

## Changes in Structure of Coral Reef Fish Communities by Destruction of Hermatypic Corals: Observational and Experimental Views<sup>1</sup>

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**ABSTRACT:** Population outbursts of the crown-of-thorns starfish, *Acanthaster planci*, have drastically altered communities in many coral reef areas of the Indo-west Pacific since the late 1960s. To understand the pattern of changes in fish communities on damaged coral colonies, direct observations and field experiments were carried out in inshore waters at Minatogawa, Okinawa Island (26°16' N, 127°42' E), in 1979 and 1980. From experiments on the effects of coral death and on the effects of decreased structural complexity of coral branches on fish communities using five colonies of staghorn coral, *Acropora* sp., we were able to predict the following changes in fish communities resulting from the destruction of living corals by *Acanthaster*. Coral polyp feeders completely disappear from dead coral colonies due to absence of their food; and the numbers of resident species and individuals decrease due to the reduction in living space or shelter when the structural complexity of dead coral colonies is decreased by bio- and physical erosion. Consequently, fish species diversity also decreases. These predicted changes are consonant with those directly observed on nine natural dead staghorn coral colonies.

ECOLOGICAL WORK ON FISH communities associated with coral reefs has rapidly expanded since the 1960s. It is widely recognized that these fish communities are highly diverse systems (Emery 1978). Many fish coexist and utilize the available resources, especially food and living space, within reef habitats. As these resources differ qualitatively and/or quantitatively among different reef habitats, we suggest that differences in the structure of fish communities should be found. Therefore, structure of the reef habitat may be an important factor in determining the diversity and structure of fish communities. There is some prior work dealing with the relationship between fish community structure and reef habitat. Alevizon and Brooks (1975), Jones and Thompson (1978), and Gladfelter, Ogden, and Gladfelter (1980) compared fish com-

munity structure on geographically separated coral reefs. Similarly, Hiatt and Strasburg (1960), Chave and Eckert (1974), Jones and Chase (1975), Goldman and Talbot (1976), and Gladfelter and Gladfelter (1978) examined community structure and distribution of fishes among various reef habitats. They found that fish community structure varies among different reef habitats. Sale (1980) summarized information on the role of resources in determining fish community structure.

From the late 1960s to the early 1970s population outbursts of the crown-of-thorns starfish, *Acanthaster planci*, were reported to occur widely on coral reefs at various localities throughout the Indo-west Pacific (Endean and Chesher 1973). On Okinawa Island the population outburst was first reported in 1969 at Seragaki on the west-central coast (Yamazato 1969) and almost all hermatypic corals along the west coast of the island were infested by 1976 (Okinawa Prefecture Tourism Development Corp. 1976).

As *Acanthaster planci* feed primarily on *Acropora*, *Pocillopora*, and *Montipora*

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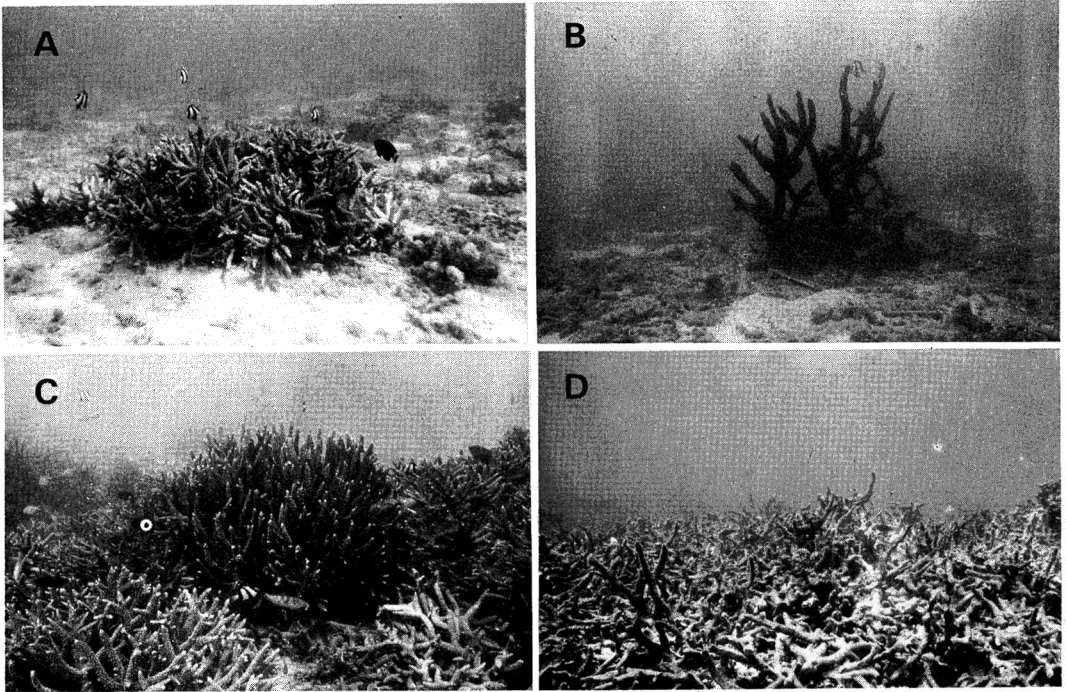


FIGURE 1. Structural changes in colony and reef of staghorn coral *Acropora* killed by *Acanthaster planci*. A, C, living coral colony and reef. Structural complexity of the coral branches is very high. B, D, dead coral colony and reef about 2 years after the attack by *A. planci*. The structural complexity has been severely decreased by bio- and physical erosion.

(Nishihira and Yamazato 1972, Nishihira et al. 1974) these hermatypic corals are heavily preyed on and damaged during *Acanthaster planci* population explosions. Immediately after staghorn *Acropora* (Figure 1A, C) are infested, the feeding scars appear white. Within a few weeks, however, the scars are coated with dark, almost black, tufts of various filamentous algae (Endean 1973, Fishelson 1973, Endean and Stablum 1973, Nakasone et al. 1974). After several months, dead coral skeletons begin breaking apart due to bio- (Fishelson 1973, MacGeachy 1977) and physical erosion, and the structural complexity of the three-dimensional coral branches decreases (Figure 1B, D). Thus, in recently infested coral reef areas, the underwater view is quite different from the usual coral reef scene.

Because hermatypic corals can be extensively damaged by such population outbursts, studies of environmental changes in infested reefs and of the population biology of

*Acanthaster planci* were initiated (Nishihira and Yamazato 1972, 1973, 1974, Endean 1973, Endean and Stablum 1973, Nishihira et al. 1974). However, few workers have examined the influence of the destruction of hermatypic corals on fish communities. In the present study, through direct observations of fish communities on natural living and dead coral colonies and field experiments, we sought to determine the effects of changes in food resources and structural complexity on fish community structure. This type of study may enable us to predict the consequences in larger *Acanthaster*-damaged reefs.

#### STUDY SITE

The site was situated inshore at Minatogawa (26°16' N, 127°42' E) on the west coast of Okinawa Island (Figure 2), where both living (L-St) and dead (D-St) coral reef areas are present. Each area was about 800 m<sup>2</sup>. The

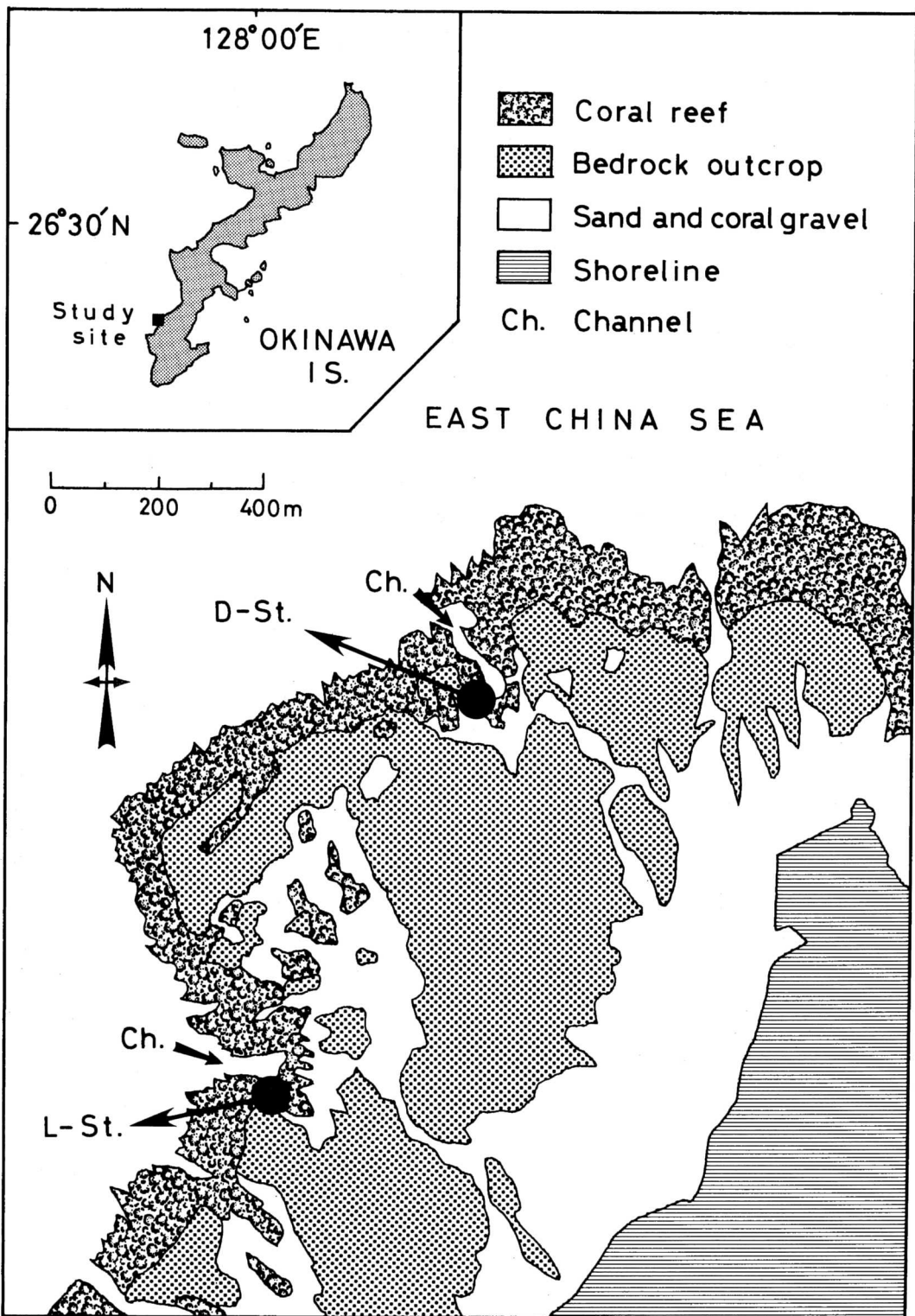


FIGURE 2. Map showing study site and its bottom types at Minatogawa, Okinawa Island.

