Marine algal flora of Sesoko Island (Okinawa, Japan): comparison between field and outdoor aquaria collections

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Data Paper

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Abstract

Benthic algae were collected from the east coast of the Sesoko Island (Okinawa, Japan, 26°38'64" N, 127°51'04" E) and from the outdoor aquaria of the Sesoko Marine Biological Station - Ryukyu University during 1995-2019. A total of 332 algal taxa, plus 49 species of Cyanobacteria, 10 species of Bacillariophyta and 2 species of seagrasses were found. The benthic flora have demonstrated no significant change in the diversity and species composition over the past 14 years.

More than half of algae living in the sea were found in the outdoor aquaria. This was thought to be facilitated by the lack of water filtration before the seawater entered the aquaria system, a variety of conditions during spore settling and the growth of thalli, as well as the absence of competition between species for substrates and resources.

Keywords: species diversity, shallow waters, outdoor aquaria, Sesoko Marine Station

Introduction

It is well known that the species composition and structure of benthic algal communities depend both on geographic background as well as local conditions surrounding the communities (Lüning 1990). Major local conditions include substrate properties (Titlyanov & Titlyanova 2013, 2014), strength and patterns of water movement (Leigh *et al*. 1987), physico-chemical composition of water (salinity, contamination) (Hurd *et al*. 2014), light intensity (Titlyanov *et al*. 2008) and biotic factors such as grazing, interspecific competition for substrate and resources (Nabivailo & Titlyanov 2006;Tolentino-Pablico *et al*. 2008). All the above-mentioned conditions for the succession of benthic algal communities are common, for both field and artificial aquaria systems.

In the artificial systems (aquaria, tanks, cultivation pools), however, some of the operating factors can be controlled, i.e. either excluded or regulated. Therefore, when studying both complex and individual effects of abiotic and biotic factors on the growth and ontogenetic development of algae or the succession of algal communities, the use of artificial systems may be preferable to natural ones. Algal cultivation in aquaria is widely used in the study of life cycles of benthic algae (Belton *et al*. 2014), competitive relationships between sessile organisms, and the impact of abiogenic and biogenic factors on the growth and development of various life forms of marine plants (Titlyanov *et al*. 2006, 2008), and also for practical purposes – growing planting material for commercial cultivation of algae. At the same time, in the study of the conditions and dynamics of successions of algal communities, artificial ponds are rarely used. However, the multi-functional research aquaria that use unfiltered seawater are faced with the problem of fouling and the aquaria system of the Sesoko Station is no exception. Eco-physiological studies of marine plants and animals at the Sesoko Station are carried out in outdoor aquaria and pools, supplied with water from the sea without filtration. The main source of biological material for aquaria is the fringing coral reef located on its east coast, in front of the Sesoko Station (Tropical Biosphere Research Center).

The authors of this article were fortunate to be able to work for several years at the Sesoko Station to study the symbiotic and competitive relationships between hermatypic corals and marine plants, both in the field and in the aquaria. Results of the studies on the physiology of hermatypic coral and partly on the benthic flora of the island have been published previously (e.g., Titlyanov *et al*. 2006, 2008).

The aim of this study was to compare species diversity, taxonomic composition, and the structure of algal communities between the fringing coral reef in front of the station and the outdoor aquaria, taking into consideration such factors as presence/absence of herbivores and variable exposure to the air.

Materials and Methods

Study site

Studies were conducted on the fringing reef of Sesoko Island (Okinawa, Japan, 26°38’64”N, 127°51’04”E), and also in outdoor aquaria at the Sesoko Station belonging to Tropical Biosphere Research Center of the Ryukyu University (Fig. 1). At the base of the recent fringing coral reef (Veron & Wallace 1984) of Sesoko Island lies a fossil coral platform with a width of 20−100 m. On the east coast of the island (opposite the station), the lagoon and reef-flat are poorly expressed, the slope of the reef is gentle and turning into a sandy bottom at a depth of 3−5 m. The surface seawater temperature averages about 29°C (the highest up to 31°C) in summer and 21°C (the lowest 18°C) in winter. The salinity of the water varies from 34.5 to 35.2 practical salinity units (PSU) depending on the season (Nakano & Nakamura 1993). Surface incident photosynthetic radiation (PAR) was 1100–1600 μmol m^{-2} s^{-1} at midday during the summer period and 800–1400 μmol m^{-2} s^{-1} during the winter season.

Sampling in the field

Algae were collected at 0-5 m depths during low tides along four transects on the eastern coast of Sesoko Island 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), 2019 (January−February). Details of sampling and processing procedures have been described elsewhere (Titlyanov *et al*. 2019a).

Dominance in algal communities was determined visually and defined as: monodominant, if one algal species occupied more than 50% of the surface area; bidominant, if two species occupied more than 50%; and polydominant, if more than two species predominated. Algae collected from different communities were stored in separate plastic bags, which were placed in the refrigerator for the processing time.

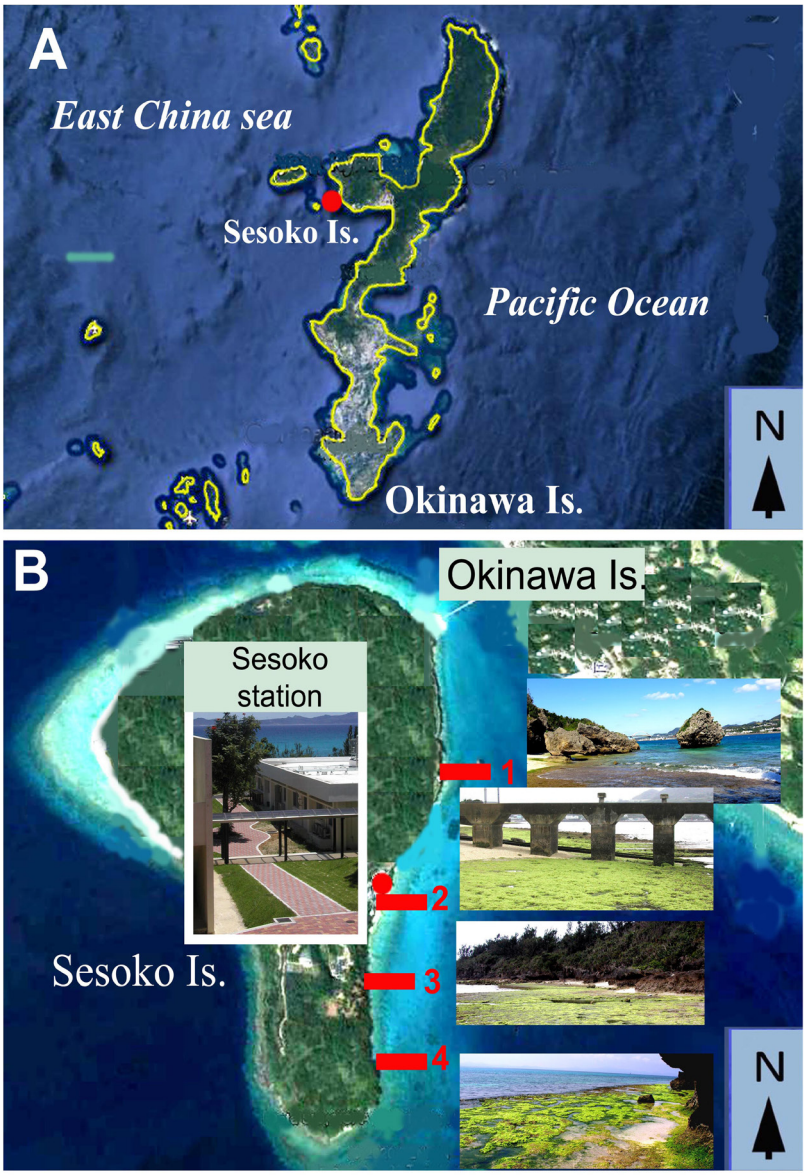

Fig. 1 Location of study site in (a) Sesoko Island on the Okinawa Island; (b) local study sites (transects, marked with numbers) for algal samplings.

Sampling in experimental outdoor aquaria

Experimental aquaria at the Sesoko Station were located in the open air at the distance of 30 m from the coastline. Seawater intake for aquaria was done by pumps in the area of a coral reef, 100 m from the coastline at a depth of 3 m. The water entered an intermediate tank, from which it is pumped into the aquaria. In the aquaria and tanks of various designs, both short-term (two to three weeks) and long-term (from one to three years) comprehensive studies of animals and plants on the coral reef of Okinawa Island are carried out. The design of all aquaria and tanks is about the same (Fig. 2). Water exchange in the aquaria was regulated by an inlet tap and the water level by the height of a drainpipe. During the experiments, the aquaria were overgrown with algae, which grew on aquaria constructions (the inlet pipes to the aquaria and outlet plastic pipes draining from the aquaria, gratings on the drain channels, bottom grids, walls of aquaria and other supports for biological objects) and biological objects (mollusc shells, damaged and dead

parts of coral fragments). Depending on the nature of the experiments, users either periodically cleaned the aquaria or did not do so until the end of the experiments.

Algae were collected in 1995 (May−October), 1997 (October−December), 1998 (January−April), 2002 (October−December), 2003 (January−September), 2005 (February–May), 2006 (November−December), 2007 (January), 2019 (January−February). Algae were completely removed from all surfaces of the aquaria structures in water and biological objects placed in the aquaria.

Results

A total of 332 species of marine algae, plus 2 species of seagrasses Thalassia hemprichii (Ehrenberg) Ascherson and Syringodium isoetifolium (Ascherson) Dandy, 49 species of Cyanobacteria and 10 species of Bacillariophyta (Table 1, 2) were recorded from the east shore and from outdoor aquaria.

Along the coastline opposite to the station, 304 species of marine macrophytes (54% species of Rhodophyta, 12% of Phaeophyceae and 34% of Chlorophyta), 45 species of Cyanobacteria, 8 species of Bacillariophyta and 2 species of seagrasses were recorded (Tables 1, 2). Among Rhodophyta (Rh), the largest number of taxa (more than 10 species) belonged to Rhodomelaceae (31 species), Ceramiaceae (18), Corallinales (15) and Wrangeliaceae (11); among Phaeophyceae (Ph), Dictyotaceae (11), Sargassaceae (8), and among Chlorophyta (Ch), Caulerpaceae (15), Cladophoraceae (12) and Ulvaceae (13) (Table 1). Among Cyanobacteria species of the Family Oscillatoriaceae (16 species) dominated (Table 2).

