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Eduard A. Titlyanov[1], Tamara V. Titlyanova[1], Tatyana L Kalita[2], Mutsunori Tokeshi[3]

[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, Kyushu University, Reihoku-Amakusa, Kumamoto 863-2507, Japan

Corresponding author: M Tokeshi, e-mail: tokeshi@ambl-ku.jp

Abstract

Changes in the benthic algal assemblages of a species-rich tropical/subtropical island were analysed using data from two extensive surveys conducted 78 years apart, one in spring 1935 and the other in spring 2013. A total of over 200 taxa of red, brown and green algae were recorded from the intertidal and the upper subtidal of two localities (Sonai and Higawa, the same sites in two surveys) on Yonaguni Island in the western Pacific. Algal assemblages underwent apparent changes in diversity and taxonomic composition from 1935 to 2013: (1) increase in total species richness; (2) decline in R:P values (i.e. the ratio of red vs brown algal species); (3) appearance/disappearance of species, but with no noticeable increase in eutrophication-indicating species. Species found in both 1935 and 2013 amounted only to a third of all recorded species. Appearance of new algal species in 2013 concerned Rhodophyta families - Rhodomelaceae, Corallinaceae and Ceramiaceae, and Chlorophyta families - Cladophoraceae and Ulvaceae, while disappearances were among Liagoraceae, Rhodomelaceae, Galaxauraceae (Rhodophyta), Caulerpaceae and Boodleaceae (Chlorophyta). In addition, epiphytic, opportunistic and cosmopolitan taxa expanded the floristic list of 2013. Analysis involving the multidimensional scaling ordination of similarity values clearly indicated large temporal variation in algal assemblages, which was considered to be associated with natural catastrophes, in particular the coral bleaching event of 1998.

Keywords: marine flora, long-term changes, coral reefs, disturbance events, anthropogenic impacts

Introduction

There has been an increasing body of literature indicating long-term changes in shallow-water algal assemblages in different regions of the world, which point to the influence of anthropogenic factors such as pollution of seawater and destruction of coastal environments on the diversity, composition and production of marine algae (e.g., Munda 1993; Piriz *et al*. 2003; Kinzie 2008; Barrett *et al*. 2009; Mumby, 2009; Titlyanov *et al*., 2011b). Studies on long-term changes are important as algal assemblages are susceptible to both large and small scale phenomena including global warming, acidification of the world's seas, storms, tsunamis, and elevated seawater temperatures (e.g., Schories *et al*.1997; Sagarin *et al*. 1999; Bartsch & Kuhlenkamp 2000; Hiscock *et al*. 2004; Schiel *et al*. 2004; Lima *et al*. 2006; Tribolett & Vroom 2007; Haraguchi & Sekida 2008; Hawkins *et al*. 2008; Vroom & Timmers 2009; Schutte *et al*. 2010). However, there is a dearth of reliable records of algal assemblages that date back over 50 years, particularly from species-rich waters of tropical-subtropical Indo-Pacific. In addition, there are often practical difficulties in carrying out long-term studies on marine flora due to the lack of control localities without anthropogenic impacts and the need for precisely matching the habitat (substrate) type(s) and the season(s) for sampling. As algal assemblages greatly vary in different microhabitats and across seasons, a comparative study encompassing widely-separated sampling occasions would require a careful 'matching' to make it meaningful.

In our earlier study of long-term changes in the Chlorophyta assemblages of the Hainan Island,China, in the tropical western-Pacific (Titlyanov *et al*. 2011b), drastic changes in flora seemed to have occurred between the 1930s and the 1990s due mainly to the destruction (degradation) of coral reefs. However, the question as to which factor(s), anthropogenic and/or natural, caused coral reef degradation remained unresolved.

In the present study, we investigated long-term changes in the algal assemblages of Yonaguni Island in the tropical/ subtropical western-Pacific, which have been relatively free from apparent anthropogenic influences. The main objective is to compare the records of shallow-water algal assemblages using sets of comprehensive survey data taken 78 years apart and to highlight the changes in flora with reference to global and local environmental changes.

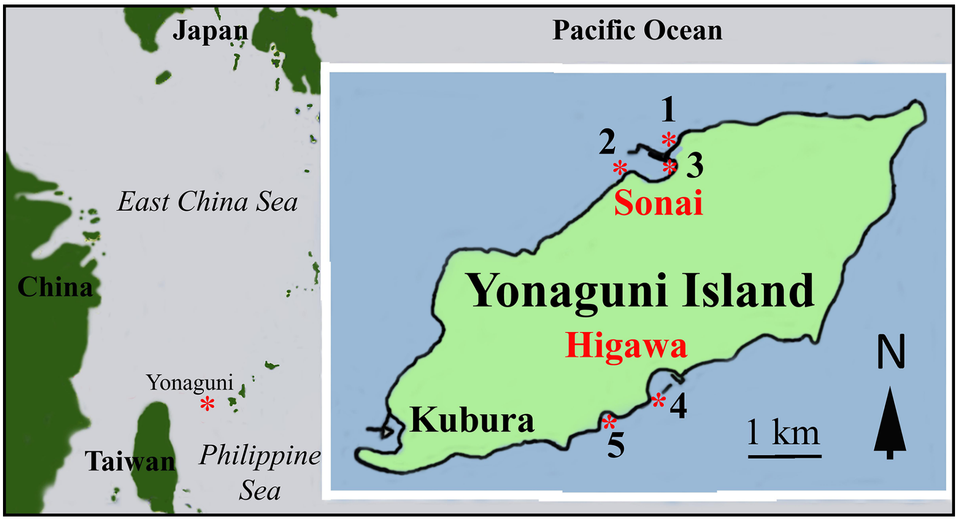

Fig. 1 Collection sites on Yonaguni Island, Japan.

Materials and Methods

Study area and algal collections

Yonaguni Island (24°27'N, 122°57'E) is located at the tropical northern periphery of the Indo-Pacific Ocean between the East China Sea and the Philippine Sea, 110 kilometers off the east coast of Taiwan (Fig. 1). The island is the most western point of Japan with an area of 28.88 km^2 with 27.5 km coastline and a population of around 1700 (density 58 km^{-2}). This region has a humid subtropical climate with a very warm summer and mild winter, with the mean summer/ winter temperature of 27.9°C and 18.2°C, respectively. Precipitation (annual mean of 2400 mm) is distributed throughout the year with the highest amount in September to November, accompanied by frequent typhoons (July to September).

The annual mean sea surface temperature (SST) is 26°C with an average seasonal range of 7-8°C. The spring and neap tidal ranges are about 2.0 m and 0.5 m, respectively

(Nohara 1970; Iryu *et al*. 1995). Yonaguni Island is strongly influenced by the Kuroshio Current (North Pacific Current), which originates in the eastern waters of Luzon Island, the Philippines, and flows northward into the East China Sea, through the Taiwan Strait (the strait between Taiwan and Yonaguni-jima) (Iryu *et al*. 1995).

Between 1935 and 2013 three expeditions were undertaken to investigate the algal flora of Yonaguni. The first collection was performed by Yukio Yamada and Takeshi Tanaka in the spring of 1935 at three localities: Sonai, Pinai (Higawa) and Kubura (Yamada & Tanaka 1938), the second additional sampling was performed in October-November 1959 by Takeshi Tanaka and Hiroshi Itono at seven localities: Sonai, Hikawa (Higawa), Kubura, Nurugan, Oodomari, Higashizaki and Urano (Tanaka & Itono 1972). A third collection was performed in March 2013 by Eduard Titlyanov and Tamara Titlyanova at two localities: Sonai and Higawa, i.e. the same localities described by Yamada & Tanaka (1938). The 2013 collection was curated and deposited at the A.V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences.

In the 2013 survey marine algae were collected from intertidal and shallow subtidal zones (up to 3 m) at five sites: Sonai - site 1 (coral reef substrates, Fig. 2), site 2 (rocky substrates, Fig. 3), site 3 (rocky substrates and concrete seaport constructions, Fig. 4); Higawa - site 4 (coral reef substrates, Fig. 5), site 5 (coral reef and soft substrates, Fig. 6).

Floristic analysis

All available data on marine macroalgal collections of 1935 and 2013 were compiled and integrated into a single table. The systematics and nomenclature followed Guiry & Guiry (AlgaeBase, http://www.algaebase.org; searched since 2013 and rechecked in 2016 for the present study).

