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ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2024, vol. 9, no. 1, pp. 108–117
https://marine-biology.ru

UDC 574.58(265.57)

MARINE ALGAL FLORA OF THE SOUTHERN ISLANDS OF JAPAN

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Received by the Editor 20.01.2023; after reviewing 28.03.2023;
accepted for publication 09.10.2023; published online 22.03.2024.

In 1995–2019, marine algae were sampled in the intertidal and upper subtidal zones of the Amakusa Archipelago (Shimoshima islands) and the southern islands of the Ryukyu Archipelago (Okinawa, Sesoko, Ieshima, Akajima, Miyako, Ishigaki, Iriomote, and Yonaguni). A total of 569 species and taxonomic forms of benthic macroalgae were identified. Out of them, 57% belonged to red algae; 15%, to brown algae; and 28%, to green algae. On these islands, 153 taxa were found for the first time. During the specified period, the benthic marine flora of individual islands was analyzed with varying degrees of care. The most thoroughly studied island of the Amakusa group was Shimoshima (14 localities during all seasons), and of the Ryukyu Archipelago, Sesoko (8 localities during all seasons). The comparison of taxonomic and biogeographic characteristics of marine floras of these two archipelagos – biodiversity of species and forms, taxonomic composition of algal communities, and potential capabilities of geographic (latitudinal) distribution of taxa – give us the grounds to classify the Shimoshima Island as a warm-temperate region of the Northern Hemisphere in East Asia, and the southern islands of the Ryukyu Archipelago, as a tropical biogeographic region.

Keywords: macroalgae, Amakusa Archipelago, southern islands of the Ryukyu Archipelago, comparison of the marine flora

The southern islands of Japan are situated in warm waters of two biogeographic regions of the Northern Hemisphere – Indo-West Pacific warm-temperate region and tropical region – in geographic latitudes from 32°23′N to 24°03′N, according to the scheme of J. C. Briggs [1974] modified by K. Lüning [1990] (Fig. 1).

The benthic marine flora of the southern islands of Japan has been fairly well studied mainly by Japanese algologists since 1897 [Okamura, 1897, 1930] and during the 1930s–2000s (see Supplement 1: https://marine-biology.ru/mbj/article/view/422/655). Only one work was dedicated to the benthic flora of Amakusa islands [Segawa, Yoshida, 1961].

The authors of the present article initiated the research on the benthic flora of the islands of the Ryukyu Archipelago in 1995 within the framework of ecological studies of Sesoko Island coral reef ecosystem (the west of Northern Okinawa) at the Tropical Biosphere Research Center Sesoko Station of the University of the Ryukyus. In parallel to eco-physiological investigations, the study of the benthic marine flora of the Amakusa Archipelago (Shimoshima islands) and the Ryukyu Archipelago (Okinawa, Sesoko, Ieshima, Akajima, Miyako, Ishigaki, Iriomote, and Yonaguni) was carried out (Fig. 1).

