Морской биологический журнал
Marine Biological Journal
2022, vol. 7, no. 3, pp. 88–102
https://marine-biology.ru

UDC [574.587:504.4](265.72.04) DOI: 10.21072/mbj.2022.07.3.08

BENTHIC ALGAE COMMUNITIES OF CORAL REEFS IN THE SANYA BAY (HAINAN ISLAND, CHINA) IN SITES HEAVILY POLLUTED WITH NUTRIENTS AND THEIR CHANGES AFTER THE POLLUTION SOURCE ELIMINATION

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Received by the Editor 22.03.2021; after reviewing 27.10.2021;
accepted for publication 19.08.2022; published online 13.09.2022.

It was previously found that extremely high concentrations of nutrients in seawater in the polluted area of a fish farm on the Luhuitou Peninsula (the Sanya Bay) cause a significant reduction in species diversity and abundance of low-productive annual and perennial red and brown algae, as well as an increase in number and biomass of highly productive green algae. In 2017–2019, for the first time, we studied changes in the number and structure of benthic algal communities over a range of tidal zones in the Sanya Bay after the pollution source elimination – the fish farm liquidation. It was shown that a decrease in the concentration of dissolved inorganic nitrogen (DIN) (from ~ 20 to 2.5 μM) and orthophosphates (from 5.0 to 0.2 μM) in seawater significantly altered diversity, species composition, and structure of benthic algal communities. One and half years after the pollution source elimination, the main indicators of the flora became, on average, close to those of the moderately polluted areas of the Sanya Bay.

Keywords: seaweeds, Hainan Island, China, eutrophication, restoration

Species diversity and floristic ratios of main algal groups vary between clean and nutrient-polluted areas, as reported in previous studies (Lapointe et al., 2005a, b ; Morand & Briand, 1996 ; Morand & Merceron, 2004). As shown in our earlier investigations, the Sanya Bay is polluted with nutrients derived from urban wastewater and waste of mariculture farms. In seawater around reefs, mean concentrations of dissolved inorganic nitrogen (hereinafter DIN) and orthophosphates are 3.3 and 0.33 μM, respectively (Li, 2011). On oceanic atolls of Australia, French Polynesia, and other tropical regions, the contents of these substances in seawater are within ranges of 0.10–0.11 and 0.03–0.06 μM, respectively (Charpy et al., 1998 ; Charpy-Roubaud & Charpy, 1994 ; Furnas et al., 1997). Meanwhile, our previous research (Titlyanov et al., 2011, 2018) revealed that diversity and composition of macroalgal species, as well as their seasonal shifts, in the Sanya Bay are likely to be similar to those of relatively clean, unpolluted areas of the Indo-Pacific Ocean.

We assumed that mean seawater pollution by dissolved forms of nitrogen and phosphorus was not high enough to cause serious changes in the marine flora of the Sanya Bay. In this regard, we continued our investigations on the benthic flora in extremely polluted coastal areas subjected to extensive discharge from a grouper fish farm (Li et al., 2021, 2016). This farm covered an area of ~ 3,500 m^2. The volume of effluents directly discharged into surrounding waters of Luhuitou reef was about 4,000 tons·$year^{-1}$. According to the data obtained in 2013–2016 (Li et al., 2016), the mean value of DIN was ~ 190 µM at the grouper farm outlet, with a range ~ 30 to ~ 700 µM. However, the value significantly decreased (down to ~ 20 µM) in intertidal and upper subtidal zones opposite the outlet and reduced down to ~ 9 µM at 100 m from the outlet (in front of the Marine Biological Station). The content of phosphates decreased from ~ 10 µM at the outlet to ~ 3 µM in the area opposite the outlet and to ~ 0.2 µM opposite the Marine Biological Station. Our previous works showed that heavily polluted areas significantly differ from moderately polluted ones in terms of floral diversity, species composition, taxonomic composition, and structure of algal communities (Li et al., 2021, 2016).

In October 2017, this fish farm was liquidated, and we had a unique opportunity to trace the dynamic restoration of the marine flora on coral reef damaged by the farm discharges. In our earlier work (Li et al., 2021), we documented a significant increase in species diversity, as well as a change in the composition of main taxonomic groups and life forms of the benthic flora in the investigated coastal area 1.5 years after the fish farm liquidation. In the present work, we aimed at studying possible changes in number and structure of benthic algal communities on the Luhuitou Peninsula coast after the elimination of the fish farm – the key source of extreme pollution for the vicinity.

MATERIAL AND METHODS

Study sites and conditions. Investigations were carried out at Luhuitou fringing reef, the Sanya Bay, Hainan Island, China. Hainan Island (Fig. 1) is located in the subtropical northern periphery of the Indo-Pacific Ocean, in the South China Sea. Main coastal ecosystems of Hainan Island shallow waters are those of coral reefs – one of the most well-known fringing reefs in China. However, almost 80 % of the fringing reefs along Hainan Island coastline were damaged because of intensive human activities in the 1970s–1990s – fishing with dynamite and coral mining for lime and construction. Recently, eutrophication of Hainan coastal waters, particularly in the shallow gulfs, increased due to growing tourist flow, hotel construction along the coast, and mariculture in coastal ponds and pools with wastes draining into the sea (Titlyanov et al., 2011).

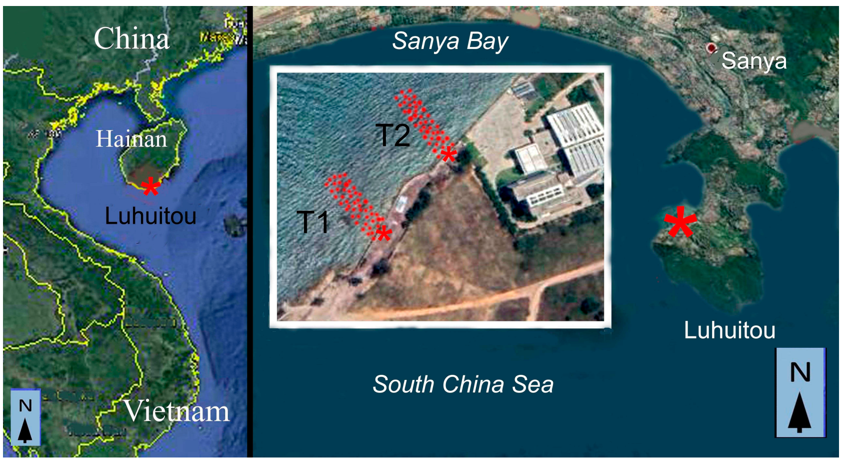

Fig. 1. Study sites on Hainan Island: T1, transect 1, opposite the former outlet of wastewater from the mariculture farm (ponds); T2, transect 2, located at the distance of 100 m from the transect 1

Sampling time and sites. Algae were sampled at the late dry season in March 2017 (while there was the fish farm), March 2018 (0.5 years after the fish farm elimination), and March 2019 (1.5 years after the elimination). In the study area, the dry season lasts from December-January to March-April. The main meteorological and hydrological characteristics of the study area during the dry seasons are given in Table 1.

