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EPIPHYTISM AMONG ALGAE OF CORAL REEFS AND ROCKY ECOSYSTEMS IN THE SOUTH CHINA AND EAST CHINA SEAS

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Epiphytism is a natural phenomenon widespread in coastal ecosystems of the World Ocean. Epiphytes are plants (algae) that grow on other plants (algae), do not compete with other organisms for substrate, and receive primarily physical support from their host. However, epiphytes are also known to have negative effects on host algae: they can reduce their productivity, cause morphological anomalies, reduce the structural strength of algal layers, and facilitate the detachment of a host thallus from the substrate during storms. This study examines the species composition and life forms of epiphytic algae in several biogeographic regions of the World Ocean, analyzes the floristic differences revealed in these regions, and determines their causes. Macroalgae were sampled in the upper, middle, and lower intertidal zones, as well as in the upper subtidal zone, on coral reefs in the South China and East China seas. Samples were collected from three randomly selected quadrats (1 m^2 in area) and beyond. Each sample was examined for the presence of epiphytes. In total, over 1,000 thalli containing epiphytes were sampled and analyzed. For the period from 1995 to 2019, the species richness, composition and distribution of epiphytic algae assemblages in ecosystems of coral reefs and hard substratum reefs in the South China Sea (Central and Southern Vietnam, Hainan Island) and East China Sea (islands of the Ryukyu and Amakusa archipelagos) were studied for the first time. More than 700 species and taxonomic forms of marine plants were registered and identified in these four regions; out of those, about 33% were found in epiphytic life form. The highest number of seaweed species was noted for coral reefs of Hainan Island (526); the lowest number of species was recorded for coastal aquatic ecosystems of the Amakusa Archipelago islands (320). The relative number of epiphytic species of algae to total number of seaweed species was the highest on the Amakusa islands. Among all the registered species of epiphytic algae, about 40% were found in obligate form, and more than 50% were facultative epiphytes. The study areas differed in the species composition of epiphytes; only 30% of species were common. The most area-specific epiphytes were recorded on the Amakusa Archipelago islands. The causes and conditions of the widespread development of epiphytism among seaweeds in various biogeographic regions of the World Ocean are discussed. The supplement to the article contains descriptions of the morphology and anatomy of thalli of 40 widespread species of epiphytes. The descriptions are provided with color photographs and elements of morphological and anatomical structures.

Keywords: marine algae, epiphytes, coral reefs, species composition

While seaweed communities are formed, some algal species settle on thalli of other species. This natural phenomenon, called epiphytism, is widespread in coastal ecosystems of the World Ocean. Epiphytism is part of a broader ecological phenomenon, epibiosis. The latter is one of complex types of interaction between organisms found in nature, when an organism grows on another, usually without parasitizing it [Wahl, 1989]. In epibiosis, the ecological relationship between the 'basiphyte' (= host) and the 'epibiont' (= species growing on the host) can be highly variable under the effect of environmental factors: light, temperature, and direct physical or chemical exposure [Thornber et al., 2016]. Epiphytes are plants that grow on other plants, bypassing competition with other organisms for substrate and receiving mostly physical support from their host [Potin, 2012].

Epiphytism in marine coastal ecosystems has been investigated since the late 19th century [Boye, 1986]. The main directions in the study of this natural phenomenon in the 20th century were the taxonomic identification of epiphytic algae and their inventory in some areas of the World Ocean, including the South China and East China seas (*e. g.*, [Abbott, Hollenberg, 1976; Pham, 1969; Segawa, Kamura, 1960; Tseng, 1983]). In the early 21st century, the key aspect of research was the analysis of epiphytism in the industrial cultivation of algae (*e. g.*, [Chirapart et al., 2022; Sahu et al., 2020]), as well as in relation to global climate changes [Albert et al., 2020]. Less attention was paid to floristic investigations of the diversity and species composition of epiphytes in algal communities in different regions of the World Ocean [Belous et al., 2021; Potin, 2012; Tsutsui et al., 2005].

The negative effect of epiphytes on the production of basiphytes is known. The settlement of epi- and endophytes often causes morphological anomalies in the host algae, which can lead to the destruction of basiphyte tissues [Correa, McLachlan, 1992, 1994; Sánchez et al., 1996], decline in the structural strength of layers, and detachment of thalli from the substrate during storms [Lein et al., 1991]. Epiphytes, when they are massively settled on thalli of macroalgae and leaves of seagrasses, shade the latter ones and significantly reduce their production [Friedlander, 1992], but at the same time, protect them from drying out in the intertidal zone of the shelf.

Epiphytic biofilms on leaves of seagrasses and thalli of macrophytes affect biogeochemical processes and chemical conditions directly in the habitat of the plant community (phyllosphere). Thus, at night, hypoxia (oxygen-free conditions) can occur at the interface between a thallus (leaf) and epiphytes, which noticeably reduces the rate of respiration of the basiphyte and also leads to the harmful formation of nitric oxide through denitrification. In the light, the formation of an epiphytic biofilm often results in reduction in photosynthetic activity due to epiphyte-induced shading caused by epiphytes in combination with accumulation of O_2 and a decrease in CO_2 concentration in the microenvironment [Brodersen, Kühl, 2022].

The studies of epiphytic algae (along with seaweeds of other life forms) in the South China and East China seas were carried out primarily by Chinese, Vietnamese, and Japanese researchers within the 1930s–1980s (*e. g.*, [Pham, 1969; Segawa, Kamura, 1960; Tseng, 1983]) and were limited to determining the taxonomic status of epiphytic algae.

From the 1980s to the 2010s, we conducted an inventory study of the benthic marine flora off the coast and islands of Southern and Central Vietnam, Hainan Island (China), and islands of the Ryukyu and Amakusa archipelagos (Fig. 1A–H).

In these regions, we carried out an inventory of the current marine benthic algal flora; also, we analyzed species, as well as life form diversity and taxonomic composition of individual algal communities. The effect of environmental factors, such as climatic conditions, seasonality, and water eutrophication, on species diversity of marine algae was studied as well. The results of these surveys are partially published [Titlyanov, Titlyanova, 2012; Titlyanov et al., 2014, 2017, 2018, 2019a, b; Titlyanova et al., 2014].

One of the aims of this work is to investigate species and life form diversity of seaweeds capable of growing epiphytically in certain areas of the tropical biogeographic region of the South China Sea and in the warm temperate region of the East China Sea. Another aim is to analyze the floristic differences revealed in the study areas and try to find out the reasons for these differences. Additionally, we considered it useful to provide photographs and descriptions of epiphytic algae that are common in the study areas.