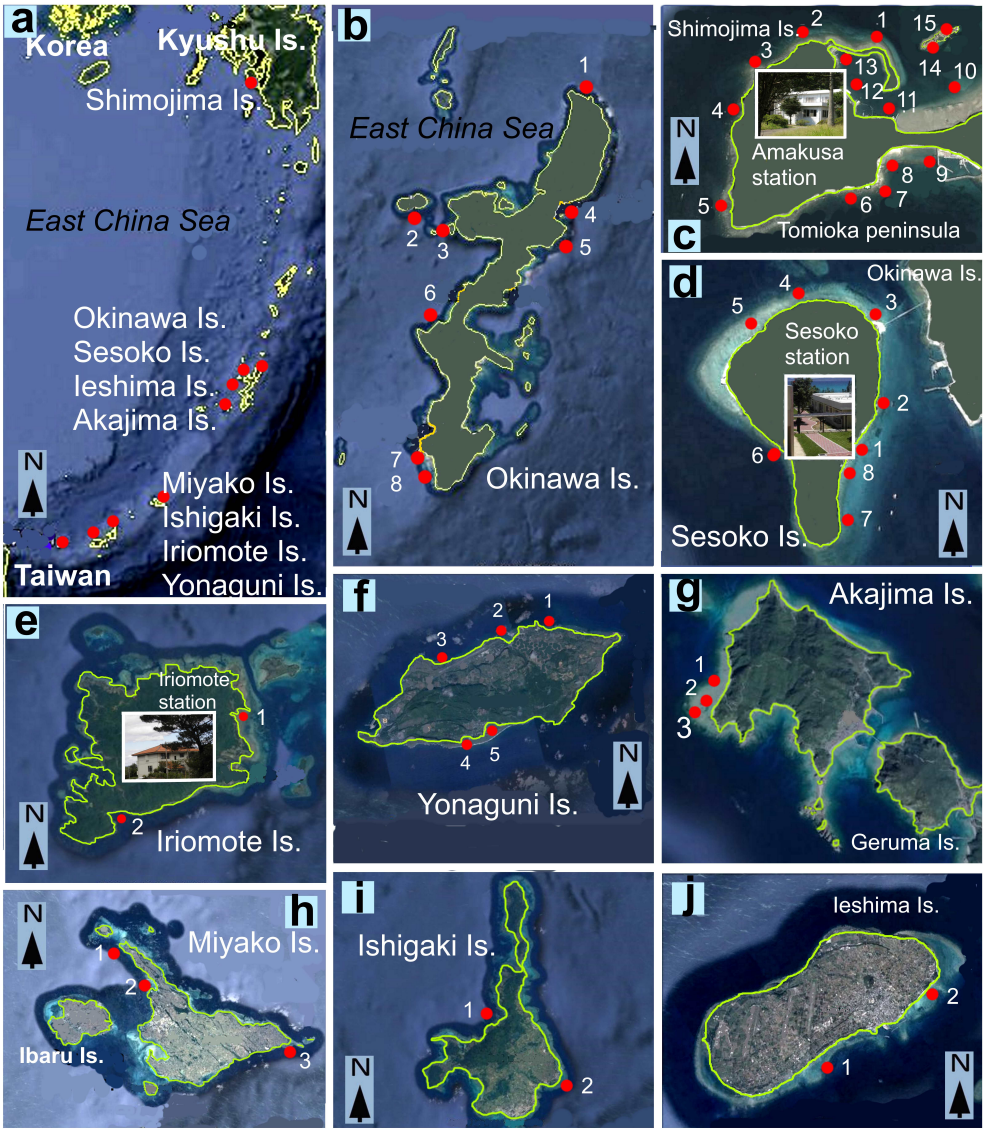

Fig. 1. Sites of algal sampling (marked with red circles) on islands of the Amakusa and Ryukyu archipelagos. A, islands where algae were sampled. B, sampling sites in Okinawa Prefecture: Cape Hedo (site 1); Ieshima Island (2); Sesoko Island (3); Oura Bay (4); Henoko point (5); Maeda coast (6); Arasaki Beach (7, 8); Ohdo coast (9). C, sampling sites along Tomioka Peninsula, Shimoshima Island: Magarizaki coast (1, 2); Akaiwa coast (3, 4); Shikizaki Bay (5); Shiraiwazaki Bay (6–8); Reihoku coast (9); Tomioka Harbor (10–13); Tsujishima Island (14, 15). D, sampling sites along Sesoko Island (1–8). E, sampling sites along Iriomote Island: Hoshidate coast (1); Kanoka coast (2). F, sampling sites along Yonaguni Island: Sonai locality (1–3); Higawa Bay (4); Tojima coast (5). G, sampling sites along Akajima Island, upper subtidal of the western coast (1–3). H, sampling sites along Miyako Island: Karimata coast (1, 2); Cape Higashi Hennasaki (3). I, sampling sites along Ishigaki Island: Shiraho coast (1); Kabira Bay (2). J, sampling sites along Ieshima Island, southeastern coast (1, 2)

Рис. 1. Места сбора водорослей (отмечены красными кружками) на островах архипелагов Амакса и Рюкю. A — острова́, где были собраны водоросли. B — места сбора в профектуре Окинава: мыс Хедо (точка 1); остров Иэдзима (2); остров Сесоко (3); залив Оура (4); мыс Хеноко (5); побережье Маэда (6); пляж Арасаки (7, 8); побережье Одо (9). C — места сбора вдоль полуострова Томиока, остров Симосима: побережье Магаризаки (1, 2); побережье Акаива (3, 4); бухта Сикизаки (5); бухта Сирайвазаки (6–8); побережье Рейхоку (9); гавань Томиока (10–13); остров Цудзисима (14, 15). D — места сбора вдоль о́строва Сесоко (1–8). E — места сбора вдоль о́строва Ириомоте: побережье Хосидате (1); побережье Канока (2). F — места сбора вдоль о́строва Йонагуни: местечко Сонай (1–3); бухта Хигава (4); побережье Тодзима (5). G — места сбора вдоль о́строва Акадзима, верхняя сублитораль западного побережья (1–3). H — места сбора вдоль о́строва Мияко: побережье Каримата (1, 2); мыс Хигаси Хеннасаки (3). I — места сбора вдоль о́строва Исигаки: побережье Сирахо (1); бухта Кабира (2). J — места сбора вдоль о́строва Иэсима, юго-восточное побережье (1, 2)

