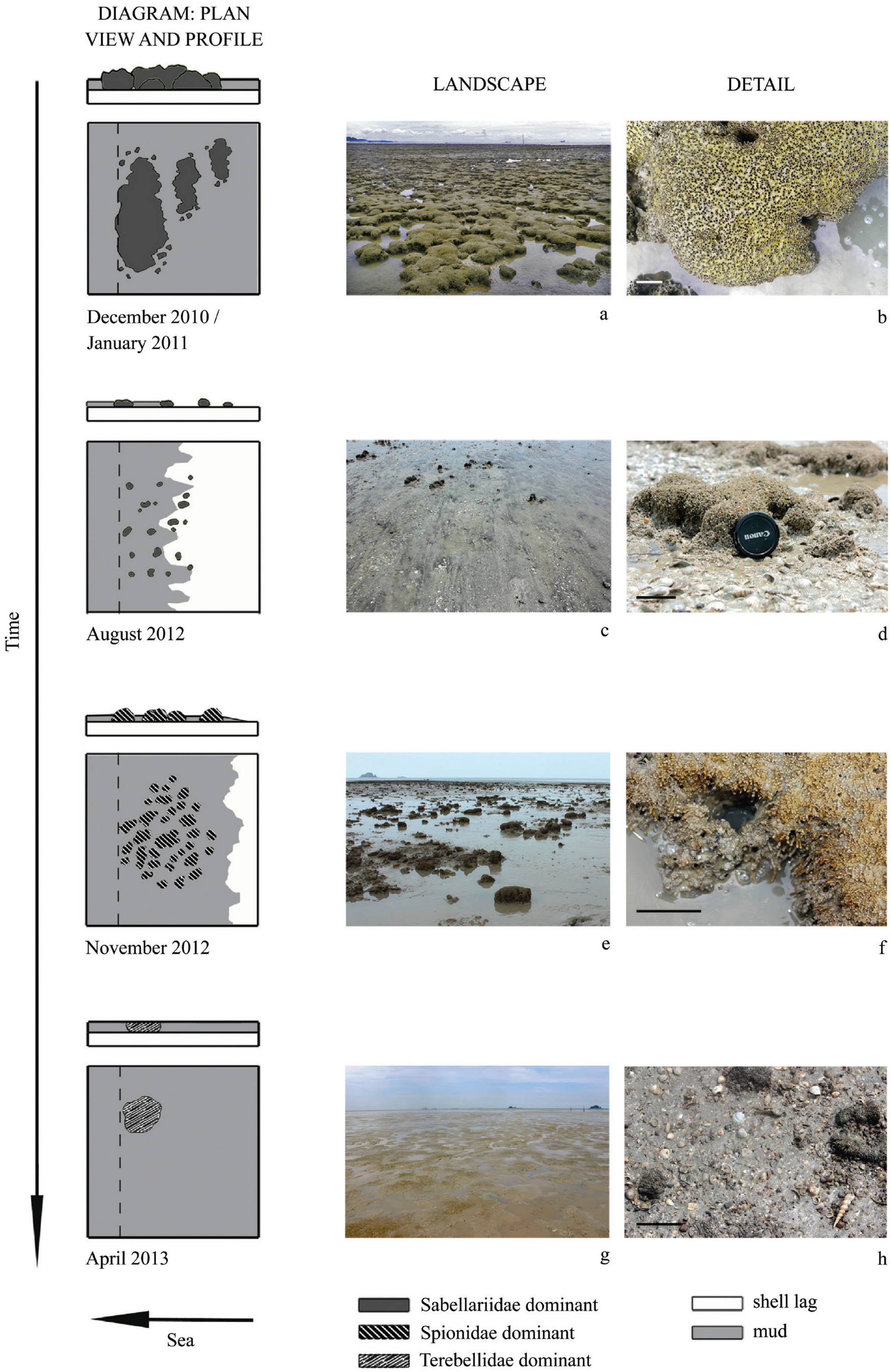

Fig. 3. Diagram illustrating the observed conditions of the polychaete communities. December 2010/January 2011: a = reef barriers; b = detail of a clump of *Sabellaria* sp. 1 (scale bar = 5 cm). August 2012: c = exposed shell bed, with erosive ridges perpendicular to the shore line with small (longest dimension: 5–20 cm) and scattered clumps of *Sabellaria* sp. 1; d = detail of a polychaete clump, on top of the shell lag (scale object's diameter = 5 cm). November 2012: e = polychaete reef, with larger and more tightly packed clumps than in c; f = detail of a clump mainly formed by tubes of spionids (scale bar = 3 cm). April 2013: g = the shore covered by a mud layer; h = detail of a patch of coarse sediments, heavily colonised by terebellid worms (scale bar = 10 cm); hatched lines: water's edge during spring low tide

