Original paper

Low species diversity of hermatypic corals on an isolated reef, Okinotorishima, in the northwestern Pacific

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Abstract Ninety-three coral species have been identified at Okinotorishima (Okinotori Island), an isolated table reef located in the center of the Philippine Sea. The species composition of the island is similar to that of other islands in the northwestern Pacific, but the number of species is small in comparison with surrounding islands. The coral fauna at the island is characterized by a unique species composition that is independent of the Ryukyu Islands, mainland Japan, Palau, and the Mariana Islands. No endemic species were found, but the dominant *Acropora* species (*A. aculeus*, *A.* sp. aff. *divaricata*, and *A. globiceps*) were morphologically different from corresponding species at the Ryukyu Islands. The relatively low species diversity at the island despite the close proximity to an area of high diversity is explained by its small habitat diversity and isolation from other islands. The island is located in a subtropical gyre and is isolated from major currents. Thus, only coral larvae with a long competency period (as long as 70 days) can settle at the island from surrounding islands. This unique species composition seems to have been maintained for at least the last 7600 years, since the last stage of sea level rise in the postglacial period (Holocene).

Keywords Okinotorishima, Northwestern Pacific, Coral fauna, Isolated reef, Biogeography

Introduction

Okinotorishima (Okinotori Island; 20°25'N, 136°05'E) is a small table reef located in the center of the Philippine Sea, northwestern Pacific (Fig. 1). Although it is located close to the Coral Triangle, which has the highest diversity of hermatypic corals (hereafter corals) with 605 species (Veron et al. 2009), the island is isolated from other islands. It is 675 km southeast of Okidaitojima and 700 km southwest of Minami-iwojima.

An isolated reef that is far from larval source reefs is separated from connectivity, and therefore there is a limited chance that larvae will recruit from other reefs (Maragos and Jokiel 1986; Glynn and Ault 2000). The probability that coral larvae will recruit to a remote island is constrained by the competency period of the larvae and the ocean currents that deliver them (Harii et al. 2002, 2007). Okinotorishima is located in a subtropical gyre and no strong currents reach the island; therefore, it can take a long time for larvae to reach the island. Moreover, the island is small and receives severe waves, and thus the diversity of habitats for corals is small. Considering these features, the biodiversity of corals at this island is expected to be small despite its close proximity to the zone with the highest coral diversity in the world.

Unfortunately, a complete list of the coral species found at the island has not yet been reported. Several studies of corals and coral reefs have been conducted by the governments of Japan and Tokyo, but lists of corals have only been published as internal reports in Japan and species identification has not been examined in detail. Therefore, the coral fauna of Okinotorishima remains unknown. In the most comprehensive map of coral biogeography in the Indo-Pacific (Veron 1993), the area around Okinotorishima is described as having a low diversity, with 40 to 50 genera, which is smaller than the diversity of the surrounding islands: 74 for the Ryukyus (Nishihira and Veron 1995), 62 for Palau (Yukihira et al. 2007), 49 for Ogasawara (Tachikawa et al. 1991), and 57 for the Mariana Islands (Randall 1995). However, the number of genera and species at Okinotorishima was not based on precise data.

A full list of the coral species at Okinotorishima would

fill a gap in our understanding of the biogeography of corals in the northwestern Pacific and would provide insight into the processes that form and maintain coral fauna at isolated islands. Here we report the first full list of coral species for Okinotorishima together with their distribution patterns on the reef, which are presented in a habitat map. The coral fauna is then compared with the fauna at surrounding islands and faunal similarities and characteristics are discussed with regard to larval competency periods and oceanic currents.

Over long time scales, some coral species will go extinct and others will recruit to a study area. The biogeographical representativeness of a site needs to be evaluated by examining the presence or absence of specific species within a certain temporal scale. Therefore, we analyzed core records to evaluate the historical diversity of corals throughout the Holocene (the last 10,000 years) and compared these data with the list of living corals.

Study site and methods

Study site

Okinotorishima, the southernmost island of Japan, is a small table reef that spans 4.5 km east-west and 1.7 km north-south (Fig. 1). It is located on a submerged arc that comprises the Kyushu-Palau ridge. A volcanic island formed on the ridge before the Miocene (24 million years ago) and subsequently became submerged (Kobayashi 2004), allowing for the growth of coral. The outer slope of the island is steep, with a 45° angle descending down to the ocean floor to depths of 3000 to 5000 m.

The reef has a flat surface (a reef flat) with a shallow lagoon (maximum depth 5.5 m) that is surrounded by a reef crest which reaches to the low water level and becomes dry during spring low tides. Two islets (Kitakojima and Higashi-kojima) on the reef flat are exposed above the high tide level. The geology of the islets is described as foraminifera and coral limestone standing on the reef flat (Tayama 1952), which implies that they are Pleistocene or Holocene limestone remnants. Three additional islets that extended above the high tide level were previously described but they have since been lost because of severe erosion.



Fig. 1 Location of Okinotorishima. Isolines are numbers of genera. Site numbers in brackets correspond to the numbers in Table 2

The island is situated at the center of the northwestern Pacific subtropical gyre, facing the northeast trade wind from November to February and the southeast trade wind from May to August. Surface seawater temperature around the island varied from 24.7 to 29.7°C (monthly averages) between May 2007 and April 2008, and the underwater light intensity at 5 m depth around noon in fair weather was as high as 1000 μ mol m⁻² s⁻¹ in May 2007 (Nakamura et al. 2011).

The North Equatorial Current flows westward along 10–15°N latitude and turns north to become the warm Kuroshio Current, which then flows along the east coast of Taiwan and west of the Ryukyu Islands. These major currents flow far from Okinotorishima.

Methods

Collection and identification of coral specimens. The Ministry of Land, Infrastructure, Transport and Tourism, Japan, has conducted a series of annual field surveys of the distribution of corals on the reef at Okinotorishima since 1988 and has produced lists of observed corals. Coral specimens were haphazardly collected from different habitats that were defined by reef topography in June 2000 and May 2006. Collected specimens were bleached using household bleach and dried. In total, 89

specimens were identified using available references (Nishihira and Veron 1995; Veron and Stafford-Smith 2000) and compared with previous coral lists to reexamine their identification (Hayashibara et al. 2006). We also made a detailed survey of the corals at the island and observed 67 species from 20 genera and 9 families. More recently, the Fisheries Agency, Japan, conducted a coral mass culture project at this island and described additional coral species (Nakamura et al. 2011). Previous lists were examined for the validity of the specimens and descriptions.

Coral species composition was compared with surrounding islands in the northwestern Pacific using lists based on monographs for Japan (mainland and Ryukyu Islands: Nishihira and Veron 1995), Taiwan (Dai 1991; Dai and Horng 2009b,a), Palau (Yukihira et al. 2007), and the Mariana Islands (Randall 1995, 2003). Similarities and dissimilarities in coral species composition among 17 sites were examined using multivariate analysis (clustering technique). Species data were converted to binary data (present or absent). The data were compiled into a matrix and "present" and "absent" data in the matrix were assigned the numbers "1" and "0," respectively, for subsequent calculations. The overall degree of similarity in species composition between a pair of sites was expressed



Fig. 2 Study site overlaid with surveyed grids (red squares) and transects (yellow and light blue lines)

using the Bray-Curtis coefficient (Bray and Curtis 1957). A cluster analysis was performed using the group average method and the software R-2.13.0.

Habitat map. A satellite image (IKONOS) of the island that was taken in July 2007 was overlaid with a 250 $\times 250 \,\mathrm{m}$ grid. Fourteen grids (total area 875,000 m²) were selected as representative areas for the different habitats available based on our field survey and previous surveys; these grids were examined in detail (Fig. 2). In addition, 21 transects (total 6800 m) were established to compensate for gaps in the grid survey. In the selected grids and transects, the coverage of corals belonging to the dominant species or genus and the coverage of turf algae were recorded with their landform and sediment type. The coverage of corals was visually determined throughout each selected grid and in 1-m-wide strips that were spaced at 10-m intervals along each transect. Coral coverage was recorded at four levels: >20%, 20-5%, <5%, and 0%. The visual method was evaluated using a point-counting method with 1400 points within a 0.4×0.6 m quadrat. The coverage of corals that was determined by this quadrat survey matched the results of the grid and transect survey. To compensate for gaps in the transect survey, a manta tow survey was conducted over the reef flat and on the outer slope all around the island to observe coral coverage (total distance 23,170 m). Additional survey was conducted on the western outer slope in 2012.

Five 20 m transects were located horizontally at a depth of 8 m. Photographs of the bottom in a 0.4×0.6 m area were taken along the transects at 1-m intervals. The 20

non-overlapping images from each transect were imported into a coral cover analysis program, CPCe (National Coral Reef Institute, USA), and 50 grid points were projected onto each image. Percent coral cover was determined using point sampling techniques (Kohler and Gill 2006).

Relative abundance of each species was marked as abundant, common, uncommon and rare based on the grid and transect survey.

Core analysis. Three cores were recovered from the reef crest and the shallow lagoon along the east-west transect (OK-1, 2, and 3 in Fig. 5), which represent the major habitat of Okinotorishima. The lengths of the cores were 20.1 (OK-1), 26.2 (OK-2), and 20.1 m (OK-3). The cores were slabbed and their lithological characteristics were described. Fossil corals in the cores were identified to species, or at least to genera. In total, seven samples were analyzed by Teledyne Inc. to obtain radiocarbon ages. The mineralogy of the dated samples was analyzed by X-ray diffraction (XRD) with a PANalytical X'Pert diffraction system to confirm that there were no alterations to the calcite. The dates were calibrated to calendar years using the calibration program CALIB Rev.5.0 (Stuiver and Reimer 1993; Stuiver et al. 2005) and the marine calibration data set Marine 04 (Hughen et al. 2004), assuming a marine reservoir effect of 400 years (Stuiver and Braziunas 1993; Stuiver and Reimer 1993).

Results

List of coral species

The coral species identified at Okinotorishima are listed in Table 1. Ninety-three species from 25 genera and 11 families were identified. The numbers of genera and species at Okinotorishima were smaller than at other islands in the northwestern Pacific (Table 2).

The major coral groups consisted of Acroporidae and Faviidae corals. The dominant species in the genus *Acropora* were *A. aculeus*, *A.* sp. aff. *divaricata*, and *A. globiceps*.