D-St was environmentally similar to the L-St (Figure 2). Both stations were about 700 m from the shoreline and surrounded by sandy areas and rocky coral reefs. Water depth was about 2.5 m at high tide and about 1 m at low tide. On the north of both stations there is a channel 7 to 10 m in depth, continuing to the outer reef slope. The stations were located about 800 m apart, separated by sandy areas and rocky coral reefs which are exposed to air at low tide. At the D-St, hermatypic corals, especially *Acropora*, were intensely infested with *Acanthaster planci* in May and June 1977, and were completely killed by the end of August 1977. During the study period coral reefs surrounding both stations were a mosaic of living and dead corals, but the area of dead coral was greater than that of living coral.

#### MATERIALS AND METHODS

Direct observations were carried out at the L- and D-Sts in August 1979 (summer) and during late March and early April 1980 (spring). Nine typical and discrete living colonies of *Acropora* sp. of from 0.1, 0.2, . . . , to 0.9 m<sup>3</sup> volumes were selected on a sandy area at L-St, and nine dead colonies of the same volumes were selected at the D-St and tagged with a plastic tag before the fish census. The volume of each colony was calculated as length  $\times$  breadth  $\times$  height measured to the nearest cm by a scaled nylon cord. In the living coral colonies more than 70% of the coral tissue was alive and the structural complexity of the three-dimensional coral branches was extremely high. In contrast, the skeletons of the dead coral colonies were coated with tufts of filamentous algae and a deposit of silt, and structural complexity had been decreased by bio- and physical erosion. Although we were not able to quantify the decreased complexity of the dead coral colonies, we believe the extent of the decrease in complexity can be represented by photographs as in Figures 1A and 1B. In the spring census the same coral colonies as in the summer census were used except for the 0.2, 0.4, 0.6, and 0.9 m<sup>3</sup> dead colonies. These four colonies collapsed, losing completely their three-dimensional structure

after the summer census, and four other dead colonies were selected for the spring census. All fishes on each colony were visually censused once a day between 8:00 A.M. and 12:00 noon using a mask and snorkel at high tide for 4 days at each station. Fishes were identified as to species, and the number of individuals of each species was counted.

Field experiments were conducted at L-St from March through May 1980. Five experimental coral colonies of *Acropora* sp. were collected from living reefs surrounding the experimental site and installed on a sandy bottom 3–4 m away from the reef. Each colony measured 1 m (length)  $\times$  1 m (breadth)  $\times$  0.2 m (height) and all were similar in size and shape. Distance between colonies was 5 m. For each newly installed colony, more than 90% of the coral tissue was living and coral branch coverage was more than 95%. Coverage was defined as a percentage of the area covered by coral branches and was determined using photographs taken from above the colony within a 50 cm  $\times$  50 cm quadrat.

Figure 3 shows the scheme for each experiment. A single colony was used for each. In Experiment C, a control, all fishes settling on the experimental colony were censused daily for 51 days after installation. In Experiments F1 and F2, fishes were censused daily for 20 days after installation. These newly installed colonies are referred to as "experimental living coral colonies." After the censuses, these colonies were exposed to air for two days, the living tissue was killed, and these colonies, now referred to as "experimental dead coral colonies," were reinstalled where the previously living colonies had been. Coral branch coverage of the dead coral colonies was at the same level as that in the living colonies. After reinstallation, all fishes on the dead colonies were censused for 28 days.

Experiments S1 and S2 were conducted using the same methods as in Experiments F1 and F2, except that coral branch coverage of the reinstalled colonies was artificially decreased to 70%, although living tissue was maintained at more than 90%. The newly installed colonies are referred to as "experimental colonies of 95% coverage," and the

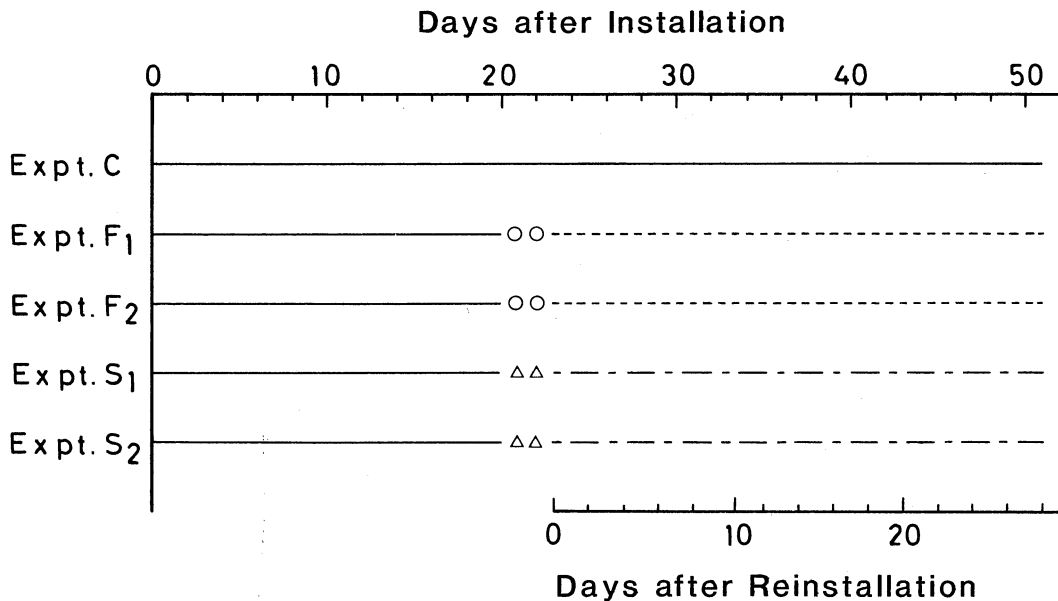


FIGURE 3. Scheme of the experiments: ———, experiment using a coral colony of which more than 90% of the tissue was living and which had coral branch coverage of more than 95%; - - - - -, experiment using a coral colony of which 100% of the tissue was dead and which had coral branch coverage of more than 95%; ———, experiment using a coral colony of which more than 90% of the tissue was living and which had a branch coverage of 70%; O, a day required to completely kill the living coral colony; Δ, a day required to decrease the coral branch coverage from 95% to 70%.

reinstalled colonies are referred to as “experimental colonies of 70% coverage.” All fishes on each colony were visually censused using a mask and snorkel for 10 minutes between 9:00 and 10:00 A.M.

Using the available data on the food habits of coral reef fishes (Allen 1975, Sano 1982), fishes censused were classified in one of six trophic categories: herbivores, zooplankton feeders, benthonic animal feeders, omnivores, coral polyp feeders, and piscivores. The category for *Parupeneus barberinoides* was tentatively determined by our underwater observations of feeding behavior because the food habits of this species have not previously been reported, and we were unable to obtain any specimens. Fishes were also grouped as either residential or visitor, using the criteria of Gooding and Magnuson (1967) and Smith and Tyler (1972). Species which stayed permanently at the colonies and which did not flee from them at our approach were determined as residents, and species which swam around near or on the colonies but which consistently fled at our approach were called

visitors. Fish species diversity was calculated using the Shannon-Weaver information formula (Shannon and Weaver 1949):

$$H' = - \sum_i P_i \log_2 P_i$$

where  $P_i$  is the proportion of the individuals of species  $i$  to all individuals in the sample.

## RESULTS

### *Fishes of Naturally Occurring Coral Colonies*

Both numbers and species of fishes were greater on the living coral colonies than on the dead coral colonies in both seasons (Table 1). In spring there were 46 species and 1973 individual fishes on the nine living coral colonies, whereas there were 30 species and 899 individuals associated with the dead coral colonies. In summer 52 species and 2720 individuals were found on the living colonies and 44 species and 1004 individuals on the dead colonies.

TABLE 1

TOTAL NUMBER OF INDIVIDUALS BY SPECIES OBSERVED DAILY ON NINE NATURAL LIVING AND DEAD CORAL COLONIES FOR 4 DAYS IN SPRING AND SUMMER AT MINATOGAWA, OKINAWA ISLAND