Table 1. Concentrations of DIN and orthophosphates (μM) in the upper subtidal zone in the study sites at high tide on the first day of algal sampling in 2018 and 2019; * denotes mean data for 4 years (Li et al., 2016)

Transect	2013–2016*		2018		2019	
	DIN*	PO_4*	DIN	PO_4	DIN	PO_4
T1	31.3 ± 17.6	4.7 ± 3.1	2.65 ± 0.26	0.24 ± 0.03	3.05 ± 0.73	0.19 ± 0.01
T2	7.1 ± 2.2	1.0 ± 0.2	2.18 ± 0.34	0.19 ± 0.02	2.35 ± 0.86	0.19 ± 0.02

Algae were sampled on foot or *via* snorkeling from a depth of 0–2 m during low tides, along two transects from the upper intertidal to the upper subtidal zone (Figs 1, 2). Transects were laid perpendicular to a shore, and algae were sampled along these transects within the bottom area of 20–30 m × 50–70 m.

Transect 1 (hereinafter T1) was laid from the fish farm outlet; transect 2 (hereinafter T2) was located at the distance of ~ 100 m (along shoreline) from T1. Samples were taken from all the substrate types. To study the species composition of the benthic flora and taxonomic composition of algal communities, we used the methods of algal sampling and material processing described in (Titlyanov et al., 2019).

Along the transects, in each tidal zone, algal turf communities (with thalli less than 5 cm in height), crust algae, and large upright-growing algae (with thalli more than 5 cm in height) were visually identified. These communities were photographed at a right angle. In communities of algal turf and crust algae, samples were taken from three randomly selected areas, with each area of ~ 100 cm^2. In communities of upright-growing algae, samples were taken from three areas as well, with each ranging 0.5–1.0 m^2. Samples were taken from all the selected algal communities – in at least three quadrats from each community. A total of 54 macrophyte communities and blue-green algae were found; out of them, 162 samples were taken and analyzed; and out of them, 170 species of macrophytes and 13 species of blue-green algae were recorded (Li et al., 2021).

Sampling was carried out from the upper intertidal to the upper subtidal zone from all the substrate types [tidal zones were divided according to (Perestenko, 1980)]. At the investigated sites, the upper intertidal zone consisted of a sloping shore (2–3 m in width), with hard substrates composed of stones and dead coral fragments of various shapes and sizes tossed by storms. The sloping shore of the middle intertidal zone (~ 10 m in width) mainly consisted of flat carbonate patches interspersed with coral debris and stones. The lower intertidal zone (~ 15 m in width) was primarily composed of dead colonies of massive and branching corals interspersed with sand and small fragments of dead branching corals. The upper subtidal zone consisted of a sloping shore (~ 50 m in width) mainly composed of dead and live colonies of massive and branching corals interspersed with sand, stones, and dead coral fragments of various shapes and sizes.

Marine algae sampling, conservation, and identification. Sampling was carried out at each site from each tidal zone. Abundance was visually determined based on photographs of analyzed quadrats – by estimating the mean substrate surface area occupied by algae. The following indicators of abundance were used: rare sighting, found only one-two times with the relative substrata coverage less than 10 %; common, recorded in most quadrats with the relative substrata coverage 10 to 50 %; and abundant, registered in communities with the relative substrata coverage 50 to 100 %. For the communities, dominance was also visually determined and defined as follows: monodominant, with one algal species occupying more than 50 % of the surface area; bidominant, with two species occupying more than 50 % of the surface area; and polydominant, with more than two species predominating.

Algae sampled from different communities were stored in separate plastic bags placed in a refrigerator for a processing time. Freshly sampled material was identified using monographic publications, results of floristic studies, and systematic articles indicated in (Titlyanova et al., 2014). The systematics and nomenclature followed (AlgaeBase, 2021). Hierarchical classification of the phylum Rhodophyta (hereinafter Rh) was carried out according to (Saunders & Hommersand, 2004). The classification system of phyla Chlorophyta (hereinafter Ch) and Ochrophyta (hereinafter Ph) followed (Tsuda, 2003, 2006). The collections of both macrophytes and their epiphytes were preserved as dried herbarium specimens and deposited in the herbarium at A. V. Zhirmunsky National Scientific Center of Marine Biology FEB RAS, Institute of Marine Biology (Vladivostok, Russian Federation).

Nutrient analysis. For nutrient analysis, bottom water samples were taken along T1 and T2 areas in the upper subtidal zones during high tide on the first day of algal sampling, immediately filtered through pre-weighed glass-fiber filters (Whatman GF/F, 47 mm), and frozen at −20 °C. DIN (NH_4, NO_3, and NO_2) and orthophosphates (PO_4) were photometrically analyzed using an autoanalyzer (model Skalar San Plus).

RESULTS

Differences in the number and structure of algal communities at variously polluted sites in March 2017. In the spring of 2017, under conditions of constant water discharge from cultivation ponds of the fish farm in the study area, differences were found in the number and structure of algal communities formed in shallow waters opposite the outlet (T1, Fig. 2A) and at the distance of 100 m from the outlet (T2, Fig. 3A).

