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# Indonesian coral reef habitats reveal exceptionally high species richness and biodiversity of diatom assemblages

Q5

 The corrections made in this section will be reviewed and approved by a journal production editor.

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## Abstract

We present the results of the first ever research on biodiversity and biogeography of marine benthic diatoms from coral reefs of the tropical islands of Indonesia, including West Borneo, East Java, South Celebes, Komodo, Rinca and Flores. The sampled islands offer a broad range of coral reef microhabitats and host diatom assemblages from seaweeds, sea grass, dead corals, scrapes from other biological surfaces, sand, rocks and other solid surfaces. The results of this study are based on the light (LM) and scanning electron microscopy (SEM) identification of diatoms only. Our taxonomic analysis revealed the presence of 911 diatom taxa representing 188 genera. Biodiversity indices such as Shannon, Simpson and Evenness as well as species richness and diatom relative abundance were calculated for each sample examined. We find that these indices were higher for Indonesia than those published for tropical oceanic islands or regions from both hemispheres, e.g. Galapagos and Martinique, but comparable to Madagascar. The non-metric multidimensional analysis showed that the type of habitat from which a particular sample was taken was of greater significance in the taxonomic composition than the geographical aspect. In terms of biogeography, cosmopolitan taxa were dominant in terms of relative abundance, but species richness was higher within tropical zonal and local forms. Many taxa were identified only at the genus level, and may turn out to be new to science.

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## Keywords:

Diversity, Biogeography, Benthic diatoms, Coral reefs, Indonesia

## 1 Introduction

Coral reefs are important natural ecosystems, hosting a wealth of biological diversity of invertebrates (corals, sea anemones, polychaetes, arthropods, mollusks and echinoderms), tropical fish, some species of sea turtles (Jackson, 2001; Hoeksema, 2007; Obura et al., 2010; Goatley et al., 2016), seaweeds and microalgae (Risjani and Abidin, 2020), and also provide important ecosystem services to local communities through tourism (Spalding et al., 2017). It is commonly accepted that coral reefs, as with any other ecosystems, are threatened due to increasing human pressure (waste, pollution, eutrophication, overfishing, extensive aquaculture), herbivory (Goatley et al., 2016) and climate-change induced water temperature and sea-level rise, and acidification (Hoegh-Guldberg, 2011). It is therefore very important that countries possessing coral reefs within their national waters set up efforts leading to coral reef conservation.

Indonesian diatoms from inland waters have been studied by Hustedt (1937), who examined samples mainly from Sumatra, Java, Bali and Celebes, and proposed numerous species new to science (see illustrations in Simonsen, 1987). Hustedt also examined marine diatoms from Miang Besar on the coast of Borneo, proposing further new species (e.g., Hustedt in Schmidt, 1927 or Hustedt, 1931–1962). In the late 19th century, Cleve and Grove (1891a, 1891b) studied a number of diatom taxa new to science, mostly representing Plagiogrammaceae De Toni, but also Fragilariaceae Kützing and Catenulaceae Mereschkowsky from the Strait of Makassar and the Philippine Islands. Later, Sterrenburg et al. (1995) studied epiphytic diatoms from sea grasses of the Spermonde Archipelago (SW Celebes). However, current knowledge on the biodiversity and biogeography of diatoms within coral reefs is extremely limited, largely as a result of problems with access (sampling) and taxonomy. Despite that, Stidolph et al. (2012) presented an illustrated series of marine benthic diatoms from the coasts of Java Island, the access of illustrated guides for this geographic region is still limited (for a review see Lobban and Jordan, 2010). An increasing interest in research on coral reef diatoms dates back to the start of the 21st century, focusing on locations such as the Great Barrier Reef (Gottschalk et al., 2007), Guam (Lobban et al., 2012), Martinique in the Western Atlantic (Desrosiers, 2014), Mascarenes (Riaux-Gobin et al. 2011a, 2011b; Al-Handal et al., 2016), Galapagos (Łopato, 2016) and Madagascar (Kryk et al., 2020).

Owing to these study efforts, significant new insights are now available on the taxonomy, geographic distribution and relative abundance, species richness and bioindices of marine benthic diatoms (e.g. Gottschalk et al., 2007; Hein et al., 2008; Lobban et al., 2012; Desrosiers, 2014; Al Handal et al., 2016; Kryk et al., 2020). Many species and genera have been described based on monoclonal strains and molecular markers have been acquired (Sato, 2008; Ashworth et al., 2012; MacGillivray & Kaczmarek 2012, 2015; Lobban and Ashworth, 2014; Li et al. 2016, 2018; Dąbek et al. 2017, 2019; Prasetya et al., 2019; Witkowski et al., 2020).

Here, we undertake a large-scale comparison between the diatom assemblages of distant geographic regions. The aim of the presented research was: 1) to analyze the species composition and biodiversity of diatom assemblages from selected islands of the Indonesian Archipelago and compare our results to previous studies; 2) to estimate the proportions of cosmopolitan, zonal (tropical) and/or potentially endemic taxa; 3) to provide the foundation for the future use of molecular methods in assessing biodiversity and phylogeny of diatom assemblages from Indonesia and beyond.

## 2 Materials and methods

### 2.1 Sampling

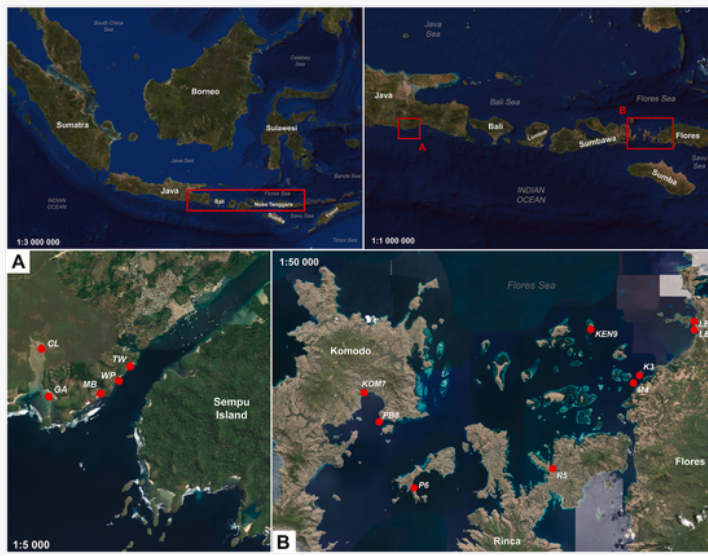
A total of 109 samples were collected from 41 sites in the Indonesian Archipelago. Samples and sites were grouped by geographic distribution into 7 study regions: 24 samples originated from W Borneo (Kalimantan), located in the southernmost part of the South China Sea in the NW extreme of the archipelago. The Celebes island (Sulawesi) region was sampled at Spermonde Archipelago in the Strait of Makassar (30 samples, assigned as SE Celebes) and at the SW coast of Buton Island (20 samples, grouped as SW Celebes). The southern tip of the Indonesian archipelago was represented by samples collected from Java. 18 samples were taken from E Java S coast (Indian Ocean), and 7 samples from E Java N coast (Sea of Java, westernmost Pacific Ocean). Additionally, one sample was separated from those two groups and represented as E Java E coast. The final 9 samples were collected from the Sea of Flores (Flores, Rinca and Komodo Islands). Whereas the Borneo and Javanese sites are included in the Sundaland Hotspot, those from Sulawesi, Komodo, Flores and Rinca belong to the Wallacea Hotspot (Myers, 2003). The latter sites are frequently referred to as the coral triangle and encompass a somewhat larger geographic region that also includes Papua New Guinea and the Philippines [Instruction: I am sorry but I am not sure how to correctly add citation with link to it. There is the missing citation of Veron et al. 2009.

Citation there should follow (Veron et al. 2009, 2011)

] (Veron et al., 2011). The locations of all samples are shown in Fig. 1 and Fig. 2. The GPS coordinates are given below (Table 1).

alt-text: Fig. 1

Fig. 1




Map of the sampling area with East Java and Komodo-Rinca-Flores sites coded. These codes appear in [Table 1](#) and [S1](#).

alt-text: Fig. 2

Fig. 2



Map of the sampling area with West Borneo, SW and SE Sulawesi sites coded. These codes appear in [Table 1](#) and [S1](#).

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Sites and their GPS coordinates within each study region. N column shows number of samples taken at each sampling site. Site codes refer to Figs. 1 and 2.

Region	Site name	Site code	GPS	N
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## Updated version

Sites and their GPS coordinates within each study region. N column shows number of samples taken at each sampling site. Site codes refer to [Figs. 1](#) and [2](#).

Region	Site name	Site code	GPS	N
W Borneo(24 samples)	Teluk Cina	LM 1	0°46'47" N 108°42'21" E	4
	Temiang	LM 2	0°46'50" N 108°42'20" E	2
	Air Tiris	LM 3	0°45'08 " N 108°43'30" E	2
	Melano Barat	LM 4	0°43'56" N 108°43'09" E	4
	Penata Besar Island (West)	PB 1	0°45'19" N 108°45'33" E	2
	Penata Besar Island (North)	PB 2	0°45'33" N 108°46'02" E	2
	Penata Besar Island (East)	PB 3	0°45'48 " N 108°45'57" E	2
	Penata Kecil Island (West)	PK 1	0°45'14" N 108°46'04" E	1
	Penata Kecil Island (East)	PK 2	0°45'04" N 108°47'35" E	2
	Seluas Island	SE	0°45'02" N 108°46'20" E	2
	Bunguran	BG	0°44'15" N 108°42'30" E	1
SE Celebes(30 samples)	Kapota Island	W1	5°20'5.09" S 123°28'55.91" E	4
	Kapota Island, seashore	W2	5°19'57.6" S 123°29'16.74" E	4
	Wangi-Wangi Island	W3	5°19' 49.38" S 123°32'13.02" E	1
	Tomea Island	W4	5°42'58.74" S 123°53'48.6" E	1
	Tomea Island, seashore	W5	5° 43' 16.86" S 123°54'6.18" E	1
	Kaledupa Island	W6	5°33'45" S 123°45'55.26" E	2
	Hoga Island (West)	W7	5°27'55.5" S 123°45'40.61" E	5
	Hoga Island (North)	W8	5°27'27.12" S 123°46'0.9" E	2
Buton Island, Bau Bau	BBNB	From 5°31'21.18" S 122°33'57.36" E to 5°31'24.9" S 122°34'2.58" E along seashore	10	
SW Celebes(20 samples)	Samalona Island	SI	5°07'34" S 119°20'34.7" E	14
	Kodingareng Keke Island	KI	5°06'22.6" S 119°17'18.5" E	6
E Java S Coast(18 samples)	Mini Beach	MB	8°26'33" S 112°40'27" E	2
	Tiga Warna Beach	TW	8°26'22" S 112°40'39" E	6
	Watu Pecah Beach	WP	8°26'33.3" S 112°40'28.2" E	3
	Clungup Beach	CL	8°26'16.2" S 112°40'05.9" E	4
	Gatra Beach	GA	8°26'34.6" S 112°40'10.4" E	3
E Java N Coast(7 samples)	Bantar Probolinggo Beach	PRO	7°46'41" S 113°16'34" E	2