SPECIES	T.C.	RESIDENCY	SPRING (1980)		SUMMER (1979)	
			LIVING CORAL	DEAD CORAL	LIVING CORAL	DEAD CORAL
<i>Apogon nubilis</i>	Z	R	40	31	329	26
<i>Atrosalarias fuscus holomelas</i>	H	R	243	117	242	37
<i>Dascyllus aruanus</i>	O	R	241	102	149	65
<i>Pomacentrus moluccensis</i>	O	R	169	28	201	47
<i>Pomacentrus flavicauda</i>	O	R	144	131	97	87
<i>Asterropteryx semipunctatus</i>	O	R	26	3	111	54
<i>Halichoeres melanurus</i>	O	V	81	69	43	60
<i>Stethojulis strigiventer</i>	Z	V	57	32	33	49
<i>Apogon cyanosoma</i>	Z	R	27	13	33	89
<i>Parapercis cylindrica</i>	O	R	31	31	30	42
<i>Scarus sordidus</i>	H	V	30	81	12	46
<i>Pomacentrus littoralis</i>	O	R	15	129	26	100
<i>Labracinus spiloptera</i>	B	R	1	5	25	23
<i>Salarias fasciatus</i>	H	R	21	23	13	22
<i>Corythoichthys haematopterus</i>	Z	R	20	11	7	10
<i>Coris variegata</i>	B	V	18	20	1	7
<i>Stegastes nigricans</i>	H	R	9	8	17	10
<i>Zebrasoma veliferum</i>	H	V	7	4	14	2
<i>Hemigymnus melapterus</i>	Z	V	9	2	13	3
<i>Epinephelus merra</i>	B	R	11	12	8	1
<i>Siganus spinus</i>	H	V	1	2	6	39
<i>Halichoeres trimaculatus</i>	B	V	5	2	2	2
<i>Chrysiptera cyanea</i>	O	R	107		128	15
<i>Labracinus melanotaenia</i>	B	R	5		29	11
<i>Gnatholepis</i> sp.	Z	R	2		18	7
<i>Siganus virgatus</i>	H	V	4		12	6
<i>Fusigobius neophytus</i>	O	R	11		5	3
<i>Plesiops coeruleolineatus</i>	B	R	9		8	1
<i>Scolopsis cancellatus</i>	B	V	4		9	1
<i>Scarus</i> sp.	H	V	2		1	3
<i>Pseudochromis melanotaenia</i>	Z	R	3	3	6	
<i>Cheilinus trilobatus</i>	B	V	2	6		4
<i>Cheilodipterus quinquelineatus</i>	B	R		9	48	56
<i>Amblygobius albimaculatus</i>	O	R		1	7	51
<i>Pomacentrus amboinensis</i>	O	R		12	3	8
<i>Labracinus cyclophthalmus</i>	B	V	7	7		
<i>Chaetodon melannotus</i>	O	V			14	1
<i>Chaetodon auriga</i>	B	V			2	1
<i>Parapercis polyophtalma</i>	B	V			1	1
<i>Gobiodon citrinus</i>	C	R	368		634	
<i>Cheiloprion labiatus</i>	C	R	193		274	
<i>Oxymonacanthus longirostris</i>	C	V	13		26	
<i>Chaetodon plebeius</i>	C	V	22		9	
<i>Chaetodon ephippium</i>	B	V	1		1	
<i>Chromis caerulea</i>	Z,O*	V	1		1	
<i>Amblyglyphidodon curacao</i>	O	V		4		5
<i>Apogon robustus</i>	B	R	4			
<i>Favonigobius</i> sp.	O	R	2			
<i>Pseudochromis xanthochir</i>	Z	R	2			
<i>Synchiropus ocellatus</i>	Z	R	2			
<i>Abudefduf sexfasciatus</i>	O	V	1			
<i>Chromis atripectoralis</i>	Z	V	1			

TABLE 1 (continued)

SPECIES	T.C.	RESIDENCY	SPRING (1980)		SUMMER (1979)	
			LIVING CORAL	DEAD CORAL	LIVING CORAL	DEAD CORAL
<i>Stethojulis bandanensis</i>	Z	V	1			
<i>Chaetodon trifascialis</i>	C	V			27	
<i>Chaetodon trifasciatus</i>	C	V			22	
<i>Fowleria aurita</i>	B	R			5	
<i>Labrichthys unilineatus</i>	C	V			5	
<i>Diodon liturosus</i>	B	V			4	
<i>Paraglyphidodon melas</i>	O	R			4	
<i>Chaetodon lineolatus</i>	B	V			2	
<i>Siganus chrysopilos</i>	O	V			2	
<i>Chaetodon auripes</i>	B	V			1	
<i>Epibulus insidiator</i>	B	V		1		
<i>Acanthurus</i> sp.	H	V				2
<i>Parupeneus trifasciatus</i>	B	V				2
<i>Pomacentrus bankanensis</i>	O	R				2
<i>Meiacanthus kamoharai</i>	O	R				1
<i>Parupeneus barberinoides</i>	B	V				1
<i>Scarus ghobban</i>	H	V				1
Total number of species			46	30	52	44
Total number of individuals			1,973	899	2,720	1,004

NOTE: T.C., trophic category; H, herbivore; Z, zooplankton feeder; B, benthonic animal feeder; O, omnivore; C, coral polyp feeder; \*, seasonal change between spring and summer in trophic category. Residency classification: R, resident; V, visitor.

A plot of the mean daily number of species against the volume of the colony shows a curvilinear relationship for both living and dead coral colonies in spring and summer (regression analysis,  $p < 0.01$ , Figure 4). We transformed the curvilinear regression to a linear one using logarithmic transformation and performed covariance analysis, which showed that the linear regression for the living coral colonies was significantly different in elevation ( $p < 0.01$ ) from that for the dead coral colonies. That is, as shown in Figure 4, the number of species was significantly greater on the living colonies in spring and summer. The mean daily number of individuals was also plotted against the volume of the colony for both living and dead colonies (Figure 5). This plot shows a significant linear relationship ( $p < 0.01$ ). Comparing the two linear regressions (by covariance analysis), the number of individuals also was found to be significantly greater in elevation on the living colonies in both seasons ( $p < 0.01$ ).

Higher species diversity values were also

obtained for living colonies in both seasons (Figure 6).

As food resources of fishes, especially coral polyps and filamentous algae, and the structural complexity of coral branches varied quantitatively with coral death, we compared fish communities on living and dead colonies by trophic category and by residency. In Figure 7 the total number of species on each living colony was compared with that on each dead colony for each trophic category. The difference between the two kinds of colonies was most distinct for the coral polyp feeders: no coral polyp-feeding fish was seen on a dead coral colony. Comparisons of the abundance of fish in other trophic categories between the two kinds of colonies showed that the total numbers of species of zooplankton feeders and omnivores were significantly greater on the living coral colonies both in spring and in summer (Wilcoxon's test, zooplankton feeders,  $p < 0.01$  for both seasons; omnivores,  $p < 0.01$  for spring and  $p < 0.02$  for summer). However, herbivores and benthonic

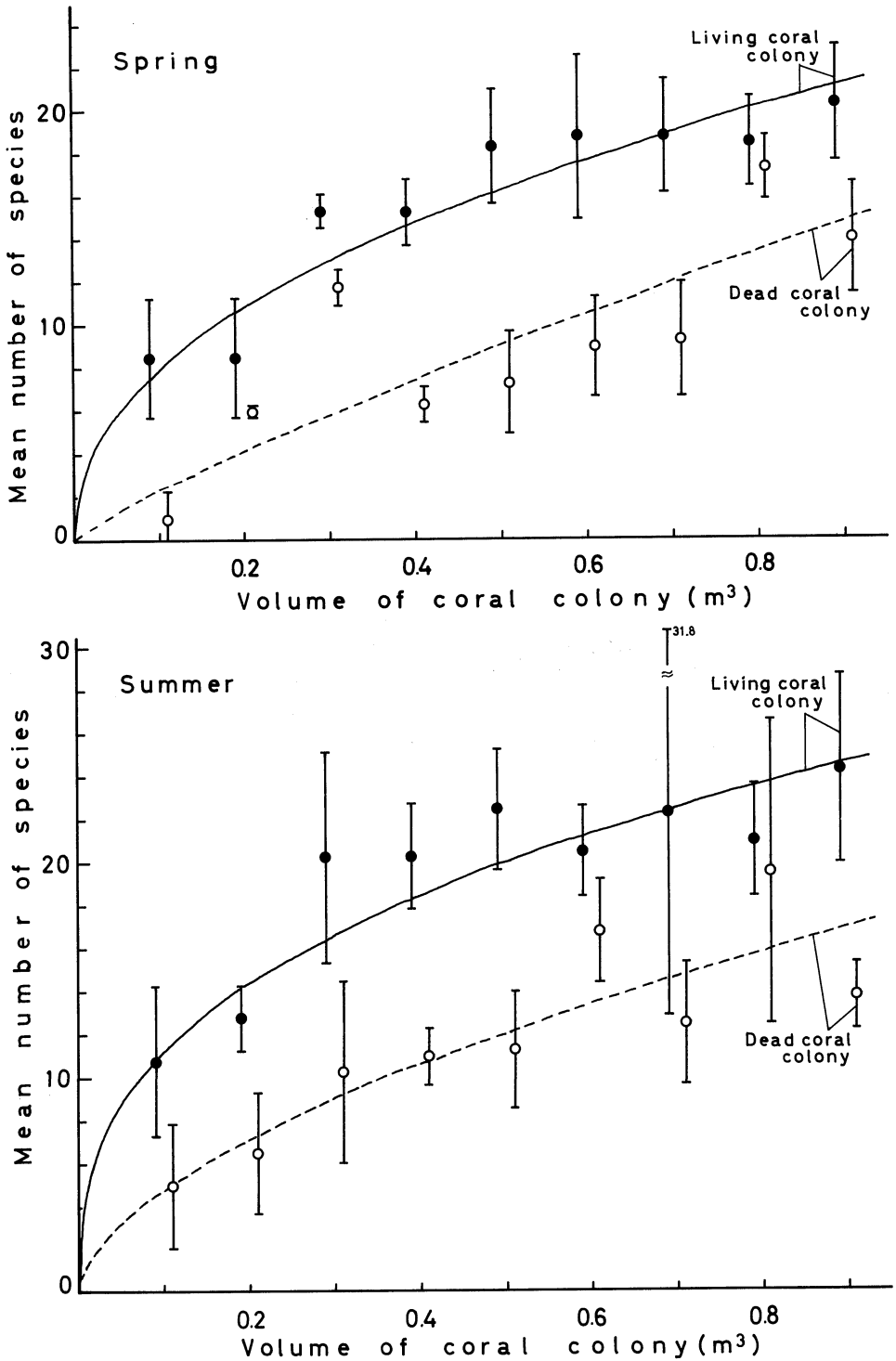


FIGURE 4. Mean daily number of species on each living and dead coral colony in spring and summer. Vertical bars indicate the 95% confidence limits of the mean. All curvilinear lines fitted with high significance (regression analysis,  $p < 0.01$ ).