Samples of the 2013 collection were identified using monographic publications, floristic studies and systematic articles by Okamura 1896, 1934; Yamada 1934, 1938, 1950; Tanaka 1936, 1941, 1956, 1960; Tseng 1936, 1938, 1983; Börgesen 1940; Egerod 1952; Dawson 1954, 1956; Segawa 1956; Taylor 1960; Durairatnam 1961; Kamura 1963;

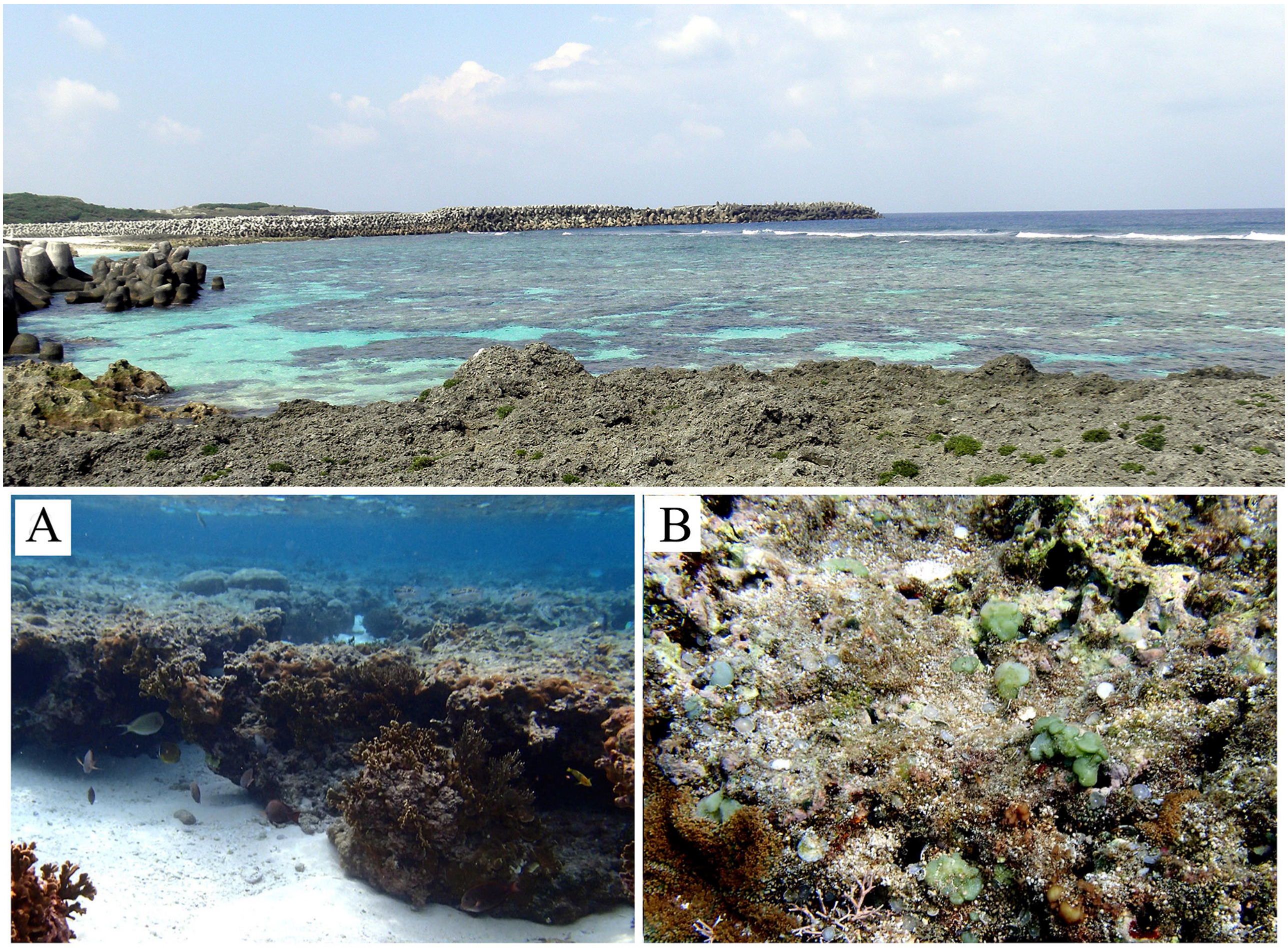

Fig. 2 Sonai, site 1 (24°28’25”N; 123° 0’13”E), lagoon of coral reef. Inset: A – patch reefs; B – An upper subtidal algal turf community with the green alga *Dictyosphaeria cavernosa* on dead colonies of hermatypic corals.

Segawa & Kamura 1960; Arasaki 1964; Trono 1968; Pham 1969; Itono 1972, 1973, 1986; Akatsuka 1973; Chiang 1962, 1973, 1997; Reyes 1976; Vinogradova 1979; Ohba & Aruga 1982; Womersley 1984; Srimanobhas *et al*. 1990; Tsuda & Kamura 1991; Kobara & Chihara 1992; Wynne 1993, 1995; Iryu *et al*. 1995; Yamaguchi & Masuda 1997; Yoshida 1998; Littler & Littler 2000, 2003; Shimada & Masuda 2000, 2002; Shimada *et al*. 2000; Leliaert & Coppejians 2003; Abbott & Huisman 2004; and Dawes & Mathieson 2008.

Changes in algal assemblages were analysed by comparing the floristic compositions in 1935 and 2013. Collections of 1935 and 2013 were comparable, as both covered (1) Sonai and Higawa sites (Fig. 1) (2) spring season, (3) intertidal to shallow subtidal zones, (4) all available habitats (coral reefs, rocky and sandy habitats, and concrete surfaces of seaport/offshore constructions). For examining changes in the proportions of different algal groups, the R:P index (ratio of the numbers of red algal species to brown algal species in a given flora, Feldmann, 1937) was calculated. Floristic similarity was analyzed using the two-dimensional non-metric multidimensional scale (n-MDS) ordination, with time periods as samples and species as variables (PRIMER v 6.0; presence/absence data; Bray-Curtis similarity). Additionally, a cluster analysis was performed on the same dataset (group average with Bray-Curtis similarities). Resulting maximum percentage similarity lines were overlaid on the n-MDS plot.

Results

Two surveys 78 years apart (1935 and 2013) resulted in a total record of 206 taxa of Rhodophyta, Phaeophyceae, Chlorophyta being identified from the intertidal and upper subtidal zones of two localities (Sonai and Higawa) on Yonaguni Island (Table 1). The algal collection of 1935 comprised 102 species and forms (Yamada & Tanaka, 1938), while the collection of 2013 comprised 172 species. In the 1935 collection, 57 species (56% of all taxa) were Rhodophyta, 8 species (8%) Phaeophyceae and 37 species (36%) Chlorophyta; in the 2013 collection, 95 species (55%) were Rhodophyta, 18 species (11%) Phaeophyceae and 59 species (34%) Chlorophyta.

Among red algae the Family Rhodomelaceae was predominant in both 1935 (16 species or 29% of all red algae) and 2013 (25 species, 25%), followed by Galaxauraceae (6 species, 10%) and Liagoraceae (5 species, 9%) in 1935 and Coralinaceae (15 species, 15%) and Ceramiaceae (11 species, 11%) in 2013. Among green algae, predominant families in the 1935 collection