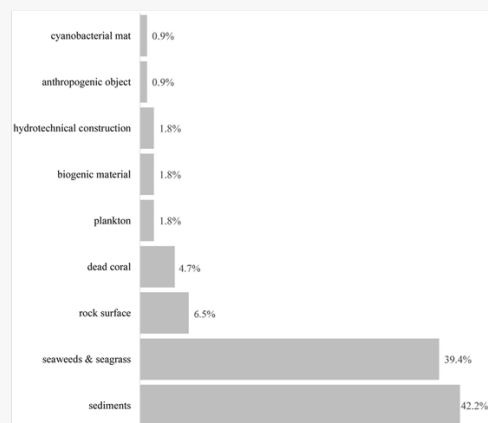
	Bohay Beach	BOH	7°42'50" S 113°33'33" E	4
	Tampora Beach	TAM	7°43'26" S 113°38'52" E	1
E Java E Coast (1 sample)	Pulau Banyuwangi Tabuhan Beach	PAL	8°02'10" S 114°27'42" E	1
Flores RincaKomodo(9 samples)	Labuan Bajo 1	LB1	8°29'46" S 119°52'36" E	1
	Labuan Bajo 2	LB2	8°30'18" S 119°52'40" E	1
	Kelor 3	K3	8°32'56" S 119°48'54" E	1
	Menjerita 4	M4	8°34'08" S 119°48'13" E	1
	Rincah 5	R5	8°39'14" S 119°42'55" E	1
	Padar 6	P6	8°40'37" S 119°33'19" E	1
	Komodo 7	KOM7	8°34'12" S 119°30'04" E	1
	Pink Beach 8	PB8	8°36'04" S 119°31'06" E	1
	Kenawan 9	KEN9	8°29'57" S 119°45'17" E	1

## 2.2 Habitats sampled

Sampling in all areas involved a variety of substrates. Most samples originated from seaweeds (*Padina* sp., *Caulerpa* sp., *Chlorodesmis fastigiata* (C.A.Agardh) S.C.Ducker, *Halimeda* sp., *Ulva* sp.,) and seagrass. *Padina* sp. were mainly sampled from deeper water, up to 2–3 m, whereas *Halimeda*, *Caulerpa* and *Ch. fastigiata* were sampled from water depths ranging between 0.5 and 1 m. *Ulva* sp. samples were usually taken from coastal habitats (rocks and rockpools). The other most common sampled habitat was a variety of sediments. Usually, this was coral sand from a water depth ranging from beach sand (splash zone) to a depth of 2–3 m. Samples were also taken from exposed sand flats (rarely mud). The E Java N coast mostly consisted of a fine gravel usually composed of coral rubble. From each sampling site, dead coral pieces were sampled as an additional kind of substrate. From each region, rock scrapes were taken from the littoral zone. Few samples were taken from biological substrates. These were scrapes from *Holoturia atra* Jaeger, a large *Conus* sp. shell, and a piece of coral. A single sample of thick microbial mat was taken from Tiga Warna beach (E Java S coast) from a dry rockpool. Likewise, a single sample was taken as a matter of curiosity from a densely overgrown backless sandal made of rubber, which we classify as an anthropogenic object. A few more samples were taken from plastic piers, classified as hydrotechnical constructions, as well as several plankton samples. The proportions of various sampled habitats are shown in Fig. 3.

alt-text: Fig. 3

Fig. 3



Proportion between different habitats sampled in this study (%).

## 2.3 Sample preparation and diatom analysis

To remove calcium carbonate and mineralized organic matter, samples were digested in 10% HCl (hydrochloric acid) and, after washing several times with deionized water, boiled in 37% H<sub>2</sub>O<sub>2</sub> (hydrogen peroxide). Thereafter, the obtained suspension was pipetted onto cover slips, left at room temperature for 24 h until evaporation of the water, and mounted onto glass slides using Naphrax<sup>®</sup>. Slides were analyzed under a light microscope (LM) Leica DMLB equipped with x100/1.40 PlanAPO and imaged with Zeiss Axio Imager 2 microscope equipped with x100/1.46 PlanAPO oil immersion objectives. All processed samples and slides in duplicate are housed at the Szczecin Diatom Culture Collection (SZCZ) with accession numbers given in the Supplementary Material (S1).

In LM, a minimum of 300 diatom valves were counted on each slide. Only full, undamaged valves were counted. If a specimen was identified based on girdle view, it was counted as two valves (Schrader and Gersonde, 1987). Although the identification of diatoms was based on LM during the counting procedure, the identification of critical taxa, e.g. very small or delicately silicified, was strongly aided by scanning electron microscope (SEM) observations. For SEM observations, samples were pipetted onto a polycarbonate membrane filter, Whatman Nuclepore with 1 µm pores, mounted onto aluminum stubs and sputter-coated with 20 nm of gold or gold-palladium alloy. SEM examination involved a Hitachi SU8000 and SU 8010 units.

The taxonomic identification was mainly based on Witkowski et al. (2000). Identification of rare and uncommon species was based on many additional publications, such as: Wachnicka and Gaiser (2007) for *Seminavis* D.G.Mann and *Amphora* Ehrenberg ex Kützing, Stepanek & Kociolek (2018) for *Amphora* and *Halamphora* (Cleve) Z.Levkov, Trobajo et al. (2013) for *Nitzschia* Hassall, Lee et al. (2013) for *Achnanthes* Bory. Also, publications such as: Stidolph et al. (2012), Lobban et al. (2012), Lobban (2018), Riaux-Gobin et al. (2008, 2010a, 2010b, 2011a, 2011b, 2015) and Al-Handal et al. (2016) were helpful for the identification of rare diatom species from coral reef habitats.

The growth form of all diatom taxa identified at the species and genus level were ordered after Round (1981) and Totti et al. (2007) into the following categories: adnate (chiefly monoraphid, plus *Amphora* and *Halamphora* among biraphid), erect = pedunculate (some bipolar centrics, araphid and some monoraphids), motile (biraphid), plocon (diatoms embedded in a substrate), tube-dwelling (diatoms living in mucilage tubes, mainly *Parlibellus*, but also some *Navicula* and *Nitzschia*), planktonic (diatoms suspended in water column). For diatoms identified as gen. et spec. indet. the growth form was not determined and they are included as nd.

## 2.4 Species richness and biodiversity indices

The simplest measure of biodiversity used in this study was species richness (S). It is the total number of taxa in a particular sample (Gray, 2000). This measure of biodiversity takes into account neither the distribution nor the abundance of species, so S does not describe the structure of the assemblage, as each species in an area is usually represented by different numbers of individuals. Therefore, another component that describes the biodiversity of a given assemblage was the relative abundance (RA). It is the abundance percentage of each species or taxa relative to the total number of all identified species in a locality. It shows how frequent or rare a species is in a defined assemblage relative to other taxa (Magurran 1988, 2004). In our study, RA was used to refer to the percentage abundance in one sample, a specific region, or the entire area of our research. Additionally, the level of biodiversity in the analyzed samples was determined using biodiversity indices, such as: Shannon biodiversity index (H') and Shannon's evenness index (E<sub>H</sub>), as well as the Simpson biodiversity index (D; Magurran, 1988). We calculated H' using the method described in Shannon (1948) with a natural logarithm (ln, cf. Shannon, 1948, cf. also Krebs, 1972, 1989). E<sub>H</sub> was calculated following Pielou (1976). The calculations of the D index were made using the method described in Simpson (1949). The disadvantage of using those biodiversity indices is that the relative role that different species played in their calculation cannot be shown. To overcome this disadvantage, we applied a rank abundance curve, also known as Whittaker plot (Whittaker, 1965; Magurran, 2004). This graph helps to understand how assemblages are different from each other in number as well as abundances of particular species. Comparisons of relative abundances curves can provide additional insight into community dynamics that will not be evident from changes in species richness or dissimilarity alone (Avolio et al., 2015).

## 2.5 Statistical analyses

The level of similarity in terms of taxonomic structure between particular samples was examined with two methods. Firstly, we constructed a dendrogram showing the relationships between individual sample species composition, with branch length showing the calculated Bray-Curtis dissimilarity index. This is a statistic feature used to quantify the compositional dissimilarity between different samples based on taxa identified in each sample (Bray and Curtis, 1957). Secondly, we applied non-metric multidimensional scaling (NMDS) with two-dimensional scaling and Bray-Curtis similarity/dissimilarity index. This defines the most fitting position of a given species in two dimensions and minimizes the stress values of the two-dimensional configuration. We used Kruskal's stress value to determine the goodness-of-fit of the calculated NMDS (Kruskal, 1964; Kruskal and Wish, 1978). Both analyses were done using PAST 3.15 software for scientific data analysis (Hammer et al., 2001). Moreover, both analyses compared additional data from our previous research on tropical oceanic island diatom biodiversity based on Nosy Be Island data (NW Madagascar; Kryk et al., 2020).



