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The diversity of molluscan faunas in marine lakes of Raja Ampat, West Papua, Indonesia

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Abstract

Marine lakes are bodies of seawater that are land-locked and maintain a subterranean connection to the surrounding sea. Here, we document the species diversity of benthic molluscs in 11 marine lakes in

* Deceased.

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Raja Ampat, West Papua, Indonesia, using the roving diving survey method. We specifically tested for relationships between species richness and lake size and the degree of connection to the surrounding sea, and tested potential environmental drivers of community structure. We recorded 73 species, belonging to the classes Gastropoda (48 species, comprising 36 genera and 25 families), Bivalvia (24 species, consisting of 17 genera and 12 families), and Polyplacophora (one species). Molluscs from marine lakes are a subset of species also occurring in coral, seagrass, mangrove, and rocky shore habitats in the open sea. We found lake communities to mostly consist of grazers and filter feeders. The number of mollusc species significantly increased with increasing connection to the surrounding sea, but not with increasing surface area, indicating that dispersal potential may be the main driving force. Furthermore, we observed no significant influence of the environment on the variation in mollusc species composition among marine lakes. Still, we observed certain species to be exclusively present in either high or low-connected lakes, indicating a potential effect of environmental filtering. Marine lakes provide a unique ecosystem for diverse mollusc assemblages and as such should be protected.

Keywords

anchialine system – biodiversity – bivalves – gastropods – marine island biogeography

Introduction

The Coral Triangle, located in the Indo-Pacific, has the highest marine biodiversity globally (Hoeksema, 2007; Asaad et al., 2018) and one of the most diverse marine animal groups in this region are molluscs (Gosliner, 2002; Wells, 2002; Wells & Kinch, 2003). Indonesia, which is part of the Coral Triangle, has a high diversity of mollusc species in coastal waters, for example in seagrass and reef flat areas in Banyuwangi, East Java with 148 species (Susintowati et al., 2019), the Tanimbar Islands, Moluccas with 152 species (Heryanto, 2018), Bunaken, North Sulawesi with 215 species (Eisenbarth et al., 2018) and Biak, Papua, with 239 species reported (Aji et al., 2018; Aji & Widyastuti, 2020). Within Indonesia, the Raja Ampat Islands of Eastern Indonesia are home to some of the highest mollusc diversity with approximately 665 species of molluscs based on rapid assessment surveys (Wells, 2002). The Raja Ampat region encompasses an area of more than 4.5 million hectares, consisting of approximately 1500 islands (Mangubhai et al., 2012; Grantham et al., 2013). Its high mollusc species richness is likely representative because of the area's ecosystem diversity, include coral reefs, seagrass beds, mangrove forests, rocky shores, soft sediment, and marine lakes (Mangubhai et al., 2012). Raja Ampat has therefore become the focus of national and global conservation efforts (Roberts et al., 2002; Asaad et al., 2018). Marine Protected Areas (MPAs) in Raja Ampat are set to protect marine ecosystems by conserving target species, as well as essential habitats (Agostini et al., 2012). Even though there have been efforts to quantify biodiversity in Raja Ampat to support conservation management strategies, peripheral systems such as marine lakes have so far been left out of surveys. The current study is the first to quantify mollusc diversity in marine lakes.

The Raja Ampat region contains an abundance of marine lakes, of which 40 have been scientifically recorded, but likely more exist (Becking et al., 2011, 2015). Marine lakes are

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anchialine systems, small bodies of landlocked seawater, maintaining marine characteristics through subterranean connections to the sea (Holthuis, 1973; Hamner & Hamner, 1998). These anchialine ecosystems can house unique and endemic species and populations (Dawson & Hamner, 2005; Becking et al., 2013; Hoeksema et al., 2015; de Leeuw et al., 2020; Maas et al., 2020). However, marine lakes in Raja Ampat are currently not explicitly included in the MPAs even though they are located in one of the MPAs in Raja Ampat region (Agostini et al., 2012; Maas et al., 2020). Marine lakes are vulnerable ecosystems that risk degradation by human activities such as tourism, aquaculture, deforestation and introduction of invasive species (Dawson et al., 2001; Patris et al., 2019; Maas et al., 2020). For example, since the discovery of marine lakes in Raja Ampat inhabited by stingless jellyfish (Becking et al., 2011, 2015), a significant increase in tourists visiting these lakes has been seen (Maas et al., 2020). The exploitation of marine lakes may have economic benefits, but may also have adverse consequences such as decline of some native species and degradation of the marine lake ecosystem (Dawson et al., 2001; Maas et al., 2020). Hence, it is important to document the diversity within marine lakes to allow adequate conservation measures to be implemented. The publication of molluscan fauna lists is one way to provide information on biodiversity for conservation purposes.

Many marine molluscs are benthic, meaning that they live in, on, or near the seabed (Bouchet et al., 2002). Benthic molluscs are diverse in the substrate they inhabit but also in their feeding types, which are related to the substrate's physical characteristics (Arruda et al., 2003). Major trophic groups of molluscs in marine coastal ecosystems can be categorized as filter feeders, consisting mostly of members of Bivalvia, and grazers, scavengers, and carnivores, predominantly represented by members of Gastropoda (Rueda et al., 2009). Trophic groups may reveal information on the species interaction and major energy pathways in the environment. Hence, the distribution of feeding types of molluscs could determine their role in the ecosystem and provide information about the condition of their ecosystem (Arruda et al., 2003). For instance, outbreaks of coralivorous molluscs of the genus *Drupella* have become notorious in the last decade that cause damage to coral (Hoeksema et al., 2013; Moerland et al., 2016). The impact of coral predators can be devastating to the health and stability of coral reefs, emphasizing the need to monitor and mitigate their effects (Scott et al., 2017). Molluscs are a prominent food source for animals at higher trophic levels (Christianen et al., 2017), and useful as biodiversity and environmental pollution indicators (Wells, 2002; Terlizzi et al., 2005; Conti et al., 2019). Because of their limited mobility and long lifespan, benthic molluscs are sensitive to local disturbances and cannot avoid deteriorating conditions within the water or sediment (Hong et al., 2020).

The species diversity within marine lakes may follow the predictions of the island biogeography theory (MacArthur & Wilson, 1967; Whittaker et al., 2017; Itescu, 2019). This theory predicts that for isolated islands, the species richness at a given point in time results from a balance of immigration and extinction rates, which in turn are influenced by the area of the island and the distance of the island to the source species pool. Therefore, we would expect more connected and larger lakes to hold a higher number of species. Lakes with a low degree of connection to the sea would have a lower immigration rate which leads to lower species richness. On the other hand, lakes with many connections have a higher chance of influx of migrants from the source species pool of the sea (Maas et al., 2018; de

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Leeuw et al., 2020). In addition, the larger the lake's area, the higher the species number because larger areas offer more space or habitat and resource availability (Whittaker et al., 2017).

The overall aim of this study was to document the species diversity and feeding types of molluscs that inhabit 11 marine lakes of Raja Ampat, West Papua, Indonesia. For this a species list and colour plates are provided for identification. We assessed whether the diversity of lake-dwelling molluscs follow the predictions of the island biogeography theory, by relating the species richness to the surface area of the lakes and to the connection to the sea. Furthermore, we determined whether the composition of species varied among the lakes and related this variation to the environmental conditions within the lakes and their degree of connectivity to the open sea.

Materials and methods

Surveys and sampling

Fieldwork was conducted from January to February 2020 in 11 marine lakes in the Misool islands, Raja Ampat region, West Papua, Indonesia (fig. 1). As there are no formal topographical names for most of the marine lakes; we followed the number codes used by de Leeuw et al. (2020) for consistency in publications. The characteristics and environmental parameters of these lakes such as lake surface area (m^2), maximum depth (m),

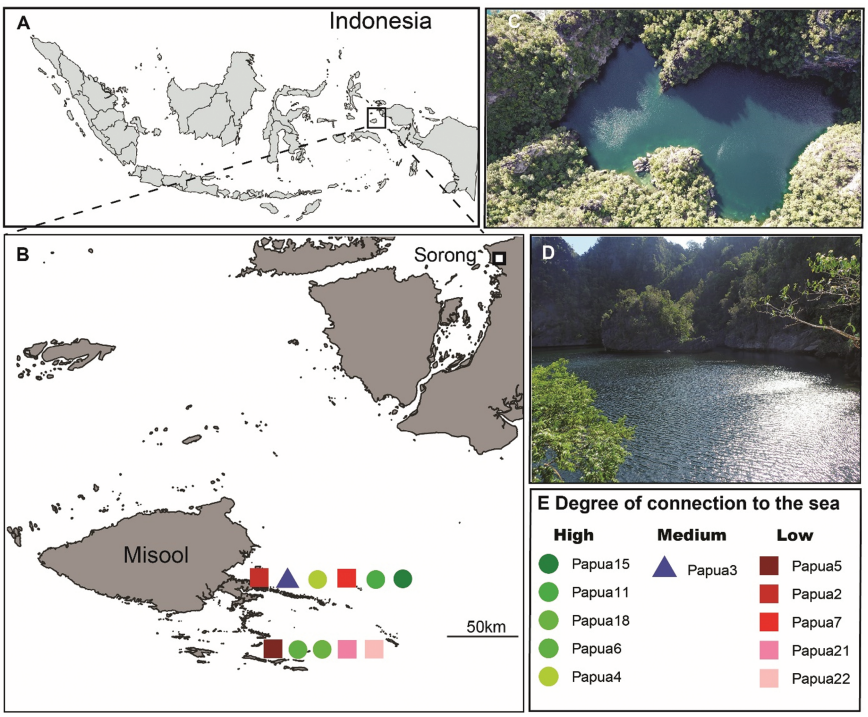

FIGURE 1 Map of sampling locations in Raja Ampat, West Papua, Indonesia. (A) Overview of Indonesia. (B) Close-up of Misool, Raja Ampat, including 11 marine lakes. (C) Aerial and (D) ground level views of a marine lake. (E) Categorization of sampling areas according to the degree of connection into three groups: High, Medium and Low. Location codes and connectivity measurements correspond with table 1.

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temperature (°C), salinity (ppt), and degree of connection to the sea (connectivity), are shown in table 1; using methods by Becking et al. (2011) and Maas et al (2018). The degree of connection to the sea was defined as a fraction resulting from dividing the maximum tidal amplitude of the lake by that of the surrounding sea, providing a theoretical minimum of 0 and maximum of 1. Additionally, the presence of mangrove, coral and seagrass within the marine lakes are also shown in table 1 as they can provide distinct microhabitats.

Occurrence data (presence/absence) of benthic molluscs species were recorded in each lake while using the roving diving survey method (Schmitt et al., 2002; Munro, 2005) performed by one person snorkeling along the perimeter of the entire lake for 8 hours (4 hours/day). Samples of each species were photographed in the field using an Olympus Tough TG-4 underwater camera. Specimens that could not be identified in the field were collected for further taxonomic identification. Voucher specimens were photographed by using a NIKON D5200 Digital SLR Camera with macro lens, and smaller sized molluscs were photographed by using an A Zeiss Stemi SV II microscope with an Olympus DP50 camera attached. Voucher specimens were deposited in *Museum Zoologicum Bogoriense* (MZB), National Research and Innovation Agency-BRIN, Indonesia. Identifications were based on the works by Abbott & Dance (2000), Dharma (2005), Huber (2010, 2015), and Okutani (2017). Additional taxonomic literature on specific gastropods families was used for specimen identification to species level: Ellobiidae (Raven & Vermeulen, 2006), Cerithiidae (Houbrick, 1992), Muricidae (Merle et al., 2011), Neritidae (Eichhorst, 2016), Potamididae (Houbrick, 1991) as well as for other families (Rudman, 1982, 1983; Gosliner, 1995; Johnson & Gosliner, 2012; Wilson & Burghardt, 2015; Krug et al., 2016; Galindo et al., 2017; Bazzicalupo et al., 2020; Papu et al., 2022). In our classification, we follow the updated taxonomy and nomenclature of MolluscaBase (Molluscabase eds, 2023).

