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# Seasonal changes in the intertidal algal communities of Sanya Bay (Hainan Island, China)

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A floristic study of marine macrophytic algae and Cyanobacteria in the splash and intertidal zones at Luhuitou reef, Sanya Bay, Hainan Island, China, was conducted during the rainy and dry seasons of 2008–2012 utilizing 148 of the most common species. Macrophytic algal diversity increased from the splash zone to the low intertidal zone, while cyanobacterial diversity decreased. In the upper and middle intertidal zones, the dominant species (primarily highly productive ephemerals) changed frequently throughout each year. In the low intertidal zone, the dominant species (mainly annual fleshy, foliose and coriaceous forms) also changed. In the dry season, species numbers were 33% higher than in the rainy season. During the rainy season, Cyanobacteria dominated the splash zone, while green and red algae dominated in increasing numbers from the upper to the low intertidal zones. During the dry season the splash zone was devoid of all macrophytic algae, and only one species of Cyanobacteria survived. In the upper intertidal, Cyanobacteria and red algae prevailed, while in the mid and low zones, red and green algae were the most diverse. In spite of heavy pollution in Sanya Bay, there was no evidence of dramatic changes in species numbers or composition, and the marine flora was similar to that of unpolluted regions in the Indo-Pacific.

Keywords: Hainan Island, intertidal, inventory, macrophytic algae, seasonality

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### INTRODUCTION

Recent studies have shown that long-term changes in the tropical marine flora can be caused by a number of natural and anthropogenic factors, and those annual and seasonal changes may be caused by both abiotic and biotic environmental factors (Fong & Zedler, 1993; Kennish, 1996; Pedersen & Borum, 1996; Kentula & DeWitt, 2003; Su *et al.*, 2009). The greatest seasonal floristic changes (especially in the intertidal zone) are known to be caused by environmental changes in light intensity, temperature, salinity, rainfall, nutrient concentration and wave action (Costa *et al.*, 2000, 2002; Ateweberhan *et al.*, 2006; Thakur *et al.*, 2008; Su *et al.*, 2009).

In the recently published sister study to this investigation, Titlyanov *et al.* (2013) investigated the distribution of algal and seagrass species in the upper subtidal zone of Sanya Bay, Hainan Island, China. In this investigation, the algal and seagrass species were shown not to have changed in species numbers and composition in spite of heavy pollution

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X. Li Email: lixiubao@scsio.ac.cn H. Huang Email: huanghui@scsio.ac.cn by dissolved inorganic nitrogen and phosphorus in the Bay. Seasonal changes did occur in the dominant subtidal species, but the turf community appeared only to change annually or periodically with stress. The present study examines the intertidal distribution of algal species during the rainy (RS) and dry seasons (DS) near the same site at Sanya Bay

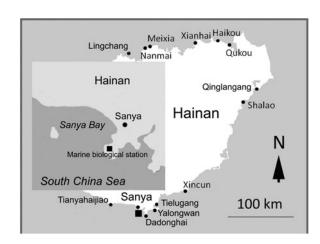


Fig. 1. Hainan Island (South China Sea, China) and the investigation area at Luhuitou reef in Sanya Bay.

where the subtidal studies took place. Hainan Island (Figure 1) is located in the South China Sea at the subtropical latitude of  $18^{\circ}10'-20^{\circ}9'N$   $108^{\circ}37'-111^{\circ}1'E$ . The annual mean sea surface temperature (SST) is  $26^{\circ}C$  (1970-2002) with an average seasonal range of  $12.1^{\circ}C$  (Sun *et al.*, 2005). The rainy season in the southern part of Hainan occurs from April to November and accounts for 95% of the yearly rainfall; the dry season occurs from November to April (Li, 2011).

The most common coastal ecosystems of Hainan Island are coral reefs. The highest biodiversity of coral reefs in Hainan occurred between the 1950s and 1960s (Gurianova, 1959) but severely decreased during the next 20 years (Hutchings & Wu, 1987; Zhang et al., 2006). Since the 1970s, at least 50% of the fringing reefs in Hainan Island have been destroyed by human activities, such as overfishing, land clearing, coral mining, aquaculture expansion and pollution (Zhang et al., 2006; Li, 2011). Recently, the eutrophication of Hainan coastal waters, particularly in the shallow gulfs, has increased due to greater tourist numbers, hotel building along the coast and mariculture in coastal ponds with wastes draining into the sea (Hutchings & Wu, 1987; Fiege et al., 1994; Zhang et al., 1996, 2004; Hodgson & Yau, 1997; Tadashi et al., 2008).

#### MATERIALS AND METHODS

### **Terminology**

To shorten our descriptions, we frequently use the historical and generalized term *algae* when referring to the following taxonomic groups listed in *AlgaeBase* (Guiry & Guiry, 2012): Rhodophyta (red algae), Heterokontophyta–Phaeophyceae (brown algae), Chlorophyta–Ulvophyceae and Siphonocladophyceae (green algae) and Cyanobacteria (blue–green algae). We also use the abbreviations Rh (Rhodophyta), Ph (Phaeophyceae), Ch (Chlorophyta) and Cy (Cyanobacteria) to clarify species affiliations. The term *macrophyte* is used to indicate only the Rh, Ph, and Ch.

### Study site, time and conditions

Investigations were conducted at Luhuitou reef, Sanya Bay, Hainan Island, China. The algae were collected from the intertidal zone in front of the Marine Biological Station of the South China Sea Institute of Oceanology (Figure 1) at the end of the rainy season 2008 (6–15 October), at the end of the dry season 2009 (6–22 April), at the end of the rainy season 2010 (15 November–3 December) and at the end of the dry season 2012 (3 February–26 April).

### Climatic characteristics of the investigated area

For two months before and one month during sampling (August–October 2008, February–April 2009, September–November 2010 and December 2011–February 2012), climatic characteristics such as SST, precipitation quantity, the average concentration of dissolved inorganic nitrogen (DIN) and orthophosphates (PO<sub>4</sub><sup>-3</sup>) in seawater were measured in the investigated area. Climatic characteristics were obtained from the weather station at the Marine Biological Station, while nutrient data were obtained at the stations close to Luhuitou reef from the Chinese Ecosystem Research

**Table 1.** Climatic characteristics of the investigated area.

Time of measurement	Surface seawater temperature (°C)	Rainfall DIN PO <sub>4</sub> <sup>-3</sup> (mm) (μM)(μM)		
August-October 2008	27.7-29.0.0	361.9	5.3	0.24
February—April 2009	24.2-26.0.8	28.3	4.8	0.40
September – November 2010	26.0-29.0.5	185.6	4.1	0.32
December 2011 – February 2012	20.0-26.0.2	14.4	4.5	0.36

Network (http://www.cern.ac.cn; Huang *et al.*, 2003). As shown in Table 1, the rainy seasons of 2008 and 2010 differed from the dry seasons of 2009 and 2012 by a lower SST (averaging  $^{\circ}$ C lower) and a rainfall that was 10 times higher (averaging 270 mm during the three months). The  $PO_4^{-3}$  was higher in dry seasons than in wet seasons (averaging 0.1  $\mu$ M) while there was no difference for DIN.

