
# Spatio-temporal variability in benthic algal assemblages on man-made and natural substrates in the Tomioka Bay (Amakusa, Japan)

Eduard A. Titlyanov, Tamara V. Titlyanova and Mutsunori Tokeshi

*Coastal Ecosystems*, 2019, vol 6, 1-21

Data Paper

# Spatio-temporal variability in benthic algal assemblages on man-made and natural substrates in the Tomioka Bay (Amakusa, Japan)

Eduard A. Titlyanov[1], Tamara V. Titlyanova[1] and Mutsunori Tokeshi[2]

[1]A.V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences, Palchevskogo 17, Vladivostok, 690059, Russia

[2]Amakusa Marine Biological Laboratory, AMBL - Kyushu University, Reihoku-Amakusa, Kumamoto, 863-2507, Japan

Corresponding author: E Titlyanov, e-mail: etitlyanov@mail.ru

## Abstract

An intensive floral survey was conducted on the spatio-temporal variability in marine benthic algal assemblages around the coasts of Tomioka Bay, Amakusa Shimoshima Island, Japan, in 2013–2015. A total of 153 species of marine macrophytes were recorded, of which 62% belonged to Rhodophyta, 20% to Phaeophyceae and 18% to Chlorophyta. Over 120 species were found on man-made substrates in the port area, of which 60% were reds, 21% browns and 19% greens. A similar number and taxonomic composition of algal species were found on natural rocky substrates in the middle part of the Tomioka Bay (outside the port) as on man-made substrates in the port. Marked seasonal varaition in the marine flora was noted, with low species diversity in summer-autumn compared with winter-spring. Consideration was also given to possible long-term changes in the algal assemblages of Amakusa with an apparent increase in tropical/subtropical taxa, probably pointing to the influence of climate change.

**Keywords**: Amakusa Shimoshima Island, Indo-Pacific, marine algae, Rhodophyta, Phaeophyceae, Chlorophyta, variation in algal assemblages

## Introduction

An increased number of studies have documented long-term changes in the benthic flora of South-East Asia, due to anthropogenic as well as natural abiotic/biotic environmental factors (Kennish 1996; Haraguchi & Sekida 2008; Su *et al*. 2009; Huang *et al*. 2013; Titlyanova *et al*. 2014; Titlyanov *et al*. 2015, 2016a, b; Li *et al*. 2016). On the other hand, seasonal changes are known to be caused by various factors including light intensity, temperature, salinity, rainfall, nutrient concentration and wave action (Costa *et al*. 2002; Ateweberhan *et al*. 2006; Thakur *et al*. 2008; Anggadiredia 2009; Su *et al*. 2009; Titlyanov *et al*. 2014a, b).

Studies on the occurrence of algae on artificial substrates in the Asia Pacific have often been linked to the issues of fouling (Zvyagintsev 2005) and our earlier investigations in the Yellow Sea, northern China, revealed variation in species diversity and composition of algae on different types of artificial substrates in and around aquacultural farms and seaports (Titlyanov & Titlyanova 2013, 2014; Titlyanov *et al*. 2016c).

The present study is a continuation of investigation into spatio-temporal variation in the marine benthic flora of the Asia-Pacific waters and aims to make floral comparisons of algal assemblages on natural and man-made substrates in the Tomioka Bay, Amakusa, Japan.

## Materials and Methods

Study site

The study was conducted around the Tomioka Bay (32°31’21”N; 130°2’31”E), Amakusa Shimoshima Island (Fig. 1), located in southwestern Japan (at the northern part of the East China Sea). Amakusa has a humid subtropical climate with hot summers and cool winters. Highest temperatures occur in August (up to 32°C), the lowest in January (c.0°C). Precipitation is significant throughout the year, being heaviest in June to July. The water temperature in the Tomioka Bay fluctuates between 14 and 28°C in the course of the year. The bay is about 3 km across and has a maximum depth of 25 m, with a tidal range of 2.6 m. Salinity stays above 30 practical salinity units (PSU) throughout the year.

The Tomioka Bay has been a local centre of fisheries activity and maritime traffic with port facilities for fishing and industrial vessels and a passenger ferry terminal. Aquacultural farms for molluscs and plantations of a green alga *Monostroma nitidum* also exist in the bay.

The port facilities have been expanded over the past century, comprising piers made of concrete and stones with extended coastal constructions with concrete slabs going into the depth. The bottom is laid with concrete blocks and natural stones, covered by sand and shellfish. The inner part of the bay is protected from strong storms, while areas outside are exposed to wave action.

Sampling and identification

Algae were collected at three sites in the fishery port (man-made substrates: concrete and concrete-stony walls of piers, concrete slabs, mooring-lines of metal and other materials) and at five sites outside of the port (natural substrates: rocky, stony, sandy and sandy bottom covered with silt) (Fig. 1). Algal sampling was conducted in 2013 (site 2 and 3 (2 March); site 2, 3, 7, 8 (15−23 April); site 2, 5, 6, 7, 8 (8−10 August)), 2014 (site 1, 3 (27−29 January)) and 2015 (sites 1, 5 (11−19 February); sites 1, 2, 3 (8−11 October)) (Fig. 1).

Collection was made by hand during low tides in the upper, middle, low intertidal and the upper subtidal zones from 0 to 2 m depth (involving snorkeling) (division into tidal zones followed Perestenko 1980). Samples were extracted from all substrate types using more than 5 quadrats from each sampling site; quadrats of two sizes (100 cm$^2$, for algal turf assemblages and 625 cm$^2$ for assemblages with large algae) were used. Quadrates were haphazardly placed, photographed and then completely cleaned of algae. Freshly collected material was identified using monographic publications, floristic studies and systematic articles indicated in Titlyanova *et al*. (2014). The abundance of taxa was determined visually by estimating mean proportional cover. The following codes were used: a single sighting (S); a rare sighting (+); common or 10−50% cover (++); abundant or 60−100% cover (+++). Dominance in an assemblage was also 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 species were involved.

The systematics and nomenclature followed Guiry & Guiry (AlgaeBase, searched in 2017). The previously known and newly recorded species for Japan were verified using Algaebase (Guiry & Guiry 2017), for Amakusa Island, the article “Fauna and flora of the sea around the Amakusa Marine Biological Laboratory. Marine algae by Sokichi Segawa and Tadao Yoshida” (1961). Hierarchical classification of the Phylum Rhodophyta is from Saunders &

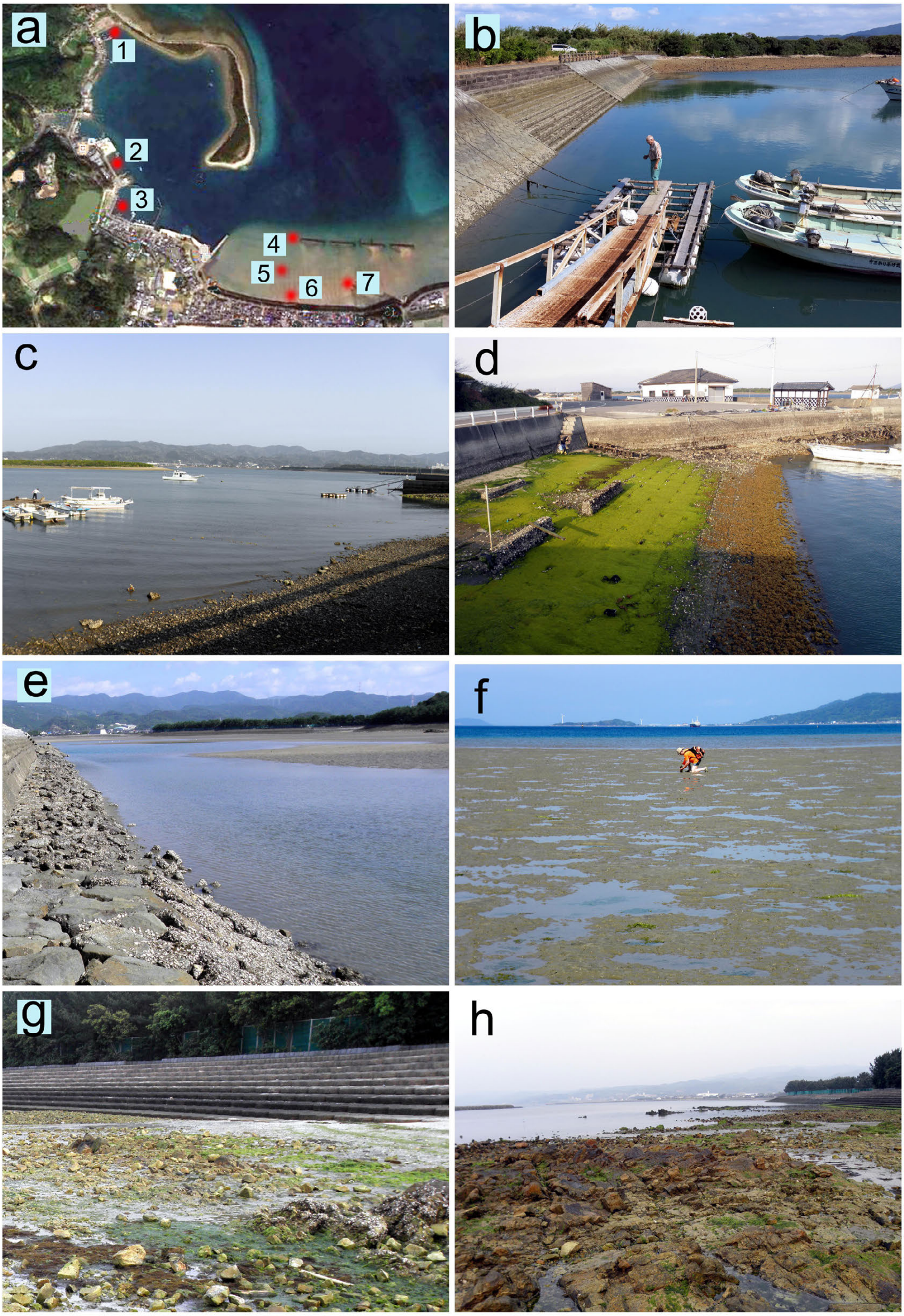


**Fig. 1** Photographs of the study sites in Amakusa Shimoshima Island: (a), aerial view of the Tomioka Bay; (b-d) Sites 1-3 in the fishery port; (e-h) Sites 4-7 outside of the port.

Hommersand (2004). The classification system of the Phyla Chlorophyta and Ochrophyta follows Tsuda (2006).

The collections of both macrophytes and their epiphytes were preserved as dried herbarium specimens and were deposited in the herbarium at A.V. Zhirmunsky Institute of Marine Biology, National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Science, Vladivostok 690041, Russian Federation.

**Results**

A total of 153 species of marine macrophytes were recorded from the shores of Tomioka (Table 1), of which 62% belonged to Rhodophyta, 20% Phaeophyceae and 18% Chlorophyta. In the fishery port (sites 1-3), 126 species were found, of which 59% were reds, 21% browns and 20% greens. Outside of the port (sites 4−7), 121 species were found with 61% reds, 22% browns and 17% greens. Ninety-