A final species list was composed based on a combination of field pictures and collected specimens (table 2, figs A1–A11 in the Appendix). We measured the shell length (L) and height (H) of bivalves, and shell length (L) and width (W) of gastropods by using Vernier calipers. Shell measurements in mm are provided in the figure legends. We provided a short characterization and species classification for all individuals (table A1 and figs A1–A11 in the Appendix). In addition, the feeding type, and associations to specific types of coastal habitat were assigned per species based on the MolluscaBase (www.molluscabase.org) and SeaLifeBase (www.sealifebase.ca). In terms of feeding types, the following types were considered: filter feeders, grazers, carnivores, spongivores, and scavengers. The following habitats where molluscs are commonly found in coastal areas were considered: coral reefs, seagrass beds, mangroves, and rocky shores.

Data analysis

After verifying assumptions of normality, Pearson correlation (r) tests were performed between species richness and connection to the sea and surface area with R v.4.0.2. (R Core Team, 2022) and visualized with the ggplot2 package (Wickham, 2016). In addition, Pearson correlation was used to test the collinearity between the connection to the sea and the environmental variables of temperature and salinity, as well as between temperature and salinity.

Next, similarity between lakes in terms of community composition was assessed using presence/absence data of species per lake. The Jaccard index was calculated for this purpose, without any additional transformations or standardizations (Real & Vargas, 1996).

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TABLE 1 Sampling stations, environmental parameters and characteristics of 11 marine lakes in Raja Ampat, Indonesia. Number codes for marine lakes following de Leeuw et al. (2020)

Lake	Connection to the sea	Surface area (m^2)	Temperature (°C)	Salinity (ppt)	Maximum depth (m)	Mangrove presence	Coral presence	Seagrass presence
Papua15	0.9 (High)	10,300	30.6 (30.3–31.2)	30.1 (29.1–30.4)	34	Y	Y	N
Papua11	0.8 (High)	27,300	30.7 (30.1–31)	27.6 (23.4–29)	9	Y	Y	Y
Papua18	0.8 (High)	7,000	31.2 (29.9–32.6)	27.6 (22.5–29.1)	5	Y	N	N
Papua6	0.8 (High)	2,950	31.8 (30.8–32.5)	28.1 (26.7–29.1)	12	N	N	N
Papua4	0.8 (High)	13,750	31.7 (31.2–32.3)	25.7 (24.4–27.2)	20	N	N	N
Papua3	0.5(Medium)	20,800	31.9 (29.4–33.2)	25.6 (19.6–32.5)	8	Y	N	N
Papua5	0.3 (Low)	3,700	31.6 (31–32.6)	28.5 (23.9–29.4)	5	N	N	N
Papua2	0.2 (Low)	12,200	33.4 (31.6–34.7)	25 (22.2–26)	7	Y	N	N
Papua7	0.2 (Low)	9,700	34.2 (31.8–35.4)	15.5 (14.9–16.5)	8	N	N	N
Papua21	0.1 (Low)	18,950	34.4 (31.9–36.1)	23.9 (20.2–25.6)	13	Y	N	N
Papua22	0.1 (Low)	23,100	36.1 (31.3–39.5)	16.8 (11.9–20.7)	12	Y	N	N

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TABLE 2 Species list of molluscs from 11 marine lakes including feeding types and coastal habitats. Lakes are ranked from low to high connection to the surrounding sea (left to right). Codes used for mollusc feeding types: FD = Filter Feeder, G = Grazer, Ca = Carnivore, Sp = Spongivore, Sc = Scavenger. Codes for coastal habitats: C = Coral, Sg = Seagrass, Mg = Mangrove, Rs = Rocky shore

		Feeding type	Habitat	Papua22	Papua21	Papua7	Papua2	Papua5	Papua3	Papua4	Papua6	Papua18	Papua11	Papua15
BIVALVIA														
Arcidae	*Acar plicata*	FD	C, Sg, Mg							1			1	1
	Barbatia amygdalumtostum	FD	C, Sg, Mg										1	1
	Barbatia trapezina	FD	C, Sg, Mg										1	1
	Lamarcka ventricosa	FD	C, Sg, Mg										1	
Cardiidae	*Tridacna squamosa*	FD	C, Sg										1	
Carditidae	*Cardita pica*	FD	C, Sg, Mg				1							
	Cardita variegata	FD	C, Sg, Mg						1				1	1
Chamidae	*Chama limbula*	FD	C										1	1
	Chama lazarus	FD	C										1	1
Cyrenidae	*Geloina papua*	FD	Mg	1	1									
Isognomonidae	*Isognomon ephippium*	FD	Sg, Mg								1	1	1	1
	Isognomon isognomum	FD	Sg, Mg				1						1	
Lucinidae	*Ctena bella*	FD	C, Sg						1					
Mytilidae	*Brachidontes* sp.	FD	C, Sg, Mg	1	1									
	Brachidontes ustulatus	FD	C, Sg, Mg				1	1	1	1	1	1	1	1
	Brachidontes striatulus	FD	C, Sg, Mg			1								
	Septifer bilocularis	FD	C, Sg, Mg										1	1
Noetiidae	*Striarca symmetrica*	FD	C, Sg				1		1					
Ostreidae	*Alectryonella plicatula*	FD	C, Sg, Mg									1	1	
	Lopha cristagalli	FD	C										1	1

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TABLE 2 Species list of molluscs from 11 marine lakes including feeding types and coastal habitats. Lakes are ranked from low to high connection to the surrounding sea (left to right). Codes used for mollusc feeding types: fd = Filter Feeder, G = Grazer, Ca = Carnivore, Sp = Spongivore, Sc = Scavenger. Codes for coastal habitats: C = Coral, Sg = Seagrass, Mg = Mangrove, Rs = Rocky shore (*cont.*)

		Feeding type	Habitat	Papua22	Papua21	Papua7	Papua2	Papua5	Papua3	Papua4	Papua6	Papua18	Papua11	Papua15
	Saccostrea sp.	FD	Mg								1			1
	Saccostrea cucullata	FD	Mg				1				1	1	1	1
Spondylidae	*Spondylus* sp.	FD	C									1	1	1
Veneridae	*Aphrodora* sp.	FD	Sg, Mg						1					
GASTROPODA														
Aplysiidae	*Stylocheilus striatus*	Gr	C, Sg, Mg					1			1			
Cerithiidae	*Cerithium coralium*	Gr	Sg, Mg			1	1		1		1		1	1
	Cerithium zonatum	Gr	Sg, Mg								1		1	
	Clypeomorus batillariaeformis	Gr	Sg, Mg									1	1	1
Chilodontaidae	*Euchelus atratus*	Gr	C, Sg				1		1					1
Chromodorididae	*Chromodoris lineolata*	Sp	C, Sg					1						
	Hypselodoris cf. *placida*	Sp	C, Sg				1							
Colloniidae	*Neocollonia pilula*	Gr	C, Sg					1		1				
Cypraeidae	*Cypraea tigris*	Gr	C, Sg					1						
	Monetaria annulus	Gr	C, Sg, Mg					1			1	1		
	Monetaria moneta	Gr	C, Sg, Mg					1			1			
	Naria miliaris	Gr	C, Sg, Mg									1		
Ellobiidae	*Auriculastra semiplicata*	Gr	Mg									1		
	Melampus adamsianus	Gr	Mg									1		

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TABLE 2 Species list of molluscs from 11 marine lakes including feeding types and coastal habitats. Lakes are ranked from low to high connection to the surrounding sea (left to right). Codes used for mollusc feeding types: fd = Filter Feeder, G = Grazer, Ca = Carnivore, Sp = Spongivore, Sc = Scavenger. Codes for coastal habitats: C = Coral, Sg = Seagrass, Mg = Mangrove, Rs = Rocky shore (*cont.*)

		Feeding type	Habitat	Papua22	Papua21	Papua7	Papua2	Papua5	Papua3	Papua4	Papua6	Papua18	Papua11	Papua15
Siphonariidae	*Siphonaria* sp.	Gr	Rs										1	1
Tegulidae	*Rochia nilotica*	Gr	C, Sg								1			
	Tectus fenestratus	Gr	C, Sg								1			
Trochidae	*Trochus maculatus*	Gr	C, Sg						1		1		1	1
Turbinidae	*Astralium calcar*	Gr	C, Sg, Mg										1	1
Vermetidae	*Thylacodes* sp.	FD	C										1	
POLYPLACOPHORA														
Chitonidae	*Acanthopleura spinosa*	Grazer	Rs										1	1
		Total		4	4	3	11	10	14	7	16	19	32	26

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The Jaccard index was performed by pairwise comparison between all lakes. The similarity levels were calculated by dividing the size of intersection with the size of the union of the sample sets, defined as $J(L1, L2) = \frac{|L1 \cap L2|}{|L1 \cup L2|}$.

Where *L1*, *L2* are two data sets from different lakes (Jaccard 1908). Consequently, the Jaccard index can range between 0 (indicating no similarity) and 1 (indicating identical sets). To calculate the percentage of similarity, the outcome was multiplied by 100, where a Jaccard index of 0.8 would indicate 80% similarity. A Nonmetric Multidimensional Scaling (NMDS) plot was used to visualize the Jaccard index to show the variation in mollusc community among lakes, using the vegan package in R (Oksanen et al., 2019).

Finally, the contribution of abiotic parameters (temperature, salinity, connection to the surrounding sea and surface area) to the community composition was assessed using the *envfit* function in the vegan package. We used the function to fit environmental vectors and species factors on the NMDS and assessed their significance. We ran *envfit* with 999 permutations to obtain r^2 and p-values to assess significant contribution to the community composition. We plotted all environmental parameters and the significantly contributing mollusc species on the NMDS.

Results

We recorded 73 species of molluscs from 11 marine lakes (table 2). We refer to voucher specimens (MZB collection) and provide a photographic overview of the species as evidence. Furthermore, we tested the relationship between species richness and connection to the surrounding sea and surface area, and visualized the mollusc communities and their potential environmental drivers.

Observed species

The recorded species belonged to the classes Gastropoda (48 species, comprising 36 genera and 25 families), Bivalvia (24 species, comprising 17 genera and 12 families), and Polyplacophora (one species). Of the 73 recorded species, *Brachidontes ustulatus* (Bivalvia) and *Littoraria scabra* (Gastropoda) were the most common, found in eight and seven lakes respectively.

The composition of species varied among the marine lakes (table 2), with certain moluscs found in only specific categories of lakes (high, medium or low connected). High connected lakes exclusively contained 14 Bivalvia species, 25 Gastropoda species and the single Polyplacophora species. More than half of the mollusc species (53%) were therefore exclusively found in high-connected lakes. For medium connected lakes, this came down to 5.5% of the species, with 2 bivalves and 2 gastropods being found exclusively in medium connected lakes. Lastly, low connected lakes exclusively contained four species of bivalves and seven species of gastropods. The rest of the species (~27%) were found in multiple types of marine lakes. Mussels from the genus *Brachidontes* were the most common mollusc in all sampling areas (present in all 11 lakes).

All recorded mollusc species are also known from coastal areas (table 2). About 48 marine-lake species (66%) are also commonly found in mangroves, 43 (58%) in seagrass, 40 (55%) in coral reefs, and nine (12%) on rocky shores. This first inventory therefore did not record species endemic to marine lakes.