 Table 1
 List of coral species at Okinotorishima (Okinotori Island)

Family		Family		Family	
Genus		Genus		Genus	
Species	ra	Species	ra	Species	ra
Pocilloporidae	10	Poritidae	14	Faviidae	
Pocillopora		Porites		Favia	
Pocillopora damicornis	r	Porites solida	с	Favia stelligera	a
Pocillopora verrucosa	а	Porites lobata	а	Favia laxa	u
Pocillopora evdouxi	a	Porites australiensis	с	Favia pallida	a
Pocillopora elegans	u	Porites lutea	с	Favia favus	c
Acroporidae		Porites mayeri	u	Favia matthaii	a
Montipora		Porites cylindrica	с	Favia rotundata	u
Montipora tuberculosa	с	Porites lichen	u	Favites	
Montipora mollis	с	Porites annae	u	Favites halicora	с
Montipora peltiformis	с	Porites rus	с	Favites flexuosa	с
Montipora turgescens	с	Siderastreidae		Favites complanata	a
Montipora incrassata	с	Psammocora		Goniastrea	
Montipora foveolata	с	Psammocora contigua	u	Goniastrea favulus	с
Montipora caliculata	с	Psammocora haimeana	u	Goniastrea pectinata	с
Montipora digitata	u	Psammocora profundacella	u	Platygyra	
Montipora hispida	с	Coscinaraea		Platygyra daedalea	с
Montipora informis	a	Coscinaraea columna	u	Platygyra sinensis	с
Montipora efflorescens	с	Agariciidae		Platygyra pini	с
Montipora grisea	с	Pavona		Platygyra contorta	с
Acropora		Pavona clavus	с	Leptoria	
Acropora gemmifera	с	Pavona duerdeni	с	Leptoria phrygia	a
Acropora verweyi	u	Pavona varians	с	Montastrea	
Acropora robusta	u	Pavona venosa	с	Montastrea curta	a
Acropora abrotanoides	с	Pavona maldivensis	с	Montastrea annuligera	u
Acropora muricata	u	Gardineroseris		Montastrea valenciennesi	с
Acropora austera	с	Gardineroseris planulata	u	Leptastrea	
Acropora tenuis	с	Fungiidae		Leptastrea purpurea	а
Acropora cytherea	u	Fungia		Leptastrea pruinosa	с
Acropora hyacinthus	с	Fungia scutaria	а	Cyphastrea	
Acropora latistella	с	Mussidae		Cyphastrea agassizi	с
Acropora nana	с	Lobophyllia		Cyphastrea serailia	а
Acropora aculeus	а	Lobophyllia hemprichii	с	Cyphastrea chalicidicum	а
Acropora valida	с	Lobophyllia corymbosa	с	Cyphastrea microphthalma	а
A. sp. aff. divaricata	а	Merulinidae		Echinopora	
Acropora elseyi	с	Merulina		Echinopora lamellosa	а
Acropora rosaria	u	Merulina ampliata	с	Echinopora gemmacea	а
Acropora florida	с	Scapophyllia		Echinopora pacificus	с
Acropora donei	с	Scapophyllia cylindrica	с	Dendrophylliidae	
Acropora globiceps	а			Turbinaria	
Acropora intermedia	с			Turbinaria reniformis	u
Isopora				Milleporidae	
Isopora palifera	u			Millepora	
Astreopora				Millepora platyphylla	с
Astreopora myriophthalma	а			Millepora exaesa	с

ra(relative abundance) a:abundant, c: common, u: uncommon, r: rare

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 Table 2
 Numbers of genera and species at 17 sites in the northwestern Pacific

no.	Site	Numb	er of	Reference
		genera	species	
1	Okinotorishima	25	93	Present study
2	Southern Mariana Islands	57	205	Randall (1995, 2003)
3	Northern Mariana Islands	43	125	Randall (1995, 2003)
4	Palau Islands	62	209	Yukihira et al. (2007)
5	Ogasawara Islands	49	180	Tachikawa et al. (1991)
6	Taiwan	68	296	Dai (1991), Dai and Horng (2009a, b)
7	Yaeyama Islands	74	368	Nishihira and Veron (1995)
8	Okinawa Islands	70	343	Nishihira and Veron (1995)
9	Miyako Islands	66	249	Nishihira and Veron (1995)
10	Amami Islands	58	226	Nishihira and Veron (1995)
11	Tanegashima	46	149	Nishihira and Veron (1995)
12	Tosa Shimizu	44	127	Nishihira and Veron (1995)
13	Amakusa	41	98	Nishihira and Veron (1995)
14	Shirahama	40	78	Nishihira and Veron (1995)
15	Kushimoto	42	95	Nishihira and Veron (1995)
16	Izu Peninsula	25	45	Nishihira and Veron (1995)
17	Tateyama	20	24	Nishihira and Veron (1995)

Acropora tenuis and A. donei comprised the second most abundant group. Interestingly, A. hyacinthus, A. muricata, and A. gemmifera were not in the majority group, yet they are dominant reef components in the western Pacific. Moreover, A. humilis, A. monticulosa, and A. digitifera, which are dominant reef builders on reef crests in the northwestern Pacific, were not found at Okinotorishima. The genera Stylophora, Seriatopora, and Pachyseris and the families Oculinidae and Pectiniidae have not been recorded at the island, but they are all common in the Ryukyu Islands. Only one Fungia species, Fungia scutaria, was found. Only two species, Lobophyllia hemprichii and L. corymbosa, were present from the Family Mussidae, and only Merulina ampliata and Scapophyllia cylindrica were present from the Family Merulinidae.

Ecomorphic features of some Acropora species

The species composition at Okinotorishima was essentially similar to other islands in the northwestern Pacific. However, the three dominant species of *Acropora* (*A. aculeus, A.* sp. aff. *divaricata,* and *A. globiceps*) were morphologically different from corresponding species in the Ryukyu Islands (Hayashibara et al. 2006).

At Okinotorishima, *A. aculeus* had larger branches and corallites and a more irregular colony shape than in the Ryukyus, and the colonies extended brown tentacles during the daytime. However, from the results of genetic comparisons using mitochondrial and nuclear molecular markers, no differences were detected between the samples from Okinotorishima and Okinawa (Hayashibara et al. in prep.).

Acropora sp. aff. divaricata at Okinotorishima had a different colony shape from A. divaricata in the Ryukyu Islands. The form of the corallites and the detailed structure of the coenosteum agreed with the description of A. divaricata (Wallace 1999). However, although colonies at Okinotorishima showed variation in shape, they did not present all of the features of A. divaricata, whose branches anastomose to form a network. For this reason, Hayashibara et al. (2006) hypothesized that the specimens from Okinotorishima were from a different species and treated them as A. sp.4? Here, we labeled the specimens as A. sp. aff. divaricata. Although there was a close relationship between the specimens during a genetic comparison, there was a distinguishable level of difference in their mitochondrial DNA (Hayashibara et al. in prep.).

The specimens of *A. globiceps* from Okinotorishima closely resembled the morphology of *A. humilis* in the Ryukyu Islands; however, their caespito-corymbose colony shape, columnar branches, and small axial corallites matched the description of *A. globiceps* (Wallace 1999). Although this species has only been recorded from the south-central Pacific (Wallace 1999), one of the authors, T. Hayashibara, confirmed that this species is distributed in Guam. Although the specimens from Okinotorishima and Guam did not differ genetically, *A. humilis* from Okinawa did differ from *A. globiceps* in the non-coding region of the mitochondrial DNA by one base (Hayashibara et al. in prep.).

Cluster analysis

The cluster analysis produced four groups among the 17 sites (Fig. 3 and in ESM Table 1). Group 1 only included one site (1: Okinotorishima). Group 2 was composed of nine sites (2: Southern Mariana Islands, 3: Northern Mariana Islands, 4: Palau Islands, 5: Ogasawara Island, 6: Taiwan, 7: Yaeyama Islands, 8: Okinawa Islands, 9: Miyako Islands and 10: Amami Islands). Group 3 consisted of five sites (11: Tanagashima, 12: Tosa Shimizu, 13: Amakusa, 14: Shirahama, and 15: Kushimoto), and Group 4 had two sites (16: Izu Penisula and 17: Tateyama). Group 2 was located in tropical and subtropical areas,

while Groups 3 and 4 were located in temperate areas of Japan. Group 1 (Okinotorishima) was located in an isolated area in the Philippine Sea.

Habitat map

The surface landform of Okinotorishima consists of an outer slope, a reef crest, and a shallow lagoon. The outer reef descends steeply to the ocean floor. Coral coverage exceeds 20% along the northern slope but is only 5 to 20%



Fig. 3 Dendrogram from average linkage clustering of coral composition at 17 sites in the northwestern Pacific

in other areas. Along the northern and eastern rims of the island, the reef crest is as wide as 200 to 300 m, with less than 5% coral coverage. The surface of the reef crest is reef rock covered with turf algae and it is exposed during low water in the spring.

The shallow lagoon contains patch reefs that are up to 10 m wide and 1 to 5 m high from the lagoon bottom. Patch reefs were generally densely covered with corals, with coral coverage exceeding 20%, particularly in the central and western patches. The dominant inhabitants of patch reefs were encrusting Faviidae (genus Cyphastrea and Echinopora), especially on the sides of the reefs. In the central part of the island, bush-like A. aculeus was dominant on the top portions of some patch reefs and corymbose A. sp. aff. divaricata and A. globiceps were also abundant. The patch reefs in the southwestern corner of the island were densely inhabited with corymbose Pocillopora damicornis. The bottom of the shallow lagoon was covered with sand and gravel, with less than 5% coral coverage. Massive Porites and Leptoria were scattered in the shallow lagoon where reef rock was exposed without gravel cover.

Corymbose, encrusting and massive types of corals are dominant on the outer slope. *Acropora robusta, Isopora palifera, Favia laxa, Favia rotundata* and *Montastrea annuligera* were only found from the outer slope.

Coral communities in reef cores

Core analyses and radiocarbon dating showed that the upper 10 m of the cores were from the Holocene. They



Fig. 4 Habitat map of Okinotorishima. Percent cover of living corals are shown by colors for each habitat





Fig. 5 Internal structure of sample cores and recovered fossil corals of the Holocene coral reef at Okinotorishima

contained rich unaltered corals overlying Pleistocene limestone with altered corals. Detailed internal structures for the cores are shown in Figure 5.

Core OK-1: this western reef crest consisted of A. globiceps, Montastrea curta, Favia stelligera, Pocillopora verrucosa, Millepora sp., massive Porites sp., corymbose types of Acropora spp., and fragments of Montipora, Cyphastrea, Favia sp. cf. pallida, massive Porites, and Pocillopora verrucosa. Core OK-2: this shallow lagoon core was divided into two units. The lower part between 13 and 10 m in depth mainly consisted of massive Porites and a few Cyphastrea fragments. The upper part between 10 m in depth and the core top was mainly composed of detritus. This detritus was composed of coral gravels (Cyphastrea, Pocillopora, massive Porites, and corymbose Acropora) and calcareous sand (e.g., Halimeda fragments and adhering foraminifera). Core OK-3: this eastern reef crest was very similar to OK-1. It consisted of A. globiceps, M. curta, F. stelligera, Pocillopora damicornis, P. verrucosa, Millepora sp., massive Porites sp., Montipora sp., corymbose types of Acropora spp., and fragments of Pocillopora eydouxi and P. verrucosa.