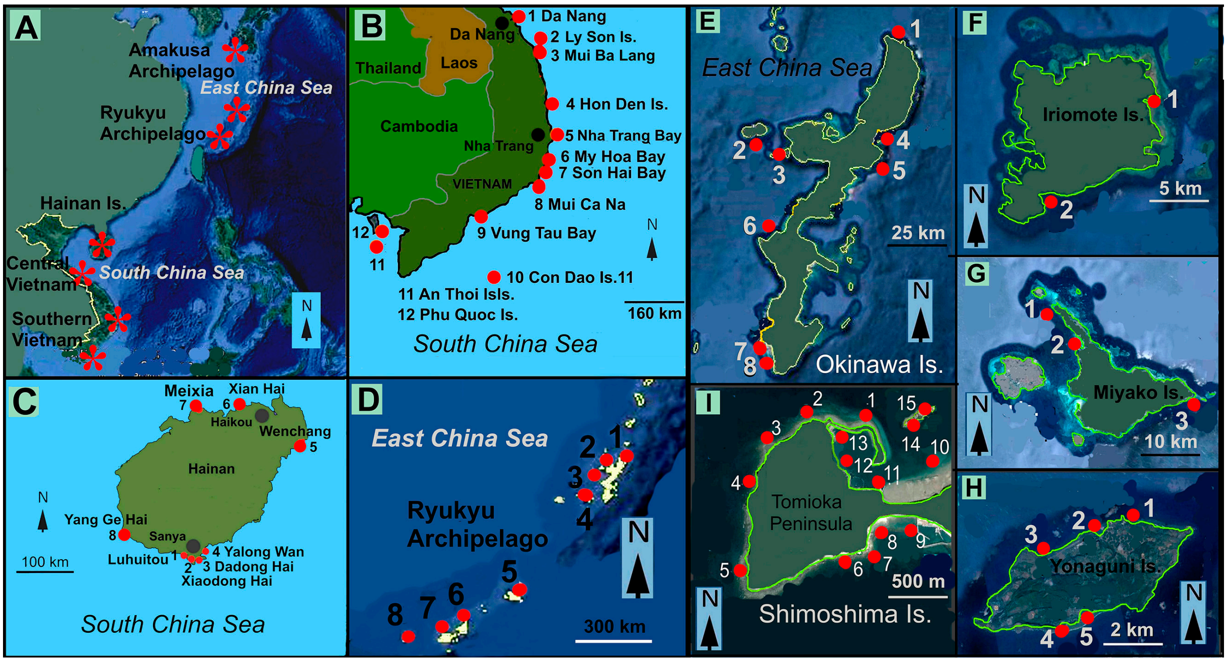

Fig. 1. Sites of algal sampling off the mainland coast and islands in the South China and East China seas. A, schematic map of the South China and East China seas; sampling sites are marked with red asterisks. B, sampling sites off the coast and islands in Central and Southern Vietnam. C, sampling sites off the coast of Hainan. D, schematic map of islands of the Ryukyu Archipelago and sampling sites: 1, Okinawa Island; 2, Sesoko Island; 3, Ieshima Island; 4, Akajima Island; 5, Miyako Island; 6, Ishigaki Island; 7, Iriomote Island; 8, Yonaguni Island. E, sampling sites in Okinawa Prefecture: 1, Cape Hedo; 2, Ieshima Island; 3, Sesoko Island; 4, Oura Bay; 5, Cape Henoko; 6, Maeda coast; 7, 8, Arasaki Beach; 9, Ohdo coast. F, sampling sites off the coast of Iriomote Island: 1, Hoshidate coast; 2, Kanoka coast. G, sampling sites off the coast of Miyako Island: 1, 2, Karimata coast; 3, Cape Higashi-Hennazaki. H, sampling sites off the coast of Yonaguni Island: 1–3, Sonai locality; 4, Higawa Bay; 5, Tojima coast. I, Shimoshima Island and Tsujishima Island (Amakusa Archipelago), sampling sites along Tomioka Peninsula: Magarizaki coast (sites 1, 2); Akaiwa coast (sites 3, 4); Shikizaki Bay (site 5); Shiraiwazaki Bay (sites 6–8); Reihoku coast (site 9); Tomioka Harbor (sites 10–13); Tsujishima Island (sites 14, 15)

MATERIAL AND METHODS

In the study areas, more than 300 benthic algal collections were made from 1981 to 2019. Approximately 70% of the collections were formed by the methods described below, and this is the material analyzed in the article.

The study of the marine flora along the coastal zone and off islands of Central and Southern Vietnam (Fig. 1A, B), using the methods described below, was conducted by us in 2002–2009 off the following sites: Hon Den Island (January 2002); Ly Son Island (March 2002); Son Hai Bay (March 2006); Cape Ca Na (April 2006); My Hoa Bay (May 2006); Nha Trang Bay (March and April 2006–2010); vicinity of Da Nang (April 2007); Vung Tau Bay (April 2008); Con Dao Islands (April 2008); Mui Ba Lang (March 2009); An Thoi Islands (March 2009); and Phu Quoc Island (March 2009).

Algal samplings along the coast of Hainan Island (Fig. 1A, C) were carried out in 2008–2019 and covered Luhuitou Peninsula (February 2012; March and May 2009; November and December 2010, 2012, and 2015; and April 2009, 2012, and 2014); Xiaodong Hai Bay (October 2008; March and April 2016, 2017, and 2019; and November and December 2016 and 2018); Dadong Hai Bay (October 2008 and April 2016); Yalong Wan Bay (March 2012); vicinity of Wenchang City (March 2012); Xian Hai Bay (April 2012); vicinity of Meixia town (April 2012); and Ying Ge Hai Bay (April 2014).

Algae were sampled in 1995–2019 along coasts of the Ryukyu Archipelago islands (Fig. 1A, D–H): on coral reefs of the western coast of Akajima Island and in two localities of Ishigaki Island (August 1995); Ieshima Island (December 2006); along the coast of Okinawa Island (November and December 2006); Arasaki Beach, Okinawa (March 2013 and February 2014); Sesoko Island (May–September 1995; October–December 1997; January–March 1998; October–December 2002; January–September 2003; July 2004; February–May 2005; November–December 2006; October 2007; and February 2014 and 2019); Yonaguni Island (March 2013); Miyako Island (March 2013); and Iriomote Island (February 2017).

Shimoshima Island and Tsujishima Island (Fig. 1A, I) of the Amakusa Archipelago were covered by algal sampling within 2012–2017 (November and December 2012; April and August 2013; January 2014; October and November 2015; and November 2017).

Field works in Central and Southern Vietnam were carried out jointly with the staff of two Vietnamese institutes: Institute of Oceanography and Institute of Technology Research and Application of the Vietnamese Academy of Science and Technology (Nha Trang City).

On the southern islands of Japan, we used the services of three marine biological stations. The Amakusa Marine Biological Laboratory (Kyushu University) is located on Shimoshima Island (Amakusa Archipelago); the Tropical Biosphere Research Center (University of the Ryukyus) is situated on Sesoko Island, Okinawa; and the Iriomote Station of the Tropical Biosphere Research Center (University of the Ryukyus) is located on Iriomote Island.

On Hainan Island, the main base for field and laboratory works was the Tropical Marine Biological Research Station of the South China Sea Institute of Oceanology of the Chinese Academy of Sciences, located in the Sanya Bay. Professor Huang Hui and Professor Li Xiubao took part in all our works and co-authored scientific articles and books (see "References" section).

Macroalgae were sampled in the upper, middle, lower intertidal, and upper subtidal zones (by snorkeling, and sometimes by scuba diving) on coral reefs of Central and Southern Vietnam, Hainan Island, islands of the Ryukyu Archipelago, and in ecosystems of rocky substrata around islands of Amakusa Archipelago.