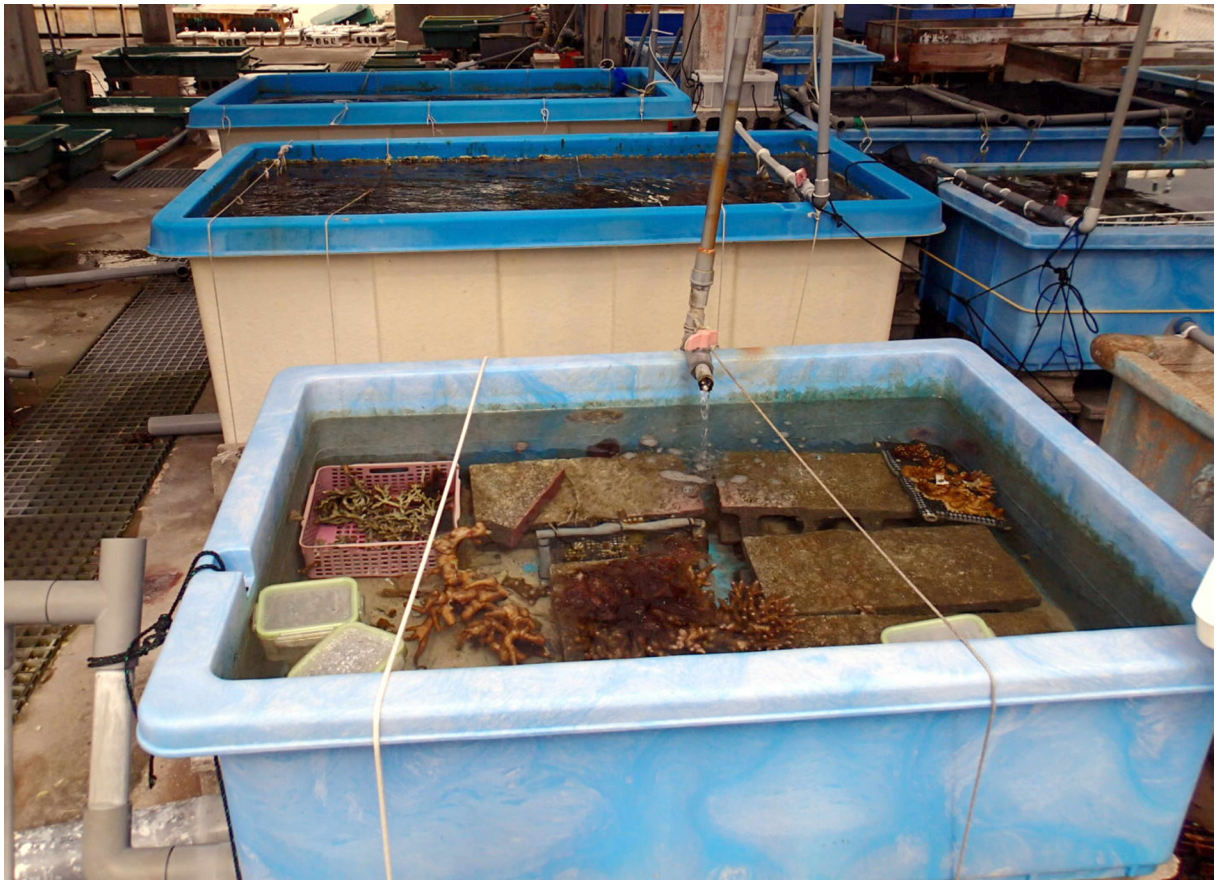

Fig. 2 Outdoor aquaria at the Sesoko Station, January 2019.

Table 1. List of the benthic algae collected from the east coast of Sesoko Island and from the aquaria of the Sesoko Marine Biological Station

Substrates: AS – artificial substrata; DC – dead and damaged corals. Life forms of algae: Epl – epilithic algae; Ep – epiphytic algae; En – endophytic algae; Ez – epizoic algae; El – endolithic algae. Tidal algal habitat: EA – the intertidal zone exposed to air; SZ – submerged zone; EA - SZ – both zones; CA – cast ashore.

Species (varieties and forms)	East coast	Aquaria
PHYLUM RHODOPHYTA		
CLASS BANGIOPHYCEAE		
ORDER BANGIALES		
Family Bangiaceae		
Bangia fuscopurpurea (Dillwyn) Lyngbye	AS	
CLASS STYLANEMATOPHYCEAE		
ORDER STYLONEMATALES		
Family Stylonemataceae		
Chroodactylon ornatum (C. Agardh) Basson	Ep, SZ	DC, Ep
Stylonema alsidii (Zanardini) K.M. Drew	Ep, EA-SZ	DC, Ep
CLASS COMSPOPOGONOPHYCEAE		
ORDER ERYTHROPELTALES		
Family Erythrotrichaceae		
Erythrotrichia carnea (Dillwyn) J. Agardh	Ep, EA-SZ	DC, Ep
Erythrocladia irregularis Rosenvinge	Ep, EA-SZ	Ep
Sahlingia subintegra (Rosenvinge) Kornmann	Ep, SZ	DC, Ep
ORDER ACROCHAETIALES		
Family Acrochaetiaceae		
Acrochaetium catenulatum M.A. Howe	Ep, SZ	Ep
Acrochaetium crassipes Børgesen	Ep, SZ	Ep
Acrochaetium microscopicum (Nägeli ex Kützing) Nägeli	Ep, SZ	DC, Ep
Acrochaetium moniliforme (Rosenvinge) Børgessen	SZ, Ep	Ep
Acrochaetium secundatum (Lyngbye) Nägeli	Ep, SZ	DC, Ep
Acrochaetium subseriatum Børgesen	Ep, SZ	Ep
ORDER NEMALIALES		
Family Galaxauraceae		
Actinotrichia fragilis (Forsskål) Børgesen	Epl, SZ	AS
Dichotomaria marginata (J. Ellis & Solander) Lamarck	Epl, SZ	
Dichotomaria obtusata (J. Ellis & Solander) Lamarck	Epl, SZ	
Galaxaura divaricata (Linnaeus) Huisman & R.A. Townsend	Epl, SZ	AS
Galaxaura rugosa (J. Ellis & Solander) J.V. Lamouroux	Epl, SZ	
Tricleocarpa cylindrica (J. Ellis & Solander) Huisman & Borowitzka	Epl, SZ	
Tricleocarpa fastigiata (Decaisne) Huisman, G.H. Boo & S.M. Boo	Epl, SZ	
Tricleocarpa fragilis (Linnaeus) Huisman & R.A. Townsend	Epl, Ez, SZ	
Family Liagoraceae		
Ganonema farinosum (J.V. Lamouroux) K.C. Fan & Yung C. Wang	Epl, EA	
Helminthocladia australis Harvey	AS	
Liagora ceranoides J.V. Lamouroux	Epl, EA-SZ	
Otohimella japonica (Yamada) Mas.Suzuki, T. Segawa, Hi. Mori & H. Nozaki	Epl, SZ	
*Trichogloea requienii (*Montagne) Kützing	Epl, SZ	
Family Yamadaellaceae		
Yamadaella caenomyce (Decaisne) I.A. Abbott	Epl, EA-SZ	
ORDER COLACONEMATALES		
Family Colaconemataceae		
Colaconema gracile (Børgesen) Ateweberhan & Prud'homme	Ep, SZ	
Colaconema hypneae (Børgesen) A.A. Santos & C.W.N. Moura	Epl, SZ	Ep
Colaconema robustum (Børgesen) Huisman & Woelkerling	Ep, SZ	

Table 1. Continued (2 of 9).

ORDER CORALLINALES		
Family Corallinaceae		
Jania adhaerens J.V. Lamouroux	Ep, SZ	
Jania capillacea Harvey	Ep, SZ	DC, Ep
Jania pedunculata var. adhaerens (J.V. Lamouroux) A.S. Harvey, Woelkerling & Reviers	Ep, SZ	
Jania pumila J.V. Lamouroux	Ep, SZ	
Jania ungulata f. brevior (Yendo) Yendo	Ep, Epl, EA-SZ	AS, Ep
Pneophyllum fragile Kützing	Ep, SZ	AS, DC
Family Hydrolithaceae		
Hydrolithon boreale (Foslie) Y.M. Chamberlain	Ep, SZ	AS, Ep
Hydrolithon farinosum (J.V. Lamouroux) D. Penrose & Y.M. Chamberlain	Ep, SZ	AS, DC, Ep
Family Lithophyllaceae		
Amphiroa anceps (Lamarck) Decaisne	Epl, SZ	
Amphiroa foliacea J.V. Lamouroux	Epl, SZ	
Amphiroa fragilissima (Linnaeus) J.V. Lamouroux	Ep, Epl, SZ	AS
Family Mastophoraceae		
Mastophora rosea (C. Agardh) Setchell	Epl, SZ	
Family Porolithaceae		
Dawsoniolithon conicum (E.Y. Dawson) Caragnano, Foetisch, Maneveldt & Payri	Ep, Epl, SZ	
Family Spongitaceae		
Neogoniolithon brassica-florida (Harvey) Setchell & L.R. Mason	Ep, Epl, SZ	AS
ORDER BONNEMAISONIALES		
Family Bonnemaisoniaceae		
Asparagopsis taxiformis (Delile) Trevisan de Saint-Léon [Falkenbergia hillebrandii, Sporophytic stage of *Asparagopsis taxiformis]*	Ep, Ez, Epl, SZ	DC, Ep
ORDER CERAMIALES		
Family Callithamniaceae		
Aglaothamnion callophyllidicola (Yamada) Boo, I.K. Lee, Rueness & Yoshida	Ep, SZ	Ep
Aglaothamnion cordatum (Børgesen) Feldmann-Mazoyer	Ep, SZ	Ep
Crouania attenuata (C. Agardh) J. Agardh	Ep, SZ	Ep
Gymnothamnion elegans (Schousboe ex C. Agardh) J. Agardh	Ep, Epl, SZ	Ep
Family Ceramiaceae		
Antithamnion antillanum Børgesen	Ep, Epl, SZ	AS, DC
Antithamnionella breviramosa (E.Y. Dawson) Wollaston	Ep, SZ	
Centroceras clavulatum (C. Agardh) Montagne	Ep, Epl, EA-SZ	AS, DC, Ep
Centroceras gasparrinii (Meneghini) Kützing	Ep, SZ	DC
Centroceras minutum Yamada	Epl, SZ	Ep
Ceramium aduncum Nakamura	Ep, EA-SZ	
Ceramium affine Setchell & N.L. Gardner	Ep, SZ	
Ceramium amamiense Itono		Ep
Ceramium borneense Weber Bosse		DC
Ceramium camouii E.Y. Dawson		DC
Ceramium cimbricum H.E. Petersen	Ep, SZ	AS, Ep
Ceramium cimbricum f. flaccidum (H.E. Petersen) G. Furnari & Serio		Ep
Ceramium cingulatum Weber-van Bosse	Ep, EA-SZ	
Ceramium clarionense Setchell & N.L. Gardner		DC
Ceramium codii (H. Richards) Mazoyer	Ep, EA-SZ	DC
Ceramium macilentum J. Agardh	Ep, EA-SZ	
Ceramium procumbens Setchell & N.L. Gardner	Ep, EA-SZ	
Ceramium serpens Setchell & N.L. Gardner		Ep
Ceramium sp.		Ez
Ceramium vagans P.C. Silva	Ep, SZ	Ep