Material partially published earlier provided the dynamics of algal growth on damaged and dead coral colonies in the sea and in aquariums of Sesoko Island [Titlyanov et al., 2008, 2010, 2018], decadal changes in algal assemblages of Yonaguni Island [Titlyanov et al., 2016], and historical changes in the marine flora of Tomioka Peninsula, Shimoshima Island [Titlyanov et al., 2019a, b]. For other islands we studied, the data are published for the first time.

The aim of this work was to present an annotated list of benthic algae in coral reef ecosystems of the Ryukyus and ecosystem of hard substrata with coral settlements of Amakusa islands, using all papers on the inventory of the benthic flora of the islands and our published and unpublished sampling data of 1995–2019. Moreover, based on a comparison of taxonomic and biogeographic characteristics of recent benthic algal floras of the islands of these two archipelagos [diversity of species and forms, taxonomic composition of algal communities, and potential opportunities for geographical (latitudinal) distribution of taxa], we aimed at assigning them to specific biogeographic regions of the Northern Hemisphere in East Asia.

MATERIAL AND METHODS

Sampling sites and time. The study of the marine flora along the coast of Okinawa Island was carried out in November–December 2006 in the following localities: Cape Hedo, Oura Bay, Henoko point, Maeda coast, and Ohdo coast; in March 2013 and February 2014, the investigation was carried out along Arasaki Beach (Fig. 1B). In the west of Northern Okinawa, along the coast of Sesoko Island, algae were collected in 1995 (May–October), 1997 (September–December), 1998 (January–April), 2002 (October–December), 2003 (January–September), 2004 (July), 2005 (February–May), 2006 (November–December), 2007 (January), 2014 (February), and 2019 (January–February) (Fig. 1D). In December 2006, marine algae were sampled along the southeastern coast of Ieshima Island (Fig. 1J). In August 1995, algal sampling was carried out on a coral reef along the western coast of Akajima Island (the group of Kerama islands) at three localities (Kubamanohama, Kushibaru, and Hanase) (Fig. 1G), Kohama Island (the group of Yaeyama islands), and at two localities of Ishigaki Island (Kabira Bay and Shiraho Reef) (Fig. 1I). In March 2013, marine algae were sampled around Yonaguni Island (Sonai, Higawa, and Tojima bays) (Fig. 1F) and along the coast of Miyako Island (Karimata locality and Cape Higashi Hennasaki) (Fig. 1H). In February 2017, algal sampling was carried out along the coast of Iriomote Island (Hoshidate and Tanaka bays) (Fig. 1E). On Shimoshima Island, marine algae were sampled in November and December 2012, April and August 2013, January 2014, October and November 2015, and November 2017 at seven localities of Tomioka Peninsula: Akaiwa, Magarizaki, Shikizaki Bay, Shiraiwazaki Bay, Tomioka Harbor, Tsujishima Island, and Reihoku-cho (Fig. 1C).

Collection, conservation, and floristic analysis of samples. Macroalgae were sampled in the upper, middle, and lower intertidal and the upper subtidal (from 0.5-m to 4-m depth during low tide) zones of Ryukyu islands by T. Titlyanova, E. Titlyanov, and O. Belous; on Amakusa islands, by T. Titlyanova, E. Titlyanov, and M. Tokeshi. In the upper subtidal zone, marine plants were sampled *via* snorkeling (by T. Titlyanova) and scuba diving (by E. Titlyanov and M. Tokeshi) during low and high tides. Algae were collected from all types of substrata. The algal samples are deposited at the A. V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences (Vladivostok, Russian Federation).

Fresh and dried specimens were identified by T. Titlyanova, E. Titlyanov, and O. Belous using the data of monographic publications, floristic studies, and systematic articles cited in previous papers [Titlyanov et al., 2011; Titlyanova et al., 2012]. The systematics and nomenclature follow AlgaeBase [2023]. Hierarchical classification of the phylum Rhodophyta is given according to [Saunders, Hommersand, 2004; Schneider, Wynne, 2013; Wynne et al., 2014]. The classification system of the phyla Chlorophyta and Ochrophyta is given in accordance with [Tsuda, 2003, 2006].