In each tidal zone, within 100–300 m^2 (depending on area of tidal zones), communities of algal turf, crust algae, and large upright growing algae were visually estimated. In the communities of algal turf and crust algae, samples were taken from three randomly selected quadrats, each measuring 100 cm^2 in area. In communities of upright growing algae, samples were also taken from three randomly selected quadrats, 1 m^2 each. Seaweeds were sampled separately from areas outside the selected quadrats as well. Mostly, algae were taken out of water along with substrate (small stones, fragments of corals, and shells) and manually (carefully) cleaned of debris in a laboratory.

Each collected fresh sample was checked for the presence of epiphytes. Epiphytic thalli were removed with tweezers from the basiphyte and taxonomically analyzed. For the survey of the epiphytic flora, only adult, healthy thalli of epiphytic algae attached to living basiphytes were selected. In total, more than 1,000 thalli with epiphytes were sampled and analyzed. Epiphytic species found on thalli of macrophytes 1–10 times were designated as single occurrences; 11–19 times, as rare; and more than 20 times, as common.

Freshly collected material was identified using monographic publications, data from floristic studies, and systematic articles listed by T. Titlyanova and coauthors [2014]. The systematics and nomenclature followed AlgaeBase [2026]. The material was identified under stationery and field optical microscopes immediately or within 2–3 days after sampling (the material was stored in a refrigerator). After identification, algal samples were herbarized or preserved in fixative solutions (7% formaldehyde in seawater). Herbarium material was deposited at the Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences (Vladivostok, Russia).

RESULTS

Among all the species we found, reds (species of the phylum Rhodophyta) accounted for 57%; greens (species of the phylum Chlorophyta), for 28%; and browns (species of the phylum Heterokontophyta), for 15%. Importantly, the taxonomic composition of epiphytic algae (Fig. 2) was different: red seaweeds significantly prevailed (70–85%), while green and brown ones were less common (10–20 and 5–10%, respectively).

The most common species of epiphytic red algae in all four study areas were those belonging to the orders Stylonematales, Erythropeltales, Acrochaetiales, Colaconematales, Corallinales, and Ceramiales. Out of brown algae, the most common species were those from the orders Ectocarpales and Sphacelariales. The most common seaweeds among the greens were epiphytes from the order Ulvales (Table 1). Most of epiphytic algae from the families covered by our collection had a fine filamentous form. Micrographs and descriptions of the most common species of epiphytes in the study areas are given in Supplement 1 (see https://marine-biology.ru/mbj/article/view/519).

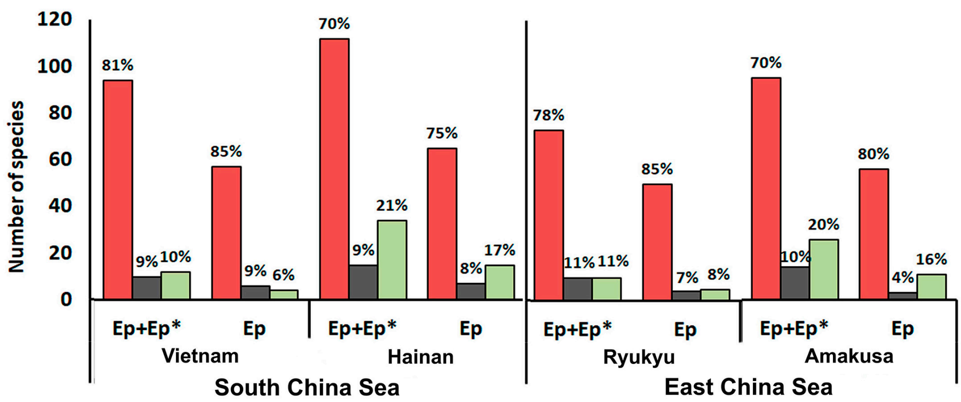

Fig. 2. Distribution of epiphytic algae in the study areas of the South China and East China seas. Ep, algae found only as epiphytes (obligate epiphytes); Ep*, algae found as epiphytes, as well as on hard substrata (facultative epiphytes); Ep + Ep*, the total number of species of obligate and facultative epiphytic algae

Among all the epiphytes we registered, about 40% of the species were in obligate form (Fig. 2, Table 1): they grew only as epiphytes on thalli of one or more species of basiphytes. Red seaweeds belonging to the orders Acrochaetiales (family Acrochaetiaceae), Colaconematales (family Colaconemataceae), and Ceramiales (family Callithamniaceae), as well as green algae from the orders Chaetophorales (family Chaetophoraceae), Ulotrichales (family Ulotrichaceae), and Ulvales (family Ulvellaceae), were found as epiphytes only.

Table 1. Seaweeds growing epiphytically in some areas of the South China and East China seas

Species, variety, and taxonomic form	Ryukyu islands	Hainan Island	Southern Vietnam	Amakusa islands
Phylum RHODOPHYTA				
Class Stylonematophyceae				
Order Stylonematales				
Family Stylonemataceae				
Bangiopsis dumontioides (P. Crouan & H. Crouan) V. Krishnamurthy		Ep		Ep
Chroodactylon ornatum (C. Agardh) Basson ♣	Ep*	Ep	Ep	Ep
Stylonema alsidii (Zanardini) K. M. Drew ♣	Ep*	Ep	Ep	Ep*
Class Compsopogonophyceae				
Order Erythropeltales				
Family Erythrotrichiaceae				
Erythrocladia irregularis Rosenvinge ♣	Ep	Ep	Ep	Ep
Erythrotrichia carnea (Dillwyn) J. Agardh ♣	Ep*	Ep	Ep	Ep*
Erythrotrichia parietalis T. Tanaka			Ep*	
Porphyrostromium japonicum (Tokida) Kikuchi		Ep		
Sahlingia subintegra (Rosenvinge) Kornmann ♣	Ep*	Ep	Ep	Ep
Class Bangiophyceae				
Order Bangiales				
Family Bangiaceae				
Bangia gloiopeltidicola Tanaka				Ep
Pyropia ishigecola (A. Miura) N. Kikuchi & M. Miyata				Ep
Pyropia suborbiculata (Kjellman) J. E. Sutherland, H. G. Choi, M. S. Hwang & W. A. Nelson				Ep*
Class Florideophyceae				
Order Acrochaetiales				
Family Acrochaetiaceae				
Acrochaetium catenulatum M. A. Howe ♣	Ep	Ep	Ep	Ep
Acrochaetium chaetomorphae (Tanaka & P. H. Hô) Heerebout		Ep	Ep	Ep
Acrochaetium crassipes (Børgesen) Børgesen	Ep		Ep	
Acrochaetium gracile var. *vietnamense* P. H. Hô			Ep	
Acrochaetium microscopicum (Nägeli ex Kützing) Nägeli	Ep	Ep	Ep	Ep
Acrochaetium moniliforme (Rosenvinge) Børgessen	Ep			
Acrochaetium sancti-thomae Børgesen			Ep	
Acrochaetium secundatum (Lyngbye) Nägeli	Ep	Ep	Ep	
Acrochaetium subseriatum Børgesen ♣	Ep	Ep	Ep	Ep
Order Colaconematales				
Family Colaconemataceae				
Colaconema bonnemaisoniae Batters		Ep		
Colaconema daviesii (Dillwyn) Stegenga	Ep	Ep	Ep	Ep
Colaconema gracile (Børgesen) Ateweberhan & Prud'homme	Ep	Ep	Ep	Ep
Colaconema hypneae (Børgesen) A. A. Santos & C. W. N. Moura ♣	Ep	Ep	Ep	Ep
Colaconema robustum (Børgesen) Huisman & Woelkerling	Ep	Ep	Ep	Ep
Order Corallinales				
Family Corallinaceae				
Jania capillacea Harvey	Ep*	Ep*		
Jania pedunculata var. *adhaerens* (J. V. Lamouroux) A. S. Harvey, Woelkerling & Reviers	Ep*	Ep*	Ep*	Ep*