### Collection, conservation and identification of marine algae

Marine macrophytic algae and Cyanobacteria were collected in the splash zone and in the upper, middle and lower intertidal zones. At the sites investigated, the splash zone consisted of a horizontal belt (up to 20 cm wide) on the vertical walls of an artificial dam built of dead colonies of massive corals. The upper intertidal zone consisted of a sloping shore (2-3 m wide) with hard substrates composed of stones and dead coral fragments of various shapes and sizes, tossed about by storms. The sloping shore of the middle intertidal zone (~10 m wide) consisted mainly of flat carbonate patches intermixed with coral debris and stones. The lower intertidal zone (~15 m wide) was composed primarily of dead colonies of massive and branched corals intermixed with sand and small fragments of dead branched corals. Algal sampling was carried out by foot or via snorkeling during low and high tides in an area 50 m wide along the shore. Marine algae were collected from all types of substrata. Quadrats of the following sizes were haphazardly placed, photographed and then completely cleared for the study:  $10 \times 10 \text{ cm}^2$  (for algal turf communities) and 25 × 25 cm<sup>2</sup> (for communities with large algae). More than 50 quadrats of hard substrata and 20 quadrats of sandy/muddy substrata were sampled during each season. Freshly collected material was identified using monographic publications, floristic studies and systematic articles indicated in Titlyanov et al. (2013).

The systematics and nomenclature followed Guiry & Guiry (2012) (AlgaeBase, searched 2012). The collections of both macrophytes and their epiphytes were preserved as dried herbarium specimens and were deposited in the herbarium at A.V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences, Palchevskogo 17, Vladivostok, 690041, Russian Federation.

### Assessment of algal communities

For qualitative studies of the species during each season, the occurrence data from all quadrats in each tidal zone were merged to compile the total counts. For quantitative assessment, the individual quadrats were used to determine both

seasonal abundance and dominance. Abundance estimates were as follows: rare species were those found in 10% or less of all quadrats studied; common species were those found in at least 50% of all quadrats studied; and abundant species were those found in all (or almost all) of the quadrats studied. In Table 2 rare, common and abundant species are marked as (+), (++) and (+++), respectively. Algal dominance was visually or photographically estimated (Titlyanov *et al.*, 2005) and defined as: mono-dominant if algal cover of a single species amounted to 50% of the surface area; bi-dominant if two species amounted to more than 50%; poly-dominant if more species (commonly 3–5) were involved.

#### RESULTS

### Diversity of species in the intertidal zones

In total 176 species of marine macrophytes and Cyanobacteria were found in the intertidal zone of Luhuitou Peninsula during the seasonality investigations. However, 28 of these taxa were exceedingly rare or found only once. These taxa were, therefore, excluded from the quantitative study. The remaining more common 148 species were chosen for the seasonality study. These species, detailed in Table 2, include 65 species (44%) of Rhodophyta, 31 species (21%) of Chlorophyta, 22 species (15%) of Phaeophyceae, and 30 species (20%) of Cyanobacteria. The 28 excluded taxa are listed in Table 3.

A summary of the year-around intertidal distribution of the 148 species is shown in Figures 2 and 3. A clear increasing gradient in species numbers was found to occur from the splash zone to the low intertidal zone ranging from only nine species in the splash zone to 124 species in the low intertidal zone. There was also a gradient in the tidal occurrence of the major algal groups. The splash zone consisted of almost entirely of blue–green algae (89% of the species). The upper intertidal zone was also dominated by blue–green algae (37% of the species), but red and green algae were also fairly diverse (each with  $\sim$ 27% of the species). The mid and low intertidal zones were both dominated by red algae ( $\sim$ 50%) followed by green algae ( $\sim$ 24%) with a lesser representation of both brown and blue–green algae.

The proportions of the various algal groups and the species composition varied between the rainy and dry seasons, and both seasonal and aseasonal species were present.

### Rainy season communities (2008, 2010)

#### DIVERSITY OF SPECIES COMPOSITION

In 2008 and 2010, 76 and 80 species were collected during each rainy season, and little variation occurred between the two years (Figure 4). Each year, approximately 50% of the species were red algae, 23% were green, 15% brown, and 12% were blue-green. The two years were combined to show the tidal zone composition (Figure 5). During the rainy seasons, nine species occurred in the splash zone, and the numbers increased in each zone towards the low intertidal zone, where 72 species occurred. The blue-green algae showed a reverse trend, with eight species occurring in the splash zone and only two in the low intertidal.

STRUCTURE OF ALGAL COMMUNITIES DURING THE RAINY SEASONS

In 2008 and 2010, algae were found in all zones investigated.

Rainy season of 2008

In the splash zone, algae were found in holes on the seaward side of dead coral boulders (Figure 6A). Two types of bluegreen algal films were found on the surface of the holes: dark blue (almost black) and bright green colour films. Coleofasciculus chthonoplastes was dominant in the community of the dark blue film. In the bright green film, Oscillatoria limosa was dominant.

In the upper intertidal zone large coral boulders were occupied by mono-dominant communities of algal turf dominated by the green alga *Ulva clathrata* (Figure 6B). Some dead coral pebbles were occupied by algal turf communities dominated by *Ceramium procumbens* (Rh) and *Cladophora vagabunda* (Ch). In the upper intertidal zone, the most widespread monodominant community was the red algal crust *Hildenbrandia rubra*. This species overgrew stones but not dead coral fragments (Figure 6C). *Parvocaulis clavatus*, *P. parvulus*, *Phyllodictyon anastomosans*, *Cladophoropsis fasciculata* (Ch), *Lobophora variegata*, *Sphacelaria rigidula* (Ph), *Gelidium pusillum*, *Parviphycus pannosus* and *Peyssonnelia rubra* (Rh) were found on some dead coral blocks in turf communities.

In the middle intertidal zone, the algal turf consisted of a bi-dominant community of *Cladophora vagabunda* (Ch) and *Ceramium* sp. (Rh), which occupied mainly the flat carbonate reef bases (Figure 6D). *Gelidium pusillum, Peyssonnelia rubra, P. conchicola* (Rh), *Neoralfsia expansa and Lobophora variegata* (Ph) occurred just outside the community. A mono-dominant community of *Hildenbrandia rubra* was also found growing on stones and pebbles.

The low intertidal zone was occupied primarily by polydominant turf algal communities with a mosaic dominance of Amphiroa foliacea, Gelidium pusillum and Lobophora variegata. Outside the main community, Dictyosphaeria cavernosa, Neomeris annulata (Ch), Gelidiella acerosa, Jania adhaerens, J. capillacea, J. ungulata f. brevior, Peyssonnelia rubra, Lithothamnion phymatodeum (Rh), Sargassum polycystum and S. sanyaense (Ph) were often found on dead coral blocks and at the base of coral reefs.

Rainy season of 2010

In the splash zone, the seaward holes of the same dead coral boulders were overgrown by blue-green algal films that were dark green in colour and covered with sand. *Microcystis reinboldii* and *Calothrix* sp. (Cy) were predominant in the film.

Hard substrate in the upper intertidal zone was occupied by a mono-dominant community of the green turf alga *Ulva clathrata*. Flat stones were frequently overgrown by a mono-dominant community of the red crustose alga *Hildenbrandia rubra*.

In the middle intertidal zone, the algal turf community consisted of a bi-dominant community of the green alga *Cladophora laetevirens* and the red alga *Parviphycus pannosus* inhabiting mainly flat carbonate reef bases. A mono-dominant community of *Hildenbrandia rubra* was common on the upper surfaces of stones where *Peyssonnelia rubra* and *P. conchicola* were also found. On the shaded surface of coral boulders, a mono-

**Table 2.** Species composition and abundance of marine algae and Cyanobacteria in the intertidal zone of the Luhuitou Peninsula 2008–2012: 1, the splash zone; 2, the upper intertidal zone; 3, the middle intertidal zone; 4, the low intertidal zone; E, epiphyte; En, endophyte; +, rare; +, common; +, abundant.