Species richness and feeding types

The highest species richness (n = 32) was found in the highly connected lake Papua 11, followed by Papua 15 (n = 26). While the lowest number of species (n = 3) was found in low-connected lake Papua 7 (fig. 2). Feeding

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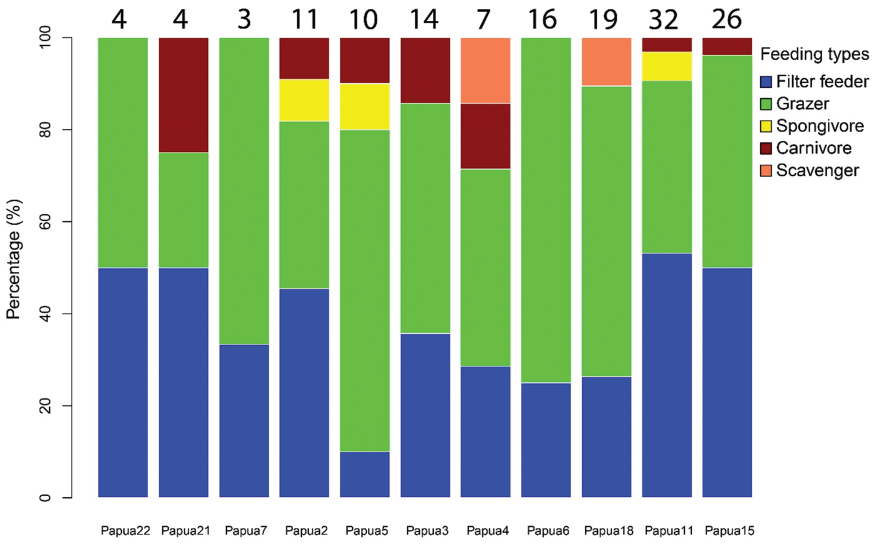

FIGURE 2 The percentage of feeding types of mollusc species from 11 lakes with the total number of species at the top of the graph. Lakes are ordered by degree of connection to the surrounding sea, ranging from low connection (left) to high connection (right).

types filter feeders and grazers were observed in all 11 marine lakes. The highest diversity of feeding types (n = 4) was found in low connected (Papua 2, Papua 5) and high connected lakes (Papua 4, Papua 11), with representatives from filter feeders, grazers, spongivores and carnivores, except for Papua 4; where the spongivore was replaced by a scavenger. The low-connected lakes Papua 22 and Papua 7; and the high-connected lake Papua 6 only harboured representatives from two feeding types, which were filter feeders and grazers. Filter feeders were mostly represented by bivalves, while most gastropods were grazers. Other gastropods were categorized into the feeding types of spongivores (Chromodorididae and Phyllidiellidae), scavengers (Nassariidae) and carnivores (Muricidae and Pisaniidae).

Drivers of species richness and community composition

Based on the Pearson correlation tests, we observed collinearity between lake connectivity and temperature ($r = -0.87$, $P < 0.001$) and salinity ($r = 0.71$, $P < 0.05$), as well as between temperature and salinity ($r = -0.86$, $P < 0.001$). Next, we investigated the relationship between species richness and composition and physical and environmental parameters. Pearson correlations showed significant correlations (fig. 3) among mollusc species richness and the connection of the marine lakes to the surrounding sea ($r = 0.78$, $P = 0.0049$) but not with the surface area of the marine lakes ($r = 0.12$, $P = 0.73$).

Non-metric Multidimensional Scaling (NMDS) ordination plot illustrates variation in composition of mollusc assemblages among the different marine lakes (fig. 4). Some clustering of lakes can be seen (high-connected lakes Papua 6 and Papua 18, and Papua 11 and Papua 15, and low-connected lakes Papua 21 and Papua 22), but most lakes appear to be distinct. The *envfit* analysis indicated that temperature ($r^2 = 0.3908$, $P = 0.142$), salinity ($r^2 = 0.4221$, $P = 0.116$), connectivity ($r^2 = 0.1908$, $P = 0.422$) and surface area ($r^2 = 0.2008$, $P = 0.408$) did not show a significant impact on the species composition among marine lakes.

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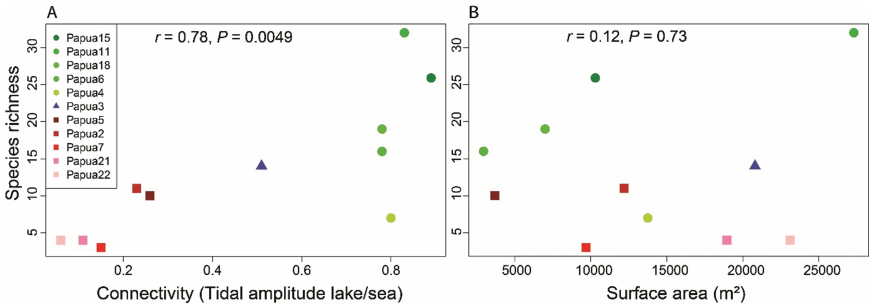

FIGURE 3 Pearson correlations among species richness of molluscs and (A) connectivity of marine lakes to the adjacent sea, and (B) surface area of marine lakes.

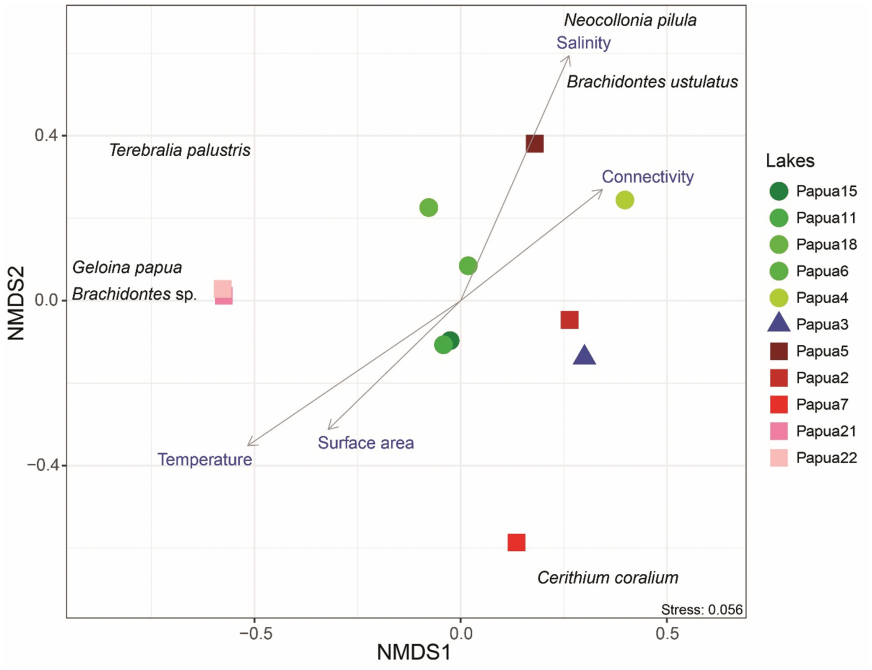

FIGURE 4 Non-metric Multidimensional Scaling (NMDS) ordination plot of mollusc assemblages from 11 marine lakes in Raja Ampat, Indonesia, based on Jaccard distances between lakes. Mollusc species that have significant influence on reshaping the species composition among marine lakes are shown *Geloina papua* (r^2 = 0.78, P = 0.02), *Brachidontes* sp. (r^2 = 0.78, P = 0.02), *Brachidontes ustulatus* (r^2 = 0.66, P = 0.018), *Cerithium coralium* (r^2 = 0.59, P = 0.017), *Neocollonia pilula* (r^2 = 0.56, P = 0.044) and *Terebralia palustris* (r^2 = 0.63, P = 0.024). The arrows represent environmental (temperature and salinity) and physical characteristics (connectivity and surface area) of the lakes.

Discussion

We conducted the first study on mollusc assemblages in marine lakes in Raja Ampat, West Papua, Indonesia and provided a species list (table 2) and field images for identification (figs A1–A11 in the Appendix). Overall, based on this inventory, the mollusc assemblages in the marine lakes contained a mixture of species that also occur in coastal coral

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reefs, seagrass beds, mangroves and rocky shores habitats. By quantifying the variation in species diversity among marine lakes and relating this variation to spatial and environmental variables, we were able to determine that the degree of connection of the marine lakes to sea positively influences the number of species in the marine lakes. The composition of mollusc faunas among marine lakes did not appear to be structured by either temperature, salinity, connectivity or surface area alone. Below, we elaborate on our findings.

Species and feeding types

The mollusc fauna of marine lakes represents a subset of species that are also known to occur in coastal areas. In our study we did not encounter any endemic species to marine lake habitats. The most common species found in all marine lakes were mussels from the genus *Brachidontes*: *Brachidontes ustulatus*, *Brachidontes* sp. and *Brachidontes striatulus*. The ability of *Brachidontes* to disperse via a planktonic phase (Safriel et al., 1980), produce byssal threads to attach to most substrates (Cheung et al., 2006), high fecundity (Morton, 1988), and their capacity to filter food under different environmental conditions (Sarà et al., 2003, 2008) could play an important role in their wide distribution among marine lakes. This genus has been found to occur extensively in Indonesian marine lakes (Tomascik & Mah, 1994; Becking et al., 2016; Maas et al., 2018; de Leeuw et al., 2020) and is widely distributed throughout the coastal ecosystems of the Indo-Pacific region (Terranova et al., 2007; Tan et al., 2021). Molecular work by de Leeuw et al. (2020) on *Brachidontes* spp. in marine lakes in Palau and Indonesia revealed that each lake contained one of six distinct genetic lineages, which could represent separate species. Within the current study in Raja Ampat, one genetic lineage inhabits lakes Papua 2-6 (de Leeuw et al., 2020), for which we have the morphological identification of *Brachidontes ustulatus*. A separate genetic lineage is present in Papua 7 (de Leeuw et al., 2020), which was morphologically identificatied as *Brachidontes striatulus* (supplementary material S1).

The second-most common species, occurring in seven out of the 11 marine lakes, was the periwinkle snail *Littoraria scabra*. These animals are mostly residing around the perimeters and mangroves of the lakes. This species disperses using planktotrophic larvae, with an estimated larval duration between three and ten weeks (Reid, 1989). *Littoraria* species have wide ranges in the Indo-Pacific and are common in estuarine ecosystems, typically being found in the intertidal zones of mudflats and rocky coasts, or on rocks and mangroves (Reid et al., 2010; Iacarella & Helmuth, 2012; Bharti & Shanker, 2021). They are the most abundant arboreal (tree-dwelling) gastropods in tropical mangrove forests (Reid, 1985; Reid et al., 2010). Many conditions in marine lakes are similar to those of estuarine ecosystems. The marine lakes where *Littoraria scabra* was found also contain mangroves.

Some species were only present in low-connected lakes with low salinity and an anoxic or hypoxic (oxygen depletion) layer at depths greater than 8 m. These species (e.g., *Geloina papua*, *Faunus ater* and *Terebralia palustris*) are also common in mangrove ecosystems where they are adapted to conditions with wide salinity fluctuations and long periods of air exposure (Morton, 1976, 1988; Fratini et al., 2008; Das et al., 2018). In addition, *Geloina* clams are known to have the ability to create chemosymbiosis with sulfide oxidizing bacteria as their symbionts. Sulfide from muddy sediment is oxidized and provides energy for the bacteria to fix CO_2 into organic compounds which then become accessible to *Geloina* (Clemente et al., 2013). These abilities may explain why *Geloina* clams are abundant

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in low-connected lakes in conditions where not many species can live.

There is an overlap in the mollusc faunas of the 11 marine lakes in comparison to previously published work on other anchialine systems. For example, bivalves (*Brachidontes* spp., oysters) and gastropods (*Drupella margariticola*, *Cerithium* spp., *Nerita* spp., *Terebralia* spp.) in marine lakes of East Kalimantan (Tomascik & Mah, 1994), West Papua (Becking et al., 2011; Maas et al., 2020), and Palau (Colin, 2009; Goto et al., 2011) have also been observed in the present study. In anchialine ecosystems in the Ha Long-Cat Ba Area in Vietnam (Nguyen Dang Ngai et al., 2015), 23 mollusc species were recorded, of which six families were not found in the current study (Buccinidae, Thiaridae, Naticidae, Pectinidae, Pteriidae and Pinnidae). In an artificial anchialine pond in northern Australia, 33 mollusc species were found, gastropods from family Cerithidae being the most abundant (Philbey & Willan, 2005). Lastly, anchialine ponds in Hawaii also contained similar species as the marine lakes in Raja Ampat (Tango et al., 2012). In terms of feeding types, the previous studies are consistent with findings of the current study, where most molluscs can be classified as grazers and filter feeders (Tomascik & Mah, 1994; Philbey & Willan, 2005; Becking et al., 2011; Tango et al., 2012; Nguyen Dang Ngai et al., 2015). Despite the variation in particular mollusc species between marine lakes in Raja Ampat and anchialine ecosystems from other locations, the overall ecological signature and diversity is similar: an abundance of primary consumers, sparse predator populations and presence of chemo-autotroph bivalves.