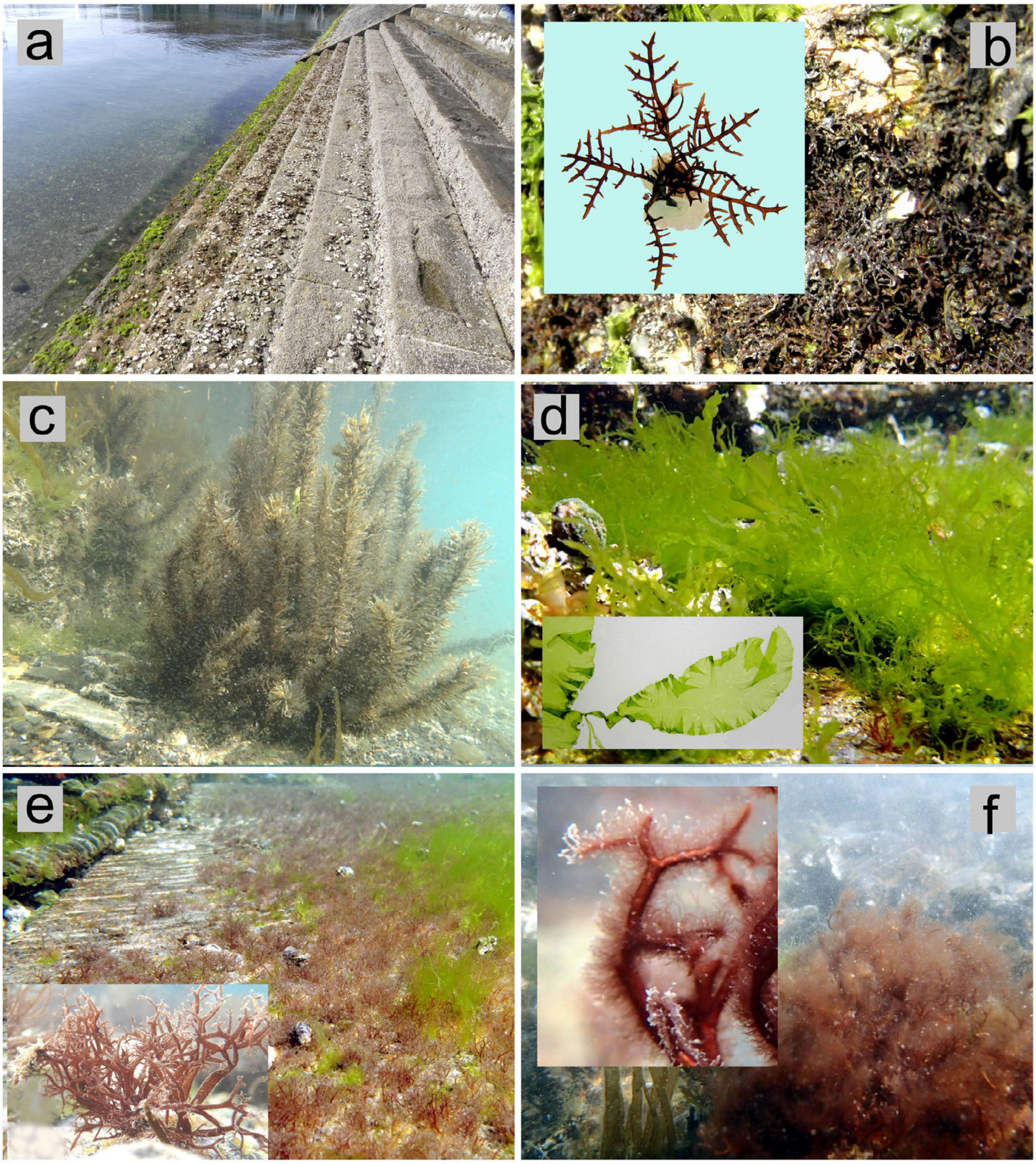


**Fig. 2** Algal assemblages on man-made substrates of Tomioka (site 1), late January 2014: (a) general view; (b) monodominant *Gelidiophycus divaricatus*; (c) monodominant *Sargassum thunbergii*; (d) bidominant *Ulva prolifera* + *U. linza*; (e) monodominant *Gloiopeltis furcata*; (f) monodominant red epiphytic alga *Bangia gloiopeltidicola* on *G. furcata*.

seven taxa or 63% of all species found occurred in both the port area and in other areas of the Tomioka Bay, 29 species (19%) were found only in the port, and 27 species (18%) only outside the port. Species occupying hard (rocky) substrates were predominant (70% of all species), followed by those growing on artificial substrata (55%) and those of epiphytic and endophytic algae (32%). Three species were found on sandy substrates, four epizoic and seven unattached (floating).

In total, 84 species (54%) were newly recorded for the Amakusa Islands and one red algal species *Antithamnionella longicellulata* Perestenko was new to Japan (Table 1). Among the collected macroalgae, species inhabiting tropical to subtropical waters of the world were predominant and amounted to 84%, 10% of the species occurring only in subtropics, 40% also occurring in the temperate zones and 16% also distributed in the Arctic (or Antarctic) areas. About 40% of all algal species found in the Tomioka Bay occur only in the Indo-Pacific and the rest of the species occur also in the Atlantic Ocean (Table 1).

Algal assemblages on man-made substrates

Around the port area of the Tomioka Bay (sites 1-3, Fig. 1a), the largest number of species was found in the low intertidal and upper subtidal zones on rocky-concrete blocks of underwater constructions (i.e. 43% of all collected species), 16% species were found on mooring ropes, 13% species lived on vertical and horizontal surfaces of concrete slabs and blocks and same number was found on metal constructions.

In winter-spring, 115 species were found on underwater constructions; of these 60% were reds, 21% browns and 19% greens. At the end of January, monodominant assemblages of a red alga *Gelidiophycus divaricatus* occurred in the upper intertidal zone at site 3 (Figs. 1a, d; 3a) and site 1 (Fig. 2). The alga occupied the surface of oyster shells attached to concrete constructions. Rocky-concrete substrates between the low intertidal and the upper subtidal zones were occupied by a brown alga *Sargassum thunbergii* (Fig. 2c). In the middle intertidal zone, two green algae *Ulva prolifera* and *U. linza* (Fig. 2d) were dominant and *Gloiopeltis furcata* (Fig. 2e, f) was also frequently found, but not *Sargassum thunbergii*. Green algae *Monostroma nitidum* and *U. prolifera* were predominant on concrete slabs in the upper and middle intertidal zones (Fig. 3d, e). In the low intertidal zone, monodominant assemblages of a brown alga *Ishige foliacea* occurred on rocky slabs and concrete blocks of fishery constructions (Fig. 3f). Monodominant assemblages of a green alga *Blidingia minima* were found only on old mooring ropes in the upper intertidal zone (Fig. 3b), monodominant assemblage of a red alga *Pyropia suborbiculata* overgrew thin plastic fishing lines in the upper and middle intertidal zones (Fig. 3c). Old mooring ropes in the low intertidal zone were overgrown with polydominant assemblages (with the structure close to algal turf communities) including *Amphiroa beauvoisii, Gelidiophycus divaricatus, Gelidium pusillum, Chondracanthus intermedius, Caulacanthus ustulatus, Polyopes affinis, Monostroma nitidum, Ulva flexuosa, U. intestinalis* and *U. prolifera* (Fig. 3g, h).

In early March, at site 3 of the port (Fig. 4a), monodominant assemblages of *Gelidiophycus divaricatus* occurred in the upper intertidal (Fig. 4b) where shells covered concrete structures, while concrete slabs were overgrown with bidominant assemblages comprising *M. nitidum* + *U. intestinalis* (Fig. 4c). The middle intertidal zone was mainly occupied by *U. intestinalis* forming a monodominant assemblage (Fig. 4d), and also bidominant assemblages composed of a brown alga *Scytosiphon lomentaria* and a green alga *U. intestinalis* (Fig. 4e). In the low intertidal zone, two monodominant assemblages of brown algae *I. foliacea* and *Colpomenia sinuosa* occupied slabs and concrete blocks (Fig. 4f-h).

At the end of April, notable changes in algal assemblages occurred at sites 2 and 3 of the port (Fig. 5), compared with the beginning of March (Fig. 4). In the upper and middle intertidal zone, bidominant (*Monostroma nitidum* + *Ulva intestinalis*) and monodominant (*U. intestinalis*) assemblages, bidominant assemblages of a brown alga *Scytosiphon lomentaria* + a green alga *U. intestinalis* were not found. Their places were occupied by *M. nitidum* (various substrates in the upper and middle intertidal), *Gracilaria vermiculophylla* (on concrete slabs in the mid intertidal) and bidominant assemblages of *M. nitidum* + *Gloiopeltis furcata* (on concrete slabs in the mid intertidal) (Fig. 5c-e) and monodominant assemblages of *Ulva prolifera* (on rocky-concrete blocks in middle intertidal) (Fig. 5f).

In the low intertidal and upper subtidal zones, algal assemblages analogous to those found in January and early March occurred on rocky-concrete substrates with the predominance of *Ishige foliacea* and *Colpomenia sinuosa*, and also on plastic floats with *Amphiroa beauvoisii, Gelidiophycus divaricatus, Gelidium pusillum, Chondracanthus intermedius, Caulacanthus ustulatus,*

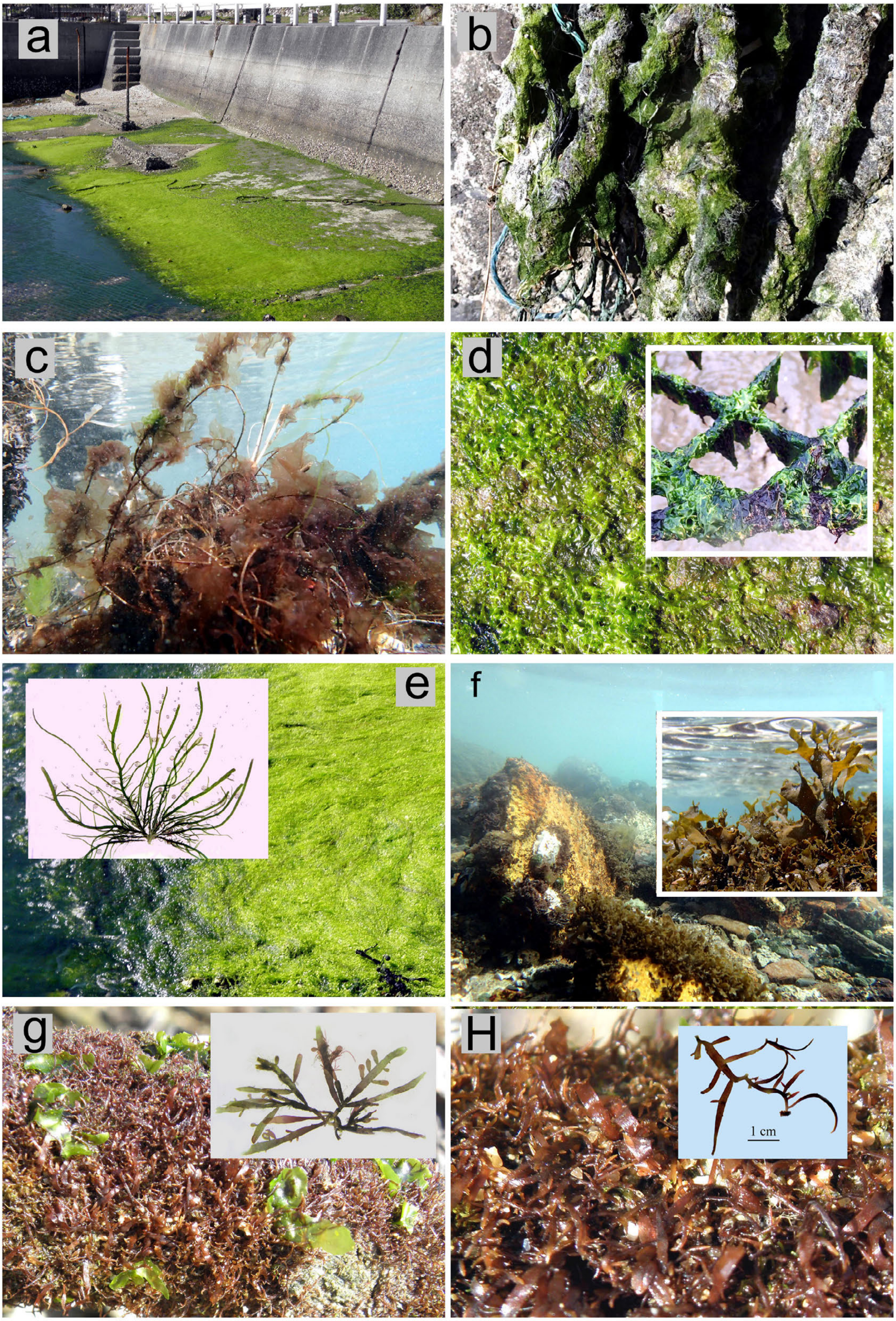


**Fig. 3** Algal assemblages on man-made substrates of Tomioka (site 3), late January 2014: (a) general view; (b) monodominant *Blidingia minima*; (c) monodominant *Pyropia suborbiculata*; (d) monodominant *Monostroma nitidum*; (e) *Ulva prolifera*; (f) monodominant *Ishige foliacea* (g) polydominant assemblage on plastic rope with *Gelidiophycus divaricatus, Gelidium pusillum* and *Chondracanthus intermedius*; (h) monodominant *Chondracanthus intermedius* on a nylon rope in the upper subtidal zone.

