

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 post-glacial 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.

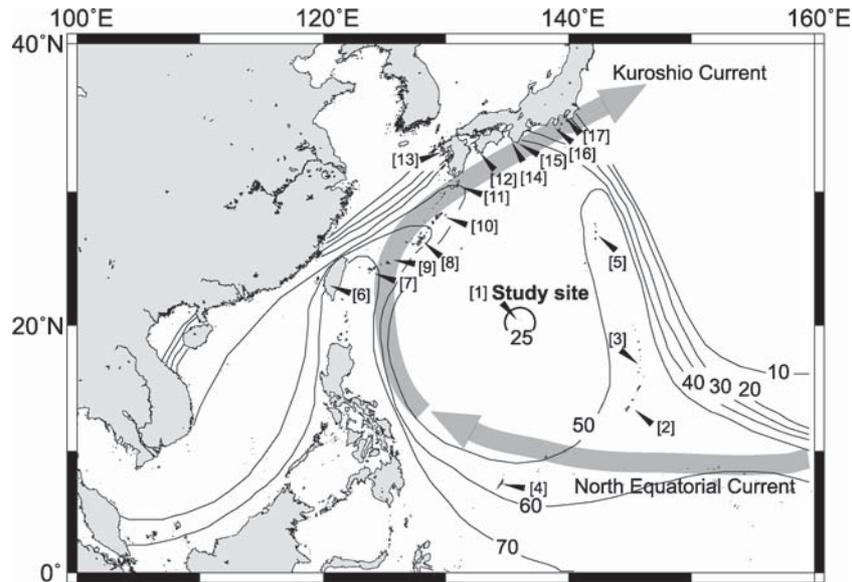


Fig. 1 Location of Okinotorishima. Isolines are numbers of genera. Site numbers in brackets correspond to the numbers in Table 2

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 $\mu\text{mol m}^{-2} \text{s}^{-1}$ 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

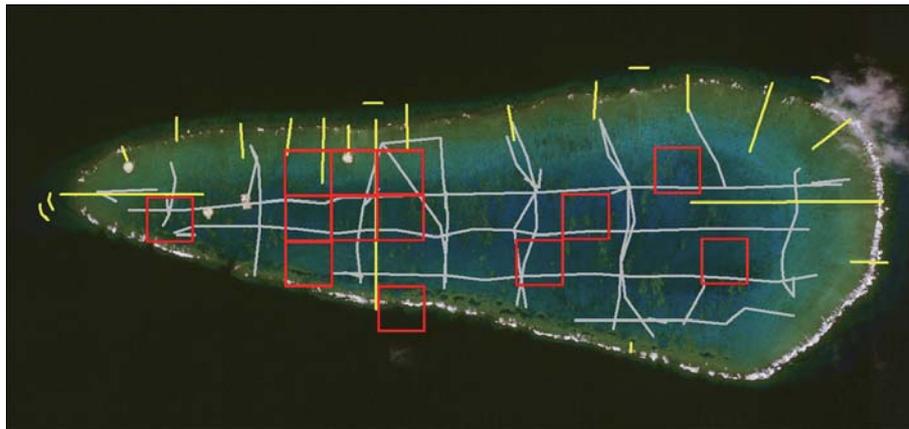


Fig. 2 Study site overlaid with surveyed grids (red squares) and transects (yellow and light blue lines)