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Species, variety, and taxonomic form	Ryukyu islands	Hainan Island	Southern Vietnam	Amakusa islands
Jania pumila J. V. Lamouroux	Ep	Ep*	Ep	Ep*
Jania ungulata f. *brevior* (Yendo) Yendo ♣	Ep*	Ep*	Ep*	Ep*
Pneophyllum confervicola (Kützing) Y. M. Chamberlain			Ep	
Pneophyllum fragile Kützing	Ep*	Ep	Ep	Ep
Family Hydrolithaceae				
Hydrolithon boergesenii (Foslie) Foslie		Ep*	Ep	
Hydrolithon boreale (Foslie) Y. M. Chamberlain ♣	Ep*	Ep	Ep	Ep
Hydrolithon farinosum (J. V. Lamouroux) Penrose & Y. M. Chamberlain ♣	Ep	Ep	Ep	Ep
Family Porolithaceae				
Metagoniolithon stelliferum (Lamarck) Ducker			Ep*	Ep*
Order Bonnemaisoniales **Family Bonnemaisoniaceae**				
Asparagopsis taxiformis (Delile) Trevisan	Ep*	Ep*	Ep*	Ep*
Bonnemaisonia hamifera Hariot		Ep		Ep
Order Ceramiales **Family Callithamniaceae**				
Aglaothamnion callophyllidicola (Yamada) Boo, I. K. Lee, Rueness & Yoshida	Ep			
Aglaothamnion cordatum (Børgesen) Feldmann-Mazoyer ♣	Ep	Ep	Ep	Ep
Crouania attenuata (C. Agardh) J. Agardh ♣	Ep	Ep	Ep	Ep
Crouania minutissima Yamada			Ep	
Gymnothamnion elegans (Schousboe ex C. Agardh) J. Agardh	Ep		Ep	
Spyridia filamentosa (Wulfen) Harvey	Ep*	Ep*	Ep*	
Family Ceramiaceae				
Antithamnion antillanum Børgesen	Ep	Ep	Ep	Ep
Antithamnionella basispora (Tokida & Inaba) Cormaci & Furnari			Ep	
Antithamnionella breviramosa (E. Y. Dawson) Wollaston		Ep	Ep	Ep
Antithamnionella elegans (Berthold) J. H. Price & D. M. John		Ep		
Antithamnionella longicellulata Perestenko				Ep
Antithamnionella spirographidis (Schiffner) E. M. Wollaston		Ep	Ep	
Centroceras clavulatum (C. Agardh) Montagne	Ep*	Ep*	Ep*	Ep*
Centroceras gasparrinii (Meneghini) Kützing	Ep		Ep*	
Centroceras japonicum Itono		Ep*		
Centroceras minutum Yamada	Ep	Ep*		
Ceramium aduncum Nakamura	Ep	Ep*	Ep	Ep
Ceramium amamiense Itono	Ep			
Ceramium boydenii E. S. Gepp				Ep
Ceramium borneense Weber Bosse	Ep	Ep*	Ep	Ep
Ceramium camouii E. Y. Dawson		Ep*		
Ceramium cimbricum H. E. Petersen ♣	Ep*	Ep	Ep	Ep
Ceramium cimbricum f. *flaccidum* (H. E. Petersen) G. Furnari & Serio	Ep	Ep		
Ceramium cingulatum Weber Bosse	Ep	Ep	Ep	
Ceramium clarionense Setchell & N. L. Gardner			Ep	
Ceramium hamatispinum E. Y. Dawson		Ep		
Ceramium macilentum J. Agardh ♣	Ep	Ep*	Ep*	Ep
Ceramium marshallense E. Y. Dawson	Ep	Ep*		Ep*
Ceramium procumbens Setchell & N. L. Gardner ♣	Ep	Ep*	Ep*	Ep
Ceramium serpens Setchell & N. L. Gardner	Ep	Ep		
Corallophila howei (Weber-van Bosse) R. E. Norris			Ep*	
Corallophila huysmansii (Weber-van Bosse) R. E. Norris		Ep	Ep*	Ep*

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Species, variety, and taxonomic form	Ryukyu islands	Hainan Island	Southern Vietnam	Amakusa islands
Corallophila kleiwegii Weber Bosse	Ep*	Ep*	Ep*	
Gayliella fimbriata (Setchell & N. L. Gardner) T. O. Cho & S. M. Boo		Ep	Ep	Ep*
Gayliella flaccida (Harvey ex Kützing) T. O. Cho & L. J. McIvor	Ep	Ep	Ep	
Gayliella mazoyerae T. O. Cho, Fredericq & Hommersand ♣	Ep*	Ep*	Ep*	Ep*
Gayliella taylorii (E. Y. Dawson) T. O. Cho & S. M. Boo		Ep*	Ep*	
Gayliella transversalis (Collins & Harvey) T. O. Cho & Fredericq	Ep*			
Pseudoceramium paniculatum (Okamura) Barros-Barreto & Maggs				Ep
Pseudoceramium tenerrimum (G. Martens) Barros-Barreto & Maggs		Ep*		Ep*
Stirkia codii (H. Richards) Barros-Barreto & Maggs	Ep	Ep		
Stirkia vagans (P. C. Silva) Barros-Barreto & Maggs	Ep	Ep	Ep*	Ep
Yoneshiguea compta (Børgesen) Barros-Barreto, Maggs & M. A. Jaramillo		Ep		
Family Delesseriaceae				
Acrosorium polyneurum Okamura				Ep
Acrosorium yendoi Yamada				Ep
Caloglossa leprieurii (Montagne) G. Martens			Ep	
Cryptopleura ramosa (Hudson) L. Newton				Ep
Dasya anastomosans (Weber Bosse) M. J. Wynne			Ep*	
Dasya pedicellata (C. Agardh) C. Agardh			Ep*	
Dasysiphonia japonica (Yendo) H.-S. Kim				Ep
Dasysiphonia sessilis (Yamada) M. M. Cassidy, C. W. Schneider & G. W. Saunders				Ep*
Heterosiphonia crispella (C. Agardh) M. J. Wynne	Ep	Ep	Ep*	Ep
Heterosiphonia pulchra (Okamura) Falkenberg		Ep		Ep
Hypoglossum attenuatum N. L. Gardner			Ep	Ep
Hypoglossum caloglossoides M. J. Wynne & Kraft			Ep	
Hypoglossum simulans M. J. Wynne, I. R. Price & D. L. Ballantine			Ep	
Nitophyllum adhaerens M. J. Wynne	Ep		Ep*	
Taenioma perpusillum (J. Agardh) J. Agardh	Ep	Ep*	Ep*	Ep*
Family Rhodomelaceae				
Acanthophora spicifera (M. Vahl) Børgesen		Ep	Ep*	
Bostrychia tenella (J. V. Lamouroux) J. Agardh		Ep*		
Bryocladia cervicornis (Kützing) F. Schmitz		Ep*		
Chondria dasyphylla (Woodward) C. Agardh				Ep
Chondria minutula Weber Bosse	Ep*	Ep		Ep
Chondria pygmaea Garbary & Vandermeulen		Ep		
Chondria repens Børgesen	Ep	Ep*	Ep*	
Chondrophycus cartilagineus (Yamada) Garbary & J. T. Harper		Ep		
Herposiphonia insidiosa (Greville ex J. Agardh) Falkenberg		Ep	Ep*	
Herposiphonia parca Setchell	Ep	Ep	Ep	
Herposiphonia secunda (C. Agardh) Ambronn ♣	Ep*	Ep	Ep	Ep
Herposiphonia subdisticha Okamura		Ep		Ep
Herposiphonia tenella (C. Agardh) Ambronn	Ep	Ep*	Ep	Ep*
Herposiphonia vietnamica Pham-Hoàng Hô			Ep	
Laurencia pinnata Yamada				Ep*
Laurencia silvae J. F. Zhang & B. M. Xia		Ep		
Leveillea jungermannioides (Hering & G. Martens) Harvey	Ep	Ep*	Ep	Ep
Lophosiphonia cristata Falkenberg		Ep		Ep
Melanothamnus ferulaceus (Suhr ex J. Agardh) Díaz-Tapia & Maggs	Ep	Ep*	Ep*	Ep*
Melanothamnus harlandii (Harvey) Díaz-Tapia & Maggs			Ep	