### 3 Results

The 109 analyzed samples yielded a total of 911 taxa representing 188 genera. Based on LM and SEM observations, we estimate that dozens of taxa will require a description as new to science; this includes both species and genera. To the best of our knowledge, at least several morphologies observed in the Indonesian Islands by SEM have never been illustrated in published sources in the past. A full taxa list with the number of identified valves in each sample, substrate and slide accession numbers from the Szczecin Diatom Culture Collection (SZCZ), as well as biogeographic affinity and growth form for each taxon are given in the Supplementary Material (S1). Dominant taxa compositions for the entire study area are presented in Table 2, and dominant taxa within each sampling area are presented in Table 3. Selected dominant taxa in particular sampled regions are illustrated with LM micrographs in Figs. 4–96.

alt-text: Table 2

Table 2

*i* The table layout displayed in this section is not how it will appear in the final version. The representation below is solely purposed for providing corrections to the table. To preview the actual presentation of the table, please view the Proof.

Relative abundance (RA) of the dominant taxa (above 1% of RA) for summed abundances within the entire study area.

RA	TAXA	
4.37%	<i>Nitzschia frustulum</i>	–
2.14%	<i>Amphora exilitata</i>	Figs. 59–62
2.02%	<i>Serratifera</i> sp. 1	Fig. 20
1.68%	Rhoicosphenioid form sp. 5	Figs. 48–50
1.66%	<i>Seminavis</i> sp. 5	Figs. 75–77
1.51%	<i>Nitzschia inconspicua</i>	–
1.40%	<i>Amphora pannucea</i>	Fig. 68
1.29%	Rhoicosphenioid form sp. 1	Figs. 51–53
1.23%	<i>Amphora wiseti</i>	Figs. 56–58
1.17%	<i>Halamphora yundangensis</i>	Figs. 70 and 71
1.13%	<i>Navicula</i> sp. 9	Figs. 46 and 47
1.11%	<i>Psammodictyon</i> sp.	Figs. 93 and 94
1.06%	<i>Halamphora acutiuscula</i>	–
1.03%	<i>Cocconeis alucitae</i>	Figs. 24 and 25

alt-text: Table 3

Table 3

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Relative abundance (RA) of the dominant taxa (above 2% of RA) within a particular region.

REGION	RA	TAXA	
W BORNEO	5.34%	Rhoicosphenioid form sp. 1	–

Updated version

Relative abundance (RA) of the dominant taxa (above 2% of RA) within a particular region.

REGION	RA	TAXA	
W BORNEO	5.34%	Rhoicosphenioid form sp. 1	–
	4.51%	Rhoicosphenioid form sp. 5	–
	4.24%	<i>Cocconeis scutellum</i>	–

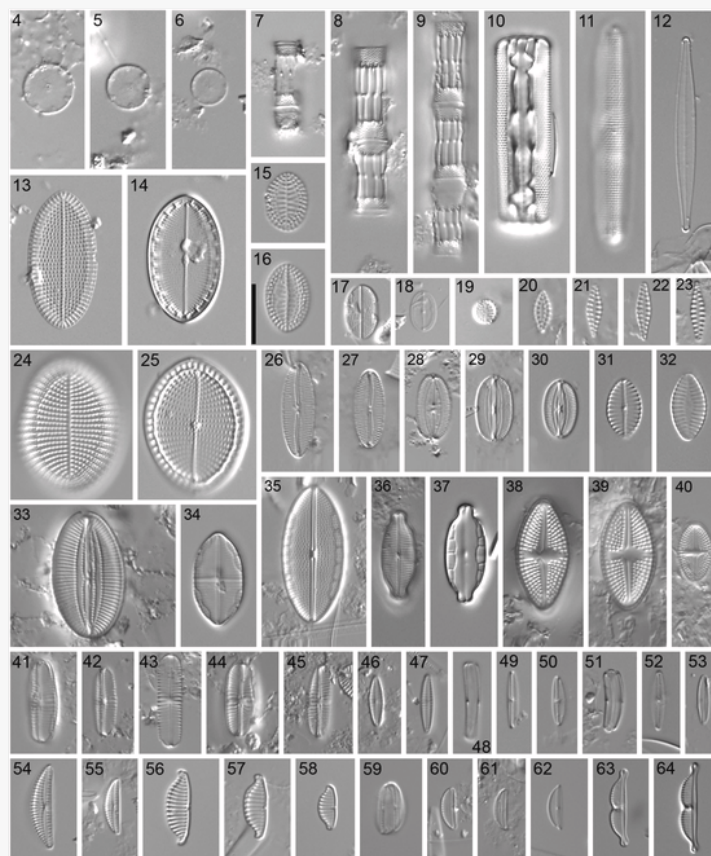


	3.66%	<i>Nitzschia frustulum</i>	–
	3.24%	<i>Amphora exilitata</i>	–
	2.44%	<i>Navicula</i> sp. 9	–
	2.16%	<i>Gomphonemopsis littoralis</i>	<a href="#">Figs. 72–74</a>
	2.04%	<i>Mastogloia ovalis</i>	<a href="#">Fig. 35</a>
<b>SE CELEBES</b>	5.92%	<i>Serratifera</i> sp. 1	–
	5.86%	<i>Nitzschia frustulum</i>	–
	5.60%	<i>Seminavis</i> sp. 5	–
	3.51%	<i>Amphora pannucea</i>	–
	2.54%	<i>Halamphora yundangensis</i>	–
	2.05%	<i>Planothidium</i> sp. 5	<a href="#">Figs. 31 and 32</a>
	2.02%	<i>Nanofrustulum</i> sp.	<a href="#">Fig. 19</a>
<b>SW CELEBES</b>	4.62%	<i>Amphora exilitata</i>	–
	4.14%	<i>Periraphis</i> sp. nov.	<a href="#">Figs. 85–88</a>
	3.86%	Rhoicosphenioid form sp. 2	–
	3.38%	<i>Nitzschia frustulum</i>	–
	3.33%	Rhoicosphenioid form sp. 5	–
	2.64%	<i>Hyalosynedra</i> sp. 2	<a href="#">Fig. 12</a>
	2.00%	<i>Amphora staurohyalina</i>	<a href="#">Figs. 67 and 68</a>
<b>E JAVA S COAST</b>	6.80%	<i>Nitzschia frustulum</i>	–
	6.29%	<i>Amphora wiseii</i>	–
	4.48%	<i>Nitzschia inconspicua</i>	–
	4.16%	<i>Fallacia</i> sp. 4	<a href="#">Figs. 26 and 27</a>
	3.84%	<i>Denticula</i> sp.	<a href="#">Figs. 78–80</a>
	2.37%	<i>Fallacia</i> ny	<a href="#">Fig. 33</a>
	2.22%	<i>Gomphonemopsis littoralis</i>	–
	2.15%	<i>Amphora helenensis</i>	<a href="#">Figs. 54 and 55</a>
<b>E JAVA N COAST</b>	13.19%	<i>Thalassiosira</i> sp. 2	<a href="#">Figs. 4–6</a>
	8.01%	<i>Luticola</i> sp. 2	<a href="#">Fig. 40</a>
	4.69%	<i>Nitzschia inconspicua</i>	–
	4.16%	<i>Minidiscus trioculatus</i>	–
	3.58%	<i>Nitzschia frustulum</i>	–
	3.35%	<i>Skeletonema tropicum</i>	<a href="#">Figs. 8 and 9</a>
	2.74%	<i>Luticola</i> sp. 1	<a href="#">Figs. 38 and 39</a>
	2.17%	<i>Skeletonema</i> sp.	<a href="#">Fig. 7</a>
	2.10%	<i>Nitzschia</i> sp. 7	<a href="#">Fig. 89</a>
<b>E JAVA E COAST</b>	6.63%	<i>Cocconeis mascarenica</i>	<a href="#">Figs. 17 and 18</a>
	5.76%	Rhoicosphenioid form sp. 1	–
	4.61%	<i>Hyalosynedra</i> sp. 2	–
	4.32%	<i>Grammatophora marina</i>	<a href="#">Figs. 10 and 11</a>
	4.32%	<i>Nitzschia</i> sp. 9	<a href="#">Figs. 81–83</a>
	4.03%	<i>Nitzschia frustulum</i>	–
	2.88%	<i>Mastogloia crucicula</i>	<a href="#">Fig. 34</a>
	2.88%	<i>Mastogloia pusilla</i> var. <i>subcapitata</i>	<a href="#">Figs. 36 and 37</a>
	2.59%	<i>Cocconeis coronatoides</i>	<a href="#">Figs. 13 and 14</a>

	2.59%	<i>Cocconeis scutellum</i> var. <i>posidoniae</i>	–
	2.31%	<i>Amphora staurohyalina</i>	–
	2.31%	<i>Navicula</i> sp. 9	–
	2.31%	<i>Serratifera</i> sp. 3	Figs. 21–23
	2.02%	<i>Amphora exilitata</i>	–
<b>FLORES RINCA KOMODO</b>	4.04%	<i>Halamphora yundangensis</i>	Figs. 70 and 71
	3.68%	<i>Amphora wiseii</i>	–
	3.68%	<i>Nitzschia inconspicua</i>	–
	3.38%	<i>Rhopalodia guettingeri</i>	Figs. 95 and 96
	3.02%	<i>Grammatophora oceanica</i>	–
	2.73%	<i>Nitzschia</i> cf. <i>asteropeae</i>	Figs. 91 and 92
	2.33%	<i>Nitzschia frustulum</i>	–
	2.04%	<i>Fallacia pseudony</i>	Figs. 29 and 30

