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Stony Corals and Their Associated Fauna Residing in Marine Lakes under Extreme Environmental Conditions

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Abstract: Tropical marine lakes are small land-locked marine waterbodies occurring in karstic coastal areas. During biodiversity surveys in 12 marine lakes in Raja Ampat, Southwest Papua province, Indonesia, we recorded at least 37 species belonging to 29 genera of hard corals. Their observed associated symbiont fauna consisted of bivalve molluscs and polychaete worms. Marine lake temperature ranged from 30.0 to 32.5 °C, acidity from pH 7.6 to 8.1, and salinity from 26.4 to 33.2 ppt. This study provides the first inventory of the marginal coral communities in the extreme habitat of marine lakes, under chronic extreme environmental conditions of higher temperatures, land-based nutrient loads, and sedimentation.

Keywords: extreme habitat; marginal coral communities; environmental limits; anchialine; Raja Ampat; Bird's Head Peninsula; Indonesia

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In recent years, there has been heightened interest in corals that live at the edge of their environmental limits as they can provide insights into how coral communities may survive and adapt to future scenarios of the marine environment [1]. Coral-populated extreme environments are considered possible resilience hotspots and climate-change refugia [1–3]. Within this line, marine lakes represent environments with elevated seawater temperatures, lower pH, and natural turbidity [4–6]. These small waterbodies are entirely surrounded by land but have a connection to the adjacent sea through subterranean channels and fissures or porous rock [4]. As such, marine lakes contain saline water and harbour marine species communities [6–9], some of which are anchialine as defined by Holthuis [10]. Marine lakes may contain endemic species of crustaceans [11,12], echinoderms [13,14], sponges [15–17], sea anemone [18,19], and benthic forams [20], some of which were observed to be involved in unique species interactions [18,19].

During biodiversity surveys in 2016, 2020, and 2023 in Raja Ampat, west of Bird's Head Peninsula (Papua, Indonesia), we encountered hard coral species in 12 marine lakes (Figure 1). All marine lakes with coral fauna appeared to have well-developed connections to the sea. These allow frequent flushing of seawater with the adjacent coast and a high influence of terrigenous runoff, resulting in low-visibility waters despite low turbulence.

The temperature across the 12 marine lakes ranged from 30.0 to 32.6 °C (Table 1), while in the nearby reefs it ranged from 29.2 to 30.9 °C. The salinity of the lakes also varied, with some of them representing brackish environments (26.4–29.1 ppt) and others that are only slightly lower in salinity (30.0–33.2 ppt) (Table 1) than coastal reefs (33.5–34.5 ppt).

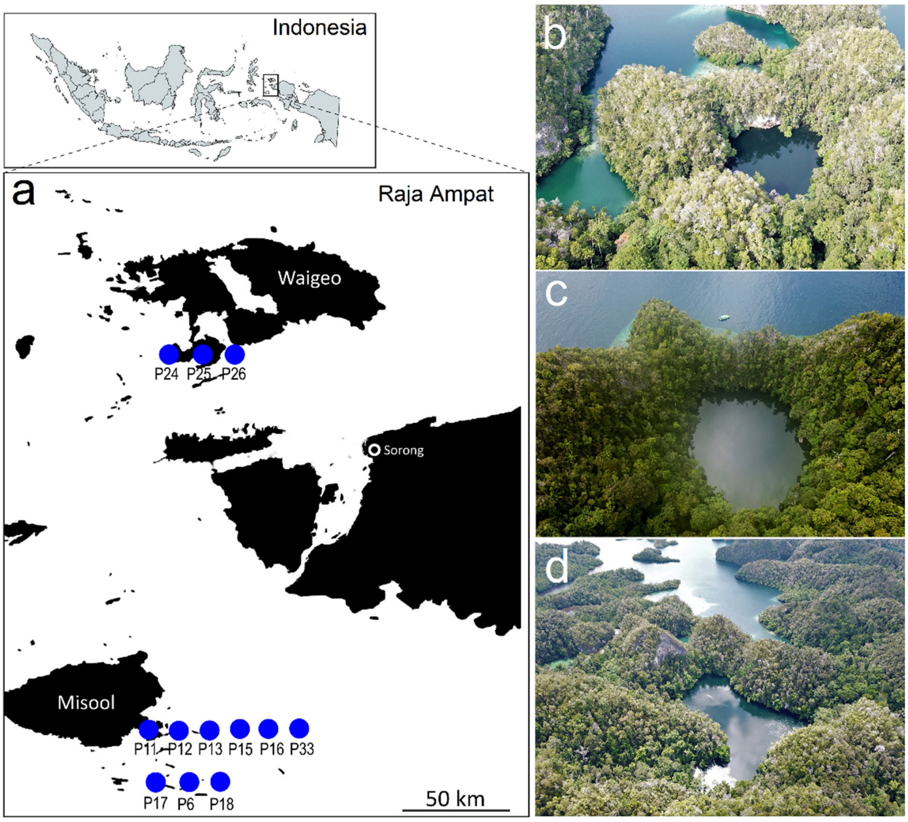

Figure 1. (**a**) Locations of 12 marine lakes with coral communities in Raja Ampat, Indonesia. (**b**–**d**) Aerial images of marine lakes: (**b**) Papua24, (**c**) Papua06, and (**d**) Papua25. See Table 1 for location codes (Photo credits: Christiaan de Leeuw).