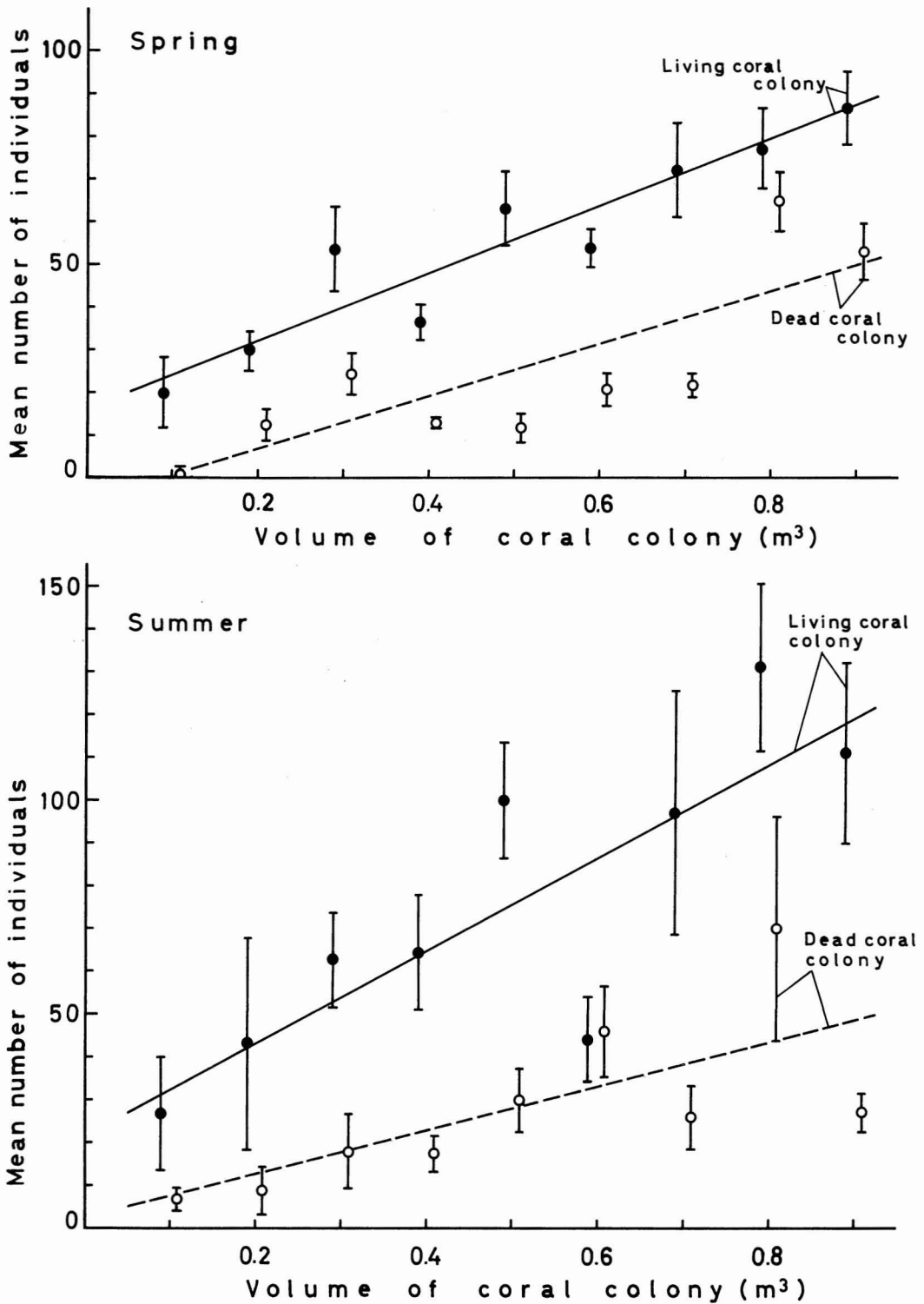


FIGURE 5. Mean daily number of individuals on each living and dead coral colony in spring and summer. Vertical bars indicate the 95% confidence limits of the mean. All linear lines fitted with high significance (regression analysis,  $p < 0.01$ ).

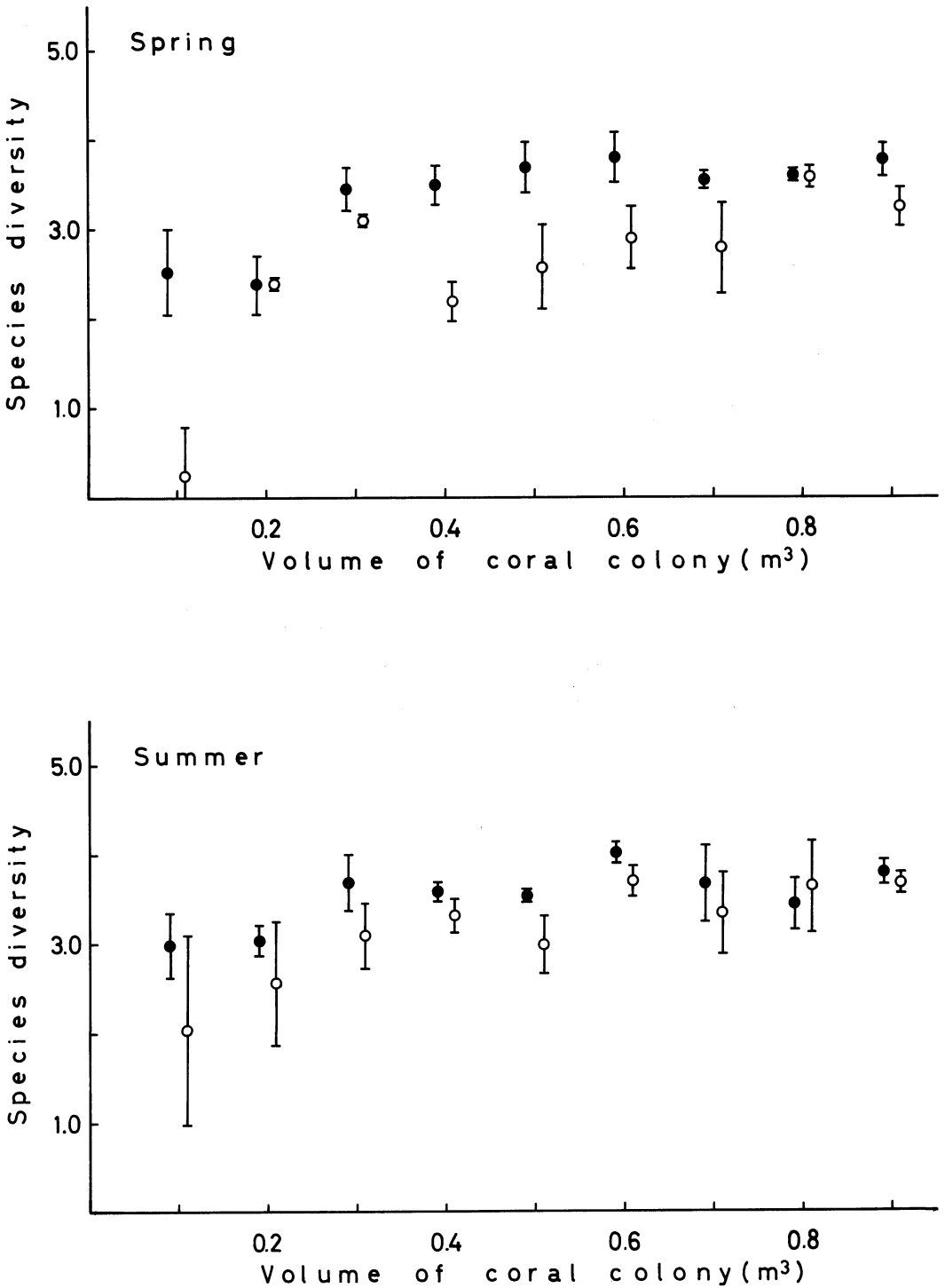


FIGURE 6. Mean daily species diversity of fishes on each living (closed circle) and dead (open circle) coral colony in spring and summer. Vertical bars indicate the 95% confidence limits of the mean.

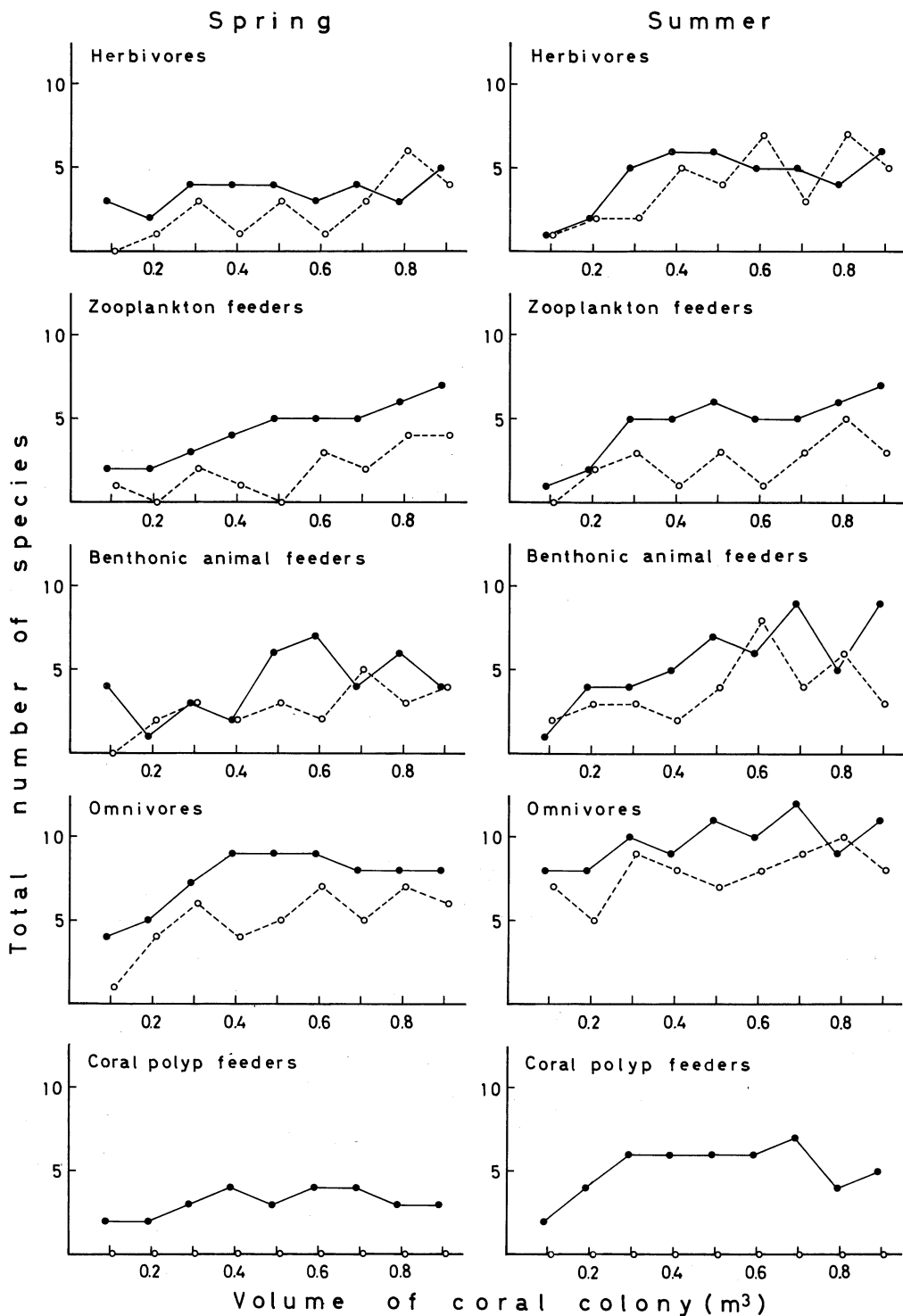


FIGURE 7. Total number of species of each trophic category on each living (closed circle) and dead (open circle) coral colony in spring and summer.