All of the species recorded from marine lakes (table 2) have also been reported from Indonesian reefs (Wells, 2002; Burghardt et al., 2006; van der Meij et al., 2009), seagrass beds (Arbi, 2011; Aji et al., 2018; Aji & Widyastuti, 2020), and mangrove forests (Yolanda et al., 2016; Adharyan Islamy & Hasan, 2020). Some mollusc species found in marine lakes are commonly associated with corals, such as *Tridacna squamosa* and *Drupella margariticola*. Giant clams of the genus *Tridacna* can contribute to coral reef ecosystem as food and shelter for reef organisms, and as reef builders or shapers due to their calcium carbonate production (Neo et al., 2015). The muricid snail *D. margariticola* is a coral predator, which may occur in small aggregations on its prey species (Hoeksema et al., 2013; Moerland et al., 2016). Indeed, most of the marine lakes that contained *D. margariticola* also housed stony corals. Remarkably, *D. margariticola* was also found in a low-connected lake with no coral (Papua 21). It is possible that *D. margariticola* in the low-connected lake has adapted to new habitat conditions and switched its diet, feeding on other available prey (Claremont, 2011; Claremont et al., 2011).

In addition, certain mollusc species in the marine lakes are also typically found in mangrove ecosystems. The mangrove *Bruguiera gymnorrhiza* was common in seven of the 11 marine lakes. The most common gastropod families that observed in marine lakes are also found in Indonesia mangrove forests, namely Cerithidae, Ellobiidae, Littorinidae, Muricidae, Neritidae and Potamididae (Yolanda et al., 2016; Adharyan Islamy & Hasan, 2020; Al Idrus et al., 2021). Most of these gastropods are herbivorous grazers, as mangrove ecosystems are rich in nutrients and organic matter.

Functional group complexity in marine lakes

In terms of functional groups, most of the mollusc species in marine lakes act as primary consumers that are likely preyed upon by higher-trophic-level animals such as fish and crabs. Primary consumers convert primary production into secondary production and transfer energy and nutrients up the food

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chain to their predators (Nagelkerken et al., 2020). The majority of the gastropods found in marine lakes are herbivores, followed by carnivores, spongivores and scavengers to lesser extents. The sole filter-feeding gastropod was the vermetid worm snail *Thylacodes* sp., which uses a mucus net for catching prey (Kusama et al., 2021), whereas, the feeding types of bivalves and chitons (*Acanthopleura spinosa*) are predominantly filter feeders and grazers, respectively. The potential food sources of bivalves mainly include microalgae/phytoplankton, particle-associated microorganisms such as bacteria, and a wide range of dissolved organic matter and detrital organics (Xu & Yang, 2007; Christianen et al., 2017). Chitons are grazers and feed mainly on microflora, macroalgae *Chlorophyta* and encrusting macroalgae (Chelazzi et al., 1987; Santini et al., 1991). Similarly, the most common gastropod *Littoraria scabra* is a generalist grazer that can ingest and assimilate great quantities of diverse foods such as filamentous algae, foliose macrophytes, microalgae, mangrove tissue and zooplankton (Alfaro, 2008). In addition, Van der Meij et al. (2009) found that regarding their feeding types, filter feeder bivalves can cope better with sediment stress than herbivorous grazer gastropods. Marine lakes tend to support more resources for mollusc primary consumers. The low percentage of carnivores demonstrates the low diversity of food sources for predatory molluscs. Based on our observations, the bottom soft and hard substrate of marine lakes are dominated by macroalgae (*Caulerpa, Cladophora, Halimeda, Padina*), turf algae and benthic cyanobacteria mats which are important food sources for primary consumers.

While the high-connected lakes harboured a higher number of species, the number and proportion of feeding types remained mostly similar across the marine lakes. Functional redundancy exists when multiple species share a trophic level and similar functional traits (Micheli & Halpern, 2005). While the number of feeding types remained at two or three regardless of lake type, the underlying species increased in number, potentially increasing functional redundancy and therefore ecosystem resilience in lakes with a higher connection to the sea. The redundancy hypothesis predicts that functional redundancy in species communities enhances community functional stability and thus resilience (Teichert et al., 2017). Future research on the food web structure, for example by using a stable isotope approach (Seidel et al., 2016; Nagelkerken et al., 2020), is needed to get a better insight into the relations of these mollusc species within the food webs of marine lakes.

Drivers of mollusc diversity and composition

We did not observe an accumulation of species with an increase of surface area of marine lakes. A larger lake area would theoretically provide a more heterogeneous habitat for species to live in, reducing competition for space and food resources, resulting in a higher diversity (Seehausen, 2006). The lack of a positive correlation between lake size and species richness could be explained by the limited size of the 11 marine lakes, ranging from 2,950 to 27,300 m^2, with an average size of 13,613 m^2. In a study on African cichlid fish species diversity found that the number of species does not correlate with lake area if the area is under 1,000 km^2 (Wagner et al., 2014). Thus, the marine lakes of Raja Ampat are perhaps too small to have a distinct effect on the number of mollusc species.

In contrast, the observed species richness in the marine lakes was strongly and positively related to the degree of connection to the surrounding sea, which is the main source of species pools. The degree of connection to the open sea may facilitate the influx of

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propagules from the local species pool. The life stages of many of the mollusc species include a pelagic phase, in the form of veliger larvae that may be dispersed considerable distances before settlement and metamorphosis (Lopez, 1988). Hence, larvae of some species can survive in the plankton for long periods of time and could enter the marine lake through subterranean tunnels and fissures, transported by tidal currents. High-connected lakes likely have shorter, wider channels resulting in higher expected species immigration than low-connected lakes, which usually have smaller fissures. Rapacciuolo et al. (2019) explored the diversity patterns of microbial and macro-invertebrate communities in marine lakes of Palau. The researchers aimed to infer potential responses and feedbacks between biotic and abiotic components of these ecosystems. The study revealed that lake isolation had a negative correlation with the alpha-diversity of macro-invertebrates in marine lakes. This finding suggests that dispersal limitation could be a contributing factor to this phenomenon.

While connection has clear implications for the permeability of lakes by species' propagules, the environmental conditions of the new habitat could then influence their survival (Belyea & Lancaster, 1999). As we observed a correlation between these environmental parameters and connectivity, it is difficult to determine which one affects species diversity. Local environments varied widely between highly and lowly connected lakes. The environments of low-connected lakes were found to be dissimilar from coastal lagoons, which may result in an additional filter for species richness. In coastal areas, environment and habitat changes affect benthic molluscs in the substrate or sediment (van der Meij et al., 2009). While, gastropods and bivalves typically tolerate a wide range of salinity and temperature (Mcmahon, 1990; Huhn, 2016; Astudillo et al., 2017; Vinagre et al., 2019), local environments represented by lowly connected lakes in this study may limit establishment success of certain mollusc species, explaining the lower species richness.

Similar to species richness (alpha-diversity), the composition of species assemblages (beta-diversity) also varied strongly among the marine lakes. However, though there appeared to be a 'lake-effect', we did not detect a significant influence of potential predictors of mollusc community composition. This is in contrast to other studies. For example, temperature and salinity were found to be the major environmental factors restricting mollusc species distribution in mangrove areas (Ashton et al., 2003; Satheeshkumar & Khan, 2012). Furthermore, Rapacciuolo et al. (2019) found that environmental constraints (including connection to the sea) explained around 50% of dissimilarity among macro-invertebrate communities in marine lakes in Palau. That we did not observe a clear effect of environment on mollusc communities could be due to that the process of chance entering the marine lakes randomizes the species composition to such an extent that it simply outweighs the effects of environmental constraints (de Leeuw et al., 2020). Another explanation could be that in our analyses, more weight was put on species presence than species absence. This is mostly done to avoid creating artefacts because the species was accidentally missed in the sampling effort. Our employment of the roving diving technique may have its limitations. We may have missed nocturnal species or infaunal or cryptic mollusc species that are mostly buried in the sediment (Bouchet et al., 2002; Rueda et al., 2009) or in limestone rock (Kleemann, 1984). A subsequent study could include sediment grabs to capture the diversity of the infaunal, cryptic, and micro-molluscs from the marine lakes.

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Conclusions

We observed a significant positive correlation between species richness and the degree of connection of the marine lakes. This suggests that dispersal limitation plays an important role in determining the number of species in the lakes. Variation in species composition among the marine lake assemblages was high, however none of our recorded variables (temperature, salinity, connection, surface area) significantly explained the variation. The results of this study show that marine lakes are important ecosystems for molluscs, as marine lakes can harbor extensive mollusc communities. The information will be useful for future studies and could set the stage for more projects to survey other yet unstudied lakes. This study emphasizes the importance of conservation and preservation of marine lakes for the health of mollusc populations, and possibly as a refuge.

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Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.22726250

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Appendix

TABLE A1 Species list from marine lakes of Raja Ampat, along with their corresponding figure, voucher number (MZB), examined material, and reference. Each voucher number represents one specimen

Species	Figure	Examined material	Reference
Acar plicata (Dillwyn, 1817)	Fig. A1A–B	MZB.Pel.2217	Huber, 2010: 130
Barbatia amygdalumtostum (Röding, 1798)	Fig. A1C–D	MZB.Pel.2218	Dharma, 2005: 242, pl. 96 fig. 3
Barbatia trapezina (Lamarck, 1819)	Fig. A1E–F	MZB.Pel.2219	Dharma, 2005: 242, pl. 96 fig. 5
Lamarcka ventricosa (Lamarck, 1818)	Fig. A1G–H	MZB.Pel.2220	Dharma, 2005: 242, pl. 96 fig. 2
Striarca symmetrica (Reeve, 1844)	Fig. A1I–J	MZB.Pel.2239	Huber, 2010: 147
Tridacna squamosa Lamarck, 1819	Fig. A2A–B	–	Huber, 2010: 311
Cardita pica Reeve, 1843	Fig. A2C–D	MZB.Pel.2221	Huber, 2010: 250
Cardita variegata Bruguière, 1792	Fig. A2E–G	MZB.Pel.2222 MZB.Pel.2223	Huber, 2010: 250
Ctena bella (Conrad, 1837)	Fig. A2H–J	MZB.Pel.2227	Huber, 2015: 87
Brachidontes striatulus (Hanley, 1843)	Fig. A2K–M	MZB.Pel.2228	Tan et al., 2021: 77–115, fig. 2.
Brachidontes sp.	Fig. A3A–F	MZB.Pel.2229	Tan et al., 2021: 77–115
Brachidontes ustulatus (Lamarck, 1819)	Fig. A3G–L	MZB.Pel.2230 MZB.Pel.2231 MZB.Pel.2232 MZB.Pel.2233	Huber, 2010: 118, 550
Septifer bilocularis (Linnaeus, 1758)	Fig. A3M–O	MZB.Pel.2237 MZB.Pel.2238	Huber, 2010: 115
Alectryonella plicatula (Gmelin, 1791)	Fig. A4A–B	MZB.Pel.2240	Huber, 2010: 183
Lopha cristagalli (Linnaeus, 1758)	Fig. A4C	–	Huber, 2010: 182
Saccostrea sp.	Fig. A4D	–	Lam & Morton, 2006
Saccostrea cucullata (von Born, 1778)	Fig. A4E	–	Lam & Morton, 2006: fig. 1
Isognomon ephippium (Linnaeus, 1758)	Fig. A4F–G	–	Huber, 2010: 176
Isognomon isognomum (Linnaeus, 1758)	Fig. A4H	–	Huber, 2010: 175
Spondylus sp.	Fig. A5A	–	Huber, 2010
Chama lazarus Linnaeus, 1758	Fig. A5B	–	Huber, 2010: 281
Chama limbula Lamarck, 1819	Fig. A5C–D	MZB.Pel.2224	Huber, 2010: 283

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TABLE A1 Species list from marine lakes of Raja Ampat, along with their corresponding figure, voucher number (MZB), examined material, and reference. Each voucher number represents one specimen (*cont.*)