alt-text: Fig 4–64

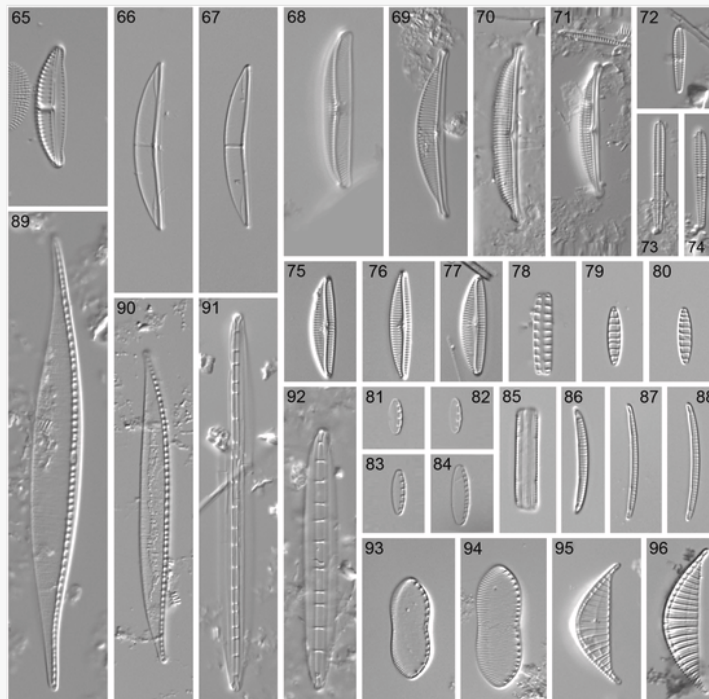
Fig 4–64



LM images of selected most dominant taxa: (4–5) *Thalassiosira* sp.; (7) *Skeletonema* sp.; (8–9) *Skeletonema tropicum*; (10–11) *Grammatophora marina*; (12) *Hyalosynedra* sp. 2; (13–14) *Cocconeis coronatoides*; (15–16) *Cocconeis dapalistriata*; (17–18) *Cocconeis mascarenica*; (19) *Nanofrustulum* sp.; (20) *Serratifera* sp. 1; (21–23) *Serratifera* sp. 3; (24–25) *Cocconeis alucitae*; (26–27) *Fallacia* sp. 4; (28) *Fallacia oculiformis*; (29–30) *Fallacia pseudony*; (31–32) *Planothidium* sp. 5; (33) *Fallacia ny*; (34) *Mastogloia crucicula*; (35) *Mastogloia ovalis*; (36–37) *Mastogloia pusilla* var. *subcapitata*; (38) *Luticola* sp. 1; (39–40) *Luticola* sp. 2; (41–42) *Dickieia* sp. 1; (43–45) *Dickieia ulvacea*; (46–47) *Navicula* sp. 9; (48–50) Rhoicosphenoid form 1; (51–53) Rhoicosphenoid form 3; (54–55) *Amphora helenensis*; (56–58) *Amphora wiseii*; (59–62) *Amphora exilitata*; (63–64) *Amphora incrassata*. Scale bar = 10  $\mu$ m.

alt-text: Fig. 65–96

Fig. 65–96



LM images of selected most dominant taxa: (65) *Amphora malectractata*; (66–67) *Amphora staurohyalina*; (68) *Amphora pannucea*; (69) *Halamphora coffeaeformis*; (70–71) *Halamphora yundangensis*; (71–74) *Gomphonemopsis littoralis*; (75–77) *Seminavis* sp. 5; (78–80) *Denticula* sp.; (81–83) *Nitzschia* sp. 9; (84) *Nitzschia aurariae*; (85–88) *Periraphis* sp.; (89) *Nitzschia* sp. 7; (90) *Nitzschia sigma*; (91–92) *Nitzschia* cf. *asteropeae*; (93–94) *Psammodictyon* sp. 1' (95–96) *Rhopalodia guettingeri*. Scale bar = 10  $\mu$ m.

### 3.1 Taxonomic composition overview by region

#### 3.1.1 W Borneo (W Kalimantan)

This region reached the highest number of 131 genera. These were represented by 458 taxa, out of which 190 were tentatively identified. Among the taxa identified, only sixteen taxa exceeded an RA of 1%. Eight taxa exceeded an RA of 2% (Table 3), and three of these were the same as in SW Celebes. The taxa present in the two regions were: Rhoicosphenioid form sp. 1 (5.3%), Rhoicosphenioid form sp. 5 (4.5%) and *Amphora exilitata* Giffen (3.2%). The remaining dominant taxa included: *Cocconeis scutellum* Ehrenberg (4.2%), *Nitzschia frustulum* (Kützing) Grunow (3.7%), *Navicula* sp. 9 (2.4%), *Gomphonemopsis littoralis* (Hendey) Medlin (2.2%) and *Mastogloia ovalis* A.W.F.Schmidt (2.0%). Beside the dominant taxa, the studied assemblages were characterized by higher numbers of *Amphora*, *Cocconeis* Ehrenberg, *Halamphora* (Cleve) Mereschkowsky, *Mastogloia* Thwaites ex W.Smith, *Navicula* Bory and *Nitzschia*.

#### 3.1.2 SE Celebes (SE Sulawesi)

In samples from this area, 91 genera were identified and represented by 390 taxa, out of which, 149 were tentatively identified. Fourteen taxa exceeded an RA of 1%. Seven taxa attained an RA >2% (Table 3) and three of them (*Nitzschia frustulum* – 5.869%, *Halamphora yundangensis* W.W.Wu, C.P.Chen & Y.H.Gao – 2.5% and *Amphora pannucea* Giffen – 3.5%) were shared with other regions. The other dominant taxa in SE Celebes included *Serratifera* sp. 1 (5.92%), *Seminavis* sp. 5 (5.6%), *Planothidium* sp. 5 (2.05%) and *Serratifera* sp. (2.02%). The most species-rich genera included *Amphora*, *Cocconeis*, *Halamphora*, *Mastogloia*, *Navicula* and *Nitzschia*.

#### 3.1.3 SW Celebes (SE Sulawesi)

This region reached the second highest number of genera of 114, represented by 407 taxa. 16 taxa exceeded 1%. Seven taxa exceeded 2% of the RA and were unique for the entire study area (Table 3), i.e. *Amphora exilitata* (4.6%) followed by *Periraphis* sp. 2 (4.1%), Rhoicosphenioid form sp. 1; 3.9%; *Nitzschia frustulum* (3.4%), Rhoicosphenioid form sp. 5 (3.3%), *Hyalosynedra* sp. 2 (2.6%) *Amphora staurohyalina* A.C.Podzorski & H.Håkansson (2.0%). The diatom assemblages of this region were characterized by an increased RA of planktonic species *Skeletonema tropicum* Cleve and clearly lower RA of small *Nitzschia* spp. including *N. frustulum*, and *N. inconspicua* Grunow which have been replaced by another set of cosmopolitans including *N. aurariae* Cholnoky, *N. martiana* (C.Agardh) Schütt, *N. sigma* (Kützing) W.Smith and *N. vidovichii* Grunow. The most species-rich genera included: *Amphora*, *Cocconeis*, *Halamphora*, *Mastogloia*, *Navicula* and *Nitzschia*.

#### 3.1.4 E Java S coast

In this region, 96 genera with 365 taxa were recorded, including 184 tentatively identified. Diatom assemblages of the E Java S coast were characterized by a low RA, with twenty-four exceeding 1% and eight species exceeding 2% (

Table 3). The highest abundances were observed for *Nitzschia frustulum* (6.8%), *N. inconspicua* (4.9%), *Amphora wiseii* Salah (6.3%) and *Fallacia* sp. 4 (4.2%). Less abundant were *Denticula* sp. (3.8%), *Fallacia ny* (Cleve) D.G.Mann (2.4%), *Gomphonemopsis littoralis* (2.2%) and *Amphora helenensis* Giffen (2.2%). The most species-rich genera were: *Nitzschia*, *Navicula*, *Fallacia* Stickle & D.G.Mann, *Halamphora*, *Amphora*, *Cocconeis* and *Psammodictyon* D.G. Mann.

### 3.1.5 E Java N coast

Diatom assemblages of this area were characterized by a lower number of taxa (156), among which 70 were tentatively identified. The number of genera was 56. A higher number of species attained the highest RA when we compare all samples analyzed in Indonesia. Eleven taxa exceeded an RA of 1% and nine taxa exceeded 2.0% (Table 3). The most dominant species was *Thalassiosira* sp. 2 (13.1%). The second of the most dominant taxa in this region was *Luticola* sp. 2 (8.04%). The remaining dominant taxa were cosmopolitan *Nitzschia inconspicua*, which achieved an RA of 4.778%, as well as planktonic forms (i.e., *Minidiscus trioculatus* (F.J.R.Taylor) Hasle 4.162%, *Skeletonema tropicum* 3.35% and *Skeletonema* sp. 2.172%).

### 3.1.6 E Java E coast

In this area, 77 diatom taxa were identified, of which 29 were tentative, from 27 genera. The diatom assemblage was different to all other regions. The RA of fifteen taxa exceeded 1% and fourteen exceeded 2% (Table 3). The highest RA was observed in the case of *C. mascarenica* Riaux-Gobin & Compère (6.8%), and a diatom that was tentatively named as Rhoicosphenioid form sp. 1 (5.8%). An increased RA was also characteristic for cosmopolitan *Grammatophora marina* (Lyngbye) Kützing (4.32%) and a few widespread cosmopolitan *Nitzschia* including: *N. frustulum* (4.0%) and *N. aurariae*. Dominant genera were *Cocconeis*, *Nitzschia*, *Amphora* and *Mastogloia*.

### 3.1.7 Flores–Rinca–Komodo

In this area, 103 genera represented by 334 taxa were identified. A significant proportion (168 taxa) have been only tentatively identified. Fourteen taxa exceeded an RA of 1%. Part of the dominant taxa were shared with other sampled areas and four taxa, out of eight with an RA exceeding 2% (Table 3), have not been observed in other areas as dominants. These were *Ropalodia guetingeri* Krammer (3.4%), *Grammatophora oceanica* Ehrenberg (3.0%), *Nitzschia* cf. *asteropeae* Lobban, Ashworth, Calao & E.C.Theriot. The remaining dominant taxa included *Halamphora yundangensis* (4.04%), *Amphora wiseii* (3.7%), *N. inconspicua* (3.7%), *N. frustulum* (2.3%) and *Fallacia pseudony* (Hustedt) D.G.Mann (2.0%). The most species-rich genera were *Cocconeis*, *Halamphora*, *Mastogloia*, *Navicula* and *Nitzschia*, from which the most dominant was *Mastogloia*.