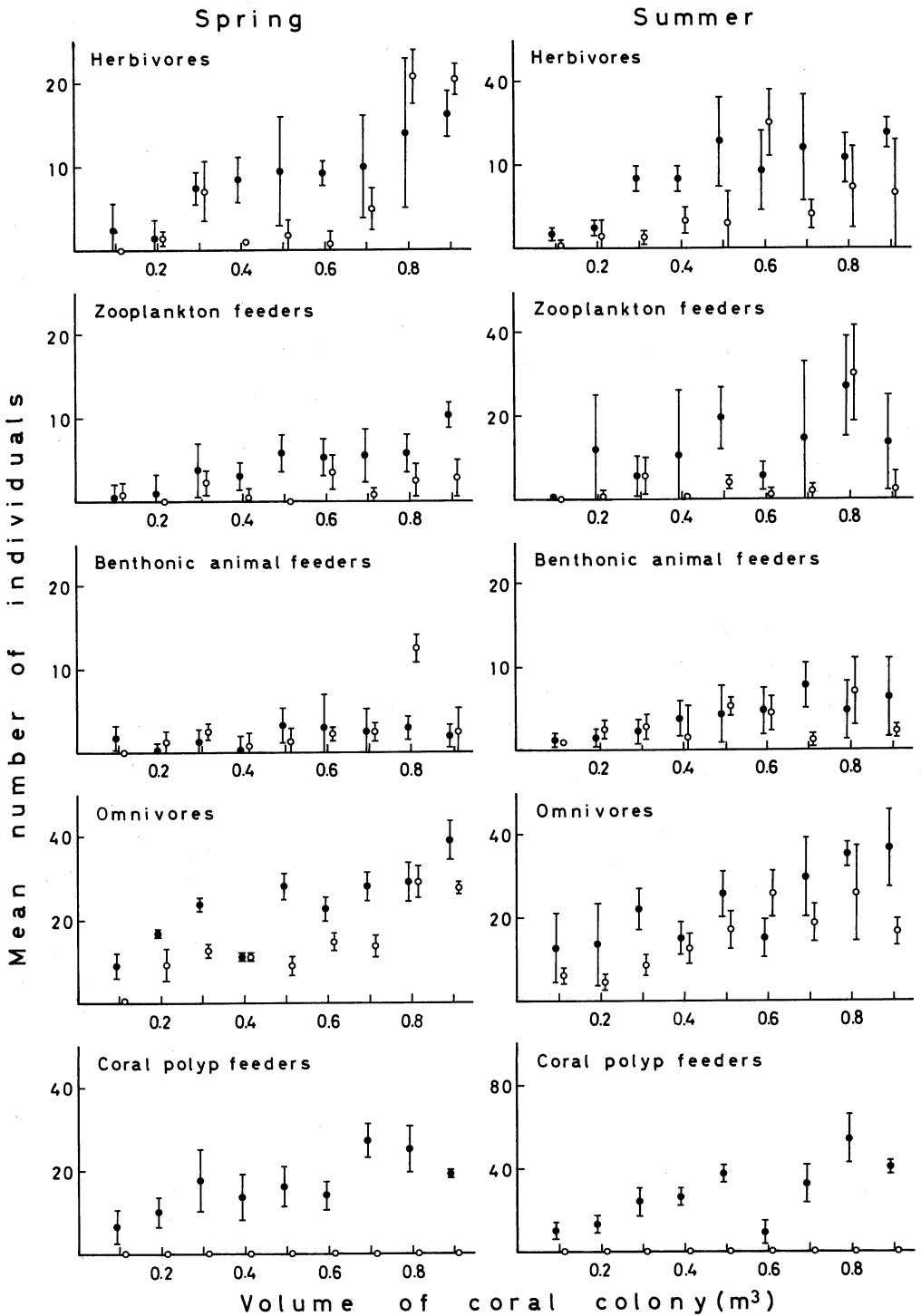


FIGURE 8. Mean daily number of individuals of each trophic category on each living (closed circle) and dead (open circle) coral colony in spring and summer. Vertical bars indicate the 95% confidence limits of the mean.

animal feeders showed no significant difference in the total numbers of species between the two kinds of colonies in either season ( $p > 0.05$ ).

The number of individuals within different trophic categories was also compared on live and dead colonies (Figure 8). Coral polyp feeders were more abundant on the living than on the dead colonies in both seasons. Herbivores, zooplankton feeders, and omnivores showed significantly greater numbers of individuals on the living coral colonies in both seasons (covariance analysis, herbivores,  $p < 0.05$  for spring and  $p < 0.01$  for summer; zooplankton feeders and omnivores,  $p < 0.01$  for both seasons). Benthonic animal feeders, however, showed no significant difference in the number of individuals on the two kinds of colonies in either season ( $p > 0.10$  for spring and  $p > 0.05$  for summer). (In this analysis the number of individuals of benthonic animal feeders on the  $0.8 \text{ m}^3$  dead coral colony in spring was omitted because it showed an unusual value which lay far from the regression line.)

The numbers of resident and visiting species and individuals on live and dead coral colonies were compared by grouping fishes as resident or visitor, except for the coral polyp feeders which were omitted because they were not found on the dead colonies. Figure 9 shows the total numbers of species and the mean daily numbers of individuals of residents and visitors on each colony. The total number of species of residents was significantly greater on the living coral colonies both in spring and in summer (Wilcoxon's test,  $p < 0.01$ ). On the other hand, the total number of visitor species was slightly more numerous on the living coral colonies in spring ( $p < 0.05$ ) but was not significantly different in summer ( $p > 0.10$ ). We also compared the numbers of individuals of residents and visitors on the two kinds of colonies. Residents were significantly more abundant on the living colonies in both seasons (covariance analysis,  $p < 0.01$ ). Visitors showed no significant difference on the two kinds of colonies in spring ( $p > 0.10$ ), but there was a slightly greater number on the dead colonies in summer ( $p < 0.05$ ).

Finally, the total number of individuals was compared species by species between the living and the dead colonies (Table 1). In both seasons residents, which were among the most abundant fishes on the living coral colonies, had smaller numbers of individuals on the dead colonies (i.e., less than half the number on the living coral colonies). These residents were the herbivore *Atrosalarias fuscus holomelas*, the zooplankton feeder *Apogon nubilus* (only summer), and the omnivores *Dascyllus aruanus*, *Pomacentrus moluccensis*, *Chrysiptera cyanea*, and *Asterropteryx semipunctatus* (only summer). Two resident coral polyp feeders, *Gobiodon citrinus*, which was the dominant species on the living coral colonies, and *Cheiloprion labiatus*, which was also abundant on them, completely disappeared from the dead coral colonies. Nor were visitor coral polyp feeders, *Oxymonacanthus longirostris*, *Chaetodon plebeius*, *C. trifascialis*, *C. trifasciatus*, and *Labrichthys unilineatus*, observed on the dead coral colonies. *Pomacentrus littoralis*, a resident omnivore, on the other hand, showed obviously greater numbers of individuals on the dead colonies in both seasons.

### Field Experiments

Two resident species, *Dascyllus aruanus* and *Gobiodon citrinus*, were dominant in the experimental colonies (i.e., the control colony in Experiment C, living coral colonies in Experiments F1 and F2, and coral colonies of 95% coverage in Experiments S1 and S2). Three resident species, *Pomacentrus flavicauda*, *Atrosalarias fuscus holomelas*, and *Cheiloprion labiatus*, also occurred on the newly installed colonies almost every day during the experimental period (80% and more in percentage occurrence excluding two cases), although they were represented by fewer individuals than the former two residents (Table 2).

In Experiment C (the control), where settlement of fishes on the colony was observed daily for 51 days, both numbers of species and of individuals remained stable from the 9th day after installation until the end of the experiment (Figure 10). The mean daily num-