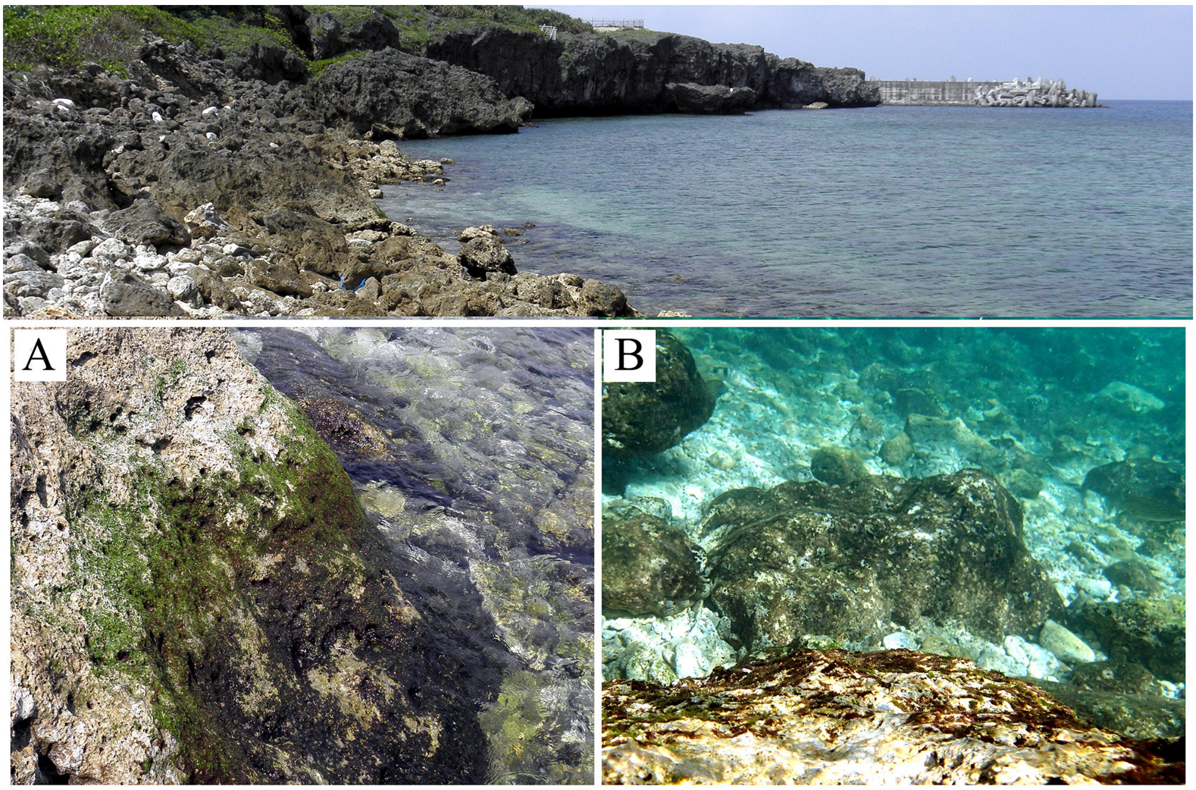

Fig. 3 Sonai, site 2 (24°28'16"N; 122°59'55"E), coast made of fossil corals and rare stones. Inset: A − mid-intertidal community of algal turf with the dominance of *Ulva pertusa* and *Gelidium pusillum*. B − turf algae in the middle and low intertidal zones.

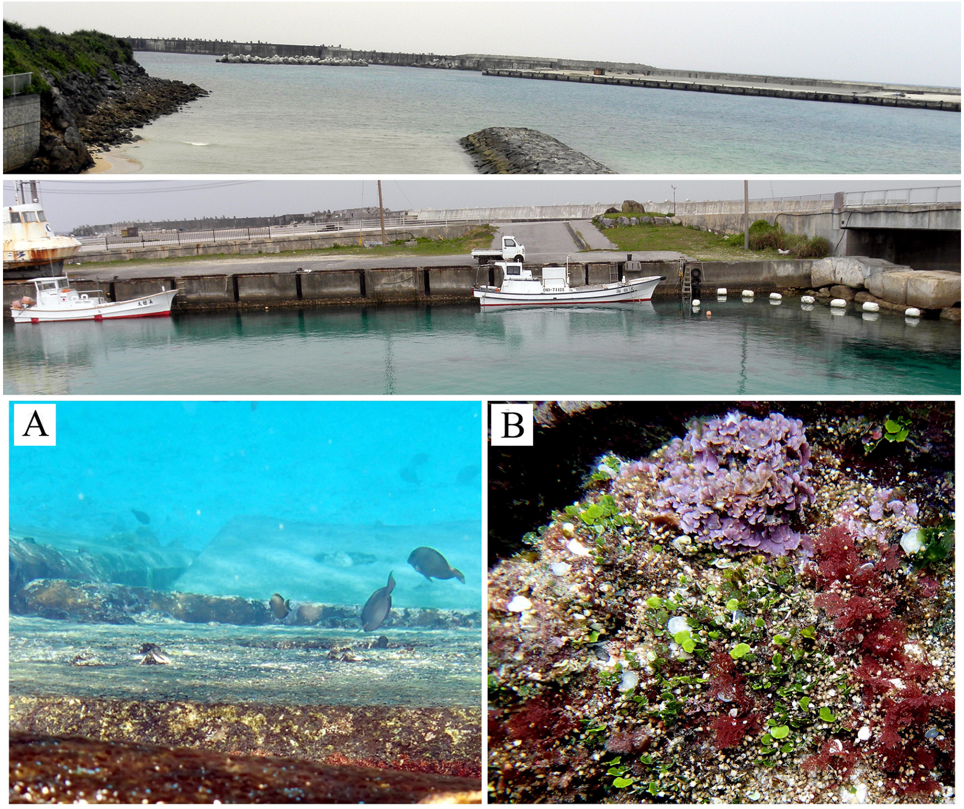

Fig. 4 Sonai, site 3 (24°28'19"N, 123°10"E), seaport. Inset: A − algal fouling on concrete seaport constructions; B − the upper subtidal turf community with the green alga *Halimeda velasquezii* and the red algae *Portieria hornemannii* and *Mastophora rosea*.

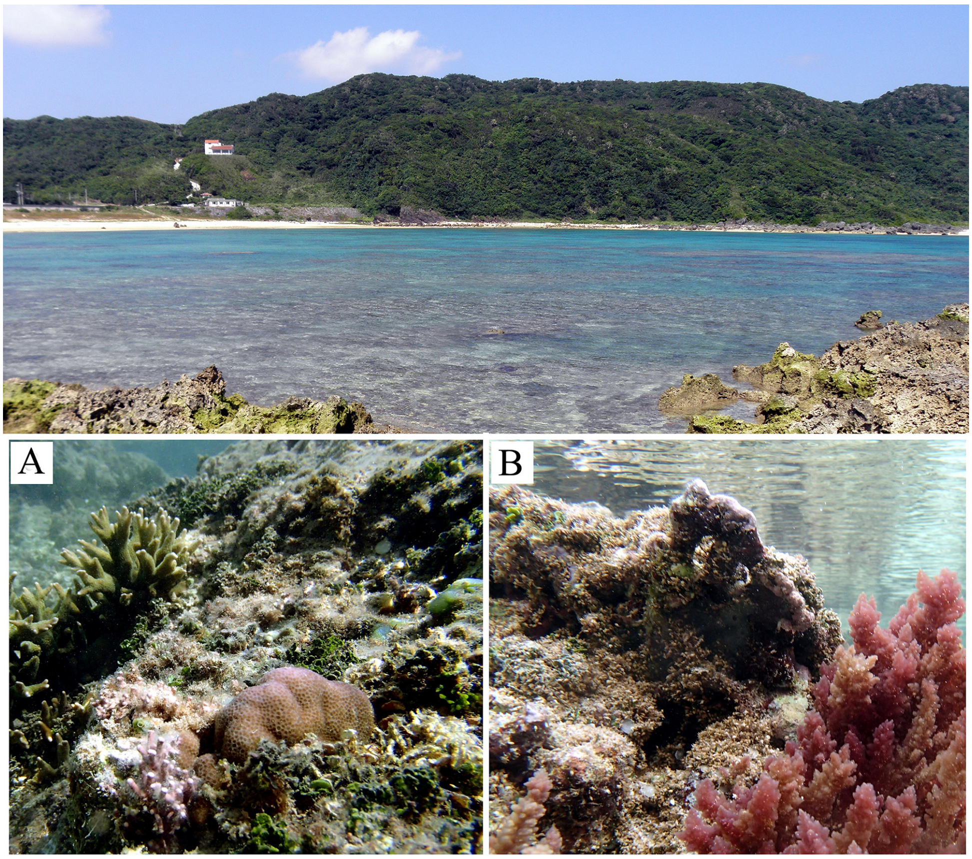

Fig. 5 Higawa, site 4 (24°26'21"N, 122°59'1"E), lagoon and reef-flat of coral reef. Inset: A − live and dead (overgrown with algal turf and calcareous red algae) in lagoon; B − dead coral colonies overgrown with turf and some upright algae, the red alga *Asparagopsis taxiformis* in front plane.

Fig. 6 Higawa, site 5 (24°26'22"N; 122°58'26"E), Kataburuhama Bay. Inset: A − live and dead coral colonies (overgrown with algal turf and calcareous red algae) in lagoon. B − the green alga *Halimeda macroloba* among sand and dead fragments of branched corals.

were Caulerpaceae (7 species, 11%) and Codiaceae (5 species, 14%), and in the 2013 collection Cladophoraceae (10 species,18%), Caulerpaceae (8 species,13%) and Codiaceae (6 species, 11%) (Table 1).

Algal species richness and composition were different between the two localities (Sonai and Higawa) (Table 2). In both the 1935 and the 2013 collection, the total number of algal species was higher in Sonai than in Higawa. The proportions of different taxonomic groups were also different between the two localities, with Rhodophyta being more predominant in Sonai than in Higawa in both 1935 and 2013. R/P values declined from 1935 to 2013, with Higawa having lower values than Sonai.