RESULTS

Species composition. The results of the present study are provided in Table (see Supplement 2: https://marine-biology.ru/mbj/article/view/422/656). It documents 569 species and taxonomic forms of benthic macroalgae sampled off the southern islands of Japan in 1995–2019; 153 species of marine algae were new records for the Amakusa and Ryukyu archipelagos (see [Titlyanov et al., 2016, 2019a, b]). The phylum Rhodophyta (Rh in Fig. 2) was comprised of 4 classes, 17 orders, 47 families, 128 genera, and 324 species (57% of all species). The phylum Ochrophyta (Oc) was comprised of 2 classes, 10 orders, 16 families, 43 genera, and 86 species (15% of all species) belonging to the class Phaeophyceae. The phylum Chlorophyta (Ch) was comprised of 2 classes, 7 orders, 23 families, 49 genera, and 159 species (28% of all species) (Suppl. 2, Fig. 2).

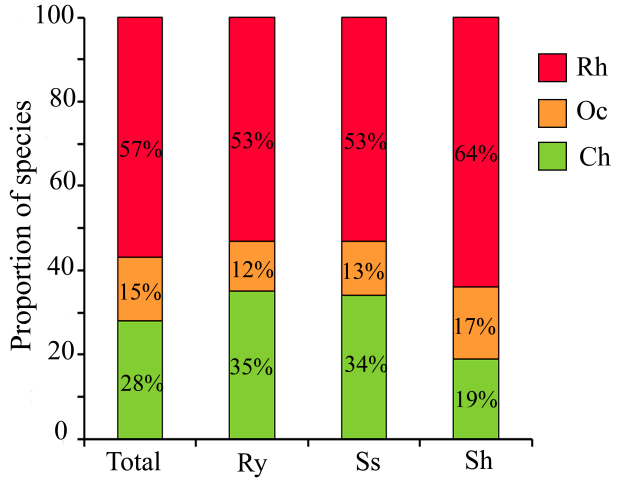

Fig. 2. Proportion of species and their taxonomic forms sampled along the islands of the Ryukyu and Amakusa archipelagos in 1995–2019. Ry, islands of the Ryukyu Archipelago; Ss, Sesoko Island; Sh, Shimoshima Island (the Amakusa Archipelago). Rh, Rhodophyta; Oc, Ochrophyta; Ch, Chlorophyta

Рис. 2. Соотношение видов и их таксономических форм, собранных на островах архипелагов Рюкю и Амакса в 1995–2019 гг. Ry — острова́ архипелага Рюкю; Ss — остров Сесоко; Sh — остров Симосима (архипелаг Амакса). Rh — Rhodophyta; Oc — Ochrophyta; Ch — Chlorophyta

Out of red algae, the highest number of taxa belonged to four orders: Ceramiales (129), Gigartinales (35), Corallinales (29), and Rhodymeniales (24). Brown algae were mostly represented by Ectocarpales (26), Dictyotales (22), and Fucales (23). Out of green algae, Bryopsidales (67), Cladophorales (47), and Ulvales (23) prevailed (Suppl. 2, Fig. 3A).

All species of our collection were found earlier by other authors in tropics and/or subtropics. Out of them, 79% were recorded in tropics and/or subtropic alone; 13% were registered in tropics and/or subtropics and in temperate latitudes as well; and 8% were noted in tropical and/or subtropical, temperate latitudes, and Arctic and/or Antarctic.

More than a half (58%) of all species of our collection were found in the seas of Pacific, Indian, and Atlantic oceans; 27% inhabited only the Indo-Pacific; and 15% inhabited only the seas of the Pacific Ocean (Fig. 4A).

On all investigated islands of the Ryukyu Archipelago, 428 species of marine algae were documented. Out of them, 54% were red algae, 12% were brown, and 34% were green (Suppl. 2, Fig. 2). Species of red algae belonged to 4 classes, 16 orders, 40 families, and 104 genera; species of brown algae, to 2 classes, 7 orders, 10 families, and 28 genera; and species of green algae, to 2 classes, 7 orders, 22 families, and 46 genera. In terms of species number, the richest families and orders were the following ones: out of red algae, Rhodomelaceae (50), Ceramiaceae (32), and families of Corallinales (23); out of brown algae, Dictyotaceae (17), Sargassaceae (11), and Scytosiphonaceae (6); and out of green algae, Caulerpaceae (23), Cladophoraceae (21), and Ulvaceae (13) (Suppl. 2, Fig. 3B). All species of our collection were previously found by other authors in tropics and/or subtropics. Out of them, 84% were registered only in tropical and/or subtropical latitudes; 8% were noted in temperate latitudes; and 8% were recorded in Arctic and/or Antarctic. Also, 28% of marine algae belonged to the Indo-Pacific, and 8% inhabited only the seas of the Pacific Ocean (Suppl. 2, Fig. 4B).