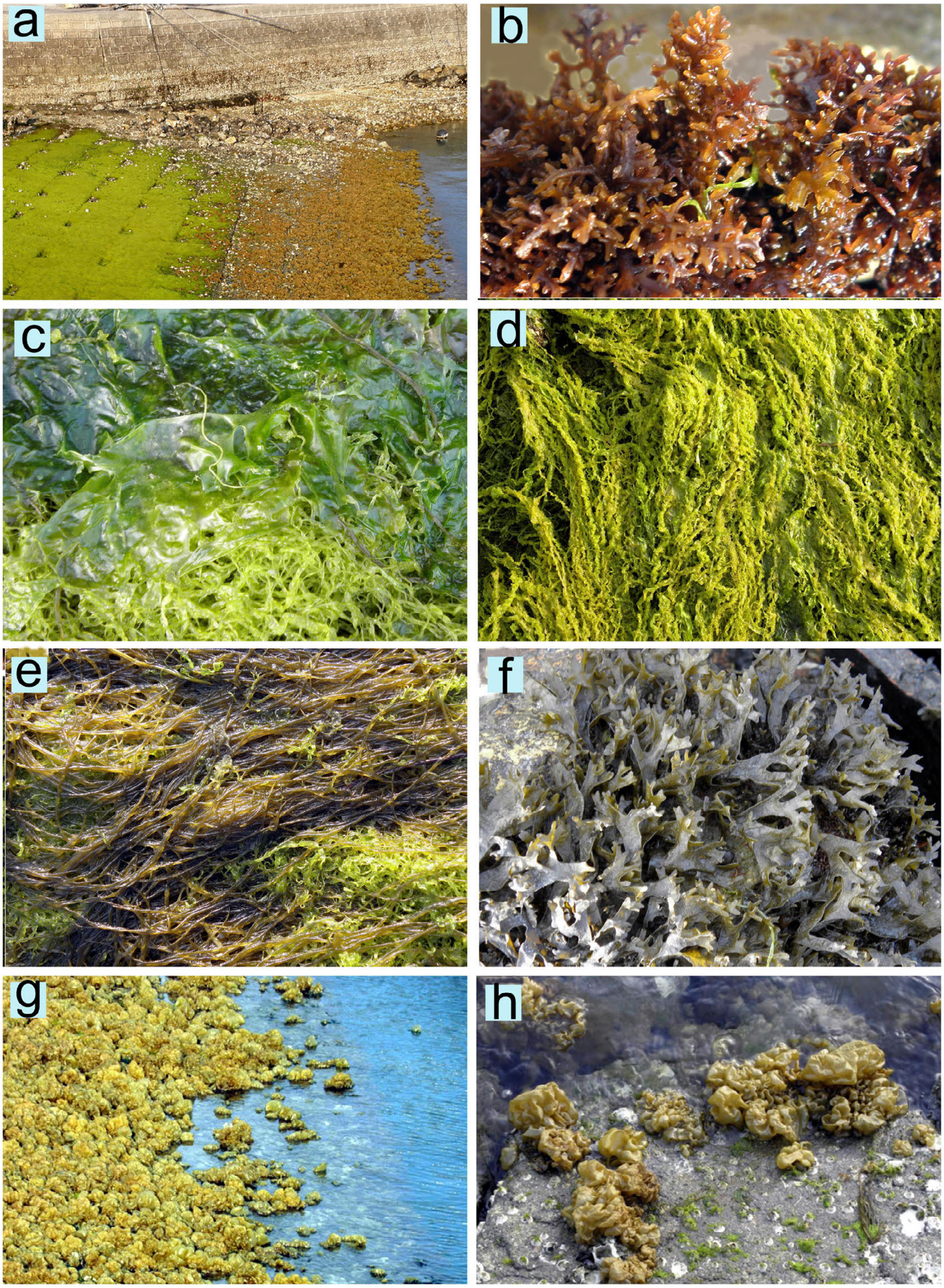


**Fig. 4** Algal assemblages on man-made substrates of Tomioka (site 3), 2 March 2013: (a) general view; (b) monodominant *Gelidiophycus divaricatus*; (c) bidominant *Monostroma nitidum* + *Ulva intestinalis*; (d) monodominant *U. intestinalis*; (e) bidominant *Scytosiphon lomentaria* + *U. intestinalis*; (f) monodominant *Ishige foliacea*; (g, h) monodominant *Colpomenia sinuosa*.

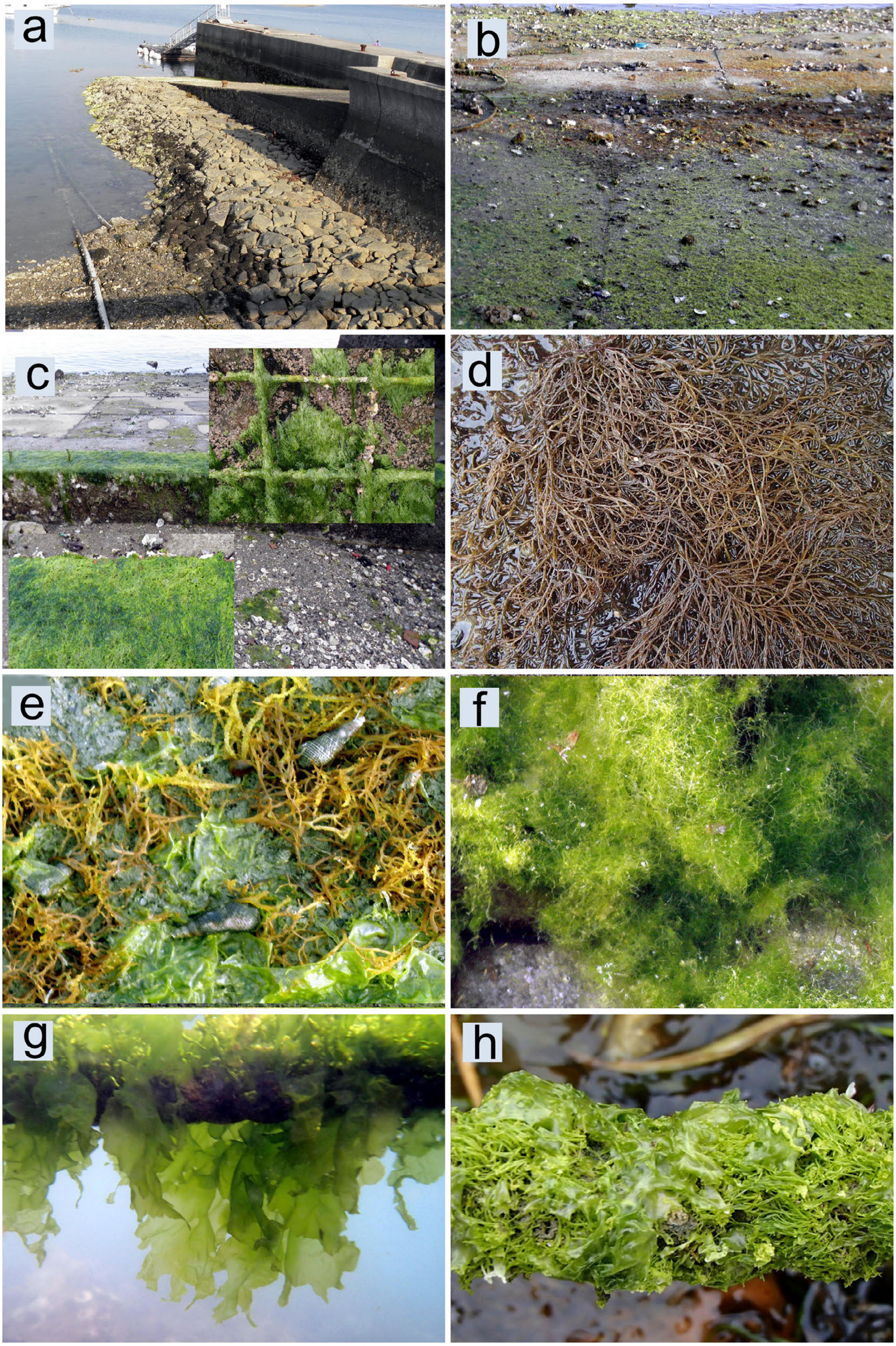


**Fig. 5** Algal assemblages on man-made substrates of Tomioka at (a) site 2 and (b) site 3, 27 April 2013: (c) monodominant *Monostroma nitidum*; (d) monodominant *Gracilaria vermiculophylla*; (e) bidominant *Monostroma nitidum* + *Gloiopeltis furcata*; (f) monodominant *Ulva prolifera*; (g) monodominant *Ulva lactuca* on plastic rope; (h) polydominant assemblage including *M. nitidum, U. prolifera* and *U. intestinalis*.

Table 1. List of algal species collected from the Tomioka Bay in 2013−2015.

Species: $, new records for Amakusa; $$, new records for Japan. Tidal zone: 1 – upper intertidal, 2 – middle intertidal, 3 – low intertidal, 4 – upper subtidal. Life form: Ep, epiphytic; Ez, epizoic; En, endophytic algae, HS, algae growing on hard substrata (epilithic), SS, algae growing on soft substrata, Af, algae growing on artificial substrata; Fl, floating algae. Geographical distribution: T – tropical, S – subtropical, M – temperate, An – Antarctic, Ar - Arctic, T,S,M,An − from tropics to Antarctic, T,S,M,Ar - from tropics to Arctic, T,S,M – from tropics to temperate zones, T,S – from tropics to subtropics, (I-P) – only in the Indo-Pacific, (P) – only in the Pacific. The abundance of taxa: rare sightings (+); common (++); abundant (+++). Win-Spr refers to data including March-April 2013, January 2014, and February 2015; Sum-Aut refers to data including August 2013 and October 2015.

| Species (varieties and forms) | Tidal zone | Life form | Geographical distribution | Abundance on man-made substrates (site 1–3) | | Abundance on natural substrates (site 4–7) | |
|---|---|---|---|---|---|---|---|
| | | | | Win-Spr | Sum-Aut | Win-Spr | Sum-Aut |
| RHODOPHYTA | | | | | | | |
| Order STYLONEMATALES | | | | | | | |
| Family STYLONEMATACEAE | | | | | | | |
| *Stylonema alsidii* (Zanardini) K.M. Drew | | Ep | T,S,M | ++ | ++ | ++ | ++ |
| Order ERYTHROPELTALES | | | | | | | |
| Family ERYTHROTRICHIACEAE | | | | | | | |
| *Erythrotrichia carnea* (Dillwyn) J. Agardh $ | | Ep | T,S,M,Ar, An | ++ | + | ++ | ++ |
| *Sahlingia subintegra* (Rosenvinge) Kornmann $ | | Ep | T,S,M | ++ | | ++ | |
| Order BANGIALES | | | | | | | |
| Family BANGIACEAE | | | | | | | |
| *Bangia gloiopeltidicola* Tanaka $ | | Ep | S,(P) | +++ | | +++ | |
| *Pyropia ishigecola* (A. Miura) N. Kikuchi & M. Miyata $ | 1,2 | HS, Af | S,(P) | ++ | | + | |
| *Pyropia suborbiculata* (Kjellman) J.E. Sutherland, H.G. Choi, M.S. Hwang & W.A. Nelson $ | 1,2 | Ez, HS, Af | T,S | ++ | | ++ | |
| Order ACROCHAETIALES | | | | | | | |
| Family ACROCHAETIACEAE | | | | | | | |
| *Acrochaetium catenulatum* M. Howe $ | | Ep | T,S,M,An | ++ | | ++ | |
| *Acrochaetium microscopicum* (Nägeli ex Kützing) Nägeli $ | | Ep | T,S,M,Ar | + | + | + | ++ |
| *Acrochaetium robustum* Børgesen $ | | Ep | T,S | | + | | ++ |
| Order COLACONEMATALES | | | | | | | |
| Family COLACONEMATACEAE | | | | | | | |
| *Colaconema daviesii* (Dillwyn) Stegenga $ | | Ep | T,S,M,Ar,An | | + | | ++ |
| *Colaconema gracile* (Børgesen) Ateweberhan & Prud'homme van Reine $ | | Ep | T,S | + | | + | |
| Order HILDENBRANDIALES | | | | | | | |
| Family HILDENBRANDIACEAE | | | | | | | |
| *Hildenbrandia rubra* (Sommerfelt) Meneghini $ | 1-2 | HS | T,S,M,Ar, An | + | | ++ | |
| Order PEYSSONNELIALES | | | | | | | |
| Family PEYSSONNELIACEAE | | | | | | | |
| *Peyssonnelia rubra* (Greville) J. Agardh $ | 4 | HS | T,S | + | | ++ | |
| Order CORALLINALES | | | | | | | |
| Family CORALLINACEAE | | | | | | | |
| *Amphiroa beauvoisii* J.V. Lamouroux $ | 3,4 | HS, Af | T,S | ++ | +++ | ++ | ++ |
| *Amphiroa ephedraea* (Lamarck) Decaisne | 4 | HS, Af | T,S | | ++ | | |
| *Corallina crassisima* (Yendo) K. Hind & G.W. Saunders | 3,4 | HS, Af | S,(P) | | | ++ | ++ |
| *Corallina pilulifera* Postels & Ruprecht | 2 | HS, Af | T,S,M,(P) | | | ++ | ++ |
| *Hydrolithon farinosum* (J.V. Lamouroux) Penrose & Y.M. Chamberlain $ | | Ep | T,S,M | + | ++ | ++ | ++ |
| *Jania ungulata* f. *brevior* (Yendo) Yendo $ | 4 | HS, Af | T,S | | +++ | | |
| *Lithophyllum okamurae* Foslie | 4 | HS, Af | T,S,(I-P) | + | + | + | + |

Table 1. Continued (2 of 5).