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Species, variety, and taxonomic form	Ryukyu islands	Hainan Island	Southern Vietnam	Amakusa islands
Melanothamnus japonicus (Harvey) Díaz-Tapia & Maggs	Ep*			Ep*
Melanothamnus pseudovillum (Hollenberg) Díaz-Tapia & Maggs		Ep		Ep
Melanothamnus savatieri (Hariot) Díaz-Tapia & Maggs	Ep	Ep		Ep
Melanothamnus sphaerocarpus (Børgesen) Díaz-Tapia & Maggs		Ep	Ep	
Melanothamnus tongatensis (Harvey ex Kützing) Díaz-Tapia & Maggs		Ep	Ep*	
Melanothamnus yendoi (T. Segi) Díaz-Tapia & Maggs				Ep
Palisada perforata (Bory) K. W. Nam		Ep*		
Polysiphonia exilis Harvey		Ep		
Polysiphonia nhatrangense Pham-Hoàng Hô			Ep	
Polysiphonia scopulorum Harvey			Ep*	
Polysiphonia subtilissima Montagne	Ep*	Ep*		Ep
Polysiphonia villum J. Agardh ♣	Ep	Ep*	Ep*	Ep*
Symphyocladia marchantioides (Harvey) Falkenberg				Ep*
Symphyocladia pumila (Yendo) S. Uwai & M. Masuda				Ep*
Tolypiocladia condensata (Weber Bosse) P. C. Silva			Ep	
Tolypiocladia glomerulata (C. Agardh) F. Schmitz	Ep*	Ep*	Ep*	
Vertebrata lanosa (Linnaeus) T. A. Christensen			Ep	
Vertebrata reptabunda (Suhr) Díaz-Tapia & Maggs		Ep		
Wilsonosiphonia howei (Hollenberg) D. Bustamante, Won & T. O. Cho		Ep		Ep
Family Wrangeliaceae				
Anotrichium tenue (C. Agardh) Nägeli		Ep	Ep*	Ep
Gordoniella yonakuniensis (Yamada & T. Tanaka) Itono		Ep		
Griffithsia japonica Okamura			Ep	Ep*
Griffithsia metcalfii C. K. Tseng	Ep*	Ep*	Ep	Ep
Griffithsia rhizophora Grunow ex Weber Bosse		Ep		Ep
Griffithsia subcylindrica Okamura		Ep	Ep	
Tiffaniella saccorhiza (Setchell & N. L. Gardner) Doty & Meñez	Ep		Ep	
Wrangelia argus (Montagne) Montagne		Ep*	Ep*	Ep*
Order Gelidiales				
Family Gelidiaceae				
Gelidium crinale var. *perpusillum* Piccone & Grunow			Ep	
Gelidium divaricatum G. Martens				Ep*
Gelidium pusillum (Stackhouse) Le Jolis		Ep*	Ep*	Ep*
Family Gelidiellaceae				
Gelidiella acerosa (Forsskål) Feldmann & Hamel		Ep*		
Gelidiella lubrica (Kützing) Feldmann & Hamel			Ep*	
Millerella pannosa (Feldmann) G. H. Boo & L. Le Gall		Ep*		
Parviphycus adnatus (E. Y. Dawson) B. Santelices		Ep*		
Family Pterocladiaceae				
Pterocladiella capillacea (S. G. Gmelin) Santelices & Hommersand	Ep			
Order Gigartinales				
Family Caulacanthaceae				
Caulacanthus okamurae Yamada				Ep*
Caulacanthus ustulatus (Turner) Kützing		Ep*		Ep*
Family Cystocloniaceae				
Hypnea cervicornis J. Agardh		Ep*		
Hypnea charoides J. V. Lamouroux		Ep*		Ep*
Hypnea esperi Bory	Ep	Ep*		
Hypnea musciformis var. *esperi* J. Agardh		Ep		

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Species, variety, and taxonomic form	Ryukyu islands	Hainan Island	Southern Vietnam	Amakusa islands
Hypnea nidulans Setchell		Ep*		
Hypnea pannosa J. Agardh		Ep*	Ep*	
Hypnea spinella (C. Agardh) Kützing	Ep	Ep	Ep*	Ep*
Hypnea valentiae (Turner) Montagne		Ep*		Ep*
Family Dumontiaceae				
Dudresnaya japonica Okamura				Ep*
Family Gigartinaceae				
Chondracanthus intermedius (Suringar) Hommersand				Ep*
Family Kallymeniaceae				
Kallymenia perforata J. Agardh				Ep*
Order Peyssonneliales **Family Peyssonneliaceae**				
Peyssonnelia rubra (Greville) J. Agardh				Ep*
Order Plocamiales **Family Plocamiaceae**				
Plocamium ovicorne Okamura				Ep*
Plocamium recurvatum Okamura				Ep
Plocamium telfairiae Harvey				Ep*
Order Rhodymeniales **Family Champiaceae**				
Champia expansa Yendo				Ep
Champia japonica Okamura	Ep			Ep
Champia parvula (C. Agardh) Harvey	Ep	Ep*	Ep*	Ep*
Champia vieillardii Kützing	Ep	Ep*		
Coelothrix irregularis (Harvey) Børgesen		Ep		
Family Lomentariaceae				
Ceratodictyon intricatum (C. Agardh) R. E. Norris		Ep		
Lomentaria corallicola Børgesen	Ep	Ep*	Ep*	
Lomentaria pinnata Segawa				Ep*
Family Rhodymeniaceae				
Botryocladia kuckuckii (Weber Bosse) Yamada & T. Tanaka	Ep			
Phylum HETEROKONTOPHYTA **Class Phaeophyceae** **Order Ectocarpales** **Family Acinetosporaceae**				
Feldmannia indica (Sonder) Womersley & A. Bailey	Ep			
Feldmannia irregularis (Kützing) G. Hamel ♣	Ep*	Ep*	Ep	Ep*
Feldmannia mitchelliae (Harvey) H.-S. Kim	Ep*	Ep*		Ep*
Hincksia conifera (Børgesen) I. A. Abbott				Ep
Pylaiella littoralis (Linnaeus) Kjellman	Ep*	Ep		
Family Ectocarpaceae				
Ectocarpus siliculosus (Dillwyn) Lyngbye	Ep		Ep	
Family Chordariaceae				
Chilionema ocellatum (Kützing) Kornmann	Ep*	Ep	Ep	
Kuetzingiella elachistaeformis (Heydrich) M. Balakrishnan & Kinkar	Ep*	Ep	Ep	
Leathesia marina (Lyngbye) Decaisne				Ep*
Myrionema strangulans Greville		Ep	Ep	
Family Scytosiphonaceae				
Colpomenia peregrina Sauvageau				Ep