## 3.2 Species richness (S) and biodiversity indices (H', E<sub>H</sub>, D)

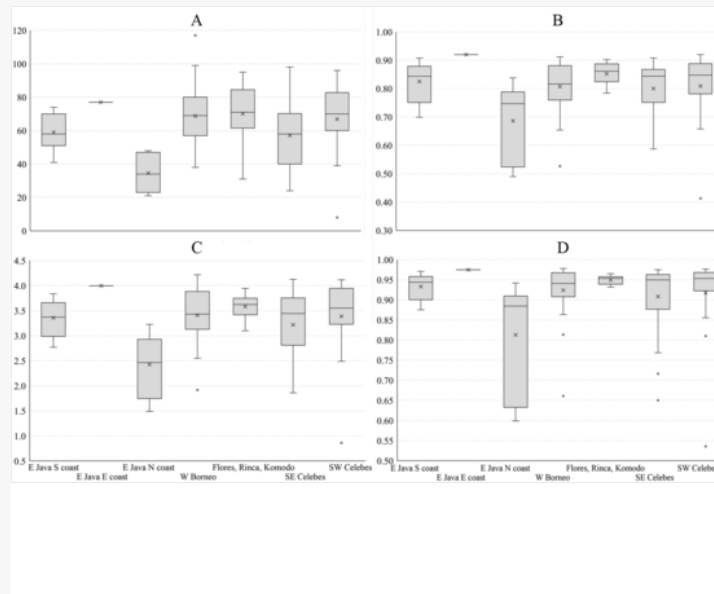
Most of the diatom assemblages of the Indonesian Archipelago were characterized by a very high number of taxa, with >100 taxa recorded in numerous samples. The highest S was observed in samples collected from W Borneo, ranging from 38 to 118, (average 69). Three regions centered around the Sea of Flores: 1) Flores–Rinca–Komodo, 2) SE Celebes and 3) SW Celebes all had similar S values, with a minimum ranging from 31 at Flores–Rinca–Komodo region to 39 at SW Celebes and a maximum ranging from 96 at SW Celebes to 98 at SE Celebes. Samples from E Java were characterized by lower S values of between 21 and 77 taxa. The lowest S value was recorded on the E Java N coast ranging from 21 to 48 (average 35). The highest on the E Java S coast with S values between 41 and 74 taxa (average 59). One sample assigned as E Java N coast from the inland-most station of Probolinggo reached 77 taxa. These areas of the lowest S were also characterized by the lowest number of identified genera. Therefore, the identified number of genera was 27, 56 and 95 on the E Java N coast, E Java E coast, and E Java S coast, respectively. In samples from Flores–Rinca–Komodo we identified 103 genera. In samples from Celebes, the number of genera was 91 and 114 for SE Celebes and SW Celebes, respectively. The highest number of genera was recorded from W Borneo with 131 genera.

As illustrated in Fig. 97, diatom assemblages of the Indonesian Archipelago were characterized by a very high biodiversity in most of the examined samples. In eight samples, the H' attained values > 4.0, with the highest value of 4.22 in W Borneo followed by 4.13 and 4.12 in SE and SW Celebes, respectively. Despite H' max values for the E Java S coast and Flores–Rinca–Komodo regions being <4.0, these two regions had biodiversity indices equally distributed with all samples falling in the range between 2.75 and 3.94. Likewise, the E Java E coast had a high H' value amounting to 3.99 (Fig. 97). The lowest H' values for the whole area were computed in samples from the E Java N coast and ranged from 1.49 to 3.23. However, the absolute lowest H' value for a particular sample (0.86) was obtained in SW Celebes. Samples of all regions reached high values of D, with the highest value of 0.98 in W Borneo followed by SW Celebes, E Java coasts and Flores–Rinca–Komodo region. However, the lowest D values were observed on the E Java N coast (average 0.59). In this region, we also notice the lowest absolute D value of all samples (0.41). Samples with high H' were characterized by highest D and vice versa (Fig. 97). In most studied samples, E<sub>H</sub> was high (>0.9). It conformed well with two other biodiversity indices with the highest scores computed for coral sand

and the lowest for seaweeds (*Halimeda* J.V. Lamouroux, *Padina* Adanson and *Ulva* Linnaeus). Similarly, to previous biodiversity indices, the lowest  $E_H$  was computed again for the same, polluted waters of the E Java N coast.

alt-text: Fig. 97

Fig. 97



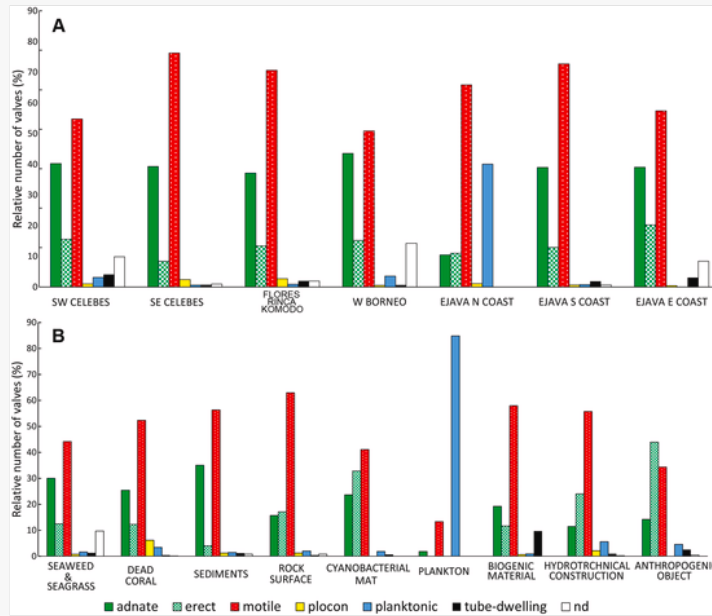
Box-Whisker's plot showing the results of biodiversity compounds for each study region. A) species richness; B) evenness; C) Shannon biodiversity index; D) Simpson biodiversity index. Mean value (x) and outliers (points) are shown in plots. **Below plots, each region is given with number of samples (n).**

### 3.3 Diatom growth forms analysis

In general, our study areas were dominated by motile diatoms that consisted of 60% of all identified valves. Adnate forms occurred with 20% and erect with almost 14%. The remaining diatom growth forms did not exceed 5%. These were plocon (4.7%), planktonic (4.5%) and tube-dwelling (1.8%) forms. We were not able to assign 1.3% of all diatom valves to any growth form and thus they are not determined (nd). Differences in growth form structure are presented in Fig. 98. All studied regions were dominated by motile diatom forms (>40% of all identified valves in each region). The highest proportion was observed in SE Celebes where motile forms consisted of 60.3%. The lowest proportion was in W Borneo and the E Java E coast with 39.5% and 44.6%, respectively. Additionally, due to increased plankton sampling, the E Java N coast was characterized by an increased proportion of planktonic diatoms to 31.2% (average for entire sample set from Indonesia was 5.5%). The second most dominant form was adnate that ranged between 8 and 33% and erect 6–16% (Fig. 98A). Differences between diatom assemblages associated with different regions were better reflected in species composition than in growth form structure. However, growth form showed interesting patterns when divided into sampled habitats (Fig. 98B). Despite that, in most of the sampled habitats, motile forms still dominated and the percentage of other forms changed among the habitats. Plankton samples were dominated by planktonic diatoms (almost 85%), accompanied by motile forms (14%) and other forms were almost absent. Moreover, samples from the cyanobacterial mat, hydrotechnical constructions and anthropogenic objects were different from the others. In these habitats we observed an increased proportion of erect and adnate forms and decrease in motile forms (Fig. 98B). In terms of the anthropogenic object, the growth structure showed almost the same percentages of both erect and motile forms (ca. 45%). Samples from the biogenic material showed the highest proportion of tube-dwelling forms, which was not that high in any other substrate (10%).

alt-text: Fig. 98

Fig. 98



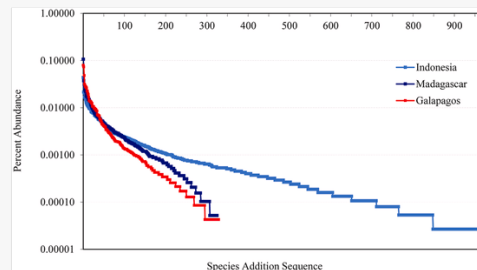
Relative diatom valve number of particular growth forms grouped by our study regions (A) and sampled habitat (B).

### 3.4 Intraregional similarity of diatom assemblages

The rank abundance curve (Fig. 99) showed that abundances in the Indonesian Island habitats that we studied were significantly different from trends in species abundance of the Nosy Be Island in NW Madagascar or in the Laguna Diablas of Isabela Island in the Galapagos (Łopato, 2016; Kryk et al., 2020). These two latter localities were characterized by significantly higher abundances of the high-ranking species than low-ranking ones, which was opposite to the Indonesian curve. In a species rank abundance curve made only for Indonesian sites, this pattern was repeated, but two sites, E Java N coast and E Java E coast deviate from this above pattern (Fig. 100). This is due to a significantly higher RA in the E Java N coast and low amount of data (one sample) for the other site.

alt-text: Fig. 99

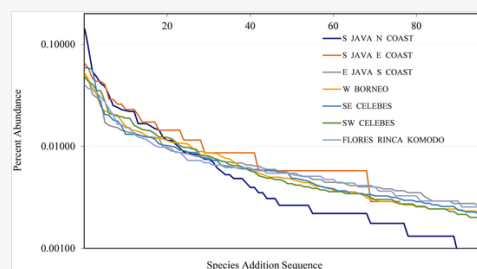
Fig. 99



Rank abundance curve comparing Indonesian data (this study), Madagascar data (Kryk et al., 2020) and Galapagos data (Łopato, 2016).

alt-text: Fig. 100

Fig. 100



Partial Rank abundance curve with 100 most abundant ranks (top of curves) grouped by study regions.

Based on the Bray-Curtis similarity/dissimilarity index, built on the taxonomic composition of all studied samples plus the Nosy Be diatom assemblage data from Kryk et al. (2020), each sampling area was separated from the remaining

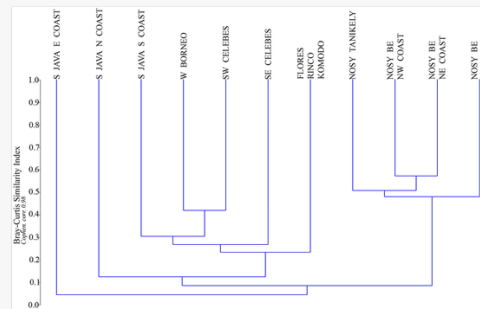


ones and constitutes a separate cluster (Fig. 101). Three distinct branches were formed with the E Java E coast (5%) and E Java N coast (15%) as two isolated regions and one larger branch formed by the remaining sites. The similarity between the remaining areas was higher and the least similar region of Flores–Rinca–Komodo (25%) graded into SE Celebes (28%). Together, these two areas graded into the south E Java S coast (30%). The two most similar areas were W Borneo and SW Celebes with 45% of taxonomical similarity. A fourth separate branch was formed by the Nosy Be diatom assemblages. In general, similarities between the particular Nosy Be areas were significantly higher than those in Indonesia. This is understandable as the sampling area in NW Madagascar was smaller compared to the Indonesian Islands.

alt-text: Fig. 101

Fig. 101

Figure Replacement Requested



Results of cluster analysis based on Bray-Curtis similarity/dissimilarity of taxonomic composition of the dominant species (exceeding 2% RA) between particular study region of Indonesia (this study) and Nosy Be, Madagascar (Kryk et al., 2020).

