Boring of Intertidal Sandstones by Isopod Sphaeroma triste in NW Borneo (Sarawak, Malaysia)

Authors: Dodge-Wan, D., and Nagarajan, R.

Source: Journal of Coastal Research, 36(2) : 238-248

Published By: Coastal Education and Research Foundation

URL: https://doi.org/10.2112/JCOASTRES-D-19-00066.1

Journal of Coastal Research	36	2	238–248	Coconut Creek, Florida	March 2020

Boring of Intertidal Sandstones by Isopod *Sphaeroma triste* in NW Borneo (Sarawak, Malaysia)

D. Dodge-Wan* and R. Nagarajan

Department of Applied Geology
Faculty of Engineering and Science
Curtin University
Miri, Sarawak, Malaysia

www.cerf-jcr.org

www.JCRonline.org

ABSTRACT

Dodge-Wan, D. and Nagarajan, R., 2020. Boring of intertidal sandstones by isopod *Sphaeroma triste* in NW Borneo (Sarawak, Malaysia). *Journal of Coastal Research,* 36(2), 238–248. Coconut Creek (Florida), ISSN 0749-0208.

Sphaeromatid isopods are known for their ability to bore into wood and friable rock and to cause damage to mangrove plant roots, wooden structures, and polystyrene dock floats in the intertidal zone. The ability of isopods to bore extensively into rock and accelerate coastal erosion is less well known and has not been previously reported in Malaysia. This study investigated the presence, the identity, and the erosive effect of rock-boring isopods in sandstones of the NW Borneo coastal region (Sarawak, East Malaysia). A multidisciplinary approach was used, including field and laboratory observations (geological and biological) of rocks and wood. This study revealed that abundant cylindrical borings in soft intertidal rock are created by the boring isopod *Sphaeroma triste* (*S. triste*). Bioerosion by this species can result in the direct removal of up to 50% of the exposed surface of the rock and penetrate the rock up to a few centimeters depth. This has a significant but localised impact on coastal erosion, contributing to the development of concavities in the rock, enlargement of joints, deepening of wave cut notches, widening of rock pools, and erosion of fallen blocks and sea-cave walls. There is evidence of modification of the isopods' mandible incisor processes by abrasion during rock boring. Although several Sphaeromatid species are known to bore into soft rocks, this is the first report and comprehensive description of boring into sandstone substrates by *S. triste*. The *S. triste* borings are compared with those made by other species reported elsewhere. In terms of neoichnology, the borings belong to deep-tier Trypanites ichnofacies, and fossil equivalents may be useful in palaeogeographic reconstructions of ancient shorelines, although they may have poor preservation potential.

ADDITIONAL INDEX WORDS: *Crustacea, Isopoda, Sphaeromatidae, coastal bioerosion, marine habitat, neoichnology, intertidal notch, Sarawak, Malaysia.*

INTRODUCTION

Bioerosion has been defined as organic erosive activity, *i.e*. the process of breakdown and/or modification of substrata by macro- and micro-organisms (Davidson *et al*., 2018; Viles, 2013). Bioerosion involves organisms scraping, grazing, boring, burrowing, or dissolving on and in substrata of varying hardness and composition in a range of environments (Kázmér and Taborosi, 2012). Boring oganisms perforate and remove consolidated rocks, whereas burrowers tunnel and displace loose unconsolidated materials. In coastal intertidal regions, common macrobioeroders include molluscs (especially bivalves, gastropods, and chitons), urchins, sponges, worms, and arthropods (crabs and isopods) (Davidson *et al*., 2018; Donn and Boardman, 1988; Kázmér and Taborosi, 2012). Bioerosion can have a profound effect on intertidal ecology as it modifies local environmental conditions at a small scale within the affected habitat. Bioerosion is also a significant geomorphological process leading to rock removal and sediment production, with the potential to modify other dynamic erosive processes (Wilson, 2013). In the intertidal and shallow marine habitats, isopods may burrow into sand, inhabit macroalgae, or bore into mangrove roots or other substrates (Arrontes, 1990; Davidson and de Rivera, 2010; De Ruyck, McLachlan, and Donn, 1991; Miranda and Thiel, 2008). Their reported boring activity is briefly reviewed here, and their potential to cause bioerosion, in the case of boring into rocks, is of specific interest.

A number of Sphaeromatid isopods have been reported to burrow or bore into various substrates and a number of locations worldwide, as listed in Table 1. Wood boring is reported among isopods of the Sphaeromatidae and Limnoriidae families (Cragg, Pitman, and Henderson, 1999; Harrison and Holdich, 1984) including in SE Asia and Borneo (Hossain and Bamber, 2013; Singh and Sasekumar, 1994). Several species of *Sphaeroma* are reported to bore into mangrove roots as well as manmade coastal wooden structures such as jetties. A number of studies have been conducted to document wood-boring species; the types of timber most frequently damaged; and possible measures to prevent damage to jetties, wharves, piers, and other marine structures (Cragg, 1988; Cragg, Pitman, and Henderson, 1999; Nair, 1984; Roszaini and Salmiah, 2015). Sphaeromatid isopods are also reported to damage polystyrene floats used in docks and marinas in several countries, including native species (*e.g.,* in Indo and West Pacific) and non-native (*i.e.* introduced) species (particularly along the Pacific coast of North America) (Carlton and Iverson, 1981; Davidson, 2012). Not only do they do extensive damage to

DOI: 10.2112/JCOASTRES-D-19-00066.1 received 14 May 2019; accepted in revision 16 August 2019; corrected proofs received 31 October 2019.
*Corresponding author: dominique@curtin.edu.my

Table 1. *List of isopods species of the genus Sphaeroma reported boring in wood, polystyrene, and rock substrates worldwide, as well as other reports for S. triste (unspecified whether boring or not).*

Substrate	Reported Species	Country and Location (With Rock Type Where Known)	References (See Footnotes)
Wood	*Sphaeroma annandalei annandalei*	India, Persian Gulf, S Africa, Brazil	1
	Sphaeroma annandalei travancorense	India	1
	Sphaeroma annandalei	Iraq	11
	Sphaeroma peruvianum	Peru, Costa Rica	1, 25
	Sphaeroma quoianum	Australia (East and West), New Zealand, USA (Pacific coast)	1, 2, 3, 4, 5
	Sphaeroma retrolaeve	Japan	1
	Sphaeroma sieboldii	Japan, West Malaysia (Penang)	1, 20
	Sphaeroma terebrans	USA (Georgia to Texas), Brazil, S Africa, India, Sri Lanka, Thailand, Indonesia, Australia (NE), Andaman Islands, Brunei , Philippines, West Malaysia (Kuala Selangor; Lumut, Perak; Endau-Rompin, Pahang)	1, 6, 7, 8, 22,23
	Sphaeroma triste	India (Little Andaman; Rameswaram) (Lakshadweep), Nicobar Islands, NE Indian Ocean, Indonesia, Australia (Qld, NT, WA), Torres Strait, Papua New Guinea, Philippines, West Malaysia (Pulau Babi Besar, Johor; Sungai Patani, Kedah; Lumut, Perak; Morib, Selangor) Brunei	1, 6, 9, 16, 17, 18, 19, 21
	Sphaeroma walkeri	West Malaysia (Lumut, Perak; Endau-Rompin, Pahang)	23
Polystyrene (including dock floats)	*Sphaeroma quoianum*	USA (Oregon, California)	2, 3
	Sphaeroma terebrans	Taiwan	2
	Sphaeroma triste	Australia (Townsville)	1
Rock	*Sphaeroma sp (S. annandalei?)*	India (SW coast: laterite and hard clay)	10
	Sphaeroma annandalei	Iraq (muddy fine sandstone rock, silty clay sediments)	11
	Sphaeroma quoianum	USA (California: sandstone; Pacific coast: peat, mud, sandstone, friable rock), Australia, New Zealand	3, 4
	Sphaeroma sieboldii	Korea (stones on mud flats)	12
	Sphaeroma triste	Indonesia (porous clay), East Malaysia (Sarawak: sandstones and siltstones)	13 (Indonesia), and this study (East Malaysia)
	Sphaeroma wadai	Japan (sandstone)	14
	Sphaeroma walkeri	Persian Gulf (soft rock)	15
Unspecified	*Sphaeroma triste*	Singapore, Philippines	24, 21

References: (1) Harrison and Holdich (1984); (2) Davidson (2012); (3) Rotramel (1975); (4) Davidson and de Rivera (2010, 2012); (5) Hass and Knott (1998); (6) Das and Roy (1984); (7) Hossain and Bamber (2013); (8) Messana et al. (1994); (9) Müller and Brusca (1992); (10) Dharmaraj and Nair (1982); (11) Mohammad (2014); (12) Kim and Kwon (1985); (13) Sidabalok (2013); (14) Murata and Wada (2002); (15) Khalaji-Pirbalouty and Wägele (2010); (16) Jones, Icely, and Cragg (1983); (17) George (1963); (18) Nair and Salim (1994); (19) Natural History Museum (2019b); (20) Natural History Museum (2019a); (21) Orrell (2019a,b); (22) Singh and Sasekumar (1994); (23) Roszaini and Salmiah (2015); (24) Bruce and Wong (2015); (25) Perry (1988).

manmade structures, but they also produce microplastic waste (Davidson, 2012).