Table 1. Continued (3 of 9).

Corallophila howei (Weber Bosse) R.E. Norris	Ep, SZ	
Corallophila itonoi (Ardré) R.E. Norris	Ep, SZ	DC
Corallophila kleiwegii Weber Bosse	Ep, SZ	DC, Ep
Gayliella fimbriata (Setchell & N.L. Gardner) T.O. Cho & S.M. Boo	Ep, Epl, SZ	
Gayliella mazoyerae T.O. Cho, Fredericq & Hommersand	Ep, SZ	DC, Ep
Gayliella transversalis (Collins & Hervey) T.O. Cho & Fredericq	Ep, SZ	DC, Ep
Family Delesseriaceae		
Dasya scoparia Harvey	Epl, SZ	
Heterosiphonia crispella (C. Agardh) M.J. Wynne	Ep, Ez, Epl, SZ	DC
Hypoglossum simulans M.J. Wynne, I.R. Price & D.L. Ballantine	Epl, SZ	
Martensia fragilis Harvey	Ep, SZ	
Nitophyllum adhaerens M.J. Wynne	Ep, SZ	
Taenioma perpusillum (J. Agardh) J. Agardh	Ep, SZ	
Family Rhodomelaceae		
Acanthophora muscoides (Linnaeus) Bory	Epl, SZ	
Acanthophora spicifera (M. Vahl) Børgesen	Epl, SZ	
Acrocystis nana Zanardini	Epl, SZ	
Bostrychia tenella (J.V. Lamouroux) J. Agardh	Epl, EA	
Chondria dasyphylla (Woodward) C. Agardh	Epl, EA	AS, DC
Chondria minutula Weber Bosse	Ep, EA	DC, Ep
Chondria repens Børgesen	Epl, SZ	Ep
Chondrophycus articulatus (C.K. Tseng) K.W. Nam	Epl, SZ	
Chondrophycus carolinensis (Y. Saito) K.W. Nam	Epl SZ	
Chondrophycus cartilagineus (Yamada) Garbary & J.T. Harper	CA	
Chondrophycus undulatus (Yamada) Garbary & Harper	Epl, SZ	
Digenea simplex (Wulfen) C. Agardh	Epl, SZ	DC
Herposiphonia parca Setchell	Ep, SZ	Ep
Herposiphonia secunda (C. Agardh) Ambronn	Ep, SZ	DC, Ep
Herposiphonia tenella (C. Agardh) Ambronn	Ep, SZ	DC, Ep
Herposiphonia subdisticha Okamura	Ep, SZ	
Laurencia brongniartii J. Agardh	Ep, SZ	
Laurencia decumbens Kützing	Epl, SZ	
Laurencia galtsoffii M. Howe	Epl, SZ	
Laurencia intricata J.V. Lamouroux	Ep, SZ	AS, DC
Laurencia obtusa (Hudson) J. V. Lamouroux	Epl, SZ	AS, DC
Laurencia pinnata Yamada	Epl, SZ	
Leveillea jungermannioides (Hering & G. Martens) Harvey	Ep, SZ	
Melanothamnus ferulaceus (Suhr ex J. Agardh) Díaz-Tapia & Maggs	Ep, SZ	
Melanothamnus savatieri (Hariot) Díaz-Tapia & Maggs	Ep, SZ	Ep
Palisada parvipapillata (C.K. Tseng) K.W. Nam	Epl, SZ	AS, DC
Palisada perforata (Bory) K.W. Nam	Epl, SZ	
Palisada yamadana (M. Howe) K.W. Nam	Epl, SZ	AS
Wilsonosiphonia howei (Hollenberg) D. Bustamante, Won & T.O. Cho	Epl, SZ	
Polysiphonia villum J. Agardh	Ep, SZ	
Polysiphonia sp.		AS, Ez
Tolypiocladia glomerulata (C. Agardh) F. Schmitz	Ep, Epl, SZ	AS, DC, Ep
Family Spyridiaceae		
Spyridia filamentosa (Wulfen) Harvey	Epl, SZ	AS, DC, Ep
Family Wrangeliaceae		
Anotrichium tenue (C. Agardh) Nägeli	Ep, SZ	DC, Ep
Gordoniella yonakuniensis (Yamada & T. Tanaka) Itono	Epl, EA-SZ	Ep
Griffithsia heteromorpha Kützing	Ep, SZ	
Griffithsia metcalfii C.K. Tseng	Ep, Epl, SZ	AS, DC, Ep
Griffithsia rhizophora Grunow ex Weber Bosse	Epl, SZ	
Griffithsia subcylindrica Okamura	Epl, SZ	
Haloplegma duperreyi Montagne	Ep, SZ	
Pleonosporium borreri (Smith) Nägeli	Ep, SZ	
Tiffaniella saccorhiza (Setchell & N.L. Gardner) Doty & Meñez	Ep, SZ	
Wrangelia argus (Montagne) Montagne	Epl, SZ	
Wrangelia penicillata (C. Agardh) C. Agardh	Epl, SZ	

Table 1. Continued (4 of 9).

ORDER GELIDIALES		
Family Gelidiaceae		
Gelidium divaricatum G. Martens	Epl, EA	
Gelidium pusillum (Stackhouse) Le Jolis	Epl, EA	
Gelidium pusillum var. *cylindricum* W.R. Taylor	Epl, EA-SZ	AS
Gelidium pusillum var. *pacificum* W.R. Taylor	Ep, EA	
Family Gelidiellaceae		
Gelidiella acerosa (Forsskål) Feldmann & G. Hamel	Epl, SZ	
Millerella pannosa (Feldmann) G.H. Boo & L. Le Gall	Epl, SZ	DC
Parviphycus adnatus (E.Y. Dawson) B. Santelices	Epl, SZ	
Family Pterocladiaceae		
Pterocladiella capillacea (S.G. Gmelin) Santelices & Hommersand	Ep, EA-SZ	Ep
ORDER GIGARTINALES		
Family Caulacanthaceae		
Caulacanthus okamurae Yamada	Epl, EA	
Caulacanthus ustulatus (Turner) Kützing	Epl, SZ	
Family Cystocloniaceae		
Hypnea cervicornis J. Agardh	Epl, SZ	
Hypnea charoides J.V. Lamouroux	Epl, SZ	
Hypnea esperi Bory	Ep, SZ	AS
Hypnea nidulans Setchell		AS
Hypnea pannosa J. Agardh	Epl, SZ	AS
Hypnea spinella (C. Agardh) Kützing	Ep, Epl, EA-SZ	DC
Hypnea valentiae (Turner) Montagne	Epl, SZ	
Family Dumontiaceae		
Dudresnaya hawaiiensis R.K.S. Lee	CA	
Family Gigartinaceae		
Chondracanthus intermedius (Suringar) Hommersand	Epl, EA-SZ	
Chondracanthus tenellus (Harvey) Hommersand	Epl, SZ	AS
Family Phyllophoraceae		
Ahnfeltiopsis flabelliformis (Harvey) Masuda	Epl, EA-SZ	
Erythrodermis haematis (Hollenberg) Denizot		DC
Family Solieriaceae		
Eucheuma denticulatum (N.L. Burman) Collins & Hervey	Epl, SZ	
Kappaphycus cottonii (Weber Bosse) Dumilag & Zuccarello	CA	
Wurdemannia miniata (Sprengel) Feldmann & Hamel	Epl, SZ	
ORDER NEMASTOMATALES		
Family Schizymeniaceae		
Titanophora weberae Børgesen	Epl, SZ	
ORDER PEYSSONNELIALES		
Family Peyssonneliaceae		
Peyssonnelia armorica (P.Crouan & H.Crouan) Weber Bosse		DC
Peyssonnelia boergesenii Weber Bosse	Epl, SZ	
Peyssonnelia conchicola Piccone & Grunow	Epl, SZ	
Peyssonnelia rubra (Greville) J. Agardh	Epl, SZ	AS
ORDER GRACILARIALES		
Family Gracilariaceae		
Gracilaria arcuata Zanardini	Epl, SZ	
Gracilaria canaliculata Sonder	Epl, SZ	AS
Gracilaria salicornia (C. Agardh) E.Y. Dawson	Epl, SZ	

Table 1. Continued (5 of 9).

