

Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan

Mitsuhiko Sano, Makoto Shimizu & Yukio Nose

Department of Fisheries, Faculty of Agriculture, University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113, Japan

ABSTRACT: Long-term changes in structure of fish communities on coral reefs infested by the coral-feeding starfish *Acanthaster planci* were determined using 20 m² visual transects. We censused a living coral reef consisting mainly of staghorn *Acropora* spp. at Sakiyama Bay and a dead coral reef with low structural complexity of coral branches (about 2 yr after *A. planci* infestation) at Amitori Bay, Iriomote Island (Ryukyu Islands, Japan) in September 1984. Two yr later, we recensused the dead coral reef, which had changed into a flat plain of unstructured coral rubble ('rubble reef'). Mean numbers of species and individuals per transect severely decreased in the following order of reef types: (1) living reef (1984), (2) dead reef (1984), and (3) rubble reef (1986). Correlated with these decreases in numbers were several patterns: (1) coral-polyp feeders completely disappeared on both dead and rubble reefs, probably due to absence of food; (2) numbers of resident species and individuals decreased on the dead reef, perhaps due to decrease in living space or shelter associated with the reduction in structural complexity of coral branches; and (3) numbers of species and individuals of both resident and visitor fishes declined on the unstructured rubble reef, likely due to shortage of living space and food.

INTRODUCTION

Population outbreaks of the coral-feeding starfish *Acanthaster planci* have been reported to occur widely on coral reefs at various localities throughout the Indo-West Pacific since the late 1960s (e.g. Endean & Chesher 1973, Endean & Cameron 1985, Yamaguchi 1986). Hermatypic corals of many reefs have been killed extensively by the starfish, and the biological and physical environment of infested reefs has changed drastically (e.g. Endean 1973, Nishihira & Yamazato 1974). After attack by *A. planci*, the skeletons of corals become coated with tufts of various filamentous algae, and after a few years the exposed skeletons of branching corals collapse due to biological and physical erosion (review by Hutchings 1986).

Some workers have found that fish community structure varies among different reef habitats (e.g. Chave & Eckert 1974, Goldman & Talbot 1976, Gladfelter & Gladfelter 1978, Gladfelter et al. 1980, Williams 1982, Bell & Galzin 1984). Thus we expected that the structure of fish communities associated with coral reefs damaged by *Acanthaster planci* would be altered as a result of environmental changes. However, previous

studies of the influence of coral destruction by *Acanthaster planci* infestation on fish communities are restricted to observations shortly after reef degradation (Bouchon-Navaro et al. 1985, Williams 1986) and comparisons of fish communities on living and dead coral colonies (Sano et al. 1984a). The present study was initiated to determine long-term changes in fish communities on large reefs 4 yr after damage by *A. planci*.

METHODS

This study was carried out in the fringing reefs of Sakiyama and Amitori bays (24° 20' N, 123° 42' E) on the western side of Iriomote Island, one of the Ryukyu Islands of Japan (Fig. 1). Both study reefs, at Sakiyama and Amitori bays, were about 300 m from the shoreline, and water depth was about 2 m at high tide and about 1 m at low tide. The Sakiyama Bay reef consisted mostly of living staghorn coral *Acropora* spp., forming high structural complexity (Fig. 2A). Live coral cover on the reef was more than 80%. At Amitori Bay, on the other hand, hermatypic corals, especially *Acropora* and *Pocillopora* spp., were intensely infested

with *Acanthaster planci* between 1981 and 1982, and were completely killed by the end of 1982 (H. Kohno pers. comm.). By September 1984 the dead coral branches were strikingly degraded by biological and physical erosion, especially by wave action, and structural complexity was very low (Fig. 2B). The dead coral skeletons were coated with filamentous and coralline algae and a deposit of silt. This reef in 1984 is referred to hereafter as 'dead coral reef'. Two yr later (September 1986) the structure of dead coral reef had degraded further due to erosion, and a flat plain of low-relief coral rubble remained (Fig. 2C, D). This reef in 1986 is referred to as 'rubble reef'. Although we were not able to quantify the decreased complexity of the dead and rubble reefs, the striking extent of the decrease in complexity can be represented by photographs (Fig. 2A to D).

Direct fish observations were carried out on the living and dead coral reefs in September 1984 and on the rubble reef in September 1986. The living reef was not censused in 1986, because predation by *Acanthaster planci* had reduced live coral cover on the reef to less than 50% of its cover in 1984. Five transects 20 m long and 1 m wide were established on each reef using a scaled nylon rope. This transect width, rather than a greater width, was found to minimize bias in visual

transect censuses in methodical tests by Sale & Sharp (1983). Using a mask and snorkel, a single diver (the first author) slowly approached each transect. 'Visitor' fishes, which swam across the transect but which consistently fled at our approach, were first censused visually for 10 min (Gooding & Magnuson 1967, Smith & Tyler 1972). 'Resident' fishes, which stayed permanently on the transect and did not flee at our approach, were then counted by swimming along the transect and carefully inspecting the entire area until all visible residents were recorded. Each transect required approximately 30 to 60 min to census. Fishes were identified to species, and the number of individuals of each species was recorded on a plastic slate. All censuses were made at high tide between 1000 and 1400 h and each transect was censused once.