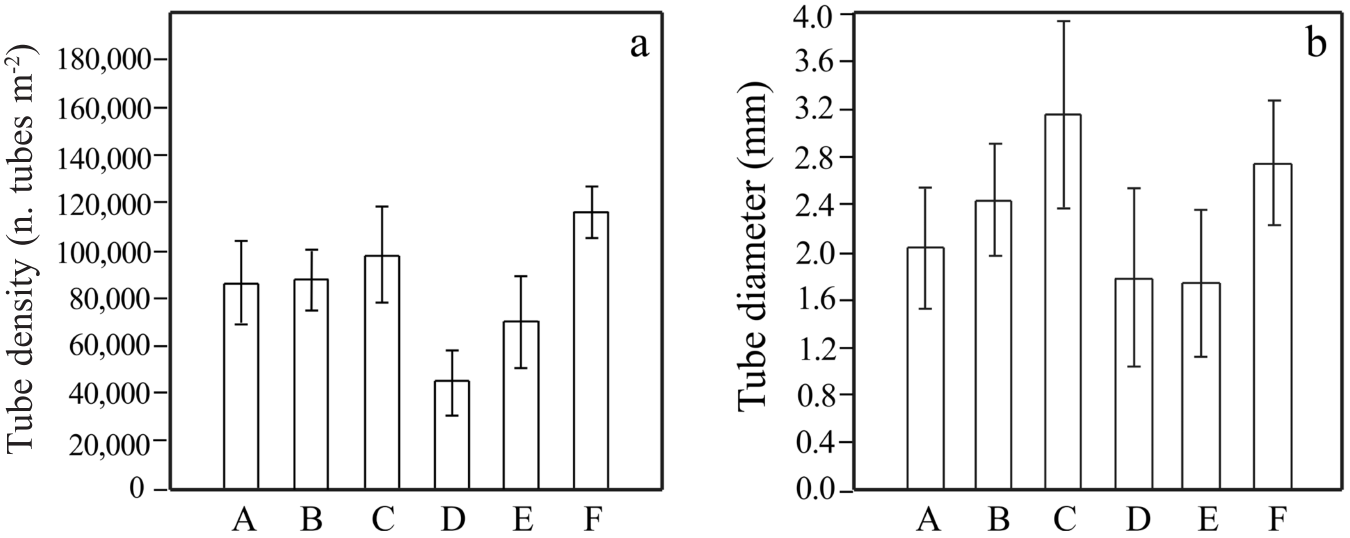

Fig. 4. Bar charts of *Sabellaria* sp. 1 tubes' density (a) and tubes' diameter (b) measured in December 2010. Bars indicate mean values, and whiskers indicate one-sigma intervals based on standard deviations.

were conducted using PAST v.2.09 (Hammer et al., 2001; Hammer & Harper, 2005).

RESULTS

Community composition. Overall, 26 species and morphospecies from 12 families were found (Fig. 2, Table 1, Online Resource 1). Five species are new records for a geographic area including the South China Sea, the Malacca Straits and the Andaman Sea (Hylleberg et al., 1986; Paxton & Chou, 2000; Aungtonya et al., 2002; Chan, 2009; Rajasekaran & Fernando, 2012; Idris & Arshad, 2013); four species plus the morphospecies *Sigambra* sp. 1 are new records for the Malay Peninsula only (Tan & Chou, 1993; Chan, 2009; Idris & Arshad, 2013).

Field surveys and measurements. In December 2010, the reef was made of several elongated barriers or patches along coast (Fig. 3a), formed by clustered and fused clumps of polychaete tubes (Fig. 3b). The barriers were several hundred metres long and 50–200 m wide. The primary builder species was *Sabellaria* sp. 1, occurring at all sites in this survey (Table 2). During spring low tide, the surveyed reef barrier spanned through the lower and middle intertidal zones, from a point at ~200 m from the supratidal sand berm, down to the sea water's edge (Fig. 1). Clusters of smaller clumps and ball-shaped structures of 50–100 cm in diameter hemmed the reef's margins (sites A, B, F; Fig. 1). The superficial substrate was muddy, and excavations indicated that the clumps grew on top of a shell lag. The clumps' height was 20–50 cm above ground level (Ribero & Polgar, 2012). The mean (± standard deviation) tube density of the primary builders per site was 89,467 ± 27,485 tubes m^{-2}, n = 30 (26,000–131,600 tubes m^{-2}; Online Resource 2). The average tube diameter was 2.3 ± 0.8 mm, n = 180 (0.5–4.5 mm; Online Resource 3).

Ten polychaete taxa were collected during this survey. In particular, the secondary tube builder *Polydora cavitensis* and the errant species *Perinereis maindroni* occurred at all sites (Table 2). *Lysidice* sp. 1, *Lysidice* sp. 2, *Neanthes willeyi* and *Lepidonotus* cf. *sublevis* were collected in the inner and back reef (sites A, B, and C, respectively; Table 2).

In January 2011, the shore was covered by mud and the condition of the sabellariid reef was essentially the same of December 2010. No samples were collected during this survey.

In August 2012, only scattered, visibly eroded clumps of *Sabellaria* sp. 1 were observed, whose mean height per site increased in a seaward direction (overall mean = 10.0 cm ± 5.0 cm, n = 13; Online Resource 4a; Fig. 3c, d). A shell lag was exposed in sites A, B and C (Figs. 1; 3c), and the superficial substrate was richer in mud towards the sea. The shell lag was crossed by numerous parallel ridges, perpendicular to the shore and partially filled with mud (Fig. 3c). Along the western exposed margin, the clumps were more eroded. Excavations showed that these clumps grew on top of the shell bed, at a depth of 10–15 cm. No buried polychaete clumps were found below the mud. Only six species were collected during this survey (Table 2). The only tubiculous polychaetes in the scattered and eroded reef clumps were *Sabellaria* sp. 1 and *Loimia verrucosa*. This survey was characterised by the presence of the errant polychaetes *Nectoneanthes oxypoda* and *Lepidonotus* sp. 1, found in the lower intertidal zone (sites E, F; Fig. 1; Table 2). *Marphysa* sp. 1 and the tubiculous *Diopatra claparedii* were also collected in this survey.

In November 2012, the polychaete clumps were both larger and more tightly packed than three months earlier (Figs. 3e, f). The shell bed was found below 15–20 cm of mud throughout the intertidal zone, except at sites A and B, where it was exposed. The mean height per site of the polychaete clumps was 11–19 cm (overall mean 14.5 cm ± 5.1 cm, n = 58; Online Resource 4b), and were mainly composed of tubes of *Polydora cavitensis* (Fig. 3f), with few scattered tubes of *Sabellaria* sp. 1. The polychaete assemblage included 17 species. The high species richness observed in this survey