ORDER HALYMENIALES		
Family Grateloupiaceae		
Grateloupia livida (Harvey) Yamada	Epl, SZ	AS
Yonagunia formosana (Okamura) Kawaguchi & Masuda	Epl, SZ	
ORDER PLOCAMIALES		
Family Plocamiaceae		
Plocamium telfairiae (W.J. Hooker & Harvey) Harvey ex Kützing	Epl, SZ	
ORDER RHODYMENIALES		
Family Champiaceae		
Champia bifida Okamura	Ep, SZ	AS
Champia japonica Okamura	Ep, SZ	Ep
Champia parvula (C. Agardh) Harvey	Ep, Epl, SZ	DC
Champia vieillardii Kützing	Ep, SZ	AS
Coelothrix irregularis (Harvey) Børgesen	Epl, SZ	Ep
Family Hymenocladiaceae		
Asteromenia anastomosans (Weber Bosse) G.W. Saunders, C.E. Lane, C.W. Schneider & Kraft	Epl, SZ	
Family Lomentariaceae		
Ceratodictyon intricatum (C. Agardh) R.E. Norris	Epl, EA-SZ	
Ceratodictyon scoparium (Montagne & Millardet) R.E. Norris	Epl, SZ	
Ceratodictyon spongiosum Zanardini	Epl, SZ	
Ceratodictyon variabile (J. Agardh) R.E. Norris	Epl, SZ	AS
Lomentaria corallicola Børgesen	Ep, SZ	Ep
Lomentaria pinnata Segawa		AS
Family Rhodymeniaceae		
Botryocladia kuckuckii (Weber Bosse) Yamada & T. Tanaka	Epl, EA	Ep
Botryocladia pyriformis (Børgesen) Kylin		AS
Botryocladia skottsbergii (Børgesen) Levring	Epl, SZ	
Chrysymenia okamurae Yamada & Segawa	Epl, SZ	DC
Chamaebotrys boergesenii (Weber Bosse) Huisman	Epl, CA, SZ	DC
Rhodymenia coacta Okamura	Epl, SZ	
PHYLUM OCHROPHYTA		
CLASS XANTHOPHYCEAE		
ORDER VAUCHERIALES		
Family Vaucheriaceae		
Pseudodichotomosiphon constricta (Yamada) Yamada	Epl, EA	AS
CLASS PHAEOPHYCEAE		
ORDER SCYTOTHAMNALES		
Family Asteronemataceae		
Asteronema breviarticulatum (J. Agardh) Ouriques & Bouzon	Epl, EA	
ORDER ECTOCARPALES		
Family Acinetosporaceae		
Feldmannia filifera (Børgesen) Pham-Hoàng Hô		DC
Feldmannia indica (Sonder) Womersley & A. Bailey	Ep, Epl, EA-SZ	AS
Feldmannia irregularis (Kützing) Hamel	Ep, Epl, EA-SZ	DC, Ep
Feldmannia mitchelliae (Harvey) H.-S. Kim	Ep, EA-SZ	AS, DC
Hincksia conifera (Børgesen) I.A. Abbott	Ep, Epl, EA-SZ	
Pylaiella littoralis (Linnaeus) Kjellman	Ep, EA-SZ	AS, DC, Ep
Family Chordariaceae		
Chilionema ocellatum (Kützing) Kornmann	Ep, EA-SZ	DC, Ep
Cladosiphon okamuranus Tokida	Epl, SZ	AS
Kuetzingiella elachistaeformis (Heydrich) M. Balakrishnan & Kinkar	Ep, EA-SZ	DC, Ep
Myrionema strangulans Greville		DC

Table 1. Continued (6 of 9).

Family Ectocarpaceae		
Spongonema tomentosum (Hudson) Kützing	Ep, EA-SZ	
Family Scytosiphonaceae		
Pseudochnoospora implexa (J. Agardh) Santiañez, G.Y. Cho & Kogame	Ep, SZ	AS, DC
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier	Epl, SZ	
Hydroclathrus clathratus (C. Agardh) M.A. Howe	Epl, SZ	
ORDER RALFSIALES		
Family Mesosporaceae		
Mesospora schmidtii Weber Bosse		DC
Family Neoralfsiaceae		
Neoralfsia expansa (J. Agardh) P.-E. Lim & H. Kawai ex Cormaci & G. Furnari	Epl, EA-SZ	AS
ORDER SPHACELARIALES		
Family Sphacelariaceae		
Sphacelaria novae-hollandiae Sonder	Epl, EA-SZ	AS, DC
Sphacelaria rigidula Kützing	Ep, EZ, EA-SZ	AS, DC, Ez
Sphacelaria tribuloides Meneghini	Ep, EA-SZ	DC
ORDER DICTYOTALES		
Family Dictyotaceae		
Canistrocarpus cervicornis (Kützing) De Paula & De Clerck	Ep, SZ	AS
Dictyopteris undulata Holmes	Epl, SZ	
Dictyota bartayresiana J.V. Lamouroux	Epl, SZ	AS
Dictyota friabilis Setchell	Epl, SZ	AS
Dictyota implexa (Desfontaines) J.V. Lamouroux	Epl, SZ	AS, DC
Lobophora variegata (J.V. Lamouroux) Womersley ex Oliveira	Ez, Epl, EA-SZ	AS, DC
Padina australis Hauck	Epl, SZ	
Padina boryana Thivy	Epl, SZ	DC
Padina gymnospora (Kützing) Sonder	Epl, SZ	
Padina minor Yamada	Epl, EA-SZ	DC
Zonaria flabellata (Okamura) Papenfuss	Epl, SZ	
ORDER FUCALES		
Family Sargassaceae		
Hormophysa cuneiformis (J.F. Gmelin) P.C. Silva	Epl, SZ	
Sargassum aquifolium (Turner) C. Agardh	Epl, SZ	
Sargassum feldmannii Pham-Hoàng Hô	Epl, SZ	
Sargassum ilicifolium (Turner) C. Agardh	Epl, SZ	
Sargassum polycystum (C. Agardh)	Epl, SZ	
Sargassum polyporum Montagne	Epl, SZ	
Sargassum thunbergii (Mertens ex Roth) Kuntze	Epl, EA-SZ	
Turbinaria ornata (Turner) J. Agardh	Epl, SZ	AS
PHYLUM CHLOROPHYTA		
CLASS CHLOROPHYCEAE		
ORDER CHAETOPHORALES		
Family Uronemataceae		
Uronema marinum Womersley		Ep
CLASS ULVOPHYCEAE		
ORDER ULOTRICHALES		
Family Gomontiaceae		
Gomontia arrhiza Hariot	Ep, EA-SZ	
Family Monostromataceae		
Monostroma nitidum Wittrock	Epl, EA	AS, DC

Table 1. Continued (7 of 9).

Family Ulotrichaceae		
Ulothrix implexa (Kützing) Kützing	Ep, EA-SZ	
Ulothrix flacca (Dillwyn) Thuret	Ep, Epl, EA-SZ	HS
ORDER ULVALES		
Family Phaeophilaceae		
Phaeophila dendroides (P. Crouan & H. Crouan) Batters	Ep, EA-SZ	
Family Ulvellaceae		
Ulvella lens P. Crouan & H. Crouan	Ep, EA-SZ	Ep
Ulvella leptochaete (Huber) R. Nielsen, C.J. O'Kelly & B. Wysor		En
Ulvella repens (Pringsheim) R. Nielsen, C.J. O'Kelly & B. Wysor		Ep
Ulvella scutata (Reinke) R. Nielsen, C.J. O'Kelly & B.Wysor	Ep, EA-SZ	DC, Ep
Ulvella viridis (Reinke) R. Nielsen, C.J. O'Kelly & B. Wysor	Ep, EA-SZ	DC, Ep
Family Ulvaceae		
Ulva australis Areschoug	Epl, EA-SZ	AS
Ulva clathrata (Roth) C. Agardh	Ep, Epl, EA	AS, DC, Ep
Ulva compressa Linnaeus	Epl, EA	
Ulva conglobata Kjellman	Epl, EA	
Ulva fasciata Delile	Epl, EA-SZ	
Ulva flexuosa Wulfen	Epl, EA	AS
Ulva intestinalis Linnaeus	Epl, EA	AS, DC
Ulva kylinii (Bliding) H.S.Hayden, Blomster, Maggs, P.C. Silva, Stanhope & Waaland	Epl, EA	
Ulva lactuca Linnaeus	Epl, EA-SZ	
Ulva prolifera O.F. Müller	Epl, -SZ	
Ulva ralfsii (Harvey) Le Jolis	Ep, Epl, EA-SZ	AS, DC
Ulva reticulata Forsskål	Ep, SZ	
Ulva rigida C. Agardh	Epl, EA-SZ	
ORDER CLADOPHORALES		
Family Anadyomenaceae		
Anadyomene wrightii Harvey ex J.E. Gray	Epl, SZ	
Microdictyon japonicum Setchell	Epl, SZ	
Microdictyon nigrescens (Yamada) Setchell	Epl, SZ	
Microdictyon okamurai Setchell	Epl, SZ	AS
Family Boodleaceae		
Boodlea coacta (Dickie) G. Murray & De Toni	Epl, SZ	AS, DC
Boodlea composita (Harvey) F. Brand	Ep, SZ	DC, Ep
Boodlea struveoides M. Howe	Epl, SZ	AS
Cladophoropsis fasciculata (Kjellman) Wille	Epl, SZ	AS
Cladophoropsis membranacea (Bang ex C. Agardh) Børgesen	Epl, EA	AS
Phyllodictyon anastomosans (Harvey) Kraft & M.J. Wynne	Epl, SZ	AS
Struvea enomotoi Chihara	Epl, SZ	
Family Cladophoraceae		
Chaetomorpha antennina (Bory) Kützing	Epl, EA	
Chaetomorpha basiretrorsa Setchell	Epl, EA	
Chaetomorpha gracilis Kützing	Epl, SZ	
Chaetomorpha linum (O.F. Müller) Kützing	Epl, EA	AS
Cladophora catenata Kützing	Epl, SZ	AS
Cladophora fuliginosa Kützing	Epl, EA-SZ	DC
Cladophora laetevirens (Dillwyn) Kützing	Epl, EA-SZ	AS, DC, Ez
Cladophora socialis Kützing		DC
Cladophora sp.		Ez
Cladophora vagabunda (Linnaeus) Hoek	Epl, EA-SZ	DC
Lychaete herpestica (Montagne) M.J. Wynne	Epl, EA-SZ	
Rhizoclonium grande Børgesen	Epl, EA-SZ	
Rhizoclonium riparium (Roth) Harvey	Epl, EA-SZ	AS
Rhizoclonium implexum (Dillwyn) Kützing	Ep, EA-SZ	DC, Ez

Table 1. Continued (8 of 9).

