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ECOLOGY

Species Composition and Distribution of Algae on the Fringing Coral Reef of Sesoko Island (Ryukyu Archipelago) before and after the Natural Catastrophe of 1998

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Abstract—The species composition and distribution of marine plants on the fringing reef of Secoko Island were studied before and after the mass coral mortality in 1998. The study showed that changes in the bottom communities that occurred after bleaching of corals were caused by the presumed development of marine plants substituting reef-building corals on the bottom. The number of algal species grew from 211 to 345. The projective cover (PC) of hard substrate with macroalgae increased: in 1998, it was 1–10% in the subtidal zone and 20–50% in the intertidal zone, while in 2002 through 2005, the PC reached 71% in the subtidal and 40–85% in the intertidal zone. It is assumed that the phase of the "plant reef" on Sesoko Island is a temporary event, and that the coral reef can recover within several decades, unless a natural catastrophe occurs again.

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Key words: macroalgae, coral reef, bleaching, "phase shift," competition.

The ecosystem of a coral reef is based on the vital activity of hermatypic reef–building corals that produce a hard carbonate substrate for the settling of benthic organisms. On healthy reefs, corals usually occupy up to 80–90% of the bottom area; they are the main primary producers of organic matter at the expense of the photosynthesis of their intracellular symbionts, namely dinoflagellate algae. Other primary producers of organic matter are benthic and planktonic marine plants; macrophytes among them yield the highest production. On a healthy coral reef, macrophytes cover from 1 to 20% of the hard substrate of the bottom [8]. The algae of coral reefs present a diverse species composition; they successfully compete with corals for substrate, space and other life resources [13].

The total area of contemporary coral reefs amounts to about 600 thousand sq. km [1]. In the last decades, a catastrophic destruction of shallow–water coral reefs took place and, consequently, their productivity and biological diversity were reduced [3]. The coral mortality and reef destruction characteristic of the entire tropical zone of the World Ocean depend mostly on water temperature increases that cause coral bleaching and expulsion of symbiotic algal cells from coral tissues (often together with the host animal cells) [3].

The most destructive consequences were recorded in 1998 after events of elevated surface seawater temperature in many areas of the World Ocean [11]. A rise of water temperature by 1–2°C in July–August caused extensive coral mortality even in the subtropical zone: up to 80% of the total coral population died on Okinawa Island [10].

Diaz-Pulido and McCook [4] show that immediately after coral bleaching and mortality dead coral colonies were colonized with marine algae and this colonization resulted in a shift from corals to algae. This "phase shift" after the mass mortality of corals was observed on the Great Barrier Reef [4] and on Caribbean coral reefs [6]. Some authors believe that the phase shift leads to the disappearance of reefs, as the algae destroy (rather than build, as corals do) the carbonate substrate, the base of the reef. The "phase shift" could be a temporary event in an active reparative processes, when corals settle on the substrate and old colonies recover [13, 20].

There is no way to predict the future fate of a coral reef without research into the contemporary structure of the reef and its species composition, i.e., the number and distribution of organisms competing for substrate, among them corals and benthic macro- and microalgae, as well as some invertebrate animals destroying the substrate. It is no less important to study competitive abilities of reef-building corals and mass algal species [4, 12].

Notwithstanding the urgency of these studies, only a few works deal with the study of the biological struc-

ture of coral reefs after catastrophes [5, 7, 8, 10, 11, 17]; these studies mostly describe changes in the species composition and projective cover of the bottom with corals. A few works concern development of algae on damaged coral reefs [4, 11]. During the period from 1995 to 2005, the species composition and distribution of algae were studied at the fringing reef of Sesoko Island. After the catastrophe in 1998, about 75 to 80% of the corals died in shallow waters around the island [10]. This study is aimed at a comparison of the composition and distribution of algal species on the fringing reef of Sesoko Island before and after the natural catastrophe in 1998.

MATERIAL AND METHODS

The investigations were conducted at the fringing reefs of the south-eastern shore (opposite the Biological Station of the University of Ryukyus) and the western shore (Sesoko Beach) of Sesoko Island, lying near Okinawa (Japan) in the East- Chinese Sea (26°38′N, 127°52′E) (Fig. 1). Algae were collected, herbarized and identified from May to October in 1995, October to December of 1997, January to April of 1998, March to December of 2002, January to March of 2003, July 2004, and February to May of 2005. The coral reef near Sesoko Island, according to the classification of Veron [21], is assigned to the fringing reef type. The coast is formed by a fossil coral reef. The reef platform is 10 to 20 m broad; the lagoon is shallow, 1 to 3 m wide. Water depth at the reef flat is about 1 m at a high tide. The reef slope is quite steep, stretches down to a depth of 30 m and passes into a sandy bottom. The surface water temperatures in the sea is, on the average, approximately +29°C (with 31°C as the maximum) in the summer and 21°C in the winter (with 18°C as the minimum). Water salinity varies from 34.5 to 35.2‰, depending on the season [14].

The object of study was algae collected by scuba-diving in the intertidal and subtidal zones at the fringing reef of Sesoko Island.

Marine plants were identified with the use of Olympus stereo and light microscopes and photographed with a Olympus Camedia 5050C digital camera. The projective algal cover of the bottom in the supralittoral, intertidal and subtidal zones was determined by the generally accepted hydrobiological method with the use of a 50x50 cm frame, in triplicate for each zone. Algae in the frame were photographed, collected, and identified in the laboratory, the number of specimens within the frame was counted for every species, and the mass of the algal species was weighed.

Color prints of the algae in the frame were made on a high-quality paper with the use of an Epson KA450PM printer, cut and weighed. The "weight" method of was applied to calculate the projective cover area of algae on the bottom [20].