Radiocarbon dates for six coral samples ranged from 4300 to 7600 cal. years BP. The oldest Holocene age (7600 cal. years BP) was obtained from the bottom of core OK-3. The uppermost portions of the reef crest were dated to 3930 and 4300 cal. years BP at OK-1 and OK-3, respectively.

Discussion

Low species diversity at Okinotorishima

The number of species, 93 species in 25 genera, at Okinotorishima (Table 1) was small when compared with Palau (209 species in 62 genera) and the Yaeyama Islands (368 species in 74 genera) to the west and Ogasawara (180 species in 49 genera) and the Mariana Islands (205 species in 57 genera) to the east in the northwestern Pacific (Table 2). The species richness is rather smaller than that previously inferred (Veron 1993).

The coral fauna at Okinotorishima was characterized by a unique species composition. In the cluster analysis (Fig. 3), species composition at the sites in Japan, from the Yaeyama Islands (site no. 7) to Tateyama (site no. 17), basically matched the grouping by Veron and Minchin (1992), which detected two main clusters: the Ryukyu Islands, with reef communities, and mainland Japan, with non-reef communities. The decrease in temperature with latitude is the major constraint that leads to a decreasing number of species. Species composition at islands in the northwestern Pacific, from Southern Mariana (site no. 2) to Taiwan (site no. 6), was categorized together with the Ryukyu Islands. The results showed that the community composition on reefs in the tropical and subtropical northwestern Pacific (Mariana Islands, Palau Islands, Ogasawara, Taiwan, and Ryukyu Islands) clustered together into one group (Group 2), with the exception of Okinotorishima. The island's species composition was dissimilar to that of the surrounding tropical and subtropical reefs, although the island is located in a tropical area. This indicates that the species composition at the island was influenced by more than just sea surface temperature.

The uniqueness of the species composition was also manifested by the abundance of *Acropora*. Although three *Acropora* species (*A. aculeus*, *A.* sp. aff. *divaricata*, and *A. globiceps*) were relatively more abundant than other *Acropora* species at Okinotorishima, they are absent or are only minor species in the Ryukyus (Hayashibara et al. 2006). On the other hand, although *A. hyacinthus* and *A. muricata* are the most abundant species at many locations in the Ryukyu and Amami Islands, they were rarely observed at Okinotorishima. *Acropora digitifera* and *A. nasuta*, which are also dominant species in Okinawa, were not found at Okinotorishima.

The small size and the high wave energy of Okinotorishima are major factors affecting the low species richness. The outer slope, reef crest, and patch reefs in the shallow lagoon were the only habitats available at this island (Fig. 4). All of the habitats receive high wave energy, and typical low energy habitats, such as deep lagoons and inner reef flats, were not available. Species of Pectinidae, Fungiidae, and Merulinidae prefer protected environments, which may explain the relatively small number of coral species from these families.

The low species diversity can also be partially attributed to the island's isolation, which limits coral recruitment from other islands. This point is discussed further in the following section.

Larval dispersal potential and low diversity

The biodiversity of hermatypic corals is maintained by connectivity among reefs through the dispersal of coral larvae (Roberts 1997). Larval dispersal is controlled by the period during which larvae can settle after spawning or release (settlement-competency period) and the speed and direction of ocean currents (Harii et al. 2007). The competency period varies among coral species, ranging from a few hours to more than 100 days with an average of several days (Harrison and Wallace 1990). In general, corals can disperse several tens of kilometers, and thus the species diversity of corals in a group of islands or reefs that are distributed within this distance is maintained because of tight connectivity among locations. However, Okinotorishima is separated from other islands and only larvae with long competency periods will be able to recruit to the island.

Some of the common species at Okinotorishima are known to have longer competency periods. The competency period of A. tenuis, one of the common species in Okinotorishima, is longer than 70 days (Richmond 1987; Nishikawa and Sakai 2003; Nishikawa et al. 2003; Harii et al. 2010). Pocillopora damicornis is known to have a long competency period that is longer than 100 days (Richmond 1987; Harii et al. 2002). The abundant and common Pocillopora species are P. verrucosa, P. eydouxi and *P. elegans*, which competency periods have not been reported, but the similar characteristics of their larvae with zooxanthellae to P. damicorns infers the potential of their long competency periods. The abundances of these species at Okinotorishima are explained by their long competency periods and their higher recruitment potential to this remote reef. On the other hand, some brooding corals such as Heliopora coerulea (Harii et al. 2002) and Stylophora pistillata (Nishikawa et al. 2003) settle soon after the release of matured larvae and they lose their settlement potential within 20 days after release. The shorter competency periods of these two corals are consistent with their absence at Okinotorishima.

Okinotorishima is situated in the center of a subtropical gyre and is isolated from the major currents of the North Equatorial Current and the Kuroshio Current. The island is exposed to a weak current of about 0.1 m s⁻¹ that runs from the southeast to the northwestern in the subtropical Pacific; this is an Ekman current that is induced by the northeastern trade wind (Maximenko et al. 2009). The other currents observed in this region are mesoscale eddies that are several hundred kilometers in diameter, have maximum velocities of 0.2 m s^{-1} , and move from east to west (Kobashi and Kawamura 2002; Qiu and Chen 2010). Therefore, the most probable route of larval transportation by these currents originates in the southeast, where the Mariana Islands are located at a distance of 1400 km. If we take 0.2 m s^{-1} as the maximum current speed from Mariana to Okinotorishima, it would take 70 days for larvae to settle. The larval competency period of the dominant corals is as long as 100 days; therefore, these species have the potential to travel this distance. On the other hand, the competency periods of corals that were not observed at Okinotorishima might be shorter than this threshold period.

Historical species composition during the last 7600 years

On the basis of identified fossil corals, the species composition at Okinotorishima has been maintained throughout the past 7600 years at least within a generic level, since the last stage of sea level rise that was followed by stabilization in the post-glacial period (Holocene). All of the fossil corals that were extracted from the cores (P. verrucosa, P. damicornis, P. eydouxi, A. globiceps, corymbose types of Acropora, M. curta, F. stelligera, Cyphastrea spp., Favia sp., massive Porites sp., Millepora sp., and Montipora sp.) are distributed in the present-day reefs. Furthermore, the fossil corals in these cores generally corresponded to the dominant species on the present reef. Therefore, the unique composition of coral species has been maintained by the dispersal potential threshold and the low habitat diversity at this small isolated reef, at least during the Holocene.

The species composition in the east Pacific region has supported the unique coral fauna at Okinotorishima. East Pacific reefs (e.g., Costa Rica, Panamá, and Galápagos Island) are generally composed of *Pocillopora* and *Porites* (Glynn et al. 1994; Glynn and Ault 2000). *Acropora* is a dominant reef builder in the northwestern Pacific, but it is not distributed in east Pacific reefs. This pattern is also mainly explained by the competency period of coral larvae and ocean currents, although other factors are also involved, such as vicariance.

Most of the fossil corals are identified as generic level or a group of the same ecomorphic species. Moreover, post-depositional taphomony has degraded the original assemblage. Even with these problems, however, the reconstructed generic-level assemblage of the fossil corals is consistent with the present coral fauna.

Conclusion

We reexamined the previous lists and specimens of corals and conducted additional survey to compile the list of coral fauna, which shows 93 species within 25 genera are present in Okinotorishima, southernmost island of Japan. The survey has been spatially dense over a small island and the list provides a sound basis for future research and any changes in ecosystem in Okinotorishima, and biogeographical studies in the northwestern Pacific. However, additional species might be found from the deep outer slope, where relatively small survey efforts have been done. The low species diversity is explained by its low environmental diversity and isolated location, which permits the recruitment of coral larvae with long competency period. However, the competency period has been known only for few species and more information for the other species is necessary for further discussion.

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References

- Bray JR, Curtis JT (1957) An Ordination of the Upland Forest Communities of Southern Wisconsin. Ecol Monogr 27: 326-349
- Dai CF (1991) Reef environment and coral fauna of southern Taiwan. Atoll Res Bull 354: 1-28
- Dai CF, Horng S (2009a) Scleractinia fauna of Taiwan. II. The robust group. National Taiwan University Press, Taipei
- Dai CF, Horng S (2009b) Scleractinia fauna of Taiwan. I. The complex group. National Taiwan University Press, Taipei
- Glynn PW, Ault JS (2000) A biogeographic analysis and review of the far eastern Pacific coral reef region. Coral Reefs 19: 1-23
- Glynn PW, Colley SB, Eakin CM, Smith DB, Cortes J, Gassman NJ, Guzman HM, Delrosario JB, Feingold JS (1994) Reef coral reproduction in the Eastern Pacific Costa-Rica, Panama, and Galapagos-Islands (Ecuador) 2. Poritidae. Mar Biol 118: 191–208
- Harii S, Yamamoto M, Hoegh-Guldberg O (2010) The relative contribution of dinoflagellate photosynthesis and stored lipids to the survivorship of symbiotic larvae of the reefbuilding corals. Mar Biol 157: 1215–1224
- Harii S, Nadaoka K, Yamamoto M, Iwao K (2007) Temporal changes in settlement, lipid content and lipid composition of larvae of the spawning hermatypic coral Acropora tenuis. Mar Ecol Prog Ser 346: 89–96
- Harii S, Kayanne H, Takigawa H, Hayashibara T, Yamamoto M (2002) Larval survivorship, competency periods and settlement of two brooding corals, Heliopora coerulea and Pocillopora damicornis. Mar Biol 141: 39–46
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) Coral reefs. Elsevier, Amsterdam, pp 133-207
- Hayashibara T, Seno K, Yoneyama S (2006) Reef-building corals on Okino-torishima. Tokyo Metropolitan Reserch on Fisheries Science 1: 87–95
- Hughen KA, Baillie MGL, Bard E, Beck JW, Bertrand CJH, Blackwell PG, Buck CE, Burr GS, Cutler KB, Damon PE, Edwards RL, Fairbanks RG, Friedrich M, Guilderson TP, Kromer B, McCormac G, Manning S, Ramsey CB, Reimer PJ, Reimer RW, Remmele S, Southon JR, Stuiver M, Talamo S, Taylor FW, van der Plicht J, Weyhenmeyer CE (2004) Marine04 marine radiocarbon age calibration, 0– 26 cal kyr BP. Radiocarbon 46: 1059–1086
- Kobashi F, Kawamura H (2002) Seasonal variation and instab-

ility nature of the North Pacific Subtropical Countercurrent and the Hawaiian Lee Countercurrent. J Geophys Res 107: 3185, doi:10.1029/2001JC001225