Fish species diversity was calculated using the Shannon-Wiener index (Shannon & Weaver 1949):

$$H' = - \sum_{i=1}^s P_i \log_2 P_i \quad (1)$$

where P_i = proportion of individuals of species i in the sample; s = number of species.

Based on available published dietary data of coral reef fishes (Hiatt & Strasburg 1960, Hobson 1974, Allen 1975, 1980, Sano et al. 1984b), fishes censused were assigned to one of 6 trophic categories: herbivores, zooplankton feeders, benthic-animal feeders, omnivores, coral-polyp feeders, and piscivores. Food habits of some fishes not previously examined were tentatively determined by our underwater observations of feeding behavior. The scientific names of all fishes censused follow the nomenclature used by Masuda et al. (1984).

RESULTS

Species of fishes and density of individuals associated with the transects at each reef are shown in Table 1. Sixty-two species were found on the living reef, while 43 and 22 species were recorded on the dead and rubble reefs, respectively. The mean numbers of species and individuals per transect decreased remarkably in the following order of reef types: (1) living reef (1984), (2) dead reef (1984), and (3) rubble reef (1986) (Table 2). Mean species diversity measured for each reef showed no significant difference between the living and dead reefs (Mann-Whitney U-test, $p > 0.20$) (Table 2). However, the diversity of the rubble reef was significantly lower than diversities of the living and dead reefs ($p < 0.05$).

Since the food resources of fishes (especially coral polyps and filamentous algae) and the structural complexity of coral branches varied with coral death, we

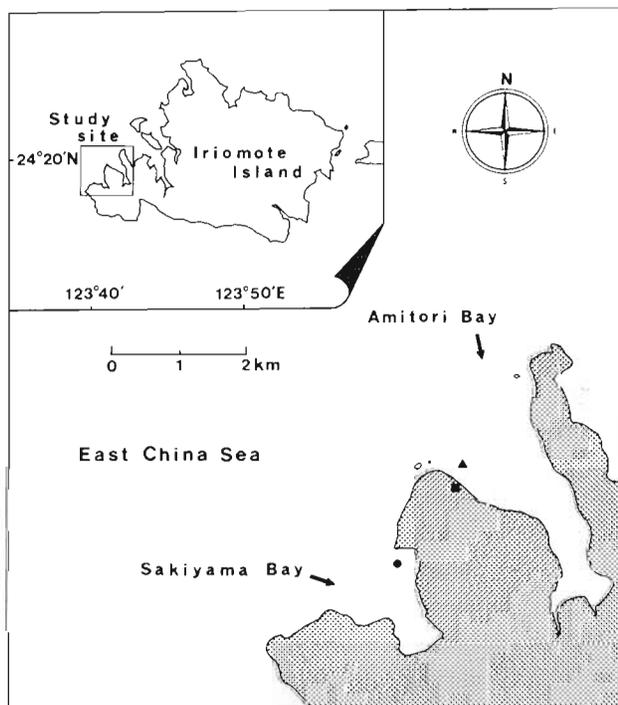


Fig. 1. Map showing study site at Iriomote Island, Ryukyu Islands, Japan. Dotted line indicates reef margin. (●) Living coral reef, 1984; (▲) dead coral reef, 1984 and rubble reef, 1986; (■) Okinawa Regional Research Center, Tokai University