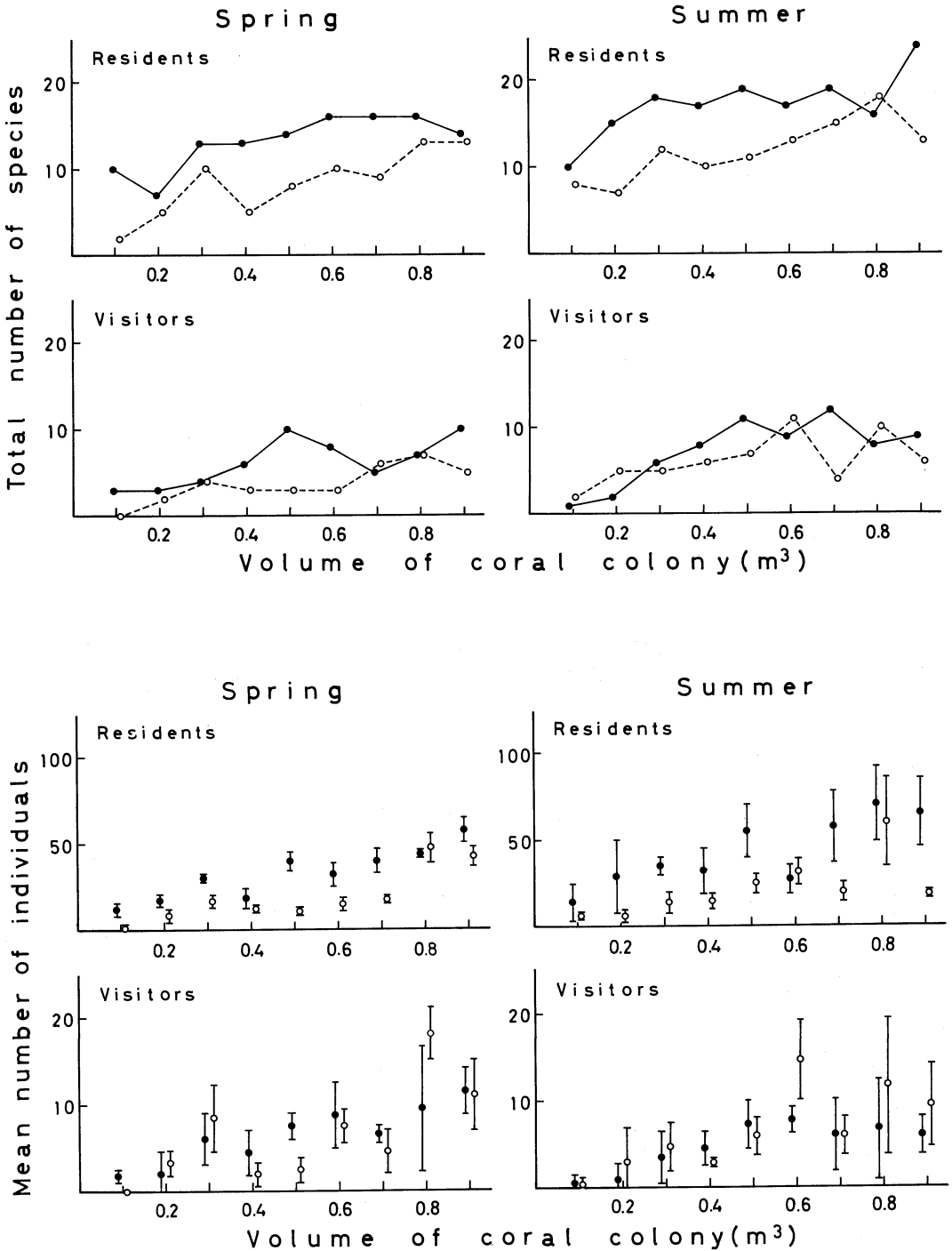


FIGURE 9. Total numbers of species and mean daily numbers of individuals of residents and of visitors on each living (closed circle) and dead (open circle) coral colony in spring and summer. Vertical bars indicate the 95% confidence limits of the mean. Coral polyp feeders on the living coral colonies were omitted in this analysis (see text).

TABLE 2

MEAN DAILY NUMBER OF INDIVIDUALS AND PERCENTAGE OCCURRENCE FOR EACH SPECIES ON EACH EXPERIMENTAL CORAL COLONY DURING THE STUDY PERIOD

SPECIES	T.C.	RESIDENCY	EXPT. C	EXPT. F1		EXPT. F2		EXPT. S1		EXPT. S2	
				LIVING CORAL	DEAD CORAL	LIVING CORAL	DEAD CORAL	95% COVERAGE	70% COVERAGE	95% COVERAGE	70% COVERAGE
<i>Dascyllus aruanus</i>	O	R	3.73(100)	3.50( 80)	4.79(100)	4.70(100)	4.11(100)	6.25(100)	6.71(100)	4.30(100)	2.82(100)
<i>Gobiodon citrinus</i>	C	R	2.90(100)	7.75(100)	0.25( 7)	6.95(100)	0.50( 32)	2.80(100)	3.82(100)	2.60(100)	2.18(100)
<i>Pomacentrus flavicauda</i>	O	R	1.94( 98)	0.80( 80)	0.50( 50)	0.15( 10)	0.61( 57)	1.95(100)	0.25( 21)	2.35(100)	1.71(100)
<i>Apogon cyanosoma</i>	Z	R	1.67( 84)			1.15( 70)	1.82(100)	1.40( 80)			
<i>Atrosalarias fuscus holomelas</i>	H	R	0.94( 92)	1.10( 80)	1.18( 96)	1.85(100)	1.32( 96)	0.35( 35)		0.90( 90)	0.86( 86)
<i>Cheiloprion labiatus</i>	C	R	0.90( 90)	1.35( 85)	0.29( 29)	2.00(100)	0.39( 39)	0.80( 80)		0.95( 95)	
<i>Coris variegata</i>	B	V	0.84( 84)	0.45( 45)	0.64( 43)	0.05( 5)	0.04( 4)	0.95( 95)	0.21( 21)	0.95( 90)	
<i>Oxymonacanthus longirostris</i>	C	V	0.61( 35)	0.55( 30)	0.04( 4)	0.40( 20)		1.35( 85)	0.21( 14)	0.65( 35)	0.25( 18)
<i>Corythoichthys haematopterus</i>	Z	R	0.55( 45)	0.35( 35)	0.82( 57)	0.50( 45)	0.71( 57)	0.45( 45)	0.79( 64)	0.35( 30)	0.36( 32)
<i>Epinephelus merra</i>	B	R	0.49( 49)	0.05( 5)	0.04( 4)			0.10( 10)			
<i>Halichoeres melanurus</i>	O	V	0.39( 39)	0.60( 50)	1.04( 96)	0.25( 25)	0.96( 79)	0.05( 5)		0.65( 60)	0.36( 36)
<i>Stethojulis strigiventer</i>	B	V	0.33( 27)	0.55( 35)	0.29( 29)	0.50( 50)	0.39( 39)	0.35( 30)	0.04( 4)	0.50( 50)	0.04( 4)
<i>Cheilinus trilobatus</i>	B	V	0.29( 29)	0.20( 20)	0.07( 7)		0.04( 4)	0.10( 10)	0.07( 7)		
<i>Parapercis cylindrica</i>	O	R	0.25( 24)	0.60( 55)	0.36( 14)	0.80( 75)	0.43( 39)	0.80( 75)	0.36( 36)	0.65( 60)	0.21( 21)
<i>Salarias fasciatus</i>	H	R	0.22( 22)	0.05( 5)	0.29( 29)	0.05( 5)		0.90( 80)	0.82( 64)	0.15( 15)	
<i>Synchiropus ocellatus</i>	Z	R	0.16( 16)								
<i>Scarus sordidus</i>	H	V	0.14( 6)	0.10( 10)	1.32( 43)	0.20( 15)	0.25( 11)	0.05( 5)			
<i>Zebrasoma veliferum</i>	H	V	0.06( 6)	0.15( 15)				0.15( 15)	0.54( 54)	0.10( 10)	0.32( 32)
<i>Hemigymnus melapterus</i>	Z	V	0.04( 4)		0.04( 4)		0.04( 4)				
<i>Chaetodon plebeius</i>	C	V	0.04( 4)	0.25( 25)		0.05( 5)		0.10( 10)	0.75( 75)	0.80( 75)	0.43( 43)

TABLE 2 (continued)

SPECIES	T.C.	RESIDENCY	EXPT. C	EXPT. F1		EXPT. F2		EXPT. S1		EXPT. S2	
				LIVING CORAL	DEAD CORAL	LIVING CORAL	DEAD CORAL	95% COVERAGE	70% COVERAGE	95% COVERAGE	70% COVERAGE
<i>Halichoeres trimaculatus</i>	B	V	0.04( 4)							0.05( 5)	0.14( 14)
<i>Scolopsis cancellatus</i>	B	V	0.04( 4)			0.65( 65)	0.50( 50)			0.20( 20)	
<i>Chaetodon trifasciatus</i>	C	V	0.04( 2)	0.10( 5)				0.30( 30)	0.11( 11)	0.20( 10)	0.32( 25)
<i>Amblygobius albimaculatus</i>	O	R	0.02( 2)								
<i>Scarus sp.</i>	H	V	0.02( 2)	0.25( 25)		0.30( 5)	0.11( 4)	0.05( 5)			
<i>Acanthurus dussumieri</i>	H	V	0.02( 2)	0.05( 5)	0.21( 11)	0.20( 20)	0.07( 4)				
<i>Scarus ghobban</i>	H	V	0.02( 2)		0.32( 29)	0.05( 5)	0.14( 11)				
<i>Chaetodon trifascialis</i>	C	V	0.02( 2)	0.05( 5)				0.10( 10)			0.07( 7)
<i>Plesiops coeruleolineatus</i>	B	R			0.54( 32)	0.05( 5)	0.14( 7)	0.10( 10)	0.04( 4)	0.10( 10)	
<i>Siganus spinus</i>	H	V		0.10( 10)	0.04( 4)	0.05( 5)	0.04( 4)	0.05( 5)			
<i>Scarus venosus</i>	H	V			0.21( 7)		0.68( 25)				
<i>Fowleria aurita</i>	B	R		0.05( 5)	0.07( 7)						
<i>Asterropteryx semipunctatus</i>	O	R			0.29( 14)					0.05( 5)	
<i>Labracinus cyclophthalmus</i>	B	R					0.25( 18)	0.10( 10)			
<i>Siganus virgatus</i>	H	V				0.05( 5)	0.04( 4)				
<i>Cheilodipterus quinquelineatus</i>	B	R				0.75( 75)	0.54( 46)				
<i>Pomacentrus moluccensis</i>	O	R				0.05( 5)					
<i>Parapercis polyophthalma</i>	B	R				0.10( 10)					
<i>Diodon liturosus</i>	B	V				0.10( 10)					
<i>Thalassoma lunare</i>	B	V					0.04( 4)				
<i>Epinephelus summana</i>	P	R					0.07( 7)				
<i>Apogon robustus</i>	B	R						0.40( 40)			
<i>Stethojulis bandanensis</i>	Z	V								0.05( 5)	
Total number of species			28	23	23	26	26	25	14	20	14

NOTE: Parentheses indicate the percentage occurrence calculated by number of days when a fish occurred on the colony/total number of census days  $\times$  100. T. C., trophic category; H, herbivore; Z, zooplankton feeder; B, benthonic animal feeder; O, omnivore; C, coral polyp feeder; P, piscivore. Residency classification: R, resident; V, visitor.