Species	Tidal zone	Tidal zone Rainy season		Dry season	
		2008	2010	2009	2012
RHODOPHYTA					
Acanthophora muscoides (Linnaeus) Bory de Saint-Vincent	4			++	++
Acanthophora spicifera (M. Vahl) Børgesen	3			+	
	4			+++	++
Acrochaetium hypneae (Børgesen) Børgesen	3			+ E	
71 ( 0 ) 0	4	+ E	+E	+ E	++ F
Acrochaetium microscopicum (Nägeli ex Kützing) Nägeli in Nägeli &	4	, –	, –	, -	++ E
Cramer	7				
Amphiroa foliacea J.V. Lamouroux	4	+++	+	+	++
Amphiroa fragilissima (Linnaeus) J.V. Lamouroux	4	+	+	+	+
Centroceras clavulatum (C. Agardh) Montagne	3	+	'	++	+++
Schilocolus curvuululli (S. 115arcii) Montaglic		++ E	++	++ E	++
Centroceras minutum Yamada	4	TT L	TT	++ E	++ E
Ceramium camouii E.Y. Dawson	4				++ E
	3			++	
Ceramium cingulatum Weber-van Bosse	3		++ E		
	4	+	++ E	+	+ E
Ceramium comptum Setchell and N.L. Gardner	2	+++			
Ceramium macilentum J. Agardh	3			+	
	4			+	
Ceramium marshallense E.Y. Dawson	4		+ E		++
Ceramium sp.	3	+++			
Ceramium tenerrimum (G. Martens) Okamura	3				++
Ceramium vagans P.C. Silva	2	+			
•	3			+	
	4	+ E	+	+	+ E
Ceratodictyon intricatum (C. Agardh) R.E. Norris	3	•	·	+	
Service week of the control of the c	4			'	+
Ceratodictyon spongiosum Zanardini	4	++	++	++	++
Champia parvula (C. Agardh) Harvey		7.7	77	+	+
Chroodactylon ornatum (C. Agardh) Basson	4			+ E	Т
Enroductyton ornatum (C. Agardii) bassoii	2				+ E
	3	1 1 17	1 17	+ E	
	4	++ E	+ E	+ E	++ E
Colaconema gracile (Børgesen) Ateweberhan & Prud'homme van Reine	3			+ E	
	4	+ E			+ E
Corallophila kleiwegii Weber-van Bosse	3				+ E
3	4	+	++ E	+ E	++ E
Erythrotrichia carnea (Dillwyn) J. Agardh	2	+ E	+	+ E	+ E
Siyunonomo cuntou (2 minyii) )i 11gurun	3	++ E	++ E	+ E	+ E
		++ E	++ E	++ E	++ E
Gayliella flaccida (Harvey ex Kützing) T.O. Cho & L.J. McIvor	4	TT L	77 L	++ E	77 L
Guyilettu fitaccittu (Harvey ex Kutzing) 1.0. Cho & L.j. Mctvoi	3	1 1 E	++ E		1 1 E
Coult lle toulouii (EV Donnes) TO Che 9 CM Per	4	++ E	++ E	++ E	++ E
Gayliella taylorii (E.Y. Dawson) T.O. Cho & S.M. Boo	3	+++		+ E	
Gelidiella acerosa (Forsskål) Feldmann & G. Hamel	4	+		+	+
Gelidium pusillum (Stackhouse) Le Jolis	2	++	+	++	
	3	++	+	+	+
	4	+++	++	+	+
Gelidium pusillum var. cylindricum W.R. Taylor	2		+	++	
	4	+	+	+	+
Gracilaria salicornia (C. Agardh) E.Y. Dawson	4			+	+
Gracilaria tenuistipitata C.F. Chang & B.M. Xia	3			+	
Herposiphonia secunda (C. Agardh) Ambronn	3			+	
	4	+ E	++ E	+	+
Herposiphonia secunda f. tenella (C. Agardh) M.J. Wynne	3		112	++	'
20. poorphornin occument is noticine (O. rigaran) 141.j. 44 yillic		+	+	+	+ E
Hildanhrandia ruhra (Sommarfalt) Managhir:	4				
Hildenbrandia rubra (Sommerfelt) Meneghini	2	+++	++	++	++
	3	++	++	+++	+++
	4	++	+	+	++
Hydrolithon farinosum (J.V. Lamouroux) D. Penrose & Y.M.	2		++ E		
Chamberlain					

Table 2. Continued

Species	Tidal zone	Rainy sea	son	Dry season	
		2008	2010	2009	2012
	3	+ E	+ E	+ E	+ E
	4	+ E	+E	+ E	++ E
Hydropuntia edulis (S.G. Gmelin) Gurgel & Fredericq	4			+	+
Hydropuntia eucheumatoides (Harvey) Gurgel & Fredericq	4	+	+	++	++
Hypnea esperi Bory de Saint-Vincent	4			+	+
Hypnea pannosa J. Agardh	4		+		+
Hypnea spinella (C. Agardh) Kützing	3	_		+ E	+
T	4	+ E	+	++	+++
Hypnea valentiae (Turner) Montagne	3			+	
I II IV I	4	+	+	++	+++
Jania adhaerens J.V. Lamouroux	4	+	+	++ ++ E	+
Jania capillacea Harvey	3	+ E	1	++ E + E	++
Jania ungulata f. brevior (Yendo) Yendo	4		+		++
Leveillea jungermannioides (K. Hering & G. Martens) Harvey	4	+	++	+ +	+++
Liagora ceranoides J.V. Lamouroux	4			+	++
Lingora teranolaes J.V. Lamouroux	3			++	++
Lithothamnion phymatodeum Foslie	4	++	+	+	++
Lithothamnion prymatoueum Posne Lithothamnion sp.	4 2	TT	Т	+	TT
Eunomanmon sp.		+	++	++	+
	3 4	+	+	+	+++
Lomentaria corallicola Børgesen	2	'	'	+++	1 1 1
zemenum zeigeen	3			+	++
	4	+	+	++	++
Neosiphonia sphaerocarpa (Børgesen) M.S. Kim & I.K. Lee	3	'	'	+	
7	4	+	++	+	++ E
Palisada perforata (C. Agardh) K.W. Nam	3	·		+++	++
<i>J. J</i>	4	+	+	+++	+++
Parviphycus adnatus (E.Y. Dawson) B. Santelices	2			++	
• •	3	+		++	
	4	+	+	+	+
Parviphycus pannosus (Feldmann) G. Furnari	2	++	++	++	
	3	++	+++	+++	++
	4	+	++	+	+
Peyssonnelia conchicola Piccone & Grunow	3	+	++	+	+
	4	+	+	++	+
Peyssonnelia inamoena Pilger	4	+	+	+	+
Peyssonnelia rubra (Greville) J. Agardh	2	+	+		
	3	++	++	++	++
	4	++	++	++	++
Pneophyllum fragile Kützing	4			+ E	+ E
Polysiphonia howei Hollenberg	4				++
Polysiphonia japonica var. savatieri (Hariot) Yoon	3			+++	
Polysiphonia scopulorum var. villum (J. Agardh) Hollenberg	4				++
Polysiphonia subtilissima Montagne	3			+	
D. 1 1: II 1 (IZ., ; ) C ( I; 0 II 1	4		+		
Pterocladiella caerulescens (Kützing) Santelices & Hommersand	4				++
Spyridia filamentosa (Wulfen) Harvey in Hooker	3			++	++
Stylonema alsidii (Zanardini) K.M. Drew	4	+ E		++ + E	+++
Stytomethia ustati (Zanatunn) K.M. Diew	3	+ E + E	++ E	+ E + E	++ E
Tolypiocladia glomerulata (C. Agardh) F. Schmitz	4	T L	7 <b>7</b> L	+ E	-T-T E
100/processing geometrianus (O. 11gartin) 1. Ocininiz	3 4			+++	+
Wrangelia argus (Montagne) Montagne	4			+ E	++
OCHROPHYTA	т			, 1	1 1
Canistrocarpus cervicornis (Kützing) De Paula & De Clerck	4			+	++
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier	3			+	++
The state of the s	4	+	+	++	++
Dictyota bartayresiana J.V. Lamouroux	4	•	'	+	+
Dictyota friabilis Setchell	4			++ E	++
Dictyota implexa (Desfontaines) J.V. Lamouroux	3			+	