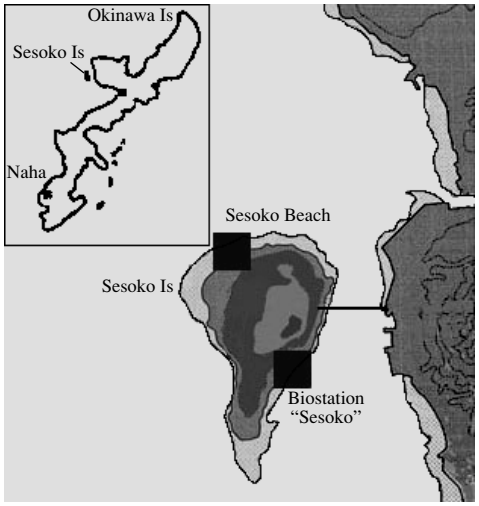

Fig. 1. Schematic map of Sesoko Is.

RESULTS

From 1995 until the natural catastrophe of 1998, our studies revealed 211 species of marine plants, of them 78 green algae (36.9%), 23 brown algae (10.9%), 96 red algae (45.5%), 9 blue-green algae (4.3%), 1 yellow-green alga (0.5%), and 4 species of sea grasses (1.9%). In the years 2002 through 2005, the list comprised 345 species (Table 1). It is interesting, that quantitative relationship of species did not change significantly: we documented 99 species of green algae (30.1%), 36 brown algae (11%), 152 red algae (46.2%), 37 blue-green algae (11.2%), 1 yellow-green alga (0.3%), and 4 species of seagrasses (1.2%). Both before and after the dramatic coral mortality (Fig. 2), the highest relative number of marine plant species was found in the intertidal collections (60%), a lower number was collected in the subtidal zone (30%), and only 10% were recorded for the supralittoral zone. The portion of epiphytic species also did not change, it made up about 15% of the total number of species. About 50% of all algae collected during the years inhabited an algal turf community, as they did before the catastrophe.

Ulva spp., *Gelidiella acerosa, Jania* spp., *Centroceras clavulatum, Bostrychia tenella*, and *Digenea simplex* dominated on the healthy coral reef. As well, *Enteromorpha* spp., *Codium* spp., *Ulva fasciata, Boodlea composita, Bornetella sphaerica, Actinotrichia fragilis, Tricleocarpa* spp., *Ganonema farinosum*, and *Liagora ceranoides* became new dominants after coral mortality. At the same time, *Cladophora catenata, Boodlea coacta, Ceratodictyon intricatum* and some other species were no longer found on the damaged reef.

The projective cover (PC) of microalgae on the hard substrate changed significantly after the catastrophe (Table 2). The PC of algae on Sesoko and some other islands of the Ryukyus made up 1–10% in the subtidal

Table 1. Algae collected on the fringing reef of Sesoko Island: before a natural catastrophe (1995–1998) and after the event (2002–2005)

List of species	Before catastrophe		After catastrophe		Community
	zone	occurrence	zone	occurrence	
CHLOROPHYTA					
Micrasterias sp.	–	–	–	+	–
Phaeophila dendroides (P. Crouan & H. Crouan) Batters	–	–	–	+	enl
Monostroma nitidum Wittrock	up. int	+++	int, up. int	+++	M
Enteromorpha clathrata (Roth) Greville	m. int	++	int	+++	T, ep
E. compressa (Linnaeus) Nees	int	+	int	+++	T
E. flexuosa (Wulfen) J. Agardh	–	–	int, l. int	+	T
E. kylinii Bliding	–	–	int	+	T
E. prolifera (O.F. Muller) J. Agardh	int	+	int	+	T
E. ralfsii Harvey	–	–	int	+	T
Ulva conglobata Kjellman	int	+++	int	+++	Ms(p)
U. fasciata Delile	int, l. int	–	int, l. int	+++	M
U. lactuca Linnaeus	int	–	int	++	Ms(p)
U. pertusa Kjellman	int, up. int	+++	int, up. int	+++	M
U. reticulata Forsskål	l. int	+	washed	+	Ms(p)
Pringsheimiella scutata (Reinke) Marchewianka	–	–	l. int	+	ep
Ulvella lens (P. Crouan & H. Crouan)	sub	+	up. int	+	ep
Verdigellas sp.	–	–	washed	+	–
Anadyomene wrightii Harvey ex J. Gray	l. int	++	int, l. int	++	T
Acrochaete viridis (Reinke) Nielsen (=*Entocladia viridis* Reinke)	l. int	+	l. int	+	ep
Acrochaete sp.	–	–	l. int	+	ep
Ectochaete leptochaete (Huber) Wille	–	–	–	+	enph
Gomontia arrhiza Hariot	l. int	+	l. int	+	ep
Microdictyon nigrescens (Yamada) Setchell	inf. lit	+	inf. lit	+	T
M. okamurai Setchell	inf. lit	+	inf. lit	+	T
M. japonicum Setchell	int	+	int	+	T
Chaetomorpha basiretrorsa Setchell	up. int	+	up. int	+	T
C. capillaris (Kützing) Børgesen	l. int	+	l. int	+	T
C. linum (O.F. Müller) Kützing	inf. lit	+	inf. lit	+	Ms(p)
C. pachynema Montagne	–	–	l. int	+	Ms(p)
C. javanica Kützing	–	–	l. int	+	T
Cladophora catenata (Linnaeus) Kützing	l. int	+	–	–	T
C. fuscicularis (Martens ex C. Agardh) Kützing	–	–	l. int	+	T
C. fuliginosa Kützing	–	–	l. int	+	T
C. laetevirens (Dillwyn) Kützing	l. int	+	l. int	+	T
C. vagabunda (Linnaeus) van den Hoek	int	+	int	++	T
Rhizoclonium grande Børgesen	int	+	int	++	T
R. implexum (Dillwyn) Kützing	inf. lit	+	inf. lit	++	T, ep
Boodlea coacta (Dickie) G. Murray & De Toni	int	+	–	–	T, f. sw
B. composita (Harvey) Brand	int	+	int	++	T, f. sw
B. struveoides Howe	–	–	int	+	T, f. sw
Struvea anastomosans (Harvey) Piccone & Grunow ex Piccone	int	+	int	+	T
Cladophoropsis herpestica (Montagne) Howe	–	–	int	+	T
C. membranacea (Hofman Bang ex C. Agardh) Børgesen	–	–	int	+	T
C. sundanensis Reinbold	int	+	int	++	T

Table 1. (Contd.)