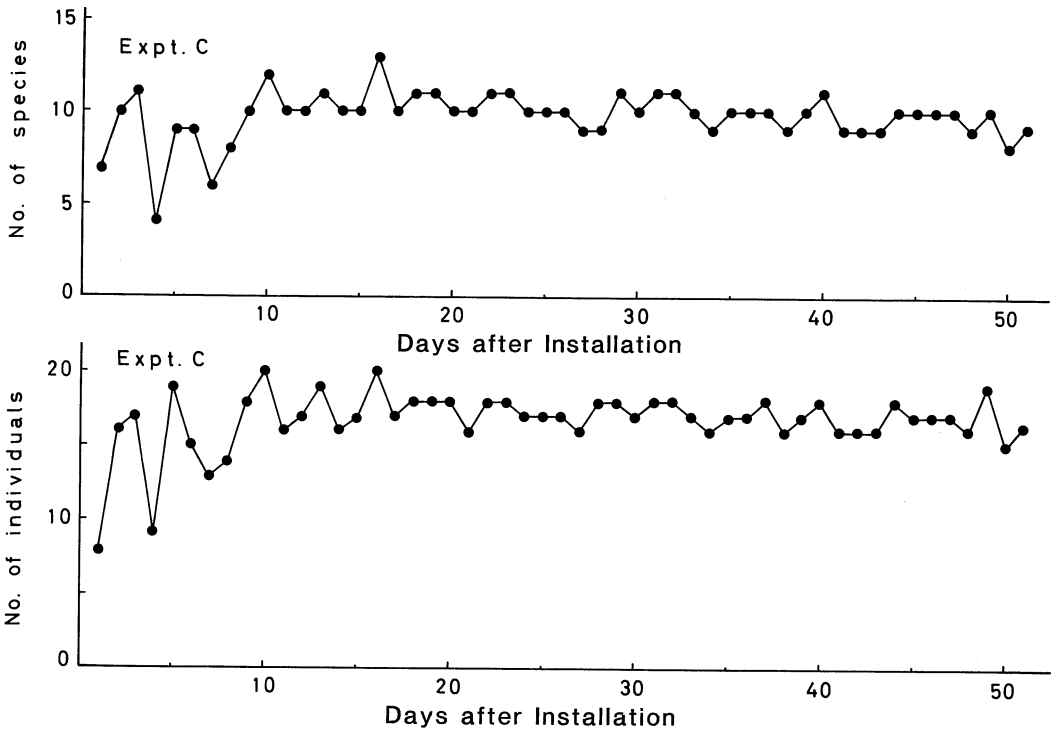


FIGURE 10. Numbers of species and of individuals on the colony in Experiment C during the study period.

TABLE 3

MEAN DAILY NUMBERS OF SPECIES AND OF INDIVIDUALS ON THE COLONY IN EACH EXPERIMENT DURING THE STABLE PERIOD

EXPERIMENT	NO. OF SPECIES	NO. OF INDIVIDUALS
Expt. C	$10.1 \pm 0.3$	$17.2 \pm 0.3$
Expt. F1 Living coral colony	$9.0 \pm 0.8$	$20.4 \pm 0.9$
Expt. F1 Dead coral colony	$8.2 \pm 0.7$	$14.3 \pm 1.4$
Expt. F2 Living coral colony	$9.4 \pm 0.5$	$22.7 \pm 0.5$
Expt. F2 Dead coral colony	$8.7 \pm 0.5$	$14.4 \pm 0.9$
Expt. S1 Coral colony of 95% coverage	$10.7 \pm 0.4$	$21.1 \pm 0.5$
Expt. S1 Coral colony of 70% coverage	$5.7 \pm 0.3$	$14.8 \pm 0.4$
Expt. S2 Coral colony of 95% coverage	$9.6 \pm 0.6$	$16.9 \pm 0.7$
Expt. S2 Coral colony of 70% coverage	$6.0 \pm 0.3$	$9.8 \pm 0.6$

NOTE: Values are mean  $\pm$  95% confidence limits of the mean.

bers of species and individuals counted during this stable period were  $10.1 \pm 0.3$  (95% confidence limits of the mean) and  $17.2 \pm 0.3$ , respectively (Table 3). Most of the dominant species, such as *Dascyllus aruanus*, *Gobiodon citrinus*, *Pomacentrus flavicauda*, and *Apogon cyanosoma*, were observed every day and their

numbers hardly varied throughout the stable period. Therefore, we assume that the numbers of species and of individuals during the stable period can be considered as the maximum population possible in the colony, and these numbers are used in the discussion which follows.

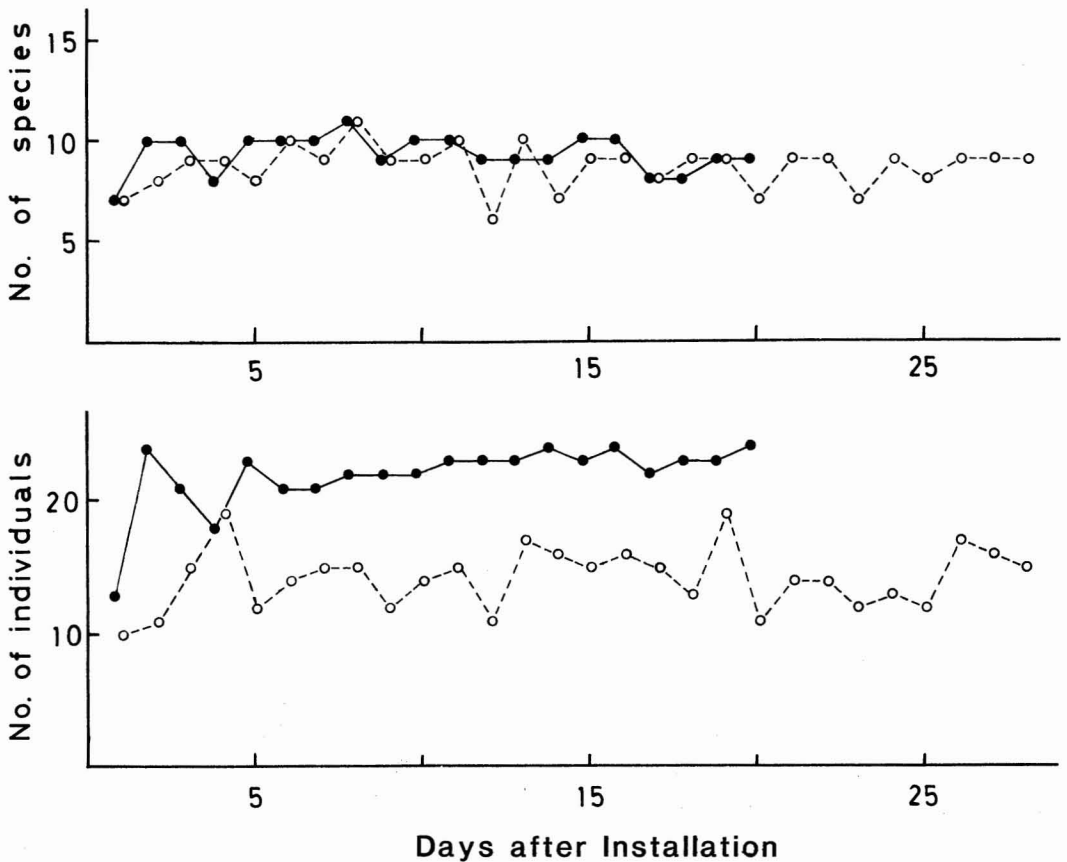


FIGURE 11. Numbers of species and of individuals on living (closed circle) and dead (open circle) coral colonies in Experiment F<sub>2</sub> during the study period.

In Experiments F1 and F2 (experimental living coral colonies and experimental dead coral colonies) there was no significant difference in the pattern of settlement of fishes, and the numbers of species and individuals stabilized about a week after installation. Nor was there a significant difference between living and dead colonies when daily numbers of species were examined during the stable period (Table 3, Figure 11) (Mann-Whitney's *U*-test,  $p > 0.10$  for Experiment F1 and  $p > 0.05$  for Experiment F2). However, the numbers of individuals were significantly greater on the living colonies than on the dead colonies ( $p < 0.01$ ).

To determine which fishes were affected by dead coral colonies, we analyzed the fishes by

trophic categories,<sup>3</sup> based on the consideration that quantitative changes in foods would have either positive or negative effects on the fishes. Coral polyps, the most important food for coral polyp feeders (Hiatt and Strasburg 1960, Hobson 1974, Sano 1982), are absent after coral is killed and filamentous algae overgrow dead coral skeletons. The results of our comparison of species and individuals during the stable period on the living and dead coral colonies are shown in Table 4 and Figure 12. More species of herbivores in Experiment F1 and more species of omni-

<sup>3</sup> The piscivores in Experiment F2 are excluded because only one species, *Epinephelus summana*, with few individuals was involved.

TABLE 4

MEAN DAILY NUMBERS OF SPECIES AND OF INDIVIDUALS DURING THE STABLE PERIOD FOR EACH TROPHIC CATEGORY ON THE LIVING AND ON THE DEAD CORAL COLONIES IN EXPERIMENTS F1 AND F2

TROPHIC CATEGORY	NUMBER OF SPECIES				NUMBER OF INDIVIDUALS			
	EXPT. F1		EXPT. F2		EXPT. F1		EXPT. F2	
	LIVING CORAL	DEAD CORAL	LIVING CORAL	DEAD CORAL	LIVING CORAL	DEAD CORAL	LIVING CORAL	DEAD CORAL
Herbivores	1.3 ± 0.5	2.5 ± 0.4	1.5 ± 0.4	1.6 ± 0.4	1.7 ± 0.6	4.2 ± 1.4	2.7 ± 0.5	2.7 ± 0.9
Zooplankton feeders	0.9 ± 0.5	1.0 ± 0.4	1.9 ± 0.5	2.1 ± 0.3	1.3 ± 0.9	1.2 ± 0.5	2.5 ± 0.7	3.1 ± 0.3
Benthonic animal feeders	1.1 ± 0.4	1.5 ± 0.4	1.7 ± 0.4	1.7 ± 0.2	1.1 ± 0.4	1.5 ± 0.4	1.7 ± 0.4	1.7 ± 0.2
Omnivores	3.2 ± 0.5	3.1 ± 0.4	2.0 ± 0.4	2.9 ± 0.3	6.3 ± 0.7	7.2 ± 0.3	5.8 ± 0.5	6.4 ± 0.4
Coral polyp feeders	2.5 ± 0.3	0.2 ± 0.2	2.3 ± 0.3	0.4 ± 0.3	10.0 ± 0.4	0.2 ± 0.2	9.9 ± 0.5	0.5 ± 0.4

NOTE: Values are mean ± 95% confidence limits of the mean.

vores in Experiment F2 were found on the dead coral than on the living coral (Mann-Whitney's  $U$ -test,  $p < 0.01$ ). In both trophic categories, however, differences between the two kinds of colonies were small with only one or two species involved. In contrast, the numbers of species of coral polyp feeders were greater on the living colonies in both experiments ( $p < 0.01$ ). No significant difference was found for species in the other trophic categories in either Experiment F1 or F2 ( $p > 0.10$ ). In both experiments the coral polyp feeders occurring on the dead colonies were almost always the two residents, *Gobiodon citrinus* and *Cheilopriion labiatus*, but both species disappeared about the 10th day after installation when filamentous algae began to overgrow the branches of the dead coral skeletons.