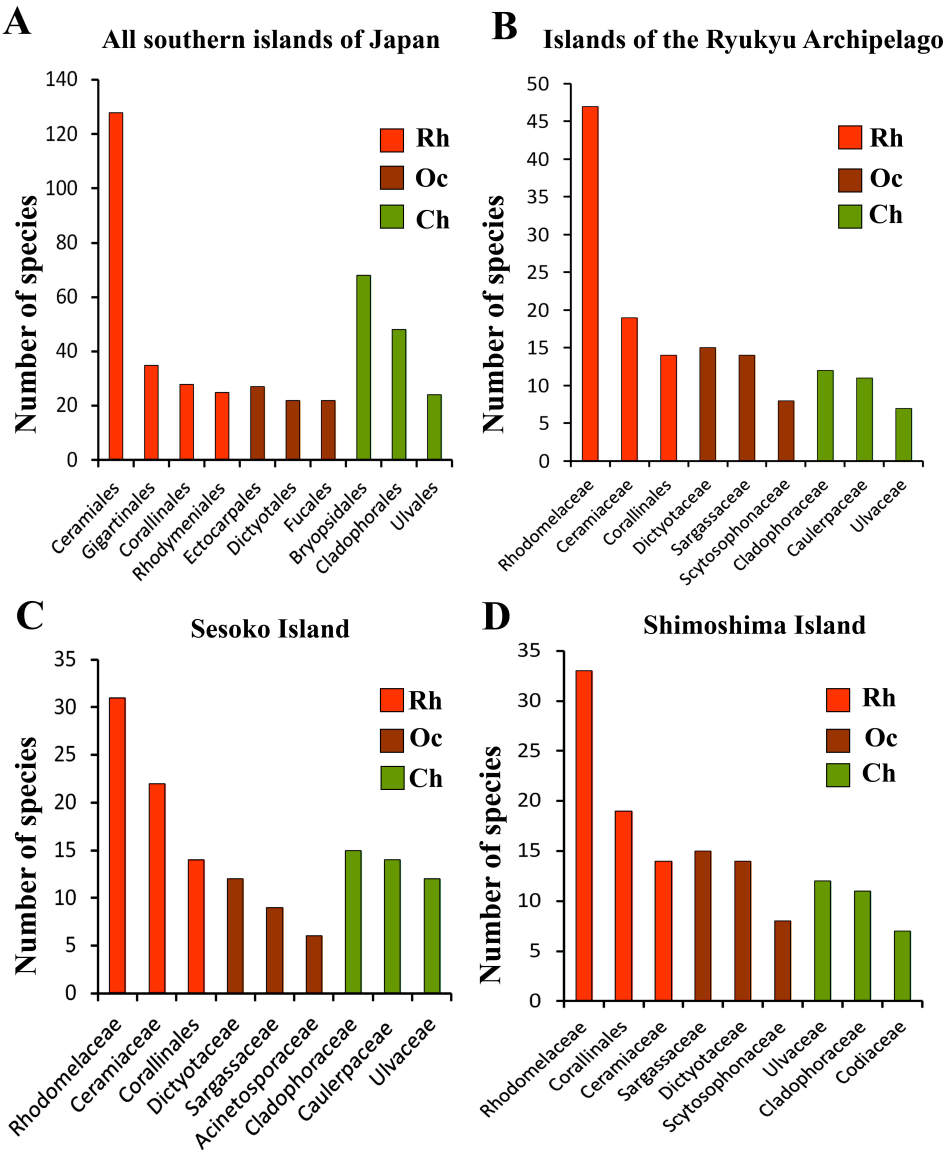

Fig. 3. Number of marine algal species in the richest taxa: A, all investigated southern islands of Japan; B, islands of the Ryukyu Archipelago; C, Sesoko Island; D, Shimoshima Island

Рис. 3. Количество видов морских водорослей в наиболее богатых таксонах: A — все исследованные южные острова́ Японии; B — острова́ архипелага Рюкю; C — остров Сесоко; D — остров Симосима