Table 2. Spatial and temporal species distributions. Upper case letters indicate sites (Fig. 1). ? = Absence/presence data for sites A and C are not available for the survey of August 2012. Shaded areas = dominant builders. Species abbreviations: Chrysopetalidae: bre = *Paleaequor breve*; Eunicidae: lys1 = *Lysidice* sp. 1, lys 2 = *Lysidice* sp. 2, mar = *Marphysa* sp. 1; Glyceridae: nic = *Glycera nicobarica*; Lumbrineridae: lum = *Lumbrineris* sp. 1; Nereididae: bur = *Ceratonereis* (*Composetia*) *burmensis*, cri = *Leonnates crinitus*, lae = *Laevispinereis* sp. 1, mai = *Perinereis maindroni*, nicon = *Nicon* sp. 1, oxy = *Nectoneanthes oxypoda*, sin = *Perinereis singaporiensis*, wil = *Neanthes willeyi*; Onuphidae: cla = *Diopatra claparedii*; Phyllodocidae: eul = *Eulalia* sp. 1; Pilargidae: cab = *Cabira* sp. 1; sig = *Sigambra* sp. 1; Polynoidae: lep1 = *Lepidonotus* sp. 1, lep2 = *Lepidonotus* sp. 2, lep3 = *Lepidonotus* sp. 3, sub = *Lepidonotus* cf. *sublevis*, tub = *Parahalosydnopsis tubicola*; Sabellariidae: sab = *Sabellaria* sp. 1; Spionidae: cav = *Polydora cavitensis*; Terebellidae: ver = *Loimia verrucosa* (see also Tab. 1).

Species	**26 Apr 2013 (Absence)**						**30 Nov 2012 (Growth)**						**7 Dec 2010 (Stagnation)**						**7 Aug 2012 (Destruction)**					
	A	B	C	D	E	F	A	B	C	D	E	F	A	B	C	D	E	F	A	B	C	D	E	F
bre						×													?		?			
bur							×												?		?			
cab						×						×							?		?			
cav						×	×	×	×	×	×	×	×	×	×	×	×	×	?		?			
cla																			?		?		×	
cri						×			×										?		?			
eul							×												?		?			
sab							×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
lae							×												?		?			
lep1																			?		?			×
lep2						×													?		?			
lep3						×	×		×			×			×		×		?		?			
lum						×			×										?		?			
lys1															×				?		?			
lys2													×						?		?			
mai						×	×		×			×	×	×	×	×	×	×	?		?			
mar						×	×	×	×	×									?		?			×
nic						×	×												?		?			
nicon							×												?		?			
oxy																			?		?			×
sig						×													?		?			
sin							×												?		?			
sub															×				?		?			
tub						×			×	×							×		?		?			
ver						×	×		×	×		×					×		?		?			×
wil									×					×					?		?			
Totals:	0	0	0	0	0	13	12	3	10	5	2	6	4	4	6	3	6	3	1	1	1	1	2	5

(Fig. 5a) was mainly due to seven nereidid species (Table 2). Except *Perinereis maindroni*, which was also found at site F, all these nereidids were found in the inner reef (site A), where the shell lag was exposed, and in the back reef (site C; Fig. 5b; Table 2).

In April 2013, the reef completely disappeared, and the whole tidal flat was covered by a superficial layer of mud (Fig. 3g). Excavations demonstrated the presence of a shell lag at a depth of 15–30 cm. No buried clumps of polychaete tubes were found. An isolated ~100 m wide patch of sand and shell debris was observed at site F, heavily colonised by *Loimia verrucosa* (Fig. 3h). Thirteen polychaete species were found here (Table 2). A few, small sabellariid clumps (height ~5–10 cm, longest dimension ~5–20 cm) were scattered inside this patch, but no live sabellariid polychaetes were found inside. These empty tubes were colonised by *L. verrucosa* and *Marphysa* sp. 1. *Parahalosydnopsis tubicola* was often observed to co-occur in the same tubes of *L. verrucosa*. The tubiculous *Polydora cavitensis* was also present in this patch, together with the predatory *Lumbrineris* sp. 1. No polychaetes were found in the other sites, but we observed pairs of openings (spaced at ~60 cm) in all other sites, possibly corresponding to large U-shaped burrows dug by polychaete worms.

Species richness: temporal and spatial patterns. Polychaete species richness varied both in time and space (Fig. 5). The highest richness was recorded in November 2012 (17 species) and the lowest in August 2012, when single representatives of six families were recorded (Fig. 5a). Except the seaward exposed margin (F), where species richness increased over time (Fig. 5b), values were higher in December 2010 and November 2012 than in August 2012 and April 2013. Overall, the number of species was higher in marginal and more exposed sites (A, F) than in internal sites (D, E), except the seaward portion of the inner reef (site B), which was less rich than the back reef (site C; Figs. 1, 5c). A similar pattern was observed in November 2012; species richness increased in a seaward direction both in August 2012 and April 2013. In December 2010, a comparable number of species was recorded at all sites (Fig. 5d).

Polychaetes' temporal and spatial distribution. The temporal and spatial species distributions (Table 2) are summarised by the dendrograms of cluster analyses (Fig. 6).

Six groups of species (T1–T6) were associated with different surveys (Fig. 6a). Groups T2 and T3 include species that were found in November 2012 and at least one more survey, including the three tube builders: *Sabellaria* sp. 1, *Polydora cavitensis* and *Loimia verrucosa*. In particular, the latter species (group T2) was collected in all surveys. *Marphysa* sp. 1 (group T2) was also collected in August 2012 (Table 2). Each of the other groups (T1, T4, T5, T6) includes species that were all collected in a single survey. In particular, T4 includes five nereidids, *Eulalia* sp. 1 and *Cabira* sp. 1, all collected in November 2012. *Leonnates crinitus* and *Cabira* sp. 1 were also collected in April 2013 (Table 2).

Four groups of species (S1–S4) are associated with different sites (Figs. 1, 6b). Group S2 includes species that were found in the back reef and the seaward exposed margin (sites C and F, respectively), plus at least two different sites. In particular, the tube builders *Sabellaria* sp. 1 and *P. cavitensis*, and the errant *Perinereis maindroni* were found at all sites. The tubiculous *L. verrucosa* was found at all sites, except the seaward portion of the inner reef (site B; Table 2). Groups S3 and S4 include species that were all collected in one site. In particular, S4 includes four nereidids, *Eulalia* sp. 1 and *Lysidice* sp. 2, which were only found in the landward portion of the inner reef (site A). In group S1, all the species were found in the seaward exposed margin (site F). *Glycera nicobarica* was also found at site A, and *Lumbrineris* sp. 1 was also found in the back reef (site C; Table 2).