Family Siphonocladaceae		
Dictyosphaeria cavernosa (Forsskål) Børgesen	Epl, EA-SZ	DC
Dictyosphaeria versluysii Weber Bosse	Ep, Epl, EA-SZ	
Siphonocladus rigidus M. Howe	Epl, EA-SZ	
Family Valoniaceae		
Valonia aegagropila C. Agardh	Epl, SZ	AS
Valonia fastigiata Harvey ex J. Agardh	Epl, SZ	AS
Valonia macrophysa Kützing		AS
Valonia utricularis (Roth) C. Agardh		AS, DC
Valonia ventricosa J. Agardh	Epl, SZ	DC, Ez
ORDER BRYOPSIDALES		
Family Bryopsidaceae		
Bryopsis australis Sonder	Epl, SZ	AS
Bryopsis hypnoides J.V. Lamouroux	Epl, SZ	
Bryopsis indica A. Gepp & E. S. Gepp	Epl, SZ	AS
Bryopsis maxima Okamura ex Segawa		AS
Bryopsis pennata J.V. Lamouroux	Epl, SZ	AS, DC
Bryopsis pennata var. *secunda* (Harvey) Collins & Hervey	Epl, SZ	
Bryopsis plumosa (Hudson) C. Agardh	Epl, SZ	AS, DC
Bryopsis ryukyuensis Yamada	Epl, EA-SZ	
Family Ostreobiaceae		
Ostreobium quekettii Bornet & Flahault	El, SZ	
Family Caulerpaceae		
Caulerpa ambigua Okamura	Ep, SZ	Ep
Caulerpa chemnitzia (Esper) J.V. Lamouroux	Epl, SZ	AS
Caulerpa cupressoides (Vahl) C. Agardh	Epl, SZ	
Caulerpa fastigiata Montagne	Epl, SZ	AS
Caulerpa lentillifera J. Agardh	Epl, SZ	
Caulerpa microphysa (Weber Bosse) Feldmann	Epl, SZ	
Caulerpa nummularia Harvey ex J. Agardh	Ep, Epl, SZ	AS, DC
Caulerpa racemosa (Forsskål) J. Agardh	Epl, SZ	AS, DC
Caulerpa racemosa var. *macrophysa* (Sonder ex Kützing) W.R. Taylor	Epl, SZ	
Caulerpa serrulata (Forsskål) J. Agardh	Epl, SZ	AS
Caulerpa serrulata f. *spiralis* (Weber Bosse) Gilbert	Epl, SZ	AS
Caulerpa serrulata f. *lata* (Weber Bosse) C.K. Tseng	Epl, SZ	AS
Caulerpa sertularioides (S.G. Gmelin) M. Howe	Epl, SZ	AS
Caulerpa verticillata J. Agardh	Epl, EA-SZ	
Caulerpa webbiana f. *tomentella* (Harvey ex J. Agardh) Weber Bosse	Epl, SZ	
Family Codiaceae		
Codium adhaerens C. Agardh	Epl, EA-SZ	DC
Codium arabicum Kützing	Epl, EA-SZ	
Codium intricatum Okamura	Epl, SZ	DC
Codium sp.	Epl, EA-SZ	
Codium repens P. Crouan & H. Crouan	Epl, SZ	
Family Derbesiaceae		
Derbesia fastigiata W.R. Taylor		AS, DC
Derbesia marina (Lyngbye) Solier	Epl, SZ	AS, DC
Derbesia tenuissima (Moris & De Notaris) P. Crouan & H. Crouan		AS, Ez
Pedobesia ryukyuensis (Yamada & T. Tanaka) Kobara & Chihara		AS
Family Dichotomosiphonaceae		
Avrainvillea erecta (Berkeley) A. Gepp & E.S. Gepp	Epl, SZ	
Avrainvillea lacerata J. Agardh	Epl, SZ	

Table 1. Continued (9 of 9).

Family Halimedaceae		
Halimeda discoidea Decaisne	Epl, SZ	
Halimeda macroloba Decaisne	Epl, SZ	
Halimeda macrophysa Askenasy	Epl, SZ	
Halimeda opuntia (Linnaeus) J.V. Lamouroux	Epl, SZ	
Halimeda tuna (Ellis et Solander) Lamouroux	Epl, SZ	
Boodleopsis pusilla (Collins) W.R. Taylor, A.B. Joly & Bernatowicz	Epl, SZ	DC
Chlorodesmis fastigiata (C. Agardh) S.C. Ducker	Epl, SZ	
Penicillus sibogae A. Gepp & E.S. Gepp	Epl, SZ	DC
Pseudochlorodesmis furcellata (Zanardini) Børgesen	Epl, SZ	AS
Rhipidosiphon javensis Montagne	Epl, SZ	AS, DC
Siphonogramen abbreviatum (W.J. Gilbert) I.A. Abbott & Huisman	Epl, SZ	
Tydemania expeditionis Weber Bosse	Epl, SZ	AS
ORDER DASYCLADALES		
Family Dasycladaceae		
Bornetella nitida Munier-Chalmas ex Sonder	Epl, SZ	AS
Bornetella oligospora Solms-Laubach	Epl, SZ	
Bornetella sphaerica (Zanardini) Solms-Laubach	Epl, EA-SZ	DC
Neomeris annulata Dickie	Epl, SZ	DC
Cymopolia vanbosseae Solms-Laubach	Epl, SZ	
Family Polyphysaceae		
Acetabularia dentata Solms- Laubach	Epl, SZ	DC
Parvocaulis clavatus (Yamada) S. Berger, U. Fettweiss, S. Gleissberg, L.B. Liddle, U. Richter, H. Sawitzky & G.C. Zuccarello	Epl, SZ	DC
Parvocaulis exiguus (Solms-Laubach) S. Berger, Fettweiss, Gleissberg, Liddle, U. Richter, Sawitzky & Zuccarello	Epl, SZ	DC
Parvocaulis parvulus (Solms-Laubach) S. Berger, Fettweiss, Gleissberg, Liddle, U. Richter, Sawitzky & Zuccarello	Epl, SZ	DC
Parvocaulis pusillus (M. Howe) S. Berger, U. Fettweiss, S. Gleissberg, L.B. Liddle, U. Richter, H. Sawitzky & G.C. Zuccarello	Epl, SZ	DC

Table 2. List of marine higher plants, cyanobacteria and diatoms collected from the east coast of Sesoko Island and from the aquaria of the Sesoko Marine Biological Station.

Species (varieties and forms)	East coast	Aquaria
PHYLUM TRACHEOPHYTA		
ORDER ALISMATALES		
Family Hydrocharitaceae		
Thalassia hemprichii (Ehrenberg) Ascherson	+	
ORDER ALISMATALES		
Family Cymodoceaceae		
Syringodium isoetifolium (Ascherson) Dandy	+	
PHYLUM CYANOBACTERIA		
ORDER PLEUROCAPSALES		
Family Dermocarpellaceae		
Cyanocystis hemisphaerica (Setchell & N.L. Gardner) Kaas		+
Dermocarpa acervata (Setchell & Gardner) Pham-Hoàng Hô	+	+
Brachytrichia quoyi (C. Agardh) Bornet & Flahault	+	
Dermocarpella hemisphaerica (Lemmermann) Lemmermann	+	+
Family Hyellaceae		
Chamaecalyx clavatus (Setchell & N.L. Gardner) Komárek & Anagnostidis	+	+
Family Xenococcaceae		
Xenococcus chaetomorphae Setchell & N.L. Gardner	+	
ORDER OSCILLATORIALES		
Family Coleofasciculaceae		
Coleofasciculus chthonoplastes (Gomont) M. Siegesmund, J.R. Johansen & T. Friedl	+	
Family Microcoleaceae		
Symploca hydnoides Kützing	+	
Trichodesmium erythraeum Ehrenberg ex Gomont *	+	
Family Oscillatoriaceae		
Leptolyngbya tenuis (Gomont) Anagnostidis & Komárek	+	+
Moorena bouillonii (L.Hoffmann & Demoulin) Engene & Tronholm	+	
Lyngbya confervoides C. Agardh	+	
Lyngbya majuscula Harvey ex Gomont	+	+
Lyngbya martensiana Meneghini ex Gomont	+	+
Lyngbya semiplena J. Agardh ex Gomont	+	+
Lyngbya sordida Gomont	+	+
Oscillatoria bonnemaisonii P. Crouan & H. Crouan ex Gomont	+	
Oscillatoria limosa C. Agardh ex Gomont	+	
Oscillatoria margaritifera Kützing ex Gomont	+	+
Oscillatoria miniata Hauck ex Gomont	+	+
Oscillatoria tenuis C. Agardh ex Gomont	+	+
Phormidium nigroviride (Thwaites ex Gomont) Anagnostidis & Komárek		+
Phormidium corium Gomont	+	+
ORDER NOSTOCALES		
Family Calotrichaceae		
Calothrix aeruginea Thuret ex Bornet & Flahault	+	+
Calothrix confervicola C. Agardh ex Bornet & Flahault	+	+
Calothrix contarenii Bornet & Flahault	+	+

Table 2. Continued (2 of 3).