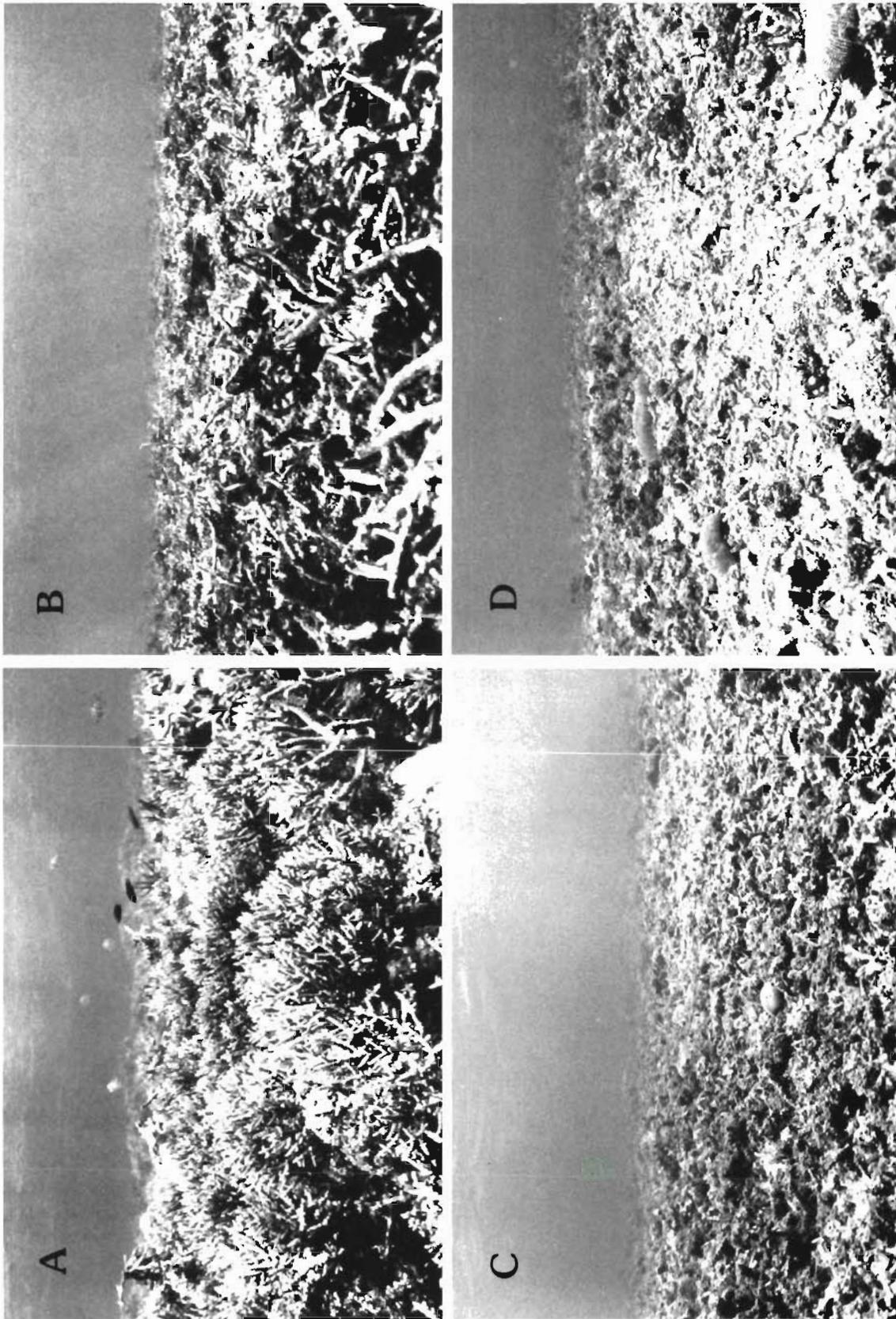


Fig. 2. Structural changes in reef of staghorn coral *Acropora* spp. killed by *Acanthaster planci*. (A) Living coral reef at Sakayama Bay. (B) dead coral reef with low structural complexity of coral branches at Amiton Bay about 2 yr after attack by *A. planci*; (C) and (D) unstructured rubble reef at Amiton Bay about 4 yr after attack

Table 1. Mean number of individuals per transect (20 m²) by species observed on each reef, listed in order of decreasing abundance on the living reef. Year each reef was sampled is included in parentheses. Dead reef and rubble reef were the same reef sampled 2 yr apart. Values are mean \pm 95% confidence limits of the mean (n=5 transects). Trophic category (TC): H, herbivore; O, omnivore; B, benthic-animal feeder; C, coral-polyp feeder; Z, zooplankton feeder; P, piscivore. Residency: R, resident; V, visitor. -: not observed