Table 1. Environmental characteristics of 12 marine lakes with hard coral fauna in Raja Ampat, Indonesia. Code names for marine lakes follow those of earlier studies [21–23]. Averages (and ranges in brackets) of temperature, salinity, and pH are based on five sites within each marine lake. Measurements were made at 1 m intervals in the depth range that the corals were observed (1–5 m). n.a. = not available.

Marine Lake Code	Temperature (°C)	Salinity (ppt)	pH	Surface Area (m^2)	Maximum Depth (m)	Mangrove Presence
Papua06	31.9 (30.8–32.5)	28.3 (26.7–29.1)	7.9 (7.9–8.0)	2950	12	No
Papua11	30.7 (30.1–31.0)	27.6 (26.4–29)	8.1 (8.0–8.1)	27,300	9	Yes
Papua12	31.2 (30.2–31.8)	32.7 (32.6–32.8)	n.a.	7160	12	Yes
Papua13	30.6 (29.0–31.3)	32.8 (32.7–32.9)	n.a.	2100	3.5	Yes
Papua15	30.6 (30.3–31.2)	30.1 (29.1–30.4)	8.1 (8.0–8.1)	10,300	34	Yes
Papua16	31.2 (31.1–31.6)	30.0 (29.5–30.1)	8.1 (8.0–8.1)	21,100	19	No
Papua17	31.7 (31.1–32.0)	n.a.	n.a.	6500	n.a.	Yes
Papua18	31.5 (29.9–32.6)	28.4 (27.2–29.1)	7.7 (7.6–7.8)	7000	4.5	Yes
Papua24	30.3 (30.0–31.1)	30.7 (30–31.1)	7.9 (7.8–7.9)	4200	6	No
Papua25	31.7 (31.1–32.1)	29.6 (27.2–30)	7.8 (7.7–7.8)	21,500	8.5	Yes
Papua26	30.6 (30.0–31.5)	29.7 (29.1–30.2)	8.1 (8.0–8.1)	16700	4.5	Yes
Papua33	30.4 (30.0–30.6)	33.0 (32.8–33.2)	n.a.	11,700	27	No

The corals were mostly present at a depth range of 0.5–5 m. In four marine lakes (Papua11, Papua12, Papua15, and Papua24) hard corals represented 10–20% of the total benthic cover [23], resembling inshore and turbid reefs in the Indo-Pacific [24–26]. For comparison, the nearby reefs in Raja Ampat can range in coral cover from 10 to 86% [23] In some marine lakes, the corals formed small reefs (Figures 2d and 3c,d), while in others, corals occurred in patches (Figure 2c). Most corals exhibit massive and encrusting growth forms. In some marine lakes, corals also exhibit foliose and branching growth forms, which contribute to increased structural habitat complexity. In the surveyed marine lakes with mangroves, the corals grow on and in between mangrove roots. Corals growing on mangrove roots is an uncommon feature, although there are reports from coastal areas in the Caribbean, such as in the U.S. Virgin Islands [27,28], Panama [29,30], and Florida [31], and also in the Indo-Pacific, such as the Great Barrier Reef [32,33].