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 250×250 m grid. Fourteen grids (total area $875,000 \text{ m}^2$) 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: $>20\%$, $20\text{--}5\%$, $<5\%$, 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 Genus Species	ra	Family Genus Species	ra	Family Genus Species	ra
Pocilloporidae		Poritidae		Faviidae	
<i>Pocillopora</i>		<i>Porites</i>		<i>Favia</i>	
<i>Pocillopora damicornis</i>	r	<i>Porites solida</i>	c	<i>Favia stelligera</i>	a
<i>Pocillopora verrucosa</i>	a	<i>Porites lobata</i>	a	<i>Favia laxa</i>	u
<i>Pocillopora eydouxi</i>	a	<i>Porites australiensis</i>	c	<i>Favia pallida</i>	a
<i>Pocillopora elegans</i>	u	<i>Porites lutea</i>	c	<i>Favia favus</i>	c
Acroporidae		<i>Porites mayeri</i>	u	<i>Favia matthaii</i>	a
<i>Montipora</i>		<i>Porites cylindrica</i>	c	<i>Favia rotundata</i>	u
<i>Montipora tuberculosa</i>	c	<i>Porites lichen</i>	u	Favites	
<i>Montipora mollis</i>	c	<i>Porites annae</i>	u	<i>Favites halicora</i>	c
<i>Montipora peltiformis</i>	c	<i>Porites rus</i>	c	<i>Favites flexuosa</i>	c
<i>Montipora turgescens</i>	c	Siderastreidae		<i>Favites complanata</i>	a
<i>Montipora incrassata</i>	c	<i>Psammocora</i>		Goniastrea	
<i>Montipora foveolata</i>	c	<i>Psammocora contigua</i>	u	<i>Goniastrea favulus</i>	c
<i>Montipora caliculata</i>	c	<i>Psammocora haimeana</i>	u	<i>Goniastrea pectinata</i>	c
<i>Montipora digitata</i>	u	<i>Psammocora profundacella</i>	u	Platygyra	
<i>Montipora hispida</i>	c	<i>Coscinaraea</i>		<i>Platygyra daedalea</i>	c
<i>Montipora informis</i>	a	<i>Coscinaraea columna</i>	u	<i>Platygyra sinensis</i>	c
<i>Montipora efflorescens</i>	c	Agariciidae		<i>Platygyra pini</i>	c
<i>Montipora grisea</i>	c	<i>Pavona</i>		<i>Platygyra contorta</i>	c
Acropora		<i>Pavona clavus</i>	c	Leptoria	
<i>Acropora gemmifera</i>	c	<i>Pavona duerdeni</i>	c	<i>Leptoria phrygia</i>	a
<i>Acropora verweyi</i>	u	<i>Pavona varians</i>	c	Montastrea	
<i>Acropora robusta</i>	u	<i>Pavona venosa</i>	c	<i>Montastrea curta</i>	a
<i>Acropora abrotanoides</i>	c	<i>Pavona maldivensis</i>	c	<i>Montastrea annuligera</i>	u
<i>Acropora muricata</i>	u	<i>Gardineroseris</i>		<i>Montastrea valenciennesi</i>	c
<i>Acropora austera</i>	c	<i>Gardineroseris planulata</i>	u	Leptastrea	
<i>Acropora tenuis</i>	c	Fungiidae		<i>Leptastrea purpurea</i>	a
<i>Acropora cytherea</i>	u	<i>Fungia</i>		<i>Leptastrea pruinosa</i>	c
<i>Acropora hyacinthus</i>	c	<i>Fungia scutaria</i>	a	Cyphastrea	
<i>Acropora latistella</i>	c	Mussidae		<i>Cyphastrea agassizi</i>	c
<i>Acropora nana</i>	c	<i>Lobophyllia</i>		<i>Cyphastrea serailia</i>	a
<i>Acropora aculeus</i>	a	<i>Lobophyllia hemprichii</i>	c	<i>Cyphastrea chalicidicum</i>	a
<i>Acropora valida</i>	c	<i>Lobophyllia corymbosa</i>	c	<i>Cyphastrea microphthalma</i>	a
<i>A. sp. aff. divaricata</i>	a	Merulinidae		Echinopora	
<i>Acropora elseyi</i>	c	<i>Merulina</i>		<i>Echinopora lamellosa</i>	a
<i>Acropora rosaria</i>	u	<i>Merulina ampliata</i>	c	<i>Echinopora gemmacea</i>	a
<i>Acropora florida</i>	c	<i>Scapophyllia</i>		<i>Echinopora pacificus</i>	c
<i>Acropora donei</i>	c	<i>Scapophyllia cylindrica</i>	c	Dendrophylliidae	
<i>Acropora globiceps</i>	a			<i>Turbinaria</i>	
<i>Acropora intermedia</i>	c			<i>Turbinaria reniformis</i>	u
Isopora				Milleporidae	
<i>Isopora palifera</i>	u			<i>Millepora</i>	
Astreopora				<i>Millepora platyphylla</i>	c
<i>Astreopora myriophthalma</i>	a			<i>Millepora exaesa</i>	c