Species	Family	TC	Residency	Living reef (1984)	Dead reef (1984)	Rubble reef (1986)
<i>Pomacentrus moluccensis</i>	Pomacentridae	O	R	55.4 \pm 6.0	13.8 \pm 10.3	0.2 \pm 0.6
<i>Atrosalarias fuscus holomelas</i>	Blenniidae	H	R	33.0 \pm 3.4	4.8 \pm 5.7	-
<i>Cheiloprius labiatus</i>	Pomacentridae	C	R	29.2 \pm 6.2	-	-
<i>Gobiodon citrinus</i>	Gobiidae	C	R	14.8 \pm 2.7	-	-
<i>Amblyglyphidodon curacao</i>	Pomacentridae	O	R	10.8 \pm 11.0	-	-
<i>Pomacentrus</i> sp.	Pomacentridae	O	R	9.2 \pm 2.8	9.0 \pm 1.2	0.2 \pm 0.6
<i>Stegastes nigricans</i>	Pomacentridae	H	R	7.8 \pm 4.1	3.2 \pm 2.7	-
<i>Chaetodon trifasciatus</i>	Chaetodontidae	C	V	7.8 \pm 2.7	-	-
<i>Ctenochaetus striatus</i>	Acanthuridae	H	V	4.4 \pm 2.9	5.6 \pm 1.4	1.6 \pm 2.3
<i>Labrichthys unilineatus</i>	Labridae	C	V	3.8 \pm 2.0	-	-
<i>Epinephelus merra</i>	Serranidae	B	R	3.2 \pm 1.6	3.2 \pm 1.0	1.0 \pm 0.9
<i>Scarus sordidus</i>	Scaridae	H	V	3.0 \pm 1.5	3.6 \pm 1.4	2.4 \pm 2.9
<i>Oxymonacanthus longirostris</i>	Monacanthidae	C	V	2.4 \pm 2.7	-	-
<i>Chaetodon trifascialis</i>	Chaetodontidae	C	V	2.0 \pm 1.2	-	-
<i>Zebrasoma scopas</i>	Acanthuridae	H	V	2.0 \pm 0.9	-	-
<i>Gomphosus varius</i>	Labridae	B	V	1.8 \pm 1.0	0.4 \pm 0.7	0.2 \pm 0.6
<i>Siganus vulpinus</i>	Siganidae	H	V	1.8 \pm 1.0	0.8 \pm 1.4	-
<i>Thalassoma hardwickii</i>	Labridae	B	V	1.8 \pm 1.0	2.2 \pm 1.0	1.6 \pm 1.4
<i>Cheilodipterus quinquelineatus</i>	Apogonidae	B	R	1.6 \pm 1.4	-	-
<i>Paraglyphidodon melas</i>	Pomacentridae	O	R	1.4 \pm 0.7	-	-
<i>Stegastes lividus</i>	Pomacentridae	H	R	1.4 \pm 0.7	-	-
<i>Gobiodon okinawae</i>	Gobiidae	C	R	1.2 \pm 3.3	-	-
<i>Chaetodon melannotus</i>	Chaetodontidae	B	V	1.2 \pm 1.0	0.4 \pm 0.7	-
<i>Hemigymnus melapterus</i>	Labridae	B	V	1.2 \pm 1.0	0.4 \pm 0.7	-
<i>Zanclus cornutus</i>	Zanclidae	O	V	1.2 \pm 1.0	0.2 \pm 0.6	-
<i>Epibulus insidiator</i>	Labridae	B	V	1.0 \pm 0.9	0.8 \pm 1.0	-
<i>Dascyllus aruanus</i>	Pomacentridae	O	R	0.8 \pm 1.4	1.0 \pm 1.8	-
<i>Meiacanthus atrodorsalis atrodorsalis</i>	Blenniidae	H	R	0.8 \pm 0.6	-	-
<i>Halichoeres melanurus</i>	Labridae	O	V	0.8 \pm 1.0	0.2 \pm 0.6	-
<i>Siganus spinus</i>	Siganidae	H	V	0.8 \pm 2.2	1.0 \pm 2.2	-
<i>Thalassoma lunare</i>	Labridae	B	V	0.8 \pm 1.0	0.8 \pm 1.0	0.6 \pm 0.7
<i>Chaetodon kleinii</i>	Chaetodontidae	O	V	0.6 \pm 1.1	0.2 \pm 0.6	0.2 \pm 0.6
<i>Centropyge vrolicki</i>	Pomacanthidae	H	R	0.4 \pm 0.7	0.2 \pm 0.6	-
<i>Chrysiptera cyanea</i>	Pomacentridae	O	R	0.4 \pm 1.1	0.4 \pm 1.1	0.2 \pm 0.6
<i>Paracirrhites forsteri</i>	Cirrhitidae	B	R	0.4 \pm 0.7	-	-
<i>Cephalopholis urodelus</i>	Serranidae	B	R	0.4 \pm 0.7	-	-
<i>Dampiera cyclophthalmala</i>	Pseudochromidae	B	R	0.4 \pm 0.7	0.4 \pm 0.7	-
<i>Chaetodon auriga</i>	Chaetodontidae	B	V	0.4 \pm 1.1	0.8 \pm 1.0	-
<i>Chaetodon leiolatus</i>	Chaetodontidae	B	V	0.4 \pm 0.7	-	-
<i>Chaetodon unimaculatus</i>	Chaetodontidae	C	V	0.4 \pm 0.7	-	-
<i>Chaetodon vagabundus</i>	Chaetodontidae	O	V	0.4 \pm 1.1	0.6 \pm 1.1	0.2 \pm 0.6
<i>Cheilinus diagrammus</i>	Labridae	B	V	0.4 \pm 1.1	-	-
<i>Chromis atripectoralis</i>	Pomacentridae	O	V	0.4 \pm 1.1	-	-
<i>Hemiochus chrysostomus</i>	Chaetodontidae	C	V	0.4 \pm 0.7	-	-
<i>Scarus oviceps</i>	Scaridae	H	V	0.4 \pm 1.1	0.6 \pm 1.1	-
<i>Scarus dimidiatus</i>	Scaridae	H	V	0.4 \pm 0.7	-	-
<i>Stethojulis strigiventer</i>	Labridae	Z	V	0.4 \pm 1.1	2.0 \pm 0.9	0.2 \pm 0.6
<i>Corythoichthys haematopterus</i>	Syngnathidae	Z	R	0.2 \pm 0.6	-	-
<i>Dascyllus melanurus</i>	Pomacentridae	H	R	0.2 \pm 0.6	-	-
<i>Epinephelus caeruleopunctatus</i>	Serranidae	P	R	0.2 \pm 0.6	-	-
<i>Aulostomus chinensis</i>	Aulostomidae	P	V	0.2 \pm 0.6	-	-
<i>Chaetodon baronessa</i>	Chaetodontidae	C	V	0.2 \pm 0.6	-	-
<i>Chaetodon bennetti</i>	Chaetodontidae	C	V	0.2 \pm 0.6	-	-
<i>Chaetodon plebeius</i>	Chaetodontidae	C	V	0.2 \pm 0.6	-	-
<i>Cheilio inermis</i>	Labridae	B	V	0.2 \pm 0.6	1.0 \pm 1.2	0.4 \pm 0.7
<i>Cheilinus chlorurus</i>	Labridae	B	V	0.2 \pm 0.6	1.0 \pm 0.9	1.0 \pm 0.9
<i>Hemigymnus fasciatus</i>	Labridae	Z	V	0.2 \pm 0.6	-	-
<i>Naso lituratus</i>	Acanthuridae	H	V	0.2 \pm 0.6	0.2 \pm 0.6	-
<i>Parupeneus trifasciatus</i>	Mullidae	B	V	0.2 \pm 0.6	2.0 \pm 0.9	1.2 \pm 1.6
<i>Siganus puellus</i>	Siganidae	H	V	0.2 \pm 0.6	-	-
<i>Thalassoma janseni</i>	Labridae	B	V	0.2 \pm 0.6	-	-
<i>Zebbrasoma veliferum</i>	Acanthuridae	H	V	0.2 \pm 0.6	-	-
<i>Hologymnosus annulatus</i>	Labridae	B	V	-	1.0 \pm 1.2	0.2 \pm 0.6
<i>Salarias fasciatus</i>	Blenniidae	H	R	-	0.8 \pm 0.6	0.2 \pm 0.6
<i>Naso</i> sp.	Acanthuridae	H	V	-	0.6 \pm 1.1	-
<i>Centropyge heraldi</i>	Pomacanthidae	H	R	-	0.4 \pm 0.7	-
<i>Cheilinus rhodochrous</i>	Labridae	B	V	-	0.4 \pm 1.1	-
<i>Choerodon anchorago</i>	Labridae	B	V	-	0.4 \pm 0.7	0.4 \pm 1.1
<i>Scarus frenatus</i>	Scaridae	H	V	-	0.4 \pm 0.7	-
<i>Stethojulis bandanensis</i>	Labridae	Z	V	-	0.4 \pm 0.7	-
<i>Halichoeres trimaculatus</i>	Labridae	B	V	-	0.4 \pm 0.7	-
<i>Apogon cooki</i>	Apogonidae	B	R	-	0.2 \pm 0.6	-
<i>Meiacanthus kamoharai</i>	Blenniidae	O	R	-	0.2 \pm 0.6	-
<i>Chaetodon rafflesi</i>	Chaetodontidae	B	V	-	0.2 \pm 0.6	-
<i>Scarus schlegeli</i>	Scaridae	H	V	-	0.2 \pm 0.6	-
<i>Pomacentrus rhodonotus</i>	Pomacentridae	O	R	-	-	3.8 \pm 1.6
<i>Parapercis cylindrica</i>	Mugiloididae	O	R	-	-	1.8 \pm 0.6
<i>Scarus</i> sp.	Scaridae	H	V	-	-	0.6 \pm 1.1
<i>Parupeneus cyclostomus</i>	Mullidae	B	V	-	-	0.2 \pm 0.6
Total number of species				62	43	22