Species	Figure	Examined material	Reference
Geloina papua (Lesson, 1831)	Fig. A5E–F	MZB.Pel.2225	Huber, 2015: 803–804
Aphrodora sp.	Fig. A5G	MZB.Pel.2241	Huber, 2010: 396
Cerithium coralium Kiener, 1841	Fig. A6A–E	MZB.Gst.23488 MZB. Gst.23489 MZB.Gst.23490	Houbrick, 1992: 61–68, figs. 37–41
Cerithium zonatum (W. Wood, 1828)	Fig. A6G–H	MZB.Gst.23493 MZB. Gst.23494	Houbrick, 1992: 193–200, figs. 141–145
Clypeomorus batillariae-formis Habe & Kosuge, 1966	Fig. A6F	MZB.Gst.23491 MZB. Gst.23492	Houbrick, 1985: 19, figs 6
Faunus ater (Linnaeus, 1758)	Fig. A7A–B	MZB.Gst.23527 MZB. Gst.23528	Dharma, 2005: 70, pl.20 fig. 13a, b
Terebralia palustris (Linnaeus, 1767)	Fig. A7C–D	MZB.Gst.23533 MZB. Gst.23534	Houbrick, R. S., 1991: 305–313, figs. 7–9.
Terebralia sulcata (Born, 1778)	Fig. A7E–F	MZB.Gst.23535 MZB. Gst.23536	Houbrick, R. S., 1991: 318–331, figs 14–21.
Cypraea tigris Linnaeus, 1758	Fig. A7G	–	Dharma, 2005: 178, pl.64 fig.1
Monetaria annulus (Linnaeus, 1758)	Fig. A7H	–	Dharma, 2005: 188, pl. 69 fig. 9
Monetaria moneta (Linnaeus, 1758)	Fig. A8A–B	MZB.Gst.23499	Dharma, 2005: 188, pl. 69 fig. 7
Naria miliaris (Gmelin, 1791)	Fig. A8C–D	–	Dharma, 2005: 186, pl. 68 fig. 15
Littoraria scabra (Linnaeus, 1758)	Fig. A8E–F	MZB.Gst.23501 MZB. Gst.23502 MZB.Gst.23503	Okutani, 2017: 802, pl. 69 fig. 3
Thylacodes sp.	Fig. A8G	–	–
Nassarius graphit-erus (Hombron & Jacquinot, 1848)	Fig. A8H	–	Dharma, 2005: 106, pl. 28 fig. 7a, b
Nassarius olivaceus (Bruguière, 1789)	Fig. A8I	–	Dharma, 2005: 106, plate 28, fig. 20a, b
Reticunassa cf. *paupera* (A. Gould, 1850)	Fig. A8J–K	MZB.Gst.23518	Galindo L.A et al., 2017: fig.2 I–L
Pollia undosa (Linnaeus, 1758)	Fig. A8L–M	MZB.Gst.23531 MZB. Gst.23532	Dharma, 2005: 100, pl. 25 fig. 22
Pollia fumosa (Dillwyn, 1817)	Fig. A8N–O	MZB.Gst.23529 MZB. Gst.23530	Dharma, 2005: 100, pl. 25 fig. 20
Chicoreus strigatus (Reeve, 1849)	Fig. A9A–B	MZB.Gst.23513 MZB. Gst.23514	Merle, et al., 2011: pl 59

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TABLE A1 Species list from marine lakes of Raja Ampat, along with their corresponding figure, voucher number (MZB), examined material, and reference. Each voucher number represents one specimen (*cont.*)

Species	Figure	Examined material	Reference
Drupella margariticola (Broderip, 1833)	Fig. A9C–F	MZB.Gst.23515 MZB. Gst.23516 MZB.Gst.23517	Dharma, 2005: 170, pl. 60 fig. 4
Stylocheilus striatus (Quoy & Gaimard, 1832)	Fig. A9G	–	Bazzicalupo et al., 2020: 552, fig.9A–B, 10, 11
Diniatys cf. *monodonta* (A. Adams, 1850)	Fig. A9H	MZB.Gst.23509	Hori (in Okutani), 2017: 1095, pl. 394 fig.7
Auriculastra semiplicata (H. & A. Adams, 1854)	Fig. A9I–J	MZB.Gst.23500	Raven & Vermeulen, 2007: 35, pl. 1 figs 6–7.
Melampus adamsianus L. Pfeiffer, 1855	Fig. A9K	MZB.Gst.23501	Raven & Vermeulen, 2007: 44, pl. 3 figs 21–23.
Melampus fasciatus (Deshayes, 1830)	Fig. A9L–M	MZB.Gst.23502	Raven & Vermeulen, 2007: 44, pl. 3 figs 24–26.
Melampus sculptus L. Pfeiffer, 1859	Fig. A9N	MZB.Gst.23503	Kurzumi (in Okutani), 2017: 1129, pl. 428 fig. 5
Melampus sp.	Fig. A9O	MZB.Gst.23504	Raven & Vermeulen, 2007: 44
Pythia pantherina (A. Adams, 1851)	Fig. A9P–Q	MZB.Gst.23505	Raven & Vermeulen, 2007: 55, pl. 6 figs 50–56.
Pteraeolidia semperi (Bergh, 1870)	Fig. A10A	–	Wilson & Burhardt, 2015: 123, figs 3A–C, 4A,C,E, 5A,C,E
Chromodoris lineolata (van Hasselt, 1824)	Fig. A10B	–	Rudman, 1982
Hypselodoris cf. *placida* (Baba, 1949)	Fig. A10C	–	Rudman, 1983
Phyllidiella nigra (van Hasselt, 1824)	Fig. A10D	–	Papu et al., 2022: 609, fig.9.3 a–f
Elysia marginata (Pease, 1871)	Fig. A10E	–	Krug et al., 2016: 18, fig.5
Elysia sp.	Fig. A10F	–	Krug et al., 2016: 18
Thuridilla gracilis (Risbec, 1928)	Fig. A10G	–	http://www.seaslugforum.net/find/thurgrac
Siphonaria sp.	Fig. A10H	–	Abbot & Dance, 2000: p. 281

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TABLE A1 Species list from marine lakes of Raja Ampat, along with their corresponding figure, voucher number (MZB), examined material, and reference. Each voucher number represents one specimen (*cont.*)

Species	Figure	Examined material	Reference
Nerita undata Linnaeus, 1758	Fig. A10I–J	MZB.Gst.23519 MZB. Gst.23520	Eichhorst, 2016: p. 584, pl. 184
Nerita striata Burrow, 1815	Fig. A10K–L	MZB.Gst.23521 MZB.Gst.23522	Eichhorst, 2016: p. 572, pl. 176
Nerita winteri Philippi, 1844	Fig. A10M–N	MZB.Gst.23523 MZB. Gst.23524	Eichhorst, 2016: p. 471, pl. 120
Neritodryas dubia (Gmelin, 1791)	Fig. A10O–P	MZB.Gst.23525 MZB. Gst.23526	Dharma, 2005: 70, pl.10 fig. 9
Eoacmaea sp.	Fig. A10Q	MZB.Gst.23506	Okutani, 2017: 744, pl. 16 fig. 9
Diodora mus Reeve, 1850	Fig. A10R–S	MZB.Gst.23507	Okutani, 2017: 779, pl. 48 fig. 9
Diodora sp.	Fig. A11A–B	MZB.Gst.23508	Okutani, 2017: 779, pl. 48 fig. 9
Euchelus atratus (Gmelin, 1791)	Fig. A11C–D	MZB.Gst.23495 MZB. Gst.23496	Okutani, 2017: 768, pl. 38 fig. 10
Neocollonia pilula (Dunker, 1860)	Fig. A11E–F	MZB.Gst.23497 MZB. Gst.23498	Okutani, 2017: 746, pl. 19 fig. 4
Rochia nilotica (Linnaeus, 1767)	Fig. A11G	–	Dharma, 2005: 64, pl. 7 fig. 1a, b
Tectus fenestratus (Gmelin, 1791)	Fig. A11H	MZB.Gst.23529	Dharma, 2005: 64, pl. 7 fig. 11
Trochus maculatus Linnaeus, 1758	Fig. A11I–J	MZB.Gst.23538	Okutani, 2017: 747, pl. 19 fig. 9
Astralium calcar (Linnaeus, 1758)	Fig. A11K–L	MZB.Gst.23540	Hinton, 1972: 2, pl. 1 fig. 16
Acanthopleura spinosa (Bruguière, 1792)	Fig. A11M	–	Dharma, 2005: 54, pl. 2 fig. 6

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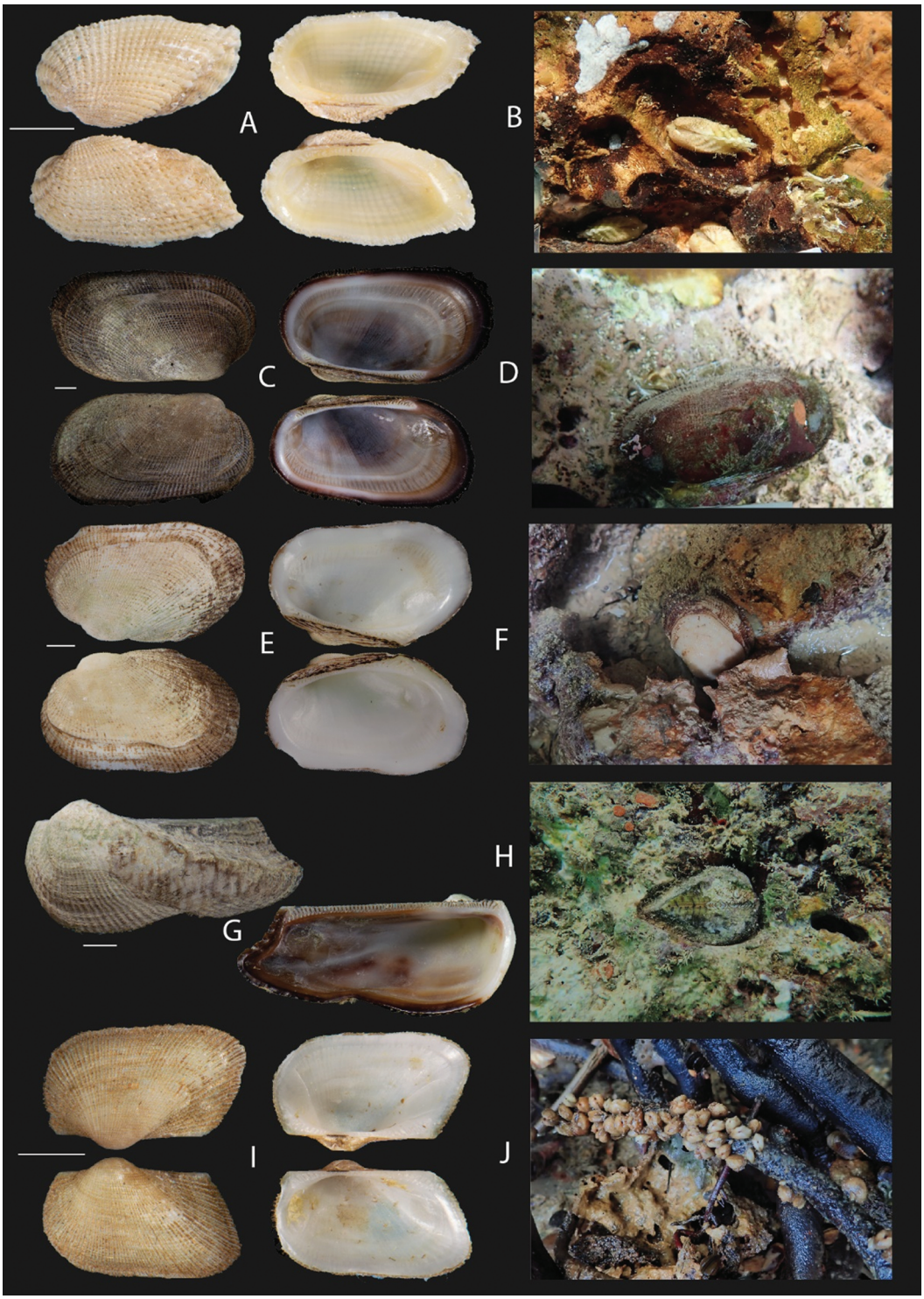

FIGURE A1 A–B. *Acar plicata* (L = 16.1 mm; H = 8.4 mm), C–D. *Barbatia amygdalumtostum* (L = 48.8 mm, H = 26.6 mm), E–F. *Barbatia trapezina* (L = 35.1 mm; H = 21.9 mm), G–H. *Lamarcka ventricosa* (L = 39.6 mm, H = 17.6 mm), I–J. *Striarca symmetrica* (L = 15 mm; H = 11 mm). Scale bars: 5 mm.