DISCUSSION

Insights on the reef's dynamics. The ecosystem's states observed during the different surveys are consistent with the four phases of a classical cycle of a sabellariid reef (Gruet, 1986). In this view, our surveys can be defined as: (i) absence or pre-settlement (April 2013); (ii) settlement or growth (November 2012); (iii) stagnation (December 2010, January 2011); (iv) destruction (August 2012). In particular, these phases are associated with a conspicuous turnover of the polychaete community's composition.

During the absence phase (April 2013), the tubiculous *Loimia verrucosa* was a dominant component of the community, forming dense aggregations. In all other surveys, *L. verrucosa* was found at lower densities in almost all the sites (Fig. 6; Table 2). This indicates that this species, being capable of colonising mud deposits, becomes dominant when no hard substrate is available in the system. The co-occurrence of *Parahalosydnopsis tubicola* in its tubes suggests a species-specific association, since *P. tubicola* has been already found in mutualistic association with the congeneric *Loimia medusa* (Savigny in Lamarck, 1818) in other parts of the Indo-Pacific (Martin & Britayev, 1998). It can be reasonably hypothesised that this isolated patch of coarser sediments was determined by the feeding and tube building activity of *L. verrucosa*. This species appears to establish and maintain patches of coarser sediments when the superficial substrate is dominated by mud deposits, possibly facilitating the establishment of sabellariid colonies in the Jeram system. *Loimia verrucosa* is a surface deposit feeder, like its congener, *L. medusa* (see Llanso & Diaz, 1994). Due to its feeding strategy, this latter species can effectively destabilise mud substrates, by decreasing the sedimentation rate of finer particles (Luckenbach, 1986). High densities of the terebellid *Lanice conchilega* (Pallas, 1766) can increase the coarse sand fraction and heterogeneity of the sediment (Rabaut et al., 2007), thus facilitating the establishment of sabellariid colonies on mud substrates (Larsonneur et al., 1994). In general, this phase was characterised by the presence of opportunistic species that both occurred in at least two different phases (group T2; Fig. 6a), and in at least two different zones (group S2; Fig. 6b), and by the absence of *Sabellaria* sp. 1, which occurred in all other phases. *Paleaequor breve*, *Sigambra*

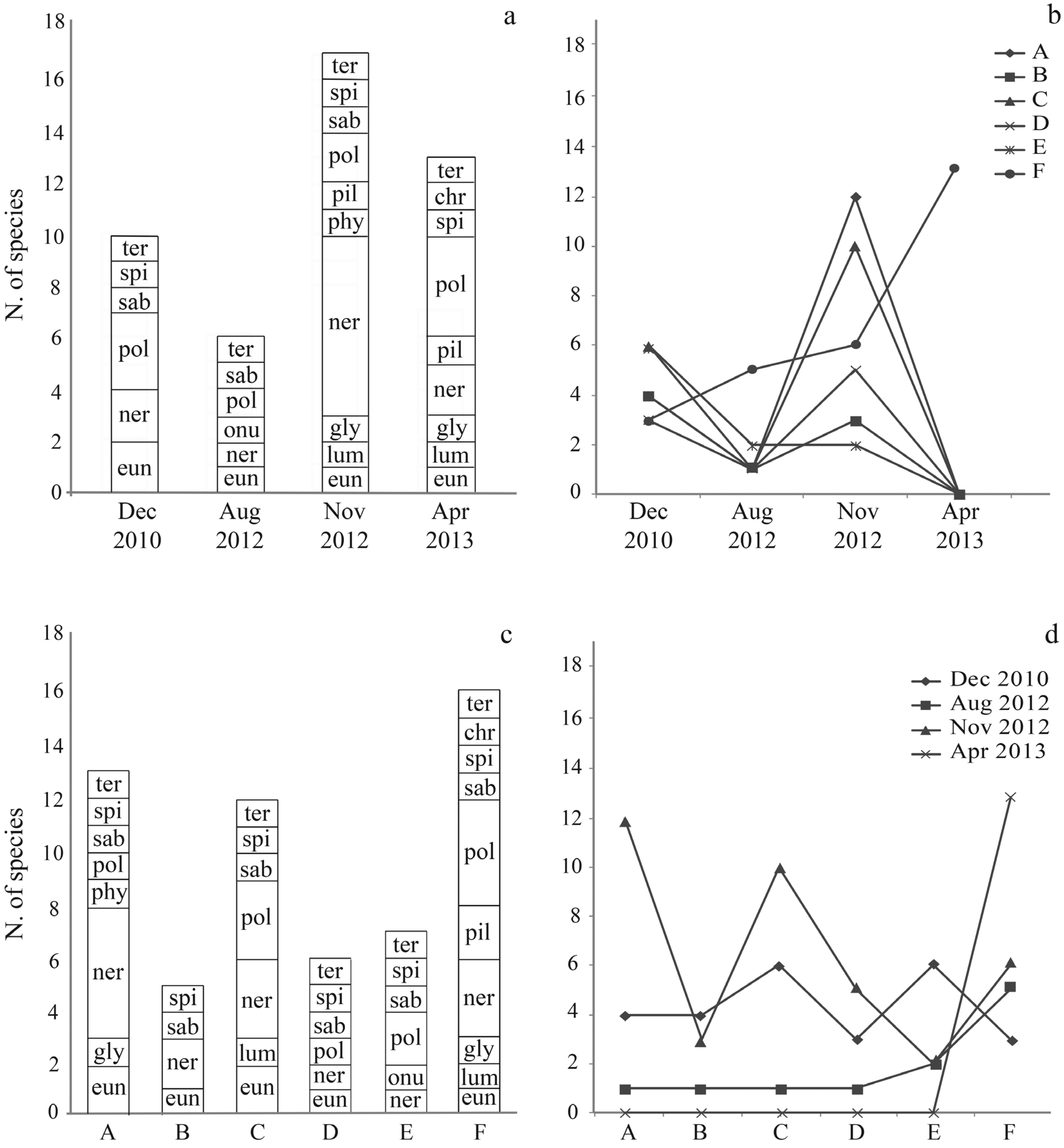

Fig. 5. Species richness (grouped by family): per survey, at all sites (a); per survey, at each site (b); per site, in all surveys (c); per site, in each survey (d); chr = Chrysopetalidae, eun = Eunicidae, gly = Glyceridae, lum = Lumbrineridae, ner = Nereididae, onu = Onuphidae, phy = Phyllodocidae, pil = Pilargidae, pol = Polynoidae, sab = Sabellariidae, spi = Spionidae, ter = Terebellidae.