compared fish communities on the 3 reefs by trophic category and by residency (Sano et al. 1984a). The mean numbers of species and of individuals per tran-

Table 2. Mean numbers of species and individuals and species diversity per transect (20 m²) on each reef. Year each reef was sampled is included in parentheses. Dead reef and rubble reef were same reef sampled 2 yr apart. Values are mean \pm 95% confidence limits of the mean (n = 5 transects)

Parameter	Living reef (1984)	Dead reef (1984)	Rubble reef (1986)
Number of species	34.6 \pm 2.9	22.6 \pm 2.1	9.8 \pm 2.0
Number of individuals	218.0 \pm 12.0	66.4 \pm 18.2	18.4 \pm 3.0
Species diversity	3.80 \pm 0.17	3.92 \pm 0.30	3.03 \pm 0.33

sect in each trophic category on each reef are summarized in Fig. 3. Zooplankton feeders and piscivores were excluded in this analysis, because fish in these categories were rare. Differences among the reefs were most distinct for the coral-polyp feeders: no coral-feeding fish were found on either dead and rubble reefs. Comparisons of the abundances of fishes in other trophic categories among the 3 reefs indicated that the lowest numbers of species and individuals were obtained from the rubble reef for all categories, except for the number of omnivorous species which showed no significant difference between the dead and rubble reefs (U-test, $p > 0.20$). Herbivores and benthic-animal feeders showed no significant differences in the number of species on the living and the dead reefs (herbivores, $p > 0.05$; benthic-animal feeders, $p > 0.20$). The number of omnivorous species, how-