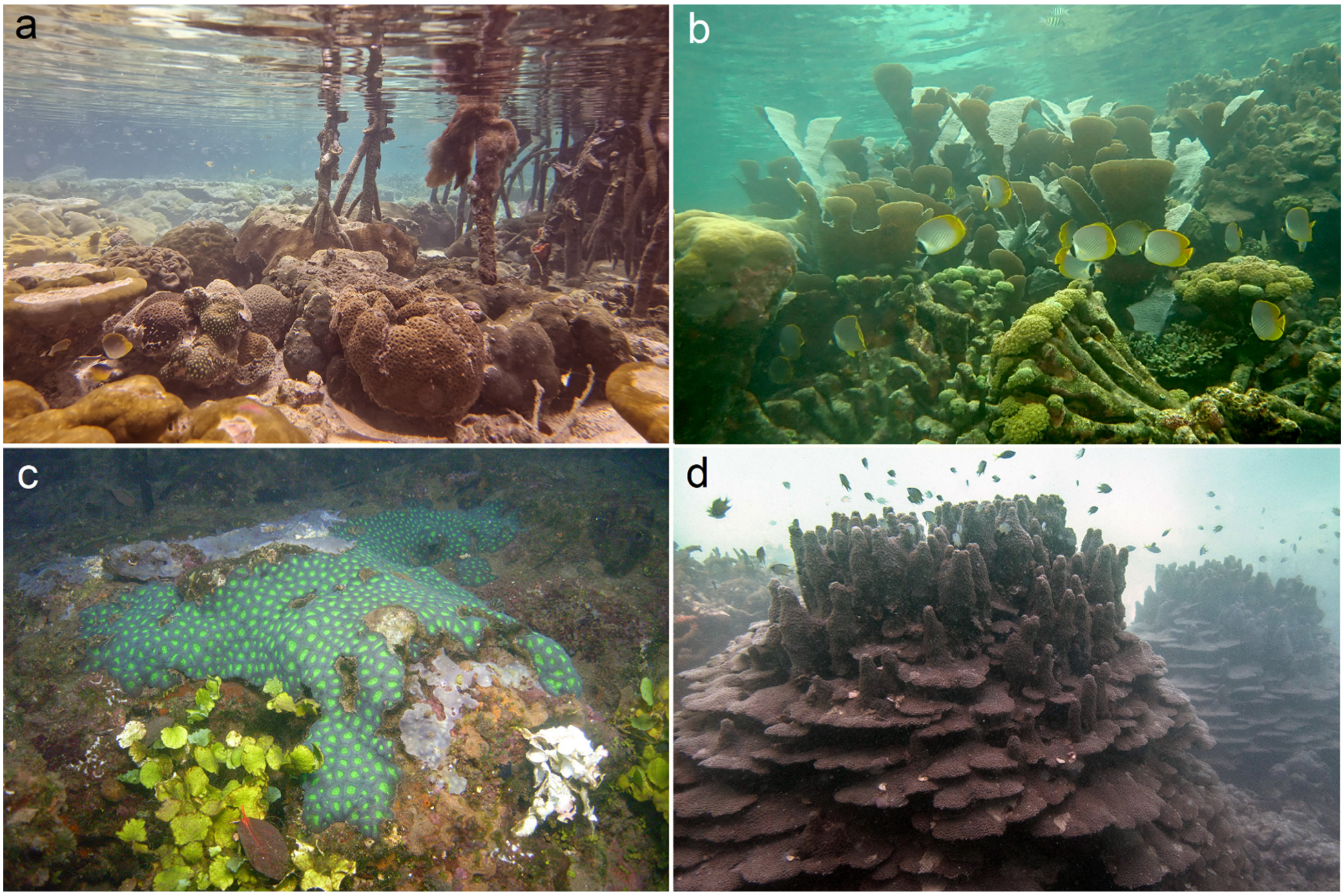

Figure 2. Impressions of coral cover and coral formations at shallow depths in marine lakes: (**a**) corals growing among and on mangrove roots; (**b**) foliose and vase-shaped corals as habitats for butterflyfishes in shallow water; (**c**) encrusting merulinid coral with the grey encrusting sponge *Lamellodysidea herbacea* and the green macroalga *Halimeda* sp.; (**d**) pillar reef formations of *Galaxea*.

Based on photographic evidence that was taken while snorkelling, 37 stony coral species of 29 genera could be distinguished, belonging to 11 scleractinian families and one hydrozoan family (Table 2; Figures 4 and 5). They were identified with the help of *Corals of the World* [34], updated with the nomenclature of *World List of Scleractinia* [35]. These corals are generally known to be sediment-tolerant, such as those belonging to the genera *Galaxea*, *Goniopora*, *Montipora*, *Pachyseris*, *Pavona*, and *Porites* [36,37]. Most of the species have previously been reported from turbid reef or mangrove environments. For example, shallow-water branching *Acropora* spp., foliose *Montipora* spp., and large massive *Porites* spp. have been recorded in turbid nearshore coral communities in the Paluma Shoals Reef Complex in the Great Barrier Reef, Australia [26].