A total of 104 species (about a half of all species found in Yonaguni) were newly recorded in 2013, while 68 species (33%) were common to both 1935 and 2013 collections and 35 species (17%) occurred only in 1935. Among Rhodophyta species newly found in 2013, the Family Rhodomelaceae had 16 species (50% of all Rhodomelaceae species recorded to date), Coralinaceae 13 species (87%) and Ceramiaceae 8 species (72%). Chlorophyta newly found in 2013 included Cladophoraceae (7 species) and Ulvaceae (4 species). Species from the families Acrochaetiaceae, Gelidiaceae, Hapalidiaceae, Cystocloniaceae, Callithamniaceae, Spyridiaceae, (Rh); Acinetosporaceae, Neoralfsiaceae (Ph) and Gomontiaceae, Ulvellaceae, Ostreobiaceae, Polyphysaceae (Ch) were recorded for the first time in the 2013 collection.

Compared with the 1935 collection, major disappearances in 2013 concerned families of red algae: Liagoraceae (50% of species), Rhodomelaceae (25%), Galaxauraceae (33%) and Wrangeliaceae (25%). In addition, no species were recorded for Solieriaceae, Sarcodiaceae, Plocamiaceae, Rhodymeniaceae in the 2013 collection. Among green algae, 42% of Caulerpaceae species and 33% of Boodleaceae recorded in 1935 were not found in 2013 (Table 1).

In terms of habitat preference, species occurring on hard substrates accounted for 81% of all species in 1935 and 70% in 2013, epiphytic species 15% (1935) and 27% (2013), while those occurring on soft substrates comprised less than 3% in both collections. Numbers of epilithic (hard-substrate) species increased from 82 (1935) to 123 (2013)

Table 1. List of species (including varieties and forms) of benthic marine algae (Rhodophyta, Phaeophyceae, Chlorophyta) found at two localities on Yonaguni Island, Japan, in two separate surveys. Nomenclature based on Guiry & Guiry (AlgalBase, 2016); algal species names of 1935 (as synonyms) are given in square brackets after current names. Distribution: T, tropical; S, subtropical; M, temperate; Ar, Arctic; An, Antarctic;I-P, Indo-Pacific. Habitat: E, epiphytic; H, hard substrate; Sf, soft substrate.

Species and forms	1935		2013		distribution	habitat
	Sonai	Higawa	Sonai	Higawa		
RHODOPHYTA						
Order STYLONEMATALES						
Family Stylonemataceae						
Stylonema alsidii (Zanardini) K.M. Drew [*Goniotrichum alsidii* (Zanardini) Howe]	+		+		T,S,M	E
Order ERYTHROPELTIDALES						
Family ERYTHROTRICHIACEAE						
Erythrotrichia carnea (Dillwyn) J. Agardh			+	+	T,S,M,Ar,An	E
Sahlingia subintegra (Rosenvinge) Kornmann [*Erythrocladia subintegra* Rosenvinge]	+	+	+	+	T,S,M	E
Order ACROCHAETIALES						
Family ACROCHAETIACEAE						
Acrochaetium microscopicum (Nägeli ex Kützing) Nägeli				+	T,S,M	E
Acrochaetium robustum Børgesen			+		T,S	E
Order COLACONEMATALES						
Family COLACONEMATACEAE						
Colaconema hypneae (Børgesen) A.A. Santos & C.W.N. Moura				+	T,S	E
Order NEMALIALES						
Family GALAXAURACEAE						
Actinotrichia fragilis (Forsskål) Børgesen	+			+	T,S,(I-P)	H
Dichotomaria marginata (J. Ellis & Solander) Lamarck [*Galaxaura clavigera* Kjellman]	+	+	+		T,S	H
Dichotomaria spathulata (Kjellman) A. Kurihara & Huisman [*Galaxaura arborea* Kjellman]	+	+			T,S,(I-P)	H
Galaxaura divaricata (Linnaeus) Huisman & R.A. Townsend [*Galaxaura fasciculata* Kjellman]	+				T,S	H
Galaxaura rugosa (J. Ellis & Solander) J.V. Lamouroux [*Galaxaura elongata* J. Agardh; G. rudis Kjellman]	+	+		+	T,S	H
Tricleocarpa cylindrica (J. Ellis & Solander) Huisman & Borowitzka [*Galaxaura fastigiata* Decaisne]	+	+		+	T,S	H
Family LIAGORACEAE						
Dermonema virens (J. Agardh) Pedroche & Ávila Ortíz			+		T,S,(I-P)	H
Ganonema farinosum (Lamouroux) Fan et Wang [*Liagora farinosa* J.V. Lamouroux]		+			T,S	H
Liagora ceranoides J.V. Lamouroux [*Liagora ceranoides* f. *leprosa* (J. Agardh) Yamada]		+	+		T,S	H
Titanophycus setchellii (Yamada) S.-M. Lin, S.-Y. Yang & Huisman [*Liagora setchellii* Yamada]		+			T,S,(I-P)	H
Trichogloea lubrica J. Agardh		+			T,S	H
Yamadaella caenomyce (Decaisne) I.A. Abbott [*Liagora caenomyce* Decaisne]	+	+	+		T,S	H

Table 1. (continued, 2 of 8)

Order GELIDIALES						
Family GELIDIACEAE						
Gelidium pusillum (Stackhouse) Le Jolis			+	+	T,S	H
Family GELIDIELLACEAE						
Gelidiella acerosa (Forsskål) Feldmann & G. Hamel	+		+	+	T,S	H
Parviphycus pannosus (Feldmann) G. Furnari			+		T,S	H
Family PTEROCLADIACEAE						
Pterocladiella caerulescens (Kützing) Santelices & Hommersand			+	+	T,S	H
Order BONNEMAISONIALES						
Family BONNEMAISONIACEAE						
Asparagopsis taxiformis (Delile) Trevisan de Saint-Léon [*Asparagopsis sanfordiana* Harvey]	+	+	+	+	T,S	H
Order CORALLINALES						
Family CORALLINACEAE						
Amphiroa anceps (Lamarck) Decaisne			+		T,S,M	H
Amphiroa beauvoisii J.V. Lamouroux			+		T,S,M,Ar,An	H
Amphiroa foliacea J.V. Lamouroux			+		T,S,(I-P)	H
Amphiroa fragilissima (Linnaeus) J.V. Lamouroux			+	+	T,S,M	H
Hydrolithon boreale (Foslie) Y.M. Chamberlain			+	+	T,S,M	E
Hydrolithon farinosum (J.V. Lamouroux) D. Penrose & Y.M. Chamberlain			+		T,S,M	E
Jania acutiloba (Decaisne) J.H. Kim, Guiry & H.-G. Choi [*Cheilosporum jungermannioides* Ruprecht ex Areschoug]	+	+	+		T,S,(I-P)	H
Jania adhaerens J.V. Lamouroux				+	T,S	H
Jania arborescens (Yendo) Yendo			+		T,S	H
Jania capillacea Harvey			+	+	T,S,(I-P)	E
Jania ungulata f. *brevior* (Yendo) Yendo			+		T,S,(I-P)	H
Mastophora rosea (C. Agardh) Setchell [*Mastophora macrocarpa* Montagne]		+	+	+	T,S,(I-P)	H
Neogoniolithon frutescens (Foslie) Setchell & L.R. Mason				+	T,S,(I-P)	H
Pneophyllum fragile Kützing			+		T,S,M	E
Titanoderma tumidulum (Foslie) Woelkerling, Y.M. Chamberlain & P.C. Silva			+		T,S,(I-P)	H
Family HAPALIDIACEAE						
Lithothamnion intermedium Kjellman			+		T,S,M	H
Order GIGARTINALES						
Family CYSTOCLONIACEAE						
Hypnea pannosa J. Agardh			+	+	T,S	H
Hypnea spinella (C. Agardh) Kützing			+	+	T,S	H
Hypnea sp.			+			H
Family SOLIERIACEAE						
Eucheuma serra (J. Agardh) J. Agardh	+				T,S,(I-P)	H
Family RHIZOPHYLLIDACEAE						
Portieria hornemannii (Lyngbye) P.C. Silva [*Chondrococcus hornemannii* (Mertens) F. Schmitz]	+	+	+	+	T,S,(I-P)	H

Table 1. (continued, 3 of 9)