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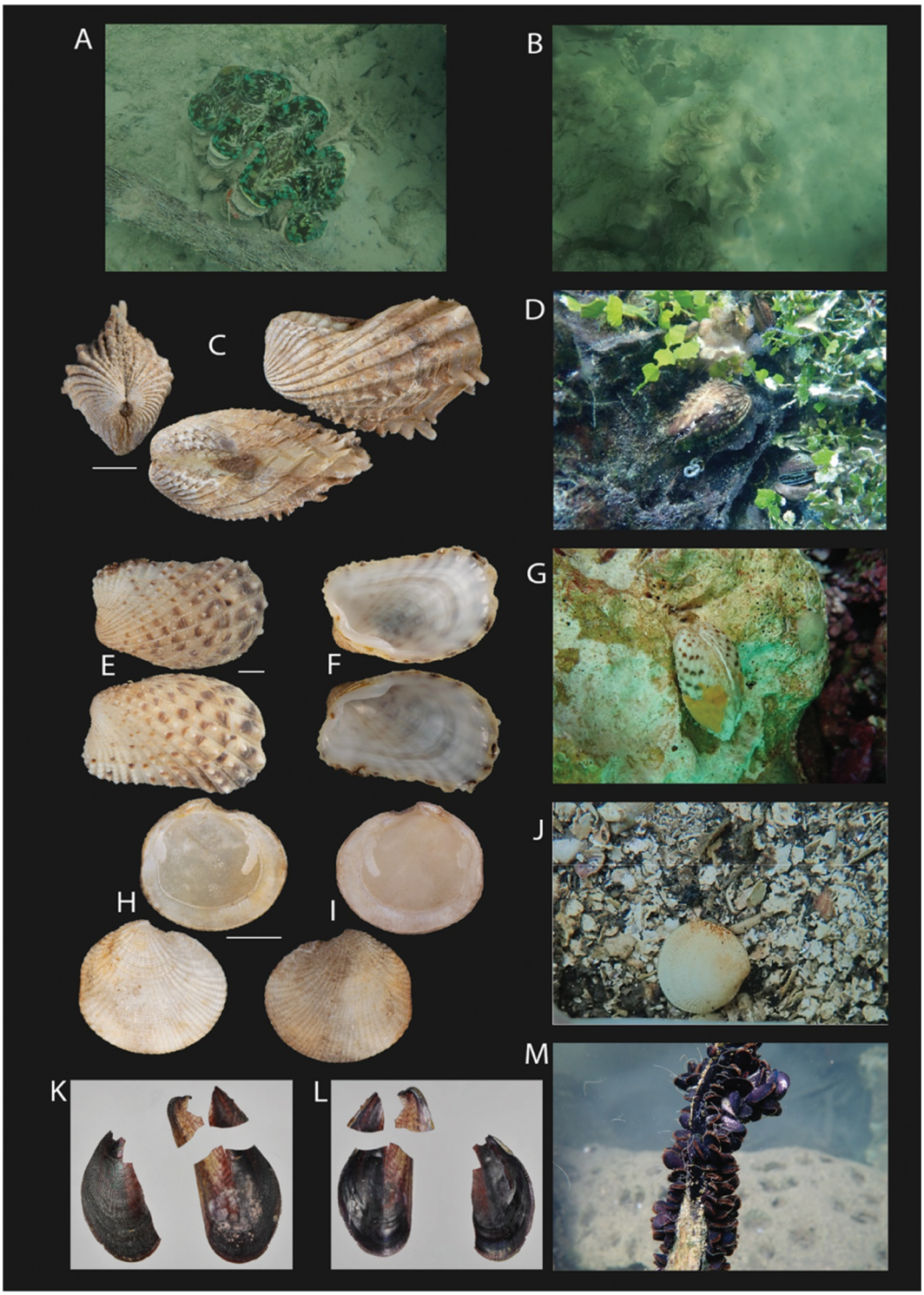

FIGURE A2 A–B. *Tridacna squamosa*, C–D. *Cardita pica* (L = 25 mm, H = 8.1 mm), E–G. *Cardita variegata* (L = 33.4 mm, H = 14.5 mm), H-J. *Ctena bella* (L = 13.4 mm, H = 12 mm), K–M. *Brachidontes striatulus*. Scale bars: 5 mm.

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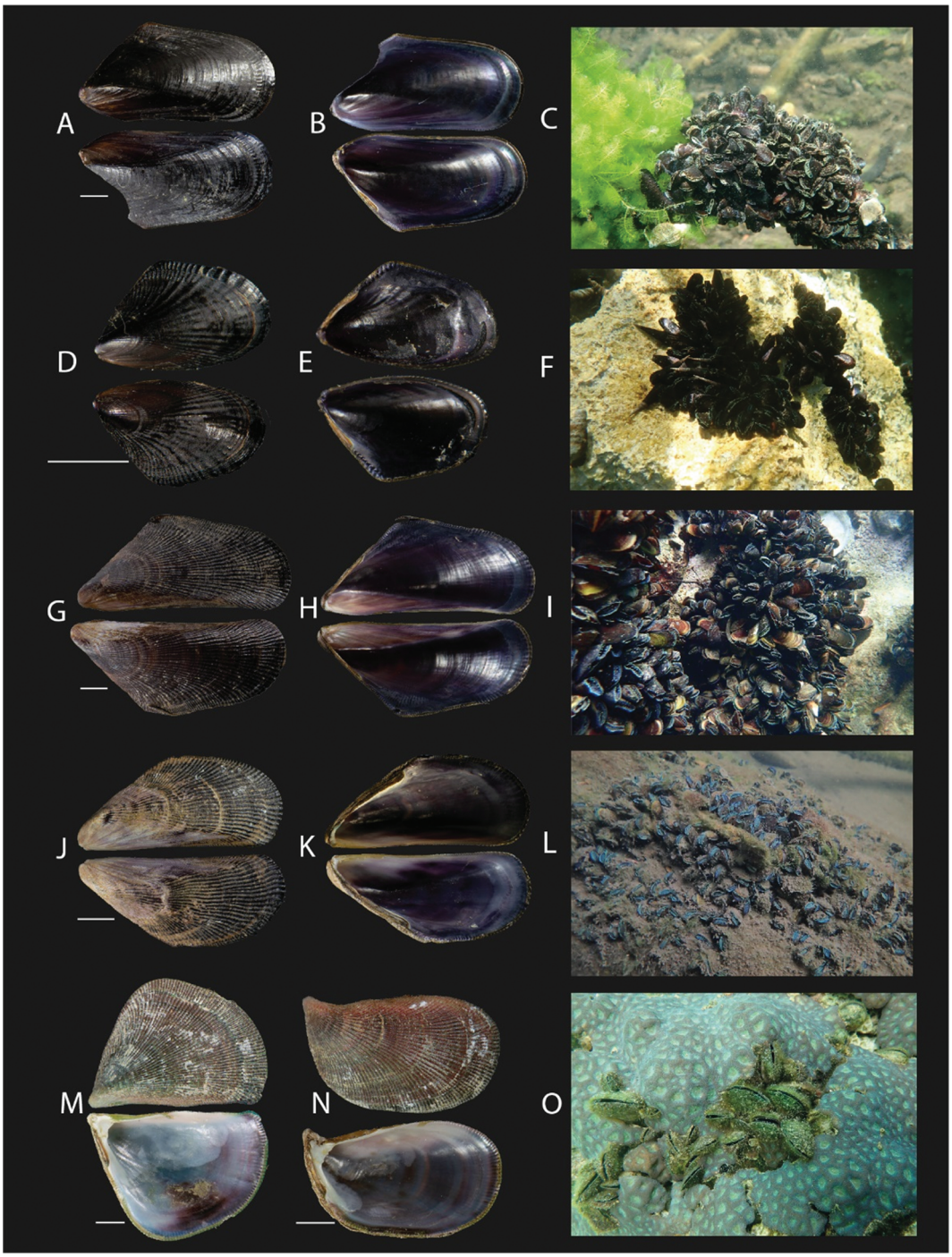

FIGURE A3 A–C. *Brachidontes* sp. (L = 35.3 mm; H = 17.7 mm) from Papua 21, D–F. *Brachidontes* sp. (L = 10.6 mm; H = 6.6 mm) from Papua 22, G–I. *Brachidontes ustulatus* (L= 40 mm; H = 17.3 mm) from Papua6, J–L. *Brachidontes ustulatus* (L = 28.4 mm; H = 12.5 mm) from Papua 18, M. *Septifer bilocularis* (L = 31.9 mm; H = 18.9 mm) from Papua11, N–O. *Septifer bilocularis* (L = 26.6 mm, W = 23.2 mm) from Papua15. Scale bars: 5 mm.

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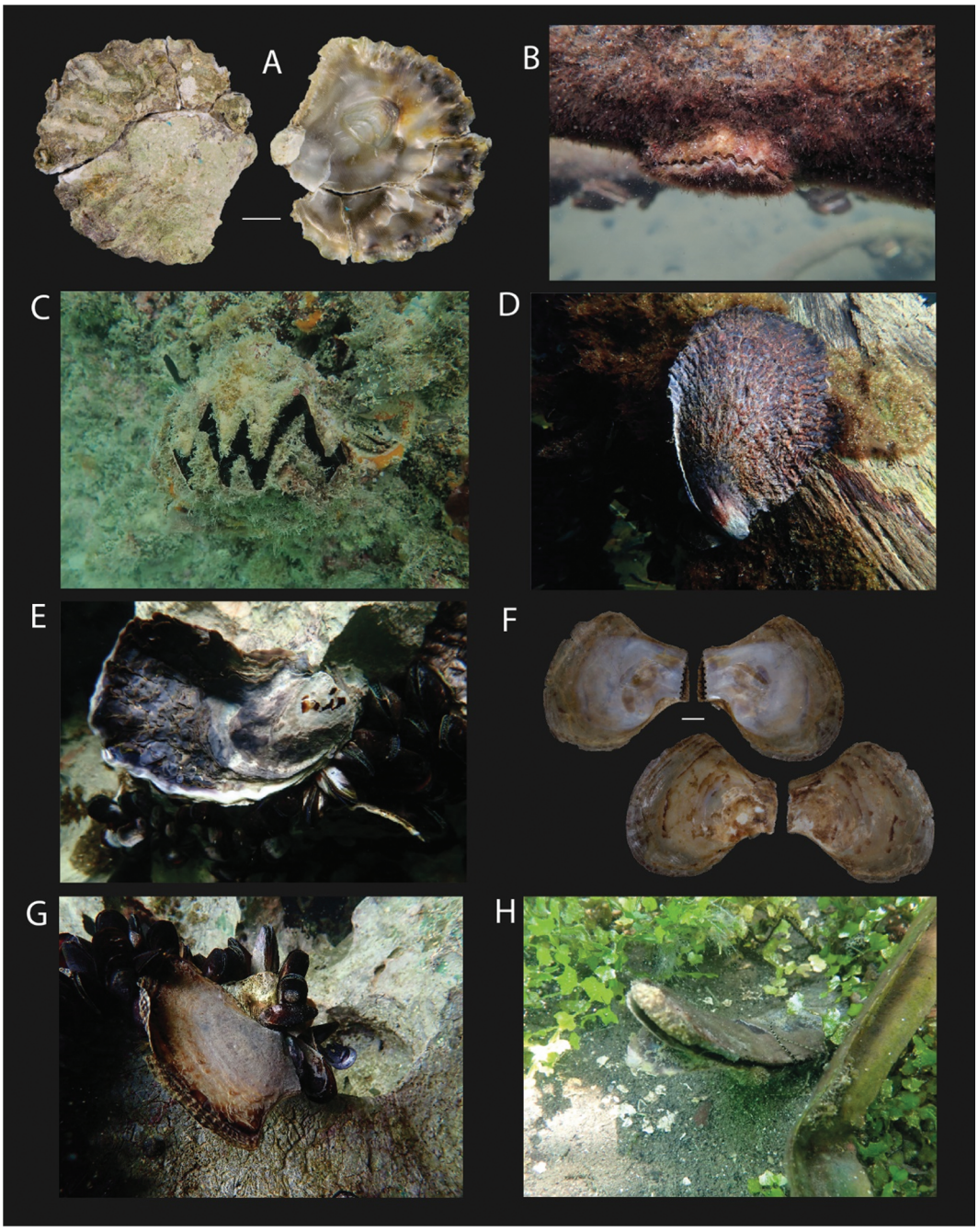

FIGURE A4 A–B. *Alectryonella plicatula* (L = 58.2 mm, H = 56.6 mm), C. *Lopha cristagalli,* D. *Saccostrea* sp., E. *Saccostrea cucullata*, F–G. *Isognomon ephippium* (L = 65 mm, H = 64 mm), H. *Isognomon isognomum.* Scale bars: 10 mm.