- Kobayashi K (2004) Origin of the Palau and Yap trench-arc systems. Geophys J Int 157: 1303-1315
- Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Comput Geosci 32: 1259–1269
- Maragos JE, Jokiel PL (1986) Reef corals of Johnston Atoll one of the worlds most isolated reefs. Coral Reefs 4: 141– 150
- Maximenko N, Niiler P, Rio MH, Melnichenko O, Centurioni L, Chambers D, Zlotnicki V, Galperin B (2009) Mean dynamic topography of the ocean derived from satellite and drifting buoy data using three different techniques. J Atmos Ocean Tech 26: 1910–1919
- Nakamura R, Ando W, Yamamoto H, Kitano M, Sato A, Nakamura M, Kayanne H, Omori M (2011) Corals mass-cultured from eggs and transplanted as juveniles to their native, remote coral reef. Mar Ecol Prog Ser 436: 161–168
- Nishihira M, Veron JEN (1995) Hermatypic corals of Japan. Kaiyusha, Tokyo
- Nishikawa A, Sakai K (2003) Genetic variation and gene flow of broadcast spawning and planula brooding coral, *Goniastrea* aspera (Scleractinia) in the Ryukyu Archipelago, southern Japan. Zool Sci 20: 1031–1038
- Nishikawa A, Katoh M, Sakai K (2003) Larval settlement rates and gene flow of broadcast-spawning (Acropora tenuis) and planula-brooding (Stylophora pistillata) corals. Mar Ecol Prog Ser 256: 87–97
- Qiu B, Chen SM (2010) Interannual variability of the orth Pacific Subtropical Countercurrent and its associated mesoscale eddy field. J Phys Oceanogr 40: 213–225
- Randall RH (1995) Biogeography of reef-building corals in the Mariana and Palau Islands in relation to back-arc rifting and the formation of the eastern Philippine Sea. Nat History Res 3: 193–210
- Randall RH (2003) An annotated checklist of hydrozoan and scleractinian corals collected from Guam and other Mariana Islands. Micronesica 35–36: 121–137

- Richmond RH (1987) Energetics, competence, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. Mar Biol 93: 527–533
- Roberts CM (1997) Connectivity and management of Caribbean coral reefs. Science 278: 1454–1457
- Stuiver M, Reimer PJ (1993) Extended ¹⁴C data base and revised CALIB 3.0 ¹⁴C age calibration program. Radiocarbon 35: 215–230
- Stuiver M, Braziunas TF (1993) Modelling atmospheric ¹⁴C influences and ¹⁴C ages of marine samples to 10,000 BC. Radiocarbon 35: 137–189
- Stuiver M, Reimer PJ, Reimer RW (2005) CALIB 5.0.
- Tachikawa H, Suganuma H, Sato F (1991) Hermatypic corals of Chichijima and Hahajima Archipelago Research Report, Tokyo Metropolitan University, Tokyo, pp 285–296
- Tayama R (1952) Coral Reefs of the South Seas. Bull Hydrographic Office, Maritime Safety Agency of Japan 11: 1-292
- Veron JEN (1993) Corals of Australia and the Indo-Pacific. University of Hawaii Press, Honolulu
- Veron JEN, Devantier LM, Turak E, Green AL, Kininmonth S, Stafford-Smith M, Peterson N (2009) Delineating the Coral Triangle. Galaxea J Coral Rreef Stud 11: 91–100
- Veron JEN, Minchin PR (1992) Correlations between sea surface temperature, circulation patterns and the distribution of hermatypic corals of Japan. Cont Shelf Res 12: 835-857
- Veron JEN, Stafford-Smith M (2000) Corals of the world. Australian Institute of Marine Science, Townsville
- Wallace C (1999) Staghorn Corals of the World. CSIRO Publishing, Collingwood
- Yukihira H, Shimoike K, Golbuu Y, Kimura T, Vector S, Ohba H (2007) Coral reef communities and other marine biotopes in Palau. In: Kayanne H, Omori M, Fabricius K, Verheiji E, Colin P, Golbuu S, Yukihira H (eds) Coral reefs of Palau. Palau International Coral Reef Center, Palau, pp 10–29

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Supplementary Table 1	A list of	hern	latypic	coral	s at tl	le 17	sites i	1 the r	orthw	vest Pa	cific.	1 and	0 rep	resent	t pres	suce a	and absence of the specific corals at the site, respectively
site no.	1	. 1	3	4	5	9	7	8	6	10	1 1	2 13	3 14	15	16	17	7 Remarks
	smidziroi-oniAO	Southern Mariana Islands	Northern Mariana Islands	sbnslsl uslands	ogasawara Islands	newieT	одвіэqілэтА втвуэвҮ	sbnslsl swamidO	миуако Атспірсіадо	Taneorashima	uzimidase20T	seulemA	smahama	Mushimoto	sluzninə ^q uzl	Таѓеуата	
Acanthastrea amakusensis	0	0	0	0	-	0		0	0			-	-	-	-	0	Micromussa amakusensis in Veron (2000)
Acanthastrea bowerbanki	0	0,	0,	0,	0,	0,		_ ,	- 0,	。, 。,	·		0,	0,	0 0	0,	
Acanthastrea echinata	0				_ ,	,		_ ,	_ ,		_ ,		- ,		0 (
Acanthastrea hemprichii Acanthastrea hillan	0 0	0 -	0 0												0 0	0 0	
Acanthastrea nuae Acanthastrea ishiaakiensis		- 0		- c	- C	- 0			- 0								
Acanthastrea lordhowensis		0	0	0		0	. 0) O		~ -	~ —	0	~ —	~ —	0	
Acanthastrea rotundoflora	0	0	0	0	0	0	-	-	0		0	0	0	0	0	0	
Acrhelia horrescens	0	1	0	0	0	-	-	-	_	0	0	0	0	0	0	0	
Acropora abrolhosensis	0	0	0	-	0	0	-	-	0	0	0	0	0	0	0	0	
Acropora abrotanoides	-	1	0	0	1		1	-	_	0	0	0	0	0	0	0	A. danai In Nishihira and Veron (1995)
Acropora aculeus	-	-	0	0	-		-	_	_	0	0	0	0	0	0	0	
Acropora acuminata	0	-	0	0	1		-	-	0	0	0	0	0	0	0	0	
Acropora akajimensis	0	0	0	0	0	0	-		0	0	0	0	0	0	0	0	A. donei in Wallace (1999)
Acropora anthocercis	0	0	0	0	-		1	-	-	_	0	0	0	0	0	0	
Acropora aspera	0	-	0	0	0			_	_	-	-			-	0	0	
Acropora austera	1	0	0	-	-		-	_	0	0	0	0	0	0	0	0	
Acropora awi	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	
Acropora azurea	0	-	-	0	0	-	0	0	0	0	0	0	0	0	0	0	
Acropora carduus	0	0	0	0	-	0	-	-	_	-	0	0	0	0	0	0	
Acropora cerealis	0	-	-		-				_	-	0	0	0	0	0	0	
Acropora clathrata	0	0	0	-	0		-	-	0	0	0	0	0	0	0	0	
Acropora copiosa	0	0	0	0	0	0	-	_	0	-	0	0	0	0	0	0	
Acropora cylindrica	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	
Acropora cytherea		0	0	0	-		-		_	_	0	0	0	0	0	0	
Acropora dendrum	0	0	0	0	-		-	0	0	0	-	-		—	0	0	
Acropora derawanensis	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	
Acropora digitifera	0	-	-	-	-				<u> </u>	_	0	—	0	0	0	0	A, japonica for the mainland Japan in Veron (2000)
Acropora divaricata	-	0	0	0	-	-	-	_	_	_	-	-	0	0	0	0	
Acropora donei	-	0	0	-	0		0	0	0	0	0	0	0	0	0	0	
Acropora echinata	0	0	0	0	0			_	_	0	0	0	0	0	0	0	
Acropora elegans	0	0	0	0	0	0			0	0	0	0	0	0	0	0	
Acropora elseyi	1	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	
Acropora exquisita	0	0	0	0	0	-	-	_	0	1	0	0	0	0	0	0	
Acropora florida		-	0	-	-		-	_	_	_	1	-	-	-	0	0	
Acropora formosa	0	-	0	1	1	-	-	-	_	1	0	0	0	0	0	0	A. muricata in Wallace (1999)

							S	upple	menta	Iry T	able 1	ŭ	ntinu	ed			
Acropora gemmifera	-	-	-	-	1	1	1	1	1	0	0	0	0	0	0	0	
Acropora glauca	0	0	0	0	0	1 (0	0	0		1		0	1	0	0	
Acropora globiceps		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Acropora grandis	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	
Acropora granulosa	0	-	0	0	-	1	1	0	-	0	0	0	0	0	0	0	
Acropora horrida	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	
Acropora humilis	0	-	1	1	1	1	1	-	0	0	0	0	0	0	0	0	
Acropora hyacinthus	-	0	0	1	-	1	-		1	-	-	-	-	-	0	0	
Acropora insignis	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	
Acropora intermedia	-	0	0	-	1	1	1	-	1	0	0	0	0	0	0	0	synonym: A. nobilis
Acropora irregularis	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	A. sukarnoi in Wallace (1999)
Acropora kimbeensis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Acropora kirstyae	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	
Acropora latistella	-	0	0	0	-	1	1		1	-	0	-	0	0	0	0	
Acropora listeri	0	0	0	0	0	1	1	0	0	-	0	0	0	0	0	0	
Acropora longicyathus	0	-	0	1	1	0	1	1	0	0	0	0	0	0	0	0	
Acropora loripes	0	-	1	-	0	1	1	1	1	-	-	-	0	0	0	0	
Acropora lovelli	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Acropora lutkeni	0	-	0	1	0	1	0	0	0	0	0	0	0	0	0	0	
Acronora microclados	C	0	0	0	_	-	-	-	0	0	0	0	0	0	0	0	
Acronora micronhthalma	0	C	0		0	_	-			C	0	C	C	0	C	C	
Acronova millenova				0	0		·		·			0				0	
Arronora mirahilis																\sim	
Act opor a min aonis Actornes mentionless		> -	> -	> -		> -		- <									
Acropora monuculosa	0		- <	- <		- 0		-	0 0	\supset					○ <	\rightarrow	
Acropora multiacuta	0	_	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Acropora muricata			0	1	-	1	-	1	-	0	0	0	0	0	0	0	synonym: A. formosa
Acropora nana	-	0	0	0	-	-	-	1	-	0	0	0	0	0	0	0	
Acropora nasuta	0	-	1	1	0	1	1	1	1	0	0	0	0	0	0	0	
Acropora nobilis	0	0	0	0	1	1	1	, ,	1	0	0	0	0	0	0	0	A. intermedia in Wallace (1999)
Acropora ocellata	0	-	-	0	0) (0	0	0	0	0	0	0	0	0	0	
Acropora palmerae	0	-	1	0	0	1	0	0	0	0	0	0	0	0	0	0	
Acropora paniculata	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	
Acropora parilis	0	0	0	0	0	0	-	0	-	0	0	0	0	0	0	0	
Acropora pichoni	0	0	0	1	0) (0	0	0	0	0	0	0	0	0	0	
Acropora pruinosa	0	0	0	0	0	0	0	0	0	0	-	-	0	0	-	0	
Acropora pulchra	0	0	0	-	-	-	-	-	-	0	0	0	0	0	0	0	
Acropora rambleri	0	-	-	0	0) 0	0	0	0	0	0	0	0	0	0	0	
Acropora robusta	-	0	0	1	-	-	1	1	-	0	0	0	0	0	0	0	
Acropora rosaria	-	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	
Acropora samoensis	0	0	0	1	0	0	1	0	-	-	0	0	0	0	0	0	
Acropora sarmentosa	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	
Acropora secale	0		0	-	-	1	1	0	1	0	0	0	0	0	0	0	
Acropora sekiseiensis	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0	0	
Acropora selago	0	-	-	0	-	1	-	0	-	0	0	0	0	0	0	0	
Acropora solitaryensis	0	0	0	0	_	_	-	0	1	-	-	-	-	-	-	0	
Acropora stoddarti	0	0	0	0	0) 0	0 (0	0	1	0	0	0	0	0	0	