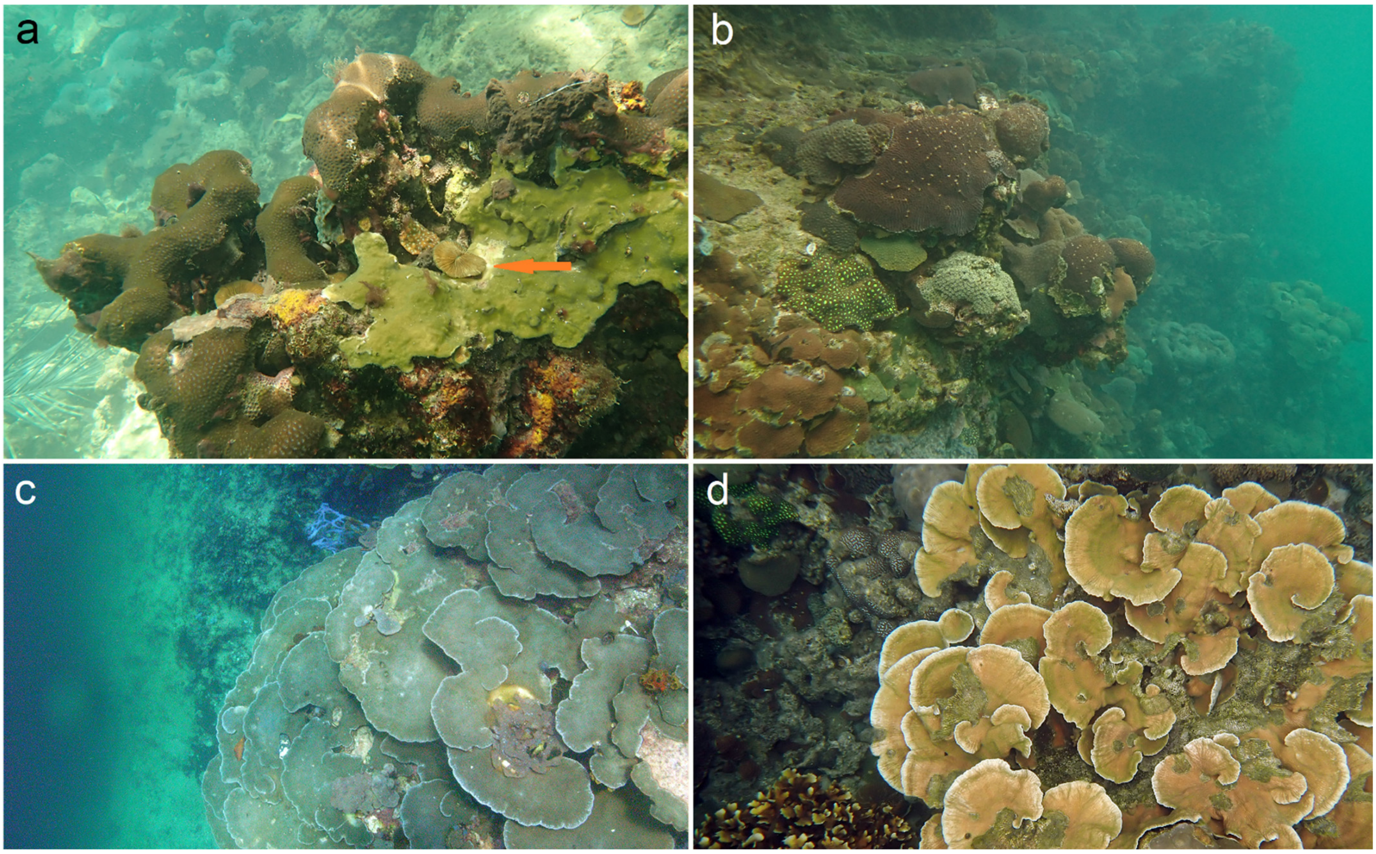

Figure 3. Impressions of coral cover and coral formations on upper reef slopes of marine lakes: (**a**) massive merulinid coral colonies and an encrusting *Porites* overtopped by a free-living mushroom coral, *Danafungia scruposa* (arrow); (**b**) encrusting and massive coral colonies; (**c**) foliose colonies of an unidentified *Montipora* species; (**d**) foliose colonies of an unidentified *Montipora* species next to a patch of *Pavona cactus*.

Table 2. Coral taxa (Scleractinia and Milleporidae) observed in 12 marine lakes of Raja Ampat, Indonesia (Figure 1).

Family	Species
Acroporidae	*Acropora* cf. *rudis*, *Montipora* spp. (2×)
Agariciidae	*Gardineroseris planulata*, *Pavona cactus*, *P. decussata*
Euphylliidae	*Coeloseris mayeri*, *Euphyllia glabrescens*, *Galexea astreata*
Fungiidae	*Danafungia scruposa*, *Fungia fungites*, *Heliofungia actiniformis*, *Lithophyllon repanda*
Leptastreidae	*Leptastrea* sp.
Lobophylliidae	*Lobophyllia* sp.
Merulinidae	*Cyphastrea* sp., *Dipsastraea* spp. (2×), *D. rotumana*, *D. speciosa*, *Echinopora* sp., *Favites* spp. (2×), *Goniastrea* sp., *Hydnophora rigida*, *Leptoria phrygia*, *Oulophyllia crispa*, *Pectinia paeonia*
Milleporidae	*Millepora tenera*
Pachyseridae	*Pachyseris speciosa*
Plerogyridae	*Plerogyra sinuosa*
Pocilloporidae	*Pocillopora damicornis*, *Seriatopora hystrix*, *Stylophora pistillata*
Poritidae	*Porites* sp., *P. cylindrica*, *P. rus*