ORDER CHROOCOCCALES		
Family Chroococcaceae		
Chroococcus turgidus (Kützing) Nägeli	+	
Family Nostocaceae		
Nostoc commune Vaucher ex Bornet & Flahault	+	+
Hydrocoryne soluta (Bornet & Grunow) I. Umezaki		+
Family Rivulariaceae		
Dichothrix fucicola Bornet & Flahault	+	+
Dichothrix sp.	+	+
Isactis plana Thuret ex Bornet & Flahault	+	
Rivularia atra Roth ex Bornet & Flahault	+	
Rivularia sp.	+	+
Family Scytonemataceae		
Scytonema ocellatum Lyngbye ex Bornet & Flahault	+	
Scytonematopsis crustacea (Thuret ex Bornet & Flahault) Kováčik & Komárek	+	+
Family Symphyonemataceae		
Brachytrichia quoyi Bornet & Flahault	+	
ORDER SPIRULINALES		
Family Spirulinaceae		
Spirulina major Kützing ex Gomont	+	+
Spirulina subsalsa Oersted ex Gomont	+	+
Spirulina subtilissima Kützing ex Gomont	+	+
Spirulina tenerrima Kützing ex Gomont		+
ORDER SYNECHOCOCCALES		
Family Leptolyngbyaceae		
Leibleinia epiphytica (Hieronymus) Compère	+	+
Leptolyngbya crosbyana (Tilden) Anagnostidis & Komárek	+	
Leptolyngbya tenuis (Gomont) Anagnostidis & Komárek	+	+
Family Merismopediaceae		
Aphanocapsa litoralis Hansgirg	+	
Family Pseudanabaenaceae		
Pseudanabaena limnetica (Lemmermann) Komárek	+	

Table 2. Continued (3 of 3).

PHYLUM BACILLARIOPHYTA		
ORDER RHAPHONEIDALES		
Family Asterionellopsidaceae		
Asterionellopsis glacialis (Castracane) Round	+	+
ORDER FRAGILARIALES		
Family Fragilariaceae		
Fragilaria hyalina (Kützing) Grunow		+
ORDER BACILLARIALES		
Family Bacillariaceae		
Cylindrotheca closterium (Ehrenberg) Reimann & J.C. Lewin	+	
Nitzschia longissima (Brébisson) Ralfs	+	+
Nitzschia sigma (Kützing) W. Smith	+	
Pseudo-nitzschia seriata (Cleve) H. Peragallo	+	+
ORDER NAVICULALES		
Family Berkeleyaceae		
Berkeleya rutilans (Trentepohl ex Roth) Grunow	+	
ORDER THALASSIONEMATALES		
Family Thalassionemataceae		
Thalassionema nitzschioides (Grunow) Mereschkowsky		+
ORDER LICMOPHORALES		
Family Licmophoraceae		
Licmophora abbreviata C. Agardh	+	+
Licmophora ehrenbergii (Kützing) Grunow	+	

Among macrophytes, the majority were found on hard natural substrate (epilithic algae, 70% species), 27% species were obligate epiphytes and 7% of species were growing on hard substrate as well as on thalli of larger algae. Five species of algae were found on mollusc shells (epizoic algae); three species were found only as algae cast ashore by waves, one species as endophytic (Phaeophila dendroides) and one species as endolithic (Ostreobium quekettii). Among the epilithic algae, there were 44% red, 13% brown, and 43% green species. Among epiphytes, red algae prevailed significantly and amounted 75% (Table 1, Fig. 3).

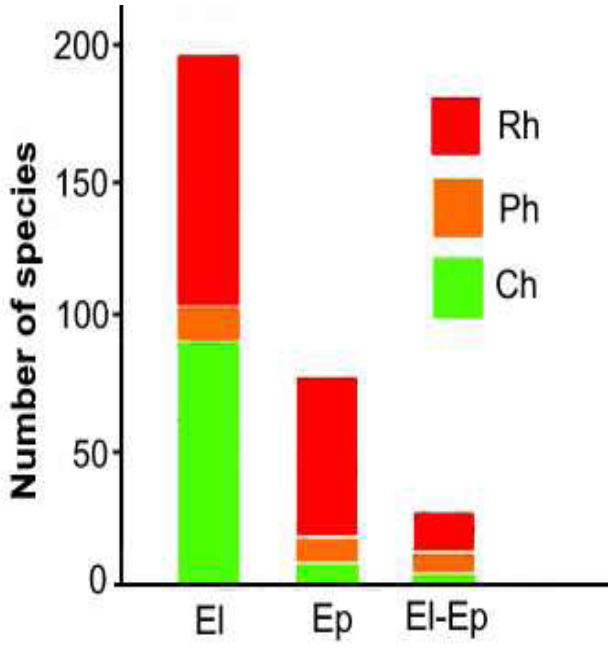

Fig. 3 Number of species inhabiting the Sesoko reef in different life forms. El – epilithic algae, Ep – epiphytes and El-Ep – as epiliths and as epiphytes. Rh – Rhodophyta, Ph – Phaeophyceae, Ch – Chlorophyta.

The largest number of species (215, or 70% species of the field collection) was found in the submerged zone (SZ, the low intertidal and upper subtidal zones), 21 species (7% of the collection) – in the intertidal zone exposed to air (EA, the upper and middle intertidal zone), 62 taxa (20% of the collection) grew in both zones (SZ and EA). Red algae prevailed in the submerged zone (61% of the collection), green algae (48%) – in non-submerged zone (Table 1, Fig. 4). Epilithic algae prevailed in both submerged and non-submerged zones (Table 1).

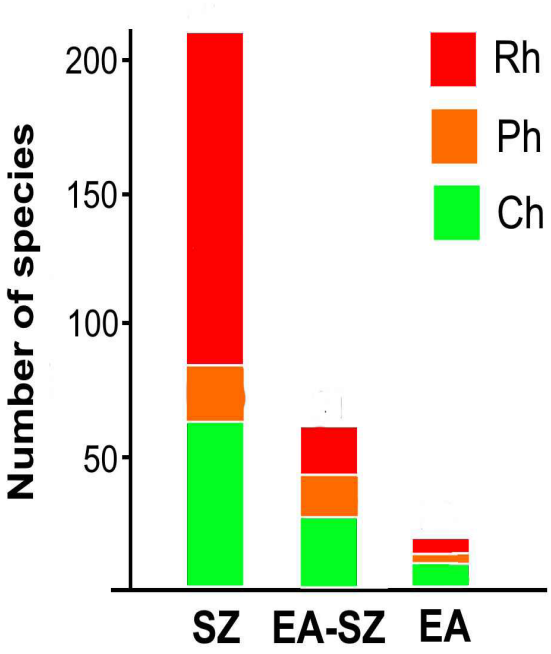

Fig. 4 Number of algae found in submerged (SZ) and in the intertidal zone exposed to air (EA) on the east coast of Sesoko Island. Rh – Rhodophyta, Ph – Phaeophyceae, Ch – Chlorophyta.

The structure of algal communities

Recent coral reefs of Sesoko Island are formed on the platform (carbonate base) of fossil reefs. Marine algal communities occupy all tidal zones from the splash zone to the upper subtidal zone.

In the splash zone and in the upper intertidal zone, during the winter seasons (January-February of 2003, 2014 and 2019), a monodominant algal turf community of *Bostrychia tenella* occurred (Rh) with accompanying species *Lyngbya majuscula* and *Symploca hydnoides* (Cy) (Fig. 5 a).

In the upper intertidal zone, the flat carbonate base of the reef and blocky remains of the fossil reef were covered by monodominant communities of the green alga *Monostroma nitidum* and the blue-green alga *Oscilatoria* sp. in winter-spring (Fig. 5b, c).

In the middle intertidal zone along the eastern coast, community of the green alga *Ulva pertusa* (Fig. 5d) prevailed and accompanied by some species such as *Bornetella sphaerica*, *Ganonema farinosum*, *Liagora ceranoides* and *Gelidium pusillum* var. *pacificum*.

In the lower intertidal zone, a polydominant community prevailed with dominant species *Chondracanthus intermedius*, *Padina minor*, *Jania ungulata* f. *brevior*, *Lobophora variegata* and accompanying species (Fig. 5e).

In the upper subtidal zone, hard substrata (not occupied by live coral colonies) were overgrown by a mosaic of polydominant algal turf community with species such as *Actinotrichia fragilis*, *Amphiroa fragilissima*, *Digenea simplex, Caulerpa racemosa* being dominant (Fig. 5f).

Algae from outdoor aquaria

In total, 218 species of algae were found in the aquaria; of these 180 species were macrophytes, 32 species Cyanobacteria and 6 species Bacillariophyta. Among macrophytes, Rhodophyta amounted to 49%, Phaeophyceae – 13% and Chlorophyta – 38%. Among the reds, the following taxa had more than 5 species: Ceramiaceae (18 species), Rhodomelaceae (14) and Corallinales (7); among browns, Dictyotaceae (7); among greens, Caulerpaceae (9), Cladophoraceae (9), and Boodleaceae (6) (Table 1). Among Cyanobacteria species of the Family Oscillatoriaceae dominated with a total of 12 species (Table 2).

Macrophytes found on artificial substrates amounted to 49%, those on experimental dead and injured coral colonies 50%, and those growing epiphytically 32%. In addition, 8 species of epizoic algae and one species of the green endophytic alga *Ulvella leptochaete* were found in the aquaria. Among macrophytes green algae were dominant (46%) on aquaria constructions (AS); red algae (47%) on dead and injured coral colonies (DC) and among epiphytes (Ep) (80% reds) (Table 1, Fig. 6).