In the upper intertidal zone along the T1 area, monodominant communities – those of *Wilsonosiphonia howei* (Hollenberg) D. Bustamante, Won & T. O. Cho, 2017 (Rh) (Fig. 2B) and *Cladophoropsis fasciculata* (Kjellman) Wille, 1910 (Ch) (Fig. 2C) – predominated. Moreover, in the T1 area, there were monodominant communities of common green algae *Ulva prolifera* O. F. Müller, 1778 and *Ulva clathrata* (Roth) C. Agardh, 1811; monodominant community of a brown crust alga *Neoralfsia expansa* (J. Agardh) P.-E. Lim & H. Kawai ex Cormaci & G. Furnari, 2012; and bidominant turf communities of *C. fasciculata* (Ch) + *W. howei* (Rh) and *U. prolifera* (Ch) + *W. howei* (Rh). Out of the species forming the communities, *Centroceras clavulatum* (C. Agardh) Montagne, 1846, *Gelidium pusillum* (Stackhouse) Le Jolis, 1863 (Rh), *Siphonogramen abbreviatum* (W. J. Gilbert) I. A. Abbott & Huisman, 2004, and *Rhizoclonium riparium* (Roth) Harvey, 1849 (Ch) were commonly found.

In the middle intertidal zone in the T1 area, monodominant communities – those of a green alga *Ulva flexuosa* Wulfen, 1803 (Fig. 2D), the red crust alga *Hildenbrandia rubra* (Sommerfelt) Meneghini, 1841, and the crustose brown alga *Ralfsia verrucosa* (Areschoug) Areschoug, 1845 (Fig. 2E) – predominated on a rocky bottom. Algal turf community of a red fine filamentous alga *C. clavulatum* (Fig. 2F) dominated on dead coral remnants. Here, the rest parts of silt-covered hard coral colonies were occupied by a monodominant community of a blue-green alga (hereinafter Cy) *Lyngbya majuscula* Harvey ex Gomont, 1892; the lower great part of hard substratum was overgrown with a bidominant community of green algae *Ulva lactuca* Linnaeus, 1753 + *Ulva fasciata* Delile, 1813.

In the lower intertidal zone along the T1 area, the surfaces of dead coral blocks were overgrown by a monodominant community of a red turf-forming alga *C. clavulatum*, with accompanying species *Acanthophora muscoides* (Linnaeus) Bory de Saint-Vincent, 1843, *Hypnea pannosa* J. Agardh, 1847, *Hypnea spinella* (C. Agardh) Kützing, 1847, *Spyridia filamentosa* (Wulfen) Harvey, 1833 (Rh), and *Caulerpa racemosa* (Forsskål) J. Agardh, 1873 (Ch) (Fig. 2G). This community occupied 90 % of substratum. Out of the algal turf, *Sargassum polycystum* (C. Agardh), 1924 (Ph), *Bryopsis pennata* J. V. Lamouroux, 1809, *U. lactuca* (Ch), and live colonies of massive hard corals were commonly found (Fig. 2H).