In comparison to wood boring, rock boring is reported in less detail and in fewer studies (Table 1). Warme and Marshall (1969, p. 773), quoting Barrows (1919), stated that isopods such as *Sphaeroma* "can erode rocks with its mandibles." Dharmaraj and Nair (1982) report destruction of laterite and hard clay embankments attributable to boring by *Sphaeroma sp*. along backwaters of the Indian SW coast. *Sphaeroma sieboldii* has been reported as actively boring stones and living in the holes in coast of Korea (Kim and Kwon, 1985). Davidson, de Rivera, and Carlton (2013, p. 116) mention isopods burrowing in "friable rock," and *Sphaeroma quoianum* is reported to accelerate erosion in salt marshes because of prodigious burrowing by dense populations in mud, clay, and peat in the Pacific coast of North America (Davidson and de Rivera, 2010, 2012). This leads to erosion rates that are $\sim$300% higher in infested areas compared with noninfested ones. *Sphaeroma triste* Heller (1865) is reported to burrow into "porous clay" exposed on beaches in Indonesia (Sidabalok, 2013, p. 53), but no description of the bioerosive activity is given. In Iraq, *Sphaeroma annandalei* is reported to create networks of burrows in a variety of materials, including friable rock (Mohammad, 2014). *Sphaeroma walkeri* is generally "not considered to be a wood-boring species," and it was suggested that the morphology of its mouthparts is "unlike that of the true wood-boring sphaeromatids" (Carlton and Iverson, 1981, p. 35, 41). The species has been reported to be found in holes and crevices, in empty barnacle shells and sponge canals, and under stones (Carlton and Iverson, 1981; Khalaji-Pirbalouty and Wägele, 2010). Khalaji-Pirbalouty and Wägele (2010, p. 9), however, report it to be a wood borer and that "it also burrows in to soft rock" in the Persian Gulf. *Sphaeroma wadai* is reported boring in intertidal sandstone in Japan; their population structure and reproductive biology have been studied in detail and related to the boring habit (Murata and Wada, 2002). These various references clearly indicate that although several Sphaeromatid species are capable of boring into soft rock substrates and that this behavior may be more widespread than currently reported, research on the bioerosive effect of species other than *S. quoianum* is generally lacking.

The potential bioerosive effect of several Sphaeromatid species, including *S. triste*, has not been previously described or studied in any detail, and previous research in the SE Asian region focuses on wood boring not rock boring. The aim of this research was to identify if and where bioerosion is occurring in the study area and to establish the identity of the species responsible. In addition, the goal was to study the morphology of the borings and their distribution and density in the rocky substrate as well as their relationship to other types of coastal erosion features described previously (Dodge-Wan and Nagarajan, 2019) to establish the potential for bioerosive effect of isopod boring. This study presents the results of initial and mainly qualitative surveys of bioerosion by isopods in sedimentary rocks outcropping within a 40-km-long stretch of the coastal region to the SW of Miri in Northern Sarawak, East Malaysia. Other forms of erosion attributable to nonbiological processes have also been researched and are described elsewhere (Dodge-Wan and Nagarajan, 2019).

METHODS

The methods include geological and biological field observations, photography, and measurement with limited sampling and laboratory analysis.

Perforations in rocks in the intertidal zone of the study area were initially noticed and photographed by the authors in 2007. Then, as part of this research, rock surfaces, and driftwood found in the intertidal zone along a 40-km stretch of coast were examined several times during low tide between June 2016 and February 2019. Surveys of cliff and wave-cut marine notch profiles were performed using tripod mounted Leica Disto D810 range meter. Survey data was plotted using AutoCAD 2014 software (Autodesk, Inc., 2019). Elevations were compared to water levels at the date and time of each survey with corresponding tide chart levels and are reported in meters above datum (mAD) with reference to Miri tide datum. Perforation density per area of rock surface was based on initial estimation in field and then measured from calibrated photographs and is described as follows: moderate (10 to 100 perforations per 100 cm^2), high (100–500 perforations per 100 cm^2), and very high (>500 perforations per 100 cm^2). Within areas of high to very high clustered abundance of perforations, 43 rock surfaces were selected and photographed with scale. The density of perforations on rock surfaces was analysed using calibrated field photographs of 5 cm $\times$ 5 cm areas, and measurements were made from all or selected parts of the photographs, as described in the text, using AutoCAD 2014 software. In addition, to establish the maximum crowding, ten areas of 1 cm^2 were selected from within photos of the highest density zones for further analysis. Within these 1 cm^2 areas, perforations were counted on the photos, and the percentage of perforated area was measured. Casts of rock surfaces with isopod perforations were made in the field on areas that appeared to be abandoned by the live isopods, such as loose boulders. Casts were made using Hardex Clear Silicone Rubber sealant RS-850 by applying approximately 10 g to the rock surface and gently pressing to inject the sealant into the perforations. Casts were used to describe perforation shape, not for quantitative measurements. Small samples of rock and wood were removed, stored in ethanol, and examined in the laboratory under binocular microscope. In addition, a small number of specimens were extracted and preserved in 70% ethanol. It is likely that isopod sampling was biased toward larger adult individuals, which are easier to collect in the field. Isopod specimens were examined using a Nikon SMZ74 stereomicroscope equipped with auxiliary 2$\times$ G-AL objective. Measurement of isopod length from anterior tip of cephalon to posterior tip of pleotelson was made dorsally using microscope crosshair graduation and micrometer scale after gently depressing the specimens to lay them flat. Width was measured at the widest part of the body. The measurement unit of variation is given in standard deviation ($\pm$). Specimens were dissected under stereomicroscope, and elements were placed on microscope slides in glycerin for examination using a Nikon Eclipse LV100NPOL polarizing/reflecting microscope equipped with a Nikon DSF12 camera. Fragile perforated rock samples were soaked in ethanol and dried and coated in blue-stained Ranger Industries liquid Ice Resin. After resin curing, rock samples were cut with rock saw for microscope examination and thin section preparation. Thin sections were polished to approximately 30-micron thickness with carborundum grit and examined using a Nikon Eclipse microscope. Measurement of perforation size ($n = 35$) and photography was performed under microscope using software NIS Elements Version 4.40 (Nikon, 2019). Isopod identification was based on the key provided by Harrison and Holdich (1984) in their worldwide review. Morphology and taxonomy are discussed briefly in the "Results" and in greater detail in Supplemental Material (Section 4).

General Characteristics of Study Area

The study area is a 40-km stretch of coast located south of the Baram and Miri River mouths and the city of Miri, in northern Sarawak (Figure 1). The coastline predominantly comprises sandy beaches with some isolated rock headlands. It trends NE-SW approximately parallel to the strike of the outcropping interbedded sandstones and mudstones. The rocks belong to the Miri and Lambir formations of Miocene age. The strata are tilted with dips ranging from 20° to subvertical. Numerous and varied erosional features occur in this dynamic coastline. The typology of erosion features in the rocky sections has been described by Dodge-Wan and Nagarajan (2019). The features range from macroscale erosion (mass wasting, rock falls, sea caves, and arches) to mesoscale features (widened joints and bedding planes, pockets, gullies, and runnels) (Dodge-Wan and Nagarajan, 2019). The isopod perforations described here are the most obvious microscale erosional feature.