Continued

Table 2. Continued

Hinksia coniforal (Bargesen) I.A. Abbott	Species	Tidal zone	Rainy seas	Rainy season		Dry season	
Hinckis confirm (Borgsen) LA. Abbott			2008	2010	2009	2012	
Hinckis configer (Bergsen)   LA Abbott	Feldmannia mitchelliae (Harvey) HS. Kim	4			++ E	++ E	
Hydroclathrus (C. Agardh) M.A. Howe						++	
Liyahrodaihris tenuis C.K. Tseng & Lu	,	4				++ E	
Hydroclathrus tenutic C.K. Teng & Lu	Hydroclathrus clathratus (C. Agardh) M.A. Howe	3			+	+	
Fuerbingfella elachistacformis (Heydrich) M. Balakrishnan & Kinkar		4			++	++	
Lobophora variegata (J.V. Lamouroux) Womersley ex Oliveira 2		4			++	++	
Labophora variagata (J.V. Lamouroux) Womersley ex Oliveira   2	Kuetzingiella elachistaeformis (Heydrich) M. Balakrishnan & Kinkar	3			++		
3		4	+	++	++	+	
A	Lobophora variegata (J.V. Lamouroux) Womersley ex Oliveira	2	+				
Neorafia expansa (J. Agardh) PE. Lim & H. Kawai ex Cormaci & 2		3	+	++	+		
Sphacelaria tribuloides Meneghini		4	+++	+++	++	+++	
Padina australis   Hauck		2	+	+	+++	+	
Padina dustralis Hauck		3	++	+	++	++	
Padina boysuna Thivy		4	+	+	++	+++	
Padina minor Yamada	Padina australis Hauck	4			++	++	
Sargassum polycystum C. Agardh  4	Padina boryana Thivy			+	+		
Sargassum polyostum C. Agardh	Padina minor Yamada	3	+	++	+	++	
Sargassum sanyaense Tseng & Lu		4			++	+++	
Sphacelaria fissca (Hudson) S.F. Gray   2	Sargassum polycystum C. Agardh	4	+	+	+	+	
Sphacelaria fusca (Hudson) S.F. Gray   2	Sargassum sanyaense Tseng & Lu	4	+	+	++	++	
Sphacelaria novae-hollandiae Sonder	Sphacelaria fusca (Hudson) S.F. Gray	2	+				
Sphacelaria novae-hollandiae Sonder		3	+				
Sphacelaria rigidula Kützing   2		4	+				
3	Sphacelaria novae-hollandiae Sonder	4	+	++	++ E	+	
Sphacelaria tribuloides Meneghini	Sphacelaria rigidula Kützing	2			+		
Sphacelaria tribuloides Meneghini		3	++	++	+		
Sphacelaria tribuloides Meneghini		4		+		+	
Turbinaria ormata (Turner) J. Agardh         4         +         +         +         +         +         +         CHLOROPHYTA         +         En         +         +         En         +         +         En         +	Sphacelaria tribuloides Meneghini		+	+	+	+++	
Acrochaete leptochaete (Huber) R. Nielsen	Turbinaria ornata (Turner) J. Agardh	4	+	+	++	+	
Acrochaete (Huber) R. Nielsen	Acrochaete geniculata (N.L. Gardner) O'Kelly	3			+ En		
Acrochaete viridis (Reinke) R. Nielsen		4			+ En		
Boodlea composita (Harvey) F. Brand	Acrochaete leptochaete (Huber) R. Nielsen	4			+ En	+ En	
Bornetella nitida Munier-Chalmas ex Sonder	Acrochaete viridis (Reinke) R. Nielsen	4				++ E	
Bornetella nitida Munier-Chalmas ex Sonder	Boodlea composita (Harvey) F. Brand	3			+		
Bornetella oligospora Solms-Laubach		4			+	+	
Bornetella sphaerica (Zanardini) Solms-Laubach		4			+	+	
Bornetella sphaerica (Zanardini) Solms-Laubach   4	Bornetella oligospora Solms-Laubach	3			+		
Strong to the content of the conte		4			+	+	
Caulerpa serrulata (Forsskål) J. Agardh	Bornetella sphaerica (Zanardini) Solms-Laubach	4			+	+	
Caulerpa serrulata (Forsskål) J. Agardh       4       ++       +         Chaetomorpha linum (O.F. Müller) Kützing       2       +       +         3       +       +       +         4       +       ++       +         Chlorochytrium cohnii E.P. Wright       4       +       ++       +         Cladophora laetevirens (Dillwyn) Kützing       2       +       ++       +       +         Cladophora socialis Kutzing       2       +       ++       + <td>Bryopsis pennata J.V. Lamouroux</td> <td>3</td> <td></td> <td></td> <td>+</td> <td></td>	Bryopsis pennata J.V. Lamouroux	3			+		
Chaetomorpha linum (O.F. Müller) Kützing       2       + <td></td> <td>4</td> <td></td> <td></td> <td>++</td> <td>+</td>		4			++	+	
3	Caulerpa serrulata (Forsskål) J. Agardh	4			++	+	
4	Chaetomorpha linum (O.F. Müller) Kützing	2	+	+			
Chlorochytrium cohnii E.P. Wright       4       ++ + + + + + + + + + + + + + + + + + +		3		+	+		
Cladophora laetevirens (Dillwyn) Kützing       2       ++       ++       +       +       ++       ++       +       +       +       ++       + <td< td=""><td></td><td>4</td><td>+</td><td>++</td><td>+</td><td>+</td></td<>		4	+	++	+	+	
3	Chlorochytrium cohnii E.P. Wright	4				++ En	
4	Cladophora laetevirens (Dillwyn) Kützing	2			++	+	
4		3	+	+++	+++		
Cladophora socialis Kutzing       2       +         4       +       +         Cladophora vagabunda (Linnaeus) Hoek       2       +++       ++         3       +++       +       +         4       ++       +       +       +         Cladophoropsis fasciculata (Kjellman) Wille       2       +       +       +       +         3       +       +       +       +       +       +         Cladophoropsis membranacea (Hofman Bang ex C. Agardh)       2       +       +       +       +         Børgesen       +				++	+		
Cladophora vagabunda (Linnaeus) Hoek	Cladophora socialis Kutzing		+				
3		4				+	
3	Cladophora vagabunda (Linnaeus) Hoek		+++	++			
4	-	3	+++			+	
Cladophoropsis fasciculata (Kjellman) Wille  2 + + + + + + + + + + + + + + + + + +				++	+		
3 + + + + + Cladophoropsis membranacea (Hofman Bang ex C. Agardh) 2 + Børgesen	Cladophoropsis fasciculata (Kjellman) Wille						
4 + + + + + Cladophoropsis membranacea (Hofman Bang ex C. Agardh) 2 + Børgesen		3				+	
Cladophoropsis membranacea (Hofman Bang ex C. Agardh) 2 + Børgesen				+			
Børgesen	Cladophoropsis membranacea (Hofman Bang ex C. Agardh)						
	•	4		++			