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Order NEMALIALES | | | | | | | |
| Family GALAXAURACEAE | | | | | | | |
| *Actinotrichia fragilis* (Forsskål) Børgesen | 4 | HS | T,S,(I-P) | + | | + | |
| *Dichotomaria falcata* (Kjellman) Kurihara & Masuda | 4 | HS | T,S,( P) | + | | | |
| *Dichotomaria marginata* (J. Ellis & Solander) Lamarck | | Fl | T,S | + | | | |
| Family SCINAIACEAE | | | | | | | |
| *Scinaia japonica* Setchell | 4 | HS | T,S | + | | + | |
| *Scinaia okamurae* (Setchell) Huisman | 4 | HS | S,(P) | | | + | |
| Order BONNEMAISONIALES | | | | | | | |
| Family BONNEMAISONIACEAE | | | | | | | |
| *Asparagopsis taxiformis* (Delile) Trevisan [=*Falkenbergia hillebrandii*, Sporophytic stage of *Asparagopsis taxiformis*] | 3 | HS | T,S | + | | ++ | |
| *Bonnemaisonia hamifera* Hariot [$] [=*Trailliella intricata* Batters] | | Ez, Ep | T,S,M | ++ | | ++ | |
| Order CERAMIALES | | | | | | | |
| Family CERAMIACEAE | | | | | | | |
| *Antithamnionella longicellulata* Perestenko [$$] | | Ep | S,M,(P) | ++ | | | |
| *Centroceras clavulatum* (C. Agardh) Montagne | 1-3 | Ep,HS,Af | T,S | + | ++ | ++ | ++ |
| *Ceramium borneense* Weber-van Bosse [$] | | Ep | T,S,(I-P) | + | | | |
| *Ceramium boydenii* E.S. Gepp | | Ep | T,S,(I-P) | + | | | |
| *Ceramium cimbricum* H.E. [$] | | Ep | T,S,M | + | ++ | ++ | |
| *Ceramium tenerrimum* (G. Martens) Okamura | | Ep | T,S | + | ++ | ++ | ++ |
| *Crouania attenuata* (C. Agardh) J. Agardh | | Ep | T,S | + | | | |
| *Gayliella fimbriata* (Setchell & N.L. Gardner) T.O. Cho & S.M. Boo [$] | | Ep | T,S,(I-P) | ++ | | | |
| *Gayliella mazoyerae* T.O. Cho, Fredericq & Hommersand [$] | | Ep | T,S | ++ | | | |
| *Pleonosporium segawae* Yoshida [$] | | Ep | S,( P) | | | + | |
| Family WRANGELIACEAE | | | | | | | |
| *Anotrichium tenue* (C. Agardh) Nägeli | | Ep | T,S | ++ | | | |
| *Griffithsia japonica* Okamura | 4 | Ep ,HS | T,S,(I-P) | | | + | |
| *Wrangelia argus* (Montagne) Montagne [$] | 3 | HS | T,S | + | | ++ | |
| Family DASYACEAE | | | | | | | |
| *Dasya sessilis* Yamada [$] | 4 | HS | T,S,M | + | | + | |
| *Dasysiphonia japonica* (Yendo) H.-S. Kim [=*Heterosiphonia japonica* Yendo] | | Ep | T,S,M | ++ | | ++ | |
| *Heterosiphonia pulchra* (Okamura) Falkenberg [$] | | Ep | T,S,M | | | ++ | |
| Family DELESSERIACEAE | | | | | | | |
| *Acrosorium yendoi* Yamada [$] | 3 | HS | S,M (P) | + | | + | |
| Family RHODOMELACEAE | | | | | | | |
| *Chondria dasyphylla* (Woodward) C. Agardh [$] | 4 | HS | T,S,M | + | | | |
| *Chondria intertexta* P.C. Silva [$] | 3 | HS | T,S,(I-P) | + | | | |
| *Chondria crassicaulis* Harvey | 3 | HS | T,S,M (I-P) | | | + | |
| *Herposiphonia tenella* (C. Agardh) Ambronn | | Ep | T,S | | | ++ | |
| *Chondrophycus undulatus* (Yamada) Garbary & Harper | 2,3 | HS, Af | T,S | + | ++ | ++ | ++ |
| *Melanothamnus japonicus* (Harvey) Díaz-Tapia & Maggs [=*Polysiphonia japonica* Harvey] | | Ep | T,S,(I-P) | | | ++ | |
| *Melanothamnus yendoi* (T. Segi) Díaz-Tapia & Maggs [=*Polysiphonia yendoi* Segi] | 3,4 | Ep,HS,SS | T,S,(I-P) | + | | ++ | |
| *Laurencia okamurae* Yamada | 3, 4 | HS, Af | T,S | + | | ++ | |
| *Palisada intermedia* (Yamada) K.W. Nam [=*Laurencia intermedia* Yamada] | 2,3 | HS, Af | T,S | ++ | ++ | ++ | ++ |
| *Polysiphonia howei* Hollenberg [$] | | Ep | T,S | | | ++ | |
| *Polysiphonia scopulorum* var. *villum* (J. Agardh) Hollenberg [$] | | Ep | T,S | + | | | |
| *Polysiphonia senticulosa* Harvey [$] | | Ep | T,S,M | + | | | |
| *Symphyocladia marchantioides* (Harvey) Falkenberg | 3 | Ep,HS,Af | T,S,M | ++ | | + | |
| *Symphyocladia pumila* (Yendo) S. Uwai & M. Masuda [$] | 3 | HS, Af | S,(P) | + | | + | |

Table 1. Continued (3 of 5).

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Order GELIDIALES | | | | | | | |
| Family GELIDIACEAE | | | | | | | |
| *Gelidiophycus divaricatus* (G. Martens) G.H. Boo, J.K. Park & S.M. Boo [=*Gelidium divaricatum* G. Martens] | 1,2 | HS, Af, Ez | T,S,(I-P) | +++ | +++ | +++ | +++ |
| *Gelidium amansii* (J.V. Lamouroux) J.V. Lamouroux | 3 | HS, Af | T,S,(I-P) | | + | | ++ |
| *Gelidium elegans* Kützing [$] | 4 | HS, Af | T,S,M,(I-P) | + | + | ++ | ++ |
| *Gelidium pacificum* Okamura [$] | 3,4 | HS | S,M,(P) | | | + | |
| *Gelidium pusillum* (Stackhouse) Le Jolis [$] | 2,3 | HS, Af | T,S | ++ | | + | |
| *Ptilophora subcostata* (Okamura) R.E. Norris | 2 | HS, Af | S,(P) | + | | | |
| Family PTEROCLADIACEAE | | | | | | | |
| *Pterocladiella tenuis* (Okamura) Shimada, Horiguchi & Masuda | 3,4 | HS | T,S,M,(P) | | | ++ | |
| Order GIGARTINALES | | | | | | | |
| Family CAULACANTHACEAE | | | | | | | |
| *Caulacanthus okamurae* Yamada [$] | 2 | Ep,HS, Af | T,S,M | ++ | | | ++ |
| *Caulacanthus ustulatus* (Mertens ex Turner) Kützing [$] | 2 | Ep,HS, Af | T,S | ++ | + | ++ | |
| Family CYSTOCLONIACEAE | | | | | | | |
| *Hypnea charoides* J.V. Lamouroux | 3 | HS, Af, Fl | T,S,(I-P) | | | ++ | |
| *Hypnea spinella* (C. Agardh) Kützing [$] | 3 | HS, Af | T,S | | ++ | | + |
| *Hypnea valentiae* (Turner) Montagne [$] | 3 | Ep,HS, | T,S | | | | + |
| Family ENDOCLADIACEAE | | | | | | | |
| *Gloiopeltis complanata* (Harvey) Yamada | 2 | HS | T,S,(I-P) | | | ++ | |
| *Gloiopeltis furcata* (Postels & Ruprecht) J. Agardh | 1-2 | HS, Af | T,S,M,(I-P) | +++ | | +++ | |
| *Gloiopeltis tenax* (Turner) Decaisne | 2 | HS, Af | T,S,(I-P) | + | | ++ | |
| Family GIGARTINACEAE | | | | | | | |
| *Chondracanthus intermedius* (Suringar) Hommersand [=*Gigartina intermedia* Suringar] | 2,3 | HS, Af | T,S,(I-P) | ++ | | ++ | ++ |
| *Chondracanthus tenellus* (Harvey) Hommersand [=*Gigartina tenella* Harvey] | 2 | HS, Af | T,S,(I-P) | + | | + | |
| *Chondrus ocellatus* Holmes [$] | 3,4 | HS, Af | T,S,M | | | ++ | + |
| Family GLOIOSIPHONIACEAE | | | | | | | |
| *Gloiosiphonia capillaris* (Hudson) Carmichael | 3 | HS, Af | T,S,M | + | | | |
| Family KALLYMENIACEAE | | | | | | | |
| *Kallymenia perforata* J. Agardh | 4 | HS, Ep | T,S | + | | + | |
| Family PHYLLOPHORACEAE | | | | | | | |
| *Ahnfeltiopsis flabelliformis* (Harvey) Masuda | 3,4 | HS, Af | T,S,(I-P) | + | ++ | +++ | |
| Family RHIZOPHYLLIDACEAE | | | | | | | |
| *Portieria hornemannii* (Lyngbye) P.C. Silva | 4 | HS | T,S,(I-P) | | | + | |
| *Portieria japonica* (Harvey) P.C. Silva | 4 | HS, Af | T,S,(I-P) | + | | | |
| Order GRACILARIALES | | | | | | | |
| Family GRACILARIACEAE | | | | | | | |
| *Gracilaria parvispora* I.A. Abbott [$] | 4 | HS,SS | T,S,(P) | | | ++ | + |
| *Gracilaria vermiculophylla* (Ohmi) Papenfuss | 2-3 | HS,SS, Af | T,S,M | + | ++ | ++ | + |
| Order HALYMENIALES | | | | | | | |
| Family HALYMENIACEAE | | | | | | | |
| *Grateloupia asiatica* S. Kawaguchi & H.W. Wang [$] | 3 | HS | T,S | | | ++ | |
| *Grateloupia elliptica* Holmes [$] | 4 | HS | T,S,M,(I-P) | | | ++ | |
| *Grateloupia filicina* (J.V. Lamouroux) C. Agardh | 3 | HS, Af | T,S,M,An | ++ | | ++ | |
| *Grateloupia imbricata* Holmes [$] | 4 | HS, Af | T,S | + | | ++ | |
| *Grateloupia sparsa* (Okamura) Chiang [$] | 4 | HS, Af | S,(P) | + | | | |
| *Pachymeniopsis lanceolata* (K. Okamura) Y. Yamada ex S. Kawabata [$] | 3 | HS, Af | T,S | + | | + | |
| *Polyopes affinis* (Harvey) Kawaguchi & Wang [$] | 3 | HS, Af | T,S,(P) | ++ | | ++ | |
| Order PLOCAMIALES | | | | | | | |
| Family PLOCAMIACEAE | | | | | | | |
| *Plocamium ovicorne* Okamura [$] | 4 | HS, Ep | S,M (P) | + | | + | |

Table 1. Continued (4 of 5).