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Species, variety, and taxonomic form	Ryukyu islands	Hainan Island	Southern Vietnam	Amakusa islands
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier		Ep*		
Dactylosiphon bullosus (D. A. Saunders) Santiañez, K. M. Lee, S. M. Boo & Kogame				Ep*
Hydroclathrus clathratus (C. Agardh) M. A. Howe		Ep*		Ep*
Myelophycus simplex (Harvey) Papenfuss				Ep*
Rosenvingea nhatrangensis E. Y. Dawson			Ep*	
Order Sphacelariales **Family Sphacelariaceae**				
Sphacelaria carolinensis Trono		Ep		
Sphacelaria novae-hollandiae Sonder ♣	Ep	Ep*	Ep*	Ep*
Sphacelaria rigidula Kützing ♣	Ep*	Ep*	Ep*	Ep*
Sphacelaria solitaria (Pringsheim) Kylin			Ep	
Sphacelaria tribuloides Meneghini	Ep	Ep	Ep*	
Sphacelaria yamadae Segawa		Ep		Ep
Order Dictyotales **Family Dictyotaceae**				
Dictyota friabilis Setchell		Ep*		Ep*
Lobophora variegata (J. V. Lamouroux) Womersley ex E. C. Oliveira		Ep*		Ep*
Zonaria flabellata (Okamura) Papenfuss				Ep*
Phylum CHLOROPHYTA **Class Chlorophyceae** **Order Chaetophorales** **Family Uronemataceae**				
Uronema marinum Womersley	Ep	Ep	Ep	
Class Ulvophyceae **Order Ulotrichales** **Family Ulotrichaceae**				
Ulothrix flacca (Dillwyn) Thuret		Ep		
Ulothrix implexa (Kützing) Kützing		Ep		Ep
Ulothrix subflaccida Wille		Ep		
Order Ulvales **Family Ulvellaceae**				
Ulvella lens P. L. Crouan & H. M. Crouan ♣	Ep	Ep	Ep	Ep
Ulvella repens (Pringsheim) R. Nielsen, C. J. O'Kelly & B. Wysor				Ep
Ulvella scutata (Reinke) R. Nielsen, C. J. O'Kelly & B. Wysor		Ep	Ep	Ep
Ulvella viridis (Reinke) R. Nielsen, C. J. O'Kelly & B. Wysor ♣	Ep	Ep	Ep	Ep
Family Ulvaceae				
Ulva clathrata (Roth) C. Agardh	Ep*	Ep		Ep
Ulva compressa Linnaeus		Ep*		Ep*
Ulva flexuosa Wulfen		Ep*	Ep*	Ep*
Ulva intestinalis Linnaeus				Ep*
Ulva prolifera O. F. Müller				Ep*
Order Cladophorales **Family Anadyomenaceae**				
Anadyomene wrightii Harvey ex J. E. Gray				Ep*
Microdictyon japonicum Setchell				Ep*
Family Boodleaceae				
Boodlea coacta (Dickie) G. Murray & De Toni				Ep*
Boodlea composita (Harvey) F. Brand	Ep*	Ep*		

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Species, variety, and taxonomic form	Ryukyu islands	Hainan Island	Southern Vietnam	Amakusa islands
Cladophoropsis fasciculata (Kjellman) Wille		Ep*		Ep
Cladophoropsis membranacea (Bang ex C. Agardh) Børgesen		Ep		Ep
Phyllodictyon anastomosans (Harvey) Kraft & M. J. Wynne		Ep*		Ep*
Family Cladophoraceae				
Chaetomorpha aerea (Dillwyn) Kützing			Ep*	
Chaetomorpha javanica Kützing		Ep*		
Chaetomorpha ligustica (Kützing) Kützing		Ep*	Ep*	
Chaetomorpha linum (O. F. Müller) Kützing				Ep*
Chaetomorpha minima F. S. Collins & Hervey		Ep*		Ep
Cladophora albida (Nees) Kützing		Ep*		
Cladophora coelothrix Kützing		Ep*		
Cladophora flexuosa (O. F. Müller) Kützing		Ep*		Ep*
Cladophora gracilis Kützing		Ep*	Ep*	
Cladophora laetevirens (Dillwyn) Kützing		Ep	Ep*	Ep*
Cladophora patentiramea (Montagne) Kützing		Ep		
Cladophora perpusilla Skottsberg & Levring		Ep*	Ep*	
Cladophora sibogae Reinbold		Ep		
Cladophora socialis Kützing		Ep*		
Cladophora vagabunda (Linnaeus) Hoek		Ep*	Ep*	Ep*
Lychaete herpestica (Montagne) M. J. Wynne	Ep*	Ep*		
Rhizoclonium implexum (Dillwyn) Kützing	Ep*	Ep		Ep*
Rhizoclonium riparium (Roth) Harvey	Ep	Ep		Ep*
Order Bryopsidales **Family Bryopsidaceae**				
Bryopsis australis Sonder		Ep		
Bryopsis pennata J. V. Lamouroux		Ep*		
Family Siphonocladaceae				
Siphonocladus rigidus M. A. Howe	Ep	Ep*		Ep*
Family Derbesiaceae				
Derbesia attenuata E. Y. Dawson			Ep*	
Derbesia marina (Lyngbye) Solier				Ep
Family Caulerpaceae				
Caulerpa ambigua Okamura	Ep*			Ep
Caulerpa vickersiae Børgesen		Ep*		
Family Halimedaceae				
Penicillus sibogae Gepp	Ep*			

Note: Ep, algae found only as epiphytes; Ep*, algae found as epiphytes, as well as living on hard substrata; ♣, the most common species of epiphytic algae (more than 20 finds in each study area).

Half of all the species we noted were common for the South China and East China seas (Table 1). We also compared the species composition of epiphytic algae sampled from different areas of the South China and East China seas: Hainan Island and Southern Vietnam; islands of the Ryukyu and Amakusa archipelagos; Amakusa islands and Southern Vietnam; and Ryukyu islands and Southern Vietnam (Fig. 3). We revealed the highest number of common species when comparing samples from Hainan Island and from Central and Southern Vietnam (South China Sea): 82 species, or 43% of the total number of species in the both collections. The lowest species similarity was established between samples from Vietnam (South China Sea) and the Amakusa islands (East China Sea): 59 species, or 32% in the both collections. The highest relative abundance of region-specific epiphytic algae (those found only in one certain region) was registered for the islands of the Amakusa Archipelago (Fig. 3): 69% of species when comparing algal collections from the islands of the Amakusa and Ryukyu archipelagos, and 56% of species when comparing algal collections from the Amakusa islands and the coast of Southern and Central Vietnam.