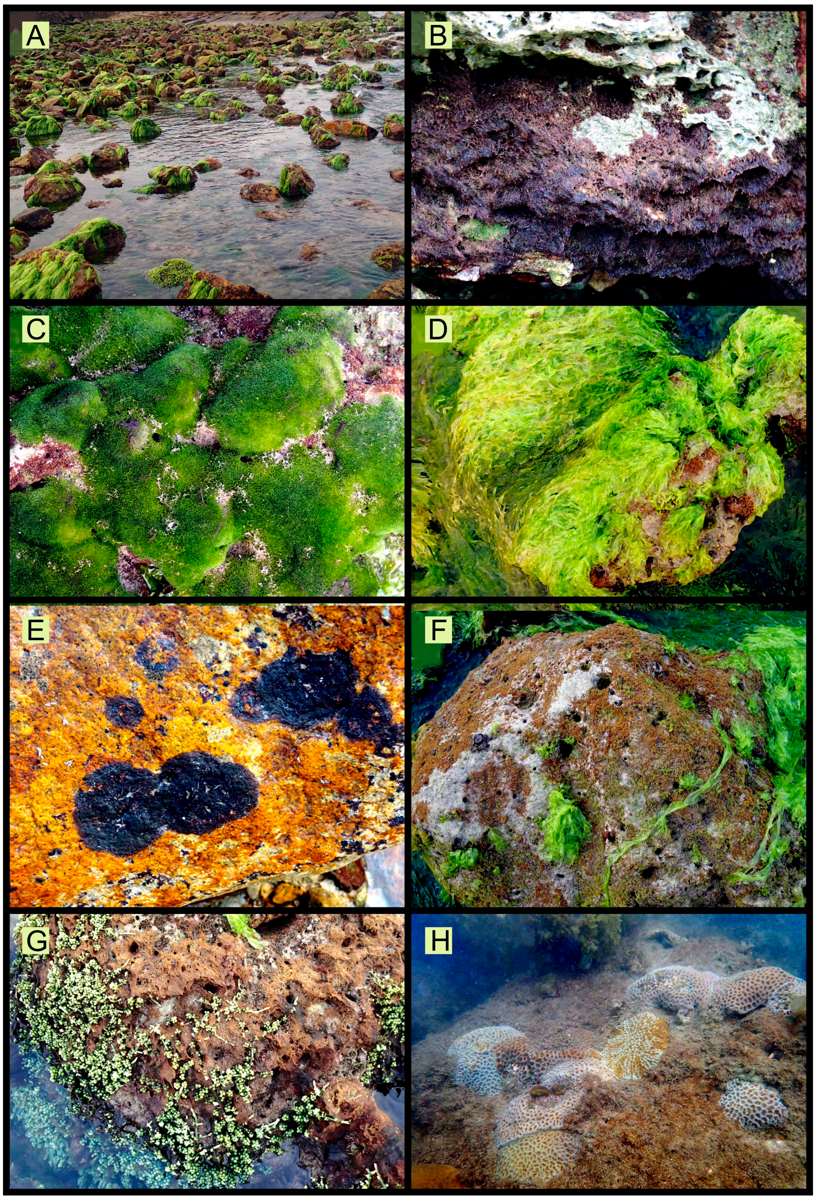

Fig. 2. Algal communities in the T1 area (heavily polluted site) in March 2017. A, the middle intertidal zone, the outlet area; B, the upper intertidal, monodominant community of a red alga *Wilsonosiphonia howei*; C, the upper intertidal, monodominant community of a green alga *Cladophoropsis fasciculata*; D, the middle intertidal, monodominant community of a green alga *Ulva flexuosa*; E, the middle intertidal, bidominant community of a red crust alga *Hildenbrandia rubra* and a brown crust alga *Ralfsia verrucosa*; F, the middle intertidal, monodominant community of the red alga *Centroceras clavulatum*; G, the lower intertidal, polydominant community of *C. clavulatum* with accompanying species *Acanthophora muscoides*, *Hypnea pannosa*, *Hypnea spinella*, *Spyridia filamentosa* (Rh), and *Caulerpa racemosa* (Ch); H, the upper subtidal, polydominant community of *C. clavulatum*, *H. pannosa*, *Hypnea valentiae*, *Jania adhaerens* (Rh), and *C. racemosa* (Ch) among young colonies of massive hermatypic corals

In the upper intertidal zone along the T2 area (Fig. 3A), at the same time, only three monodominant communities – those of *U. prolifera* (Ch) (Fig. 3B), *W. howei* (Rh) (Fig. 3C), and *N. expansa* (Ph) (Fig. 3D) – were common. Out of the species forming the communities, *C. fasciculata*, *U. clathrata* (Ch), and *C. clavulatum* (Rh) were found as well.

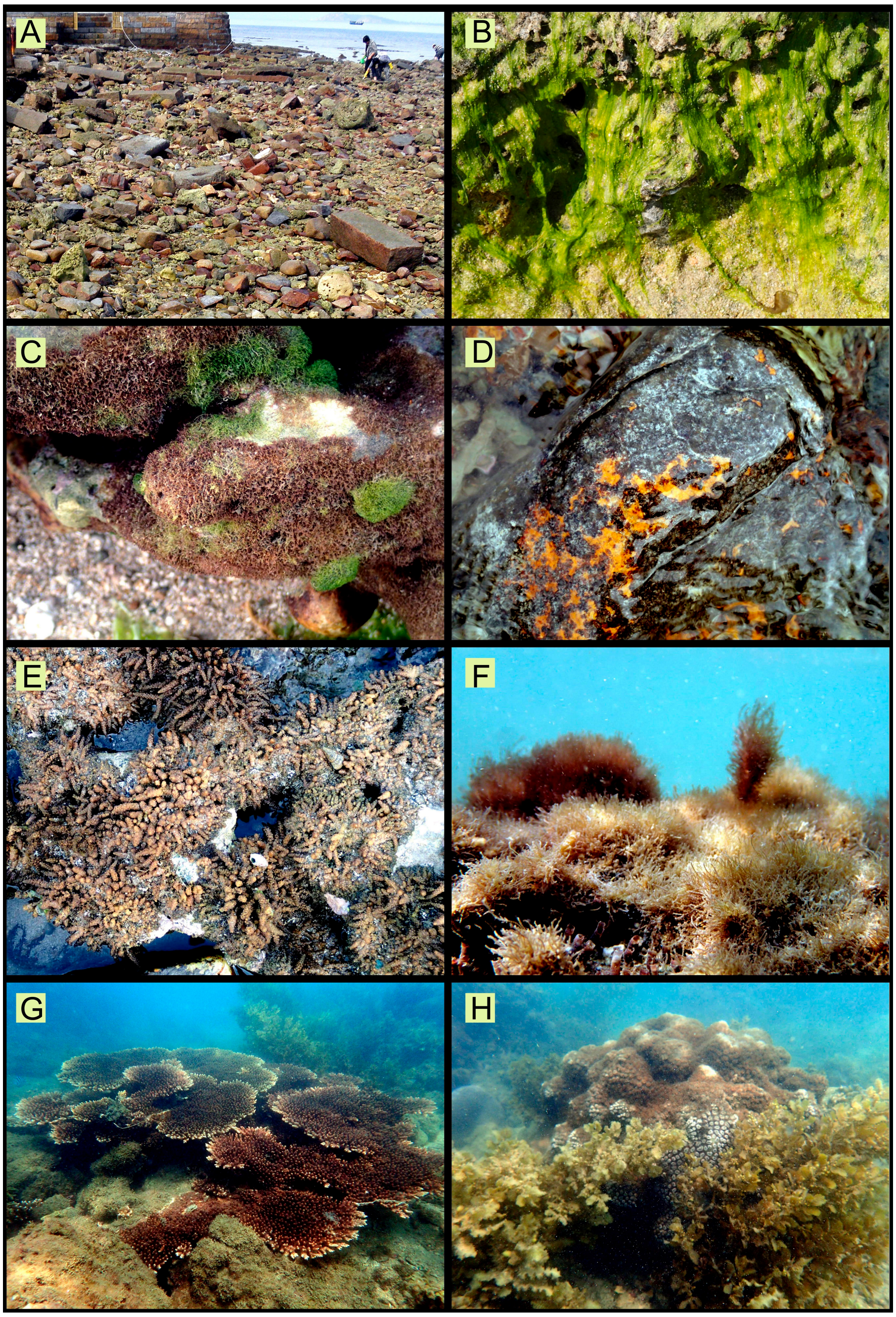

Fig. 3. Algal communities along the T2 area (moderately polluted area) in March 2017. A, the upper intertidal zone near the outlet at low tide; B, the upper intertidal, monodominant community of *Ulva flexuosa* (Ch); C, the upper intertidal, bidominant community of *Wilsonosiphonia howei* (Rh) + *Cladophoropsis fasciculata* (Ch); D, the middle intertidal, bidominant community of the red crust alga *Hildenbrandia rubra* and the brown crust alga *Ralfsia verrucosa*; E, the middle intertidal, mosaic polydominant community with a dominance of *Palisada perforata*, *Centroceras clavulatum*, and *Gelidiella bornetii* (Rh); F, the middle intertidal, polydominant turf community with a mosaic dominance of *Amphiroa fragilissima*, *C. clavulatum*, and *Jania adhaerens* (Rh); G, the upper subtidal, hermatypic corals and polydominant community of *C. clavulatum* (Rh) with accompanying species; H, lower intertidal to upper subtidal, with *Sargassum ilicifolium*, *S. polycystum*, and *S. sanyaense* (Ph) forming dense bed

In the middle intertidal zone along the T2 area, a mosaic polydominant community predominated occupying mainly a hard base of a flat carbonate substrate (Fig. 3E); the following species dominated – *Palisada perforata* (Bory) K. W. Nam, 2007, *C. clavulatum*, *Gelidiella bornetii* (Weber-van Bosse) Feldmann & C. Hamel, 1934 (Rh), *L. majuscula* (Cy), and *Lobophora variegata* (J. V. Lamouroux) Womersley ex Oliveira, 1977 (Ph) – growing on vertical surfaces of reef bases and coral blocks. Monodominant communities of the red alga *H. rubra* and the brown alga *R. verrucosa* occupied rocky substratum (as in the T1 area).