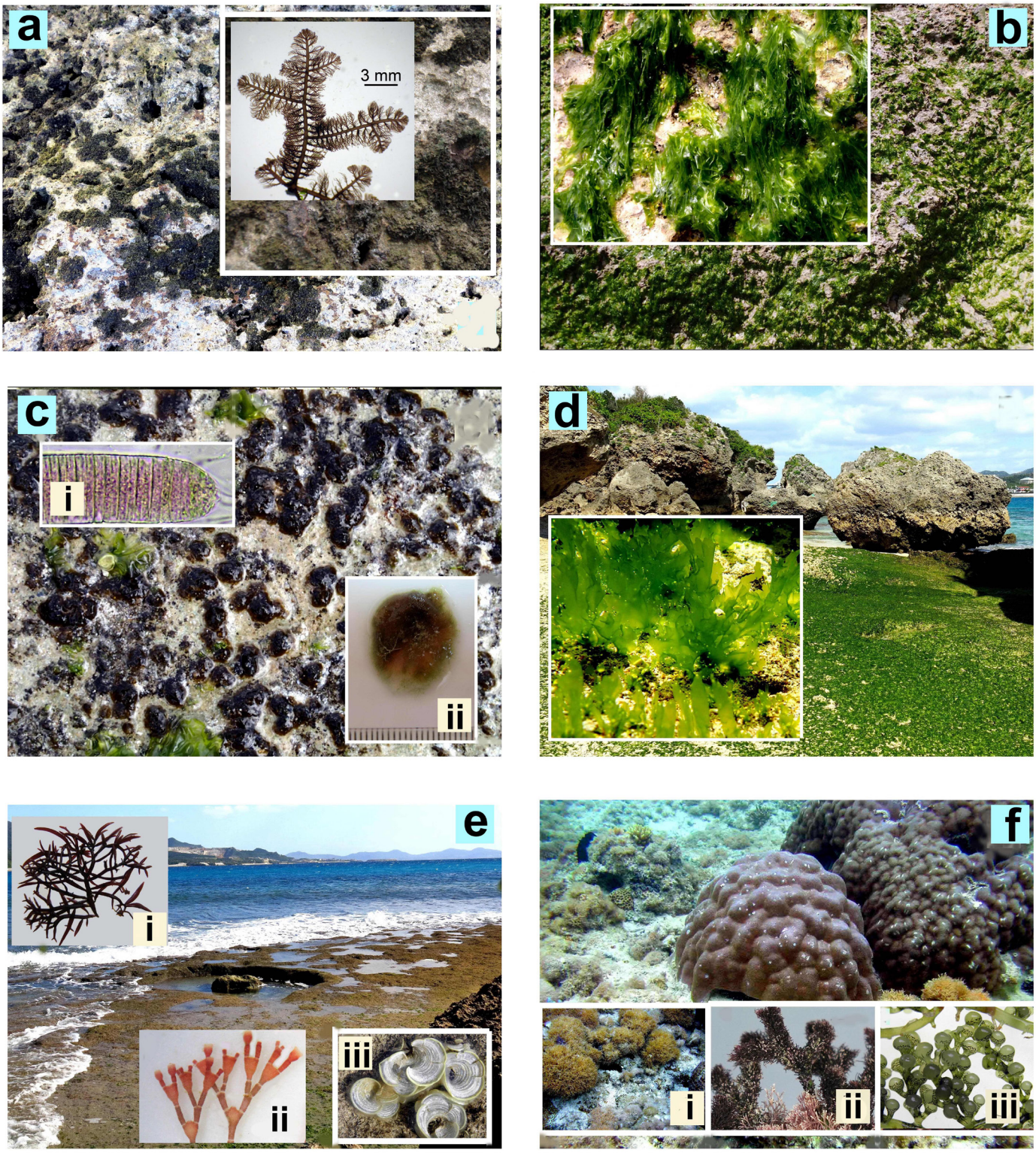

Fig. 5 Algal communities on fringing coral reefs of Sesoko Island: (a) the splash zone occupying by monodominant community of the red alga *Bostrychia tenella*. (b) the upper intertidal zone, monodominant community of the green alga *Monostroma nitidum*. (c) the upper intertidal zone, monodominant community of a colonial cyanobacteria *Oscilatoria* sp. (Inset (i) – fragment of filament in close view, inset (ii) – separate colony). (d) the middle intertidal zone, monodominant community of a green alga *Ulva pertusa*. (e) the low intertidal zone, mosaic polydominant community of algal turf with the dominance of *Chondracanthus intermedius* (Inset i), *Jania ungulata* f. *brevior* (Inset ii), *Padina minor* (Inset iii), *Hypnea spinella*, *Caulerpa racemosa*, etc. (f) the upper subtidal zone, mosaic polydominant community of algal turf with the dominance of red algae *Actinotrichia fragilis* (Inset i), *Amphiroa fragilissima*, *Digenea simplex* (Inset ii), *Caulerpa racemosa* (Inset iii).

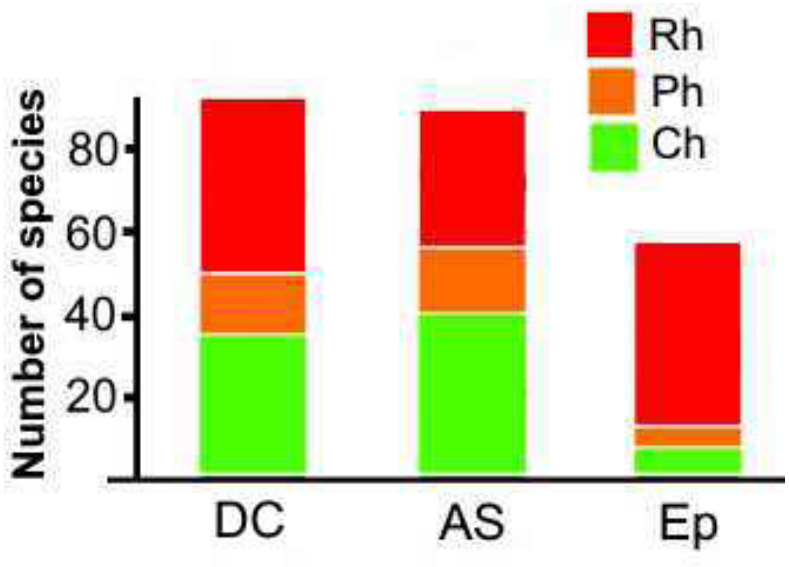

Fig. 6 Number of species of marine algae of different taxonomic groups found in aquaria growing on natural substrata (DC, damaged and dead fragments of hard corals), on artificial substrata (AS, aquaria constructions) and epiphytically (Ep). Rh – Rhodophyta, Ph – Phaeophyceae, Ch – Chlorophyta.

Algal communities in aquaria under different conditions

On the walls of outlet tube of all aquaria system, only bidominant community of the red alga *Polysiphonia* sp. and the green alga Bryopsis australis with accompanying species *Chondracanthus tenellus* (Rh) were found (Fig. 7a). The algae were overgrown with epiphytes *Colaconema hypneae* and *Sahlingia subintegra* (Rh).

Dense bidominant community *Bryopsis plumosa* and *Polysiphonia* sp. were found on outlet tubes of the outdoor aquaria and grilles under the tubes (Fig. 7b). In the community, accompanying species such as *Valonia fastigiata*, *Ulva clathrata*, *U. flexuosa* (Ch), *Griffithsia metcalfii* (Rh), *Calothrix* spp. and *Phormidium* spp. (Cy) were found.

Monodominant community of the green alga *Valonia fastigiata* with accompanying species *Hypnea nidulans*, *Caulerpa racemosa* and *Bryopsis plumosa* overgrew the upper parts of outlet tubes in the aquaria (Fig. 7c). The most widespread epiphytes were the red algae *Asparagopsis taxiformis* (sporophytic stage) and *Hydrolithon farinosum*.

The first settlers on well-lit vertical walls of the aquaria, made of fiberglass and epoxy resin, were red encrusting algae from the order Corallinales (*Hydrolithon farinosum*, *H. boreale*, *Pneophyllum fragile*, *Neogoniolithon brassica-florida*), and other species such as *Turbinaria ornata*, *Dictyota friabilis*, *Lobophora variegata* (Ph) (Fig. 7d), *Asparagopsis taxiformis*, *Laurencia intricata* (Rh) settled on the crusts. *Caulerpa chemnitzii*, *Derbesia tenuissima*, *Ulva intestinalis* and *Valonia fastigiata* grew in shaded sites.

At the bottom of the tanks and various objects placed here, mainly mosaic polydominant algal communities were formed. Metal and plastic objects were primarily overgrown with coralline crusts and other algae. In the most shaded sites, long-living (annual) green algae such as *Bryopsis australis*, *Caulerpa chemnitzia*, *C. nummularia*, *C. racemosa*, *Derbesia tenuissima* and *Valonia fastigiata* (Ch) dominated. *Dictyota implexa* (Ph), *Coelothrix irregularis*, *Hypnea esperi*, *Hypnea spinella*, *Laurencia intricata* (Rh) grew in the most illuminated places.

Algae also occupied natural substrata placed in the aquaria. Long-living (annual) *Galaxaura divaricata, Hypnea esperi* (Rh), *Dictyota friabilis* and *D. implexa* (Ph) overgrew dead fragments of coral colonies. Polydominant algal turf communities were formed on the injured surfaces of coral colonies during 6 months (Titlyanov *et al*. 2006). In the turf, mainly red algae (*Jania capillacea, Centroceras clavulatum, Corallophila kleiwegii, Gayliella flaccida, Laurencia intricata*, etc.) dominated (Fig. 7e). On the shells of living molluscs, monodominant communities of fine filamentous green algae such as *Bryopsis australis*, *B. plumosa*, *Derbesia tenuissima*, *Cladophora laetevirens* were formed (Fig. 7f).