Within this area, sedimentary rocks were found outcropping in the intertidal zone at and around four specific sites, described here below in order from NE to SW (Table 2). Taman Selera is a long, narrow sandy beach adjacent to a rocky headland consisting of massive sandstones with wave cut notch and intertidal platform. Tusan and Peliau beaches are backed by tilted interbedded sandstone and mudstone cliffs with shallow wave cut notch and sea caves. Bungai beach comprises two bays with corrugated sandstone and mudstone surfaces exposed at low tide. Further details of the sites are given in the Supplemental Material (Section 2). At all sites, variable amounts of driftwood and anthropogenic debris (jetsam) occur, depending on tidal conditions and daily and seasonal weather conditions (monsoon). The climate is tropical with annual average rainfall of approximately 2700 mm (Dodge-Wan and

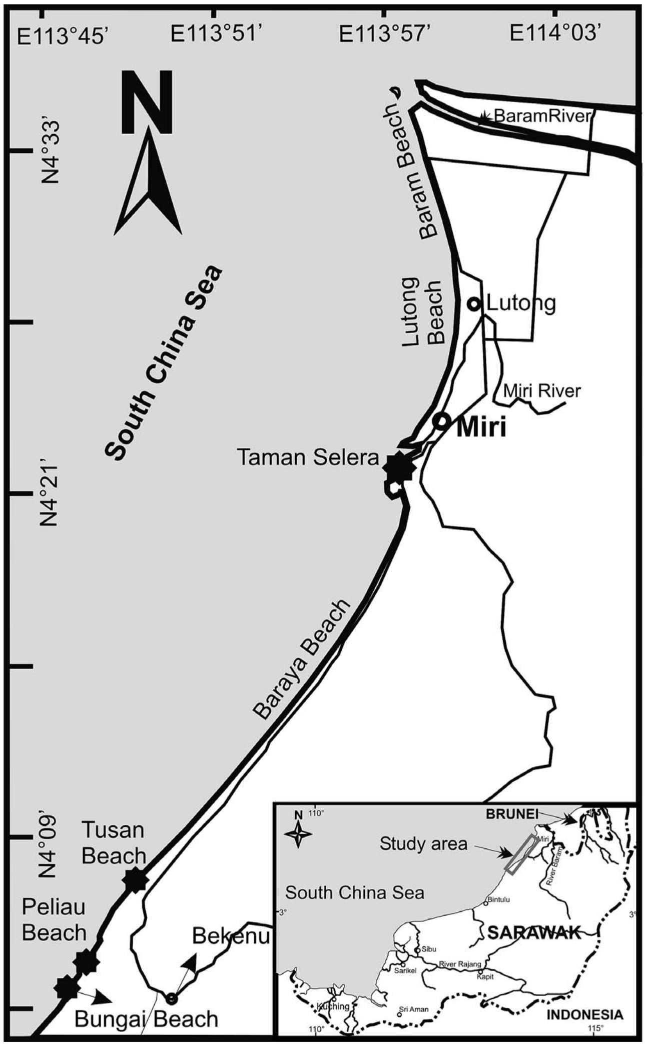

Figure 1. Map of north Sarawak (East Malaysia) showing coastline and location of sites with sandstone outcrops in intertidal zone where isopod bioerosion was observed (black stars). Distance from Taman Selera to Tusan Beach is 32 km.

Nagarajan, 2019). The tidal range is approximately 1.9 m (*i.e.* microtidal) and mixed, with a dominance of diurnal (Lim and Kho, 2010). Spring tide elevations range from 2.0 mAD (high) to 0.1 mAD (low), whereas neap tides range from 1.3 mAD (high) to 0.9 mAD (low). As a result of the tidal pattern, the intertidal zone may be periodically exposed to harsh sun when low tide occurs during daytime. Salinity varies from 21 to 30 ppt (Anandkumar, 2016) because of influence of freshwater through streams and rivers (Baram, Miri, and Sibuti rivers). At Tusan, a major stream occurs close to the site, which might explain the slightly lower salinity values. At Taman Selera and at Tusan beach, a film of freshwater may flow on the exposed rock surface above the intertidal zone after heavy rain.

RESULTS

Along the coastline between Miri and Bungai beaches, where interbedded sequences of relatively soft sandstones, siltstones, and mudstones are exposed in the intertidal zone, significant but localized areas of high and moderately dense isopod perforations on the rock surfaces are common. Hence, the phenomenon is not rare along this coastline. The isopod populations appear to be widespread and well established in this habitat. They have been present at the Tusan site since at least 2007 and perhaps much longer.

Distribution within Intertidal Habitat

Within the intertidal zone, isopod perforations are observed in the upper half of the intertidal zone. It should be noted that the lower half of the intertidal zone is generally covered with sand (below 1 mAD). The highest isopod perforations are found in the splash and spray zone up to 1 m above spring high tide level. Within the splash zone, isopod perforations are present but are quite rare and appear to be uninhabited (abandoned). The zone in which isopod perforations are most abundant—and the live animals are found—has a vertical extent of approximately 1 m ranging from around 1.6 mAD (*i.e.* 30 cm above neap high tide) to the top of the beach sand, which is at 0.5 to 1.2 mAD. In addition to isopods, the organisms observed within the intertidal zone include barnacles, small turban shaped gastropods (<1 cm long), sea slaters, rare oysters, small mussels, hermit crabs, microalgae, and fine green filamentous algae (Figure 2A). Barnacles and gastropods are common and locally clustered on rock surfaces. However, the surfaces that are intensely perforated with live isopods inside the borings are generally devoid of other macrofauna. Barnacles are common on erosion-resistant, hard, iron-rich crusts that are not colonized by isopods (Figure 3). Isopod borings that are unoccupied, *i.e.* abandoned, may subsequently be colonized by algae growth, barnacles, bryozoans, and gastropods.

Three species of isopod were identified within the study area. They are *S. triste* (Heller, 1865), *Dynamenella trachydermata* (Harrison and Holdich, 1984), and *Iais singaporensis* (Menzies and Barnard, 1951). It is possible that further investigation would reveal additional isopod species in the intertidal zone. *Sphaeroma triste* is by far the most common species in this area and was found extensively in perforated rocks at all four sites and is abundant at Tusan and Peliau beaches (Table 2). It was also found, but more rarely, in perforated wood that is immobilized in the intertidal zone, such as old bridge supports

Table 2. *Locations where rock-boring isopods were observed along the coast of Sarawak (East Malaysia) from Miri (in NE) to Bungai beach (in SW).*

Site Name	Latitude (Degrees N)	Longitude (Degrees E)	Extent	Habitat	Salinity (ppt)*
Taman Selera beach (Miri)	4.36775	113.96630	Minor infestation	Rock and wood	27–30
Tusan beach	4.12917	113.82482	Heavy infestation, several sites	Rock and wood	21–28
Peliau beach	4.07842	113.79462	Heavy infestation, several sites	Rock	ND
Bungai beach	4.06290	113.78391	Minor infestation, several sites	Rock	27–30