In the lower intertidal zone along the T2 area, a mosaic polydominant community of turf-forming algae overgrew dead coral blocks (Fig. 3F), with a mosaic dominance of *Amphiroa fragilissima* (Linnaeus) J. V. Lamouroux, 1816, *C. clavulatum*, *S. filamentosa*, *Hypnea valentiae* (Turner) Montagne, 1841, *Jania adhaerens* J. V. Lamouroux, 1816 (Rh), *Padina minor* Yamada, 1925 (Ph), and *Dictyosphaeria cavernosa* (Forsskål) Børgesen, 1932 (Ch). The green alga *C. racemosa* represented an often-overgrowing polydominant community of algal turf occupying silt- and sand-covered hard substrata. Upright-growing brown algae with large thalli of genera *Dictyota*, *Padina*, *Sargassum*, and *Turbinaria* were commonly found in the communities and on free substrata.

In the upper subtidal zone along the T2 area, hard substrata were occupied by hermatypic corals with coverage of ~ 50 %, and the rest surface of carbonate reef basis was overgrown by algal communities, primarily by polydominant mosaic algal turf communities with the following dominant species: *C. clavulatum*, *H. pannosa*, *H. valentiae*, *J. adhaerens*, and *S. filamentosa* (Rh) (Fig. 3G). A monodominant community of the green alga *C. racemosa* occupied ~ 10 % of the sand-covered hard substratum (coral reef base). *Sargassum ilicifolium* (Turner) C. Agardh, 1820, *S. polycystum*, and *Sargassum sanyaense* Tseng & Lu, 1997 (Ph) formed dense bed from the low intertidal zone to the upper subtidal zone (Fig. 3H).

Dynamic changes in the structure of algal communities in variously polluted sites after cessation of the discharge of waste from the fish farm. The transect 1, 2018. Six months after the fish farm liquidation, significant changes occurred in the structure and diversity of algal communities (Fig. 4).

In the upper intertidal zone, vertical walls of rocky boulders were partially occupied by monodominant communities (as in 2017) – those of *U. prolifera* (Ch) and *R. verrucosa* (Ph). Small niches of a stone retaining wall were overgrown by a new community – the red alga *Bostrychia tenella* (J. V. Lamouroux) J. Agardh, 1863 and the green alga *S. abbreviatum* with accompanying *R. riparium* (Fig. 4B).

The red alga *W. howei* which formed a dense monodominant community in these niches earlier was rare. Among epiphytes, *R. riparium* (Ch) and *Hydrolithon farinosum* (J. V. Lamouroux) D. Penrose & Y. M. Chamberlain, 1993 (Rh) dominated, as well as blue-green algae *Chroococcus turgidus* (Kützing) Nägeli, 1849 and *Stanieria sphaerica* (Setchell & N. L. Gardner) Anagnostidis & Pantazidou, 1991.

In the middle intertidal zone along the T1 area, stones were occupied by monodominant crust communities of *H. rubra* (Rh) and *N. expansa* (Ph) (as in 2017). Fossil reef base was overgrown by a community of the blue-green alga *L. majuscula* formed in 2017. A polydominant community of algal turf – with a dominance of *Millerella pannosa* (Feldmann) G. H. Boo & L. Le Gall, 2016 (Rh), *R. riparium*, and *U. clathrata* (Ch) (Fig. 4C) – covered remnants of massive coral colonies. Here, we also found *C. fasciculata*, *Chaetomorpha linum* (O. F. Müller) Kützing, 1845 (Ch), and *Coleofasciculus chthonoplastes* (Thuret ex Gomont) M. Siegesmund, J. R. Johansen & T. Friedl, 2008 (Cy), as well as epiphytes – *Erythrotrichia carnea* (Thuret ex Gomont) M. Siegesmund, J. R. Johansen & T. Friedl, 1883 (Rh) and *Myrionema strangulans* Greville, 1827 (Ph). On some flat rocks, a monodominant community of *W. howei* (Rh) was registered (Fig. 4D).