List of species	Before catastrophe		After catastrophe		Community
	zone	occurrence	zone	occurrence	
C. zollingeri (Kützing) Reinbold	int	+	int	++	Mat
Cladophoropsis sp.	int	+	int	+	T
Dictyosphaeria cavernosa (Forsskål) Børgesen	int	++	int	+++	Ms(p)
D. versluysii Weber-van Bosse	int	+	int	+	Ms(p)
Siphonocladus rigidus Howe	l. int	+	l. int	+	ep
Ventricaria ventricosa (J. Agardh) Olsen & J. West	l. int	++	l. int	+	Ms(p)
Valonia aegagropila C. Agardh	l. int	++	l. int	+	Mat
V. fastigiata Harvey ex J. Agardh	l. int	+	l. int	+	Mat
V. macrophysa Kützing	l. int	+	l. int	+	Ms(p)
V. utricularis (Roth) C. Agardh	l. int	+	l. int	+	Ms(p)
Bryopsis harveyana J. Agardh	l. int, inf. lit	+	l. int, inf. lit	+	T
B. indica A. Gepp & E. Gepp	l. int, inf. lit	+	l. int, inf. lit	+	T, ep
B. pennata Lamouroux	l. int	+	l. int	+	T
B. plumosa (Hudson) C. Agardh	l. int, inf. lit	+	l. int, inf. lit	+	T
B. ryukyuensis Yamada	–	–	l. int, inf. lit	+	T
Derbesia attenuata Dawson	–	–	sub	+	T
D. fastigiata Taylor	–	–	inf. lit	+	T
D. marina (Lyngbye) Solier	inf. lit	+	inf. lit	+	T
Codium adhaerens (Cabrera) C. Agardh	int, inf. lit	++	int, l. int	++	Ms(p)
C. intricatum Okamura	l. int, inf. lit	++	l. int, inf. lit	+++	Ms(p)
C. repens P. Crouan & H. Crouan	l. int, inf. lit	+	l. int, inf. lit	++	Ms(p)
Caulerpa cupressoides (Vahl) C. Agardh	l. int	+	l. int	+	T
C. fastigiata Montagne	int	+	int	+	T
C. lentillifera J. Agardh	–	–	int	+	T
C. macrophysa (Sonder ex Kützing) *G. Murray*	int	+	int	+	T
C. microphysa (Weber-van Bosse) Feldmann	l. int	+	l. int	+	T
C. nummularia Harvey ex J. Agardh	int	+	int	++	T
C. racemosa (Forsskål) J. Agardh	int	+	int	+	T
C. racemosa (Forsskål) Weber-van Bosse var. *clavigera* (Turn.) Weber-van Bosse	int	+	–	–	T
C. racemosa var. *corynephora* (Montagne) Weber-van Bosse	–	–	int	+	T
C. racemosa (Forsskål) J. Agardh var. *peltata* (Lamouroux) Eubank in Stephenson	int, inf. lit	+	int, l. int	+	T
C. serrulata (Forsskal) J. Agardh	int, inf. lit	+	int, inf. lit	+	T
C. serrulata var. *serrulata* f. *lata* (Weber-van Bosse) Tseng	int, inf. lit	+	int, inf. lit	+	T
C. serrulata J. Agardh var. *serrulata* f. *spiralis* (Weber-van Bosse) Gilbert	int, inf. lit	++	int, inf. lit	++	T
C. sertularioides (S. Gmelin) Howe	l. int, inf. lit	+	l. int	++	T
C. vickersiae Børgesen	–	–	int	+	T
C. webbiana Montagne f. *tomentella* (Harvey) Weber-van Bosse	int	+	–	–	T
Caulerpella ambigua (Okamura) Prud'homme van Reine & Lokhorst	l. int	+	l. int	+	T
Ostreobium quekettii Bornet & Flahault	–	+	–	++	enl
Penicillus sibogae Gepp	–	–	–	+	ep
Avrainvillea erecta (Berkeley) A. Gepp & E. Gepp	m. int	+	m. int	+	Ms(p)
Boodleopsis pusilla (Collins) W.R. Taylor, Joly & Bernatowicz	inf. lit	+	inf. lit	+	Ms(p)

Table 1. (Contd.)