Family DUMONTIACEAE						
Rhodopeltis borealis Yamada	+		+		T,S,(I-P)	H
Family CAULACANTHACEAE						
Caulacanthus okamurae Yamada	+		+	+	T,S,(I-P)	H
Order PLOCAMIALES						
Family SARCODIACEAE						
Sarcodia montagneana (J.D. Hooker & Harvey) J. Agardh [*Sarcodia ceylanica* Harvey ex Kützing]	+				T,S	H
Order PEYSSONNELIALES						
Family PEYSSONNELIACEAE						
Peyssonnelia distenta (Harvey) Yamada	+		+		T,S,(I-P)	H
Order PLOCAMIALES						
Family PLOCAMIACEAE						
Plocamium telfairiae (W.J. Hooker & Harvey) Harvey ex Kützing	+	+			T,S	H
Order HALYMENIALES						
Family HALYMENIACEAE						
Halymenia formosa Harvey ex Kützing [*Halymenia durvillei* var. *formosa* (Harvey ex Kützing) Reinbold]	+				T,S,(I-P)	H
Yonagunia formosana (Okamura) Kawaguchi & Masuda [*Carpopeltis formosana* Okamura]	+		+		T,S,(I-P)	H
Order RHODYMENIALES						
Family CHAMPIACEAE						
Champia parvula (C. Agardh) Harvey	+		+	+	T,S,M	H
Champia vieillardii Kützing			+		T,S	H
Coelothrix irregularis (Harvey) Børgesen			+	+	T,S	H
Family LOMENTARIACEAE						
Ceratodictyon intricatum (C. Agardh) R.E. Norris [*Gelidiopsis intricata* (C. Agardh) Vickers]	+		+	+	T,S	H
Ceratodictyon repens (Kützing) R.E. Norris [*Gelidiopsis repens* (Kützing)]	+		+		T,S	H
Ceratodictyon spongiosum Zanardini		+	+	+	T,S,(I-P)	H
Lomentaria corallicola Børgesen			+	+	T,S	H
Family RHODYMENIACEAE						
Botryocladia kuckuckii (Weber-van Bosse) Yamada & T. Tanaka	+				T,S,(I-P)	H
Chrysymenia kaernbachii Grunow		+			T,S,(I-P)	H
Erythrocolon podagricum J. Agardh	+				T,S,(I-P)	H
Order CERAMIALES						
Family CERAMIACEAE						
Antithamnion antillanum Børgesen			+	+	T,S	E
Antithamnion pectinatum (Montagne) J. Brauner			+		T,S,M,Ar,An	E
Centroceras clavulatum (C. Agardh) Montagne		+	+	+	T,S	H, E
Centroceras japonicum Itono			+		T,S,(I-P)	H, E
Ceramium cimbricum H.E. Petersen			+	+	T,S,M	E
Ceramium cingulatum Weber-van Bosse			+		T,S	E

Table 1. (continued, 4 of 8)

Ceramium macilentum J. Agardh			+		T,S,(I-P)	H, E
Ceramium sp.	+		+	+		E
Corallophila howei (Weber-van Bosse) R.E. Norris			+		T,S,(I-P)	E
Corallophila kleiwegii Weber-van Bosse			+		T,S,(I-P)	E
Gayliella flaccida (Harvey ex Kützing) T.O. Cho & L.J. McIvor				+	T,S	E
Reinboldiella warburgii (Heydrich) Yoshida & Mikami [*Carpoblepharis warburgii* Heydrich]	+	+			T,S,(I-P)	E
Family CALLITHAMNIACEAE						
Aglaothamnion cordatum (Børgesen) Feldmann-Mazoyer				+	T,S	E
Family DELESSERIACEAE						
Hypoglossum attenuatum N.L. Gardner			+		T,S	H
Martensia flabelliformis Harvey ex J. Agardh	+				T,S,(I-P)	H
Zellera tawallina G. Martens			+		T,S,(I-P)	H
Family RHODOMELACEAE						
Acanthophora aokii Okamura	+	+			T,S,(I-P)	H
Acanthophora spicifera (M. Vahl) Børgesen [*Acanthophora orientalis* J. Agardh]		+	+		T,S	H
Acrocystis nana Zanardini	+		+		T,S,(I-P)	H
Bostrychia tenella (J.V. Lamouroux) J. Agardh			+	+	T,S	H
Chondria minutula Weber-van Bosse				+	T,S	E
Chondria repens Børgesen			+	+	T,S,(I-P)	E
Chondria sp.			+			H
Palisada concreta (A.B. Cribb) K.W. Nam			+		T,S,(I-P)	H
Palisada intermedia (Yamada) K.W. Nam [*Laurencia intermedia* Yamada]			+		T,S	H
Chondrophycus undulatus (Yamada) Garbary & Harper [*Laurencia undulata* Yamada]	+				T,S	H
Digenea simplex (Wulfen) C. Agardh	+	+	+	+	T,S	H
Herposiphonia insidiosa (Greville ex J. Agardh) Falkenberg		+			T,S,(I-P)	Sf
Herposiphonia parca Setchell			+	+	T,S	E
Herposiphonia secunda (C. Agardh) Ambronn				+	T,S	E
Herposiphonia subdisticha Okamura	+				T,S,(I-P)	E
Herposiphonia tenella (C. Agardh) Ambronn			+	+	T,S	H, E
Leveillea jungermannioides (K. Hering & G. Martens) Harvey		+		+	T,S,(I-P)	E
Neosiphonia ferulacea (Suhr ex J. Agardh) S.M. Guimarães & M.T. Fujii			+	+	T,S	H ,E
Polysiphonia fragilis Suringar	+				T,S,(I-P)	E
Polysiphonia howei Hollenberg			+		T,S	H
Polysiphonia japonica var. *savatieri* (Hariot) Yoon			+		T,S	H
Polysiphonia scopulorum var. *villum* (J. Agardh) Hollenberg			+		T,S	E
Polysiphonia sp.	+		+	+		E
Laurencia mariannensis Yamada	+				T,S,(I-P)	H
Laurencia pinnata Yamada			+		T,S,(I-P)	H
Palisada parvipapillata (C.K. Tseng) K.W. Nam			+		T,S,(I-P)	H
Palisada perforata (Bory de Saint-Vincent) K.W. Nam [*Laurencia papillosa* (C. Agardh) Greville]	+	+		+	T,S,M,An	H

Table 1. (continued, 5 of 8)

Amansia glomerata C. Agardh	+		+		T,S,(I-P)	H
Neurymenia fraxinifolia (Mertens ex Turner) J. Agardh	+	+	+		T,S,(I-P)	H
Spirocladia loochooensis (Yendo) Yoshida [*Wrightiella loochooensis* Yendo]	+				T,S	H
Tolypiocladia glomerulata (C. Agardh) F. Schmitz [*Roschera glomerulata* (C. Agardh) Weber-van Bosse]	+		+	+	T,S,(I-P)	E
Vidalia obtusiloba (Mertens ex C. Agardh) J. Agardh			+		T,S	H
Family WRANGELIACEAE						
Anotrichium tenue (C. Agardh) Nägeli			+	+	T,S	E
Griffithsia japonica Okamura			+		T,S,(I-P)	H, E
Griffithsia metcalfii C.K. Tseng			+	+	T,S,(I-P)	E
Gordoniella yonakuniensis (Yamada & T. Tanaka) Itono [*Spermothamnion yonakuniensis* Yamada et Tanaka]	+		+		T,S,(I-P)	E
Gymnothamnion elegans (Schousboe ex C. Agardh) J. Agardh [*Plumaria ramosa* Yamada & Tanaka]	+				T,S	E
Haloplegma duperreyi Montagne	+		+		T,S	H
Ptilothamnion cladophorae (Yamada & T. Tanaka) G. Feldmann-Mazoyer [*Spermothamnion cladophorae* Yamada & T. Tanaka]	+				T,S,(I-P)	E
Wrangelia argus (Montagne) Montagne			+		T,S	H
Family SPYRIDIACEAE						
Spyridia filamentosa (Wulfen) Harvey				+	T,S	H
OCHROPHYTA						
Class PHAEOPHYCEAE						
Order SCYTOTHAMNALES						
Family ASTERONEMATACEAE						
Asteronema breviarticulatum (J. Agardh) Ouriques & Bouzon [*Ectocarpus breviarticulatus* J. Agardh]	+		+	+	T,S	H
Order ECTOCARPALES						
Family ACINETOSPORACEAE						
Feldmannia indica (Sonder) Womersley & A. Bailey			+		T,S	E
Feldmannia irregularis (Kützing) G. Hamel			+		T,S,M	E
Feldmannia mitchelliae (Harvey) H.-S. Kim			+		T,S,M	E
Order RALFSIALES						
Family NEORALFSIACEAE						
Neoralfsia expansa (J. Agardh) P.-E. Lim & H. Kawai ex Cormaci & G. Furnari			+	+	T,S	H
Order ECTOCARPALES						
Family SCYTOSIPHONACEAE						
Chnoospora implexa J. Agardh	+				T,S	H
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier				+	T,S,M,An	H
Order SPHACELARIALES						
Family SPHACELARIACEAE						
Sphacelaria novae-hollandiae Sonder			+		T,S	E, H
Sphacelaria rigidula Kützing			+	+	T,S,M,An	H
Sphacelaria sp.		+		+		E