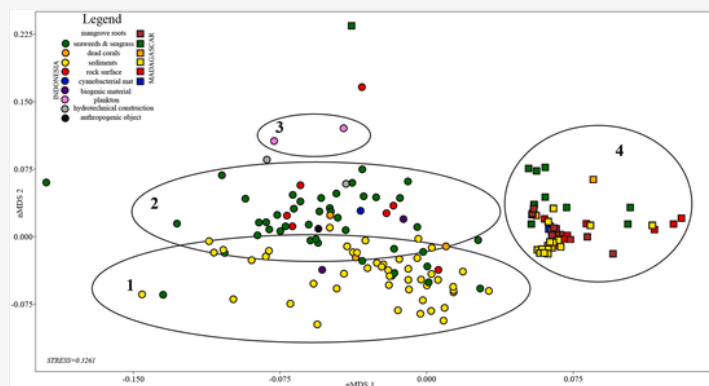
Replacement Image: Fig.101.dissimilarity.tif

Replacement Instruction: dissimilarity instead of similarity

In the NMDS ordination of the Indonesia samples, we have included the Nosy Be diatom data grouped in six categories based on the same principles as in this study (Fig. 102). NMDS results showed 4 groups of habitats that were characterized by similar taxonomic compositions (see Fig. 102). Group 1 with sediment samples, which also included coral sand. Group 2 with samples taken from seaweeds and group 3 that contained plankton forms. Group 4 constituted as a whole the Nosy Be diatoms except one sample taken from seaweed and seagrass, which was characterized by a very strong dominance of *Cocconeis scutellum* (sample NB10E in Kryk et al., 2020). The stress value was 0.32 providing a fair representation in reduced dimensions.

alt-text: Fig. 102

Fig. 102



Non-metric multidimensional scaling (nMDS) based on full taxonomic composition of samples from Indonesia (this study) and Madagascar (Kryk et al., 2020). Different colours marked in legend (top-left) indicate each habitat. Distinguishable groups are marked: 1 – domination of samples taken from sediment; 2 – domination of samples taken from seaweeds and sea grass; 3 – domination of planktonic samples; 4 – Madagascar assemblages as clearly separated from Indonesian assemblages.

## 4 Discussion

### 4.1 Identified number of genera and species



It is evident that tropical littoral diatom assemblages are very rich in genera and species though they also show a very strong intraregional variability (Hendey, 1971; Montgomery, 1978; Frankovich et al., 2006; Gottschalk et al., 2007; Hein et al., 2008; Ashworth et al., 2012; Lobban et al., 2012; Lobban and Ashworth, 2014; Riaux-Gobin et al., 2015; Al-Handal et al., 2016; Lobban, 2018; Kryk et al., 2020, this study). To the best of our knowledge, the highest numbers of genera identified in coral reef habitats thus far amounted to 127 in Martinique and to >120 in Guam (Desrosiers, 2014; Protistcentral.org), respectively. The diversity of genera in studies from the Galapagos, NE Australia, Madagascar and Bahamas were much lower and amounted to 65, 55, 82 and 94, respectively (Hendey, 1971; Gottschalk et al., 2007; Hein et al., 2008; Kryk et al., 2020). So far, the Indonesian diatom assemblages with 188 genera appear to host the highest number of genera identified during a particular study (this study). Likewise, the number of 911 taxa identified in samples from Indonesia exceeds any of the published records for coral reefs. The number of taxa identified from coral reefs ranged from 784 in Martinique (Desrosiers, 2014), significantly exceeding 500 in Guam (Lobban et al., 2012; Lobban, 2018), 379 species from Bahamas (Hein et al., 2008), 329 taxa from Nosy Be, NW Madagascar (Kryk et al., 2020) and 209 in NE Australia (Gottschalk et al., 2007). In the Galapagos, littoral diatoms were studied by Hendey (1971) and by Łopato (2016). Hendey (1971) identified 180 taxa, whereas Łopato (op. cit.) identified 331 taxa.

## 4.2 Biodiversity

A review of the diatomological literature published over several decades revealed that only a few studies have been completed on the biodiversity of tropical marine littoral diatom assemblages where the biodiversity indices have been computed (Gottschalk et al., 2007; Hein et al., 2008; Łopato, 2016; Bąk et al., 2017; Kryk, 2020, this study). This is especially the case when the data are compared to the equivalent biodiversity estimates on temperate diatom assemblages from coastal sediments (e.g. Hendey, 1977; Underwood, 1994; Weckström & Juggins, 2005; Ulanova and Snoeijis, 2006; Çolak Sabanci, 2011; Dalu, 2016), tropical rocky substrates (Siqueiros-Beltrones and Romero, 2004), mangrove roots (Siqueiros-Beltrones et al., 2005) and seaweeds and sediments (Car et al., 2019). Most studies exploring diatom assemblage biodiversity preferred to use  $H'$  and  $E_H$ , whereas Gottschalk et al. (2007) applied the Bulla Evenness Index (Bulla, 1994), which makes a direct comparison to our results somewhat problematic. In general, diatom diversity indices of the tropical coral reef assemblages are very high (Kryk et al., 2020, this study). In the Nosy Be Island diatom assemblages,  $H'$  exceeded 4.0 in several samples with a mean value exceeding 3.5 (Kryk et al., 2020). In our results,  $H'$  was even higher and more than 10 samples exceeded 4.0. All samples with  $H'$  exceeding 4.0 were taken from coral sand. Therefore, the major factor driving high biodiversity was coral sand substrate, possibly combined with increased water depth. This is best illustrated by Indonesian samples in which the number of species exceeded 80 (max. 118 in sample SZCZ 26956 taken from coral sand in Seluas Island, W Borneo at water depth exceeding 2m). Among 17 samples with the highest  $S$  (>80), 15 were taken from coral sand and only 2 from seaweeds. Whereas some of the seaweed samples revealed high biodiversity indices, none of those samples exceeded a  $H'$  of 4.0. The highest  $H'$  on seaweeds was computed in sample SZCZ27005 (3.996) taken from *Padina* sp. in the W Java E coast with  $S = 77$ . The lowest  $H'$  values were computed for seaweeds in both Nosy Be and Indonesia (Kryk et al., 2020, this study). Low  $H'$  values were also characteristic for strongly human impacted sampling sites of the E Java E coast. The Indonesian diatom assemblages showed high biodiversity indices, similar to values from tropical Nosy Be (Kryk et al., 2020), however, some studies dealing with epiphytic and epipelagic diatoms from the Mediterranean (Adriatic Sea) showed a significantly higher  $H'$ . Car et al. (2019), although with  $S$  values lower than in our study, had  $H'$  values exceeding even 5.0. Similar  $H'$  values > 5.0 were computed by Hein et al. (2008) in the tropical diatom assemblages from the Bahamas (seaweeds, seagrass, sediment and actively developing stromatolites) and by Siqueiros-Beltrones et al. (2005) in mangrove roots from the tropical Pacific coast of Mexico. However, a closer look at the methods in the above referred papers showed that the very high  $H'$  values are in part an artefact of the mathematical formula of the Shannon-Wiener equation. In Kryk et al. (2020), and in this study, we used natural logarithms whereas all the above authors applied  $\log_2$ , this small change substantially increases the  $H'$  values. If we consider the above methodologic difference, the  $H'$  of Indonesian and Madagascar diatoms assemblages are the highest thus far computed (exceeding 9.0 when  $\log_2$  is used). The low  $H'$  and high RA which is observed among planktonic and pollution resistant species as shown in the E Java N coast, was associated with higher pollution levels in this region (c.f. Risjani et al., 2014, 2020a; 2020b; Anggraini et al., 2020a; Triaji et al., 2017), which originated from plastic litter (Anggraini et al., 2020b; Buwono et al., 2021) and other anthropogenic waste. Sediment load was an effect of the riverine discharge from the adjacent delta and largely originated from the volcanic mud and revealed that organic rich sediments of the delta retained genotoxic compounds (Risjani et al., 2020a).