Continued

Table 2. Continued

Species	Tidal zone	Rainy seas	on	Dry season	
		2008	2010	2009	2012
Dictyosphaeria cavernosa (Forsskål) Børgesen	3	++		+	++
	4	++	++	+	++
Neomeris annulata Dickie	4	+	+	+	+
Ostreobium quekettii Bornet & Flahault	1		++		
	4				+ En
Parvocaulis clavatus (Yamada) S. Berger, U. Fettweiss, S. Gleissberg, L.B. Liddle, U. Richter, H. Sawitzky & G.C. Zuccarello	2	+			
	3	+		++	
	4	+			
Parvocaulis exiguus (Solms-Laubach) S. Berger, U. Fettweiss, S. Gleissberg, L.B. Liddle, U. Richter, H. Sawitsky, H. & G.C. Zuccarello	3			++	
D I (01 I 1 1) 0 D II D II O	4	+		+	+
Parvocaulis parvulus (Solms-Laubach) S. Berger, U. Fettweiss, S. Gleissberg, L.B. Liddle, U. Richter, H. Sawitsky & G.C. Zuccarello	2	+			
	3	+		+	
DI II II .	4	+		+	+
Phyllodictyon anastomosans (Harvey) Kraft & M.J. Wynne	2	+			
	4	+	+++	+	+
Rhizoclonium riparium (Roth) Harvey	3	+ E		+	
	4	++ E	+ E	+	+ E
Rhizoclonium riparium var. implexum (Dillwyn) Rosenvinge	2			+	
	3		+	++	
	4	+	++	+	+ E
Ulva clathrata (Roth) C. Agardh	2	+++	+++	+++	+
	3	+	+ E	+++	+ _
	4	++	++	++	+ E
Ulva flexuosa Wulfen	2	+			+
	3				+
	4	+	+	+	+
Ulva lactuca Linnaeus	3			++	+
III III ODANII	4	+	+	++	+
Ulva prolifera O.F. Müller	4	+	+	+	+
Ulvella lens P.L. Crouan & H.M. Crouan	4	+ E	++ E	+ E	+ E
Valonia aegagropila C. Agardh	4		+		+
CYANOBACTERIA					
Aphanocapsa litoralis Hansgirg	1	++			
Caladada a susais a Manasiakia	2				++
Calothrix aeruginea Woronichin	4			ı P	++
Calothrix confervicola (Dillwyn) C. Agardh	3	+		+ E	
Calathriu contarenii (Zanardini) Bornet & Flahault	2				++
Calothrix sp. Chamaecalyx swirenkoi (Sirsov) Komárek & Anagnostidis	1		+++		
	2				++
Chroococcus turgidus (Kützing) Nägeli Coleofasciculus chthonoplastes (Gomont) M. Siegesmund, J.R.Johansen and T. Friedl	2 1	+++	+		++
J.R.Jonansen and T. Friedi	1	+++			
	4			+++	++
Gardnerula xishaensis Tseng & Hua	2	++			
Hyella caespitosa Bornet & Flahault	2				++
Lyngbya aestuarii Liebman ex Gomont	3			+	
	4			+	
Lyngbya confervoides C. Agardh ex Gomont	4				+
Lyngbya majuscula Harvey ex Gomont	2			++	
	3			+++	
	4	++	+++	++	
Lyngbya martensiana Meneghini ex Gomont	3	+			
Lyngbya semiplena J. Agardh ex Gomont	2			++	
	4		+++	+	
Mastigocoleus testarum Lagerheim ex Bornet & Falhault	1		++		
	2				++
	4			++	

Continued

Table 2. Continued

Species	Tidal zone	Rainy seas	son	Dry season	1
		2008	2010	2009	2012
Microcystis reinboldii (Richter) Forti	1		+++		++
	2				+++
Oscillatoria bonnemaisonii (P.L. Crouan & H.M. Crouan) P.L. Crouan & H.M. Crouan ex Gomont	2			++	
	3			+	++
Oscillatoria limosa C. Agardh ex Gomont	1	+++			
	2		+		
	3		+++	++	+
	4			+	++
Oscillatoria margaritifera Kützing ex Gomont	3	++			
	4			+	++
Oscillatoria princeps Vaucher ex Gomont	4				++
Oscillatoria sancta Kützing ex Gomont	2				++
	3		++		
Oscillatoria sp.	1	++			
Phormidium nigroviride (Thwaites ex Gomont) Anagnostidis & Komárek	3				+
Phormidium simplicissimum (Gomont) Anagnostidis & Komárek	2				++
Phormidium sp.	2		++		
•	4			+++	
Planktothrix agardhii (Gomont) Anagnostidis & Komárek	4			+++	
Spirulina major Kützing ex Gomont	1	++			
Spirulina subtilissima Kützing ex Gomont	2		++		
Trichocoleus tenerrimus (Gomont) Anagnostidis	2				++
Ç	4				++

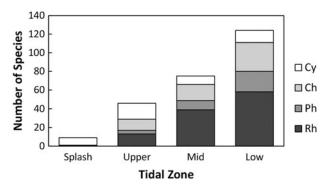
dominant community of the red crustose alga *Lithothamnion* sp. was common. In the intertidal pools, fragments of dead branched corals were covered by a blue–green algal film composed of *Oscillatoria limosa*. Outside of the investigated communities, the green algae *Ulva clathrata*, *Chaetomorpha linum* and the brown alga *Padina minor* were also found.

The low intertidal zone was commonly occupied by turf algal communities and included a poly-dominant community (Figure 6E) dominated by the green alga *Cladophora laetevirens* and the red algae *Parviphycus pannosus* and *Corallophila kleiwegii*.

Vertical walls of dead coral blocks were inhabited by a mono-dominant community of the brown alga Lobophora variegata. On dead coral fragments dwelled Gelidium pusillum, Jania adhaerens, Peyssonnelia rubra, P. conchicola, Hypnea pannosa (Rh), Sargassum polycystum, S. sanyaense (Ph) and Cladophora vagabunda (Ch). On gravelly/sandy bottoms between dead coral blocks, the red alga Ceratodictyon spongiosum and the seagrass Thalassia hemprichii were common. Communities of blue-green algae dominated by Lyngbya semiplena and L. majuscula often covered the turf communities.

Table 3. Rarely found species excluded from the seasonality study.