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Order RHODYMENIALES | | | | | | | |
| Family RHODYMENIACEAE | | | | | | | |
| *Rhodymenia intricata* (Okamura) Okamura [$] | 3 | HS | T,S,(P) | + | | + | |
| Family CHAMPIACEAE | | | | | | | |
| *Champia parvula* (C. Agardh) Harvey [$] | 2-4 | Ep,HS, Af | T,S,M | + | + | ++ | ++ |
| Family LOMENTARIACEAE | | | | | | | |
| *Fushitsunagia catenata* (Harvey) Filloramo & G.W. Saunders [=*Lomentaria catenata* Harvey] | 4 | HS, Af | T,S,(I-P) | ++ | | ++ | |
| *Lomentaria hakodatensis* Yendo [$] | 4 | HS, Af | T,S,M | + | | ++ | |
| OCHROPHYTA | | | | | | | |
| Class PHAEOPHYCEAE | | | | | | | |
| Order ECTOCARPALES | | | | | | | |
| Family ACINETOSPORACEAE | | | | | | | |
| *Feldmannia irregularis* (Kützing) Hamel [$] | | Ep | T,S | ++ | | | |
| *Feldmannia mitchelliae* (Harvey) H.-S. Kim [$] | 2 | HS, Af | T,S,M | ++ | ++ | | ++ |
| Family PETROSPONGIACEAE | | | | | | | |
| *Petrospongium rugosum* (Okamura) Setchell & N.L. Gardner | 2 | HS, Af | T,S,(I-P) | ++ | | ++ | |
| Family CHORDARIACEAE | | | | | | | |
| *Leathesia marina* (Lyngbye) Decaisne | 2,3 | Ep,Fl | S,M,Ar | | | ++ | |
| Family SCYTOSIPHONACEAE | | | | | | | |
| *Colpomenia bullosa* (De A. Saunders) Yamada | 3,4 | HS, Af | T,S,(I-P) | ++ | | + | |
| *Colpomenia wynnei* K.M. Lee, R. Riosmena-Rodriguez, K. Kogame & S.M. Boo [$] | 3 | HS, Af | S,(P) | ++ | | ++ | |
| *Colpomenia sinuosa* (Mertens ex Roth) Derbès & Solier | 2-4 | HS, Af | T,S,M,An | +++ | +++ | + | ++ |
| *Hydroclathrus clathratus* (C. Agardh) M. Howe | 3 | HS, Af | T,S | + | ++ | + | |
| *Myelophycus simplex* (Harvey) Papenfuss [$] | 2 | HS, Af | | ++ | | ++ | |
| *Petalonia fascia* (O.F. Müller) Kuntze | 2 | HS, Af | S,M,Ar | ++ | | + | |
| *Scytosiphon lomentaria* (Lyngbye) Link | 2,3 | HS, Af | T,S,M,An | +++ | | ++ | |
| Order RALFSIALES | | | | | | | |
| Family NEORALFSIACEAE | | | | | | | |
| *Neoralfsia expansa* (J. Agardh) P.-E. Lim & H. Kawai ex Cormaci & G. Furnari [$] | 1,2 | HS, Af | T,S | ++ | ++ | +++ | +++ |
| Order SPHACELARIALES | | | | | | | |
| Family SPHACELARIACEAE | | | | | | | |
| *Sphacelaria novae-hollandiae* Sonder [$] | | Ep | T,S | ++ | | | |
| *Sphacelaria rigidula* Kützing [$] | 2 | Ep, HS, Af | T,S,M,An | + | + | | + |
| Order DICTYOTALES | | | | | | | |
| Family DICTYOTACEAE | | | | | | | |
| *Dictyopteris prolifera* (Okamura) Okamura | 4 | HS | T,S | | | ++ | |
| *Dictyota dichotoma* (Hudson) J.V. Lamouroux | 4 | HS, Af | T,S,M,An | | | + | |
| *Dictyota coriacea* (Holmes) I.K. Wang, Hy.S. Kim & W.J. Lee [=*Pachydictyon coriaceum* (Holmes) Okamura] | 4 | HS, Af | S,(P) | + | | ++ | |
| *Lobophora variegata* (J.V. Lamouroux) Womersley ex Oliveira | 3 | Af, HS | T,S | + | | + | |
| *Padina arborescens* Holmes | 4 | HS, Af | T,S,(I-P) | | + | +, | + |
| *Padina gymnospora* (Kützing) Sonder [$] | 4 | HS | T,S | | | + | |
| Order LAMINARIALES | | | | | | | |
| Family Alariaceae | | | | | | | |
| *Undaria pinnatifida* (Harvey) Suringar | 4 | HS, Af | S,M | | + | + | + |
| Order ISHIGEALES | | | | | | | |
| Family ISHIGEACEAE | | | | | | | |
| *Ishige foliacea* Okamura | 2,3 | HS,Af | S(P) | +++ | | +++ | + |
| *Ishige okamurae* Yendo | 2, 3 | HS, Af | S(P) | | +++ | +++ | +++ |

Table 1. Continued (5 of 5).

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Order FUCALES | | | | | | | |
| Family SARGASSACEAE | | | | | | | |
| *Sargassum fusiforme* (Harvey) Setchell [=*Hizikia fusiforme* (Harvey) Okamura] | 3 | HS | T,S,(I-P) | + | | ++ | |
| *Sargassum giganteifolium* Yamada [$] | | Fl | T,S,(P) | + | | | |
| *Sargassum horneri* (Turner) C. Agardh | | Fl | T,S,(I-P) | + | | + | |
| *Sargassum macrocarpum* C. Agardh [$] | | Fl | S,(P) | + | | | |
| *Sargassum patens* C. Agardh | | Fl | T,S,(P) | | | + | |
| *Sargassum piluliferum* (Turner) C. Agardh | 4 | HS, Fl | T,S,(P) | + | | + | |
| *Sargassum thunbergii* (Mertens ex Roth) Kuntze | 3 | HS, Af | T,S | +++ | ++ | +++ | + |
| *Sargassum yamadae* Yoshida & T. Konno [$] | | Fl | S,(P) | + | | + | |
| CHLOROPHYTA | | | | | | | |
| Order CHLAMYDOMONADALES | | | | | | | |
| Family CHLOROCHYTRIACEAE | | | | | | | |
| *Chlorochytrium cohnii* E.P. Wright [$] | | En | T,S,M | ++ | | ++ | |
| Order ULOTRICHALES | | | | | | | |
| Family GOMONTIACEAE | | | | | | | |
| *Collinsiella cava* (Yendo) Printz [$] | 2 | HS, Af | T,S,(P) | + | | | |
| Family MONOSTROMATACEAE | | | | | | | |
| *Monostroma nitidum* Wittrock | 1,2 | HS, Af | T,S | +++ | | +++ | |
| Order ULVALES | | | | | | | |
| Family KORNMANNIACEAE | | | | | | | |
| *Blidingia minima* (Nägeli ex Kützing) Kylin [$] | 1 | Af | T,S,M | ++ | | | |
| Family ULVELLACEAE | | | | | | | |
| *Ulvella lens* P. Crouan & H. Crouan [$] | | Ep | T,S,M | ++ | | | |
| *Ulvella leptochaete* (Huber) R. Nielsen, C.J. O'Kelly & B. Wysor [$] | | En | T,S,M,Ar | ++ | | | |
| *Ulvella scutata* (Reinke) R. Nielsen, C.J. O'Kelly & B. Wysor [$] | | Ep | T,S,M,Ar | ++ | | ++ | |
| *Ulvella viridis* (Reinke) R. Nielsen, CJ. O'Kelly & B. Wysor[$] | | En | T,S,M,Ar,An | ++ | + | ++ | |
| Family ULVACEAE | | | | | | | |
| Percursaria percursa (C. Agardh) Rosenvinge [$] | | HS, Fl | T,S,M,Ar | ++ | | | |
| *Ulva australis* Areschoug [$] [= *Ulva pertusa* Kjellman] | 2,3 | HS, Af | T,S | + | ++ | ++ | ++ |
| *Ulva conglobata* Kjellman | 2 | HS, Af | T,S | ++ | | + | |
| *Ulva clathrata* (Roth) C. Agardh [$] | 1,2 | HS, Ep, Af | T,S,M,Ar,An | ++ | + | ++ | |
| *Ulva flexuosa* Wulfen [$] | 1-3 | HS, Af | T,S,M,Ar,An | ++ | ++ | ++ | ++ |
| *Ulva intestinalis* Linnaeus [$] | 2 | HS, Af | T,S,M,Ar,An | +++ | | ++ | ++ |
| *Ulva lactuca* Linnaeus | 2-4 | HS, Af | T,S,M,Ar | ++ | +++ | ++ | ++ |
| *Ulva linza* Linnaeus | 2 | HS, Af | T,S,M,Ar,An | ++ | | ++ | |
| *Ulva prolifera* O.F. Müller [$] | 1,2 | Ep,HS,Af | T,S,M,Ar | +++ | ++ | +++ | ++ |
| Order CLADOPHORALES | | | | | | | |
| Family CLADOPHORACEAE | | | | | | | |
| *Chaetomorpha minima* Collins & Hervey [$] | | Ep | T,S | + | | | |
| *Cladophora flexuosa* (O.F. Müller) Kützing [$] | 4 | HS, Af | T,S,M, An | | ++ | | |
| *Cladophora laetevirens* (Dillwyn) Kützing [$] | 2,3 | Ep,HS,Ez | T,S,M | | ++ | ++ | ++ |
| *Cladophora vagabunda* (Linnaeus) Hoek [$] | 3 | HS, Af | T,S,M | + | | | |
| *Rhizoclonium riparium* (Roth) Harvey [$] | 2 | HS, Af | T,S,M,Ar | + | | + | |
| Family PSEUDOCLADOPHORACEAE | | | | | | | |
| *Pseudocladophora conchopheria* (Sakai) Boedeker & Leliaert [$] | 2,3 | Ez | S,(P) | ++ | ++ | ++ | |
| Order BRYOPSIDALES | | | | | | | |
| Family BRYOPSIDACEAE | | | | | | | |
| *Bryopsis plumosa* (Hudson) C. Agardh [$] | | Af | T,S,M,Ar,An | + | | | |
| Family CODIACEAE | | | | | | | |
| *Codium cylindricum* Holmes | 4 | HS | T,S,(P) | | | + | |
| *Codium fragile* (Suringar) Hariot | 4 | HS | T,S,M | | | + | + |
| *Codium repens* P. Crouan & H. Crouan [$] | 4 | HS, Af | T,S | + | ++ | + | |

*Polyopes affinis*. By the end of April, monodominant and polydominant assemblages of green algae with the dominance of *Ulva lactuca, U. prolifera, U. intestinalis U. flexuosa* and *Codium repens* were formed on ropes constantly immersed in seawater (Fig. 5g, h).

In summer-autumn 42 species were found on underwater man-made substrates, of which 55% were reds, 21% browns and 19% greens. Marked changes in algal assemblages were observed In mid-August in the upper and middle intertidal zones (Fig 6): all previously existing assemblages (except for the monodominant assemblage of *Gelidiophycus divaricatus*) were degraded. Monodominant assemblages of a blue-green alga *Lyngbya majuscula* (Fig. 6c) occupied concrete slabs and blocks in the upper intertidal zone. The low intertidal zone was still dominated by the brown algae *Colpomenia sinuosa, Ishige foliacea and I. okamurae*, which formed multi-species assemblages (Fig. 6d). Single-standing old wooden poles and nylon ropes were overgrown with

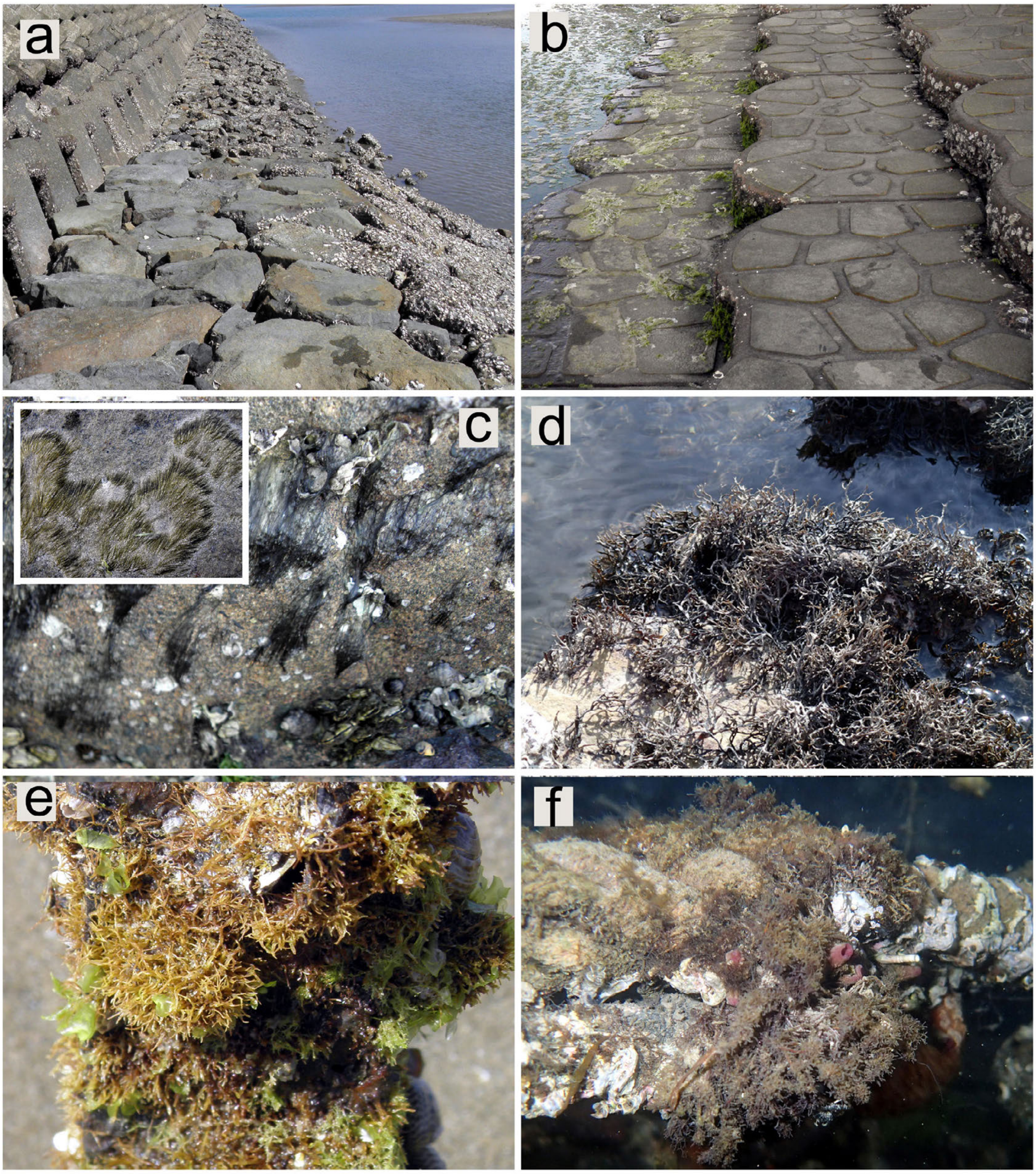


**Fig. 6** Algal assemblages on man-made substrates of Tomioka, 8-10 August 2013, at (a) site 4, and (b) site 6: (c) monodominant *Lyngbya majuscula* in the upper intertidal zone; (d) monodominant *Ishige okamurae* in the low intertidal zone; (e, f) polydominant *Gelidiophycus divaricatus, Jania ungulata, Amphiroa beauvoisii, Hypnea spinella*, and *Ulva* spp. on old wooden pole and nylon rope.

assemblages comprising *Gelidiophycus divaricatus, Jania ungulata* f. *brevior, Amphiroa beauvoisii, Hypnea spinella* and *Ulva* spp. (Fig. 6e, f).