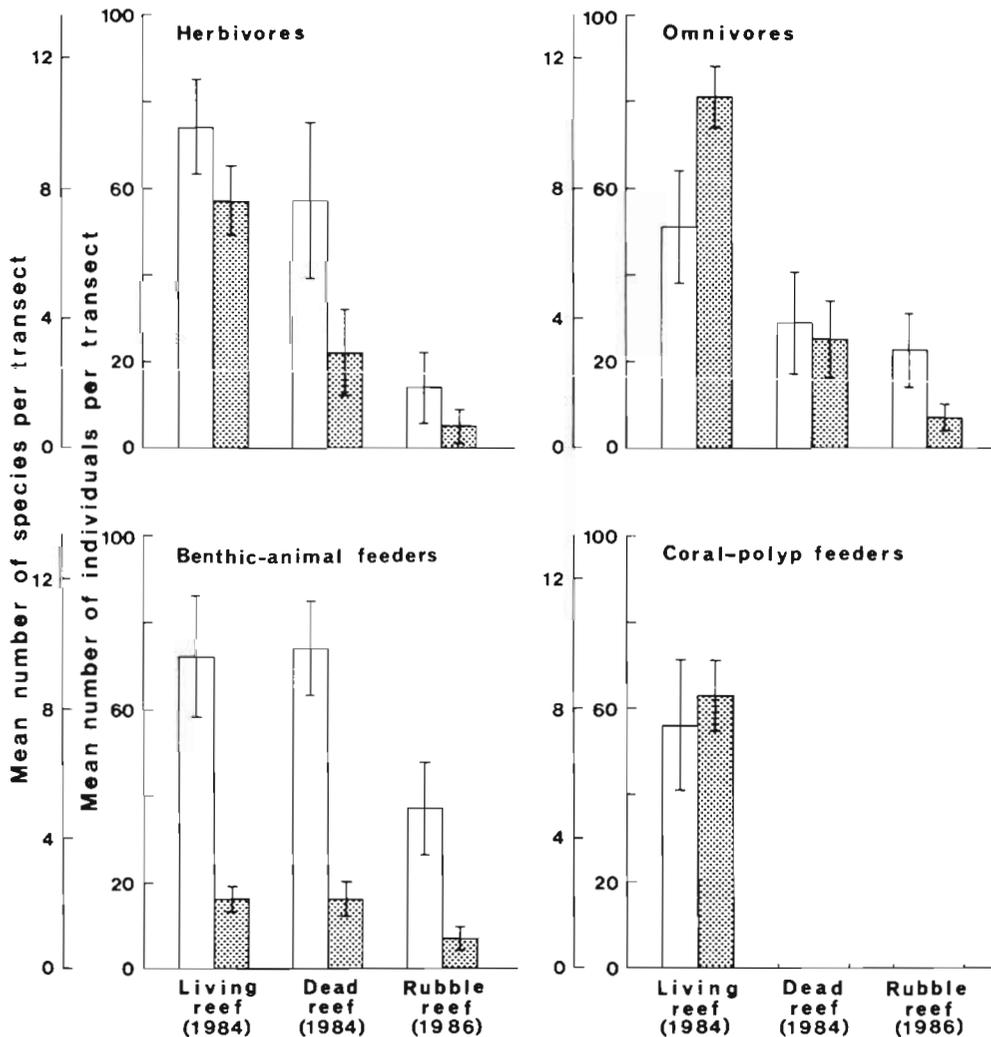


Fig. 3. Mean numbers of species (open bars) and of individuals (stippled bars) per transect for each trophic category on each reef. Vertical lines indicate 95% confidence limits of the mean (n=5 transects). Year each reef was sampled is included in parentheses

ever, was significantly greater on the living reef compared with the other reefs ($p < 0.05$). Much greater numbers of herbivorous and omnivorous individuals were counted from the living than the other reefs, but number of individuals of benthic-animal feeders showed no significant difference between the living and dead reefs ($p > 0.20$).

Fig. 4 compares the numbers of resident and visiting species and individuals on the 3 reefs, except for the coral-polyp feeders which were omitted because they were not found on the dead and rubble reefs. In the numbers of resident species and individuals, the following significant differences among the reefs were found: living reef $>$ dead reef $>$ rubble reef (U-test, $p < 0.05$). The differences in the numbers of visitor species and individuals are as follows: living reef = dead reef $>$ rubble reef, with all differences significant at $p < 0.05$. To provide a more detailed analysis, fishes known to be herbivores, omnivores, and benthic-animal feeders were grouped as either resident or visitor (Fig. 5). For all trophic categories, resident and visitor fishes showed almost the same decreasing trends among the reefs as in Fig. 4, with a few exceptions, such as the number of species of resident omnivores on the rubble reef.

Finally, the mean number of individuals per transect was compared species by species among the 3 kinds of reefs (Table 1). Most of the abundant fishes on the living reef decreased severely in abundance or completely disappeared on the rubble reef. For instance, the resident omnivore *Pomacentrus moluccensis*,

which was the predominant species on the living reef, was markedly less numerous on the dead reef and was represented by a single individual on the rubble reef. Conversely, *Parupeneus trifasciatus*, a visitor benthic-animal feeder, showed significantly greater number of individuals on the dead than on the living reefs (U-test, $p < 0.05$). The 2 resident omnivores, *Pomacentrus rhodonotus* and *Parapercis cylindrica*, occurred on the rubble reef with distinctly high abundance. All individuals of the latter 3 species were juveniles.