List of species	Before catastrophe		After catastrophe		Community
	zone	occurrence	zone	occurrence	
Chlorodesmis fastigiata (C. Agardh) Ducker	int, m. int	+	int, m. int	+	Ms(p)
Pseudochlorodesmis furcellata (Zanardini) Borgesen	–	–	l. int	+	Ms(p)
Halimeda discoidea Decaisne	inf. lit	+	inf. lit	+	Ms(p)
H. macroloba Decaisne	–	–	int	+	Ms(p)
H. macrophysa Askenasy	–	–	inf. lit	++	Ms(p)
H. opuntia (Linnaeus) Lamouroux	int, inf. lit	+	int, inf. lit		Ms(p)
H. tuna (Ellis & Solander) Lamouroux	l. int, inf. lit	+	l. int, inf. lit	++	Ms(p)
Tydemania expeditionis Weber-van Bosse	inf. lit	+	–	–	Ms(p)
Rhipidosiphon javensis (Montagne) Gepp	int, inf. lit	+++	int, inf. lit	+++	T
Cymopolia van-bosseae Solms-Laubach	inf. lit	sgl	–	–	Ms(p)
Dasycladus vermicularis (Scopoli) Krasser	l. int	sgl	–	–	Ms(p)
Bornetella nitida Sonder	int, inf. lit	+	int, inf. lit	+	Ms(p)
B. oligospora Solms-Laubach	int, inf. lit	+	int, inf. lit	+	Ms(p)
B. sphaerica (Zanardini) Solms-Laubach	int, inf. lit	++	int, inf. lit	+++	Ms(p)
Neomeris annulata Dickie	l. int, inf. lit	++	l. int, inf. lit	++	Ms(p)
N. bilimbata Koster	–	–	l. int, inf. lit	+	Ms(p)
Acetabularia clavata Yamada	inf. lit	+	inf. lit	+	Ms(p)
A. dentata Solms- Laubach	int, inf. lit	++	int, inf. lit	+++	Ms(p)
A. exigua Solms-Laubach	inf. lit	++	inf. lit	++	Ms(p)
A. parvula Solms- Laubach	l. int, inf. lit	+	l. int, inf. lit	++	Ms(p)
A. pusilla (Howe) Collins	inf. lit	–	inf. lit	+	Ms(p)
PHAEOPHYTA					
Ectocarpus elachistaeformis Heydrich	–	–	l. int	+	ep
E. siliculosus (Dillwyn) Lyngbye	–	–	l. int	+	ep
Ectocarpus sp.	–	–	l. int	+	ep
Feldmannia irregularis (Kützing) G. Hamel	–	–	l. int, inf. lit	++	ep
Hincksia indica (Sonder) Papenfuss et Chihara	l. int, inf. lit	+	l. int, inf. lit	+	ep
H. mitchelliae (Harvey) P. Silva	l. int, inf. lit	+	l. int, inf. lit	+++	T, ep
Pilayella littoralis (Linnaeus) Kjellman	–	–	int	+	ep
Ralfsia expansa (J. Agardh) J. Agardh	int	+	int	++	Ms(p)
Chilionema ocellata (Kützing) Kuckkuck	–	–	l. int, inf. lit	++	ep
Chnoospora implexa J. Agardh	inf. lit	++	inf. lit	++	Ms(p)
Colpomenia sinuosa (Mertens ex Roth) Derbes & Solier	l. int	++	l. int	++	Ms(p)
Hydroclathrus clathratus (C. Agardh) Howe	inf. lit	+	inf. lit	+	Ms(p)
Sphacelaria novae-hollandiae Sonder	l. int	+	l. int	++	T, ep
S. rigidula Kützing	l. int	++	l. int	++	T, ep
S. tribuloides Meneghini	l. int	++	l. int	++	T, ep
Dictyota dichotoma (Hudson) Lamouroux	l. int	+	l. int	+	Ms(p)
D. friabilis Setchell	–	–	l. int	+	T
D. humifusa Hörnig, Schnetter & Coppejans	–	–	l. int	++	Ms(p)
D. linearis (C. Agardh) Greville	l. int	+	l. int	+	T
D. patens J. Agardh	l. int	+	l. int	+	T
Dictyota sp.	–	–	int	+	T
Dictyopteris undulata Holmes	–	–	up. int	++	T
Dictyopteris sp.	–	–	up. int	++	T
Lobophora variegata (Lamouroux) Womersley ex Oliveira	l. int, inf. lit	++	l. int, inf. lit	++	Ms(p)
Dictyerpa stage of *Padina* [Vaughaniella stage]	int	+	int	+	T

Table 1. (Contd.)

List of species	Before catastrophe		After catastrophe		Community
	zone	occurrence	zone	occurrence	
Padina australis Hauck	int. pl	+	int. pl	+	Ms(p)
P. boryana Thivy	int. pl	++	int. pl	++	M
P. gymnospora (Kützing) Sonder	int, int. pl	+	–	–	Ms(p)
P. minor Yamada	int, inf. lit	+	int, inf. lit	+	Ms(p)
Cladosiphon okamuranus Tokida	m. int	+	m. int	+	Ms(p)
Hormophysa cuneiformis (J. Gmelin) P. Silva	inf. lit	+	inf. lit	+	Ms(p)
Sargassum crassifolium J. Agardh	inf. lit	+	inf. lit	++	Ms(p)
S. cristaefolium (=*duplicatum*) C. Agardh	–	–	int. pl	++	Ms(p)
S. feldmannii Pham Hoang Ho	–	–	inf. lit	++	Ms(p)
S. polycystum C. Agardh	–	–	inf. lit	+	Ms(p)
S. thunbergii (Mertens) C. Kuntze	int, int. pl	++	int, int. pl	++	Ms(p)
Turbinaria ornata (Turner) J. Agardh	l. int, inf. lit	++	l. int, inf. lit	+++	Ms(p)
RHODOPHYTA					
Stylonema alsidii (Zanardini) K. Drew	l. int, inf. lit	+	l. int, inf. lit	+	ep
Chroodactylon ornatum (C. Agardh) Basson	–	+	–	+	ep
Erytrotrichia carnea (Dillwyn) J. Agardh	l. int, inf. lit	+	l. int, inf. lit	+	ep
Erythropeltis subintegra (Rosenvinge) Kornmann et Sahling	–	–	l. int, inf. lit	++	ep
Porphyra crispata Kjellman	–	–	sub	+	Ms(p)
Acrochaetium catenulatum Howe	–	–	l. int	+	ep
A. crassipes (Børgesen) Børgesen	–	–	l. int	+	ep
A. gracile Børgesen	–	–	l. int	+	ep
A. moniliforme (Rosenvinge) Børgessen	l. int	+	l. int	+	ep
A. occidentale Børgessen	–	–	l. int	+	ep
A. seriatum Børgesen	–	–	l. int	+	ep
A. subseriatum Børgessen	–	–	l. int	+	ep
A. virgatulum (Harvey) Bornet	–	–	l. int	+	ep
Acrochaetium sp.	l. int	+	l. int	+	ep
Rhodochorton sp.	int	+	–	–	ep
Liagora ceranoides Lamouroux	–	–	l. int, inf. lit	++	Ms(p)
Liagora sp.	l. int, inf. lit	++	l. int, inf. lit	++	Ms(p)
Ganonema farinosum (Lamouroux) Fan & Wang	l. int, inf. lit	+	l. int, inf. lit	+	Ms(p)
Trichogloeopsis pedicellata (Howe) Abbott & Doty	–	–	l. int, inf. lit	sgl	Ms(p)
Yamadaella caenomyce (Decaisne) Abbott	inf. lit	+	inf. lit	+	Ms(p)
Trichogloea requienii (Montagne) Kützing	inf. lit	+	inf. lit	+	Ms(p)
Actinotrichia fragilis (Forsskål) Børgesen	inf. lit	++	inf. lit	++	Ms(p)
Galaxaura fasciculata Kjellman	inf. lit	+	inf. lit	++	Ms(p)
G. marginata (Ellis et Solander) Lamouroux	–	–	int	++	Ms(p)
G. obtusata (J. Ellis & Slander) J.V. Lamouroux	–	–	inf. lit	+	Ms(p)
G. subfruticulosa Chou	inf. lit	+	inf. lit	++	Ms(p)
Tricleocarpa fragilis (Linnaeus) Huisman & Townsend (=*Galaxaura oblongata*)	inf. lit	+	inf. lit	++	Ms(p)
T. cylindrica (Ellis et Solander) Huisman & Borowitzka (=*Galaxaura fastigiata*)	inf. lit	+	inf. lit	++	Ms(p)
Gelidiella acerosa (Forsskål) Feldmann et Hamel	int	++	int	++	T
G. adnata Dawson	int	+	int	+	T
G. pannosa (J. Feldmann) J. Feldmann & G. Hamel	–	–	int	+	T
Gelidiella sp.	int	+	int	+	T