The assessment of the relationship between the substrate and the assemblage structure has been approached through the diatom growth form. We have sampled and studied diatom assemblages from several kinds of substrate from the coral reefs of the Indonesian Islands, but due to the scarcity of the published data any direct comparison of our results with those published is barely possible. In a few papers published on coral reef diatoms assemblages, the analysis of the growth form has been neglected (cf. Gottschalk et al., 2007; Desrosiers et al., 2014; Kryk et al., 2020). Whereas our study involved hard substrate (rock scrapes), sediments and seaweeds, the published data are rather focused on a solitary kind of substrate either epiphytic, epilithic or soft sediments (Totti, 2003; Totti et al., 2007) with a strong predominance of epiphytic assemblages (cf. Polifrone et al., 2020 and references therein). When we analyzed the

assemblage structure in terms of their geographic origin, they all show a more or less similar pattern with a very strong dominance of motile forms (due to a wealth of biraphid diatom taxa) followed by adnate ones with numerous monoraphids and by erect forms with *Achnanthes* spp. toxariids and fragilarioids. Much lower abundance characterized the tube dwelling forms (e.g. *Parlibellus*) and plocon which attained increased abundances in Sulawesi (Celebes) coasts, Flores–Rinca–Komodo and S and E coast of East Java. The only remarkable difference from the above pattern was observed in the N coast of East Java where the assemblage was dominated by planktonic forms followed by motile ones. More interesting are our observations when particular substrates are considered in terms of assemblage structure. Motile forms are still dominant, followed by adnate, but the difference between them is much weaker than when the regions are considered. The above pattern is consistently observed for all substrates distinguished except plankton and the anthropogenic object with the former dominated by planktonic forms and the latter dominated by erect forms followed by motile and adnate forms. In the cyanobacterial mat, motile dominated but the second group in terms of growth form were erect followed by adnate forms. Our results are, in general, consistent with published records of epilithic assemblages from the Adriatic Sea (Totti et al., 2007) and epiphytic assemblages on selected seaweeds from the North Atlantic in Iceland (Totti et al., 2009), but differ strongly from epiphytic ones from Gran Canaria Island in the Atlantic Ocean (Polifrone et al., 2020). In the latter study, involving diatom assemblages from selected Gelidiales, adnate were dominant followed by erect forms with a minor participation of motile forms. The authors interpret the dominance of adnate forms as an indication of the mature assemblage. However, on seaweeds from the Iceland coast, the assemblage was dominated by either adnate, erect or motile forms depending (in part) on seaweed architecture and on environmental factor impact. As illustrated in our study, the diatom assemblage on seaweeds and seagrass are roughly similar to the dead coral assemblage, but differ from the sediment associated assemblage with a much lower participation of erect forms. Interestingly, the backless sandal that had been long kept in the water had a diatom assemblage that would fit some epiphytic type of Totti et al. (2007) and of Polifrone et al. (2020). This would mean that the seaweeds and dead coral that we studied in Indonesia hosted diatom assemblages that had not achieved maturity (cf. Polifrone et al. 2020). On the other hand, the rock scrapes follow the assemblage pattern observed by Totti et al. (2007) on an artificial rock substrate subject to colonization in the Adriatic Sea.

### 4.3 Biogeography

Many researchers assume that geographic isolation has no significant importance for microorganisms and new species described in isolated places should not be treated as endemic entities but rather as adapted to specific ecological niches (e.g. Finlay, 2002; Fenchel and Finlay, 2004). In fact, the hypothesis that those microorganisms that are the easiest to identify and most common (diatoms), inhabiting tropical islands, are at least in significant parts cosmopolitan taxa, has been corroborated by the use of molecular phylogeny on benthic diatoms of NW Madagascar, Nosy Be Island by Kryk et al. (2020). Previous research involving sequencing of *Paralia* spp. and *Haslea* spp. strains showed that some of them are globally distributed but others are limited in geographic distribution to particular tropical zones ([Instruction: The same problem as previously. Entire paper has two authors publications with "and" between. There is the only one place where it is "&" instead. In references section, this reference has citation set to be MacGillivray and Kaczmarska, and yet, it is still shown as &. It should be (MacGillivray and Kaczmarska 2012, 2015; ... )]MacGillivray & Kaczmarska 2012, 2015; Gastineau et al., 2014). Others studies showed that the presence of diatom taxa with broad tropical ranges in coral reefs of the Western Indian Ocean coasts and in the SE Pacific (Li et al. 2015, 2018). Yet Lobban et al. (2012), Ashworth et al. (2012), Dąbek et al. (2017, 2019), Li et al. (2016,2020; but see also Kryk et al., 2020) have clearly shown numerous taxa limited in their distribution to particular sites. Our analysis of the published research given above involving the use of molecular methods and identification of processed samples allowed us to distinguish three major groups of diatom taxa in terms of their biogeography:

- 1) **cosmopolitan species**, including some adapted and also distributed in cold water areas, but rather in the Arctic and Greenland than the Southern Ocean. The species principally inhabiting northern and southern temperate zones plus the subtropics and tropics belong to this group. Recently Gastineau et al. (2014), Li et al. (2018) and Kryk et al. (2020; but see also Dąbek et al., 2017, 2019) showed coral reefs inhabited by some globally distributed taxa and the identity of some of these taxa were confirmed with molecular markers. Included in this group are e.g.: *Biremis lucens* (Hustedt) K.Sabbe, A.Witkowski & W.Vyverman, *Cocconeis scutellum*, *C. convexa* Giffen, *Catenula adhaerens* (Mereschkowsky) Mereschkowsky, *Melosira lineata* (Dillwyn) Agardh, *M. nummuloides* Agardh, *Nitzschia inconspicua*, *Psammodiscus nitidus* (W.Gregory) Round & D.G.Mann, *Delphineis surirella* (Ehrenberg) G.W.Andrews, *Plagiogramma minus* (W.Gregory) Ch.Li, Ashworth & Witkowski, *Plagiogrammopsis minima* (Salah) K.Sabbe & Witkowski;
- 2) **zonal species** that can inhabit either cold, temperate or tropical water regions, sometimes in the case of tropical forms expanding their geographic distribution limits into warm temperate waters (i.e., tropical taxa in the Mediterranean and in the Western Pacific coasts of South China, Korea and Japan) or polar species in the cold temperate waters (Hasle and Syvertsen, 1990; Álvarez-Blanco and Blanco, 2014; Mock et al., 2017; Dąbek et al., 2019). Examples included in this group are taxa belonging in e.g.

*Cyclophora* Castracane, *Diplomenora* Blazé, *Hyalosynedra* D.M. Willimas & Round, *Mastogloia* spp., *Microcostatus* J.R. Johansen & J.C. Sray, and *Neofragilaria* Desikachary, Prasad & Prema, but also *Halamphora* and *Schizostauron* Grunow. In fact, the recent application of molecular methods in biogeography shows that tropical planktonic diatoms can reach a high abundance in the Mediterranean (e.g. *Skeletonema tropicum* in Sarno et al., 2005);

- 3) **local species** described from the tropics and absent outside of the habitat type and surrounding areas. Solely in the Indo-Pacific, this group includes a few hundred taxa (Guam, Indonesia, Madagascar, Polynesia). These are some taxa, including genera e.g. *Astrosyne* Ashworth & Lobban, *Brassiereia* M.K. Hein & Winsborough, *Castoridens* Ashworth, Li & Witkowski, *Hanicella* Lobban & Ashworth, *Psammotaenia* Ashworth, Li & Witkowski that have never been found outside of their type habitat despite an intense diatom search in marine littoral regions in recent years. Similar observations are valid for many taxa described from the tropics and representing e.g. *Talaroneis* Kooistra & De Stefano, *Schizostauron* and *Haslea* Simonsen.

Any estimates on the proportions between the above groups are very difficult and could be premature taking into account the number of taxa that are preliminarily identified only to the genus level or have tentative names. In recent research on tropical diatom assemblages, tentatively identified taxa constituted the majority of all distinguished taxonomic units. In the diatom assemblages from the Great Barrier Reef in NE Australia, Gottschalk et al. (2007) identified 78 taxa to the species level, but 131 to the genus level. Kryk et al. (2020) reported a very high proportion of diatoms identified only to the genus level (218 out of all 332 identified taxa). From our previous studies (Dąbek et al., 2017; Li et al. 2015, 2018; Kryk et al., 2020) and published sources (Gottschalk et al., 2007; Ashworth et al., 2012), we see that dominant diatom species inhabiting various coral reefs are zonal (i.e. tropical species). These species belong to genera such as *Cyclophora*, *Hanicella* Lobban & Ashworth, *Cocconeis*, *Amphicocconeis* De Stefano & Marino, *Paralia* Heiberg, *Pinnularia* Ehrenberg, *Gedaniella* Li, Witkowski & Ashworth, *Serratifera* Ashworth, Li & Witkowski, *Neofragilaria*, *Psammoneis* Sato, Kooistra & Medlin, *Schizostauron*, *Nanofrustulum* Round, Hallsteinsen & Paasche, *Talaroneis*, *Castoridens* Ashworth, Li & Witkowski, *Cratericulifera* Li, Witkowski & Ashworth. Despite zonal species, diatom assemblages of coral reefs are also inhabited by local and cosmopolitan species. The occurrence of cosmopolitan diatom species in coral reefs often depends on a specific habitat (e.g., *Planolithidium* Round & Bukhtiyarova in sand). Again, it is hard to make any estimate regarding the proportion between zonal and local elements as long as the unidentified or tentatively identified diatom taxa exceed 50% of the species recorded for particular regions. In tropical regions like Indonesia, the genetic biodiversity of marine macroalgae has been studied only from Madura, Celebes and Lombok (Risjani and Abidin, 2020). The only representative of Indonesian diatoms subject to genomic research is so far *Haslea nusantara* from the NW coasts of Sea of Java (Prasetya et al., 2019). However, there have been numerous research initiatives that involved isolation and sequencing from other tropical, temperate and cold-water regions including diatom taxa we have identified in samples from Indonesia. All taxa biogeography affiliation is available as supplementary data (S1).

#### 4.4 Taxonomic comments

In our study, among the dominant species (RA >1%; Table 3), four species were cosmopolitan, four zonal and six of local distribution. In Indonesian habitats, genera with the highest species number included *Amphora*, *Cocconeis*, *Fallacia*, *Halamphora*, *Mastogloia*, *Navicula* and *Nitzschia*, however, particular species were shared between all regions, except cosmopolitan *N. frustulum* and *N. inconspicua* and zonal tropical *H. yundangensis* and *A. pannucea*. Among *Amphora*, an increased RA was observed in the case of e.g. *A. arenaria* Donkin, *A. graeffeana* Hendeby, *A. helenensis*, *A. hyalina* Kützing, *A. obtusa* W. Gregory, *A. ocellata* Ehrenberg, which are all considered cosmopolitan forms (Witkowski et al., 2000). Less abundant were *Amphora* species described from the Florida coastal region including *A. lunulata* Wachnicka & Gaiser and *A. montgomeryi* Wachnicka & Gaiser and other zonal forms e.g. *A. exilitata*. *Cocconeis* taxa with highest RA were of mixed affinity, whereas the highest RA attained tropical diatoms such as: *C. mascarenica*, *C. alucitae* Riaux-Gobin & Compère, *C. coronatoides* Riaux-Gobin & Romero, *C. cupulifera* Riaux-Gobin, Romero, Compère & Al-Handal, *C. dapaalstriata* Riaux-Gobin, Romero Compère & Al-Handal, *C. napukensis* Riaux-Gobin, Compère, Coste, Straub & Taxböck followed by cosmopolitan ones e.g., *C. molesta* Kützing, *C. convexa* and *C. scutellum*. *Halamphora* was represented by mostly cosmopolitan species including *H. coffeaeformis* (C. Agardh) Mereschkowsky, *H. luciae* (Cholnoky) Levkov and *H. tenerrima* (Aleem & Hustedt) Levkov. A few *Halamphora* species were unnamed or belonged to zonal forms e.g., *Halamphora yundangensis*. *Mastogloia* was the most diverse genus (up to 20 species) and only a few of them attained an increased RA including *M. crucicula* (Grunow) Cleve, *M. ovalis*, *M. corsicana* Grunow, *M. barbadensis* (Greville) Cleve, *M. grunowii* Schmidt and *M. similis* Hustedt, with *M. crucicula* and *M. corsicana* distributed in temperate and tropical oceans and the remaining taxa inhabiting the tropical zone. *Navicula* was represented by more than a dozen species, but none of them attained an increased RA. *Navicula borowkeae* Witkowski, Lange-Bertalot & Metzeltin, *N. johannrossii* Giffen, *N. viminea* Hustedt, and very large and robust *Navicula* cf. *zosteretii* Grunow all known only from the Western Indian Ocean (Giffen, 1971; Witkowski et al., 2000) were observed in selected samples. Species belonging to *Nitzschia* except *N. frustulum*, *N. inconspicua* (see above) and *Nitzschia* cf. *asteropeae* did not attain an