DISCUSSION

Our data indicate that the structures of coral reef fish communities are substantially altered by *Acanthaster planci*-induced coral death and associated changes in habitat structure. Species number and density of fishes on *A. planci*-damaged reefs decrease, and remain low several years after infestation.

Sano et al. (1984a) discussed the probable course of events in the structure of coral reef fish communities when corals are killed by *Acanthaster planci*, using natural and experimental *Acropora* colonies at Okinawa Island, Japan. The most negative effect of coral destruction on the fish communities was that coral-polyp feeders, which were relatively abundant on the living reef, completely disappeared from the dead and the rubble reefs. Endean & Stablum (1973), Reese (1981), Bouchon-Navaro et al. (1985), and Williams (1986) made similar observations.

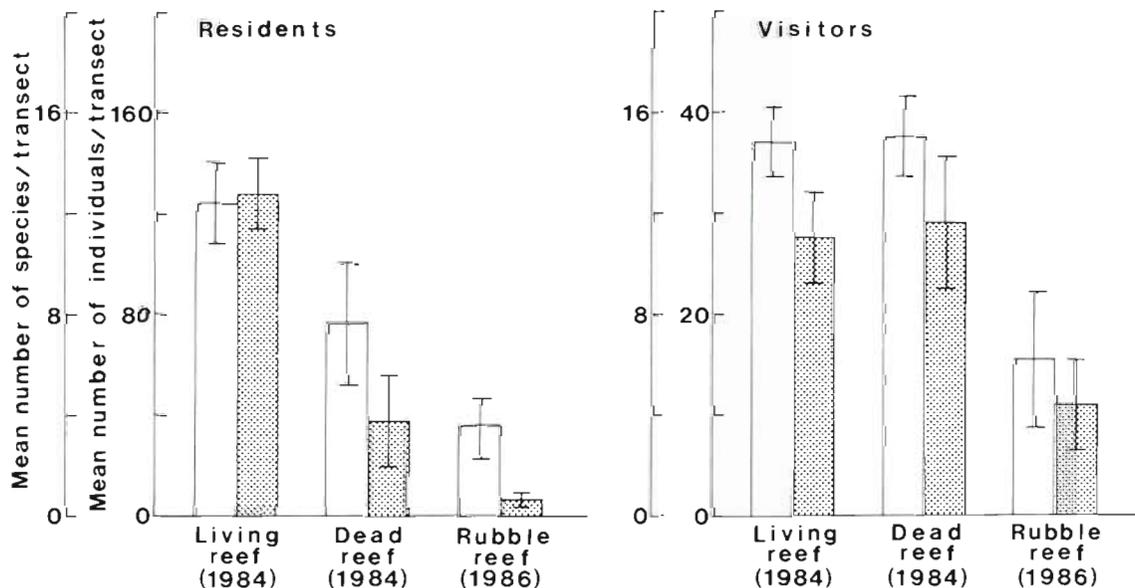


Fig. 4. Mean numbers of species (open bars) and of individuals (stippled bars) per transect for residents and visitors on each reef. Vertical lines represent 95% confidence limits of the mean ($n=5$ transects). Coral-polyp feeders on the living reef were omitted in this analysis (see text). Year each reef was sampled is included in parentheses