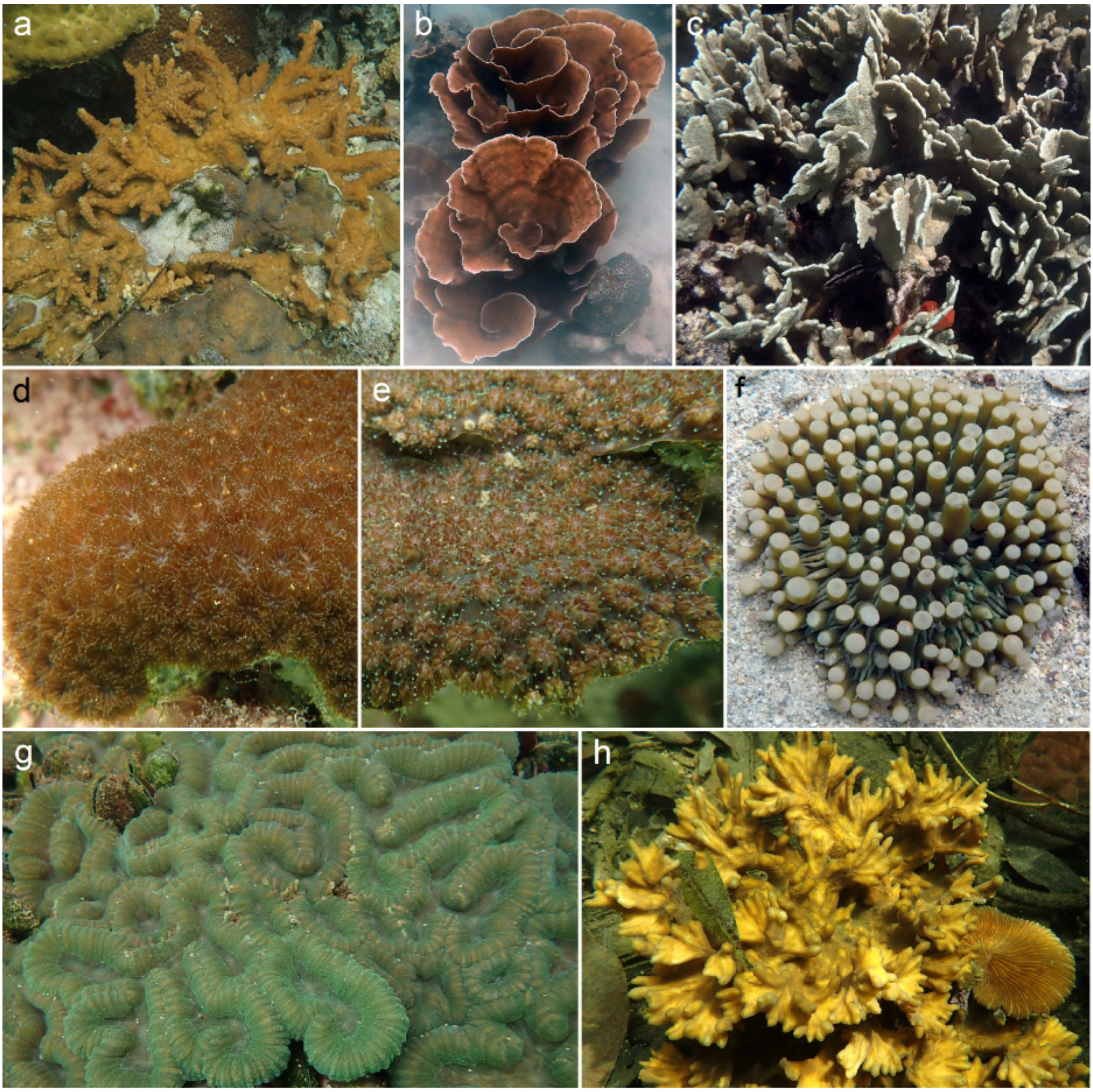

Figure 4. Selection of stony coral species observed in marine lakes: (**a**) *Acropora* cf. *rudis*, (**b**) *Montipora* sp., (**c**) *Pavona decussata*, (**d**) *Coeloseris mayeri*, (**e**) *Galaxea astreata*, (**f**) *Heliofungia actiniformis*, (**g**) *Lobophyllia* sp., and (**h**) *Pectinia paeonia*.

Hard corals have been reported in marine lakes before, but little information has been given on the species composition or their diversity. In Palau, which harbours numerous marine lakes, Hamner and Hamner [4] reported the presence of corals in the marine lake Ketau without further specification of species identities, coral cover or coral growth forms. The water in Lake Ketau was isothermal with an average temperature of 29.5 °C, with salinity around 30.5 ppt. Lake Ketau has the general appearance and fauna of the adjacent outside lagoon, with a high diversity of coral-reef fish and many species of corals found in the shallow areas near the islands [4]. Colin [5] reported on coral communities in Palau's Heliofungia Lake and displayed images of a dense cover of free-living *Heliofungia actiformis*, as well as encrusting corals with large populations of *Septifer* mussels growing on them, and a foliose coral (*Echinopora lamellosa*) growing on a slope of the lake. In Ha Long Bay (Vietnam), four marine lakes have been reported to have coral, although specific species were not mentioned: Lake Dau Be (with a narrow strip of coral reef distributed sparsely around the lake), Lake Qua Bang (narrow strip of corals), Lake Bui Xam (a belt of massive corals), and Hang Du II Lake (the rocky shores of the lake are partially covered by a belt of corals) [38,39]. In Indonesia, Tomascik and Mah [40] reported the coral *Alveopora tizardi* from the marine Kakaban Lake in East Kalimantan province. However, we did not encounter this species in our surveys. Notably, no other coral species have previously been identified in Indonesian marine lakes.