Table 1. (continued, 6 of 8)

Sphacelaria tribuloides Meneghini				+	T,S	H
Order DICTYOTALES						
Family DICTYOTACEAE						
Canistrocarpus cervicornis (Kützing) De Paula & De Clerck			+	+	T,S	H
Dictyopteris repens (Okamura) Børgesen	+		+	+	T,S	H
Dictyota implexa (Desfontaines) J.V. Lamouroux			+	+	T,S	H
Dictyota friabilis Setchell			+		T,S	H
Lobophora variegata (J.V. Lamouroux) Womersley ex Oliveira			+	+	T,S	H
Padina boryana Thivy [*Padina commersonii* Bory]	+		+		T,S	H
Padina gymnospora (Kützing) Sonder [*Padina crassa* Yamada]		+			T,S	H
Order FUCALES						
Family SARGASSACEAE						
Sargassum ilicifolium (Turner) C. Agardh [*Sargassum duplicatum* (J. Agardh) J. Agardh]	+	+	+		T,S,(I-P)	H
Turbinaria ornata (Turner) J. Agardh		+	+		T,S,(I-P)	H
CHLOROPHYTA						
Class ULVOPHYCEAE						
Order ULOTRICHALES						
Family MONOSTROMATACEAE						
Monostroma nitidum Wittrock			+	+	T,S	H
Order ULVALES						
Family ULVELLACEAE						
Ulvella viridis (Reinke) R. Nielsen, C.J. O'Kelly & B. Wysor			+		T,S,M,Ar,An	E
Ulvella scutata (Reinke) R. Nielsen, C.J. O'Kelly & B. Wysor			+		T,S,M,Ar,An	E
Family ULVACEAE						
Ulva australis Areschoug [*Ulva pertusa* Kjellman]	+	+	+	+	T,S,M	H
Ulva clathrata (Roth) C. Agardh			+	+	T,S,M,Ar,An	H
Ulva compressa Linnaeus			+	+	T,S,M,Ar,An	H
Ulva conglobata Kjellman			+		T,S,(I-P)	H
Ulva flexuosa Wulfen			+	+	T,S,M,Ar,An	H
Ulva sp. [*Enteromorpha* sp.]		+	+	+		H
Order CLADOPHORALES						
Family ANADYOMENACEAE						
Anadyomene wrightii Harvey ex J.E. Gray			+	+	T,S,(I-P)	H
Microdictyon okamurae Setchell	+	+			T,S,(I-P)	H
Microdictyon nigrescens (Yamada) Setchell	+	+	+		T,S,(I-P)	H
Family CLADOPHORACEAE						
Chaetomorpha antennina (Bory) Kützing		+	+		T,S	H
Chaetomorpha linum (O.F. Müller) Kützing	+			+	T,S,M,Ar,An	H
Chaetomorpha minima F.S. Collins & Hervey			+		T,S,M	H
Cladophora herpestica (Montagne) Kützing			+	+	T,S	H

Table 1. (continued, 7 of 8)

Cladophora laetevirens (Dillwyn) Kützing			+	+	T,S,M	H
Cladophora prolifera (Roth) Kützing	+	+			T,S,M	H
Cladophora rugulosa G. Martens				+	T,S,M	H
Cladophora sibogae Reinbold	+	+		+	T, S	H
Cladophora vagabunda (Linnaeus) Hoek				+	T,S,M	H, E
Rhizoclonium grande Børgesen			+		T,S,(I-P)	H
Rhizoclonium implexum (Dillwyn) Kützing			+		T,S,M	E
Family BOODLEACEAE						
Boodlea coacta (Dickie) G. Murray & De Toni	+	+	+	+	T,S,(I-P)	H, E
Cladophoropsis fasciculata (Kjellman) Wille	+	+	+	+	T,S	H
Cladophoropsis membranacea (Hofman Bang ex C. Agardh) Børgesen				+	T,S	H
Phyllodictyon anastomosans (Harvey) Kraft & M.J. Wynne			+		T,S	H
Struvea okamurae Leliaert [*Chamaedoris orientalis* Okamura & Higashi]	+	+			T,S,(I-P)	H
Family SIPHONOCLADACEAE						
Boergesenia forbesii (Harvey) Feldmann [*Valonia forbesii* Harvey]	+	+			T,S	H
Dictyosphaeria cavernosa (Forsskål) Børgesen	+	+	+	+	T,S	H
Dictyosphaeria versluysii Weber-van Bosse	+	+	+	+	T,S	H
Siphonocladus rigidus M.A. Howe			+		T,S	H
Family VALONIACEAE						
Valonia aegagropila C. Agardh			+	+	T,S	H
Valonia fastigiata Harvey ex J. Agardh	+	+	+		T,S	H
Valonia macrophysa Kützing			+	+	T,S	H
Valonia ventricosa J. Agardh			+	+	T,S	H
Valoniopsis pachynema (G. Martens) Børgesen	+	+		+	T,S	H
Order BRYOPSIDALES						
Family BRYOPSIDACEAE						
Bryopsis pennata J.V. Lamouroux			+		T,S	H
Bryopsis pennata var. *secunda* (Harvey) Collins & Hervey [*Bryopsis harveyana* J. Agardh]	+	+	+		T,S	H
Family DICHOTOMOSIPHONACEAE						
Avrainvillea lacerata J. Agardh		+		+	T,S,(I-P)	H
Family OSTREOBIACEAE						
Ostreobium quekettii Bornet & Flahault			+	+	T,S,M,Ar,An	En
Family CAULERPACEAE						
Caulerpa cupressoides (Vahl) C. Agardh		+			T,S	H
Caulerpa chemnitzia (Esper) J.V. Lamouroux [*Caulerpa racemosa* var. *laetevirens* Weber-van Bosse]	+	+	+	+	T,S	H
Caulerpa lentillifera J. Agardh				+	T,S,(I-P)	H
Caulerpa microphysa (Weber-van Bosse) Feldmann			+		T,S	H
Caulerpa racemosa (Forsskål) J. Agardh [*Caulerpa racemosa* var. *clavifera* (Turner) Weber-van Bosse]		+	+	+	T,S	H
Caulerpa serrulata (Forsskål) J. Agardh			+	+	T,S	H

Table 1. (continued, 8 of 8)

Caulerpa serrulata var. [*boryana*] f. *occidentalis* (Weber-van Bosse) Yamada & Tanaka		+	+	+	T,S,(I-P)	H
Caulerpa sertularioides (S.G. Gmelin) M.A. Howe	+				T,S	H
Caulerpa taxifolia (M. Vahl) C. Agardh				+	T,S	H
Caulerpa webbiana f. *elegans* Yamada & Tanaka		+			T,S,(I-P)	H
Caulerpa webbiana f. *tomentella* (Harvey ex J. Agardh) Weber-van Bosse		+			T,S	H
Caulerpella ambigua (Okamura) Prud'Homme van Reine, Lokhorst			+	+	T,S	H
Family UDOTEACEAE						
Chlorodesmis caespitosa J. Agardh [*Chlorodesmis formosana* Yamada]		+	+		T,S	H
Rhipidosiphon javensis Montagne [*Udotea javensis* (Montagne) A. Gepp & E.S. Gepp]	+	+	+		T,S	H
Udotea orientalis A. Gepp & E.S. Gepp	+	+			T,S,(I-P)	Sf
Family CODIACEAE						
Codium adhaerens C. Agardh	+		+		T,S,M,Ar,An	H
Codium repens P.L. Crouan & H.M. Crouan		+	+		T,S	H
Halimeda macroloba Decaisne		+		+	T,S,(I-P)	Sf
Halimeda opuntia (Linnaeus) J.V. Lamouroux		+	+	+	T,S	H/Sf
Halimeda borneensis W.R.Taylor				+	T,S	Sf
Halimeda velasquezii W.R. Taylor [*Halimeda opuntia* f. *intermedia* Yamada]	+	+	+	+	T,S,(I-P)	H
Family DERBESIACEAE						
Halicystis pyriformis Levring			+	+	T,S,(I-P)	E
Pedobesia ryukyuensis (Yamada & T. Tanaka) Kobara & Chihara [*Derbesia ryukyuensis* Yamada & T. Tanaka]		+	+		T,S,(I-P)	H
Class DASYCLADOPHYCEAE						
Order DASYCLADALES						
Family DASYCLADACEAE						
Bornetella sphaerica (Zanardini) Solms-Laubach [*Bornetella ovalis* Yamada]	+	+	+	+	T,S,(I-P)	H
Neomeris annulata Dickie		+		+	T,S	H
Neomeris mucosa M.A. Howe	+	+	+	+	T,S	H
Family POLYPHYSACEAE						
Parvocaulis parvulus (Solms-Laubach) S. Berger, Fettweiss, S. Gleissberg, L.B. Liddle, U. Richter, Sawitzky & Zuccarello			+	+	T,S	H

and epiphytic ones from 13 (1935) to 39 (2013).