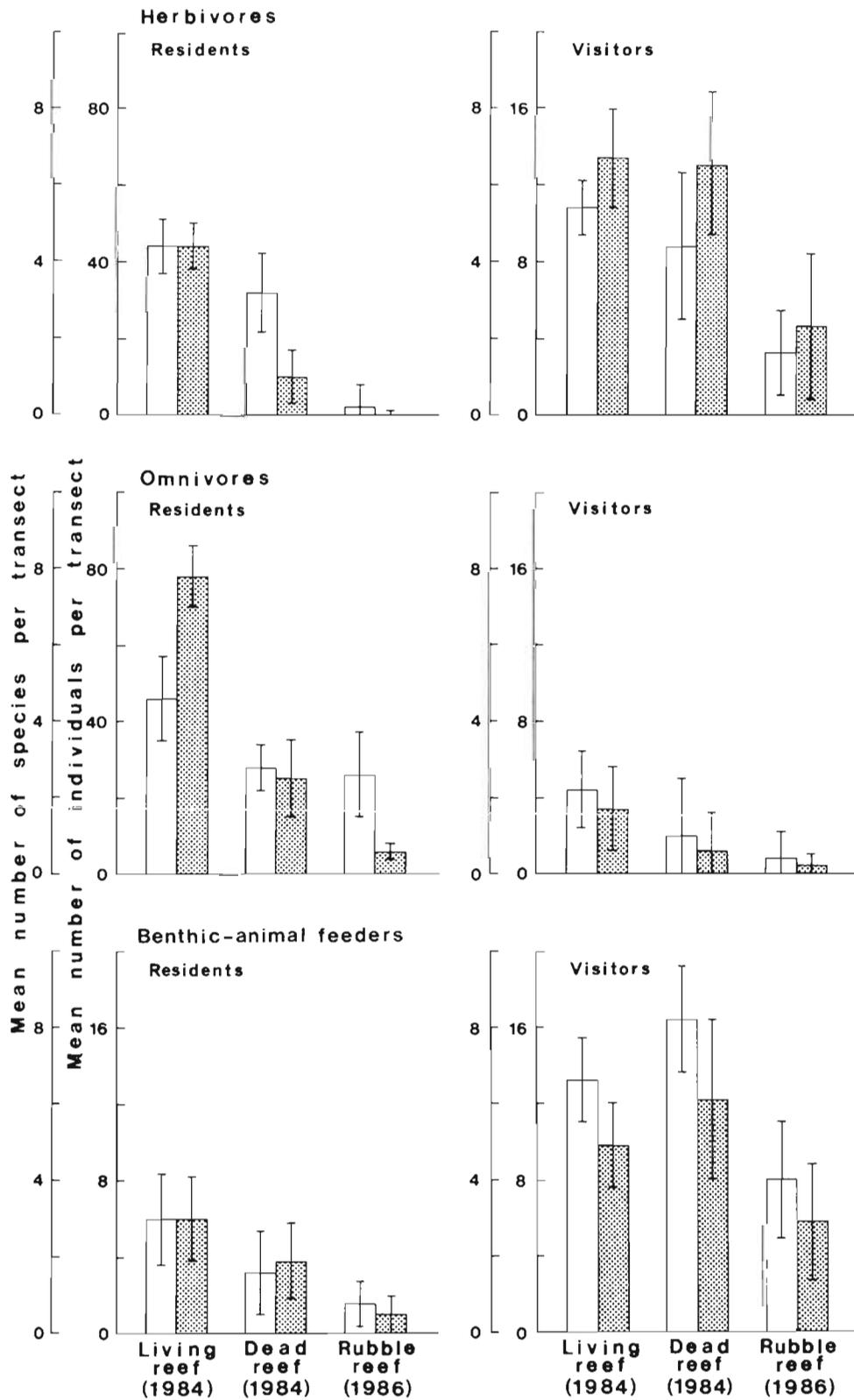


Fig. 5. Mean numbers of species (open bars) and of individuals (stippled bars) per transect for residents and visitors of each trophic category on each reef. Vertical lines indicate 95% confidence limits of the mean (n=5 transects). Year each reef was sampled is included in parentheses

The numbers of resident species and individuals markedly decreased on the dead reef with low structural complexity (about 2 yr after *Acanthaster planci* infestation) and on the unstructured rubble reef (about 4 yr after infestation). The numbers of visitors, on the other hand, showed no significant difference between the living and the dead reefs, but significantly decreased on the rubble reef. The decreases in resident and visitor fish abundance on the unstructured rubble reef may be due to shortage of 2 main resources, living space and food. It seems that visitors as well as residents are negatively affected because of the collapse of their refuge and resting sites when a flat plain of unstructured coral rubble is formed on a large scale. Although we did not examine food resource abundance on the rubble reef, there is evidence indicating decreases in food abundance in such cases. For instance, Alldredge & King (1977) and Porter et al. (1977) reported that collections from rubble coral contained many fewer demersal zooplankters than those from living coral. Kohn (1967), Kohn & Leviten (1976), and Sano (1982) have shown that topographically complex reef habitats support more benthic invertebrates such as decapods and gastropods than low-relief reefs. On the other hand, the decreases in resident numbers on the dead reef are probably due to a decrease in only living space or shelter (Sano et al. 1984a). This explanation may be supported by the fact that visitors in each trophic category did not significantly decrease on the dead reef compared with resident species (Fig. 5). If the abundance of available food markedly decreased on the dead reef, visitor species which were not closely dependent on coral for cover should have decreased in numbers also.

Several workers have demonstrated that fish species richness and diversity are positively correlated with topographic complexity of coral reef habitats (Risk 1972, Alevizon & Brooks 1975, Luckhurst & Luckhurst 1978, Gladfelter et al. 1980, Carpenter et al. 1981). With only the exception of fish species diversity on the dead coral reef, our results provide further confirmation of these findings.

Walsh (1983) investigated the immediate impact of a catastrophic storm on coral reef fish communities at Kona, Hawaii. The resulting longer-term changes in community structure showed quite different results from our observations. He found no decreases in species and population abundances on quadrats at various habitats after the storm despite considerable storm-induced habitat destruction. We cannot explain this apparent contradiction. Our data suggest that the presence of live coral cover and spatial complexity of the habitat are important factors limiting population abundance of many fishes at Iriomote Island.

We were unable to examine natural variation in

species number and abundance of fishes on the reefs at the different locations (i.e. Sakiyama Bay vs Amitori Bay) and times (1984 vs 1986). We cannot confirm that the changes in fish community structure on the dead and the rubble reefs were other than natural variation. Compared with the natural variation in fish community structure indicated by recent studies (e.g. Williams 1986), however, severe changes were observed on the infested reefs. We believe that the observed changes probably resulted from coral destruction by *Acanthaster planci*.

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