**From Anandkumar et al. (2015)*

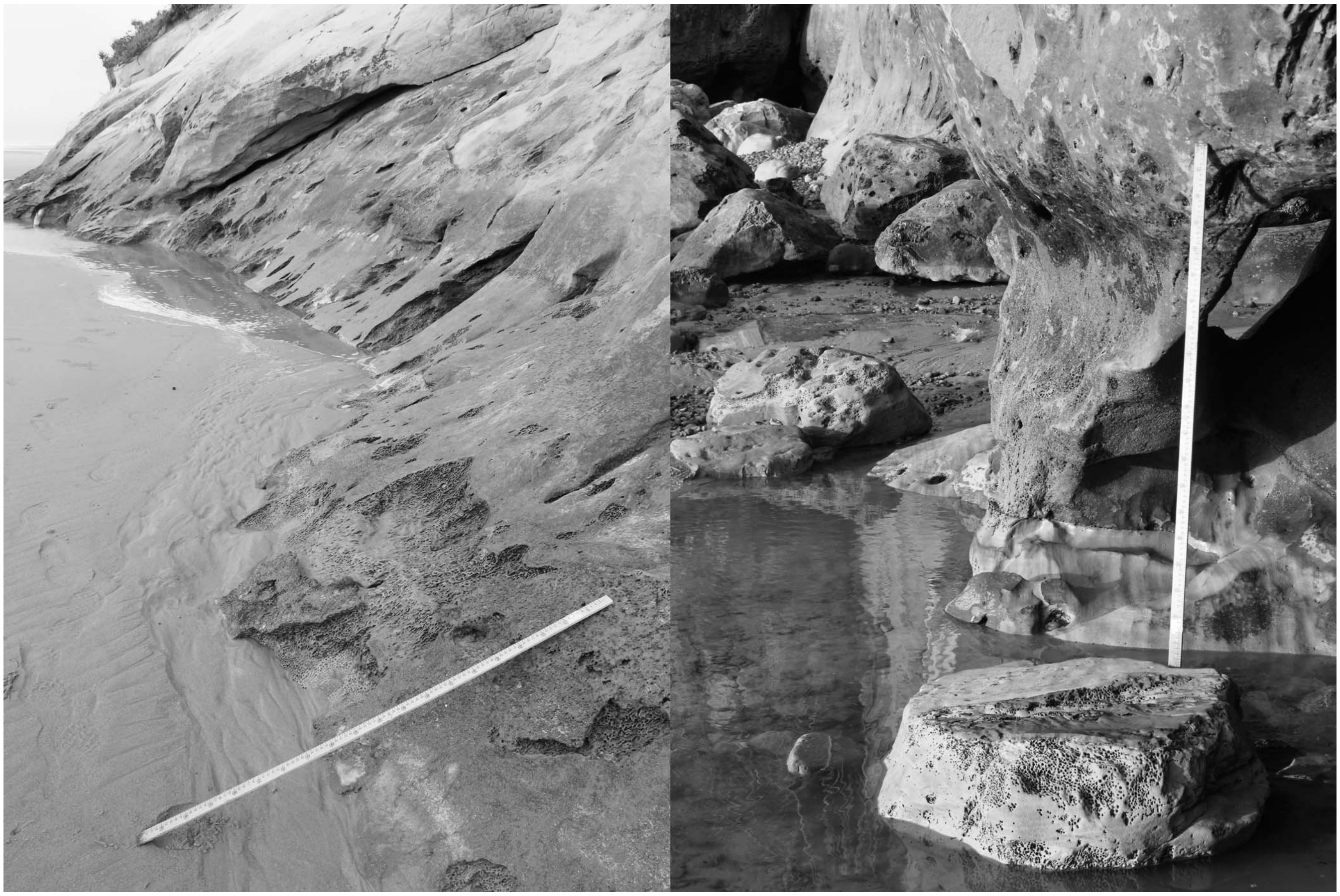

Figure 2. Dipping rock strata with shallow wave cut notch in the intertidal zone at Tusan (A) and Peliau (B), showing typical enhanced erosion due to clustering of abundant isopod perforations. Particularly high density of isopod perforations is noted in rock surface concavities as well as on the joint faces (as on subvertical joint towards middle of photo A) and on fallen blocks (as in foreground photo B). Ruler is 1-m long. Strata dip angle is approximately 42° in (A) (Tusan) and 82° in (B) (Peliau). Photos taken on 12 and 13 July 2018 at spring low tide.

and large items of driftwood embedded in the beach. The rock perforations, which are the focus of this study, are attributed only to *S. triste* as no evidence of any other rock boring species was found. *Sphaeroma triste* is the most abundant and is found exclusively within perforations in rock or wood (except when disturbed), and there is clear evidence that it is the perforation maker in these rocks (see below, description of species). Although *S. triste* was also found in wood, it does not appear to be the perforation maker in wood. The wood is riddled with dense shipworm perforations. *Dynamenella trachydermata* was found in wood, on algal covered rock surfaces, and among the sediments in shallow rock pools at Taman Selera beach, but the species is quite rare. It was not found boring into rock or inhabiting the perforations in the rocks, which were found to be exclusively occupied by *S. triste* at all the sites. The general intertidal habitat for *D. trachydermata* is thought to overlap somewhat with that of *S. triste*, but with a tendency to be found lower in the intertidal zone, where red algae, limpets, and small mussels are also more common. The species has previously been recorded in Singapore (Bruce and Wong, 2015). The smaller asellotan isopod species *I. singaporensis* was found commensal on specimens of *S. triste*. *Iais singaporensis* has been previously described commensal on wood-boring specimens of *S. triste* in West Malaysia (Müller and Brusca, 1992).

Distribution on Rock Surfaces

The bioerosion, or perforations, by *S. triste* are present in exposed soft rocks with borings noted in sandstone and siltstone including clay-rich siltstone but not in mudstones. They are present on *in situ* rocks forming wave-cut platforms and cliffs, as well as on large boulders in the intertidal zone. They are not present on small mobile pebbles or on rock surfaces that are sand covered. The distribution is very clustered (*i.e.* patchy). Some parts of the rock surfaces are heavily infested, whereas others are almost free of perforations. Perforations are observed on rock surfaces of any orientation (vertical, sloping at any angle, horizontal, or overhanging). The perforations are found on strata bedding surfaces, joint surfaces, rims of rock pools, and other rock surface irregularities formed by erosion. Perforations are preferentially located where the rock is relatively soft. These

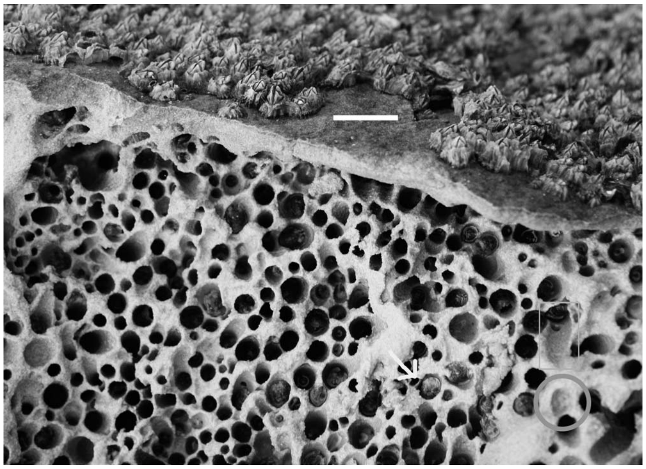

Figure 3. Detail of rock surface with iron-rich crust showing high density of isopod perforations in soft sandstone below the crust and numerous barnacles encrusting on the harder crust surface above. Photo 17 November 2007 Tusan site. Note: The *Sphaeroma triste* isopods are visible in many of the perforations in lower half of photo (*e.g.,* at the arrow). The perforated rock has been further eroded, and some former cylindrical perforations have been reduced to their hemispherical blind ends (*e.g.,* at circle), whereas others show erosion of the lateral walls (*e.g.,* at rectangle). Scale bar is 1cm.

Figure 4. Detail of freshly broken soft sandstone rock at Tusan beach in NW Sarawak, Malaysia, showing numerous burrows occupied by the isopod *Sphaeroma triste*. The animals are predominantly positioned with their heads toward the blind ends of borings. Some borings are occupied by more than one individual (at arrow for example). Coin is 18-mm diameter. The original rock surface prior to breakage was approximately parallel to the top of the photo.

soft rocks are easily broken by a weak blow with a light hammer or cut by a penknife, and small hand specimens can be crushed manually. Perforations are not found on hard rock surfaces that require heavy hammer blows to be broken, such as well-cemented sandstones, or on surfaces that are coated in millimeter-thick iron crusts (Figures 2 and 3). The harder surfaces are more commonly colonized by barnacles (Figure 3). Perforations also frequent the walls of erosion-enlarged joints. On wave-cut platforms, perforations are more common on the vertical rims of rock pools or other irregularities of the rock surface rather than on flat horizontal rock. Some perforations are found in the intertidal zone inside sandstone sea caves and on rock-surface concavities, as shown on Figure 2.

Position of Live Isopods in the Rock Perforations

Many, or most, of the perforations in the rock within the intertidal zone are occupied by isopod individuals, all of which are *S. triste* species. When undisturbed, the live isopods are most commonly positioned with their anterior end facing the blind end of the shaft (Figures 3 and 4), and their exopods, which extend beyond the posterior margin of the pleotelson, are visible close to the orifice of the shaft. When disturbed, the isopods turn around and may exit the shafts or roll up inside. It is not uncommon to observe two individuals in the same shaft (Figure 4). Occasionally borings are occupied by a group of numerous juveniles. In the upper intertidal zone and in the splash zone, there are also numerous abandoned uninhabited isopod borings.