sp. 1 and *Lepidonotus* sp. 2 were exclusively found in this phase (Table 2).

The settlement or growth phase (November 2012) corresponded to the richest polychaete assemblage, and the dominant tube builder was the spionid *Polydora cavitensis*. This species was collected in all the sites and in almost all surveys (Table 2). Spionids are typical pioneer species, which can rapidly colonise disturbed habitats during post-disturbance and early-successional phases (e.g., *Polydora ligni* Webster, 1879 = *Polydora cornuta* Bosc, 1802; see Grassle & Grassle, 1974; Pearson & Rosenberg, 1978; Gallagher et al., 1983; Zajac, 1991). The nereidids, four ones exclusively collected in this phase (Table 2), include species found in soft substrates, and species opportunistically colonising both soft and hard substrates, such as *Ceratonereis* (*Composetia*) *burmensis* and *Perinereis singaporiensis*, respectively (Paterson et al., 2004; Metcalfe & Glasby, 2008). This reasonably indicates that the unusually high number of nereidid species during this phase in Jeram (e.g., Frith et al., 1976; Nakao et al., 1989; Sarkar et al., 2005) is related to the higher habitat complexity offered by the highly heterogeneous substrate

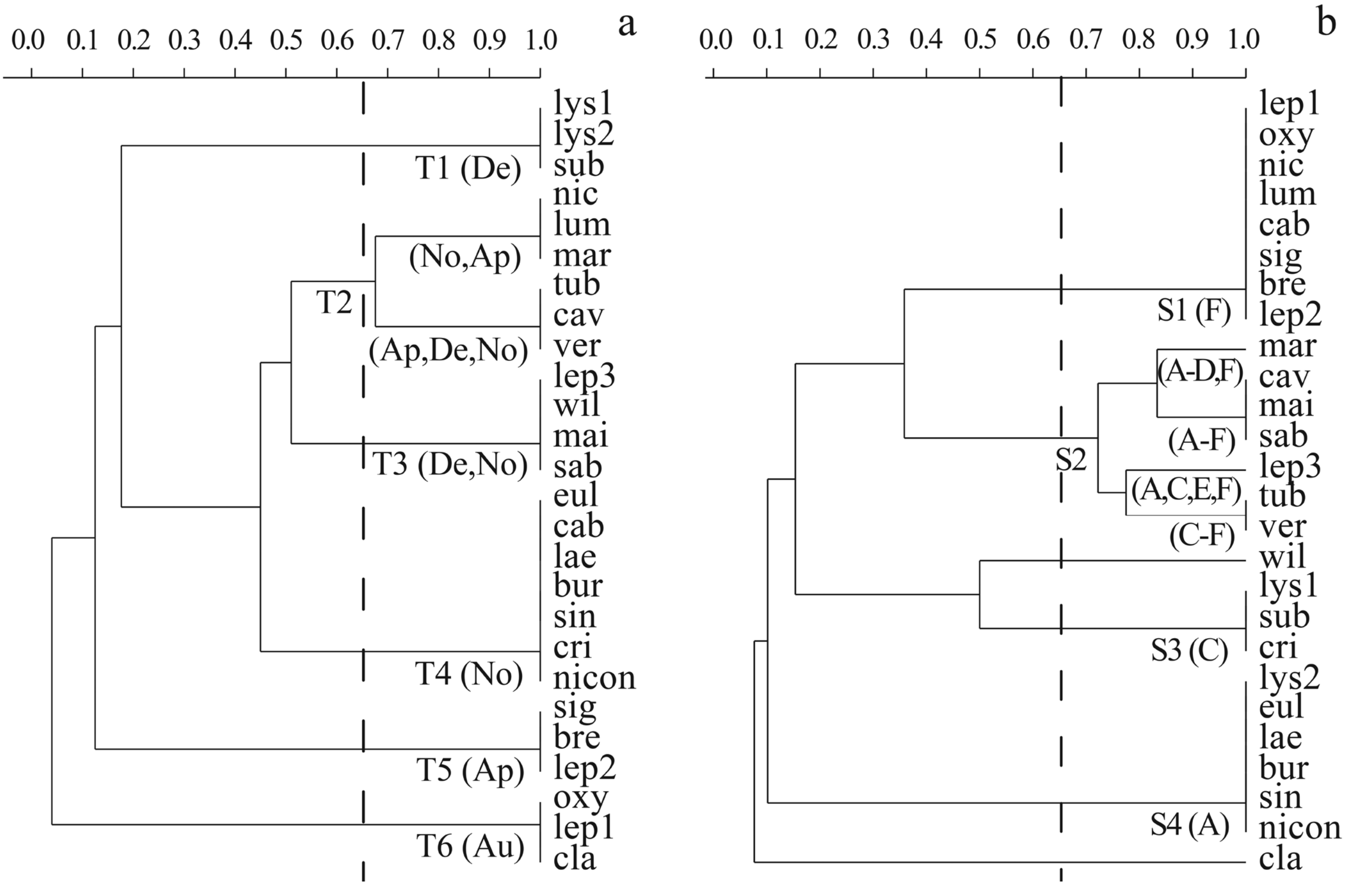

Fig. 6. Hierarchical cluster analyses of species relative to time (a) and space (b). In (a), six groups of species (T1–T6) are associated with different surveys; in parentheses: surveys in which all the group's components were found (De = 7 December 2010; No = 30 November 2012; Au = 7 August 2012; Ap = 26 April 2013; Fig 2). In (b), four groups of species (S1–S4) are associated with different sites; *in parentheses*: sites where all the group's components were found (A–F; Fig. 1); 'wil' (found at sites B and C) and 'cla' (found at site E) were not included in any group. Vertical dashed lines: 0.65 similarity cut-off value. Species' abbreviations as in Table 2.