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

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

no.	Site	Number 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: Tanegashima, 12: Tosa Shimizu, 13: Amakusa, 14: Shirahama, and 15: Kushimoto), and Group 4 had two sites (16: Izu Peninsula 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%

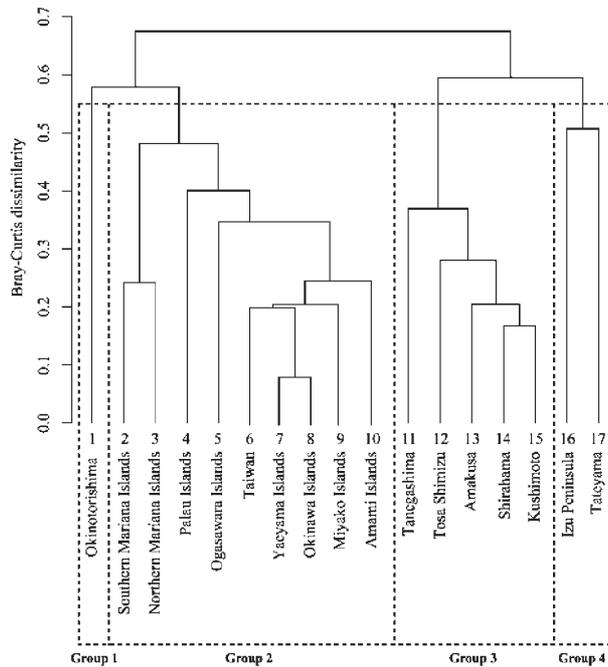


Fig. 3 Dendrogram from average linkage clustering of coral composition at 17 sites in the northwestern Pacific

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

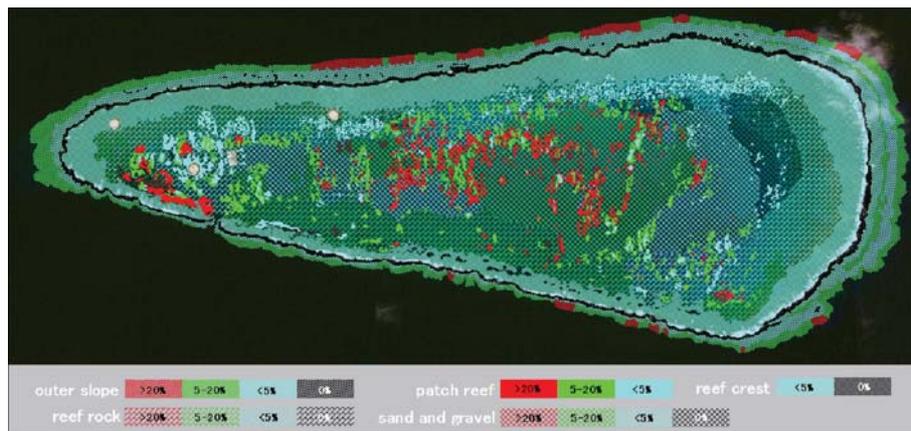


Fig. 4 Habitat map of Okinotorishima. Percent cover of living corals are shown by colors for each habitat