Morphology of Isopod *S. triste* from North Sarawak

Identification of the Sarawak specimens is based on taxonomy and the descriptions of *S. triste*, *S. quoianum*, *S. walkeri*, and *Sphaeroma terebrans*, provided by Harrison and Holdich (1984), as well as of *S. walkeri* by Jacobs (1987). Descriptions of *S. annandalei* and *Sphaeroma silvai* (Khalaji-Pirbalouty and Wägele, 2010) were also compared for completeness. The description provided in the Supplemental Material (Section 4) confirms the identity of the species. It is the first description of rock-boring isopods from East Malaysia and enables comparison with wood-boring *S. terebrans*, which is the only other sphaeromatid species reported in this region to date (Hossain and Bamber, 2013). Supplemental Table 1 summarizes the characteristics of *S. triste* and *S. terebrans* based on this and previous studies. Among the adult specimens examined ($n = 26$), body length ranges from 5.9 to 9.9 mm. The average length is 7.9 mm ($\pm$1.2). The width at the widest part ranges from 2.9 mm to 5.0 mm, with an average of 4.0 mm ($\pm$0.6). The length/width ratio ranges from 1.8 to 2.1, with an average of 2.0. The widest part of the body is between pereonites 5 and 7, where the lateral margins are relatively straight in dorsal view (Supplemental Figures 1a–c).

Morphology of the Rock Borings by *S. triste*

At the scale of the rock outcrop, there is no preferred orientation, but a strong tendency for the borings to be generally perpendicular to the rock surface occurs at the bore orifice (Figure 4). In any one area of the perforated zone, the majority of the bore shafts are subparallel with infrequent shafts at a slightly different angle (Figure 4). There is no crosscutting or branching of the borings, which are all simple hollow tubes. Two closely spaced adjacent shafts may be connected where the thin wall between them has been breached or eroded. The perforations are essentially regular cylindrical shaped with a circular transversal section and

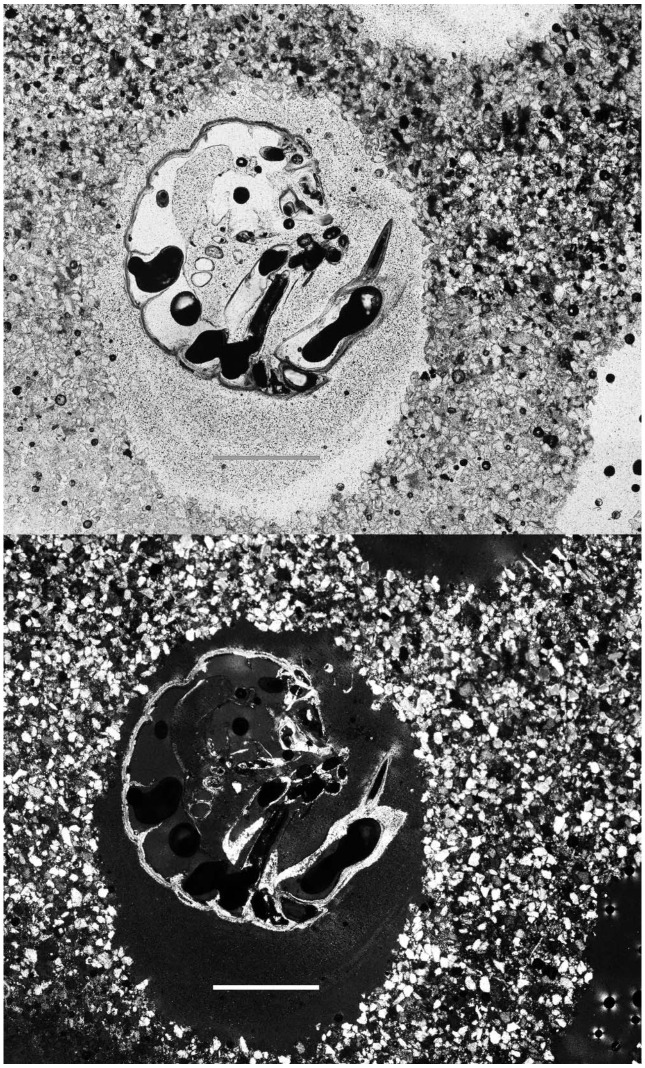

Figure 5. Thin section of sandstone with three isopod borings, one of which contains an isopod in longitudinal section and partially rolled (top image is in plain polarized light, and bottom image is in crossed polarized light). Scale bars are 1 mm. The cross-section is not exactly perpendicular to the axis of the boring, hence it appears oval rather than round. Note: The section passes through one of the isopod's mandible incisor processes that shows a blunt shape (visible in top photo). The black blobs within the isopod's body are where 800-grit carborundum polishing powder has penetrated the body cavities. Both images are a mosaic of 12 individual photos taken with the microscope's lowest magnification (50×) to cover a total field of view of approximately 6 mm by 5 mm.

parallel to subparallel walls in longitudinal section (Figure 4; Supplemental Figure 3). The perforations end in a hemispherical termination at the blind end. The isopods are able to curve around their transversal axis to exit their boring (Figure 5). No obvious changes occur in the cross-section diameter from orifice to blind end, with no swellings or taperings (Figure 4). The isopods fit relatively tightly inside their borings, with only a small gap between the animal's body and the shaft wall (Figure 5). The spacing between adjacent borings is variable depending on infestation density at the site, but it is commonly less than several millimeters and as little as ~150 microns, with possibility of breaching of the wall, *i.e.* two adjacent borings becoming connected. The borings' diameters are generally well sorted in size, with most falling in the 3.0- to 4.0-mm range. Maximum observed diameter was 4.85 mm. When compared with the average width of adult specimens, which is 4.0 mm, the typical shaft diameters appear low. It is likely that some perforations were formed by smaller individuals than those sampled and/or that the isopod body fits very snuggly in its boring. This appears to be the case, as observed under microscope and in field. It is also possible that the isopod bodies are more curved transversally (at coxal plate sutures) when live in their borings than when examined in the laboratory. The length of the borings is variable, most commonly around 2 cm, with maximum length exceeding 3 cm. This is several times the length of the adult *S. triste* body. At low tide, the isopod body does not generally protrude outside the bore, although the endopod and exopod in particular may be visible close to the orifice of the boring and extending beyond apex of pleotelson (Supplemental Figure 3). Borings that are actively occupied by isopods have clean, smooth walls with no obvious deposits, fill material, or other irregularities (Figures 4 and 5; Supplemental Figure 3).

Density of Perforations and Impact on Erosion

As noted previously, some areas of rock surface are totally devoid of perforations. At the scale of the whole outcrop, it is estimated that overall less than approximately 10% of the surface in the intertidal zone is affected by perforations of various densities. Where perforations occur, the density is variable, but the perforations are commonly clustered in localized areas showing high to very high abundance, as illustrated in Figures 2 and 3. The abundances recorded in 43 surfaces are given in histogram (Supplemental Figure 4). The average density of perforations in areas of clustered high to very high abundance is 4.6 perforations/cm^2 surface. Approximately 60% of the high-density surfaces have four to seven perforations/cm^2, which can be considered typical. The highest density recorded over any of the 25-cm^2 surfaces examined was 8.3 perforations/cm^2. Within the areas of high to very high abundance, some variability in the distribution over the rock surface occurs within a few centimeters. Analysis of photographs shows that perforation density does not exceed 11/cm^2, which is believed to be the upper crowding limit. As stated previously, the perforations do not cross-cut each other. Eleven perforations per square centimeter corresponds to approximately 51% to 54% of the total surface being perforated.

The results indicate that in areas of high to very high density of perforations, the isopod boring activity has a significant erosive effect by direct removal of rock from the outcrop surface. Within maximum density zones, where up to 11 perforations/cm^2 can occur, this effect is equivalent to the removal of up to 51% to 54% of rock from the top 2 to 3 cm of outcrop. Within high to very high density zones, with on average four perforations/cm^2, the effect is equivalent to the removal of approximately 19% of the rock from the top 2 to 3 cm of outcrop.

DISCUSSION

Sphaeroma triste has previously been described from many localities in the Central Indo-Pacific biogeographic realm, where it is considered a native species. The localities range from Lakshadweep Archipelago (off the west coast of India) (Nair and Salim, 1994) to Queensland, Australia (Harrison and Holdich, 1984), which is from latitude 11° N to 27° S and from longitude 72° E to 153° E across much of Central Indo-Pacific. Hence, it is not surprising to find it on the coast of North Sarawak, as reported here for the first time.