Table 1. (Contd.)

List of species	Before catastrophe		After catastrophe		Community
	zone	occurrence	zone	occurrence	
Pterocladiella capillacea (Gmelin) Santelices & Hommersand	–	–	l. int	+	T
Gelidium pusillum (Stackhouse) Le Jolis	int	+	int, up. int	++	T
G. divaricatum Martens	int	+	int	+	T
Wurdemannia miniata (Sprengle) Feldmann & Hamel	int, up. int	+	int, up. int	++	T
Peyssonnelia conchicola Piccone & Grunow in Piccone	–	–	l. int, inf. lit	+	Ms(p)
P. inamoena Pilger	–	–	l. int, inf. lit	+	Ms(p)
Jania adhaerens Lamouroux	int, inf. lit	+++	int, inf. lit	+++	T, ep
J. capillacea (Yendo) Yendo	int, inf. lit	+++	int, inf. lit	+++	T, ep
J. ungulata f. *brevior* (Yendo) Yendo	int, inf. lit	++	int, inf. lit	++	T, ep
Amphiroa fragilissima (Linnaeus) J.V. Lamouroux	l. int	+	l. int	++	Ms(p)
Hydrolithon farinosum (J.V. Lamouroux) Penrose & Y.M. Chamberlain	int	+	int	++	ep
Porolithon sp.	sub	–	sub	+	Ms(p)
Pneophyllum conicum (E.Y. Dawson) Keats, Y.M. Chamberlain & Baba	–	–	int, inf. lit	+	Ms(p)
P. fragile Kützing	int, inf. lit	+	int, inf. lit	+	ep
Mastophora rosea (C. Agardh) Setchell	–	–	int, inf. lit	++	M
Titanophora pulchra Dawson	–	–	washed	sgl	–
Gelidiopsis intricata (C. Agardh) Vickers	inf. lit	++	inf. lit	++	T
G. scoparia (Montagne & Millardet) De Toni	–	–	inf. lit	+	T
G. variabilis (J. Agardh) Schmitz	l. int, inf. lit	+	l. int, inf. lit	+	T
Lomentaria corallicola Børgesen	int	+	int	+	T
L. mauritiana Børgesen	int	+	int	+	T
Chryzymenia okamurai Yamada et Segawa	–	+	washed	+	–
Coelarthrum boergesenii Weber-van Bosse (=*C. coactum* Okamura)	l. int, inf. lit	+	l. int, inf. lit	+	Ms(p)
Botryocladia skottsbergii (Børgesen) Levring	int	+	–	–	T
Coelothrix irregularis Børgesen	int, inf. lit	+	int, inf. lit	++	
Eucheuma denticulatum (Burman) Collins et Harvey	l. int	sgl	washed	sgl	–
Gracilaria arcuata Zanardini	int	+	int	+	Ms(p)
G. blodgettii Harvey	–	–	int	+	Ms(p)
G. coronopifolia J. Agardh	–	–	int	+	Ms(p)
G. salicornia (C. Agardh) Dawson	int	+	int	+	Ms(p)
Ceratodictyon intricatum (C. Agardh) R.E. Norris	int	+	–	–	Ms(p)
C. spongiosum Zanardini	l. int, inf. lit	++	l. int, inf. lit	++	Ms(p)
Caulacantus ustulatus (Mertens ex Turner) Kützing	int	+	int	++	T
Hypnea cervicornis J. Agardh	–	–	int	+	T, ep
H. charoides Lamouroux	l. int	+	l. int	+	T
H. boergesenii Tanaka	–	–	l. int	+	T
H. esperi Grunov	int	+	int	+	T, ep
H. nidulans Setchell	int	+	–	–	T
H. pannosa J. Agardh	l. int, inf. lit	+	l. int, inf. lit	++	T
H. spinella (C. Agardh) Kützing	int, inf. lit	+	int, inf. lit	++	T, ep
H. valentiae (Turner) Montagne	l. int, inf. lit	+	l. int, inf. lit	+	T
Ahnfeltiopsis flabelliformis Harvey	–	–	–	+	Ms(p)
Cruoriella sp.	–	–	l. int	sgl	Ms(p)
Erythrodermis sp.	–	–	l. int	+	Ms(p)

Table 1. (Contd.)