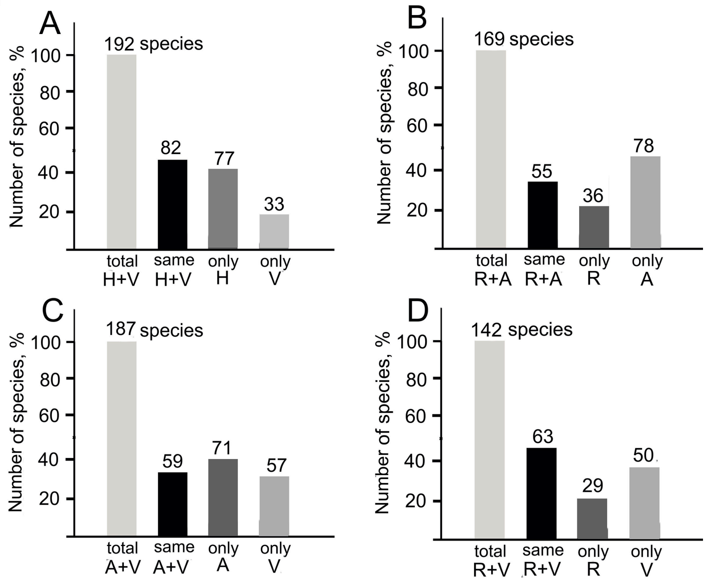

Fig. 3. Comparison of the species composition of collections of epiphytic algae from different areas of the South China and East China seas: A, Hainan Island and Southern Vietnam; B, islands of the Ryukyu and Amakusa archipelagos; C, Amakusa islands and Southern Vietnam; D, Ryukyu islands and Southern Vietnam

DISCUSSION

Species richness and taxonomic composition of the epiphytic algal flora in the study areas of the South China and East China seas. During our work, over 700 species and taxonomic forms of marine seaweeds were found and identified in four regions of the South China and East China seas; out of those, more than 30% were recorded in epiphytic life form. In algal collections from Central and Southern Vietnam, epiphytic algae accounted for 28%; from Hainan Island, 30%; from the islands of the Ryukyu Archipelago, 22%; and from the islands of the Amakusa Archipelago, 42%. Earlier, in the 1950s–1960s, Pham Hoang Ho registered 440 species of seaweeds in Southern Vietnam, of which 18% were found in epiphytic form [Pham, 1969]. In the book *Common Seaweeds of China* [Tseng, 1983], 454 species were described, and out of those, 12% were epiphytes. Comparison of our data with the material of Pham Hoang Ho and C. Tseng gives reason to assume that the recent benthic algal flora of the South China Sea is 1.5 times richer in epiphytic algae than the flora in the middle of the 20th century. However, in our opinion, the discrepancy in richness of epiphytic algae sampled by us and preserved in the earlier collections of other researchers can be explained chiefly by different methods of sampling and processing the material and also by the difference in surveyed habitats. We collected fine filamentous and unicellular epiphytes from fresh material, used stereoscopic microscope, and immediately began identification of samples. Our Vietnamese and Chinese colleagues mostly processed dry herbarium specimens, which did not facilitate the complete collection of epiphytic algae.

The highest number of seaweed species was registered on coral reefs of Hainan Island; the lowest, in the coastal aquatic ecosystems of the Amakusa Archipelago. At the same time, the relative number of epiphytic algal species to the total number of seaweed species was the highest on the Amakusa islands. The lowest species similarity was revealed between samples from Vietnam and the Amakusa Archipelago. The collection of seaweeds from the Amakusa islands differed from other ones in having noticeably higher relative number of region-specific epiphytic species.

We are inclined to assume that the difference we registered in the relative content of epiphytic algae in the flora of these two regions of the South China and East China seas is mediated by the climatic conditions within their habitats. We showed earlier that recent benthic floras off the coast and islands of Vietnam, Hainan Island, and the Ryukyu islands belong to those of the tropical biogeographic region, while the flora of the Amakusa islands is related to that of the warm temperate region [Titlyanov et al., 2019b]. Apparently, the development of epiphytism in the tropical biogeographic region is less intense than in the warm temperate region, presumably due to the effect of high temperatures on epiphytic algae throughout the dry season: it causes algae drying, and also death or inhibition of their growth in the intertidal zone [Titlyanov et al., 2014, 2019a].

Among all marine algal species we found in the study areas, about half were red algae. At the same time, in the samples of epiphytic algae, reds could account for more than 80%. Similar data were obtained earlier by Pham Hoang Ho. In the marine algal collection from the coast and islands of Southern Vietnam, red seaweeds also prevailed among epiphytes [Pham, 1969]. Reds dominated among epiphytes in cold waters of the Russian Far East seas as well [Zhigadlova, 2011]. According to the latest data by O. Belous and T. Titlyanova [2021], 57 species of epi- and endophytes were found on thalli of the brown alga *Punctaria plantaginea* (Roth) Greville in Peter the Great Bay, Sea of Japan; this accounted for 18% of the total number of algal species recorded in this location [Skriptsova, 2019]. Among fouling algae on *P. plantaginea*, fine filamentous and microscopic forms of red and brown species predominated.

About 40% of all the epiphytes we revealed were in obligate form, *i. e.*, these species grew only as epiphytes. Red algae representing the orders Acrochaetiales (family Acrochaetiaceae), Colaconematales (family Colaconemataceae), and Ceramiales (family Callithamniaceae), as well as green seaweeds from the orders Chaetophorales (family Chaetophoraceae), Ulotrichales (family Ulotrichaceae), and Ulvales (family Ulvellaceae), were found only as epiphytes.

Basiphytic algae. Chemical, morphological, and anatomical factors either contributing to the attachment and growth of epiphytes or preventing it. It is well known that the intensity of epiphytic colonization of macrophytes depends on internal factors: morphological, anatomical, and chemical properties of thalli of basiphytes and also on such habitat conditions, as grazing pressure, resistance to desiccation, and wave action [Jasim et al., 2022; Levin, Mathieson, 1991; Potin, 2012; Weinberger, Friedlander, 2008; Zhigadlova, 2011]. As shown, tropical red algal species are more active in terms of chemical defenses against fouling than other taxa. The antifouling effect of green algae is insignificant [Jasim et al., 2022]. Old or damaged thalli are often more susceptible to colonization by epiphytes, since their built-in chemical defenses are weakened [Levin, Mathieson, 1991; Potin, 2012].

For example, the fouling of the red alga *Palmaria* Stackhouse, 1802 was more active than the fouling of other species in the cold waters of the Kamchatka Peninsula due to peculiarities of *Palmaria* anatomy: a large number of cavities in its cortical layer that appear after the release of mature tetraspores and are easily accessible for settlement and fixation of epi- and endophytes. Also, it results from the fact that epibionts use biologically active substances released by a basiphyte during maturation [Zhigadlova, 2011].

Another example of the distribution of epiphytes being determined by the morphological and anatomical features of the host is reported by E. Martinez and J. Correa [1993]; the researchers combined field and laboratory works and showed that green epiphytic algae *Sporocladopsis* sp. were limited to the sori of their kelp hosts, *Lessonia nigrescens* Bory and *L. trabeculata* Villouta & Santelices (Heterokontophyta), and did not penetrate into neighboring vegetative tissues of basiphytes.