This study has shown that rock boring by *S. triste* is common in soft sandstone rocks in the intertidal zone along the coast of North Sarawak, although the distribution is very localized, generally ranging from nil on unsuitable rock surfaces to a density that commonly reaches four to seven perforations/cm^2. Hence, the presence of rock-boring isopods, where it occurs, has a significant erosive effect by direct removal of 20% to 50% volume of rock from the intertidal outcrop surface. Within maximum density zones, where up to 11 perforations/cm^2 may occur, this is equivalent to the removal of up to 51% to 54% from the top 2 to 3 cm of rock. On the regional scale, however, the volume of direct rock removal is much less because of the highly localized distribution of isopod perforations, which are estimated to occur on significantly less than 10% of intertidal exposed rock.

In addition to the direct action of isopods, the presence of the perforations also has an indirect effect on erosion. The perforations increase the surface area of rock exposed to erosion and significantly weaken the outer few centimeters of the rock mass in these soft clastic rocks. It is noted that the remnant walls of rock between adjacent perforations are thin, often reduced to millimeters or less. This is likely to enhance the effect of other agents of erosion operating in this part of the intertidal zone. Evidence of this is shown by originally cylindrical perforations being reduced in length to their hemispherical blind ends (Figure 3, red circle) and their lateral walls being eroded leaving a half tube (Figure 3, blue rectangle). Isopod perforations contribute to formation of wave-cut notch, to localized enlargement of joints and concavities of the rock surface, to widening of rock pools as well as to gradual destruction of fallen boulders and blocks. Evidence of this enhanced erosion is obvious in numerous rock surfaces showing eroded isopod perforations. The clustered isopod perforations also contribute to the formation of wave-cut notch. Similar bioerosive effect with enhanced cliff erosion and notch deepening has been documented by Cadée, Checa, and Rodriguez-Tovar (2001) in Spain. They estimated that in the case of a cliff comprising fine-grained clastic rocks along the Atlantic coast, up to 40% of the upper 5 cm of cliff was open because of bioerosion by *Paragnathia* isopods and the *Bledius* beetle. The burrowing effect of *S. quoianum* in peat and mud has been reported to reduce stability of marsh bank sediments in San Diego and San Francisco Bays, leading to enhanced erosion attributable to undercutting and collapse of the banks (Talley, Crooks, and Levin, 2001). This differs from the Sarawak situation, as no undercutting or collapse effect was found associated with *S. triste* borings in sandstone rocks of this study. Two criteria appear to control the localized distribution of *S. triste* perforations within the upper intertidal zone: rock hardness and shelter from desiccation and/or exposure to sunlight. The latter could explain their presence on joint surfaces and rock-surface concavities. However, it is uncertain if this is entirely because of habitat preference or the result of erosion of already perforated rock surfaces, leading to formation and enhancement of the concavities, or a combination of both. The distribution of perforations does not appear to be related to the intensity of wave action.

The rock borings by *S. triste* are nonbranching, cylindrical perforations with circular cross-section and hemispherical blind end. They are of variable length, often over 2 cm, and their diameter is generally between 3 and 4 mm. The dimensions are smaller than those of burrows created by the invasive species *S. quoianum*, which forms burrows of 5- to 7-mm width in peat and mud (Davidson and de Rivera, 2012; Talley, Crooks, and Levin, 2001). Rotramel (1975) reports that *Sphaeroma* species turn on their longitudinal axes while burrowing, which produces a nearly cylindrical burrow, as appears to be the case here. *Sphaeroma triste* borings are simple with no enlargements or other features. This contrasts with the burrow complexity reported for *S. terebrans* in mangrove wood (Messana *et al.*, 1994; Thiel, 1999) as well as the branching and interconnectivity of *S. quoianum* burrows in peat and mud (Talley, Crooks, and Levin, 2001). Messana *et al.* (1994) also report that the young *S. terebrans* dig holes on the internal surface of the adult's burrow. No branching, complexity, nor diggings on the internal surfaces were observed in *S. triste* borings. In terms of neoichnology, the rock borings of *S. triste* are considered to belong to the *Trypanites* ichnofacies (Buatois and Gabriela Mángano, 2011); they are sharp walled and formed in lithified substrate (hard ground). They are deep-tier borings in the sense described by Bromley and Asgaard (1993) because they penetrate the rock to over 2-cm depth as opposed to shallow rasping and etching marks on the rock surface. As mentioned previously, isopods are more commonly known for their wood boring and hence would generally be associated with the *Teredolites* ichnofacies (Gingras, Maceachern, and Pickerill, 2004).

For *S. quoianum*, individual and burrow densities of up to tens of thousands per square meter are not unusual (Talley, Crooks, and Levin, 2001). The data from Sarawak suggests that for *S. triste* in areas of high density in the intertidal zone where habitat is suitable, there might typically be four to seven perforations per square centimeter, or 40,000 to 70,000/m^2. This study indicates that maximum crowding limit for *S. triste* is 11 individual perforations per square centimeter, and this could lead to direct removal of approximately 50% of the outer 3 cm of rock, which is approximately 15 L/m^2. At more typical density of perforations, direct removal would be about half of that. Experimental studies indicated that 100,000 adult *S. quoianum* could remove 72 L of sandstone in two months from a similar surface (Davidson and de Rivera, 2012). This study did not measure the time required for isopods to create the borings and/or the rate of further penetration of the bioerosive front into the rock mass as the external perforated zone is eroded. Davidson, Rumrill, and Shanks (2008, p. 149) indicate that *S. quoianum* has the ability to "rapidly colonize intertidal substrata and in a matter of weeks completely riddle wood and other substrata." The purpose of boring activity by *S. triste* has not been investigated in this study. In general, boring and burrowing by isopods may be for defense from predators, protection from environmental stresses at low tide, for feeding, for mating and reproduction, or a combination of these (Cragg, Pitman, and Henderson, 1999; Davidson, Rumrill, and Shanks, 2008; Talley, Crooks, and Levin, 2001). In the case of North Sarawak populations, the position of the borings suggests that they provide protection from desiccation, from sunlight exposure, and possibly also from wave agitation. Negative phototaxis and preference for concavities has also been noted in wood boring by *S. terebrans* (Messana *et al*., 1994). Rotramel (1975) noted that the body position of *S. quoianum* within shafts is consistent with a filter-feeding mechanism as the movement of the pleopods creates a current over and then under the animal. Wood-boring species of sphaeromatids are reported to be filter feeders, but it is believed that they use their burrows as a dwelling place for protection rather than as a food source (Aung Si, Bellwood, and Alexander, 2002; Brusca and Iverson, 1985; Cragg, Pitman, and Henderson, 1999; Rotramel, 1975; Talley, Crooks, and Levin, 2001). *Sphaeroma terebrans* is reported to perform parental care, with juveniles inhabiting small pockets within the parental burrow or branching off into their own burrows (Messana *et al*., 1994). Those authors report 15% of burrows were occupied by couples and 5% by families. This study in Sarawak did not address population composition or ecology; however, it is common to find several individuals in one boring and some borings contain groups of juveniles. The lack of isopod boring or perforations in mudstones suggests that the presence of clay in the isopod dwelling may be a limiting factor for *S. triste* and that there is a preference for soft sandstone. It is not known at which stage of life the individuals start to bore, how long it takes an isopod to excavate a perforation, and whether boring is performed year round or if it is seasonal.

Further research would be required to clarify exactly how *S. triste* performs the boring in rock, but the blunt mandibular incisor process of the Sarawak specimens is a strong indication that the mandibles are used. It is likely that the incisor processes become blunted by abrasion from contact with angular quartz grains of the rock during this boring. To the authors' knowledge, this blunting has not been described previously.

CONCLUSIONS

In Northern Sarawak, the species *Sphaeroma triste* was found to be a common rock borer, with heavy infestations and significant bioerosion observed at several sites where soft sandstones and siltstones of Miocene age outcrop in the intertidal zone. The *S. triste* community has been present and well established here since at least 2007 and perhaps much longer. The Sarawak specimens' morphology match that of northern specimens from New Guinea described by Harrison and Holdich (1984) with four tubercles on the pleotelson. The incisor processes of the adult Sarawak specimens were found to generally be blunt and rounded, not bifid, and this is inferred to be a specific consequence of abrasion attributable to rock boring in sandstone reported here for the first time. In addition to abundant *S. triste*, two other isopod species were also observed: *D. trachydermata* (infrequent, not rock boring) and *I. singaporensis* (commensal on *S. triste*).