							•1	Iqqué	ement	tary T	able]	0	ontin	ned			
Acropora striata	0	_	_	-	0	0	_	0	1	1	0	0	0	0	0	0	
Acropora subglabra	0	0	_	_	0	_	_	-	0	0	0	0	0	0	0	0	
Acropora subulata	0	0	_	_	-	-	_	0	-	1	1	0	0	0	0	0	
Acropora surculosa	0	_	_	0	0	0	_ _	0	0	0	0	0	0	0	0	0	
Acropora tanegashimensis	0	0	_	0	0	0	_	0	0	-	0	0	0	0	0	0	
Acropora tenella	0	_	_	0	0	-	0	0	0	0	0	0	0	0	0	0	
Acropora tenuis	-	_	_	_	0	_	_	-	-	0	0	0	0	0	0	0	
Acropora teres	0	_	_	0	0	0	_	0	0	0	0	0	0	0	0	0	
Acropora tumida	0	0	_	0	0	0		0	0	0	1	0	-	-	0	-	
Acropora valenciennesi	0	0	_	0	0	_	_	-	0	0	0	0	0	0	0	0	
Acropora valida	1	_	_	0	0	_		-	1	-	1	-		-	0	0	
Acropora vaughani	0	_	~	1	1			-	0	0	0	0	0	0	0	0	
Acropora verweyi	-	_	_	_	0			0	Γ	-	0	0	0	0	0	0	
Acropora wallaceae	0	0		0	0	. 1	_	0	0	0	0	0	0	0	0	0	
Acropora willisae	0	0	_	0	1)		0	-	0	1	0	0	0	0	0	
Acropora yongei	0	0	_	_	_	_		0	0	0	0	0	0	0	0	0	
Alveopora allingi	0	_	_	_	0)		-	0	0	0	0	0	0	0	0	
Alveopora catalai	0	0	_	0	0	0	0	0	0	0	0	0	0	0	0	0	
Alveopora excelsa	0	0	_	0	0			0	-	-	0	0	-	-	0	0	
Alvenna fenestrata		_	_	C			_	0	C	С	C	C	C	C	C	C	
Alvennora ianonica														·			
Alternation and and a second sec					> -			> -						- <			
Alveopora sponglosa	0 0		_						- <			- <	- <				
Alveopora tizardi	0	_	_	0					0	0	0	0	0	0	0	0	
Alveopora verrilliana	0	_	_	0	0	_	_	-	-	0	0	0	0	0	0	0	
Anacropora forbesi	0	0	_		0	_	_	-	0	0	0	0	0	0	0	0	
Anacropora matthaii	0	0	_	0	0	_	_	0	0	0	0	0	0	0	0	0	
Anacropora puertogalerae	0	0	_	0	0		_	0	0	0	0	0	0	0	0	0	
Anacropora reticulata	0	0	_	0	0		0	0	0	0	0	0	0	0	0	0	
Anacropora spinosa	0	0	_	0	0	0	0	0	0	0	0	0	0	0	0	0	
Astreopora expansa	0	0	_	0	0	0	_	0	0	0	0	0	0	0	0	0	Astreopora explanata in Nishihira and Veron (1995).
Astreopora explanata	0	0	_	0	1	-	0	0	0	-	0	0	0	0	0	0	A. expansa in Veron (2000).
Astreopora gracilis	0	_	_	0	-	-	_	1	-	0	-	0	0	-	0	0	
Astreopora incrustans	0	0	_	0	-	-	_	0	-	1	1	0	-	-	0	0	
Astreopora listeri	0	_	_		0	_	_	1	-	0	0	0	0	0	0	0	
Astreopora macrostoma	0	0	~	0	0	0	_	0	0	-	0	0	0	0	0	0	
Astreopora myriophthalma	1	_	_	1	_	_	_	-	-	-	1	-	0	0	0	0	synonym: A. eliptica
Astreopora ocellata	0	_	_	0	_	_	0	0	0	0	0	0	0	0	0	0	
Astreopora randalli	0	_	_	0	0	0	_	0	0	0	0	0	0	0	0	0	
Astreopora suggesta	0	0	_	0	0	_	0	0	0	0	0	0	0	0	0	0	
Australomussa rowleyensis	0	0	_	0	0	_	_	-	-	0	0	0	0	0	0	0	
Barabattoia amicorum	0	0	_	0	_	_		-	-	-	1	-		1	0	0	
Blastomussa merleti	0	0	_	0	0	_	_	-	1	0	0	0	0	0	0	0	
Blastomussa wellsi	0	0	~	0	0	_	_	-	-	-	-	-	0	-	0	-	
Boninastrea boninensis	0	0	_	0	1	0	_	0	0	0	0	0	0	0	0	0	
Cantharellus jebbi	0	0	_	1	0	0	_	0	0	0	0	0	0	0	0	0	
Catalaphyllia jardanei	0	0	_	0	0	0	_	0	0	0	0	0		-	0	0	

							Ś	uppleı	nenta	ry Tal	ole 1	Cor	tinue	Ч			
Caulastrea curvata	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	
Caulastrea echinulata	0	0	0	0) 1	1	-	0	-	0	0	0	0	0	0	0	
Caulastrea furcata	0	0	0	1	_	1		-	1	0	0	0	0	0	0	0	
Caulastrea tumida	0	0	0	1	-	1	-	-	1	1	1	1	_	-	0	-	
Coeloseris mayeri	0	0	0	-	- 1	-	-		0	0	0	0	0	0	0	0	
Coscinaraea columna	1	-	1	1	_	1	-	-	1	1	1	1	_	_	_	0	
Coscinaraea crassa	0	0	0	0)	0	-	0	-	-	0	0	-	0	0	0	
Coscinaraea exesa	0	0	0	1		0	-	0	0	0	0	0	0	0	0	0	
Coscinaraea hahazimaensis	0	0	0	0	0	0	0	0	0	-	-	0	0	-	-	0	
Coscinaraea monile	0	0	0	0	0	0		0	0	-	1	0	0	0	-	0	
Coscinaraea wellsi	0	0	0	0	0	0	-	-	0	0	1	0	0	0	0	0	
Ctenactis albitentaculata	0	-	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Ctenactis crassa	0	0	0	1) 1	-	-	-	-	0	0	0	0	0	0	0	
Ctenactis echinata	0		0	1		1		1	-	0	1	0	0	0	0	0	
Cycloseris costulata	0	-	1	1		1		1	0	0	0	0	0	0	0	0	synonym: <i>Fungia costulata</i>
Cycloseris curvata	0	0	0	0	0	-	1	0	0	0	0	0	0	0	0	0	
Cycloseris cyclolites	0		0	0	_	0		-	-	0	0	1	-	-	-	-	
Cycloseris fragilis	0	0	0	0) 1	0	0	0	0	0	0	0	0	0	0	0	
Cycloseris hexagonalis	0	1	0	1	0	-	0	-	0	0	0	0	0	0	0	0	
Cvcloseris patelliformis	0	0	0	0	0	-	-	0	0	-	0	0	-	0	0	0	
Cycloseris sinensis	0	-	0	1)	-	0	0	0	0	0	0	0	0	0	0	
Cycloseris somervillei	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Cycloseris tenuis	0	-	0	0) 1	0	0	0	0	0	0	0	0	0	0	0	
Cycloseris vaughani	0	-	0	1	_	1		-	1	0	0	1	0	0	0	0	
Cynarina lacrymalis	0	0	0	1) 1	-	-	-	0	-	1	1	-	_	0	0	
Cyphastrea agassizi	1	0	0	0	0	-		0	-	0	0	0	0	0	0	0	
Cyphastrea chalcidicum	-	-	-	1	_	-	-	-	1	1	1	_	_	-	-		
Cyphastrea decadia	0	0	0	0	0	-	-	1	0	0	0	0	0	0	0	0	
Cyphastrea japonica	0	0	0	0	_	-	-	0	1	1	1	_	_	-	-	0	
Cyphastrea microphthalma	-	-		-	-	1		-	1	-	1	1	0	-	0	-	
Cyphastrea ocellina	0		1	0	0	-	0	0	0	0	0	0	0	0	0	0	
Cyphastrea serailia	-		1	0	_	-		-	-	-	1	-		-	-	-	
Diaseris distorta	0	-	0	-	0	-		0	0	0	0	0		0	0	0	
Diaseris fragilis	0	-	0	1		-	-	-	0	0	0	0	0	0	0	0	
Diploastrea heliopora	0	-	0	1	-	1		-	0	0	0	0	0	0	0	0	
Echinophyllia aspera	0		-	-	_	-	-	-	-	1	1	_	_	-	_		
Echinophyllia costata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Echinophyllia echinata	0	-	0	0	_	-	-	-	1	0	1	_	0	0	0	0	
Echinophyllia echinoporoides	0	0	0	-		-		-	1	0	0	0	0	0	0	0	
Echinophyllia nishihirai	0	0	0	0	0	1	-	-	0	0	1	0	0	0	0	0	Echinomorpha nishihirai in Veron (2000)
Echinophyllia orpheensis	0	0	0	0	_	-	-	-	0	0	0	0	0	0	0	0	
Echinophyllia patula	0	0	0	0	0	-	-	0	0		0	0	0	0	0	0	
Echinopora gemmacea	1	0	0	0	- 1	-	-	-	-	0	0	0	0	0	0	0	
Echinopora lamellosa	1	-	-	_	_	1	-	-	-	-	-	0	0	0	0	0	
Echinopora mammiformis	0	0	0		0		0		0	0	0	0	0	0	0	0	
Echinopora pacificus	1	0	0	0	-	-	_	0	1	0	0	0	0	0	0	0	