The brown seaweed *Ascophyllum nodosum* (Linnaeus) Le Jolis forms extensive thickets in rocky tidal habitats protected from waves on the Northwestern Atlantic. This fucoid alga is the host for an obligate epiphyte, the red alga *Vertebrata lanosa* (Linnaeus) T. A. Christensen, and two facultative epiphytes, the browns *Elachista fucicola* (Velley) Areschoug and *Pylaiella littoralis* (Linnaeus) Kjellman. *V. lanosa* can occur throughout most of the length of the host leaves, but largely predominates in the middle leaf segments. Having usually a smooth surface due to their young age, distal segments bound two epiphytic brown algae. By creating small wounds that mimic scratches, the researchers stimulated the spread of epiphytes over the entire surface of the host leaves. It was demonstrated that *V. lanosa* can colonize damaged distal leaf segments during the growth and reproduction season (summer and autumn). The authors suggest that the absence of surface irregularities on distal segments of the host fronds, specifically small bounds, is the main factor explaining the absence of *V. lanosa* there [Longtin, Scrosati, 2009].

In total, during our works in the study areas, epiphytes were found on thalli of 40% of the species sampled. The highest number of cases of epiphytes settlement was observed on complex thalli of algae from the families Galaxauraceae, Corallinaceae, Rhodomelaceae, Cystocloniaceae, Rhodymeniaceae (Rhodophyta), Scytosiphonaceae, Dictyotaceae, and Sargassaceae (Heterokontophyta). Epiphytes were not found on red seaweeds of filamentous and fine filamentous forms from the orders Stylonematales, Erythropeltales, Bangiales, Acrochaetiales, Colaconematales, and Ceramiales (family Delesseriaceae), as well as on green algae representing the orders Ulvales (family Ulvellaceae), Bryopsidales (family Udoteaceae), and Dasycladales (family Dasycladaceae).

The positive effect of reducing the concentration of pollutants on the intensity of epiphytism after the closing of fish farms in the Sanya Bay (Hainan Island) was revealed by us before [Li et al., 2016, 2021]. The content of nutrients in the seawater opposite the outlet decreased by more than an order of magnitude and became almost equal to the mean value for the Sanya Bay. Six months after the removal of the fish farm, the population density of the dominant species of green and brown epilithic algae and their biomass significantly dropped, while the number of species of epiphytic algae increased. In this case, we associate the reason for a rise in the number of epiphytic algae with an increase in diversity and shift in the taxonomic composition of basiphytic algae.

When studying seasonal changes in the benthic flora of tropical regions, a boost in the diversity of epiphytic algae was observed in summer and autumn [Titlyanov et al., 2014, 2019a]. An increase seemed to be governed by the formation in this late growing season of areas suitable for settlement of epiphytes on old basiphytic thalli: the ones with various types of damage, with mature or sporulated reproductive organs, with diseased or dead areas, and with other changes in morphology and anatomy [Levin, Mathieson, 1991; Potin, 2012].

Conclusions. Based on years of research involving inventory of the benthic marine flora of four regions of the South China and East China seas, the state and development of epiphytism in tropical and warm-temperate biogeographic regions were analyzed. In the study areas, epiphytic algae accounted for about half of the total number of seaweed species recorded. A greater development of epiphytism was revealed in the warm-temperate biogeographic regions (East China Sea, islands of the Amakusa Archipelago). Among epiphytic species, red algae predominated. Two groups of species were distinguished: obligate epiphytes and facultative ones. The former settled only on living (and healthy) thalli of algae, and the latter also attached to other types of substrata. Among obligate epiphytes, red algae in fine filamentous and filamentous forms prevailed. As shown, the study areas differed not only in the number of epiphytic algal species found, but also in the species composition. Only 30% of epiphytic species of all taxonomic groups were common to the study areas. Most of the region-specific epiphytes were registered on the Amakusa islands (warm-water temperate biogeographic region).

Not all the species of marine seaweeds encountered were colonized by epiphytes: those were most often noted on thalli of red and brown algae which have a complex structure of thalli.

The species diversity of the epiphytic flora increased with a decline in the concentration of pollutants in parallel with a rise in the total number of species of benthic algae. An increase in the diversity of epiphytic algae was observed in summer and autumn, which is probably associated with the climacteric period of succession of the algal community: a weakening of the chemical defenses of basiphytes against settlers and appearance of convenient surfaces for settling.

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ЭПИФИТИЗМ СРЕДИ ВОДОРОСЛЕЙ КОРАЛЛОВЫХ РИФОВ И КАМЕНИСТЫХ ПРИБРЕЖНЫХ ЭКОСИСТЕМ В ЮЖНО-КИТАЙСКОМ И ВОСТОЧНО-КИТАЙСКОМ МОРЯХ

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Эпифитизм — природное явление, широко распространённое в прибрежных экосистемах Мирового океана. Эпифиты — это растения (водоросли), растущие на других растениях (водорослях), не конкурирующие с другими организмами за субстрат и получающие в основном физическую поддержку от хозяина. В то же время известно негативное влияние эпифитов: они могут снижать продуктивность, вызывать морфологические аномалии, уменьшать структурную прочность слоёв и способствовать отрыву таллома хозяина от субстрата во время штормов. Работа посвящена изучению видового состава и жизненных форм водорослей-эпифитов в некоторых биогеографических районах Мирового океана, а также анализу флористических различий, выявленных в этих районах, и установлению причин их возникновения. Макроводоросли были собраны в верхней, средней и нижней литорали и в верхней сублиторали на коралловых рифах в Южно-Китайском и Восточно-Китайском морях. Образцы отбирали из трёх случайно выбранных квадратов (площадь 1 м^2) и с участков за их пределами. Каждый образец проверяли на наличие эпифитов. Всего собрано и проанализировано более 1000 талломов с эпифитами. Видовое богатство, состав и распространение эпифитных водорослей в экосистемах коралловых рифов в Южно-Китайском море (Центральный и Южный Вьетнам, остров Хайнань) и Восточно-Китайском море (острова́ архипелагов Рюкю и Амакса) за период с 1995 по 2019 г. изучено впервые. В этих четырёх регионах обнаружено и идентифицировано более 700 видов и таксономических форм морских растений, из которых около 33 % являются эпифитами. Наибольшее количество видов водорослей собрано на коралловых рифах острова Хайнань (526); наименьшее количество видов обнаружено в прибрежных водных экосистемах островов архипелага Амакса (320). Количество эпифитов относительно общего числа видов водорослей было максимальным на островах Амакса. Среди зарегистрированных видов эпифитных водорослей около 40 % встречались в облигатной форме, а более 50 % были факультативными эпифитами. Районы исследований различались по видовому составу эпифитов, и только 30 % видов были общими. Наиболее специфичные для района эпифитные виды отмечены на островах архипелага Амакса. В статье обсуждаются причины и условия широкого развития эпифитизма среди водорослей в различных биогеографических районах Мирового океана. Приложение к публикации содержит описания морфологии и анатомии талломов 40 широко распространённых видов эпифитов. Описания сопровождаются цветными фотографиями с деталями морфологических и анатомических структур.

Ключевые слова: морские водоросли, эпифиты, коралловые рифы, видовой состав