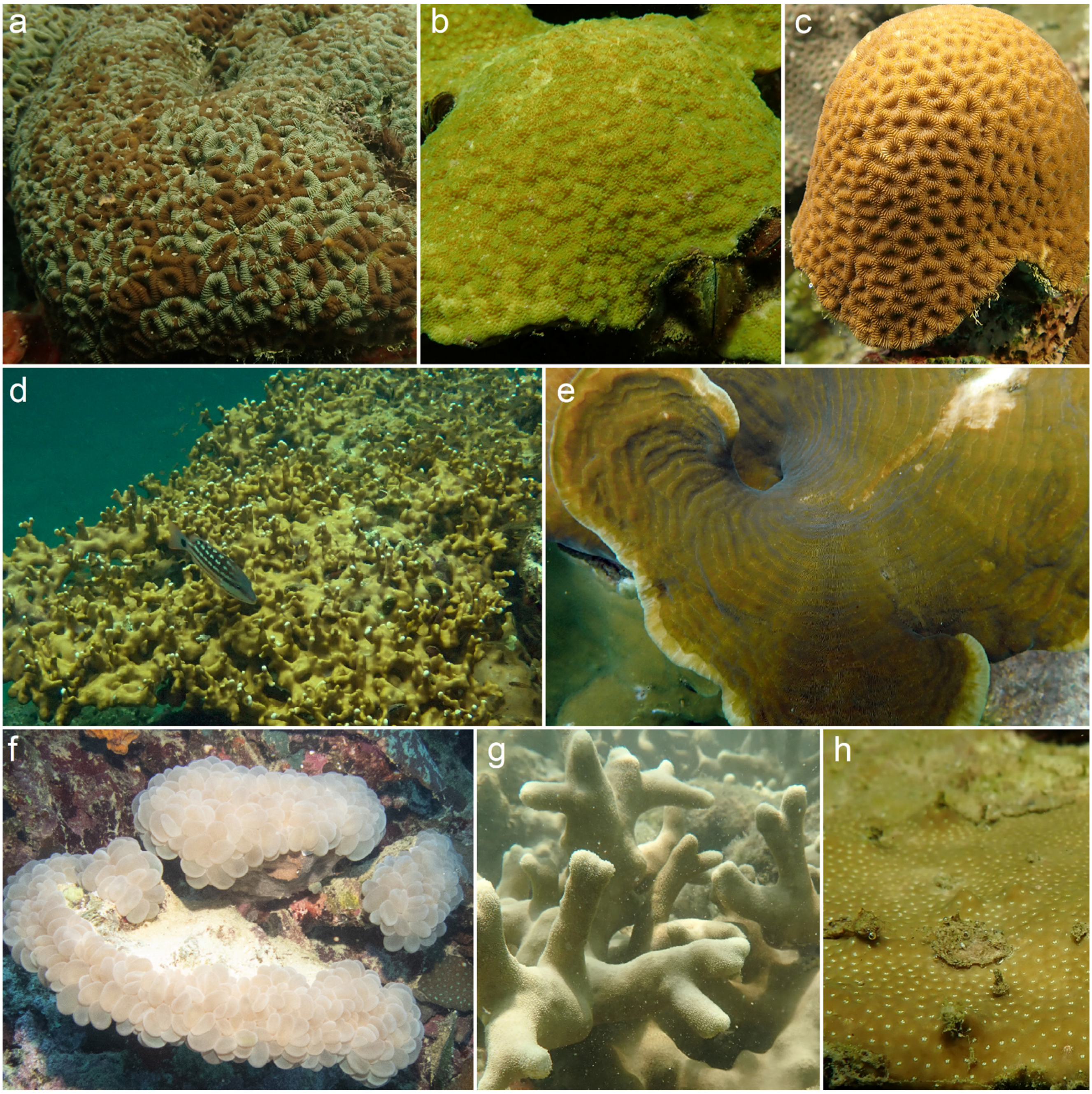

Figure 5. Selection of stony coral species observed in marine lakes (continued): (**a**) *Dipsastraea* sp., (**b**) *Echinopora* sp., (**c**) *Goniastrea* sp., (**d**), *Millepora tenera*, (**e**) *Pachyseris speciosa*, (**f**) *Plerogyra sinuosa*, (**g**) *Porites cylindrica*, and (**h**) *Porites rus*.

It is striking that some corals in marine lakes are associated with high numbers of filter feeders (Figures 6 and 7). Records of coral-associated animals can be relevant because of their role as possible bioindicators [41–44]. Since filter-feeding invertebrates generally appear to be most abundant in relatively shallow, eutrophic water [45], marine lakes could be favourable environments for these organisms.