In the two collections, the 'global' species inhabiting the tropical and subtropical waters of the world were predominant (47 and 49% of all species found in 1935 and 2013, respectively), followed by those restricted to the tropics and subtropics of the Indo-Pacific (46 and 28%). Species inhabiting tropical to temperate zones amounted to 5% (1935) and 12% (2013), while latitudinally cosmopolitan species inhabiting tropical to Arctic/Antarctic zones amounted to 2 and 11%, respectively (Fig. 7). The total number of tropical species increased from 93 (in 1935) to 139 (in 2013), while the number of cosmopolitan algae increased from 8 to 33 species. At the same time, the proportion of tropical species dropped from 91% in 1935 to 81% in 2013, and that of cosmopolitan species increased from 8 to 19%.

Floristic similarity of four assemblages, Sonai 1935, Sonai

Table 2. Number of species and R/P ratios in the collections of 1935 and 2013 at Sonai and Higawa sites on Yonaguni Island, Japan.

	1935		2013	
	Sonai	Higawa	Sonai	Higawa
Rhodophyta (Rh)	46	26	81	47
Phaeophyceae (Ph)	5	4	15	10
Chlorophyta (Ch)	23	34	47	40
total	74	64	143	97
R/P	9.2	6.5	5.4	4.7

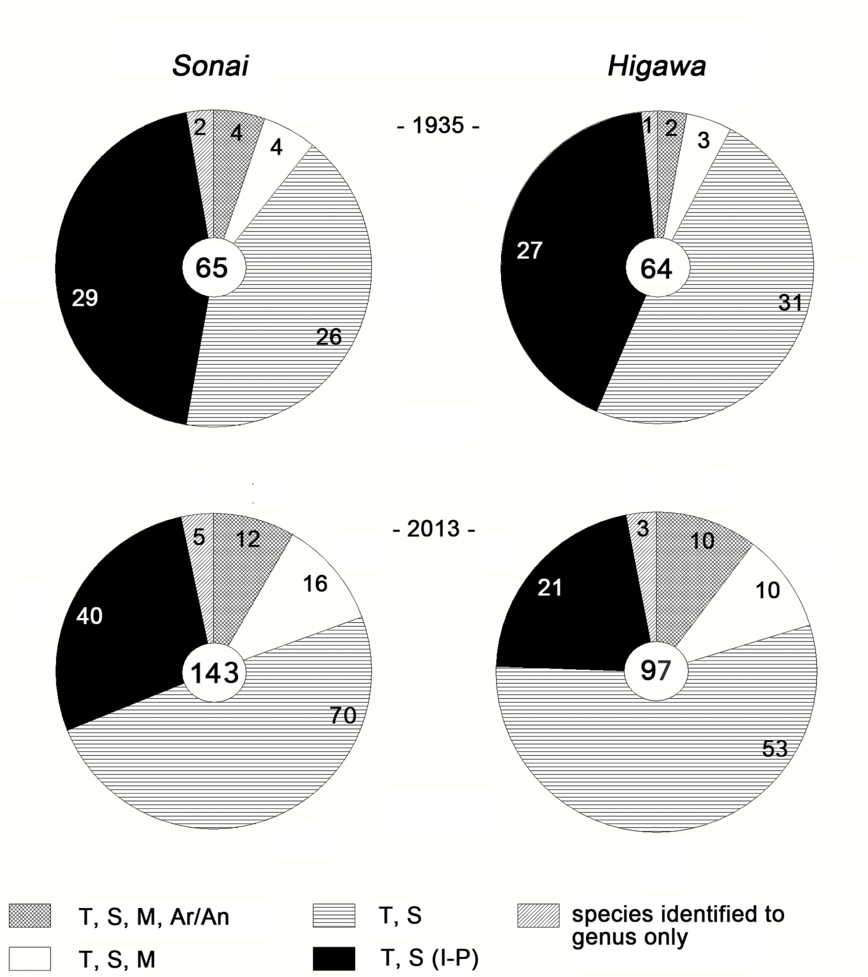

Fig. 7 Number of species with different distributional ranges in algal collections of 1935 and 2013. T, S, M, An/Ar − cosmopolitan species, occurring in tropics to the Arctic/Antarctic. T, S, M − species occurring in tropical to temperate waters. T,S − tropical and subtropical species inhabiting the Pacific, Indian and Atlantic Oceans. T,S,(I-P) − tropical and subtropical species of the Indo-Pacific.

2013, Higawa 1935 and Higawa 2013, is shown in a two-dimensional n-MDS plot (Fig. 8A). The overlay of the MDS plot with the cluster dendrogram similarity lines indicates the respective maximum boundary values for distinct clusters (Fig. 8B). The overall similarity of all assemblages (across locality and time) was 35%, while within each of 1935 and 2013 assemblages maximal similarity was >50%, clearly indicating that the temporal variation was larger than the spatial one (Fig. 8).

Discussion

The present study confirms that the floristic characteristics of Yonaguni are close to those of undisturbed, clear-water coral reefs in the Indo-Pacific where algal assemblages consist of 50−60% Rhodophyta, 20−30% Chlorophyta and 10−20% Phaeophyceae with a R:P index > 4.0 (Womersley 1981; Lewis & Norris 1987; Silva 1992; Silva *et al*. 1987, 1996; Zhang 1996; Tsuda 2003, 2006; Huisman & Borowitzka 2003).

The maximum value of similarity between the assemblages of 1935 and 2013 in these localities amounted to 35% only, indicating substantial changes in the marine flora during the past 78 years. The changes refer to the following: (1) increase in the number of species of all taxa; (2) decline in the values of R:P index; (3) changes in algal species composition due to the appearance of new species and disappearance of species found in 1935 (species occurring in both 1935 and 2013 amounted to a third of all recorded for Yonaguni). In connection with these, it is worth considering the possible characteristics of local variation

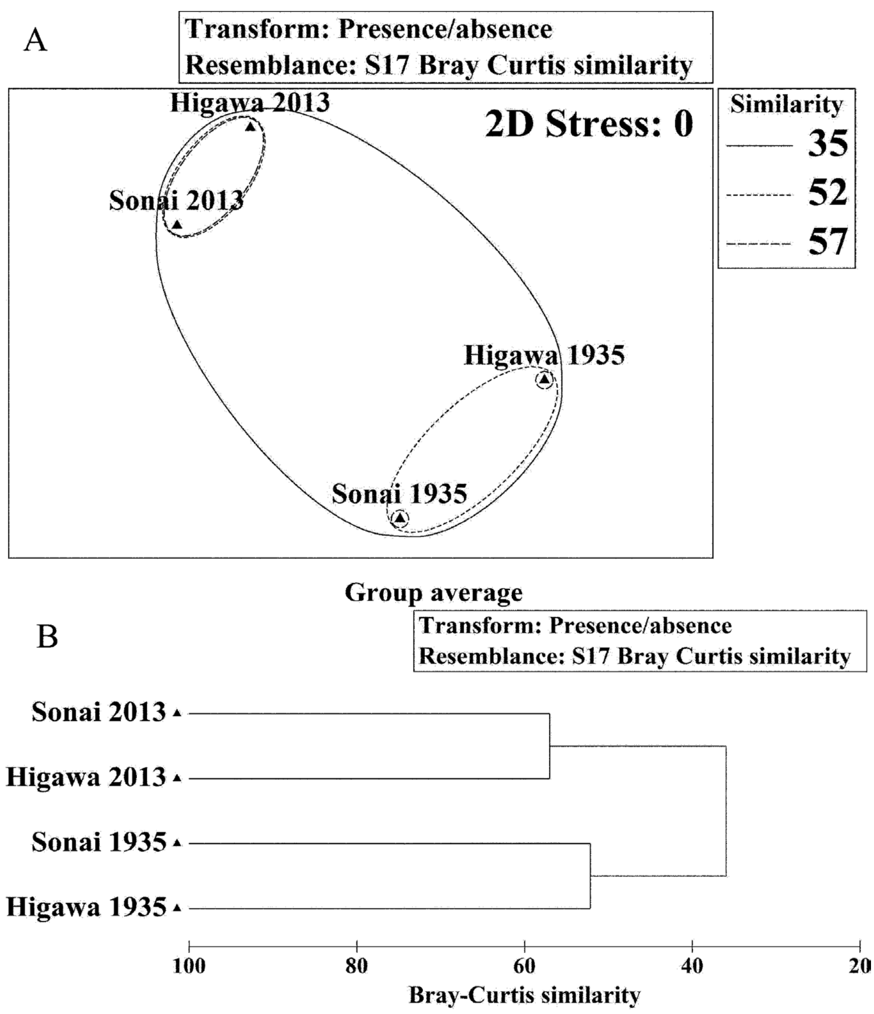

Fig. 8 Patterns of (A) floristic similarity and (B) clustering in non-metric multidimensional scaling ordination (n-MDS) of Sonai and Higawa (Yunaguni Island) samples collected in 1935 and 2013. The low stress value indicates no distortion in the compression of the multidimensional data into two dimensions. The groups indicated derive from a parallel cluster analysis showing the respective maximum similarity boundary value. Similarity values shown in the key are percentages.

in environments and global climatic changes over the past century that might have contributed to long-term changes in the flora of Yonaguni Island. It is known that factors such as anthropogenic stress, global climatic changes and other natural catastrophes exert substantial influences on the diversity and composition of taxa (families, genera, species and their forms) (Fong & Paul 2011; Titlyanov & Titlyanova 2012).