conditions. Several other polychaetes were also found in the previous phase, such as *Marphysa* sp. 1, *Lumbrineris* sp. 1 and *Glycera nicobarica* (group T2; Fig. 6a), when they all occurred in a more seaward direction (Table 2). Other species were also found in the next stagnation phase, such as the tubiculous *Sabellaria* sp. 1 and *L. verrucosa*, and *P. tubicola* (groups T2, T3; Fig. 6a).

During the stagnation phase (December 2010), three species (*Lysidice* sp. 1, *Lysidice* sp. 2 and *Lepidonotus* cf. *sublaevis*) were exclusively found in this phase, in the higher intertidal zone (group T1; Fig. 6a). The presence of the eunicids *Lysidice* sp. 1 and *Lysidice* sp. 2 only when the sabellariid reef was best developed may reflect a preference for reefal habitats for some members of this group. Three species only occurred in this and in the previous phase (group T3; Fig. 6a; Table 2).

During the destruction phase (August 2012), the superficial substrate was dominated by shell deposits. The thick shell bed typically inhibits sediment-destabilising infaunal borers (taphonomic inhibition, sensu Kidwell & Jablonski, 1983), as also noted by Seilacher (1984) in Jeram. Given the mutually exclusive occurrence of sediment-stabilising and destabilising species in soft-bottom ecosystems (Posey, 1987; Volkenborn et al., 2009), the inhibition of bioturbators would further facilitate sediment-stabilising tube-builders, promoting a shift from a community dominated by infaunal organisms to a community dominated by epibenthic organisms (Reise, 2002), thus preparing the conditions for the pre-settlement phase, and completing the cycle. The three species (*Lepidonotus* sp. 1, *Nectoneanthes oxypoda* and *Diopatra claparedii*) which characterise this phase (group T6; Fig. 6a) occurred in the lower intertidal zone (sites E, F). The other species were opportunists, which occurred in at least three different phases and five different sites (Table 2).

Species richness: spatial and temporal patterns. The observed temporal patterns of species richness are largely consistent with Gruet's model (1986), with lower levels at all sites except F during the absence phase (April 2013), highest levels during the settlement or growing phase (November 2012), intermediate levels during the stagnation phase (December 2010), and again lower levels during the destruction phase (August 2012). Similar temporal patterns of species richness were observed in other benthic intertidal communities of polychaetes and other organisms, such as aggregations of *Lanice conchilega*, reefs of *Sabellaria alvelolata*, and seagrass communities (Cunningham et al., 1984; Kirkman, 1985; Van Hoey et al., 2008). Such patterns are consistent with the general properties of ecological successions (Connell, 1978; Pearson & Rosenberg, 1978).

The observed pattern of spatial variability of the species richness is consistent with the more homogeneous conditions of the core site D, relative to the more heterogeneous conditions of the marginal zones, which are characterised by higher levels of habitat diversity, such as crevices and pools (Cunningham et al., 1984), forming ecotones. The lower richness of site B is possibly an effect of the smaller size of the reef patches in this area. During the absence phase (April 2013), the unsuitable conditions of more terrestrial zones probably determined the observed increasing trend of species richness in a seaward direction. During the growing phase (November 2012) the overall spatial pattern was particularly evident, while it was less apparent during the stagnation phase (December 2010), probably due to the generally more homogeneous conditions of this latter phase. During the destruction phase (August 2012), the pattern was analogous to that observed during the absence phase, although less extreme.

Polychaetes' spatial and temporal distribution. Cluster analyses showed that this community includes both opportunists, associated with different phases and sites, and specialists, which were only found in specific phases and sites. In particular, the three tubiculous frame builders (*Polydora cavitensis*, *Sabellaria* sp. 1 and *Loimia verrucosa*) occurred in more sites and in more phases, while errant polychaetes tended to be associated with specific phases or sites.

This suggests that numerous errant species depend on more specific microhabitat conditions, which can be provided by the structures built by the pioneer tubiculous builders. In fact, most of the errant species found only in the seaward exposed margin (site F) during the absence phase (e.g., *Glycera nicobarica*, *Leonnates crinitus*, *Lepidonotus* sp. 3, *Lumbrineris* sp. 1, *Marphysa* sp. 1), occurred in higher intertidal areas during the growth phase, where the builders established a reef. This suggests that the builders acted as ecosystem engineers, being the first to re-colonise the middle and upper intertidal zones from the lower intertidal zone during the growth phase, thus mediating the colonisation of these zones by several errant species. In this view, builders would have facilitated a terrestrialization process, enabling the colonisation of the middle and upper intertidal zone by species that would be otherwise restricted to the lower intertidal zone.

Insights on reef dynamics: the 'Jeram model'. Our observations are consistent with the 'Jeram model' outlined by Seilacher (1984). According to this model, the reef grows on top of the residual shell bed, which is exposed by storm events, and the mud gradually deposits at the base of the reef during inter-storm periods (overall positive sedimentary balance). This model predicts alternating periods of muddy and shelly substrates with associated epibenthic and infaunal communities, driven by fluctuating hydrodynamic conditions.