Rhodophyta	Rhodophyta (continued)
Acrochaetium daviesii (Dillwyn) Nägeli	Sahlingia subintegra (Rosenvinge) Kornmann
Acrochaetium secundatum (Lyngbye) Nägeli	
Actinotrichia fragilis (Forsskål) Børgesen	Ochrophyta, Phaeophyceae
Antithamnion antillanum Børgesen	Myrionema strangulans Greville
Ceramium cimbricum H.E. Petersen	
Ceramium borneense Weber-van Bosse	Chlorophyta
Ceratodictyon scoparium (Montagne & Millardet) R.E. Norris	Anadyomene wrightii Harvey ex J.E. Gray
Champia vieillardii Kützing	Chaetomorpha gracilis Kützing
Chondrophycus parvipapillatus (C.K. Tseng) Garbary & J.T. Harper	Cladophora horii Hoek & M. Chihara
Erythrocladia irregularis Rosenvinge	Gomontia polyrhiza (Lagerheim) Bornet & Flahault
Griffithsia rhizophora Grunow ex Weber-van Bosse	Penicillus sibogae A. Gepp and E.S. Gepp
Herposiphonia parca Setchell	Phaeophila dendroides (P.L. Crouan & H.M. Crouan) Batters
Hydrolithon boreale (Foslie) Y.M. Chamberlain	Ulothrix flacca (Dillwyn) Thuret
Lophosiphonia cristata Falkenberg	Ulothrix implexa (Kützing) Kützing
Neosiphonia tongatensis (Harvey ex Kützing) M.S. Kim & I.K. Lee	Ulva compressa Linnaeus
Pterocladiella capillacea (S.G. Gmelin) Santelices & Hommersand	Ulva ralfsii (Harvey) Le Jolis



**Fig. 2.** Composition of the tidal zones by algal group. Cy, Cyanobacteria; Ch, Chlorophyta; Ph, Phaeophyceae; Rh, Rhodophyta.

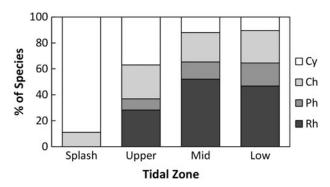


Fig. 3. Percentage composition of the tidal zones by algal group.

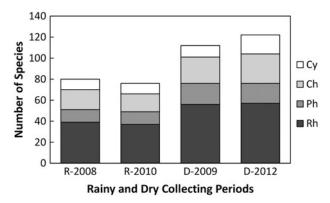


Fig. 4. Species diversity during the four collecting periods.

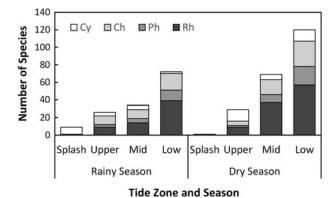


Fig. 5. Seasonal occurrence of algae by tidal zone.

### Algal communities during dry seasons (2009, 2012)

#### DIVERSITY OF SPECIES COMPOSITION

In 2009 and 2012, 112 and 122 species, respectively, were found during the dry seasons. Here as well, there was only a slight variation between the years (Figure 4). The increase in species numbers during 2012 is due primarily to the occurrence of seven additional blue-green algal species during this year. However, the overall proportion of the species groups was still very similar. Approximately 48% of the species were red algae, 23% were green, 27% were brown algae and 10–15% were blue-green. The tidal distribution of the major groups during the combined years (Figure 5) revealed a more extreme distribution trend, with only one species occurring in the splash zone and 120 occurring in the low intertidal. During the dry seasons, the blue-green algal diversity increased irregularly through the tide zones from one species in the splash zone to 13 in the low intertidal zone.

### STRUCTURE OF ALGAL COMMUNITIES DURING THE DRY SEASONS

Dry season of 2009

During this season, the large coral boulders in the upper intertidal zone were occupied by a mono-dominant community of the crustose brown alga *Neoralfsia expansa* and by algal turf communities dominated by the red alga *Lomentaria corallicola* and the green alga *Ulva clathrata*.

In the middle intertidal zone, the algal turf community consisted of a mono-dominant community of the red alga *Polysiphonia japonica* var. *savatieri*, which occupied mainly the flat carbonate reef bases. A mono-dominant community of *Ulva clathrata* occupied large boulders, where the main accompanying species were *Parviphycus adnatus* and *Herposiphonia secunda* f. *tenella*. A mono-dominant community of the red alga *Hildenbrandia rubra* was common on the upper surface of stones. On the shaded surface of the coral boulders, a mono-dominant community of the red crustose alga *Lithothamnion* sp. was common.

The low intertidal zone was also commonly occupied by turf algal communities, where *Acanthophora spicifera*, *Palisada perforata*, *Tolypiocladia glomerulata* (Rh) dominated. More than 30 species were found outside of these communities. Blue–green algae often occurred on the algal turf and consisted of two kinds of spots ranging from 100 to 600 cm² in size: dark brown spots dominated by *Coleofasciculus chthonoplastes* and *Oscillatoria* spp. and green spots of irregular form dominated by *Planktothrix agardhii* and *Lyngbya majuscula*.

### Dry season of 2012

During this season, the upper intertidal zone was mainly occupied by a poly-dominant community of blue-green algae found in the surface layer (2 mm thick) of dead coral blocks. Chroococcus turgidus, Microcystis reinboldii, Hyella caespitosa, Aphanocapsa litoralis, Chamaecalyx swirenkoi, Phormidium simplicissimum, Calothrix contarenii and Mastigocoleus testarum were common. The green algae Ulva flexuosa, U. clathrata and Cladophora laetevirens were also present.

In the middle intertidal zone, the carbonate base of the reef flat was occupied by a mono-dominant community of

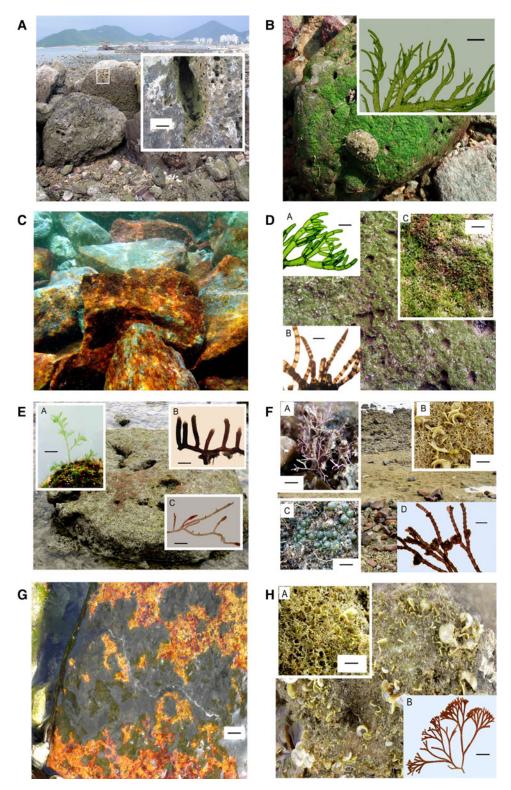


Fig. 6. Sampling sites and algal communities in Luhuitou reef. Sampling sites (in white frame) at the splash zone (A: rainy season, 2008); the upper intertidal mono-dominant community of algal turf (B, insert: the dominant green alga *Ulva clathrata*, rainy season, 2008); the upper intertidal mono-dominant community of the crustose red alga *Hildenbrandia rubra* (C: rainy season, 2008); the middle intertidal bi-dominant community of *Cladophora vagabunda* and *Ceramium* sp. (D, inserts: (A) *Cladophora vagabunda*; (B) *Ceramium* sp.; (C) algal community, rainy season, 2008); low intertidal turf algal communities where *Cladophora laetevirens* (insert A), *Parviphycus pannosus* (insert B), and *Corallophila kleiwegii* (insert C) were dominating (E: rainy season, 2010); the middle intertidal mono-dominant community of *Centroceras clavulatum* (F, inserts: (A, B, C) the accompanying species *Jania capillacea, Padina minor* and *Dictyosphaeria cavernosa*, relatively; insert: (D) the dominant species *Centroceras clavulatum*; the dry season, 2012); the middle intertidal mono-dominant community of *Neoralfsia expansa* overgrowing the crustose red alga *Hildenbrandia rubra* (G: dry season, 2012); the low intertidal poly-dominant community of algal turf (H, inserts: (A, B) the dominant species *Padina minor* (*Vaughaniella* stage) and the red calcareous alga *Jania ungulate*, dry season, 2012). Scale bars: A, 1 cm; B, 1 mm; D, 200 μm (A–B) and 5 mm (C); E, 1 mm (A), 300 μm (B) and 500 μm (C); F, 2 mm (A), 1 cm (B), 5 mm; C) and 400 μm (D); G, 5 mm; H, 1 cm (A) and 1 mm (B).