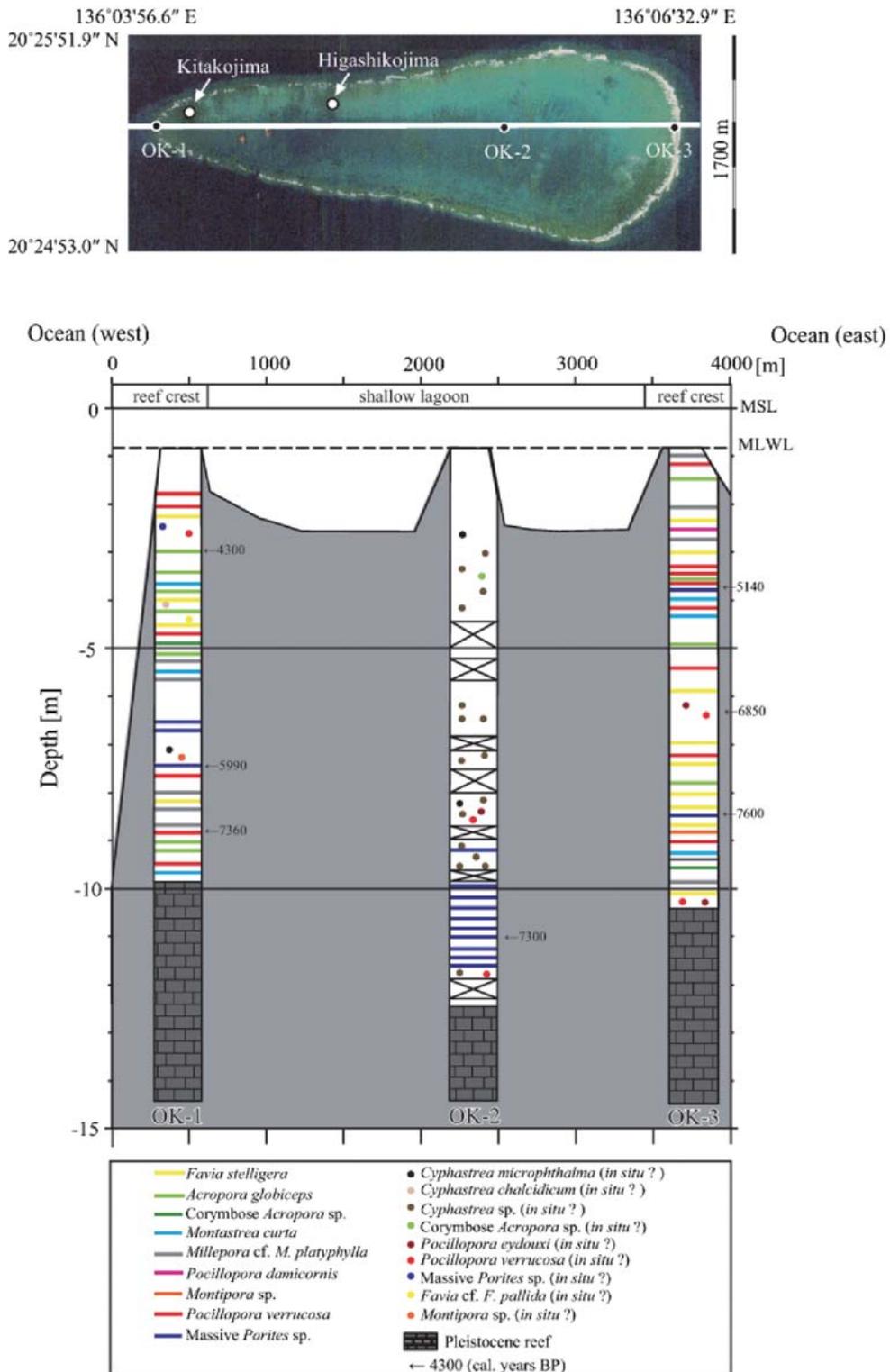


Fig. 5 Internal structure of sample cores and recovered fossil corals of the Holocene coral reef at Okinotorishima

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. damicornis* 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 taphonomy 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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