In early October, in the port area of Tomioka Bay (sites 1-3), *Gelidiophycus divaricatus* (Fig. 7a) overgrew concrete blocks covered by *Tetraclita japonica, Chthamalus challengeri* and *Saccostrea* spp. in the upper and low intertidal zones, and concrete slabs were partly covered by young *Ulva* spp. (1-3 mm long) (Fig. 7b). Substrates exposed to the surf were occupied by a red alga *Ahnfeltiopsis flabelliformis*. An epizoic green alga *Pseudocladophora conchopheria* (Fig. 7e) was found forming a dense monodominant assemblage on an intertidal gastropod *Lunella coronatus coreensis* (Récluz, 1853) (see Osawa & Tokeshi 2018). Nylon ropes temporarily exposed to the air were covered by *Cladophora laetevirens, C. flexuosa, Ulva prolifera, U. lactuca, U. flexuosa* and *Codium repens*). The ropes constantly immersed in seawater were overgrown mainly by red coralline algae *Amphiroa beauvoisii, Amphiroa ephedraea, Jania ungulata* f. *brevior* and a green alga *U. lactuca* (Fig. 7c, d, f, g). *Hypnea spinella, Colpomenia sinuosa* and *Ishige okamurae* were also found on concrete blocks in the low intertidal and upper subtidal (Fig. 7h).

Algal assemblages on natural substrates

In winter-spring season, 113 species were found on natural substrates (sites 4-7), of these about 62% were red algae, 22% brown and 16% green. In mid April 2013, in the upper and middle intertidal zone at sites 4, 6, 7 (Fig. 1a, e, g, h), rocky substrates (Fig. 8a) were covered by a red alga *Gelidiophycus divaricatus*, green algae *Monostroma nitidum* and *Ulva prolifera*, a brown crust alga *Neoralfsia expansa* and also by assemblages of *M. nitidum* + *Gloiopeltis furcata* (Fig. 8b-e). Other common species were *Pyropia suborbiculata, Corallina pilulifera, Hildenbrandia rubra, Gloiopeltis complanata, G. tenax, Chondracanthus intermedius, Centroceras clavulatum, Chondrophycus undulatus* (Rh), *Petrospongium rugosum, Myelophycus simplex, Scytosiphon lomentaria* (Ph), *Ulva clathrata, U. intestinalis* and *U. linza* (Ch).

In the low intertidal zone, bidominant assemblages of *Ishige foliacea* + *I. okamurae* and monodominant assemblages of *Ishige okamurae* and of *Sargassum thunbergii* (Fig. 8f−h) were found. Other algal species include *Amphiroa beauvoisii, Corallina crassisima,*

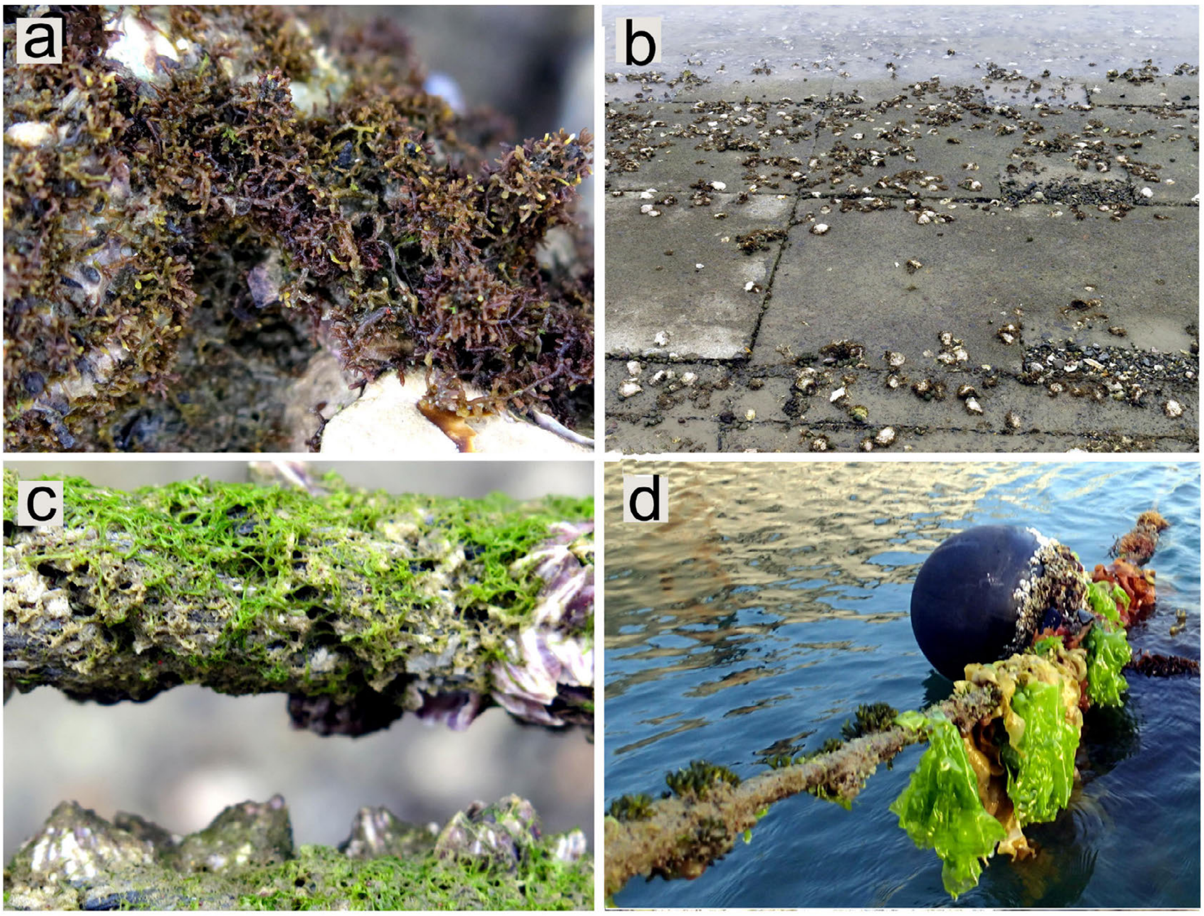


**Fig. 7a-d** Algal assemblages from Tomioka (sites 1-3, mostly man-made substrates), 8-10 October 2015: (a) monodominant *Gelidiophycus divaricatus*; (b) green algal sprouts on concrete slabs in the middle intertidal zone; (c, d) *Cladophora* spp., *Ulva* spp. and *Codium repens* on ropes temporarily exposed to air.

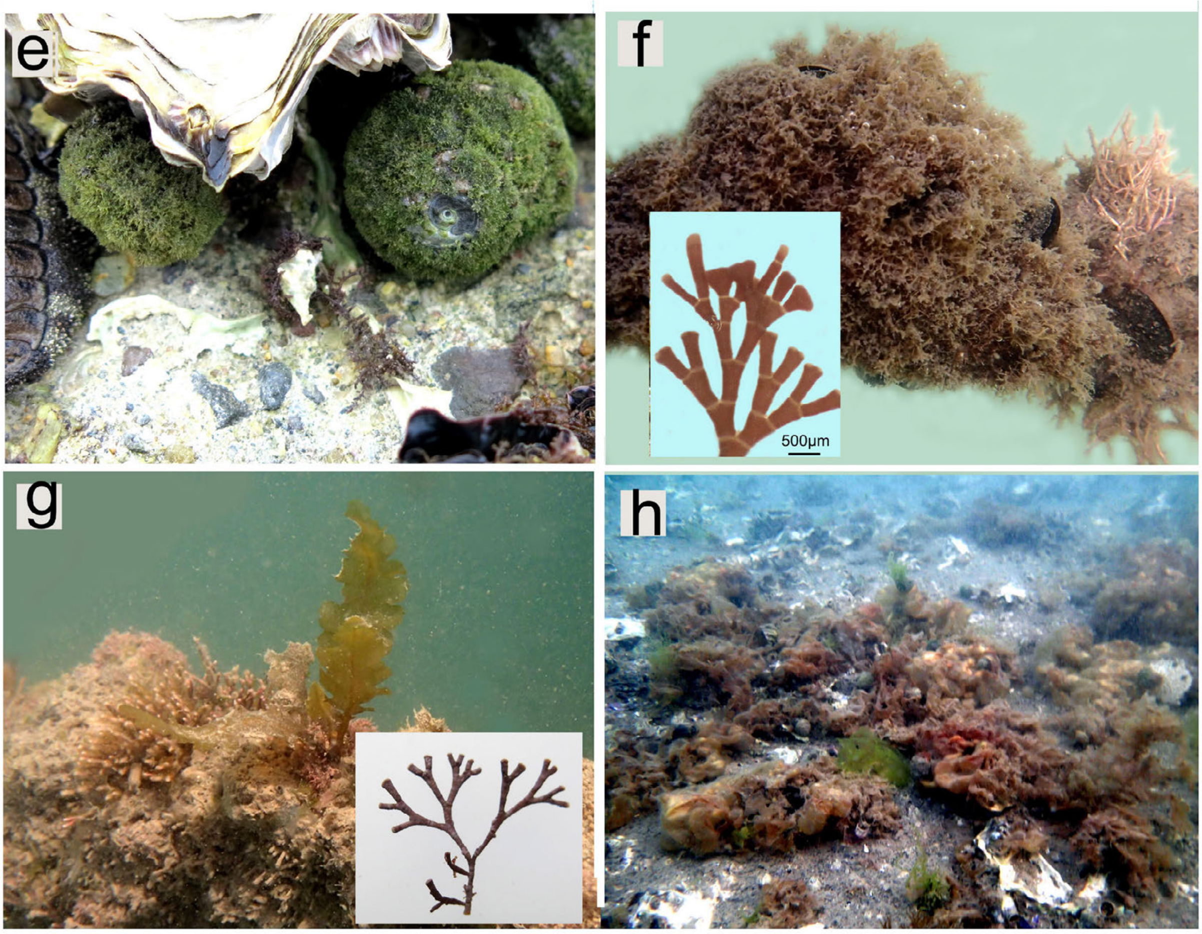


**Fig. 7e-h** Algal assemblages from Tomioka (sites 1-3), 8-10 October 2015: (e) a gastropod *Lunella coronatus coreensis* overgrown by monodominant *Pseudocladophora conchopheria*; (f, g) ropes constantly immersed in seawater covered by (f) *Jania ungulata* f. *brevior* and (g) *A. ephedraea*; (h) *Colpomenia sinuosa* on concrete blocks in the upper intertidal zone.

*C. pilulifera, Gelidium elegans, Pterocladiella tenuis, Hypnea charoides, C. intermedius, Peyssonnelia rubra, Grateloupia asiatica, G. elliptica, G. filicina, Polyopes affinis, Fushitsunagia catenata, Centroceras clavulatum, Chondrophycus undulatus, Laurencia okamurae* (Rh), *Colpomenia durvillei, S. lomentaria, Dictyopteris prolifera, Dictyota coriacea, Sargassum fusiforme* (Ph), *Ulva lactuca, U. flexuosa* and *Cladophora laetevirens* (Ch) (Table 1).