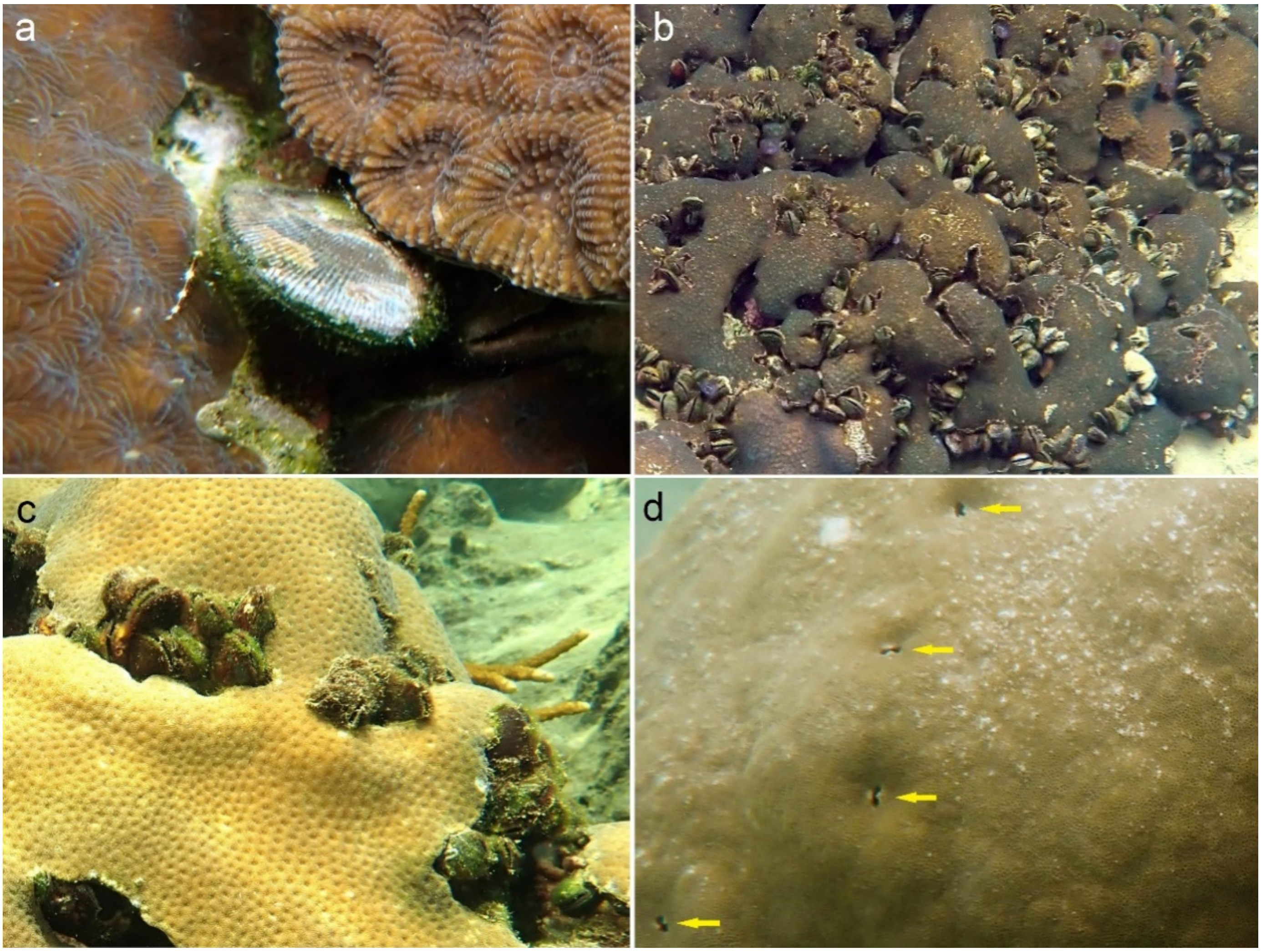

Figure 6. Coral-associated mytilid bivalves: (**a**) single specimen of *Septifer bilocularis* settled in between two merulinid corals; (**b**,**c**) clusters of *S. bilocularis* settled inside crevices and patches of dead surface areas of scleractinian corals; (**d**) characteristic orifices (arrows) of boring mussels (*Leiosolenes* sp.) in a massive *Porites* colony.

Clusters of the box mussel bivalve, *Septifer bilocularis* (family Mytilidae), were present in high densities over the upper surface of massive coral colonies and inside crevices (Figure 6a–c). Boring mussels of the genus *Leiosolenus* (previously also known as *Lithophaga*) of the same family lived inside massive *Porites* corals, showing their characteristic orifices [46–49] scattered over their host's surface (Figure 6d). The shell ribs of *Septifer bilocularis* resemble those of *Brachidontes* spp., which were also found to be abundant in the lakes but not in association with corals [22]. Since *S. bilocularis* has also been reported to occur in cryptic upper-sublittoral habitats in dead coral [50], its presence on live coral can perhaps be explained by settlement on small patches of dead surface area of the living host. Interestingly, no bivalves of the genus *Pedum* (family Pectiniidae) were observed, even though these scallops are commonly observed inside crevices in massive corals on coral reefs across the Indo-West Pacific [51–53], including eastern Indonesia [54,55].