							Ś	upple	menta	ary Ta	ble 1	Con	tinue	_		
Euphyllia ancora	0	0	0	0	1	-	-	-	1	1	-	1	_	1	-	
EuchvIlia cristata		C	0	0	0			C	С	C	C	C	0	0	0	
Euphyllia divisa	• C	0	0	_	0	_	0	. —	0	0	0	0	0	0	0	
Euphyllia glabrescens	0	-	1	0	1	-	-	1	1	0	0	0	0	0 0	0	
Euphyllia paraancora	0	0	0	0	0	0	0	0	0	0	0	0	0	0 0	0	
Euphyllia paraglabrescens	0	0	0	0	0	0	0	0	0	1	0	0	0	0 0	0	
Euphyllia yaeyamaensis	0	0	0	0	0	_	-	0	-	0	0	0	0	0 0	0	
^F avia danae	0	-	0	0	0	_	-	0	0	-	_	0	0	0 0	0	
Favia favus	1	-	-	1	1	-		-	-	-	-	-	-	1 0	0	
^F avia helianthoides	0	-	-	1	0	-	-	0	0	0	-	-	0	1	0	
Favia laxa	1	0	0	1	0	—	-	-	0	1	1	-	0	1 0	0	
^F avia lizardensis	0	0	0	0	1	-	-	-	-	1	-	-	0	1	0	
Favia maritima	0	-	0	1	1	-		0	-	0	0	0	0	000	0	
⁴ avia matthaii	-	-	-	1	1	-	-	-	-	0	0	0	0	000	0	
Favia maxima	0	0	0	0	1	-	1	-	-	1	1	0	-	000	0	
Favia pallida	-	-	-	1	-	-	-	-	-	-	_	-	0	1	0	
^F avia rotumana	0	1		0	1	-	1	1	-	1	0	0	0	000	0	
^F avia rotundata	-	0	0	1	1	1	-	-	0	-	0	0	0	1 0	0	
^F avia speciosa	0	0	0	-	1	-	-	-	1	1	1	1	1	1	1	
Favia stelligera	-	1	1	1	0	1	1	1	1	0	0	0	0	0 0	0	
^L avia veroni	C	0	0	0	-	-	-	-	-	-	_	-	_	1	0	
Eavier vietnamensis		C	C	0			C	C	C	C	C	C	C	0	C	
Favitas abdita		~ -		~ -	> -	> -	~ -		~ -		\sim					
	0		- <	- <									- 0			
H avites chinensis	0,			-	 								→ -	0 - 0 -		
avites comptanata	_	ο,	ο,	0 (_ ,	_, ,	_, ,	0,	_, ,	_, ,	_ ,	_ ,	_, ,	_ ,))	
Favites flexuosa	1	-	-	0	1		-	-		1	-	_	_	1	0	
Favites halicora	1	0	0	_	1	-		-	0	0	0	0	0	0	0	
Favites pentagona	0	0	0	1	1	-	-	-	-	-	-	-	_	1	0	
Favites russelli	0	1	-	0	1	_	-	-	-	1	-	-	, ,	1	0	
Favites stylifera	0	0	0	0	0	_	1	0	-	0	0	0	0	000	0	
⁴ ungia concinna	0	1		-	0	_	-	-		0	0	0	0	0 0	0	
^F ungia danai	0	1	0	1	0	_	1	1	0	0	0	0	0	000	0	
^F ungia fungites	0	1	-	1	0	_	-	-		0	1	0	0	0	0	
^F ungia granulosa	0	-	0	_	0	-	-	-	-	0	0	0	0	0	0	
^F ungia horrida	0	-	0	-	0	0	0	0	0	0	0	0	0	000	0	
^F ungia moluccensis	0	0	0	-	0	-	-	-	0	0	0	0	0	000	0	
^F ungia paumotensis	0	1	0	1	0	-	1	1	-	0	0	0	0	0 0	0	
^F ungia repanda	0	-	0	-	1	-			-	0	0	0	0	000	0	
^F ungia scabra	0	0	0	0	0	-	-	-	0	0	0	0	0	000	0	
⁴ ungia scruposa	0	0	0	-	0	-	-	0	1	0	0	0	0	000	0	
^F ungia scutaria	Γ		-	1	1	-		-	-	-	0	0	0	000	0	synonym: Fungia gravis
⁴ ungia spinifer	0	1	0	-	0	0	-	-	0	0	0	0	0	0 0	0	
⁴ ungia (Pleuactis) taiwanesis	0	0	0	0	0	0	0	0	0	0	0	0	0	000	0	
Fungia tenuis	0	0	0	1	0	0	0	0	0	0	0	0	0	0 0	0	Cycoloseris tenuis in Randall (1995)
^E ungia valida	0	0	0	0	0	-	-	-	1	0	0	0	0	0	0	
Galaxea astreata	0	0	0	1	_	-	-	-	0	0	-	0	0	0	0	

							S	ıppleı	nenta	ury Tâ	able 1	C	ntinue	p			
Galaxea fascicularis	0	-	1	0	1	1	1	-	_	1	_	_	0	0	0	0	
Galaxea horrescens	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Gardineroseris planulata	1	,	-		1	_	1	-	_	_	_	0	0	0	0	0	
Goniastrea aspera	0	0	0	1	-	_	1	1	_	_	_	_	0	-	-	0	
Goniastrea australiensis	0	0	0	1	1	-	1	-	0	1	_		1	1	-	0	
Goniastrea deformis	0	0	0	0	0	0	0	0	0	0	_		1	-	-	-	
Goniastrea edwardsi	C	-	1	0	0	-	1	1	1	_		_	0	0	0	0	
Goniastrea favulus		0	0	0	0	_	_		_	_			-	_	-	0	
Goniastrea palanensis	• 0	C	C	-	0	0	C	0	0				C	C	C	C	
Goniastrea pectinata		, 	, 	·	, 	~ 	, .	, 	, 	, —	. –			0	0	0	
Goniastrea retificrais	- 0	·	. –	. –	. –	. –	. –	. –		. –) –	\sim) C	
Contrastrea relijor mus	0 0			- <	- <				- <					- 0			
Goniopora burgosi	0	D (0	0	0			- 	- 	 	_			0 0	0 (
Goniopora cellulosa	0	0	0	0	0	0	0	0	0	_	_	_	0	0	0	0	
Goniopora columna	0		-	1	0	1	1	1	_	_	0	<u> </u>	0	0		-	
Goniopora djiboutiensis	0	-	0	0	1	1	-	0	1	1	-	0	0	0	0	0	
Goniopora eclipsensis	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
Gonionora fruticosa	C	-	-	-	-	0	_	_	_	C	0	0	0	0	C	0	
Gonionara lahata			. –				. –	. –					>	~ —	>	>	
	0 0			> <							_ (_		- <	- (- <	
Goniopora minor	0	-	-	0	0	_	_	_	_	_	_	_	0	0	0	0	
Goniopora pandoraensis	0	-	0	0	0	0	-	0	_	0	0	_ _	0	0	0	0	
Goniopora pendulus	0	0	0	0	-	0	0	0	0	0	_	_	0	-	0	0	
Goniopora polyformis	C	С	С	0	0	0	C	0	0	c	0	-	C	C	С	C	
Gontonora somaliansis		-	-	0	-		-	-	_	_							
	-	- <	- <						- <					> <			
Contopora stokest	0		> <		> <	, c	_ ,	_ ,	- - (> ,) (\supset	
Goniopora stutchburyi	0	0	0	0	0	_	_	-	0	0			1	-	0	0	
Goniopora tenuidens	0	-	1	0	0	_	1	1	_	0	_	_	0	0	0	0	
Gyrosmilia interrupta	0	0	0	0	0	0	1	0	0	0	0	<u> </u>	0	0	0	0	
Halomitra pileus	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	
Heliofuncia actiniformis	С	0	0	1	0	1	1	0	-	0	0	0	0	0	0	0	
Hernolitha limax	0	, -		-	0		_	-		_	_	_	0	С	0	0	
Hernolitha weberi		-	C	-	-	0	_	0	-				0	0	C		
Heteronsammia cochlea				- 0	~ c		- 0	~ -						\sim	\sim	\sim	
Index opsumma cornea	> <					> -							> -	> -			
11 Junophora vorisai	> <	> -		> -	> -		> -	> -	- c	- > -	 					> -	
nyanophora exesa	0		> <	_ ,		_, ,									- (- (
Hydnophora grandis	0	0	0	-	0	I	0	0	0	0		_	0	0	0	0	
Hydnophora microconos	0		-	-	0	-	_	-	_	_		_ _	0	0	0	0	
Hydnophora pilosa	0		0	0	0	0	0	0	0	0	0	<u> </u>	0	0	0	0	
Hydnophora rigida	0	0	0	1	0	-	1	1	_	_	0	<u> </u>	0	0	0	0	
Isopora brueggemanni	0	0	0	Ļ	0	-	1	-	_	0	0	0	0	0	0	0	synonym: Acropora bruggemanni
Isopora cuneata	0	0	0	0	0	1	1	1	0	0	-	0	0	0	0	0	synonym: A. cuneata
Isopora palifera	1	-	1	1	1	-	1	-	-	_	0	0	0	0	0	0	synonym: A. palifera
Leptastrea bewickensis	0	0	0	0	1	0	1	1	0	_	_	0	0	0	0	0	
Leptastrea bottae	0	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
Leptastrea inaequalis	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	
Leptastrea pruinosa	1	0	0	1	1	1	1	1	-	_	_	_	0	0	1	0	
Leptastrea purpurea	-	-	1	1	1	1	1	1	-	_	_		1	1	-	-	