Centroceras clavulatum (Figure 6F). The brown crusts of Neoralfsia expansa overgrew the red alga Hildenbrandia rubra on stones and pebbles (Figure 6G). Outside of the C. clavulatum community, H. rubra often occurred.

In the low intertidal zone, the flat surfaces of dead coral blocks were overgrown by a poly-dominant community of the turf-forming brown alga *Padina minor* (*Vaughaniella* stage) and the red calcareous alga *Jania ungulata* f. *brevior* (Figure 6H). Underneath the ledges and on the vertical walls of dead coral blocks, a mono-dominant community of the red crustose alga *Lithothamnion* sp. was overgrown by *Lobophora variegata* (crustose form), *N. expansa* and *Peyssonnelia rubra*. These algae were also found outside of the *Lithothamnion* sp. community on horizontal surfaces as well as on vertical walls.

On the border between the intertidal and upper subtidal zones and in intertidal pools, the poly-dominant algal turf community included *Palisada perforata*, *Spyridia filamentosa*, *Hypnea spinella* and *H. valentiae* (Rh).

### Comparison of algal communities during the rainy and dry seasons

The total number of species increased by 33% from the rainy to the dry season, changing from 93 species to 138 species (Table 2, Figure 7). The seasonal increase impacted the species in the major groups at the following amounts: Rhodophyta (33%), Phaeophyceae (38%), Chlorophyta (29%), and Cyanobacteria (33%). Clearly, all groups were effected. There was considerable overlap of species between the seasons as indicated in the 'All Season' column. This is the result of the occurrence of both season-specific and aseasonal species.

A number of the algae were season specific, occurring only during the rainy or dry season, but many were also aseasonal, occurring during both seasons (Figure 8). Of the 148 species followed during the study, 56% occurred during both seasons, 37% were specific to only the dry season, and 7% were specific to only the rainy season. Seasonal specificity occurred in all groups. In the cyanobacteria, 64% were seasonal (rainy season(RS):dry season(DS):rainy and dry seasons(R&DS) = 6:13:11) and the majority of the species occurred only during the dry season. In the other groups, most of the species were aseasonal. In the Chlorophyta, only 35% were seasonal (RS:DS:R&DS = 1:10:20). In the Rhodophyta, 37% were seasonal (RS:DS:R&DS = 2:23:40),

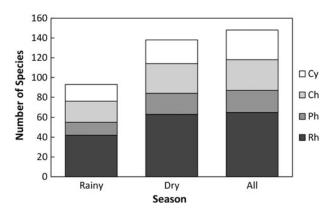


Fig. 7. Seasonal occurrence of the species.

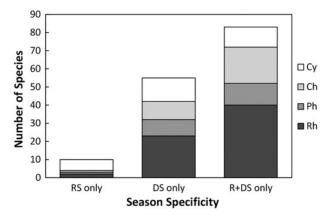


Fig. 8. Composition of season-specific algal groups.

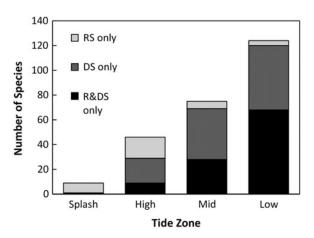


Fig. 9. Tidal distribution of season-specific algae. RS, rainy season; DS, dry season; R&DS, rainy and dry seasons.

and, in the Phaeophyceae, 45% were seasonal (RS:DS:R&DS = 1:9:12). There was some tidal separation of the season-specific algae (Figure 9). Not remarkably, rainy seasonal species were most common in the splash and high intertidal zones. Dry seasonal and aseasonal species increased progressively from the high to the low intertidal zone, where aseasonal species were predominant at 55% of the species (RS:DS:R&DS = 4:56:68).

### DISCUSSION

Our study of the flora of the intertidal zone of Luhuitou reef has shown that marine macroalgae occupy mostly the hard substrata including the rocky bottom, carbonate reef bases, dead coral colonies and their debris. Living scleractinian corals were observed only in the lower intertidal zone. Intertidal algal communities included mainly turf and crustose algae. In the upper subtidal zone, fleshy, frondose and foliose algae enriched the algal turf communities.

### Species diversity

The proportion of the species groups at Luhuitou reef (Sanya Bay) during our study was revealing. Including the rare species, a total of 176 taxa of macroalgae and blue—green algae (40% of all marine algae found in Hainan) were found in the intertidal zone. These consisted of 56% red, 28% green, 16% brown, and 10% blue—green algae. Similar floristic proportions were also found in the upper subtidal zone at Luhuitou reef (Titlyanov *et al.*, 2013). Surprisingly, these proportions fell well within the limits of those known for coral reefs in the Indo-Pacific that are situated in regions with insignificant pollution. In these regions macroalgae have been found to be 50–60% red, 20–30% green and 10–20% brown (Lewis & Norris, 1987; Silva *et al.*, 1987; Zhang, 1996; Huisman & Borowitzka, 2003; Tsuda, 2003, 2006).

In the literature (Morand & Briand, 1996; Morand & Merceron, 2004; Lapointe et al., 2005a, b), floristic ratios of the major algal groups are reported to change dramatically between clean and polluted regions, but, in spite of significant pollution with dissolved inorganic nitrogen and phosphorus in Sanya Bay (Titlyanov et al., 2011b), the intertidal floristic ratios remained the same as those in unpolluted regions. However, we did find some subtle indicators of pollution. Four species that are most common in nitrogen-enriched areas were present in the Bay: Ulva intestinalis, U. lactuca, U. linza and Caulerpa racemosa.

# Seasonal changes in species diversity and community structure in the different tidal zones

During our study the largest number of species was found during the dry seasons as compared to the rainy seasons (DS:RS = 138:93) (Table 2; Figure 3). In our opinion, this was caused by: (1) optimal conditions for the occurrence and development of algae-ephemerals (especially blue-green algae) and algae-epiphytes; and (2) the mass occurrence of young annual plants. The decrease in species richness in the intertidal zone that occurred during rainy seasons seems to be connected with the temperature drop and decrease in salinity, especially in the upper and middle intertidal zones. There was no evidence that it was caused by seawater pollution in Sanya Bay (Table 1). The annual species die off was visually noticeable during the rainy season, with the detachment and drifting ashore of the algal thalli.

Species number and composition at different tidal zones during the dry and rainy seasons showed significant differences (Table 2; Figure 5). The splash area was inhabited mainly by blue-green algae. During the dry seasons, the lack of storms and lack of high humidity and high temperature led to the near absence of algae in this zone.