The most significant factor of anthropogenic origin concerns the eutrophication of seawater. Increased concentrations of dissolved inorganic and organic nitrogen and phosphorus lead to increases in the production of green seaweeds, green algal blooms of filamentous and thin blade-like forms, and in some cases the appearance of new species (e.g. Malta & Verschuure 1997; Lapointe *et al*. 1997, 2005a, b, c; Diaz-Pulido & McCook 2002; Gartner *et al*. 2002; McClanahan *et al*. 2006; Sfriso & Curiel 2007; Titlyanov *et al*. 2008, 2011a; Lapointe & Bedford 2010). It is well known that seaweeds are good indicators of environmental changes; green algae in particular have been used to detect eutrophication (Lapointe *et al*. 2005a), with species such as *Ulva compressa*, *U. lactuca*, *U. prolifera*, *Cladophora laetevirens*, *C. liniformis*, *Chaetomorpha linum* being known as sewage indicators (Burrows 1971; Barile, 2004).

However, the present marine flora at the Sonai seaport (presumably the most human-impacted locality of the Yonaguni coast) did not show attributes of eutrophication. Among the above mentioned species of green algal indicators, we found only *Ulva compressa*, *Cladophora laetevirens* and *Chaetomorpha linum* and only in small quantities as well as others filamentous and thin blade-like forms of green algae. This suggests that the Yonaguni algal assemblages have existed under relatively 'pristine' conditions over these decades, in contrast to the algal assemblages of the tropical Hainan Island that clearly reflected the effects of eutrophication and habitat degradation (Titlyanov *et al*. 2011b).

Diaz-Pulido *et al*. (2007) suggested that the potential impacts of increased sea surface temperatures on species such as crustose calcareous algae include increased metabolism, increased production, and changes in seasonal reproductive patterns. However, given the diversity of forms and species, the probability of widespread decimation of turf algae may be low. Although 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, as yet we have no proof of this. According to our data, algal species richness of Yonaguni Island (located on the tropical - subtropical boundary) increased by well over 50% and the number of cosmopolitan species (inhabiting warm as well as cold waters) quadrupled from 1935 to 2013. It remains to be seen whether observed changes in the proportions of tropical species and of cosmopolitan species in the Yonaguni algal assemblages are anything indicative of the effects of global ocean warming.

To our knowledge there is no concrete evidence of the influence of ocean acidification on tropical algal assemblages. Experiments show that enrichment of seawater with carbonic acid may have strong effects on all primary producers, including tropical seaweeds. However, acidification enhances photosynthesis and growth of only those marine plants that rely on dissolved carbonic acid (but not bicarbonate as for the red alga *Gracilaria*) as a main source of carbon (Friedlander & Levy 1995; Israel *et al*. 2005). Acidification negatively affects calcareous algae, evoking net dissolution of algal-derived $CaCO_3$ and sometimes leading to their bleaching and mortality (Anthony *et al*. 2008; Jokiel *et al*. 2008; Kuffner *et al*. 2008). Of 104 newly found species that were not recorded in 1935, the Families Rhodomelaceae (16 species, 50% of species found at two localities) and Corallinaceae (13 species, 87%) were predominant, possibly indicating the absence of acidification effects on the marine flora of Yonaguni Island.

Tsunamis and strong storms/typhoons can cause extensive damages to coastal assemblages, especially coral reefs (Woodley *et al*. 1981; Glynn 1990). At local scales, mortality of hard corals is associated with the loss of architectural complexity and reef flattening after direct impacts of these extreme events through the breakage of coral skeletons. In marine systems tsunamis and storms may not only remove or bury subtidal marine plant populations, but they may also help form new landscape patches. Following disturbance events, biodiversity declines, newly formed substrata appear in the form of sand banks and banks of coral fragments, dead and damaged coral colonies providing the space for sessile organisms at the reef base (Massel & Done 1993; Trenberth & Shea 2006; Manzello *et al*. 2007; Rogers *et al*. 2008; Alvarez-Filip *et al*. 2009).

Unusually high sea temperatures (30-31°C) combined with periods of slack winds, calm seas, cloudiness, high solar radiation, and in some areas, reduced salinity due to flooding and typhoons cause bleaching and subsequent mortality of hermatypic corals (Titlyanov & Titlyanova 2008). Bleaching, degradation and expulsion of zooxanthellae lead to reduced photosynthesis, tissue growth, regeneration and coral calcification, consequently resulting in increased susceptibility to diseases and coral death (Lesser *et al*. 2007). On some reefs, up to 100% of corals died in the next few months after bleaching (Baker *et al*. 2008).

Severe natural catastrophes in coral reef areas result in the formation of new substrates comprised of dead or damaged hermatypic corals and also of stones and/or sand, which are rapidly colonized by sessile organisms such as seaweeds, sponges, hydroids, gorgonians and other organisms. Natural catastrophes can evoke the replacement of one group of dominant organisms by another in an ecosystem (Petraitis & Dudgeon 2004; Glynn & Enochs 2011). Numerous observations showed that strongly damaged coral reefs were transformed into a seaweed-dominated state (coral reef ''phase shifts'') (Done 1992; Knowlton 1992; McManus & Polsenberg 2004). However, Bruno *et al*. (2009) analyzed 3581 quantitative surveys of 1851 reefs performed between 1996 and 2006 to determine the frequency and degree of macroalgal dominance in coral reefs around the world and indicated that the replacement of corals by macroalgae as the dominant benthic functional group is less common and less geographically extensive than thought. These give credence to the view that coral reef "phase shifts" represent temporary states of coral reefs in an overall recovery process to a coral-dominant state (Titlyanov & Titlyanova 2012).

Natural catastrophes in the Ryukyu Archipelago are not a rare phenomenon. There are often typhoons, earthquakes with tsunamis, and elevated seawater temperatures leading to bleaching and mass mortality of corals (Nakano 2004). On Yonaguni Island during the last century, two strong earthquakes, one in 1947 (M 7.4) and the other in 1966 (M 7.8), were recorded. Mass coral bleaching of 1998 also affected the coastal areas of the Yonaguni Island (personal communication of Dr. Yoshikatsu Nakano). Unfortunately, there is no documented information on damages caused to the underwater landscape of Yonaguni Island during the period between 1935 and 2013. However, our observation of a fringing coral reef along the Sonai coast in 2013 showed that this reef was flattened by tsunamis or severe typhoons (Fig. 2) at some time in the last century, and some dead coral colonies (overgrown with algal turf and calcareous algae) located in lagoons behind the reef-flat pointed to coral reef damages by bleaching events (Figs 2, 4).

The nature of changes in the algal assemblages of Yonaguni Island as recognized through carefully matched surveys of 1935 and 2013 suggests that these were evoked by natural catastrophes and in all probability by the mass coral bleaching of 1998. This conjecture is reinforced by the following observations: (1) high (>50%) macroalgal cover on hard substrata; (2) extensive algal turf cover on the upper flat part of dead patch reefs in lagoons; (3) high species richness, especially of Corallinaceae and the appearance of cosmopolitan and opportunistic species. Thus, our collection and observations made in 2013, undertaken 15 years after the natural catastrophe (coral bleaching) of 1998, suggest that that the coral reefs of this island are still largely in the process of recovery. It remains to be seen how these algal assemblages may respond to environmental changes in the future, especially in relation to increased threats of further seawater temperature rise, ocean acidification, bleaching and typhoon/tsunami damages.

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