increased RA and were represented among others by cosmopolitan forms e.g. *N. sigma*, *N. vidovichii*. Potentially new to science and locally distributed *Nitzschia* species involved a few sigmoid species, however, with low RA. Additionally, quite a large group of cosmopolitan species were represented by *Diploneis interrupta* (Kützing) Cleve, *D. crabro* Ehrenberg, *D. coffeaeiformis* (Grunow) Cleve, *Grammatophora marina*, *G. oceanica*, *Petroneis marina* (Ralfs) D.G.Mann, *P. granulata* (Bailey) D.G.Mann, *Plagiogramma minus*, *Psammodictyon coarctata* D.G. Mann and *Trachyneis aspera* (Ehrenberg) Cleve. Quite common were also newly established genera *Hendeyella* Ashworth, Witkowski & Ch. Li and *Cratericulifera* (Li et al., 2016). Whereas the former genus is typical for temperate and tropical waters, the latter is typical only for tropical waters (Indian Ocean, Western Atlantic). Additionally, we identified some planktonic species (*Chaetoceros salsugineus* Takano, *Minidiscus trioculatus*, *Skeletonema tropicum*, *Thalassionema nitzschioides* (Grunow) Mereschkowsky, *Thalassiosira* sp., *T. binata* Fryxell, *T. cedarkyensis* Prasad and *T. minima* Gaarder and two mud dwelling species of unidentified *Luticola*. However, benthic taxa were dominant, including the presence of a few tube dwelling species of *Navicula* and *Parlibellus* E.J. Cox with one apparently unknown *Parlibellus* sp. Among the enumerated benthic genera and particularly among *Nitzschia* and *Navicula* occurred small species, e.g., *Navicula* has been represented by small needle-like species in which LM are not identifiable and can represent either *N. diserta* Hustedt, *N. dilucida* Hustedt or *N. salinicola* Hustedt or be a species new to science. *Fallacia* was represented by several cosmopolitan taxa such as *F. nummularia* (Greville) D.G.Mann, *F. ny*, *F. pseudony* and *F. subforcipata* (Hustedt) D.G.Mann. *Cocconeis* was represented by cosmopolitan taxa including *C. scutellum*, *C. pseudograta* Hustedt and *C. convexa*, but also tropical elements with *C. carinata* Riaux-Gobin, Ector & Witkowski, *C. sigillata* Riaux-Gobin & Al-Handal, and *C. mascarenica*. Most *Halamphora* species seem to be unidentifiable and we suspect they represent species new to science, although *H. coffeaeiformis* was rarely present in some samples. With the progress of SEM examination, the numbers of documented taxa new to science are increasing, just to mention two tiny species tentatively accommodated in *Rhoicosphenia* or better rhoicosphenioid forms, showing taxonomic affinity to *Rhoicosphenia* Grunow and *Campylopyxis* Medlin. We consider this species as representing a genus new to science based on preliminary SEM investigations. Interestingly, this genus predominantly occurs in seaweed samples, but is observed in all sampled regions, even in the poor environmental conditions of the E Java N coast.

## 5 Conclusions

No coral reef systems studied thus far has revealed such a high species richness and biodiversity of the diatom assemblages as observed in Indonesia. The scores for Indonesian Archipelago coral reefs are nearly double the scores for other tropical islands including the margins of the Indo-Pacific and Western Caribbean. Likewise, we observed very high numbers of unknown taxa at the species and generic level. Our results are in line with the diversity of other organisms and in particular corals, for which the area has been named a coral triangle, and coral reef fish.

- The diversity of diatom assemblages is similar throughout the regions studied and is ordinated in accordance with human pressure. The highest values of the indices were observed in pristine coastal areas throughout the regions studied with West Kalimantan revealing the highest scores and the human impacted north coast of East Java with the lowest ones.
- In terms of biogeography, a quantitative dominance of cosmopolitan species was observed, however, in terms of species richness, tropical zonal elements and taxa observed locally are dominant. Furthermore, species compositions showing some intraregional variability did not differentiate between the islands (even the most remote) studied. The Bray-Curtis ~~similarity~~ **dissimilarity** showed three clades, with easternmost Java and north coast of East Java as two separate clades and the remaining areas in one large clade but with fairly low similarity. Therefore, the diatom assemblages studied appear to be relatively homogenous and characterize the whole area beginning from West Kalimantan through Java, Sulawesi to Flores–Rinca–Komodo, i.e. fitting well with the ‘coral triangle’ concept.
- NMDS ordination showed the type of habitat as the most important factor in differentiation of the diatom assemblages with sediment and seaweeds as two major groups, whereas geography was not recognized as a differentiation factor of the diatom assemblages. The most sampled habitat, i.e. coral sand or more general sediment, revealed the most diverse diatom assemblages and was followed by seaweeds, in particular *Padina* sp.
- This research is thought to be the first step in exploring the bioindication potential of the marine benthic diatoms to assess the environmental health of the Indonesian coastal waters which sustain millions of inhabitants. Likewise, as the background for the planned research with use of molecular methods for recovering the molecular phylogeny of the Indonesian coral reefs habitats.

## CRedit authorship contribution statement



**Yenny Risjani:** sampling, Conceptualization, Funding acquisition, Writing – original draft. **Andrzej Witkowski:** Resources, Conceptualization, Formal analysis, Writing – original draft. **Adrian Kryk:** Data curation, Conceptualization, Methodology, Writing – original draft. **Yunianta:** Resources, Conceptualization, Writing – original draft. **Ewa Górecka:** Data curation, Methodology, Writing – original draft. **Marta Krzywda:** Data curation, Methodology, Writing – original draft. **Ikha Safitri:** Resources, Funding acquisition, Methodology, Writing – original draft. **Ajuk Sapar:** Resources, Funding acquisition, Methodology, Writing – original draft. **Przemysław Dąbek:** Resources, Methodology, Writing – original draft. **Sulastri Arsad:** Resources, Methodology, Writing – original draft. **Evgeniy Gusev:** Data curation, Resources, Methodology, Writing – original draft. **Rudiyansyah:** Resources, Funding acquisition, Methodology, Writing – original draft. **Łukasz Peszek:** Methodology, Formal analysis, Writing – original draft. **Rafał J. Wróbel:** Methodology, Formal analysis, Writing – original draft.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2021.107551>.

## Q4 Uncited References

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 The corrections made in this section will be reviewed and approved by a journal production editor. The newly added/removed references and its citations will be reordered and rearranged by the production team.

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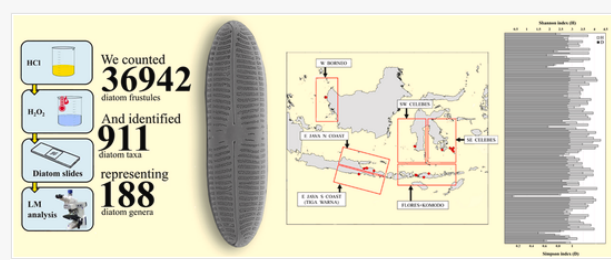
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## Graphical abstract

alt-text: Image 1



## Highlights

- The first ever research on marine benthic diatoms from Indonesian coral reefs.

- Identified were 911 diatom taxa representing 188 genera.
  - Species richness and diversity much higher than in any coral reefs studied till now.
  - Cosmopolitan taxa were dominant in terms of relative abundance.
  - Species richness was higher within tropical zonal and local taxa.
- 

## Appendix A Supplementary data

The following is the Supplementary data to this article:

 [Multimedia Component 1](#)

### Multimedia component 1

alt-text: Multimedia component 1

## Queries and Answers

Q1

**Query:** Please confirm that the provided email “andrzej.witkowski@usz.edu.pl” is the correct address for official communication, else provide an alternate e-mail address to replace the existing one, because private e-mail addresses should not be used in articles as the address for communication.

**Answer:**

Q2

**Query:** Have we correctly interpreted the following funding source(s) and country names you cited in your article: Ministry of Education and Culture, Indonesia; Ministry of Science and Higher Education, Poland?

**Answer:**

Q3

**Query:** Please provide the volume number or issue number or page range or article number for the bibliography in Ref(s). Al-Handal et al., 2016.

**Answer:** Micronesia had non-standard volume numbering by year. It has been corrected. Volume 2016, issue 3, pages 1-78.

Q4

**Query:** Uncited references: This section comprises references that occur in the reference list but not in the body of the text. Please position each reference in the text or, alternatively, delete it. Any reference not dealt with will be retained in this section. Thank you.

**Answer:** Please, add Veron et al., 2009 according to the comment in text

Q5

**Query:** Please confirm that given names and surnames have been identified correctly and are presented in the desired order and please carefully verify the spelling of all authors' names.

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**Query:** Your article is registered as a regular item and is being processed for inclusion in a regular issue of the journal. If this is NOT correct and your article belongs to a Special Issue/Collection please contact [d.ramesh@elsevier.com](mailto:d.ramesh@elsevier.com) immediately prior to returning your corrections.

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