The mud can completely cover the shell lag before the reef can be re-established, as we observed in April 2013. During this absence phase, our observations suggest that terebellid polychaetes may facilitate the re-establishment of the colonies of sabellariids in the lower intertidal zone by establishing patches of coarser superficial sediments. During the growth phase, as we observed in November 2012, the reef would expand due to the growth of pioneer polychaete builders, as also observed by Seilacher (1984), in "post-storm conditions". This allows numerous associated species to colonise the middle and upper intertidal zones, migrating in a landward direction. The presence of an exposed shell lag in the upper intertidal zone (sites A, B) during this phase indicates that only extensive destructive events affecting the middle and lower intertidal zone are able to effectively destroy the reef, while minor destructive events can maintain the community at an early successional stage. During any prolonged absence of destructive events, the reef can expand and colonise large portions of the intertidal flat, as observed in December 2010 and January 2011. At any time, the height of the reef clumps above the ground level is then the result of the average growth rate of the polychaete clumps, the action of erosive processes, and mud sedimentation rates. The reef can then be destroyed by storm events that are sufficiently strong to erode both the mud layer and the reef along large sections of the intertidal zone, such as those that possibly occurred during the summer monsoon that preceded our observations of August 2012.

If the reef is affected only by stronger storm events, the cycle's periodicity might be more irregular than monsoons, or even follow longer atmospheric cycles, as observed in other polychaete reefs (e.g., El Niño Southern Oscillation; Pohler, 2004).

Intense storms and monsoons can also affect the salinity of the tidal flat, especially if rain spells occur prevalently during low tide (Broom, 1982). The lethal effect of low salinity levels caused by tropical storms has been documented in estuarine and shallow subtidal benthic communities (Boesch et al., 1976), and might prevail or act in synergy with the effects of storms' mechanical erosion on *Sabellaria* reefs. In fact, other species of *Sabellaria* are rather intolerant of low salinity levels (Holt et al., 1998).

Our observations further suggest that the ecological succession triggered by drastic environmental changes in this ecosystem might also be driven by specific synecological interactions (e.g., Connell & Slatyer, 1977; Seilacher, 1984; Zajac & Whitlatch, 1985).

No other intertidal sabellariid reefs were previously recorded along the west coast of the Malay Peninsula. This might be due to a lack of specific environmental conditions needed for larval settlement and tube construction, such as appropriate grain size composition of sediments and suspended particles, respectively (Naylor & Viles, 2000). In fact, the Jeram shore has a divergent grain size composition compared to other tidal flats along the west coast of the Malay Peninsula, with smaller percentages of clay, silt and very fine sand, and higher percentages of fine sand and coarse shell material (Chong et al., 2012), consistent with the typical habitat of *Sabellaria* species. In this case, during the growth phase sabellariid larvae may re-colonise the tidal flat recruiting from small remnants of reef patches survived after the destruction phase. It appears improbable that the source of the larvae is a subtidal portion of the reef, since *Sabellaria* species often have species-specific depth ranges (Holt et al., 1998; Pohler, 2004). However, the recent discovery of gregarious polychaete patches on the intertidal shore of Tanjung Bungah (Penang, Malaysia, Mahadi Mohammad pers. comm.), suggests that other unrecorded reefs or patches can possibly occur along the west coast of the Malay Peninsula, and that larval recruitment might occur from other sites. In general, the knowledge of frame-building polychaetes is considerably fragmentary in this region, as suggested by other authors (Paxton & Chou, 1994; Idris & Arshad, 2013).

Concluding remarks. A systematic and quantitative investigation of the influence of climatic conditions and synecological interactions on this reef is needed in order to test the discussed hypotheses. The large number of new species and first records found in this study also highlights the need for further research and taxonomic surveys in this scarcely studied region. Specific monitoring programs and conservation policies should be adopted to sustainably manage this reef, and document the presence and state of similar biogenic structures along the coasts of the Malay Peninsula.

ACKNOWLEDGEMENTS

Thanks to Salvatore Milli (University of Rome La Sapienza) for his revision of the manuscript, and to Colin George Moore (Heriot-Watt University, Edinburgh) and Ralph Vorberg (Marine Science Service, Dassendorf) for their constructive comments. Thanks to Charlotte Watson (Museum and Art Gallery of the Northern Territory, Darwin) for her help in the discrimination of the chrysopetalid species. Thanks to A. Sasekumar (University of Malaya, Kuala Lumpur) for his assistance during the first survey, to Laura Ribero for her help in the field, in the laboratory and for her comments, and to Hj. Hussin Azhar (University of Malaya, Kuala Lumpur) and Mahadi Mohammad (Universiti Sains Malaysia, Penang) for their communications.

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SUPPLEMENTARY MATERIAL

Online resource 1. Reference specimens deposited at the Museum and Art Gallery of the Northern Territory (NTM), Darwin.