Out of the islands of the Ryukyu Archipelago, the highest number of species (329) were sampled along the coast of Sesoko Island (26°38′N, 127°51′E); out of them, 55% were red algae, 12% were brown, and 33% were green (Suppl. 2, Fig. 2). Species of red algae were represented by 4 classes, 16 orders, 38 families, and 94 genera; brown algae, by 2 classes, 7 orders, 10 families, and 26 genera; green algae, by 2 classes, 6 orders, 21 families, and 42 genera. The highest species richness was registered for the following orders and families. Out of red algae, Rhodomelaceae (32), Ceramiaceae (23), and families of Corallinales (14) prevailed; out of brown algae, Dictyotaceae (12), Sargassaceae (9), and Acinetosporaceae (5); and out of green algae, Cladophoraceae (14), Caulerpaceae (14), and Ulvaceae (11) (Suppl. 2, Fig. 3C). In the collection representing Sesoko Island, 83% of all species belonged to tropics and/or subtropics alone; 8%, temperate latitudes; 9%, Arctic and/or Antarctic. Moreover, 28% of algae represented only the Indo-Pacific, and 7%, the seas of the Pacific Ocean (Suppl. 2, Fig. 4C).

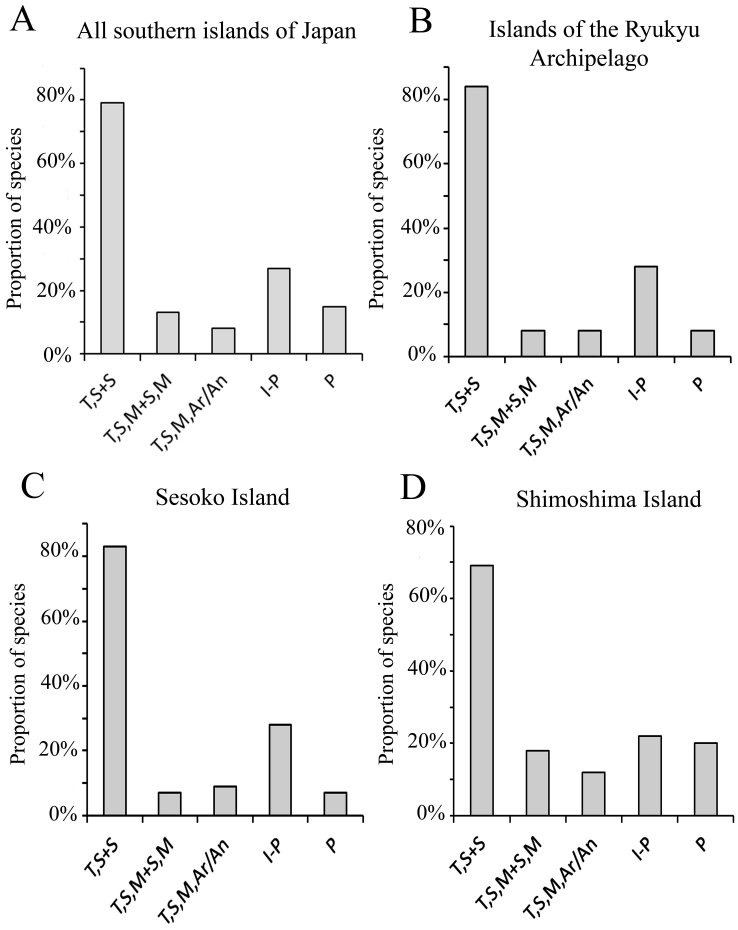

Fig. 4. Geographic distribution of marine algae off the southern islands of Japan. A, all investigated southern islands of Japan; B, islands of the Ryukyu Archipelago; C, Sesoko Island; D, Shimoshima Island. T, S + S, previously found inhabiting only the tropics and/or subtropics; T, S, M + S, M, previously found in tropical and/or subtropical and temperate latitudes; T, S, M, Ar / An, previously found in tropical and/or subtropical, temperate latitudes, and Arctic and/or Antarctic; I-P, inhabiting only the Indo-Pacific; P, found living only in the seas of the Pacific Ocean

Рис. 4. Географическое распространение морских водорослей на южных островах Японии. A — все исследованные южные острова́ Японии; B — острова́ архипелага Рюкю; C — остров Сесоко; D — остров Симосима. T, S + S — ранее найдены только в тропиках и/или субтропиках; T, S, M + S, M — ранее найдены в тропических и/или субтропических и умеренных широтах; T, S, M, Ar / An — ранее найдены в тропических и/или субтропических, умеренных широтах и Арктике и/или Антарктике; I-P — обитают только в Индо-Тихоокеанском регионе; P — встречаются только в морях Тихого океана