In the upper intertidal zone, a few more species were found in the dry seasons than in the rainy seasons (DS:RS = 29:26). During both seasons, opportunistic ephemeral algae (Parviphycus pannosus, Erythrotrichia carnea and Ulva clathrata) were widespread throughout the upper intertidal zone, as were the perennial mono-dominant crustose algae (Hildenbrandia rubra (Figure 6C) and Neoralfsia expansa (Figure 6G)). During the dry seasons, blue–green algae were the most diverse. We think that blue–green algae and opportunistic macroalgae in the upper intertidal zone thrived during the dry season due to their tolerance to drying and to the absence of competition for the space with other algae in these extreme conditions (Nabivailo & Titlyanov, 2006). During the rainy season, rainfall and moderate temperature

promoted the growth of green algae (*Ulva clathrata* and *Cladophora laetevirens*) in the upper intertidal zone (Titlyanov *et al.*, 2011a).

In the middle intertidal zone, more than twice the number of species were found during the dry seasons than in the rainy seasons (DS:RS = 69:34). The higher diversity during the dry seasons in this zone was influenced by several factors. Conditions in the upper and middle intertidal zones in Sanya Bay differed not only by the duration of the exposure to air, but also by substrata. In the middle zone, hard substrata were covered by the dense layers of muddy and sandy sediments. In the upper intertidal zone, the sediments were almost absent. Marine plants inhabiting the middle intertidal zone were partially or completely submerged in the sediments, which remained wet during the low tide. The constant exposure to water provided better conditions for macroalgal attachment and growth than the often dry and hot substrate in the upper intertidal zone, and also the damp layer sheltered the spores of many annual algae. During the rainy seasons, layers of muddy and sandy sediments in the mid intertidal zone retained rain water, negatively influencing the diversity of algal species.

In the upper and middle intertidal zones, the main algal communities were mono- and bi-dominant algal crust or turf communities, overgrown by epiphytes (Figure 6F). Species composition and dominant species (mainly highly productive opportunistic red and green ephemerals) often changed more than once during each season.

The number and composition of the algal species in the low intertidal zone also changed with the seasons. This zone had many more species during the dry seasons than during the rainy seasons (DS:RS = 120.72) (Figure 5). Of these species, 55% were common to the both seasons, 42% grew only in the dry seasons and 3% only in the rainy seasons. The large number of species common to both seasons (i.e. growing during most of the year) emphasizes the moderate growing conditions in this zone. The majority of settled species were annuals and perennials, and the epiphytes were ephemerals. Significant decline in species number during the rainy season was caused by natural cycles, such as the death and detachment of annual and old perennial thalli. Algal communities in the lower intertidal included mainly poly-dominant algal turf communities (Figures 6E and 6H) and, less often, associations of large foliose, fleshy and leathery algae. The seasonal changes in this zone were most apparent in species dominance. The dominant species are not only short-lived opportunistic algae, but also annual or perennial fleshy, foliose and leathery algae. Here the change of dominant and accompanying species in turf communities depends mainly on annual periodicity in the replacement of old plants by newly grown ones, and detachment of algal turf patches from the substratum at least once per year.

The seasonal changes in species composition and composition of algal communities in the low intertidal zone at Luhuitou were somewhat different to those that occurred in the upper subtidal zone (Titlyanov *et al.*, 2013). Here the changes in species numbers and their composition between the seasons were less extreme: 80% of the macroalgae were common to both seasons, 15% occurred only during the dry season and 2% were found only during the rainy season.

The changes in the intertidal zones appear to be caused by extreme external factors. In the upper intertidal zone factors such as high ultraviolet and visible radiation in combination

with high temperature during the dry season and with seawater desalinization and frequent storms during the rainy season. These extreme factors lead to a decrease in production and to a decay of nonresistant (especially long-lived) algae (Lüning, 1990; Ateweberhan et al., 2006), and provide open space for ephemeral, opportunistic and highly productive algae (McCook et al., 2001; Nabivailo & Titlyanov, 2006). Biotic factors also influence the diversity and structure of algal communities. Herbivorous fish are known to consume different species during the high tides of different seasons, and some crustaceans are also known to change their diets with the seasons (Clements & Choat, 1993; Hughes & Seed, 1995; Kennish et al., 1996; Cannicci et al., 2007). However, this influence is insignificant at Luhuitou Peninsula because of constant overfishing and invertebrate sampling in Sanya Bay.

Investigations of factors influencing seasonal changes in algal species composition in other tropical and subtropical regions do not contradict our results and conclusions. In Nanwan Bay in southern Taiwan (the nearest to Hainan Island), species diversity on the lower reef flat and the reef slope (the low intertidal and upper subtidal zones) showed insignificant seasonal variations (Tsai et al., 2004). However, essential changes were observed in the intertidal zone of other subtropical and tropical regions. On coral reefs in Brazil, most of the taxa (23) were present during the summer rainy season (February-March). In the rocky intertidal of the Colombian Caribbean, the macroalgal community was most diverse in October, which historically has been the rainiest and calmest month of the year (García & Díaz-Pulido, 2006). On the Great Barrier Reef in Australia, extensive ephemeral blooms of small, fleshy brown macroalgae, such as Chnoospora and Hydroclathrus, have been observed on shallow reef flats predominantly during winter and early spring (Díaz-Pulido et al., 2007). The authors of these studies believe that replacement in the vegetation at shallow sites is induced by sharp changes in climate that occur during seasonal changes. On the north-west coast of India (Port Okha), Thakur with coauthors (2008) found that seasonal variation in species composition of stranded seaweeds was correlated with natural species succession. The seaweed growing season on the Okha coast is spread over seven months, running from November to May. During this period, extensive growth and succession of different types of seaweed associations have been observed. On coral reefs in Okinawa, natural changes in vegetation are connected with a succession of algal communities that occurs in late spring (May-June) when extensive bands of drift algae were found on the shore (Titlyanov et al., 2006).

We assumed that the pollution in Sanya Bay would greatly affect the composition of macroalgae and Cyanobacteria in the intertidal of Luhuitou reef. However, our investigation revealed that there was little impact on the floristic proportions of the algae. The species composition of the tide zones and their seasonal shifts were not unlike algal community structure in relatively clean, unpolluted regions of the Indo-Pacific. Overall, species numbers increased from the rainy to the dry seasons and also from the high to the low intertidal zones. In the splash zone, a tightly adhering film of crustose and filamentous blue–green algae was present during the dry seasons. In all three lower zones during all seasons, turf and occasional crustose algae provided the main cover, with occasional upright fronds protruding

through the turf in the low zone. In the splash and upper intertidal zones the dominance of blue-green and green algae, primarily seasonal ephemerals, seemed to be due to their ability to endure or quickly recover from the extremely erratic environmental conditions in these zones. In the mid intertidal zone, a greater diversity of ephemeral red and green algae occurred, particularly during the dry season. In this zone, mud and sand frequently covered the algae and their spores, insulating them from any adverse conditions. The low intertidal zone was dominated primarily by red and brown algae that were mainly aseasonal annuals and perennials. Their occurrence and successional patterns were supported by the more stable environment and influenced by predictable annual changes in the overall flora. In our qualitative studies of macroalgal and cyanobacterial distribution, we could find no obvious influence of the urban and maricultural pollution common to Sanya Bay. However, these primarily nutritive pollutants may not yet have reached lethal amounts for the species. Continued pollution of the Bay may eventually be great enough to cause a change in the dominant algal species and heavily influence the future ecosystem of this region.

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