Registration No.	**Family**	**Genus**	**Species**	**Author and date**
NTM W25328	Polynoidae	*Lepidonotus*	cf. *squamatus*[1]	(Linnaeus, 1758)
NTM W25329	Polynoidae	*Parahalosydnopsis*	*tubicola*	Pettibone, 1977
NTM W25330	Nereididae	*Perinereis*	*maindroni*	Fauvel, 1943
NTM W25331	Pilargidae	*Cabira*	sp. 1	
NTM W25332	Spionidae	*Polydora*	*cavitensis*	Pillai, 1965
NTM W25333	Glyceridae	*Glycera*	*nicobarica*	Grube, 1868
NTM W25334	Spionidae	*Polydora*	*cavitensis*	Pillai, 1965
NTM W25335	Nereididae	*Nicon*	sp. 1	
NTM W25336	Nereididae	*Neanthes*	*willeyi*	(Day, 1934)
NTM W25337	Spionidae	*Polydora*	*cavitensis*	Pillai, 1965
NTM W25338	Nereididae	*Perinereis*	*singaporiensis*	(Grube, 1878)
NTM W25339	Nereididae	*Perinereis*	*maindroni*	Fauvel, 1943
NTM W25340	Nereididae	*Leonnates*	*crinitus*	Hutchings & Reid, 1991
NTM W25341	Nereididae	*Perinereis*	*maindroni*	Fauvel, 1943
NTM W25342	Spionidae	*Polydora*	*cavitensis*	Pillai, 1965
NTM W25343	Terebellidae	*Loimia*	*verrucosa*	Caullery, 1944
NTM W25344	Terebellidae	*Loimia*	*verrucosa*	Caullery, 1944
NTM W25345	Terebellidae	*Loimia*	*verrucosa*	Caullery, 1944
NTM W25346	Terebellidae	*Loimia*	*verrucosa*	Caullery, 1944
NTM W25347	Phyllodocidae	*Eulalia*	sp. 1	
NTM W25348	Nereididae	*Composetia*	*burmensis*[2]	(Monro, 1937)
NTM W25349	Nereididae	*Laevispinereis*	sp. 1	
NTM W25375	Nereididae	*Perinereis*	*maindroni*	Fauvel, 1943
NTM W25376	Terebellidae	*Loimia*	*verrucosa*	Caullery, 1944
NTM W25377	Nereididae	*Leonnates*	*crinitus*	Hutchings & Reid, 1991
NTM W25378	Glyceridae	*Glycera*	*nicobarica*	Grube, 1868
NTM W25379	Polynoidae	*Lepidonotus*	sp. 2	
NTM W25380	Spionidae	*Polydora*	*cavitensis*	Pillai, 1965
NTM W25381	Polynoidae	*Lepidonotus*	cf. *squamatus*[1]	(Linnaeus, 1758)
NTM W25382	Pilargidae	*Cabira*	sp. 1	
NTM W25383	Pilargidae	*Sigambra*	sp. 1	
NTM W25384	Polynoidae	*Parahalosydnopsis*	*tubicola*	Pettibone, 1977

[1] Reported as *Lepidonotus* sp. 3 in this study.
[2] Reported as *Ceratonereis* (*Composetia*) *burmensis* in this study.

Online resource 2. *Sabellaria* sp. 1 tubes' density per site (tubes m^{-2}) (December 2010). At each site, 1–2 photos of polychaetes clumps containing 2–4 quadrats of 5×5cm were made; A–F = study sites.

A	**B**	**C**	**D**	**E**	**F**
76,400	105,200	102,000	26,000	50,800	116,400
66,800	74,800	119,200	51,200	91,200	99,600
104,800	90,400	123,200	55,600	83,600	107,600
96,800	81,200	82,400	45,200	58,000	125,600
		90,400			127,200
		74,000			114,800
					131,600
					112,000

Online resource 3. Tubes' diameter of *Sabellaria* sp. 1 per site (mm) (December 2010). Clusters of 30 adjacent tubes were measured at each site; A–F = study sites.

A	**B**	**C**	**D**	**E**	**F**
0.8	1.5	1.5	0.1	1.0	2.0
1.0	1.7	1.9	0.5	1.0	2.1
1.2	1.7	2.0	0.7	1.1	2.2
1.4	1.8	2.1	1.0	1.1	2.2
1.5	1.9	2.3	1.0	1.2	2.3
1.6	2.0	2.3	1.0	1.2	2.3
1.6	2.0	2.4	1.1	1.2	2.3
1.7	2.0	2.5	1.2	1.3	2.3
1.8	2.1	2.6	1.3	1.3	2.4
1.8	2.2	2.8	1.3	1.3	2.4
1.9	2.3	2.9	1.4	1.3	2.5
1.9	2.3	2.9	1.4	1.4	2.5
1.9	2.3	3.1	1.4	1.5	2.5
2.0	2.4	3.1	1.6	1.5	2.5
2.0	2.4	3.2	1.6	1.5	2.6
2.2	2.5	3.4	1.7	1.6	2.7
2.2	2.6	3.4	1.8	1.6	2.7
2.2	2.7	3.4	1.9	1.6	2.8
2.2	2.7	3.4	2.1	1.7	2.8
2.3	2.7	3.5	2.1	1.8	2.8
2.4	2.8	3.5	2.1	1.9	2.8
2.4	2.8	3.7	2.2	1.9	2.8
2.4	2.8	3.7	2.2	2.1	2.9
2.4	2.8	3.8	2.2	2.3	3.1
2.4	2.8	4.0	2.4	2.4	3.3
2.5	2.9	4.1	2.5	2.5	3.3
2.6	3.0	4.1	2.9	2.6	3.4
2.6	3.0	4.2	3.2	2.9	3.5
2.9	3.1	4.3	3.2	2.9	3.7
2.9	3.3	4.5	3.4	3.2	4.3

Online resource 4. Height (cm) of polychaete clumps above the ground level in August 2012 (a) (data not available for sites D and E); and November 2012 (b). In December 2010, heights of clumps were 20–50 cm (Ribero & Polgar, 2012); in April 2013, the reef disappeared: the patch of coarser sediments colonised by terebellids was at the ground level; ordinals in the first column = replicates; SD = standard deviation.

a	**A**	**B**	**C**	**D**	**E**	**F**
1	4.3	8.6	14.1			18.9
2	3.7	7.7	12.3			15.7
3	3.2	7.1	7.8			12.2
4			14.4			
mean	3.7	7.8	12.2			15.6
SD	0.6	0.8	3.0			3.4

b	**A**	**B**	**C**	**D**	**E**	**F**
1	12.0	13.0	10.0	12.0	6.0	19.5
2	10.5	19.0	11.5	22.0	8.0	22.0
3	10.0	15.0	13.0	16.0	10.5	13.5
4	9.5	17.5	9.5	18.0	10.0	23.5
5	11.0	19.0	13.0	11.0	8.5	5.5
6	10.5	20.5	10.0	19.0	9.0	12.0
7	13.0	23.0	12.0	8.0	17.0	26.0
8	12.0	18.0	8.5	16.0	20.0	24.0
9	14.0		14.0	15.0	10.0	21.0
10	8.0		19.0	17.0	21.0	22.0
mean	11.1	18.1	12.1	15.4	12.0	18.9
SD	1.8	3.1	3.0	4.1	5.3	6.5