								Supj	plem	entai	.y Ta	ble 1	Col	atinu	ed		
Leptastrea transversa	0	1	1	_		_	1	1	1	1	0	0	0	0	0	0	0
Leptoria irregularis	0	0	0	0	0	_	1	1	-	1	0	0	0	0	0	0	0
Leptoria phrygia	-	_	_	_	_	_	1	-	-	-	0	0	0	0	0	0	0
Leptoseris amitoriensis	0	0	0	0	0	~	1	0	0	0	0	0	0	0	0	0	0
Leptoseris explanata	0	-	-	_	_	_	1	1	-	-	0	0	0	0	0	0	0
Leptoseris foliosa	0	1	0	0	0		1	1	1	1	0	0	0	0	0	0	0
Leptoseris gardineri	0	-	0	0	0	_	1	0	-	0	0	0	0	0	0	0	0
Leptoseris hawaiiensis	0	-	-	_	_	_	1	1	-	1	-	0	0	0	0	0	0
Leptoseris incrustans	0	_	-	0	_	_	1	0	0	0	0	0	0	0	0	0	0
Leptoseris mycetoseroides	0	1	1	0	_	_	1	1	-	-	-	-	-	-	-	-	-
Leptoseris papyracea	0	-	0	0	0	_	1	1	-	0	0	0	0	0	0	0	0
Leptoseris scabra	0	-	-	0	_	_	1	1	_	1	0	-	0	0	0	0	0
Leptoseris solida	0	1	1	0	0	_	1	1	0	0	-	0	0	0	0	0	0
Leptoseris striata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptoseris tubulifera	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptoseris yabei	0	0	0	_	_	_	1	-	_	-	-	0	0	0	0	0	0
Lithophyllon lobata	0	0	0	0	0		1	1	-	-	0	0	0	0	0	0	0
Lithophyllon mokai	0	0	0	1	_	_	0	0	0	0	0	0	0	0	0	0	0
Lithophyllon undulatum	0	0	0	0	_	_	1	1	0	0	-	-	-	-	-	0	0
Lobophyllia corymbosa	-	1	_	_	_	_	1	1	-	1	-	0	0	0	0	0	0
Lobophyllia flabelliformis	0	0	0	0	_	_	0	0	0	0	0	0	0	0	0	0	0
Lobophyllia hataii	0	1	0	1	_	_	1	1	-	-	-	0	-	0	1	0	0
Lobophyllia hemprichii	-	-	-	_	_	_	-	-	-	-		0	-	-	-	0	0
Lobophyllia pachysepta	0	0	0	0	_	_	1	1	_	0	0	0	0	0	0	0	0
Lobophyllia robusta	0	0	0	0	0	_	1	1	0	1	-	0	-	0	1	0	0
Madracis asanoi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0
Madracis kirbyi	0	1	0	1	0		0	0	0	0	0	0	0	0	0	0	0
Merulina ampliata	-	-	0	_	_	_	1	1	-	-	-	0	0	0	0	0	0
Merulina scabricula	0	0	0	1	_	_	1	1	1	1	-	0	0	0	0	0	0
Montastraea annuligera	1	0	0	1	_	_	1	1	0	0	0	0	0	0	0	0	0
Montastraea colemani	0	0	0	1	0		0	0	0	0	0	0	0	0	0	0	0
Montastraea curta	_	-	1	_		_	1	-	-	-	-	-	-	-	-	0	0
Montastraea magnistellata	0	1	1	1	_	_	1	1	-	1	-	-	0	0	0	0	0
Montastraea multipunctata	0	0	0	0	0	_	1	1	0	0	-	0	0	0	0	0	0
Montastraea valenciennesi	1	0	0	-	_	_	1	1	-	1	-	1	-	0	1	0	0
Montipora aequituberculata	0	0	0	_	_	_	-	-		-	-	0	0	0	0	0	0
Montipora altasepta	0	0	0	1	_	_	1	0	0	0	0	0	0	0	0	0	0
Montipora angulata	0	0	0	_	_	_	1	1	0	-	0	-	0	0	0	0	0
Montipora cactus	0	0	0	0	_	_	1	_	0	0	0	0	0	0	0	0	0
Montipora caliculata	1	-	1	0	_	~	-	0		0	0	0	0	0	0	0	0
Montipora capitata	0	0	0	-	0	_	1	0	0	0	0	0	0	0	0	0	0
Montipora cebuensis	0	0	0	0	<u> </u>	_	1	0	0	0	0	0	0	0	0	0	0
Montipora danae	0	1	0	0	_	_	1	1	1	1	-	1	0	0	1	0	0
Montipora digitata	-	0	0	_	_	_	1	1	1	1	0	0	0	0	0	0	0
Montipora efflorescens	-	0	0	_	_	_	1	1		0	0	0	0	0	0	1	0
Montipora effusa	0	0	0	0	0		1	-	0	-	0	-	-	0	-	0	0

								Jupple	ement	ary T	able	0	ontinu	led			
Montipora floweri	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	
Montipora foliosa	С	Ļ	0	0	-	1	1	1	-	0	0	0	0	0	0	0	
Montinora foveolata	~ —	-			0			-	-	0	0	0	0	C	0	C	
Montinora friahilis		C	С	C	C	C		C	C		C	C	C	C	C	C	
Montipora gaimardi	• c	0	0	0	0	0		0	0	0	0	0	0	0	0	0	
Montipora granulosa		. 	C	C	C	C		C	C	C	C	C	C	C	C	C	
Montipora grisea	~ —	. <u></u>	-	0	C		. –	. —	C	C	C	C	C	C	C	C	
Montinora hirsuta		0	- C	. –				0		0			• C	• C			
Montpot a nu suta Montinora hisnida	> -				>	> -		> -	>		>	> -					
Montipora hispica Montipora hoffmaistari	- <			- 0	- -	- .		• •	- -		- 0	- 0					
Montpola hojjmetstert	> -																
Monupora Incrassata) (0	-		- ,		> •	- 0	,	> ,	⊃ ,	⊃ •	> •	-	> <	
Montipora informis	-	0	0	0	0	_	1	Ι	0	-	-	-	-	-	0	0	
Montipora lobulata	0		-	0	0	0	0	0	0	0	0	0	0	0	0	0	
Montipora mactanensis	0	0	0	0	0	0	1 0	0	0	0	0	0	0	0	0	0	
Montipora malampaya	0	0	0	-	0	0	1 0	0	0	0	0	0	0	0	0	0	
Montipora millepora	0	0	0	0	-	1	1	1	0	0		-	-	-	0	0	
Montipora mollis	-	0	0	0	-	-	-	-	-	-			-	-	0	0	
Montinora monasteriata		. 	-	. 	-	. <u></u>	-	-	C		-	C	С	C	C	C	
Montinora nodoca						· -					• <			~ <			
			> <	> -			> - > -						> <	> <	> <		
Montipora petitjormis	-	0	0	-	0	_	1	0	0	0	0	0	0	0	0	0	
Montipora samarensis	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	
Montipora spongodes	0	0	0	-	-	1	1 0	0	0	-		-	1		0	0	
Montipora spumosa	0	0	0	0	0	1	1	0	-	-	0	0	0	-	0	0	
Montinora stellata	0	С	С	-	_	_	-	-	-	С	С	С	С	С	С	С	
Montinora taiwaneris								- C		0							
Montpola turbanchists	> -	- c	> -	> -			> - > -	> -									
Monupora tupercutosa	-	- •	- •		0,					, ⊂	> .	⊃ ,	0	0	0	⊃ ∘	
Montipora turgescens	-	0	0	0	_	-	1	-	-	-			-	, - 1	,	0	
Montipora undata	0	0	0	0	-	1	1	1	1	-		0	0	0	0	0	
Montipora venosa	0	-	-	-	-	-	1	0	-	0	0	0	0	0	0	0	
Montipora verrilli	0	-	-	0	0	0	0 0	0	0	0	0	0	0	0	0	0	
Montipora verrucosa	0	1	1	0	-	1	1	1	-	0	0	0	0	0	0	0	
Montipora vientnamensis	0	0	0	-	0	0	0 0	0	0	0	0	0	0	0	0	0	
Mycedium elephantotus	0	-	0	1	1	1	1 1	1	1	1		-	1	-	-	0	
Mycedium robokaki	0	0	0	0	1	1	1 0	0	0	0	0	0	0	0	0	0	
Oulastrea crispata	С	0	0	0	-	1	1	0	1	-		-	1	-	-	1	
Oulonhvllia hennettae	• c	С	С	-	0	-	-	-		0	0	С	С	С	0	С	
Oulonbullia cuicna					. –		. –	-									
Outopristita ci ispu	> <			> -	- <		- 0	- <		- <	- <	- <					
Oulopnyuia tevis	0	> <) (, c)))	> •	> <	> <	> <	> <	> <	> <	> <	> <	synonym: <i>Ошорнуша стъра</i>
Oxypora glabra	0	0	0	-	0	_	1 0	_	0	0	0	0	0	0	0	0	
Oxypora lacera	0	0	0	-	-	1	1	1	-	-	-	-	1	-		0	
Pachyseris rugosa	0	0	0		-	-	1	1	-	0	0	0	0	0	0	0	
Pachyseris speciosa	0	-	-	-	0	1	1	1	1	-		0	0	0	0	0	
Palauastrea ramosa	0	0	0	-	0	0	1	1	0	0	0	0	0	0	0	0	
Pavona bipartita	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
Pavona cactus	0	-	0			-	1	-	-		0	0	0	0	0	0	
Pavona clavus	-	-	-	0	-	1	1	0	0	0	0	0	0	0	0	0	

		Pavona minuta in Nishihira and Veron (1995)											Pectinia ayleni in Veron (2000)									Plerogyra sinuosa in Veron (2000)																				
0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	-	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
-	0	0	0	0	0	0	0	0	-	-	0	0	-	_	-	0	0	0	-	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	-	-	0	0	-	-		0	0	0	0	0	0	0	0	0	-		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
_	0	-	-	0	0	0	0	0	-	1	0	0	-	-	-	0	-	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
_	С	0	_	C	0	C	C	C	-	C	0	C	_	1	_	0	-	C	0	С	0	C	0	C	-	_	C	-	0	0	_	C	C	0	С	0	0	С	C	_	0	C