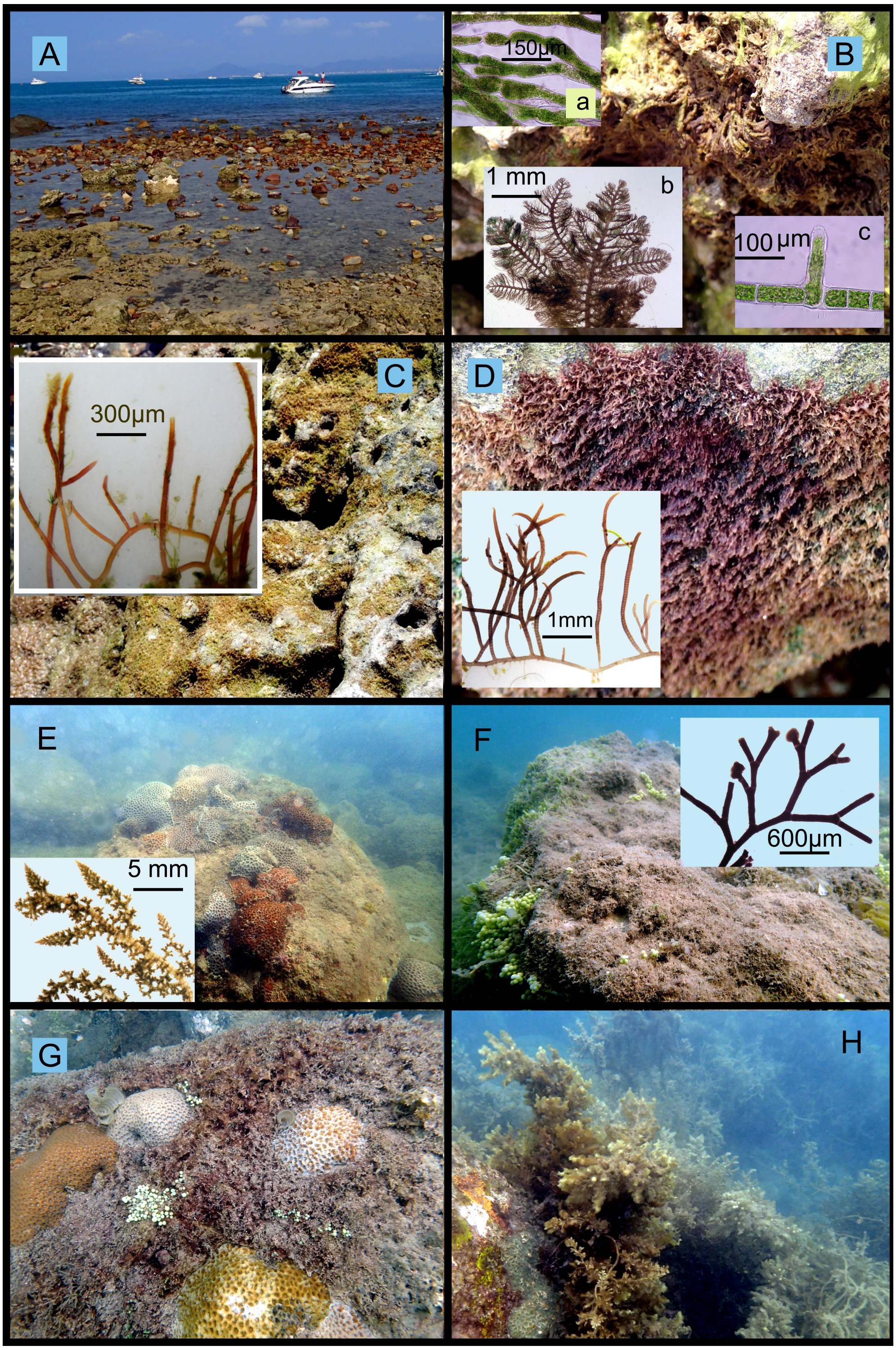

Fig. 4. Algal communities along the T1 area in March 2018. A, the middle intertidal zone opposite the former outlet of the fish farm; B, the upper intertidal, bidominant community of *Siphonogramen abbreviatum* (Ch) (insert **a**) + *Bostrychia tenella* (Rh) (insert **b**), with an epiphytic alga *Rhizoclonium riparium* (Ch) (insert **c**); C, the middle intertidal, polydominant community with a dominance of the red alga *Millerella pannosa* (insert) and green algae *Ulva clathrata* and *R. riparium*; D, the middle intertidal, monodominant community of *Wilsonosiphonia howei* (Rh); E and F, the lower intertidal, polydominant community with a dominance of *Tolypiocladia glomerulata* (E, insert), *Jania adhaerens* (F, insert), *Centroceras clavulatum*, and *Gelidium pusillum* var. *cylindricum* (Rh); G, the upper subtidal, polydominant community of algal turf with a dominance of *J. adhaerens*, *C. clavulatum*, *Asparagopsis taxiformis*, and *T. glomerulata* (Rh); H, the upper subtidal, *Sargassum polycystum* (Ph) thickets

In the lower intertidal zone along the T1 area, the remnants of coral colonies were overgrown by a polydominant community (as in 2017), but with other species predominating – *Tolypiocladia glomerulata* (C. Agardh) F. Schmitz, 1897, *J. adhaerens*, *C. clavulatum*, and *Gelidium pusillum* var. *cylindricum* W. R. Taylor, 1945 – and with common species accompanying – *M. pannosa*, *H. spinella*, *Melanothamnus ferulaceus* (Suhr ex J. Agardh) Diaz-Tapia & Maggs, 2017, *Caulacanthus ustulatus* (Mertens ex Turner) Kützing, 1843 (Rh), *Sphacelaria rigidula* Kützing, 1843 (Ph), and *C. linum* (Ch) (Fig. 4E, F). Out of the species forming the community, *R. verrucosa*, *Sphacelaria novae-hollandiae* Sonder, 1845, *P. minor*, and *S. polycystum* (Ph) were common.

In the upper subtidal zone along the T1 area in 2018, as in 2017, a polydominant algal turf community dominated, with different composition of dominating species [*J. adhaerens*, *C. clavulatum*, *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon, 1845, and *T. glomerulata*], as well as accompanying species of epilithic algae [*Peyssonnelia rubra* (Greville) J. Agardh, 1851 and *S. filamentosa*] and epiphytes [*Herposiphonia tenella* (C. Agardh) Ambronn, 1880, *Gayliella mazoyerae* T. O. Cho, Fredericq & Hommersand, 2008, *Melanothamnus savatieri* (Hariot) Díaz-Tapia & Maggs, 2017, and *Wrangelia argus* (Montagne) Montagne, 1856 (Rh)] (Fig. 4G). Out of the species forming the community, *S. polycystum* (Ph) and *C. racemosa* (Ch) were common (Fig. 4H).

Transect 1, 2019. In the spring of 2019, 1.5 years after the fish farm elimination, some alterations in the marine flora were detected in the intertidal and upper subtidal zones compared with the spring of 2018.

In the upper intertidal zone, rocky boulders, as always, were occupied by a monodominant community of the crust alga *N. expansa* (Ph). In niches of these boulders, a bidominant community of *W. howei* (with the blue-green epiphytic alga *C. chthonoplastes*) + *B. tenella* (Rh) and a bidominant community of *P. howei* (Rh) + *C. fasciculata* (Ch) [with accompanying *Bostrychia* sp. (Rh), *Rhizoclonium grande* Børgesen, 1935 (Ch), *S. abbreviatum* (Ch), and *Ceramium camouii* E. Y. Dawson, 1944 (Rh)] dominated. Moreover, the fossil reef base was covered with black film composed of blue-green algae – *Kyrtuthrix maculans* (Gomont) I. Umezaki, 1958, *C. chthonoplastes*, *Scytonematopsis crustacea* (Thuret ex Bornet & Flahault) Kovályk & Komárek, 1988, and *C. turgidus*.