List of species	Before catastrophe		After catastrophe		Community
	zone	occurrence	zone	occurrence	
Haematocelis sp.	–	–	l. int	sgl	Ms(p)
Plocamium telfairiae (W. Hooker & Harvey) Harvey ex Kützing	–	–	l. int, inf. lit	+	Ms(p)
Chondracanthus intermedius (Suringar) Hommersand	int	+	int	+	T
Rhodymenia coacta Okamura	int	+	–	–	Ms(p)
R. anastomosans Weber-van Bosse	–	–	int. pl	+	Ms(p)
Rhodymenia sp.	–	–	int	+	Ms(p)
Rhodopeltis borealis Yamada	–	–	inf. lit	+	Ms(p)
Portieria hornemanni (Lyngbye) P. Silva	–	–	inf. lit	+	Ms(p)
Champia parvula (C. Agardh) Harvey	int	+	int	++	T, ep
C. japonica Okamura	int	+	int	+	T, ep
C. vieillardii Kützing	–	–	l. int	+	T, ep
Asparogopsis taxiformis (Delile) Trevisan	inf. lit	+	inf. lit	+	Ms(p)
Falkenbergia hillebrandii (Bornet) Falkenberg (=sporophyte of *A. taxiformis*)	l. int, inf. lit	+	l. int, inf. lit	++	ep
Dudresnaya japonica Okamura	–	–	washed	+	–
D. hawaiiensis R. K. S. Lee	–	–	washed	+	–
Gymnothamnion elegans (Schousbold ex C. Agardh) J. Agardh	int	–	int	+	ep
Antithamnion lherminieri (P. Crouan & H. Crouan) Bornet ex Nasr	l. int	+	l. int	+	ep
Antithamnion sp.	l. int	+	l. int	+	ep
Antithamnionella sp.	–	–	l. int	+	ep
Anotrichium tenue (C. Agardh) Nägeli	int	+	int	++	T, ep
Aglaothamnion callophyllidicola Yamada	int	+	int	+	ep
Wrangelia argus (Montagne) Montagne	int	+++	int	+++	T
W. dumontii (Dawson) Abbott	–	–	int	+	T
W. penicillata (C. Agardh) C. Agardh	–	–	int	+	T
Spyridia filamentosa (Wulfen) Harvey	int, int. pl	++	int, int. pl	+++	ep
Corallophila apiculata (Yamada) R. Norris (=*Centroceras apiculatum* Yamada)	l. int	++	l. int	++	ep
Centroceras clavulatum (C. Agardh) Montagne	int	+++	int	+++	T, ep
C. inerme Kützing	int	+	int	+	T, ep
Ceramium aduncum Nakamura	–	–	int	+	T, ep
C. cingulatum Weber-van Bosse	l. int	+	l. int	+	T, ep
C. codii (Richards) Mazoyer	–	–	l. int	+	T, ep
C. fastigiatum Harvey	–	–	l. int	++	T, ep
C. fimbriatum Setchell & Gardner	l. int	+	l. int	+	T, ep
C. flaccidum (Kützing) Ardissone	l. int	++	l. int	++	T, ep
C. howei Dawson	l. int	+	l. int	+	T, ep
C. macilentum Dawson	–	–	l. int	+	T, ep
C. paniculatum Okamura	–	–	l. int	+	T, ep
C. procumbens Setchell & Gardner	–	–	l. int	+	T, ep
C. sympodiale Dawson	–	–	l. int	+	T, ep
Pleonosporium borrieri (Smith) Nägeli	–	–	l. int	+	ep
Spermothamnion sp.	l. int	+	l. int	+	ep
Crouania attenuata (C. Agardh) J. Agardh	int	++	int	++	T, ep
Crouania sp.	–	–	int	+	T, ep
Griffithsia metcalfii Tseng	int	++	int	++	T, ep
G. subcylindrica Okamura	int	+	int	+	T, ep

Table 1. (Contd.)

List of species	Before catastrophe		After catastrophe		Community
	zone	occurrence	zone	occurrence	
G. japonica Okamura	–	–	int	+	Ms(p)
G. weber-van-bosseae Børgesen	–	–	int	+	T, ep
Haloplegma duperreyi Montagne	–	–	washed	+	–
Dasya mollis Harvey	int	+	int	+	Ms(p)
Dasya sp.	–	–	int	+	Ms(p)
Heterosiphonia crispella (C. Agardh) Wynne	l. int	+	l. int	+	T, ep
Hypoglossum sp.	l. int	+	l. int	+	ep
Martensia pavonia (J. Agardh) J. Agardh	–	–	washed	sgl	–
Taenioma perpusillum J. Agardh (J. Agardh)	l. int	+	l. int	++	ep
Nitophyllum adhaerens Wynne	–	–	–	++	T, ep
Polysiphonia ferulacea Suhr ex J. Agardh	l. int	+	l. int	+	T, ep
P. japonica Harvey var. *savatieri* (Hariot) Yoon	l. int	+	l. int	+	T, ep
Polysiphonia sp.	up. int	+	up. int	+	T, ep
Bostrychia tenella (Lamouroux) J. Agardh	up. int, sup. lit	+++	up. int, sup. lit	+++	M
Herposiphonia parca Setchell	int	+	int	+	ep
H. secunda (C. Agardh) Ambronn f. *secunda* (C. Agardh) Wynne	int	++	int	++	ep
H. secunda (C. Agardh) Ambronn f. *tenella* (C. Agardh) Wynne	int	++	int	++	ep
Lophosiphonia villum (J. Agardh) Setchell & Gardner	l. int	+	l. int	++	T, ep
Tolypiocladia glomerulata (C. Agardh) Schmitz	l. int	++	l. int	++	T, ep
Acanthophora muscoides (Linnaeus) Bory de Saint-Vincent	–	–	int	+	T
A. spicifera (Vahl) Børgesen	int. pl	++	int. pl	++	T
Leveillea jungermannioides (Martens et Hering) Harvey	int	+	int	++	T, ep
Laurencia brongniartii J. Agardh	l. int	+	l. int	+	T
L. cartilaginea Yamada	–	–	l. int	+	T
L. implicata J. Agardh	–	–	l. int	+	T
L. obtusa (Hudson) J.V. Lamouroux	int	+	int	++	T
L. okamurae Yamada	–	–	int	+++	M
L. parvipapillata Tseng	int	+	int	+	T
L. papillosa (C. Agardh) Greville	int	+	int	+++	M
L. perforata (Bory de Saint-Vincet) Monagne	–	–	int	+	T
L. saitoi Perestenko	l. int	+	–	–	T
L. yamadana Howe	l. int	+	–	–	T
Chondria repens Børgesen	l. int	++	l. int	++	T
C. dasyphylla (Woodward) C. Agardh	int	+	int	+	T
C. minutula Weber-van Bosse	–	–	int	+	T
Chondria sp.	int	+	int	+	T
Digenea simplex (Wulfen) C. Agardh	l. int, inf. lit	+++	l. int, inf. lit	+++	T
Acrocystis nana Zanardini	int	+	int	+	T, ep
CYANOPHYTA					
Dermocarpella clavata (Setchell & Gardner) Pham Hoang Ho	–	–	–	+	ep
Dermocarpa acervata (Setchell & Gardner) Pham Hoang Ho	–	–	–	+	ep
Aphanocapsa littoralis Hansgirg	–	–	–	++	ep
Symploca hydnoides (Harvey) Kützing	sup. lit	+	sup. lit	+	Ms(p)