On sandy substrates in the middle part of Tomioka Bay (site 5), some species such as *Gracilaria parvispora, G. vermiculophylla* and *Neosiphonia yendoi* were attached to small shells and coarse sand grains, some algae were either not attached to the ground, or just washed in (probably detached from hard substrates).

In summer-autumn, 41 species of algae were found at site 4−7: 66% reds, 23% browns and 11% greens. On rocky substrates, algal assemblages consisted of red algae *Gelidiophycus divaricatus, Chondrophycus undulatus*, and brown algae *Neoralfsia expansa* and *Ishige okamurae* (Fig. 9a). Moreover, *Corallina pilulifera* (Fig. 9b), *Chondracanthus intermedius and Champia parvula* (Fig. 9c), *Centroceras clavulatum, Feldmannia mitchelliae* (Fig. 9d), *Ulva intestinalis* (Fig. 9e) were often observed. In the low intertidal and upper subtidal zones, patchy assemblages comprising *C. undulatus* (Fig. 9f), *I. okamurae, C. sinuosa* (Fig. 9g), *Ulva lactuca* (Fig. 9h) and *Cladophora laetevirens* predominanted on rocky substrates. On sandy substrates (site 5), *Gracilaria vermiculophylla* and *G. parvispora* which were recorded in winter were rarely found in summer-autumn.

In summer-autumn, newly-recorded species include epiphytic red algae *Colaconema daviesii, Acrochaetium robustum, Hypnea valentiae* and *Caulacanthus okamurae* growing on larger algae. On the other hand, some epiphytes common in winter-spring such as *Ceramium cimbricum, Heterosiphonia pulchra, Herposiphonia tenella, Neosiphonia howei, N. japonica* (Rh), *Leathesia marina* (Ph) and *Ulvella scutata* (Ch) were not found.

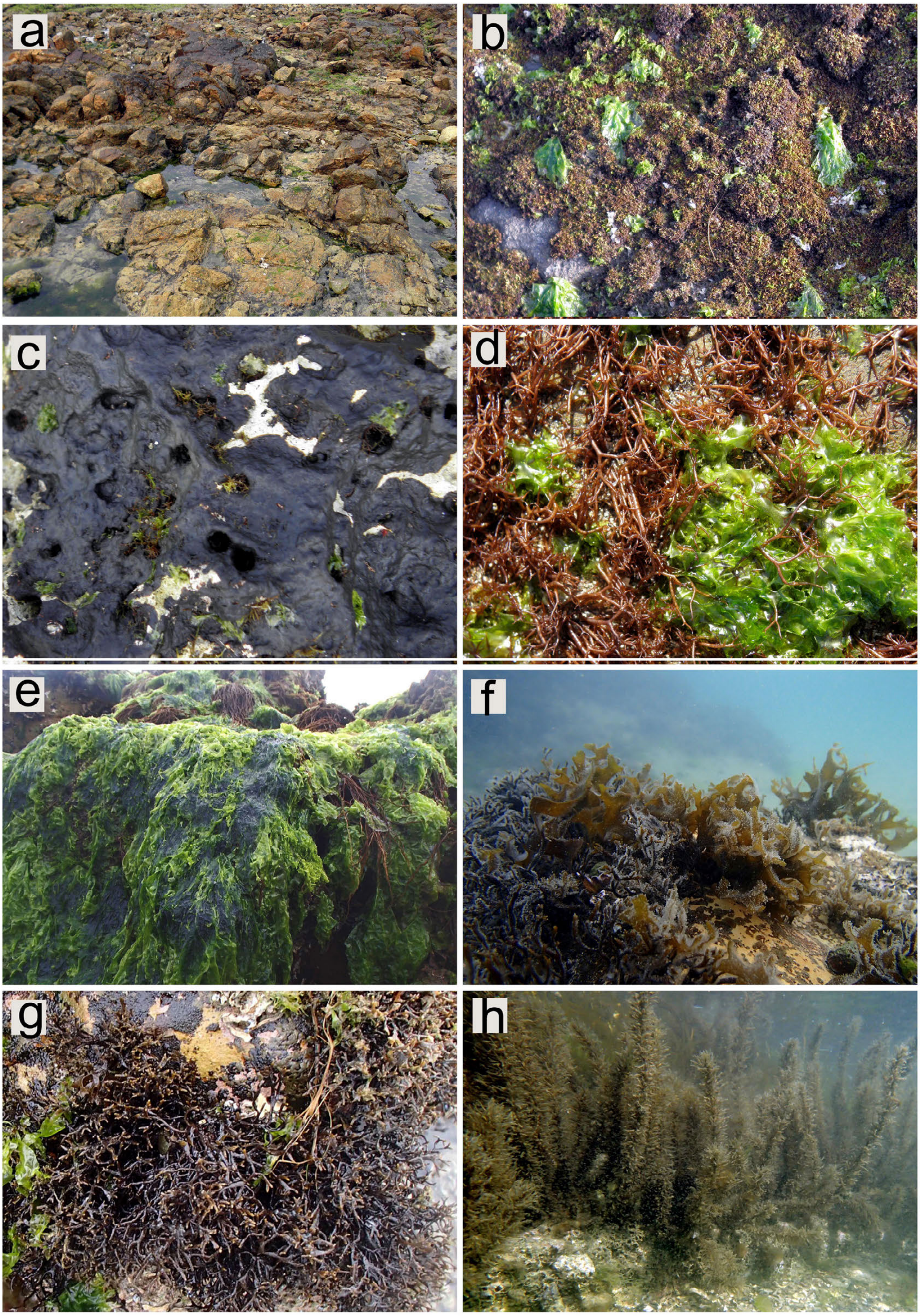


**Fig. 8** Algal assemblages on natural substrates of Tomioka (sites 4, 6, 7), 18 April 2013: (a) Rocky substrates at site 7. Assemblages in the upper and middle intertidal zones: (b) monodominant *Gelidiophycus divaricatus*; (c) a brown crust alga *Neoralfsia expansa*; (d) bidominant *Monostroma nitidum* + *Gloiopeltis furcata*; (e) monodominant *M. nitidum*. Assemblages of the low intertidal and upper subtidal zones: (f) bidominant *Ishige foliacea* + *I. okamurae*, and monodominant assemblage of (g) *I. okamurae* and of (h) *Sargassum thunbergii*.

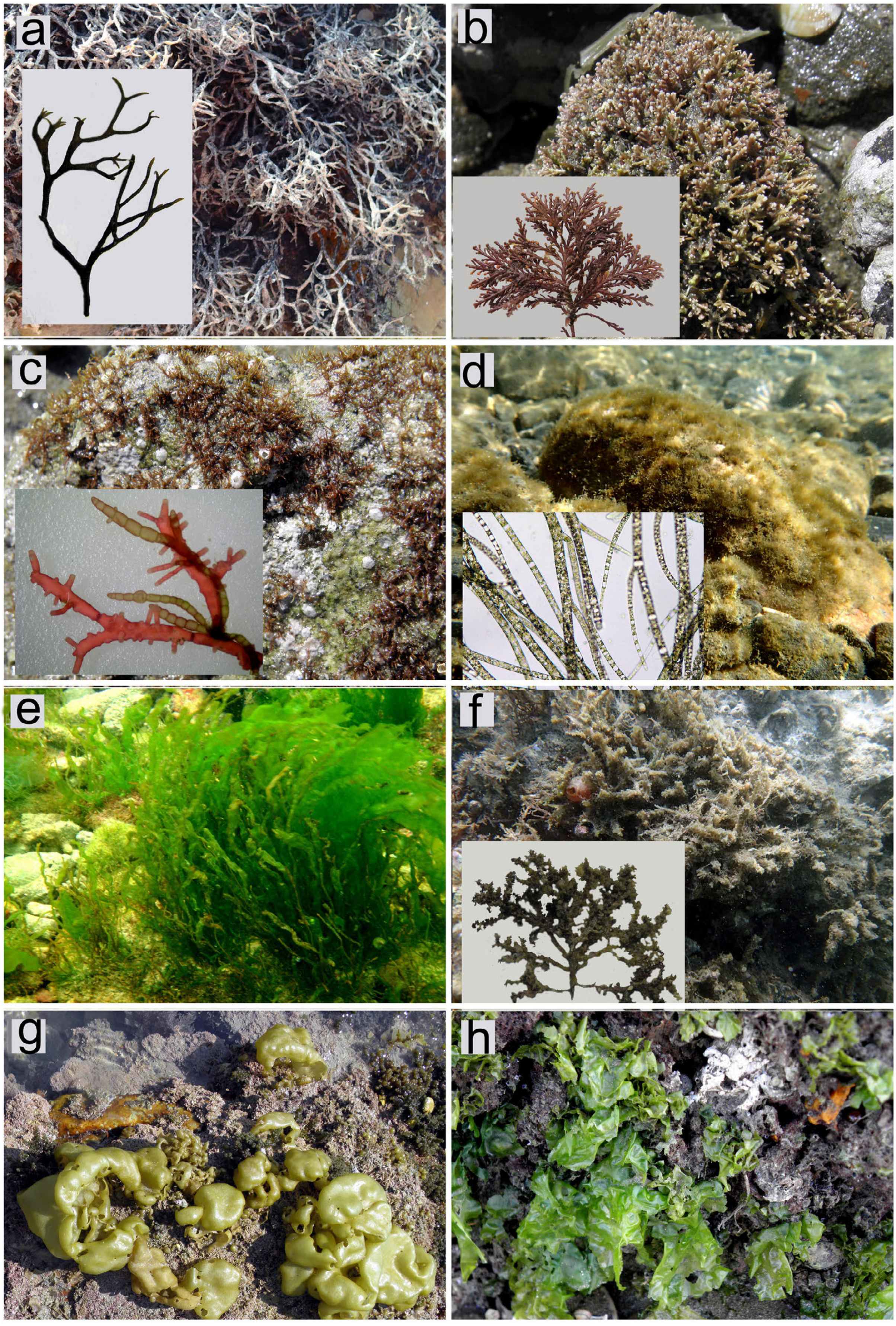

**Fig. 9** Algal assemblages on natural substrates of Tomioka (sites 4-7), August 2013: (a) monodominant *Ishige okamurae*; (b) monodominant *Corallina pilulifera*; (c) bidominant *Chondracanthus intermedius* + *Champia parvula* (insert: *C. parvula* epiphytic on *Amphiroa foliacea*); (d) monodominant *Feldmannia mitchelliae*; (e) monodominant *Ulva intestinalis*; (f) *Chondrophycus undulatus*; (g) *Colpomenia sinuosa*; (h) *Ulva lactuca* in polydominant assemblage.

## DISCUSSION

### Species diversity

The present study documents a total of 153 species of red, brown and green marine algae from the Tomioka Bay, AmakusaShimoshima Island. The Phylum Rhodophyta comprised 17 orders, 32 families, 61 genera and 95 species (62% of all species). Ochrophyta comprised 7 orders, 10 families, 17 genera and 31 species (20% of all species) and Chlorophyta comprised 5 orders, 9 families, 13 genera and 27 species (18% of all species). The ratio of numbers of red algal species to brown algal species (R:P index, Feldmann, 1937) was 3.1 and the ratio of red and green algae to brown ones (R+C)/P (Cheney 1977) = 3.9.

All species of our collection earlier were found in the tropical or subtropical regions of the world ocean (Guiry & Guiry 2017). About half of the species of our collection belong to the Indo-Pacific flora; the others inhabit also the Atlantic Ocean. In Amakusa we did not find any alien species from other biogeographic regions. One of the floristic features of the Tomioka Bay in comparison with other, more southern localities in the western Pacific such as Hainan Island (Titlyanova *et al*. 2014) and islands of the Ryukyu Archipelagoes (Okinawa, Miyako, Ishigaki, Iriomote and Yonaguni (Titlyanov *et al*. 2016b)) is the presence of cosmopolitan taxa which are distributed from tropics to temperate zones and sometimes to Arctic and Antarctic. The occurrence in Amakusa of red and brown algae such as *Corallina pilulifera, Antithamnionella longicellulata, Dasya sessilis, Chondria dasyphylla, Gloiopeltis furcata, Gracilaria vermiculophylla, Ahnfeltiopsis flabelliformis*, *Lomentaria hakodatensis* (Rh), *Leathesia marina, Scytosiphon lomentaria* and *Undaria pinnatifida* (Ph) confirm the point.