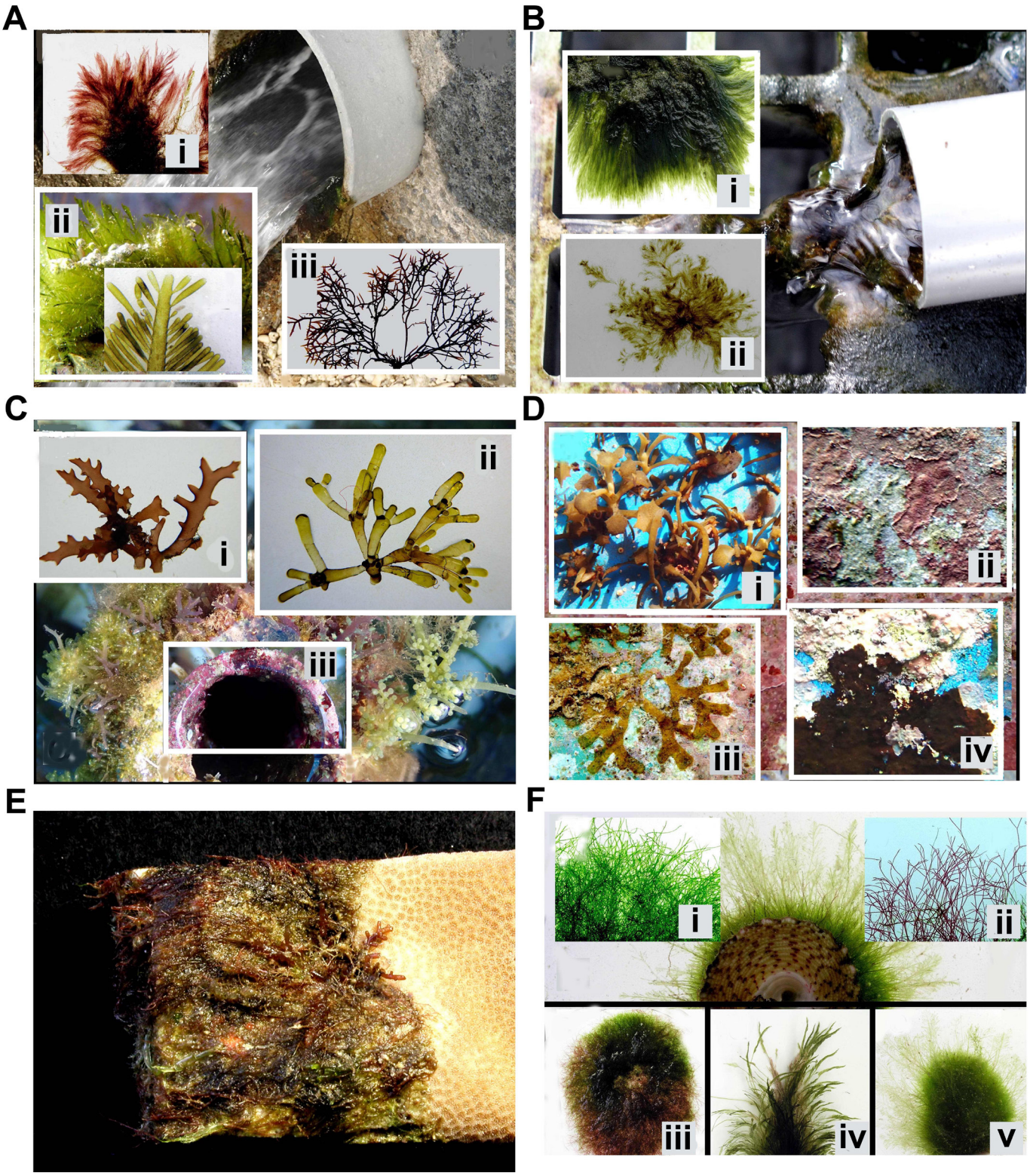

Fig. 7 Macrophytes on aquaria constructions and biological objects: (a) bidominant community *Polysiphonia* sp. and *Bryopsis australis* on the wall of outlet tube of all aquaria system. Insets: (i) *Polysiphonia* sp.; (ii) *Bryopsis australis;* (iii) accompanying species *Chondracanthus tenellus*. (b) bidominant community *Bryopsis plumosa* and *Polysiphonia* sp. in outdoor aquariums on outlet tube and grille under the tube. Insets: (i) *Bryopsis plumosa*; (ii) *Polysiphonia* sp. (c) monodominant community *Valonia fastigiata* with accompanying species on the outlet tube in aquarium. Insets: (i) *Hypnea nidulans*; (ii) *Valonia fastigiata*; (iii) red crust algae, first settlers on the plastic outlet tube. (d) algae on the aquaria side walls. Insets: (i) *Turbinaria ornata*, (ii) red crust algae; (iii) *Dictyota friabilis*; (iv) *Lobophora variegata*. (e) polydominant algal turf community formed on injured surface of colony fragment of the coral *Porites lutea*. (f) monodominant community of the green alga *Bryopsis pennata* on a mollusc shell. Insets: (i) *Cladophora catenata*; (ii) *Ceramium* sp.; (iii) bidominant community of the red alga *Ceramium* sp. and the green algae *Cladophora catenata*, (iv) *Derbesia tenuissima*, (v) *Bryopsis pennata.*

DISCUSSION

Diversity and taxonomic composition of the benthic flora of the eastern coast of Sesoko Island

The benthic marine flora of the islands of the Ryukyu archipelago is well studied (Tanaka 1956, 1960, 1963, 1964, 1965; Segawa & Kamura 1960; Akatsuka 1973; Itono 1971, 1973, 1986; Kamura 1963, 1977; Kamura & Iida 1981; Ohba & Aruga 1982; Ui 1986; Tsuda 1991; Ohba 1995; Ohba *et al*. 2006). Part of the studies (Titlyanov *et al*. 2006, 2008; Sergeeva *et al*. 2007) was devoted to the inventory of the benthic flora of Sesoko Island. Earlier, we have shown that decadal changes in the benthic flora in various tropical and subtropical regions of the Asia-Pacific region occurred under the influence of both natural and anthropogenic factors. Temporary increase in water temperature by 1.5−2.0°C and associated bleaching and mortality of corals were particularly notable (Sergeeva *et al*. 2007; Titlyanov *et al*. 2016a), coupled with anthropogenic factors such as irrational human exploitation of ecosystems (Titlyanov *et al*. 2016b) and eutrophication of the environment (Lapointe *et al*. 1997; Li *et al*. 2016; Titlyanov *et al*. 2019b).

The species composition and distribution of marine plants on a fringing reef of Sesoko Island were investigated in 1995–1998, before the bleaching event in July-August 1998 and after the event, in 2002–2005. The bleaching event led to mass coral mortality, followed by a "phase shift" from the abundance of reef-building corals to that of macroalgae with the number of algae species increasing from 211 to 345 species, while the composition of the main large taxa of the benthic flora did not change (Sergeeva *et al*. 2007). The authors supposed that the "plant reef" phase in Sesoko Island may be temporary, and the coral reef may recover within several decades not only with a decrease in area of the substrate covered by algae, but also with a decrease in algal species diversity. However, as the present work showed, the species diversity of algae on the damaged coral reef of Sesoko Island did not decrease from 2005 to 2019. It was shown that only on the east coast of Sesoko Island about 300 species of algae were collected from 2005 to 2019. This comparison primarily showed that the benthic flora of the east coast was practically no different from other coasts of the island in terms of diversity and species composition. In addition, we did not find a large difference in the diversity and species composition of algae between the 2002–2005 collection and the 2014–2019 collection, indicating the relative stability of flora throughout this period.

Structure of algal communities in shallow zones exposed to the air (EA) and submerged (SZ)

The upper and middle intertidal zones (EA) are occupied by mono- and bidominant algal turf communities and encrusting algae. The lower intertidal and upper subtidal zones (SZ) are occupied by a mosaic of polydominant communities and communities of large upright-growing algae (e.g., *Sargassum thunbergii*). The largest number of species (70% species of the field collection) was found in the submerged zone, 7% species of the collection – in the intertidal zone exposed to air and 20% of the collection grew in both zones (SZ and EA). In the SZ communities, red algae prevailed, while in EA communities green algae did. In both zones, there were approximately twice as many epilithic algal species as epiphytic ones. The structure of algal communities in the intertidal and upper subtidal zones of Sesoko Island was close to that of other localities in the East Asia warm-temperate biogeographic regions (Lüning 1990; Saunders & Hommersand 2004; Titlyanov *et al*. 2015, 2016a, b, 2019b).

Algae in outdoor aquaria

50% of field-collected taxa were found in the aquaria and most species (84%) found in the aquaria were also collected from the sea. All species found in the aquaria were typical of Asia-Pacific region. Aquaria flora varied little from field flora in terms of taxonomic composition and relative abundances of epilithic and epiphytic algae.

In our view, the high diversity of algae in the aquaria of the Sesoko Station may be related with (1) flow of unfiltered seawater carrying reproductive bodies of seaweed species from a nearby coral reef to the aquaria; (2) lack of predators and competitors in the aquaria; (3) relatively benign environmental conditions in the aquaria. This, however, should be set against the fact that c. 40% of species in the field collection were not found in the outdoor aquaria, which must also be related to a combination of factors.

In outdoor aquaria, various algal associations were formed in dependence on local external conditions. We were able to identify some of them. In long-term experiment (more than six months, Titlyanov *et al*. 2006) we

traced the dynamics of polydominant community formation of algal turf (the most common community of coral reefs in the submerged zone). Algal turf was formed only on a natural substrate: injured or dead coral fragments. Parallel experiments on the formation of algal communities on natural substrata in the sea showed similar dynamics in these processes (Titlyanov *et al*. 2008).

On artificial substrates in the aquaria, various algal associations were formed. The structure of the associations depended mainly on the rate of water movement and light intensity. Plastic and metal structures of the aquaria were primarily overgrown with encrusting algae, among which species from the order Corallinales dominated, and then algae from other orders settled on the crusts. Fouling of the substrata by pioneer coralline algae did not depend on water flow, but on light intensity: extremely shaded or most lighted constructions overgrew less. On the sidewalls of the aquaria, initially overgrown by coralline crusts, various species of algae grew in mosaics, without any specific associations. Polydominant algal associations were mainly formed on objects at the bottom of the aquaria used over 6 months under conditions of low water flow. At the most shaded sites, in these associations, long-lived (annual) green algae such as *Caulerpa* spp., *Valonia fastigiata*, etc, dominated.

Algae settling in places with a fast flow of water (inflow and outlet pipes, protectors covering the outlet gutters) formed mono- or bidominant communities, mainly from highly productive green and red filamentous algae. These associations differed from others by high density of thalli and greater biomass per surface area of the substrate. Sometimes fine filamentous green and red algae formed dense mono- and bidominant communities on live molluscs.

Our study suggests that the benthic flora of the coral reef on the east coast of Sesoko Island have experienced no significant change in terms of diversity and species composition over the past 14 years. Little changes were also recognised in the structure and distribution of algal communities on the reef. In the zone exposed to air, mono- and bidominant communities of algal turfs with the dominance of green algae prevailed. In the submerged zone, polydominant (mosaic) turf communities with the dominance of red algae prevailed.

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