								Sup	plen	nenta	ry T	ble 1	Co	ntinu(ed		
Pavona danai	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0
Pavona decussata	0	-	0	0	_	-	-	-	-	-	1	1	_	0	-	0	0
Pavona divaricata	C	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pavona duerdeni	~ -	-	_	_	-	-	_	-	-	-	_	0	-	0	0	0	0
Pavona explanulata	- 0	-	0		-	<i>.</i>	<i>.</i>	.	-	-	-	. 	<i>.</i>	C	C	. <u></u>	C
Pavona frondifera		C	C	C	C	-	-	-	-	-	-	C	C	C	C	C	C
Pavona maldivensis		-	-	0	-	-	0	-	0	-	-	0	0	0	0	0	0
Pavona varians		-	-	-	-	-	_	-	-	-	-	0	0	0	0	0	-
Pavona venosa	. –	-	-	1	-	-	-	-	-	Г	0	0	0	0	0	0	0
Pectinia alcicornis	0	0	0	1	0	0	-	-	-	0	0	0	0	0	0	0	0
Pectinia lactuca	0	0	0	1	0	-	-	-	-	1	0	-	-	-	-	0	0
Pectinia paeonia	0	-	0	0	0	1	-	1	-	1	0	0	1	-	1	0	0
Pectinia teres	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0
Physogyra lichtensteini	0	0	0	1	0	1	-	-	-	0	0	0	0	0	0	0	0
Physophyllia ayleni	0	0	0	0	-	0	-	0	0	0	0		-		-	0	0
Platygyra contorta	1	0	0	0	0	0	-	-	-	1	1	-	-	-	-	-	0
Platygyra daedalea	1	-	-	-	-	-	-	-	-	-	-		-		-		0
Platygyra lamellina	0	0	0	0	0	-	-	-	-	0	0	0	0	0	0	0	0
Platygyra pini	1	-	-	1	-	-	-	1	1	1	0		-	0	0	0	0
Platygyra ryukyuensis	0	0	0	0	-	-	-	-	-	-	0	0	0	0	0	0	0
Platygyra sinensis	-	0	0	1	0	-	-	-	-	1	-	0	0	0	-	0	0
Platygyra verweyi	0	0	0	0	0	0	-	-	0	-	-	0	0	0	0	0	0
Platygyra yaeyamaensis	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0
Plerogyra eurysepta	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0
Plerogyra simplex	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plerogyra sinuosa	0	0	0	1	0			-	-	1	0	0	0	0	0	0	0
Plesiastrea versipora	0	-	-	0	-	-	-	-	-	-	1		-		-	-	-
Pocillopora damicornis	1	-	-	0	-	-	-	-	-	-	1	-	-	-	-	0	0
Pocillopora elegans	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pocillopora eydouxi	1	-	-	1	-	-	-	-	-	-	0	-	0	0	0	0	0
Pocillopora ligulata	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pocillopora meandrina	0	-		0	0	-	-	1	0	0	0	0	0	0	0	0	0
Pocillopora verrucosa	1	-		-	-	-	-	-	-	-	-		0	0	0	0	0
Pocillopora woodjonesi	0	-	-	0	0	-		0	-	0	0	0	0	0	0	0	0
Podabacia crustacea	0	-	0	-	0	-	-	-	-	-	0	0	0	0	0	0	0
Podabacia motuporensis	0	0	0	1	0	0	-	0	-	0	0	0	0	0	0	0	0
Polyphyllia talpina	0		0	-	0	-	-	-	-	-	0	0	0	0	0	0	0
Porites annae	1	-	0	-	-	-	-	-	-	0	0	0	0	0	0	0	0
Porites aranetai	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0
Porites attenuata	0	0	0	1	0	0	-	-	0	1	0	0	0	0	0	0	0
Porites australiensis	1	-	-	1	0	-	-	-	-	0	0	0	0	0	0	0	0
Porites cylindrica	1	-	0	1	0	-	-	-	-	0	0	-	0	0	0	0	0
Porites deformis	0	0	0	0	0	0	-	0	-	0	0	0	0	0	0	0	0
Porites evermanni	0	0	0	0	0	0	-	1	0	0	0	0	0	0	0	0	0
Porites heronensis	0	0	0	0	1	0	0	-	0	1	1	-	-	-	-	-	-
Porites horizontalata	0	-	1	1	0	0	-	1	-	0	0	0	0	0	0	0	0

							Supp	lemei	itary [[able]	0	ontinu	ed		
Porites latistella	0	_)	0	0	1	1	0	0	0	0	0	0	0	0
Porites lichen	1		0	1	1	1	1	1	1	0	0	0	0	0	0 synonym: Porites eridan
Porites lohata			_	0	-	-	-	-	0	_	0	0	0	0	0
Porites lutea				-	-	-	. 	-	C	-	C	C	C	C	. 0
Porites maveri		_	0	0	C		0		0	0	0	0	0	0	0
Porites murranensis	, c		C	-	-	-	. .	0	C	C	C	C	C	C	- 0
Porites neorosensis			0	0	0	•	. 0	00	0	C		° C	0	0	0
Porites niorescens			. –	0	-	-	, <u> </u>	, –	° C	C	C	C	0 0		, U
Porites okinawensis			0	0	·	0	·	. 0	0	C		C	0	, 	0
Porites rus	, - -		_	0	-	-	-		0	0	0	0	0	0	0
Porites sillimaniani	0	_	0	0	0	-	-	0	0	0	0	0	0	0	0
Porites solida	1	0	0	0	1	-	-	1 0	0	0	0	0	0	0	0
Porites stephensoni	0		0	0	1	-	-	1 0	0	0	0	0	0	0	0
Porites vaughani	0	0	0	0	0	-	1	0	0	0	0	0	0	0	0
Psammocora contigua	1	0	(-	1	-	-	1	-	0	0	0	0	0	0
Psammocora decussata	0	_	0	0	0	0	-	0	0	0	0	0	0	0	0
Psammocora digitata	0		1	-	1	-	-	1	0	0	0	0	0	0	0
Psammocora explanulata	0	0)	0	0	0	0	0	0	0	0	0	0	0	0
Psammocora haimeana	1		1	1	1	1	1	0	0	0	0	0	0	0	0
Psammocora nierstraszi	0		-	0	0	-	1	0	-	0	0	0	0	0	0
Psammocora obtusangula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psammocora profundacella	1		0	1	1	-	1	1	1	1	1	1	-	-	1
Psammocora stellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psammocora superficialis	0	0)	1	1	-	1	1	-	1	-	1	-	-	1
Psammocora vaughani	0	_) 1	1	0	1	1	0	0	0	0	0	0	0	0
Pseudosiderastrea tayamai	0	_	0	0	1	1	1	0	0	0	0	0	0	0	0
Sandalolitha dentata	0	0) 1	0	1	0	0	0	0	0	0	0	0	0	0
Sandalolitha robusta	0		1	0	1	-	-	1	0	0	0	0	0	0	0
Scapophyllia cylindrica	1		0	1	1	Ļ	-	0	0	0	0	0	0	0	0
Scolymia australis	0		0	0	0	0	0	0	0	0	0	0	0	0	0
Scolymia vitiensis	0	_	0	1	1	-	-	1 0	0	0	0	0	0	0	0
Seriatopora aculeata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Seriatopora caliendrum	0	Ŭ	0	0	1	-	-	1	0	0	0	0	0	0	0
Seriatopora hystrix	0	_	-	0	1	1	-	1	0	0	0	0	0	0	0
Seriatopora stellata	0	_		0	1	0	0	0	0	0	0	0	0	0	0
Siderastrea savignyana	0	_	0	0	1	0	0	0	0	0	0	0	0	0	0
Stylaraea punctata	0	Ŭ	0	0	0	0	0	0	0	0	0	0	0	0	0
Stylocoeniella armata	0		-	0	-	1	1	1 0	0	1	0	-			0
Stylocoeniella cocosensis	0	_	0	0	0	-	0	0	0	0	0	0	0	0	0
Stylocoeniella guentheri	0	_	0	0	1	1	-	1	-	1	-	-		0	0
Stylophora pistillata	0	<u> </u>	1	0	1	-		1	1	1	-	0	0	0	0
Symphyllia agaricia	0	_	0	-	1	1	-	1	-	1	0	0	0	0	0
Symphyllia radians	0	_	0	-	1	1	-	1	-	1	0	0	0	0	0
Symphyllia recta	0	_	0	1	1		-	1	0	1	0	0	0	0	0
Symphyllia valenciennesii	0	Ŭ	0	1	-	1	1	1	0	1	-	-	-	0	0
Trachyphyllia geoffroyi	0	_		-	0	1	-	0	-	-	-	-	-	0	0

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							•1	lqquõ	emen	tary J	able	ŭ	ontinu	ed			
Turbinaria frondens	0	0	0	1	1	_	_	_	1	1	1	-	-	0	0	0	
Turbinaria irregularis	0	0	0	0	1	0	1	1	0 1	-	-		-	1	0	0	
Turbinaria mesenterina	0	0	0	1	-	1	_	_	1 1	-	-	0	0	0	0	0	
Turbinaria peltata	0	0	0	1	1	1	C	1	1 1	-	-	-	-	1	0	0	
Turbinaria reniformis	1		-	1	-	-	_	_	1		-	0	0	0	0	0	
Turbinaria stellulata	0	-	1	1	1	1	1	1	1 1	-	-	0	-	-	0	0	
Zoopilus echinatus	0	0	0	1	0	0	-	- 0	0 0	0	0	0	0	0	0	0	
Heliopora coerulea	0	-	-	1	1	1	1	-	1	0	0	0	0	0	0	0	
Tubipora musica	0	-	0	0	1	1	1	_	1	0	0	0	0	0	0	0	
Millepora dichotoma	0	-	-	0	0	1	1	_	1 0	0	0	0	0	0	0	0	
Millepora exaesa	1	1	1	0	0	0	1	1	1 0	0	0	0	0	0	0	0	synonnym: Millepora tuberosa
Millepora intricata	0	0	0	1	0	1	-	_	1	0	0	0	0	0	0	0	
Millepora murrayi	0	0	0	0	0	1	_	_	1 1	0	0	0	0	0	0	0	
Millepora platyphylla	1	-	-	1	-	1	-	_	1	0	0	0	0	0	0	0	
Millepora tenella	0	0	0	-	0	-	1	-	1 0	0	0	0	0	0	0	0	
Number of genera (81)	25	57	43	62	49	58 7	4	0	6 55	3 46	44	41	40	42	25	20	
Number of specieses (465)	93	205	125	209	180 2	96 30	58 3.	43 2.	49 22	6 149	127	98	78	95	45	24	

Data sources

Site 1 Okinotorishima: this study.

Randall RH (1995) Biogeography of reef-building corals in the Mariana and Palau Islands in relation to back-arc rifting and Sites 2 and 3 Southern and Northern Mariana Islands:

the formation of the eastern Philippine Sea. Natural History Research 3: 193-210

Randall RH (2003) An annotated checklist of hydrozoan and scleractinian corals collected from Guam and other Mariana Islands. Micronesica 35-36: 121-137

Sites 4 Palau Islands:

Yukihira H, Shimoike K, Golbuu Y, Kimura T, Vector S, Ohba H (2007) Coral reef communities and other marine biotopes in Palau. In: Kayanne H, Omori M, Fabricius K, Verheiji E, Colin P, Golbuu S, Yukihira H (eds) Coral Reefs of Palau. Palau International Coral Reef Center, Palau, pp10-29

Sites 5 Ogasawara Islands:

Tachikawa H, Suganuma H, Sato F (1991) Hermatypic corals of Chichijima and Hahajima Archipelago Research Report, Tokyo Metropolitan University, Tokyo 285-296

Site 6 Taiwan:

Dai CF (1991) Reef environment and coral fauna of southern Taiwan. Atoll Research Bulletin 354: 1-28

Dai CF, Horng S (2009b) Scleractinia Fauna of Taiwan. I. The Complex Group. National Taiwan University Press, Taipei Dai CF, Horng S (2009a) Scleractinia Fauna of Taiwan. II. The Robust Group. National Taiwan University Press, Taipei

Dat CF, Horng S (2009b) Scietractinia Fauna of Tatwan. I. The Complex Group. National Tatwan University Press, Tat Sites 7 to 17 Ryukyu Islands to mainland Japan

Nishihira M, Veron JEN (1995) Hermatypic Corals of Japan. Kaiyusha, Tokyo

Other references

Veron JEN, Stafford-Smith M (2000) Corals of the world. Australian Institute of Marine Science, Townsville MC, Qld, Australia

Hayashibara T, Seno K, Yoneyama S (2006) Reef-building corals on Okino-torishima. Tokyo Metropolitan Reserch on Fisherics Science 1: 87-95

Wallace C (1999) Staghorn Corals of the World. CSIRO Publishing, Collingwood