Table 1. (Contd.)

List of species	Before catastrophe		After catastrophe		Community
	zone	occurrence	zone	occurrence	
Lyngbya bouillonii Holffmann & Demoulin	–	–	int	+	T
L. epiphytica Hieronymus	int	+	int	+	ep
L. confervoides C. Agardh	int	+	int	+	T
L. majuscula (Dillwyn) Harvey	–	–	int	++	T
L. polychroa (Meneghini) Rabenhorst (=*L. sordida* Gomont)	int	+	int	+	T
L. semiplena (C. Agardh) J. Agardh	–	–	int	+	T
Lyngbya sp.	int	+	int	+	T
Oscillatoria limnetica Lemmermann	–	–	int	+	T
O. margaritifera (Kützing) Gomont	–	–	l. int	+	T
O. miniata (Zanardini) Gomont	–	–	l. int	+	T
O. tenuis C. Agardh	–	–	l. int	+	T
Oscillatoria sp.	int	+	int	+	T
Phormidium corium (C. Agardh) Kützing	–	–	l. int	+	T
P. crosbyanum Tilden	–	–	l. int	+	T
P. tenue (Menighini) Gomont	–	–	l. int	++	T
Phormidium sp.	–	–	l. int	+	T
Spirulina major Kützing	–	–	int	sgl	T
S. subsalsa Oersted	int	+	int	+	T
S. subtilissima Kützing	–	–	int	+	T
Spirulina sp.	–	–	int	+	T
Calothrix confervicola (Dillwyn) C. Agardh	–	–	int	+	ep
C. crustacea Thuret	–	–	int	+	ep
C. parasitica (Chauvin) Thuret	–	–	int	+	ep
C. scopulorum (Weber et Mohr) C. Agardh	–	–	int	+	ep
Calothrix sp. 1	int	+	int	++	ep
Calothrix sp. 2	int	+	int	++	ep
Schizothrix sp.	–	–	int	+	T
Nostoc commune Vaucher	–	–	int	+	T
Hormothamnion sp.	–	–	int	+	T
Rivularia bornetiana?	–	–	int	+	T
Rivularia spp.	–	–	int	+	T
Dichothrix sp.	–	–	int	++	T
Brachytrichia quoyi (C. Agardh) Bornet & Flahault	–	–	int	+	T
XANTHOPHYTA					
Pseudodichotomosiphon constricta (Yamada) Yamada	int	+	int	+	T
ANTHOPHYTA					
Thalassia hemprichii (Ehrenberg) Ascherson	m. int	+	m. int	+	Ms(p)
Cymodocea serrulata (R. Brown) Ascherson et Magnus	m. int	+	m. int	+	Ms(p)
Halophila ovalis (R. Brown) Hook	m. int	+	m. int	+	Ms(p)
Syringodium isoetifolium (Ascherson) Dandy	–	+	washed	+	

Note: Zones: int, intertidal; up. int, upper intertidal; m. int, middle intertidal; l. int, low intertidal; sub, subtidal; inf. lit, infralittoral; sup. lit, supralittoral; int. pl, intertidal pools; washed, washed ashore. Communities: ep, epiphytic; enph, endophytic; enl, endolithic; Ms(p), mosaic in polydominant community; M, monodominant; T, algal turf (algal community widespread in tropical waters, usually less than 3 cm high); f. sw, free-swimming; Mat, algal community growing as mat. Occurrence: –, not found; +++, more than 10 specimens per 1 cm^2; ++, less than 10 specimens per 1 cm^2; +, less than 1 specimen per 1 cm^2; sgl, single.

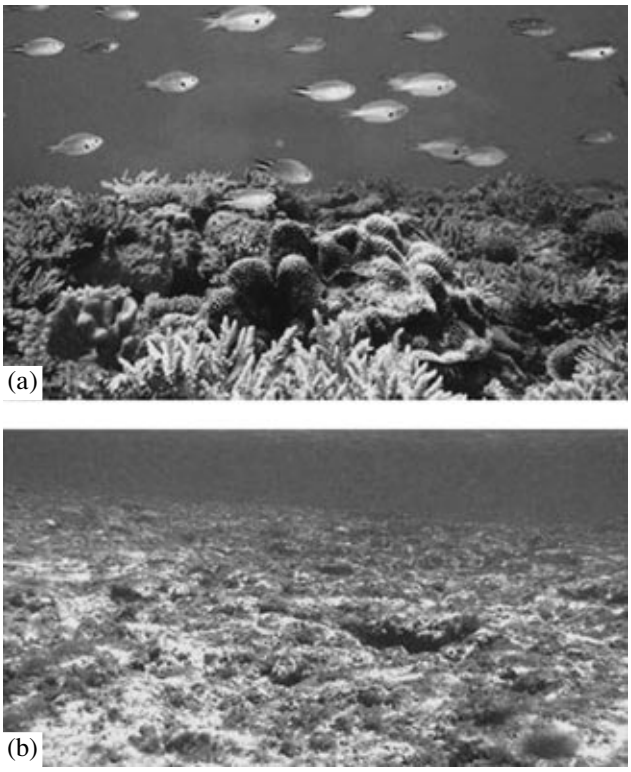

Fig. 2. Reef flat of the fringing reef of Sesoko Is., opposite Sesoko beach locality in 1995 (a) and 2005 (b).

zone and 20–50% in the intertidal zone before the catastrophe and markedly increased after the catastrophe to reach up to 40–85% in the intertidal zone and up to 71% in the subtidal zone. The biomass of mass algal species inhabiting the lower intertidal zone in 2005was as high as 310.8 g/m^2 for *Ulva*, 246.8 g/m^2 for *Digenea simplex*, and 85.32 g/m^2 for *Codium* sp.