In the middle intertidal zone, some alterations were recorded as well. The fossil carbonate base was covered by a dense mat of blue-green algae, with a dominance of *Lyngbya sordida* Gomont, 1892, *Lyngbya martensiana* Meneghini ex Gomont, 1892, and *K. maculans*. In a polydominant community of algal turf, the composition of dominant species changed as well. There, dominant species were *M. pannosa*, *P. howei* (Rh), *C. fasciculata*, and *R. grande* (Ch). Common algal species were *P. minor* (Ph), *Ceratodictyon intricatum* (C. Agardh) R. E. Norris, 1987, and *Jania capillacea* Harvey, 1853 (Rh), as well as an epiphyte *S. crustacea* and accompanying blue-green algae *C. chthonoplastes* and *K. maculans*.

In the lower intertidal zone, a polydominant algal turf community was enriched with new dominants species [*C. ustulatus* (Rh) and *S. novae-hollandiae* (Ph)] and with accompanying ones [*J. adhaerens*, *Herposiphonia secunda* (C. Agardh) Ambronn, 1880, *S. filamentosa*, *Pterocladiella caerulescens* (Kützing) Santelices & Hommersand, 1997, *H. spinella* (Rh), *S. rigidula*, *L. variegata* (Ph), *Anadyomene wrightii* Harvey ex J. E. Gray, 1866, and *C. racemosa* (Ch)]. Out of epiphytes, the most common ones were *E. carnea*, *Sahlingia subintegra* (Rosenvinge) Kornmann, 1989, *Acrochaetium microscopicum* (Nägeli ex Kützing) Nägeli, 1858, *H. farinosum*, *Ceramium aduncum* Nakamura, 1950, *Ceramium cimbricum*

H. E. Petersen, 1924, *Ceramium vagans* P. C. Silva, 1987, *G. mazoyerae*, and *M. ferulaceus* (Rh). Out of the algal turf, *Padina australis* Hauck, 1887 and *S. polycystum* (Ph) were the species forming upright-growing communities on remnants of coral colonies.

In the upper subtidal zone, a mosaic polydominant algal turf community occupied all substrata between colonies of live corals. *J. adhaerens*, *T. glomerulata*, *H. spinella* (Rh), and *C. racemosa* (Ch) were the main dominant species. *P. australis*, *S. polycystum*, and *S. sanyaense* (Ph) were common ones. The richness and species composition of epiphytes in the upper subtidal zone were similar to those of the lower intertidal zone.

Transect 2, 2018 and 2019. Alterations in the marine flora along the T2 area were registered only in the structure of polydominant communities. The composition of dominant and accompanying species changed only partially. The diversity and structure of mono- and bidominant communities remained the same as in 2017.

In 2018, the composition of dominant species changed in polydominant communities in the middle intertidal and upper subtidal zones. Specifically, in the middle intertidal zone, dominant species – *P. perforata* (Rh), *L. variegata* (Ph), and *C. racemosa* (Ch) – were not found, while *H. pannosa*, *H. spinella* (Rh), and *Caulerpa sertularioides* (S. G. Gmelin) M. Howe, 1905 (Ch) appeared. In the upper subtidal zone, dominant species – *A. fragilissima*, *J. adhaerens*, and *H. valentiae* (Rh) – were not registered (as it was before), while *J. capillacea*, *H. secunda*, *P. caerulescens* (Rh), and communities of upright-growing *S. sanyaense* and *P. australis* (Ph) appeared.

In 2019, insignificant changes in the flora along T2 were recorded only in the composition of dominant species in polydominant communities.

DISCUSSION

Adaptation of the coral reef ecosystem to moderate and extremely high nutrient concentrations. Earlier, we showed that DIN and orthophosphate levels in seawater of Luhuitou and Xiaodong Hai reefs (as most likely across all the Sanya Bay) are higher (3–5-fold and 10-fold, respectively) than those in clean waters of insular coral reefs (Titlyanov et al., 2011). About the same DIN and orthophosphate levels were noted as threshold concentrations for degradation of coral reefs resulting from eutrophication and subsequent macroalgal blooms at Kaneohe Bay in Hawaii, fringing reefs of Barbados, and inshore reefs within the lagoons of the Great Barrier Reef (Bell, 1992 ; Done, 1929 ; Hughes, 1994 ; Lapointe et al., 1997 ; Lapointe, 1997 ; Smith et al., 1981). In coral reefs, the concentrations of nutrients above the threshold ones are reported to induce growth and accumulation of biomass by frondose macroalgae provoking superabundant macroalgal blooms. Evidently, reefs exposed to chronic nutrient enrichment increase their primary productivity which can be mainly attributed to expansion of macroalgae.

Our previous floristic surveys at the Sanya Bay (Titlyanov et al., 2011, 2019) showed that this site is occupied by algal communities and species typical for healthy coral reefs. At the same time, bloom of green benthic macroalgae was observed in a few local areas of the Sanya Bay coast (Li et al., 2016). Moreover, Luhuitou reef is characterized by a high species diversity of hermatypic corals; among them, there are branching corals of genera *Acropora* and *Pocillopora* – indicators of healthy reefs (Fong & Paul, 2011 ; Littler et al., 2006 ; McManus & Polsenberg, 2004 ; Raffaelli et al., 1998 ; Rosenberg, 1985). In our opinion, the Luhuitou coral reef ecosystem in most sites of the coast has adapted to conditions of increased (moderate) nutrient concentration. It is currently stable; there are no signs of degradation, except for spots with heavy pollution, for example, the area of water flow from fish ponds. In the latter case, corals could lose their competitive ability in the struggle for the substrate and give way to highly productive algal species, and the coral reef might eventually turn into a "plant reef". However, our monitoring studies of the benthic flora in the area of constant heavy pollution by nutrients (2012–2017) did not reveal signs of ongoing degradation of the coral reef (alterations either in diversity or species composition of macrophytes and mass species of hermatypic corals) and its turning into a "plant reef" (Li et al., 2021, 2016). This gives reason to assume that the ecosystem of coral reefs can adapt to extremely high concentrations of nutrients. The main adaptive changes in the ecosystem to heavy pollution could be summarized as follows:

1) biomass of green algae in the upper and middle intertidal zones (exposed to air at low tide) and brown algae in the submerged zone (lower intertidal) increased significantly (by several times);
2) species diversity of green algae in the upper and middle intertidal zones increased, while species diversity of brown and red algae in the submerged zone decreased;
3) number of mono- and bidominant communities of algae in the upper intertidal zone increased, while polydominant communities in the middle intertidal zone disappeared;
4) in the communities of the upper and middle intertidal zones, absolute and relative numbers of dominant species in green algal communities increased, while the number of dominant red algae decreased over a range of tidal zones;
5) in polydominant communities, the species composition of both dominant and accompanying species changed.

Some of the listed above changes in the flora that occurred during nutrient water pollution were previously known, such as accumulation of green algal biomass (Fong & Paul, 2011 ; Lapointe, 1997 ; Littler et al., 2006 ; Raffaelli et al., 1998 ; Rosenberg, 1985) and increase in diversity (Li et al., 2021), while other alterations were recorded for the first time. The significance of these changes representing the ecosystem homeostasis could be ascertained only with a further long-term study of the reef ecosystem under conditions of heavy pollution.

Changes in the ecosystem under sharp decrease in nutrient concentration from heavy to moderate. In (Li et al., 2021), it is shown as follows: after the fish farm liquidation, concentration of nutrients in seawater opposite the outlet (T1) and at 100 m from it (T2) dropped by more than an order of magnitude; it is almost equal to the mean value for the Sanya Bay (Li, 2011 ; Li et al., 2016). At the same time, the values of indicators of other major environmental factors in 2017, 2018, and 2019 did not differ significantly.

In parallel, the following main alterations in the flora were recorded during the transition from heavy to moderate water enrichment with nutrients: for a year and a half, the taxonomic composition changed, the relative number of red algae increased, and the relative number of green algae decreased. The maximum similarity of the flora for T1 and T2 areas increased after the farm liquidation by 18 % and reached the value of 82 %. These alterations occurred mainly due to enrichment of the local benthic flora with unproductive annual species of red algae and depletion of highly productive species of green algae – ephemeral filamentous and membrane forms. These changes in species and taxonomic composition of the flora resulted in a decrease in the number of dominant species (mainly green o nes) and a sharp (even 6 months after the farm elimination) decrease in the mass of vegetation cover (Li et al., 2021).

As shown in this paper, within a year and a half after the fish farm liquidation, changes occurred in the number and structure of algal communities. Specifically, in the intertidal zone, the number of monodominant and bidominant algal turf communities decreased; in the middle intertidal zone, a polydominant algal turf community was formed; and in the lower intertidal and upper subtidal zones, the composition of dominant and accompanying species partially changed.

Along the T2 area (moderate pollution), alterations in the marine flora for 1.5 years were barely noticeable, and the only significant interannual change was registered in the composition of dominant and accompanying species in polydominant communities. Nature and dynamics of changes in the benthic flora along T1 give reason to talk about the adaptation of the ecosystem to new conditions of mineral nutrition by establishing homeostasis.

Conclusion. Our current findings once again confirmed our previously obtained data that the benthic flora in the Sanya Bay greatly varies in diversity, species composition, taxonomic composition, and the structure of algal communities in variously polluted coastal areas. Extremely high concentrations of nutrients in seawater near the outlet of polluted wastewater caused significant depletion in species diversity and abundance of unproductive annual and perennial red and brown algae, as well as enrichment of highly productive green species with opportunistic and often ephemeral algae. For the first time, we showed that a sharp decrease in nutrient concentration near the fish farm one year and a half after its liquidation resulted in a partial-to-complete restoration of macroalgal species diversity. We assumed that coral reef ecosystems on Hainan Island in areas with various (even extreme) nutrient pollution adapted to these conditions.

This work was financially supported by the National Natural Science Foundation of China (41476134), the Open Project of State Key Laboratory of Marine Resource Utilization in South China Sea (DX2017003), the Foundation of Hainan University (KYQD(ZR)1805), and the grant "China–Russia special funds 2018–2019" from the Chinese Academy of Sciences.

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СООБЩЕСТВА БЕНТОСНЫХ ВОДОРОСЛЕЙ КОРАЛЛОВЫХ РИФОВ ЗАЛИВА САНЬЯ (ОСТРОВ ХАЙНАНЬ, КИТАЙ) В МЕСТАХ, СИЛЬНО ЗАГРЯЗНЁННЫХ БИОГЕННЫМИ ВЕЩЕСТВАМИ, И ИХ ИЗМЕНЕНИЯ ПОСЛЕ УСТРАНЕНИЯ ИСТОЧНИКА ЗАГРЯЗНЕНИЯ

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Ранее установлено, что экстремально высокие концентрации биогенных веществ в морской воде в районе стока загрязнённых вод рыбной фермы на полуострове Лухуэйтоу (залив Санья) приводят к значительному сокращению видового разнообразия и обилия низкопродуктивных одно- и многолетних красных и бурых водорослей, а также к увеличению количества и биомассы высокопродуктивных зелёных водорослей. С 2017 по 2019 г. впервые были изучены изменения в количестве и структуре донных водорослевых сообществ в приливно-отливных зонах залива Санья после устранения источника загрязнения — ликвидации рыбной фермы. Показано, что снижение концентрации растворённого неорганического азота (DIN) (с ~ 20 до 2,5 μM) и ортофосфатов (с 5,0 до 0,2 μM) в морской воде существенно изменило разнообразие, видовой состав и структуру бентосных водорослевых сообществ. Через 1,5 года после ликвидации источника загрязнения основные показатели флоры стали близки в среднем к таковым умеренно загрязнённых участков залива Санья.

Ключевые слова: водоросли, остров Хайнань, Китай, эвтрофикация, восстановление