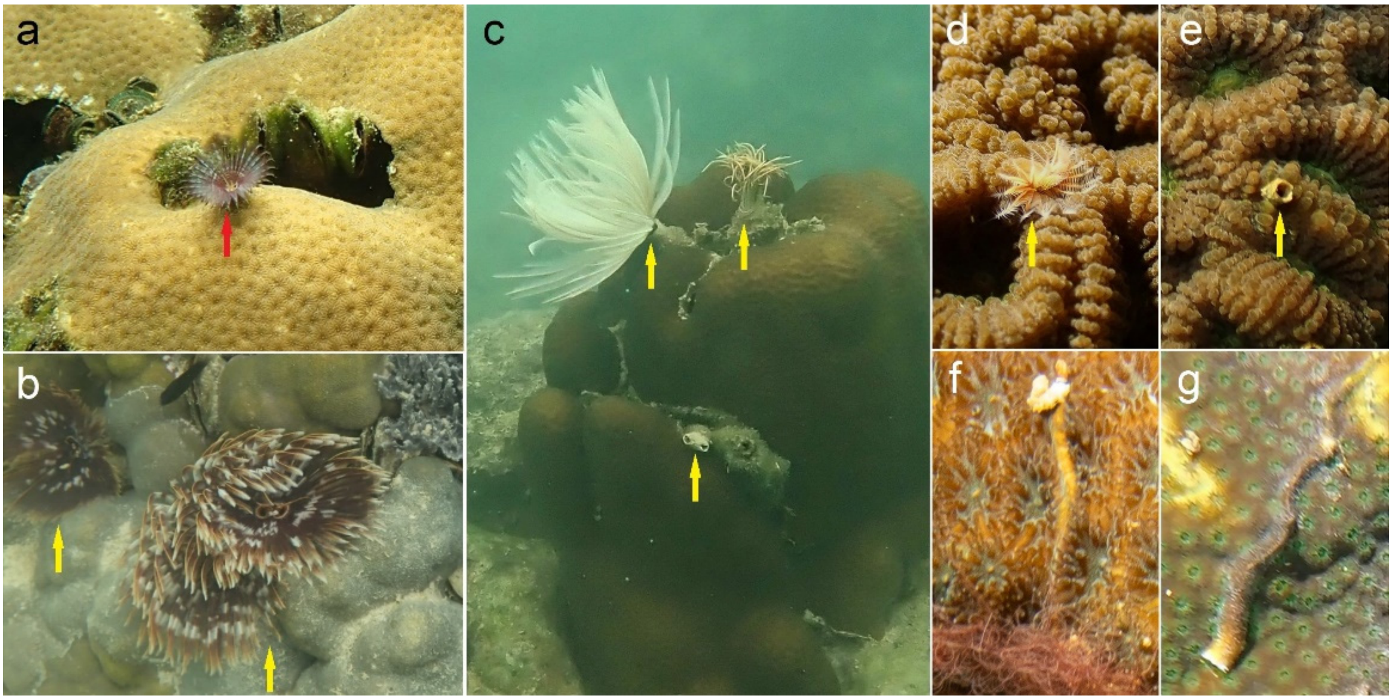

Figure 7. Coral-associated tube worms. Sabellidae: (**a**) *Acromegalomma* sp. (red arrow); (**b**,**c**) colour varieties of *Sabelastarte* sp. (possibly *S. spectabilis*) in massive *Porites* colonies (yellow arrows). Serpulidae: *Floriprotis sabiuraensis* with (**d**,**e**) tubes almost entirely implanted in a *Dipsastraea* host coral (yellow arrows), both with extended arioles (**d**) and retracted (**e**), and another one (**f**) showing its tube partially embedded and its ariole partially retracted; (**g**) tube of an unknown serpulid, possibly *Spirobranchus* sp.

Filter-feeding coral-associated tube worms were less abundant than the mussels in the lakes; they belonged to the polychaete families Sabellidae (Figure 7a–c) and Serpulidae (Figure 7d–g). The Sabellidae, popularly known as feather duster worms, have just recently been discovered to form associations with live corals in both the Indo-Pacific and in the Caribbean, where they may cause damage to their hosts [56,57]. Records of sabellids living on dead corals are more common than on live corals [58–62].

The only serpulid worm that could be identified was *Floriprotis sabiuraensis* (Figure 7d–f), a coral symbiont, which has been reported from various hosts and localities across the Indo-Pacific [49,63–65]. The calcareous tube of an unknown serpulid was found attached to the surface of a massive coral (Figure 7g). It does not show the ring-like structures (peristomes) of *Floriprotis* tubes [64,66] and also not the sharp spike at the tube opening, as seen in most *Spirobranchus* species [67,68]. It could be an individual belonging to the *Sprirobranchus tetraceros* species complex, such as in *S. schmardi* [69], which do not always develop such spikes (ten Hove, personal communication).

Boring sponges may also occur in marine lakes and have here only been recorded from limestone rock but not yet from corals [70,71], as those in open-sea reefs [71–74]. Other large, striking coral-associated fauna, such as worm snails [75–77], barnacles, and gall crabs [49,78,79], were also not observed in the marine lakes of Raja Ampat, and should therefore receive more attention in future studies.

In conclusion, the coral communities and their associated fauna that we have found in the marine lakes of Raja Ampat can be classified as extreme and marginal following the framework by Schoepf et al. [1]. The coral communities in marine lakes survive under chronic extreme environmental conditions of higher temperature, land-based nutrient loads, and sedimentation, and have a species diversity that is lower in comparison to clearwater coastal coral communities. The marine lakes in the current study that contained stony corals had an average temperature of 30.4 °C, which is markedly higher than the average temperatures of 27.9 to 28.5 °C recorded in the reefs of Raja Ampat since 2009 [80–82].

Our study is a first assessment of the stony coral diversity of marine lakes. The list of corals that we present here (Table 2) is a first qualitative compilation based on photographic evidence. Future work will require a systematic documentation of the coral biodiversity, which will likely result in additional species records. Further research will assess to what extent these marine lakes can serve as natural laboratories, where resident coral communities are experiencing conditions of future climate scenarios (high temperature and low pH) combined with local stressors on water quality (e.g., sedimentation and eutrophication).

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