The distribution of isopod rock borings in the north Sarawak coast covered by this study shows high abundance but low diversity because only one species, *S. triste*, was found to be rock boring. Distribution is localized and dependent on rock hardness, which appears to be a limiting factor. There are few or no borings in hard sandstone or where mineralized crusts have formed on the rock surface. The latter may be colonized by barnacles. The position of the isopod borings on the rock surfaces suggests that the borings provide shelter from environmental stresses of desiccation and strong sunlight during low tide. The *S. triste* borings are commonly located in the upper half of the intertidal zone and more rarely in the splash zone. Average densities of four to seven borings per square centimeter are common in highly infested areas. The maximum crowding limit appears to be 11 perforations per square centimeter of rock surface. The borings are nonbranching, almost straight round cylinders of 3 to 4 mm diameter. They are approximately perpendicular to the rock surface, which may be horizontal, sloping, vertical, or overhanging. The borings have hemispherical blind ends and have variable lengths with some over 3 cm long. During low tide, the isopods inhabit the borings with their heads pointing inward toward the blind end; it is common to find more than one individual in a single boring, and some borings contain groups of juveniles. Although the effect of boring on the erosion rate has not been fully quantified, in areas of highest abundance the organisms are capable of directly removing as much as 20% to 50% of the outer few centimeters of rock. This bioerosion has an indirect impact on other forms of erosion and leads to deepening of concavities on the rock surface, widening of joints and rock pools as well as enhancing the formation of a wave-cut notch and erosion of fallen blocks. As erosion removes weakened perforated surface material, bioerosion may continue because the isopods bore deeper into the substrate.

Further research is warranted to better understand the regional distribution of this and other isopod species as well as to quantify their bioerosive activity, in particular the rate of infestation and the pace of boring as well as to establish any seasonal variations of the activity. Preservation of rock borings by Sphaeromatid isopods in the rock record, similar to that of other deep-tier endolithic organisms, may have the potential to facilitate identification of fossil rocky shores in ancient stratigraphic sequences, and hence this research is of neoichnological interest. However, their indirect enhancement of mechanical erosion may lead to relatively poor preservation in the rock record. Furthermore, the capacity of Sphaeromatids, some of which are invasive species, to damage manmade timber structures justifies further studies into their ecology and habitat preferences.

ACKNOWLEDGMENTS

The authors wish to thank Curtin University Malaysia for use of facilities and other assistance during the course of this research. The authors also thank Curtin students Chu Wai Hsin, James Glenda Ruran, and Ilyas Bin Yusnawannie for their assistance during field work.

LITERATURE CITED

Anandkumar, A., 2016. Ecological Risk Assessment of the Miri Coast, Sarawak, Borneo—A Biogeochemical Approach. Malaysia: Curtin University, Ph.D. dissertation, 381p.

Anandkumar, A.; Rameshkumar, G.; Ravichandran, S.; Rethna Priya, E.; Nagarajan, R., and Leng, A.G.K., 2015. Occurrence of cymothoid isopod from Miri, East Malaysian marine fishes. *Journal of Parasitic Diseases*, 39(2), 206–210. doi:10.1007/s12639-013-0320-7

Arrontes, J., 1990. Diet, food preference and digestive efficiency in intertidal isopods inhabiting macroalgae. *Journal of Experimental Marine Biology and Ecology*, 139(3), 231–249. doi:10.1016/0022-0981(90)90149-7

Aung Si; Bellwood, O., and Alexander, C.G., 2002. Evidence for filter-feeding by the wood-boring isopod, *Sphaeroma terebrans* (Crustacea: Peracarida). *Journal of Zoology*, 256(4), 463–471. doi:10.1017/S095283690200050X

Autodesk, Inc., 2019. https://knowledge.autodesk.com/support/autocad/learn?sort=score

Barrows, A.L., 1919. The occurrence of a rock boring isopod along the shore of San Francisco Bay, California. *University of California Publications in Zoology*, 19, 299–316.

Bromley, R.G. and Asgaard, U., 1993. Two bioerosion ichnofacies produced by early and late burial associated with sea-level change. *Geologische Rundschau,* 82(2), 276–280.

Bruce, N.L. and Wong, H.P.-S., 2015. An overview of the marine Isopoda (Crustacea) of Singapore. *Raffles Bulletin of Zoology*, Supplement 31, 152–168.

Brusca, R.C. and Iverson, E. W., 1985. A guide to the marine Isopod Crustacea of Pacific Costa Rica. *Revista de Biologia Tropical*, Universidad de Costa Rica, 33 (Supplemento 1).

Buatois, L.A. and Gabriela Mángano, M., 2011. *Ichnology: Organism-Substrate Interactions in Space and Time*. Cambridge, UK: Cambridge University Press, 358p.

Cadée, G.C.; Checa, A.G., and Rodriguez-Tovar, J., 2001. Burrows of *Paragnathia* (Crustacea: Isopoda) and Bledius (Arthropoda: Staphylinidae) enhance cliff erosion. *Ichnos*, 8(3–4), 255–260. doi:10.1080/10420940109380193

Carlton, J.T. and Iverson, E.W., 1981. Biogeography and natural history of *Sphaeroma walkeri* Stebbing (Crustacea: Isopoda) and its introduction to San Diego Bay, California. *Journal of Natural History*, 15(1), 31–48. doi:10.1080/00222938100770031

Cragg, S.M. 1988. The wood-boring Isopod, *Sphaeroma*: A threat to maritime structures in warm waters. *In:* Houghton, D.R.; Smith, R.N., and Eggins, H.O.W. (eds.), *Biodeterioration 7*. Dordrecht, The Netherlands: Springer, pp. 727–732. doi:10.1007/978-94-009-1363-9_94

Cragg, S.M.; Pitman, A.J., and Henderson, S.M., 1999. Developments in the understanding of the biology of marine wood boring crustaceans and in methods of controlling them. *International Biodeterioration and Biodegradation*, 43(4), 197–205.

Das, A.K. and Roy, M.K.D., 1984. A note on the marine borers of mangroves of Little Andaman, India. *Bulletin of Zoological Survey India,* 6 (1–3), 95–98.

Davidson, T.M., 2012. Boring crustaceans damage polystyrene floats under docks polluting marine waters with microplastic. *Marine Pollution Bulletin,* 64(9), 1821–1828. doi:10.1016/j.marpolbul.2012.06.005

Davidson, T.M.; Altieri, A.H.; Ruiz, G.M., and Torchin, M.E., 2018. Bioerosion in a changing world: a conceptual framework. *Ecology Letters,* 21(3), 422–438. doi:10.1111/ele.12899

Davidson, T.M. and de Rivera, C.E., 2010. Accelerated erosion of saltmarshes infested by the non-native burrowing crustacean *Sphaeroma quoianum*. *Marine Ecology Process Series,* 419, 129–136. doi:10.3354/meps08836

Davidson, T.M. and de Rivera, C.E., 2012. Per capita effects and burrow morphology of a burrowing isopod (*Sphaeroma quoianum*) in different estuarine substrata. *Journal of Crustacean Biology,* 32(1), 25–30. doi:10.1163/193724011X615299

Davidson, T.M.; de Rivera, C.E., and Carlton, J.T., 2013. Small increases in temperature exacerbate the erosive effects of a non-native burrowing crustacean. *Journal of Experimental Marine Biology and Ecology,* 446, 115–121. doi:10.1016/j.jembe.2013.05.008

Davidson, T.M.; Rumrill, S.S., and Shanks, A.L., 2008. Colonization and substratum preference of an introduced burrowing crustacean in a temperate estuary. *Journal of Experimental Marine Biology and Ecology,* 354(1), 144–149. doi:10.1016/j.jembe.2007.10.015

De Ruyck, A.M.C.; McLachlan, A., and Donn, T.E., Jr., 1991. The activity of three intertidal sand beach isopods (Flabellifera: Cirolanidae). *Journal of Experimental Marine Biology and Ecology*, 146(2), 163–180.

Dharmaraj, K. and Nair, B.N., 1982. Destruction of laterite and hard clay embankments by boring Sphaeromatids (Isopoda: Flabellifera). *Indian Journal of Marine Sciences,* 11(1), 93–95.