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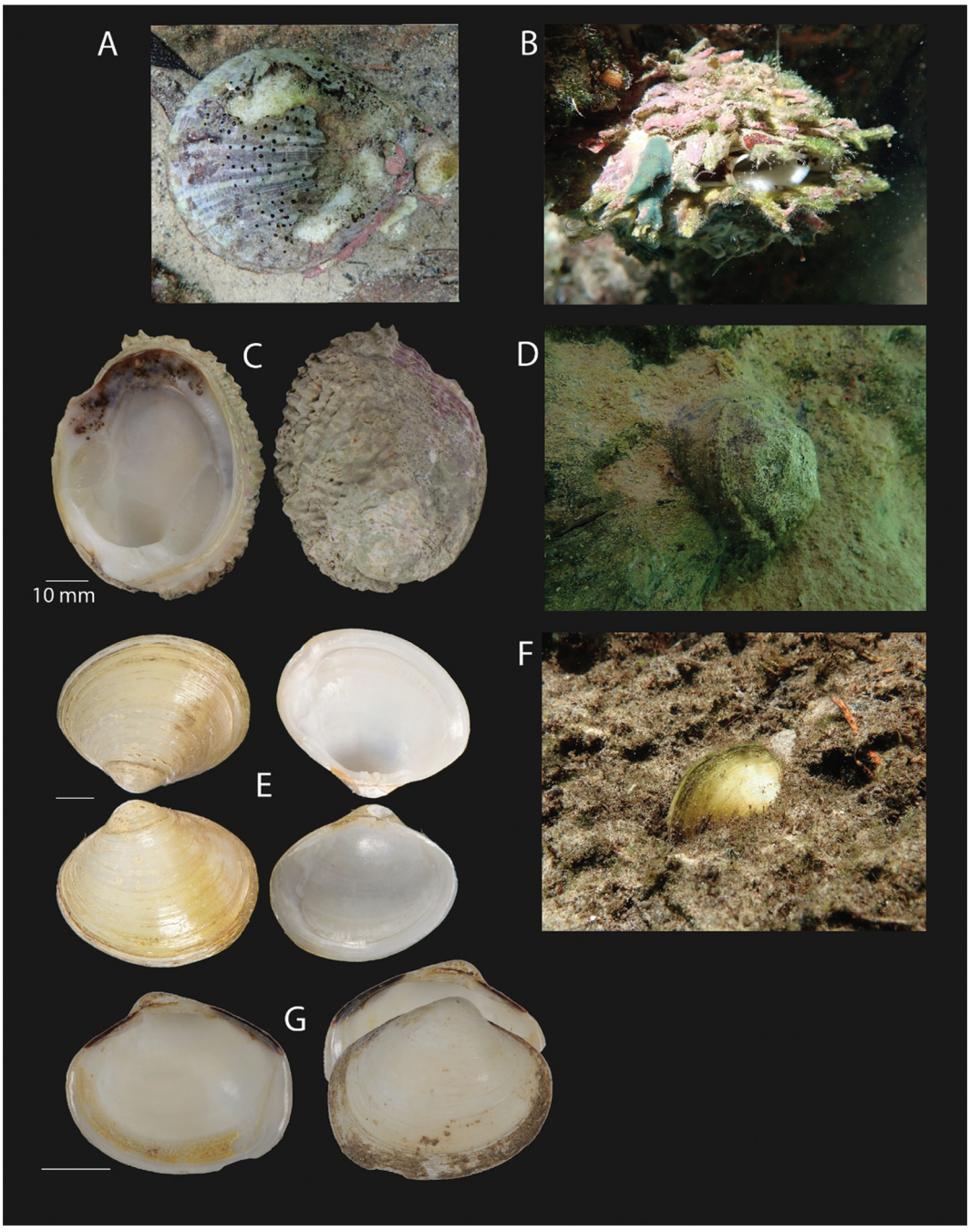

FIGURE A5 A. *Spondylus* sp., B. *Chama Lazarus*, C–D. *Chama limbula* (L = 62.8 mm, H = 49.8 mm), E-F. *Geloina papua,* juvenile (L = 26.6 mm, H = 41.4 mm), G. *Aphrodora* sp. (L = 16.4 mm, H = 1.3 mm). Scale bars: 5 mm, unless stated otherwise.

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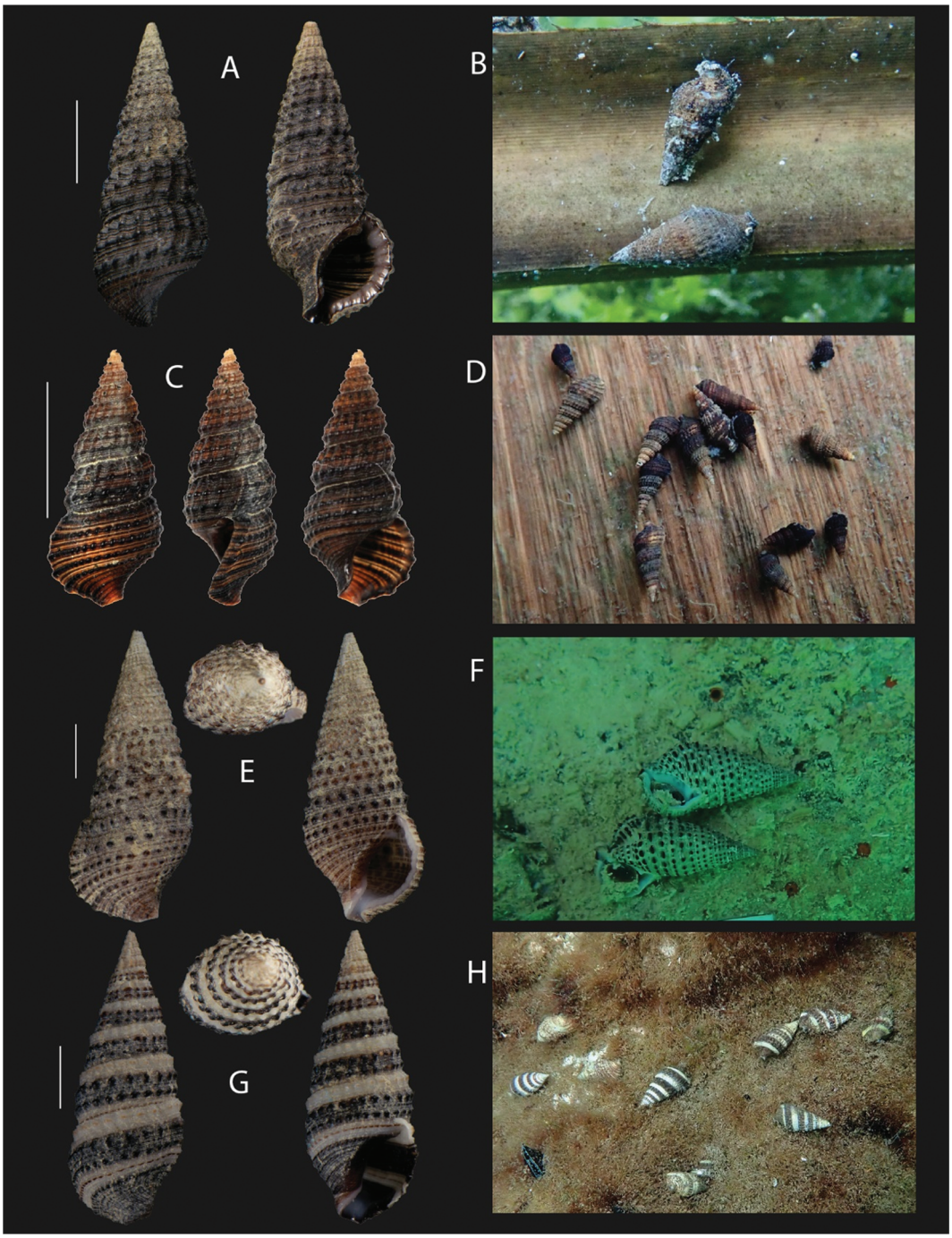

FIGURE A6 A–B. *Cerithium coralium* (L = 18.5 mm, W = 6.64 mm) from medium connected lake Papua 3, C–D. *Cerithium coralium* dwarf form (L = 9.5 mm, W = 4.4 mm) from low connected lake Papua 7, E. *Cerithium coralium* (L = 27 mm, W = 11.3 mm) from high connected lake Papua 11, F. *Clypeomorus batillariaeformis*, G–H. *Cerithium zonatum* (L = 23.5 mm, W = 9.5 mm). Scale bars: 5 mm.

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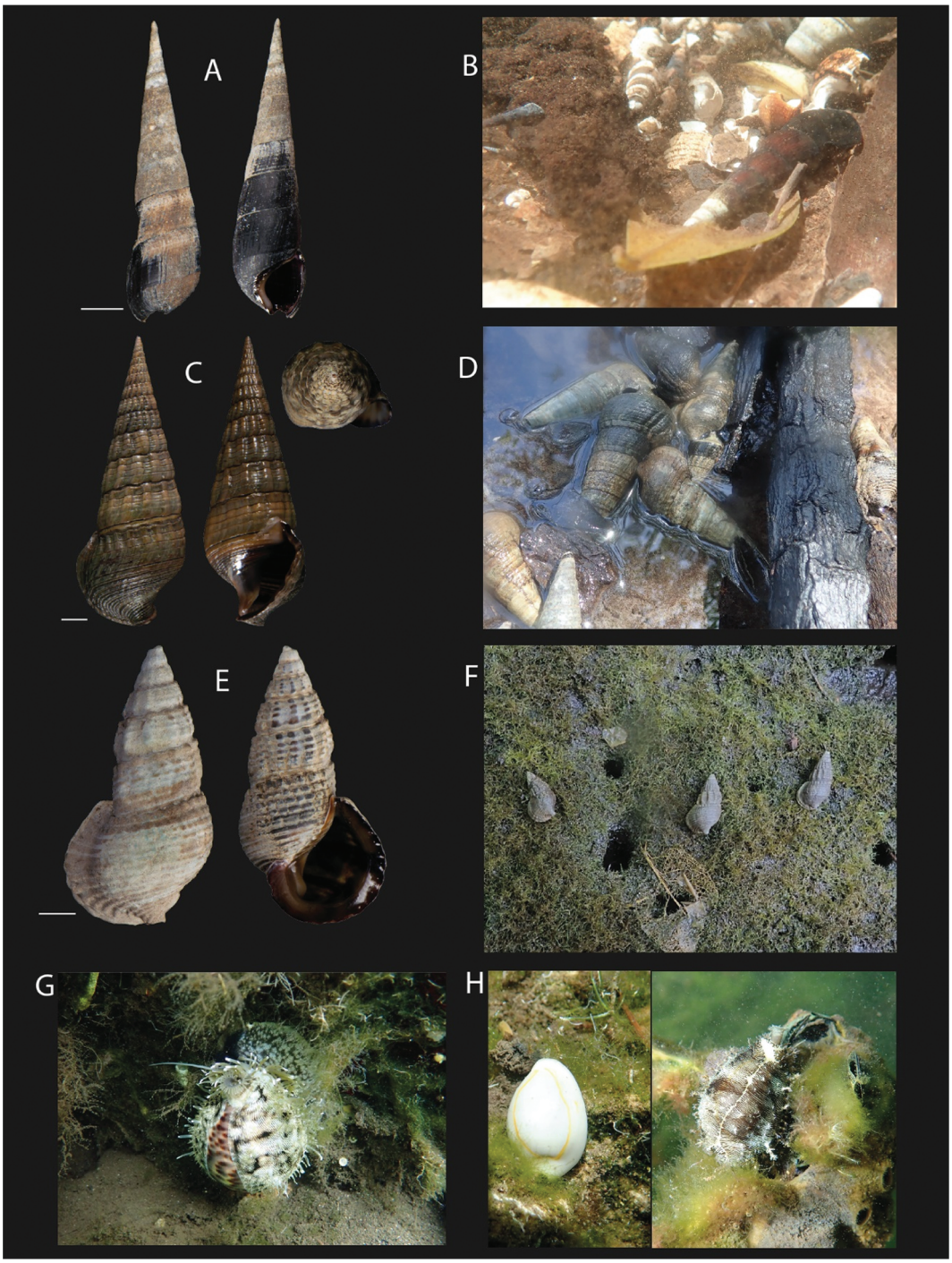

FIGURE A7 A–B. *Faunus ater* (L = 35.8 mm, W = 8.7 mm), C–D. *Terebralia palustris* (L = 56.1 mm, W = 22.5 mm), E–F. *Terebralia sulcata* (L = 37.8 mm, W = 19.7 mm), G. *Cypraea tigris*, H. *Monetaria annulus*. Scale bars: 5 mm.