Off the most northern island of investigated ones, Shimoshima (the largest island of the Amakusa Archipelago, 32°31′N, 130°02′E), located 6° north of Sesoko Island, we sampled 321 species and forms. Out of them, 63% were red algae, 17% were brown, and 20% were green (Suppl. 2, Fig. 2). Species of red algae represented 4 classes, 17 orders, 40 families, and 93 genera; species of brown algae, 1 class, 8 orders, 13 families, and 28 genera; and species of green algae, 1 class, 5 orders, 20 families, and 30 genera. The highest species richness was registered for the following families: out of red algae, Rhodomelaceae (33), families of Corallinales (20), and Ceramiaceae (13); out of brown algae, Sargassaceae (15), Dictyotaceae (14), and Scytosiphonaceae (8); out of green algae, Ulvaceae (12), Cladophoraceae (10), and Codiaceae (7) (Suppl. 2, Fig. 3D). In the collection of algae sampled off Shimoshima Island, 69% were tropical and/or subtropical species; 18% were species of temperate latitudes; and 13% were species of Arctic and/or Antarctic. Moreover, 22% inhabited only the Indo-Pacific, and 20% belonged to species inhabiting only the seas of the Pacific Ocean (Suppl. 2, Fig. 4D).

DISCUSSION

The floristic diversity and composition of macrophytes from islands of the Ryukyu Archipelago sampled by us in 1995–2019 were close to those for other islands in the Indo-Pacific, where coral reefs are the main ecosystem, algal species richness is characterized by 400 taxa, and the floristic composition is reported to be as follows: 50–60% of red algae, 20–35% of green algae, and 10–20% of brown algae [Huisman, Borowitzka, 2003; Lewis, Norris, 1987; Silva, 1992; Silva et al., 1987, 1996; Tseng, 1983; Tsuda, 2003, 2006; Zhang, 1996].

Taxonomic diversity, species richness of above-mentioned families, a group of species, or an indicator species of coral ecosystems of the seas of Southeast Asia, and potential latitudinal distribution of marine algae of the Ryukyu Archipelago are close to those of other coral reefs studied by us in the South China and East China seas lying in tropical and subtropical latitudes [Belous et al., 2021; Titlyanov et al., 2011, 2014, 2015, 2016; Titlyanova et al., 2014].

Taxonomic characteristics of the benthic marine flora on Shimoshima Island of the Amakusa Archipelago differed significantly from those for the southern islands of the Ryukyu Archipelago. On the Amakusa Archipelago, the relative number of red algae was higher by 9%, and brown algae, by 5%. At the same time, the relative number of green algae was lower by 14% than on Ryukyu islands. Taxonomic diversity of green algae on Shimoshima Island was significantly lower than that for the southern islands of the Ryukyu Archipelago: the values were lower by 1 class, 2 orders, 2 families, 16 genera, and 82 species. Moreover, green algae of two archipelagos differed in composition of families with the highest species richness. Specifically, on Ryukyu islands, those were Cladophoraceae, Caulerpaceae, and Ulvaceae; on Amakusa islands, Ulvaceae, Cladophoraceae, and Codiaceae. Algal collections from the archipelagos differed in relative number of species belonging to various geographical zones. The collection from Shimoshima Island contains less species (by 14%) representing tropics and subtropics alone than the collection from Ryukyu islands, as well as relatively more species belonging to temperate latitudes (by 11%) and Arctic and/or Antarctic (by 3%). Also, there are 13% more species which inhabit only the seas of the Pacific Ocean.

According to the scheme of marine biogeographic regions provided by J. C. Briggs [1974] and modified by K. Lüning [1990], Kyushu Island and the Amakusa Archipelago (southern islands of Japan) are located on the border between the warm-temperate region and cold-temperate region, and the southern islands of the Ryukyu Archipelago are situated on the border between the warm-temperate region and tropical biogeographic region. Data presented by us on taxonomic diversity of marine algae on the Amakusa and Ryukyu archipelagos give the grounds to suppose that the recent benthic flora of these archipelagos belongs to two different biogeographic regions.

As known, the marine flora of biogeographic temperate regions in both hemispheres differs in species diversity and the values of R/P index (number of Rhodophyta species divided by number of Phaeophyceae species) and C/P index (number of Chlorophyta species divided by number of Phaeophyceae species) [Belous et al., 2013; Lewis, Norris, 1987; Nguyen et al., 2013; Perestenko, 1980, 1994; Pham, 1969; Santelices et al., 2009; Titlyanov et al., 2015; Titlyanova et al., 2014]. It can be summarized that an average of about 200 species of benthic macroalgae were found in the cold-temperate region, and more than 400 species were recorded in the tropical biogeographical region. Both in the Northern and Southern hemispheres, the marine flora of cold waters is enriched with brown algae, and the flora of warm waters is enriched with red and green algae. The indices R/P and C/P in a given flora are very important characteristics of biogeographic regions. Their values for the marine flora of cold waters are 1.0–2.0 and 0.3–0.8, respectively; for the marine flora of warm waters, 2.5–4.0 and 0.5–1.0, respectively; and for the marine flora of tropical waters, 3.0–4.5 and 1.0–2.0, respectively [Santelices et al., 2009].