Dodge-Wan, D. and Nagarajan, R., 2019. Typology and mechanisms of coastal erosion in siliciclastic rocks of the NW Borneo coastline (Sarawak, Malaysia): a field approach. *In*: Ramkumar, Mu.; James, R.A.; Menier, D., and Kumaraswamy K. (eds.). *Coastal Zone Management: Global Perspectives, Regional Processes*. Amsterdam, The Netherlands: Elsevier, pp. 65–98.

Donn, T.F. and Boardman, M.R., 1988. Bioerosion of rocky carbonate coastlines on Andros Island, Bahamas. *Journal of Coastal Research*, 4(3), 381–394.

George, R.Y., 1963. The occurrence of the wood-boring crustacean *Sphaeroma triste* Heller on the Indian coast. *Current Science,* 32(4), 168–169.

Gingras, M.K.; Maceachern, J.A., and Pickerill, R.K., 2004. Modern perspectives on the Teredolites Ichnofacies: Obersvations from Willapa Bay, Washington. *Palaios,* 19(1), 79–88. doi: 10.1669/0883-1351(2004)019<0079:MPOTTI>2.0.CO;2

Harrison, K. and Holdich, D.M., 1984. Hemibranchiate sphaeromatids (Crustacea, Isopoda) from Queensland, Australia, with a world-wide review of the genera discussed. *Zoological Journal of the Linnean Society,* 81(4), 275–387.

Hass, C.G. and Knott, B., 1998. Sphaeromatid isopods from the Swan River, Western Australia: Diversity, distribution, and geographic sources. *Crustaceana*, 71(1), 36–46.

Heller, C., 1865. Crustaceen. *In:* Reiseder Osterreischischen Fregatte "Novara" um die Erde in den Jahren 1857, 1858, 1859. *Zoologischer Theil,* 2(3), 1–280, pls 1–25.

Hossain, M.B. and Bamber, R.N., 2013. New record of a wood-boring isopod, *Sphaeroma terebrans* (Crustacea: Sphaeromatidae) from Sungai Brunei estuary, Brunei Darussalam. *Marine Biodiversity Records,* 6, e18. doi:10.1017/S1755267212001261

Jacobs, B.J.M., 1987. A taxonomic revision of the European, Mediterranean and NW African species generally placed in *Sphaeroma* Bosc, 1802 (Isopoda: Flabellifera: Sphaeromatidae). *Zooliogische Verhandelingen*, 238, 3–71.

Jones, D.A.; Icely, J.D., and Cragg, S.M., 1983. Some corallinid isopods associated with wood from Papua New Guinea, including three new species (Isopoda: Corallanidae). *Journal of Natural History,* 17(6), 837–847.

Kázmér, M. and Taborosi, D., 2012. Bioerosion on the small scale—Examples from the tropical and subtropical littoral. *Monostori Jubilee Volume, Hantkeniana,* 7(7), 37–94.

Khalaji-Pirbalouty, V. and Wägele, J.-W., 2010. A new species and a new record of *Sphaeroma* Bosc, 1802 (Sphaeromatidae: Isopoda: Crustacea) from intertidal marine habitats of the Persian Gulf. *Zootaxa*, 2631, 1–18.

Kim, H.S. and Kwon D.H., 1985. The systematic study of the family Sphaeromatidae (Crustacea, Isopoda, Flabellifera) from Korea. *INJE Journal*, 1(2), 143–165.

Lim, Y.S. and Koh, S.L., 2010. Analytical assessments on the potential of harnessing tidal currents for electricity generation in Malaysia. *Renewable Energy,* 35(5), 1024–1032. doi:10.1016/j.renene.2009.10.016

Menzies, R.J. and Barnard, J.L., 1951. The isopodan genus *Iais* (Crustacea). *Bulletin of the Southern California Academy of Sciences,* 50(3), 136–151.

Messana, G.; Bartolucci, V.; Mwaluma, J., and Osore, M., 1994. Preliminary observations on parental care in *Sphaeroma terebrans* Bate 1866 (Isopoda Sphaeromatidae), a mangrove wood borer from

Kenya. *Ethology Ecology & Evolution*, 6(sup. 1), 125–129. doi:10.1080/03949370.1994.10721985

Miranda, L. and Thiel, M., 2008. Active and passive migration in boring isopods *Limnoria spp*. (Crustacea, Peracarida) from kelp holdfasts. *Journal of Sea Research,* 60(3), 176–183. doi:10.1016/j.seares.2008.06.002

Mohammad, M.K., 2014. Existence and ecology of the burrowing isopod *Sphaeroma annandalei* Stebbing, 1911 (Crustacea; Isopoda; Sphaeromatidae) in Lake Razzaza, Kerbala Province, Central Iraq. *Advances in Bioresearch,* 5(1), 178–184. http://www.soeagra.com/abr/march_2014/29.pdf

Müller, H.G. and Brusca, R.C., 1992. Validation and redescription of *Iais singaporensis* Menzies and Barnard, 1951, a commensal with *Sphaeroma triste* Heller, 1865, from a Malaysian coral reef. *Zoologischer Anzeiger,* 229(1/2), 73–82.

Murata, Y. and Wada, K., 2002. Population and reproductive biology of an intertidal sandstone-boring isopod, *Sphaeroma wasai* Nunomura, 1994. *Journal of Natural History*, 36(1), 25–35. doi:10.1080/00222930110087401

Nair, N.B., 1984. The problem of marine timber destroying organisms along the Indian coasts. *Proceedings of the Indian Academy of Sciences (Animal Sciences),* 93(3), 203–223.

Nair, N.B. and Salim, M., 1994. Marine timber destroying organisms of the Andaman-Nicobar Islands and Lakshadweep Archipelago. *Records of the Zoological Survey of India*, Occasional Paper No. 159, 1–87.

Natural History Museum, 2019a. *Natural History Museum (London) Collection Specimens*. https://www.gbif.org/occurrence/1056052345

Natural History Museum, 2019b. *Natural History Museum (London) Collection Specimens*. https://www.gbif.org/occurrence/1056754291

Nikon, 2019. https://www.nikon.com/products/microscope-solutions/lineup/img_soft/nis-elements/

Orrell, T., 2019a. *NMNH Extant Specimen Records. Version 1.20. National Museum of Natural History, Smithsonian Institution. Occurrence dataset*. https://www.gbif.org/occurrence/1318667199

Orrell, T., 2019b. *NMNH Extant Specimen Records. Version 1.20. National Museum of Natural History, Smithsonian Institution. Occurrence dataset*. https://www.gbif.org/occurrence/1321865560

Perry, D.M., 1988. Effects of associated fauna on growth and productivity in the red mangrove. *Ecology,* 69(4), 1064–1075.

Roszaini, K. and Salmiah, U., 2015. Resistance of five timber species to marine borer attack. *Journal of Tropical Forest Science*, 27(3), 400–412.

Rotramel, G., 1975. Filter-feeding by the marine boring isopod, *Sphaeroma quoyanum* H. Milne Edwards, 1840 (Isopoda, Sphaeromatidae). *Crustaceana*, 28(1), 7–10. doi:10.1163/156854075X00793

Sidabalok, C.M., 2013. List of marine isopods recorded from Indonesian waters. *Marine Research Indonesia,* 38(1), 49–66.

Singh, H.R. and Sasekumar, A., 1994. Distribution and abundance of marine wood borers on the west coast of Peninsular Malaysia. *Hydrobiologia,* 285(1–3), 111–121. doi:10.1007/BF00005659

Talley, T.S.; Crooks, J.A., and Levin, L.A., 2001. Habitat utilization and alteration by the invasive burrowing isopod, *Sphaeroma quoyanum*, in California salt marshes. *Marine Biology*, 138(3), 561–573.

Thiel, M., 1999. Reproductive biology of a wood-boring isopod, *Sphaeroma terebrans*, with extended parental care. *Marine Biology,* 135(2), 321–333. doi:10.1007/s002270050630

Viles, H.A., 2013. Organic weathering. *In:* Goudie, A. (ed.), *Encyclopedia of Geomorphology*. Abingdon, United Kingdom: Routledge, pp. 727–730.

Warme, J.E. and Marshall, N.F., 1969. Marine borers in calcareous terrigenous rocks of the Pacific Coast. *American Zoologist,* 9(3), 765–774. http://www.jstor.org/stable/3881678

Wilson, B., 2013. *Biogeography of the Australian North West Shelf*. Amsterdam: Elsevier, 640p.