DISCUSSION

The fringing reef of Sesoko Island was characterized by a relatively high species diversity of marine plants: 211 species were found during the period from 1995 to 1998. For comparison, coral reefs in the southern Pacific are inhabited by about 360 algal and seagrass species [9]. After the mass coral mortality and algal colonization of the newly formed substrate (dead corals), the number of marine plants at the reef of Sesoko Island increased by 134 species. Further, the number of dominant algal species increased. Before the catastrophe, a major portion of the bottom was occupied by *Gelidiella acerosa, Digenea simplex* and *Jania* spp.; after the catastrophe *Ulva, Codium, Galaxaura* and other species were added. We assume that the appearance of algal species new to the reef of Sesoko Island resulted from the absence of competition for substrate and other resources with both competitive algal species typical for the area and, probably, corals. Very likely, the competition for substrate and resources may later lead to a reduction of the number of species at the expense of non-competitive settlers. It is necessary to conduct another survey of algae on the reef of Sesoko Island after three or five years, in order to check this assumption.

Presently, the projective cover of algae on the bottom amounts to 40–85% in the intertidal zone and 50–80% in the subtidal zone (compared with 50% in the intertidal zone and no more than 10% in the subtidal zone before the catastrophe in 1998). Similar catastrophes in other areas of the World Ocean were also followed by an increase of the PC of the bottom: e.g., a 75% rise in waters of the western Sumatra [2] and a 90% rise on the reefs of Mayotte Island, in the southwestern Indian Ocean [16]. The increase in the projective algal cover of the bottom and the increase in species diversity did not destroy a quantitative relationship between species of the main taxonomic groups of marine plants. Both before the catastrophe and after it, the relationship between algae types on the Sesoko Island was as follows (average records): 31% for green algae, 46.1% for red algae, 10.7% for brown algae, 10.7% for blue-green algae, and 1.5% for other species. No changes were noted in the relative number of species inhabiting different parts of the phytal: 60% were found in the intertidal zone, 30% in the subtidal, and 10% in the supralittoral zone. The type of algal communities did not change either: algal turf mats and mosaic algal communities including large–thallus plants *Turbinaria ornata, Sargassum* spp., *Codium* spp., and *Ulva* spp. remained the most widespread on the reef of Sesoko Island, as it was before.

Thus, it was established that bleaching and mass mortality of corals at the fringing reef of Sesoko Island was followed by a "phase shift", and, as a result, marine plants occupied practically the entire area of a newly-formed substrate (the surface of dead coral colonies and their fragments that covered the bottom), the number of algal species and their total biomass distinctly increased. If the documented trend lasts for a longer time (a few decades) and surviving coral colonies and planulae settling on the substrate loose the competition with algae for the substrate, the coral reef of Sesoko Island, overgrown with algae and unable to build hard substrate (i.e. its own base) is likely to be destroyed. However, studies on competitive relationships between corals and algae on the damaged reef of Sesoko Island [19, 20] showed that, in most cases, corals win the struggle between coral polyps and algal communities. Thus, for example, in artificial injuries inflicted on massive and branched corals, polyps overgrew more than 100 algal species. Only toxic cyanobacteria of the genus *Lyngbya* were an insuperable hindrance to coral growth.

In 2005, we found young colonies of massive and branched corals in the intertidal and subtidal zones of Sesoko Island, this observation indicates a recovery of the reef not only through regeneration of old injured

Table 2. Projective cover (PC) of hard substrate with macroalgae before and after the nature catastrophe on the Ryukyus

Locality	PC of algae on hard substrate in %	Zones and depths of algae growths	Reference
	1997		
Opposite Sesoko Biological Station	From 1 to 20	No data	Nonaka, 2004
	Before 1998		
Western part of Sesoko Island	~5	Sublittoral, 2 m	Titlyanov (unpublished data)
Opposite Sesoko Biological Station	<30	No data	Loya et al., 2001
	~50	Intertidal zone	Titlyanov (unpublished data)
	~10	Sublittoral, 2 m	Ditto
North of Daito Is.	<1	No data	Nonaka, 2004
Miyako Islands	From 2 to 20, grasses and algae	No data	Kajiwara, Matsumoto, 2004
	After 1998		
Opposite Sesoko Biological Station	<85	No data	Sakai, 2004
	<85	No data	Loya et al., 2001
Akajima	<65	No data	Iwao, 2004
Minnajima and Iejima	<75	No data	Sakai, 2004
Western coasts of Okinawa Is.	<95	No data	Sakai (unpublished data)
	2005		
Opposite Sesoko Biological Station	40.22 ± 29.7	Upper intertidal zone	Our data
	78.99 ± 11.67	Middle intertidal zone	″
	62.06 ± 6.6	Lower intertidal zone	″
	71.63 ± 8.43	Sublittoral zone 1.5 m	″
Western Sesoko Is.	38.40 ± 14.8	Infralittoral zone	″
	33.41 ± 2.03	Middle intertidal zone	″
	49.21 ± 10.4	Lower intertidal zone	″

corals, but also as a result of the settlement of new colonies [see also 17]. Evidently, the "phase shift" on the reef of Sesoko Island is a temporary event, and the coral reef is able to recover in its original or modified state, unless a catastrophe occurs again.

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