One of key indicators of the benthic flora in the tropical biogeographic region is the richness of algal species and forms in families of the order Ceramiales (Rhodophyta) and in Caulerpaceae, Boodleaceae, and Valoniaceae (Chlorophyta) [Belous et al., 2021; Titlyanov et al., 2015]. Main identification characteristic of the benthic flora of the warm-temperate region in the Northern Hemisphere in East Asia is the most actively settling representative of the warm-water genus *Sargassum* C. Agardh, 1820 [Belous et al., 2013].

Our sampling in 2012–2017 on Shimoshima Island [Titlyanov et al., 2019a] allowed documenting more than 300 species of benthic macroalgae with a significant prevalence of red algae (63%) over brown and green algae. R/P value for sampled algae was 3.6, and C/P value was 1.1. Those correspond to the flora of warm-temperate regions and give us the grounds to classify Shimoshima Island of the Amakusa Archipelago, with its benthic flora, as part of the warm-temperate region.

On Sesoko Island, 6° south of Shimoshima Island, in 1995–2019, we recorded more than 300 species and forms of marine algae, with red and green algae prevailing. R/P value of sampled algae was 4.4, and C/P value was 2.6. All found species belonged to tropical latitudes; in these calculations, we also used material from our earlier works [Titlyanov et al., 2008, 2010, 2018, 2019b]. In the collection, species of red and green algae of tropic-specific families prevailed: Rhodomelaceae, Ceramiaceae (Rhodophyta), and Caulerpaceae (Chlorophyta).

On Yonaguni Island (southwest of Okinawa islands, 8° south of Shimoshima Island), only at three localities, we sampled about 200 species of marine algae; out of them, as well as on Sesoko Island, red (59%) and green algae (31%) prevailed. R/P value was 6.1, and C/P value was 3.2 [Titlyanov et al., 2016]. Thus, the main indicators of the taxonomic diversity of benthic floras for the most studied islands, Sesoko and Yonaguni, give us the grounds to assign the southern islands of the Ryukyu Archipelago (from N26° and south), with their benthic flora, to the tropical biogeographic region.

Conclusion. A total of 569 species of marine benthic algae were found off the southern islands of Japan; out of them, 153 species were registered for the first time. The comparison of taxonomic and biogeographic characteristics of marine floras of the Amakusa and Ryukyu archipelagos – biodiversity of species and forms, taxonomic composition of algal communities, and potential capabilities of geographic distribution of taxa – give us the grounds to classify Shimoshima Island as a warm-temperate region of the Northern Hemisphere in East Asia, and the southern islands of the Ryukyu Archipelago, as a tropical biogeographic region.

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МОРСКАЯ ФЛОРА ЮЖНЫХ ОСТРОВОВ ЯПОНИИ

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С 1995 по 2019 г. на литорали и в верхней сублиторали архипелага Амакса (остров Симосима) и южных островов архипелага Рюкю (Окинава, Сесоко, Иэдзима, Акадзима, Мияко, Исигаки, Ириомоте и Йонагуни) были собраны морские водоросли. Всего обнаружено 569 видов и таксономических форм бентосных макроводорослей, из них 57 % принадлежат к красным водорослям, 15 % — к бурым, 28 % — к зелёным. Новыми для этих островов были 153 вида водорослей. В течение указанного периода бентосную морскую флору отдельных островов анализировали с разной степенью тщательности. Среди островов архипелага Амакса самым изученным был Симосима (исследовано 14 точек во все сезоны), а среди островов архипелага Рюкю — Сесоко (8 точек во все сезоны). Сравнение таксономических и биогеографических характеристик морских флор этих двух архипелагов: биоразнообразия видов и форм, таксономического состава водорослевых сообществ и потенциальных возможностей географического (широтного) распространения видов — даёт нам основания классифицировать остров Симосима как теплоумеренный регион Северного полушария в Восточной Азии, а южные острова архипелага Рюкю — как тропический биогеографический регион.

Ключевые слова: макроводоросли, архипелаг Амакса, южные острова архипелага Рюкю, сравнение морской флоры