The present study indicates that the marine flora of the Tomioka Bay is characteristic of subtropical water of the Indo-Pacific where algal assemblages consist of 50−60% Rhodophyta, 20−30% Chlorophyta and 10−20% Phaeophyceae with R:P = 3.0-5.0 and (R+C)/P = 4.0−6.0 (Womersley 1981; Lewis & Norris 1987; Silva *et al*. 1987, 1996; Silva 1992; Zhang 1996; Tsuda 2006; Huisman & Borowitzka 2003). The present data indicate that the recent flora of the northwestern part of the Amakusa Island group belongs to the Indo-west Pacific tropical region, which is characterized by high species diversity and an effective geographical isolation in comparison with other biogeographic regions of the Pacific, Indian and Atlantic oceans (survey, Lüning 1990).

### Possible long-term changes in the flora of Tomioka Bay

The benthic marine flora of Amakusa was studied in the late 1950s (around the Amakusa Marine Biological Laboratory, Kyushu University at 6 sites including the Tomioka Bay) by Segawa & Yoshida (1961). Their collections included a total of 202 species, of which 56% were reds, 30% browns and 14% greens, which would yield values of R:P and (R+C)/P indices as 1.8 and 2.3, respectively. According to the literature (Cheney 1977; Luning 1990) R:P and (R+C)/P indices in the range 1.0−2.0 and 3.0−4.0, respectively, are characteristic of the flora of cold waters in temperate latitudes. A large difference in the measured indices between the early collection of S. Segawa and T. Yoshida and our collection (R:P = 3.1; (R+C)/P = 3.9) gives us reason to emphasise changes in the species composition of benthic algae of the island that have occurred over the last 60 years. These changes were in the direction of flora enrichment with green algae and probably with a decrease in brown algae. It is also confirmed by the composition of taxonomic groups among new findings (84 taxa) in our collection where red algae amounted to 61%, green algae 26%, and brown algae only 13% (Table 1). In addition, C:P and (C+R)/P indices were 2.0 and 6.7, respectively.

Thus, it is reasonable to suggest that over the last 60 years, the benthic flora of Tomioka Bay has undergone changes in species composition through the settlement of warm-water species of red and green algae and a decrease of cold-water brown algae. Probably this shift in taxonomic composition towards an increased number of warm-water red and green algae is associated with climate warming. Hawkins *et al*. (2008) postulated that the most probable effect of ocean warming on coastal marine flora is the spread of tropical seaweeds into colder regions of temperate latitudes. This seems to fit the observed situation in Amakusa, which is located to the north of the Indo-west Pacific tropical region. It should be noted, however, that this suggestion of decadal changes in the marine flora of the Amakusa Islands may require further confirmation based on more data.

### Spatio-temporal variability in algal communities

It is notable that similar numbers and compositions of algae were observed in shallow areas inside and outside the fishing port, with the majority of predominant species being common in the two localities. The largest number of algae was found on rocky natural substrates and on rocky-cement blocks of underwater constructions of the port (c. 70% of all found). On these subtidal substrates, mosaic, multi-species assemblages of annual and perennial algae were formed. At the same time, in the upper and mid intertidal, mono- and bidominant assemblages of algae-ephemerals were observed. Temporary communities of green algae-ephemerals also occurred on intertidal mooring plastic ropes and polydominant assemblages of annual and perennial algae on subtidal ropes.

Overall, no marked differences in species diversity and composition of algae were noted between man-made underwater concrete constructions of the port and natural substrates of the Tomioka Bay, suggesting that natural and artificial hard substrates both offer appropriate habitats for algal spore settlement and growth.

Species richness or the number of species increased (nearly doubled) from the upper/mid intertidal zone to the low intertidal and the upper subtidal zones. While information is scarce for subtropical and tropical algal communities on hard natural substrata (Lüning 1990), similar results were obtained in the southern part of Hainan Island (Sanya Bay) where species richness was found to increase 1.7 times from the middle to the low intertidal zone (Titlyanov *et al*. 2014a, b). It has been suggested that the intertidal zone is populated only by algal species tolerant of strong light (visible and ultraviolet), extremely high temperatures, desiccation and desalination (Lüning 1990). Interestingly, in heavily polluted waters of the Sanya Bay, Hainan, species diversity of algae in the middle intertidal zone was enhanced by accumulating mud and sand that frequently covered algae and their spores, thus insulating them from adverse conditions (Titlyanov *et al*. 2014a).

Our study clearly showed seasonal variation in algal assemblages, with a markedly higher number of species in winter-spring than in summer-autumn. Lüning (1990) suggested that sesonal changes in the benthic flora of tropical and subtropical regions could result from monsoon-caused periodic changes in the external conditions: water and air temperatures, salinity, sedimentation and force of waves and currents. Hovewer, our previous work in Hainan Island (Titlyanov *et al*. 2014a, b) and the present one in Amakusa showed that not all seasonal changes in the marine flora depend on monsoons. Indeed, in the intertidal zone, marine plants are exposed to rapid changes in environmental factors resulting in partial or complete algal replacement. As has been shown, the greatest number of species occurs in winter-spring, which may be enhanced by the disturbances associated with seasonal gale-force winds (probably favourable for the growth of ephemeral and epiphytic algae). This, however, may require confirmation based on further data collection and analysis.

**Acknowledgements**

We are grateful to Drs. Seiji Arakaki, NiNi Win and Yumiko Osawa of the AMBL - Kyushu University for various forms of support, especially during the first two authors' stay in Amakusa.

**References**

Anggadiredja JT (1998) Seaweed diversity on the Warambadi Seashore Sumba Island: Substrata and seasonal phenomenon. Prosiding Seminar Riptek Kelautan Nasional, 68–77.

Ateweberhan M, Bruggemann JH & Breeman AM (2006) Effects of extreme seasonality on community structure and functional group dynamics of coral reef algae in the southern Red Sea (Eritrea). Coral Reefs 25, 391–406.

Cheney DF (1977) R and C/P, a new and improved ratio for comparing seaweed floras. Journal of Phycology, 13 (Supplement), 12.

Costa OSJr, Attrilla MJ, Pedrinib AG & De-Paulab JC (2002) Spatial and seasonal distribution of seaweeds on coral reefs from southern Bahia, Brazil. Botanica Marina 45, 346–355.

Feldmann J (1937) Recherches sur la vegetation marine de la Mediterranée. La côtes des Albères. Revue Algologique 10, 1–33.

Guiry MD & Guiry GM (2017) AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. Available at: http://www.algaebase.org (accessed 19 July 2017).

Haraguchi H & Sekida S (2008) Recent changes in the distribution of Sargassum species in Kochi, Japan. Kuroshio Science 2(1), 41–46.

Hawkins SJ, Moore PJ, Burrows MT, Poloczanska E, Mieszkowska N, Herbert RJH, Jenkins SR, Thompson RC, Genner MJ & Southward AJ (2008) Complex interactions in a rapidly changing world: responses of rocky shore communities to recent climate change. Climate Research 37, 123–133.

Huang H, Li XB, Titlyanov EA, Ye C, Titlyanova TV, Guo YP & Zhang J (2013) Linking macroalgal $\delta^{15}$N-values to nitrogen sources and effects of nutrient stress on coral condition in an upwelling region. Botanica Marina 56 (5-6), 471–480.

 

Huisman JM & Borowitzka MA (2003) Marine benthic flora of the Dampier Archipelago, Western Australia. In Wells FE, Walker DI & Jones DS (eds) The marine flora and fauna of Dampier, Western Australia. Perth: Western Australian Museum, pp. 291–344.

Kennish R. (1996) Diet composition influences the fitness of the herbivorous crab Grapsus albolineatus. Oecologia 105, 22–29.

Lewis JE & Norris JN (1987) A history and annotated account of the benthic marine algae of Taiwan. Smithsonian Contributions to the Marine Sciences 29, 1–38.

Li X, Titlyanov EA, Zhang J, Titlyanova TV, Zhang G & Huang H (2016) Macroalgal assemblage changes on coral reefs along a natural gradient from fish farms in southern Hainan Island. Aquatic Ecosystem Health & Management 19(1), 74–82.

Lüning K (1990) Seaweeds: their environment, biogeography and ecophysiology. New York: John Wiley & Sons.

McCook LJ, Jompa J & Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19, 400–417.

Osawa Y & Tokeshi M (2018) *Lunella* shell damages and epibionts: what are interspecific relations? Coastal Ecosystems 5, 1-13.

Perestenko LP (1980) Algae of Peter the Great Bay. Leningrad: Nauka.

Saunders GW & Hommersand MH (2004) Assessing red algal supraordinal diversity and taxonomy in the context of contemporary systematic data. American Journal of Botany 91, 1494–1507.

Segawa S & Yoshida T (1961) Fauna and flora of the sea around the Amakusa Marine Biological Laboratory. Part III. Marine algae. Tomioka, Reihokucho-cho, Amakusa Kumamoto-ken, Japan [In Japanese], 24 pp.

Silva PC (1992) Geographic patterns of diversity in benthic marine algae. Pacific Science 46, 429–437

Silva PC, Basson PW & Moe RL (1987) Catalog of the benthic marine algae of the Philippines. Smithsonian Contributions to the Marine Sciences 27, 1–179.

Silva PC, Basson PW & Moe RL (1996) Catalogue of the benthic marine algae of the Indian Ocean. University of California Publications in Botany 79, 1–1259.

Su SW, Chung IC & Lee TM (2009) Temporal dynamics of rockyshore macroalgal assemblage structures in relation to coastal construction threats in Orchard Island (Taiwan): impacts of turbidity and nutrients on the blooms of *Galaxaura oblongata* and a red alga-spong symbiose *Ceratodictyon/Haliclona*. Kuroshio Science 3, 63–80.

Thakur MC, Reddy CRK & Jha B (2008) Seasonal variation in biomass and species composition of seaweeds stranded along Port Okha, northwest coast of India. Journal of Earth System Science 117, 211–218.

Titlyanov EA, Titlyanova TV (2013) Algal fouling of underwater structures at lobster farms in Nhatrang Bay (Vietnam). Russian Journal of Marine Biology 39(5), 321–330.

Titlyanov EA, Titlyanova TV (2014) Marine fouling plants in Dalian and Bayuquan seaports (China). In Adrianov AV, Lutaenko KA & Sun X-X (eds) Marine Biodiversity and Ecosystem Dynamics of the Northwest Pacific Ocean. Science Press: Beijing, pp. 201–209.

Titlyanova TV, Titlyanov EA & Kalita TL (2014) Marine algal flora of Hainan Island: a comprehensive synthesis. Coastal Ecosystems 1, 28–53.

Titlyanov EA, Titlyanova TV & Belous OS (2015) Checklist of the marine flora of Nha Trang Bay (Vietnam, South China Sea) and decadal changes in the species diversity composition between 1953 and 2010. Botanica Marina 58(5), 367–377.

Titlyanov EA, Titlyanova TV, Xia BM & Bartsch I (2016a) Retrospective Analysis of Diversity and Species Composition of Marine Macroalgae of Hainan Island (China) Ocean Science Journal 51(3), 1. Available online at http://link.springer.com −22 http://dx.doi.org/10.1007/s12601-016-

Titlyanov EA, Titlyanova TV, Kalita TL & Tokeshi M (2016b) Decadal changes in the algal assemblages of tropical-subtropical Yonaguni Island in the western Pacific. Coastal Ecosystems 3, 16–37.

Titlyanov EA, Titlyanova TV, Pham VH (2016c) Marine plant fouling of submerged surfaces of lobster farms in Nha Trang Bay (Vietnam). In Adrianov AV & Lutaenko KA (eds.) Biodiversity of the western part of the South China Sea. Vladivostok, Dalnauka, Chapter 9, pp. 449–480.

Titlyanov EA, Titlyanova TV, Huang H & Li XB (2014a) Seasonal changes in benthic algal communities of the upper subtidal zone in Sanya Bay (Hainan Island, China). Journal of Marine Biological Association UK 94(1), 51–64.

Titlyanov EA, Titlyanova TV, Li XB, Hansen GI & Huang H (2014b) Seasonal changes in the intertidal algal communities of Sanya Bay (Hainan Island, China). Journal of Marine Biological Association UK 94(5), 879–893.

Tsuda RT (2006) Checklist and bibliography of the marine benthic algae within Chuuk, Pohnpei, and Kosrae States, Federated States of Micronesia. Honolulu, HA: Bishop Museum Pacific Biological Survey, 43 pp.

Womersley HBS (1981) Biogeography of Australasian marine algae. In Clayton MN & King RJ (ed.) Marine botany an Australasian perspective. Longman Cheshire, Melbourne, pp. 292–307.

Zhang S (1996) The species distribution of the seaweeds in the coast of China seas. Chinese Biodiversity 4, 139–144 [In Chinese].

Zvyagintsev AYu (2005) Marine fouling in the northwestern part of the Pacific Ocean. Vladivostok, Dalnauka.

Published: 15 June 2019