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FIGURE A8 A–B. *Monetaria moneta* (L = 28.9 mm, W = 19.8 mm), C–D. *Naria miliaris*, E–F. *Littoraria scabra* (L = 13 mm, W = 7.4 mm), G. *Thylacodes* sp., H. *Nassarius graphiterus*, I. *Nassarius olivaceus*, J–K. *Reticunassa* cf. *paupera* (L = 7.1 mm, W = 3.8 mm), L–M. *Pollia undosa* (L = 23.9 mm, W = 12.8 mm), N–O. *Pollia fumosa* (L = 19.1 mm, W = 11 mm). Scale bars: 5 mm.

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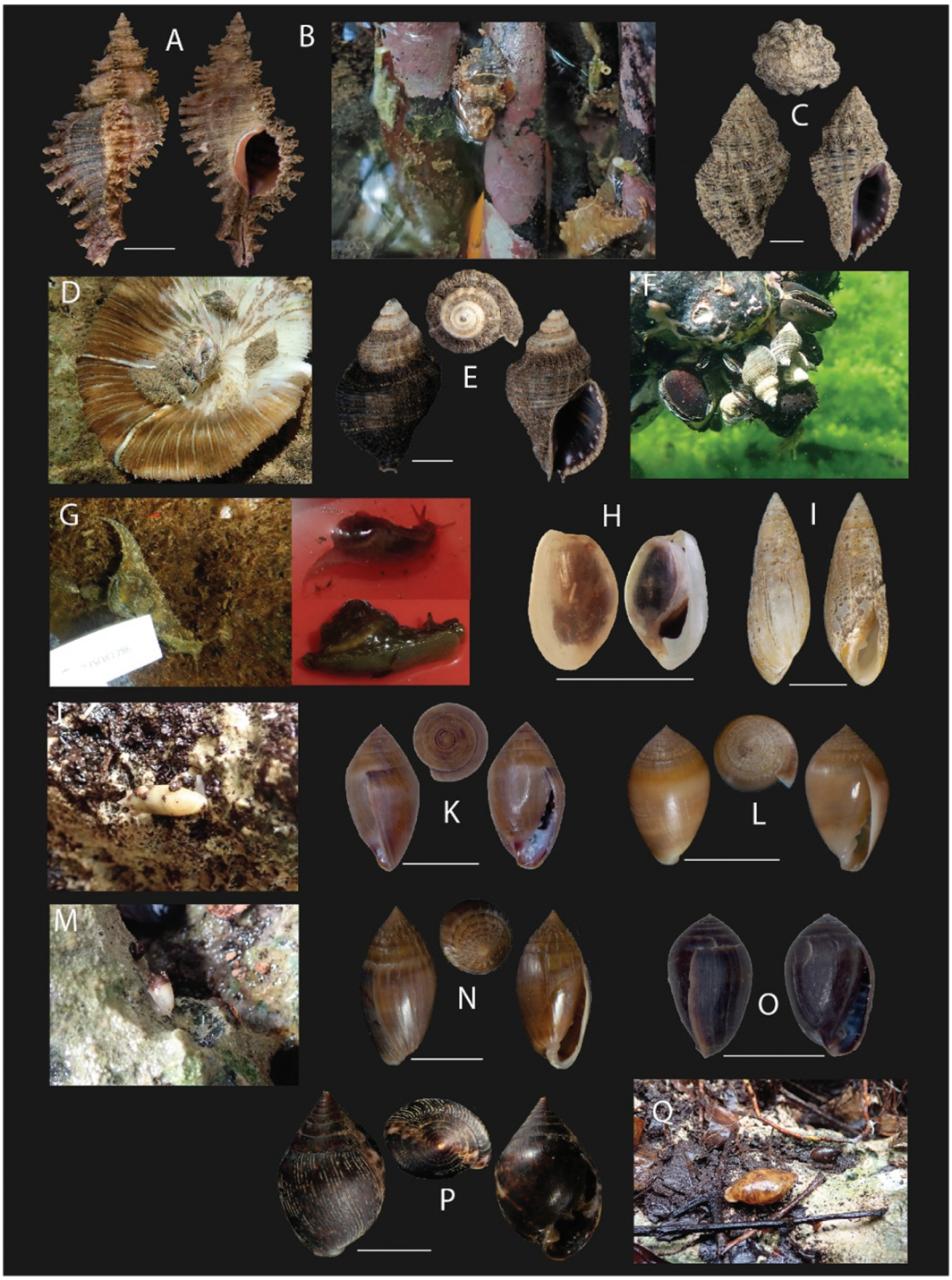

FIGURE A9 A–B. *Chicoreus strigatus* (L = 25.2 mm, W = 12.1 mm), C–D. *Drupella margariticola* (L = 26.4 mm, W = 13 mm) from Papua 11 and Papua 15, E–F. *Drupella margariticola* (L = 21.8 mm, W = 12.3 mm) from Papua 21, form living in a marine lake without coral growth, G. *Stylocheilus striatus*, H. *Diniatys monodonta* (L = 5.2 mm, W = 3.2 mm), I–J. *Auriculastra semiplicata* (L = 16.9 mm, W = 5.3 mm), K. *Melampus adamsianus* (L = 9.7 mm, W = 5.2 mm), L–M. *Melampus fasciatus* (L = 7.4 mm, W = 5.2 mm), N. *Melampus sculptus* (L = 11.3mm, W = 5.4 mm), O. *Melampus* sp. (L = 7.2 mm, W = 4.5 mm), P–Q. *Pythia pantherina* (L = 11.3 mm, W = 7.1 mm). Scale bars: 5 mm.

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FIGURE A10 A. *Pteraeolidia semperi*, B. *Chromodoris lineolata*, C. *Hypselodoris* cf. *placida*, D. *Phyllidiella nigra*, E. *Elysia marginata*, F. *Elysia* sp., G. *Thuridilla gracilis*, H. *Siphonaria* sp., I–J. *Nerita undata* (L = 21 mm, W = 14.4 mm), K–L. *Nerita striata* (L = 15 mm, W = 11.1 mm), M–N. *Nerita winteri* (L = 12.1 mm, W = 8.7 mm), O–P. *Neritodryas dubia* (L = 14.9 mm, W = 9.8 mm), Q. *Eoacmaea* sp. (L = 9.3 mm, W = 4 mm), R–S. *Diodora mus* (L = 13.4 mm, W = 5.8 mm). Scale bars: 5 mm.

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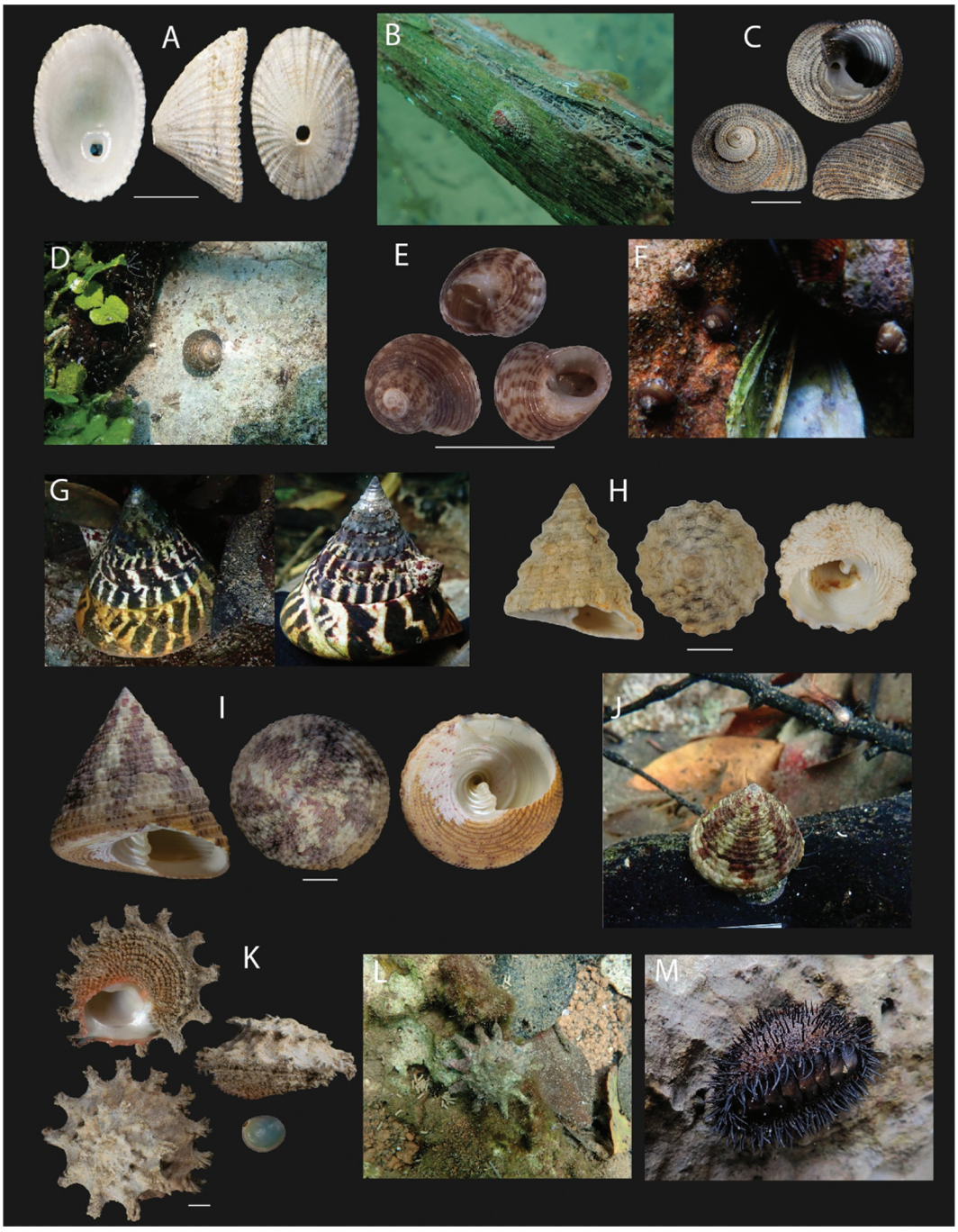

FIGURE A11 A–B. *Diodora* sp. (L = 13.5 mm, H = 7.3 mm), C–D. *Euchelus atratus* (L = 13 mm, W = 10 mm) E–F. *Neocollonia pilula* (L = 5 mm, W = 4.5 mm), G. *Rochia nilotica*, with young on the adult, H. *Tectus fenestratus* (H = 17.5 mm, W = 16 mm), I–J. *Trochus maculatus* (L = 27.8 mm, W = 28.7 mm), K–L. *Astralium calcar* (L = 18.5 mm, W = 38.4 mm) with operculum, M. *Acanthopleura spinosa.* Scale bars: 5 mm.

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