Even though the numbers of individuals of herbivores and omnivores in Experiment F1 were greater on the dead than on the living coral colonies ( $p < 0.01$  for herbivores and  $p < 0.05$  for omnivores), the numbers of individuals of these two categories in Experiment F2 showed no significant difference between the two kinds of colonies ( $p > 0.10$ ). However, the numbers of individuals of coral polyp feeders decreased markedly on the dead colonies in both experiments. Numbers of individuals in the other trophic categories (i.e., the zooplankton feeders and the benthonic animal feeders) were not significantly different

in either experiment on living and dead colonies ( $p > 0.10$ ).

In Experiment F1, on the dead coral colonies, there were sudden rises in the numbers of individuals of herbivores on the 14th, 15th, and 27th days after installation (Figure 12). Similar increases occurred in Experiment F2 several times on and after the 13th day. These increases were due to the arrival of small schools of visiting scarid fishes that occasionally appeared on the dead coral colonies where they fed on filamentous algae.

In Experiments S1 and S2 we examined the effects of decreased structural complexity of coral branches on the absolute and relative abundance of fishes. There were no significant differences in the pattern of settlement of fishes in Experiments S1 and S2, and the numbers of species and of individuals on coral colonies of both 95% and 70% coverage were stable from about the 6th day after installation. The numbers of species and of individuals during the stable period were obviously greater on the coral colonies of 95% coverage compared with the coral colonies of 70% coverage (Table 3, Figure 13). These results are associated with fishes that are dependent on the structure of coral branches. The fishes were grouped as resident or visitor and the numbers of species and individuals in each group were compared on the two types of coral colonies (Table 5, Figure 14). Greater numbers of residents were seen on the coral

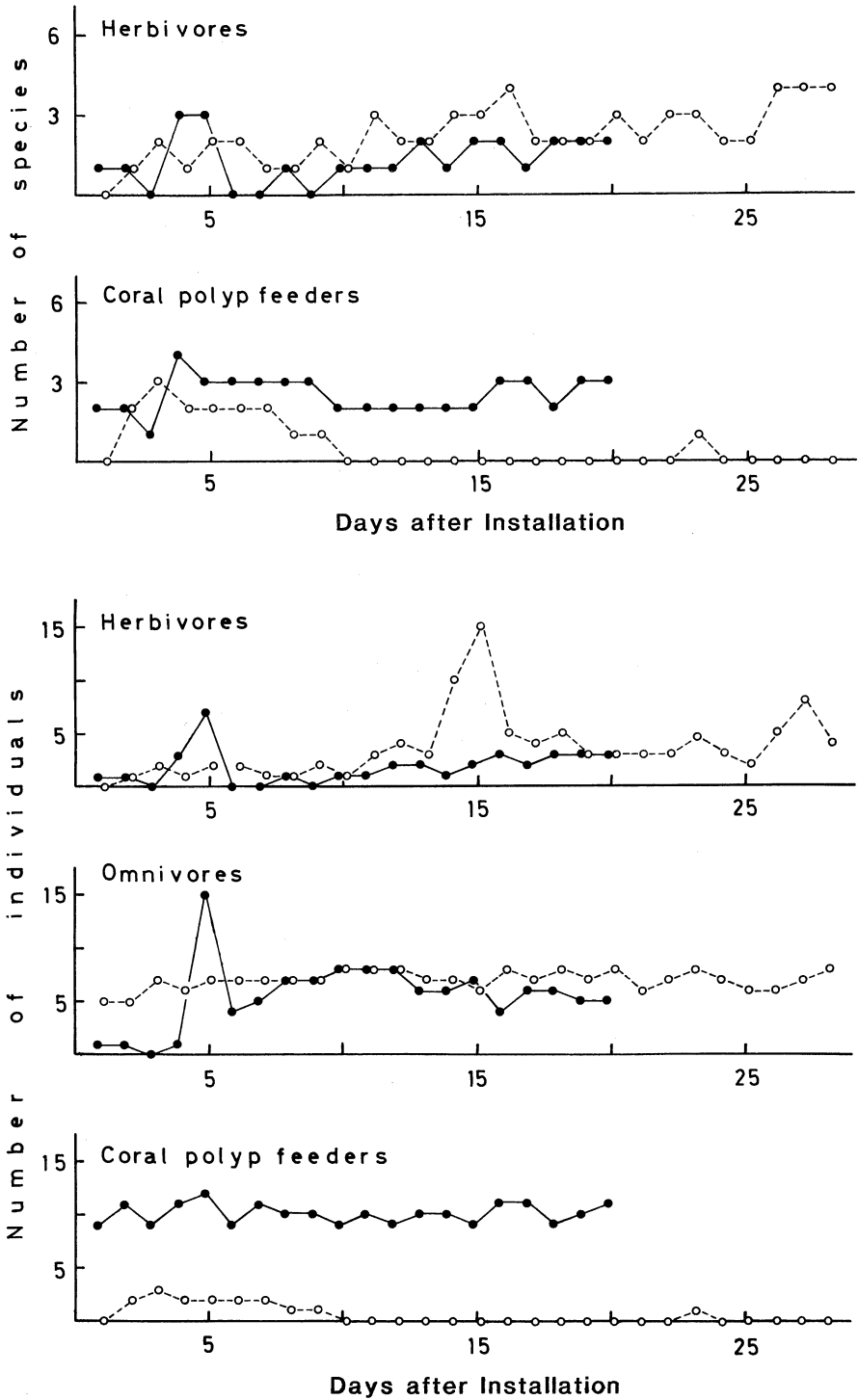


FIGURE 12. Numbers of species and of individuals for each trophic category, herbivores, omnivores, and coral polyp feeders, on living (closed circle) and dead (open circle) coral colonies in Experiment  $F_1$  during the study period.

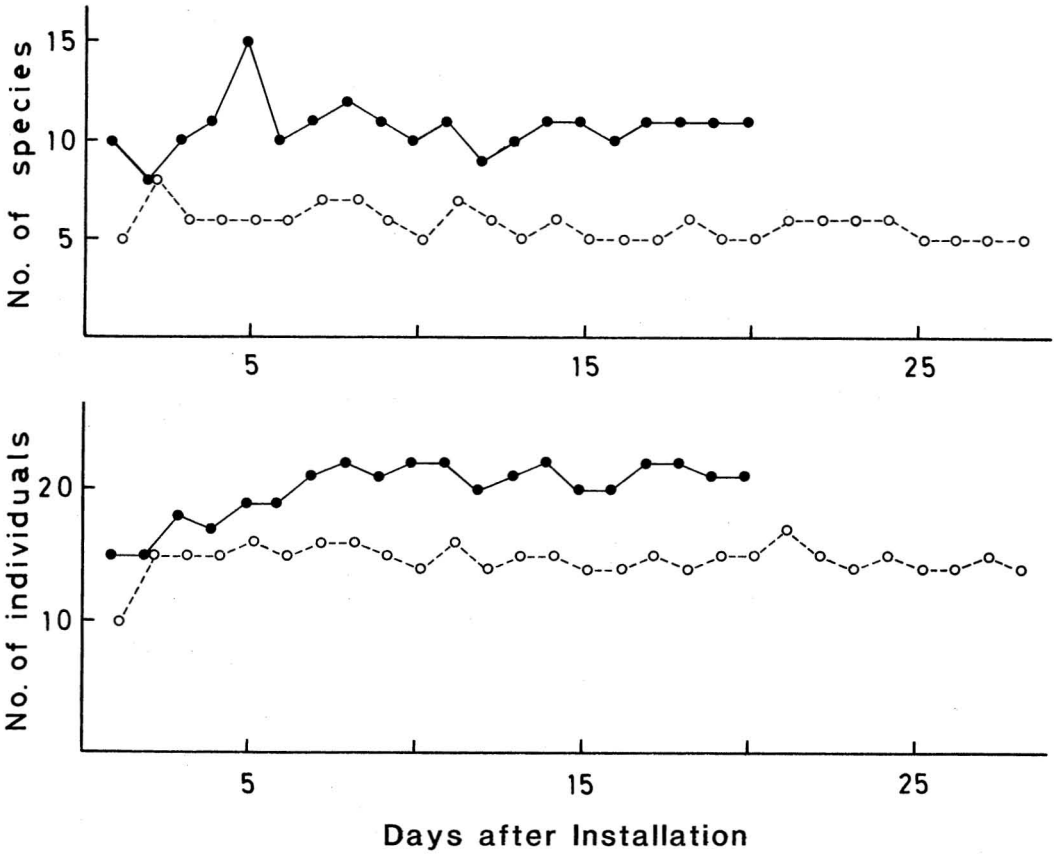


FIGURE 13. Numbers of species and of individuals on the coral colonies of 95% (closed circle) and 70% (open circle) coverage in Experiment S<sub>1</sub> during the study period.

TABLE 5

MEAN DAILY NUMBERS OF SPECIES AND OF INDIVIDUALS DURING THE STABLE PERIOD FOR EACH GROUP, RESIDENTS AND VISITORS, ON THE CORAL COLONIES OF 95% AND 70% COVERAGE IN EXPERIMENTS S1 AND S2

RESIDENCY	NO. OF SPECIES				NO. OF INDIVIDUALS			
	EXPT. S1		EXPT. S2		EXPT. S1		EXPT. S2	
	95% COVERAGE	70% COVERAGE	95% COVERAGE	70% COVERAGE	95% COVERAGE	70% COVERAGE	95% COVERAGE	70% COVERAGE
Residents	8.1 ± 0.4	3.9 ± 0.3	6.8 ± 0.4	4.4 ± 0.3	18.1 ± 0.6	13.0 ± 0.4	13.7 ± 0.8	8.1 ± 0.6
Visitors	2.5 ± 0.4	1.7 ± 0.3	2.8 ± 0.6	1.6 ± 0.3	3.0 ± 0.4	1.8 ± 0.3	3.3 ± 0.8	1.7 ± 0.3

NOTE: Values are mean ± 95% confidence limits of the mean.

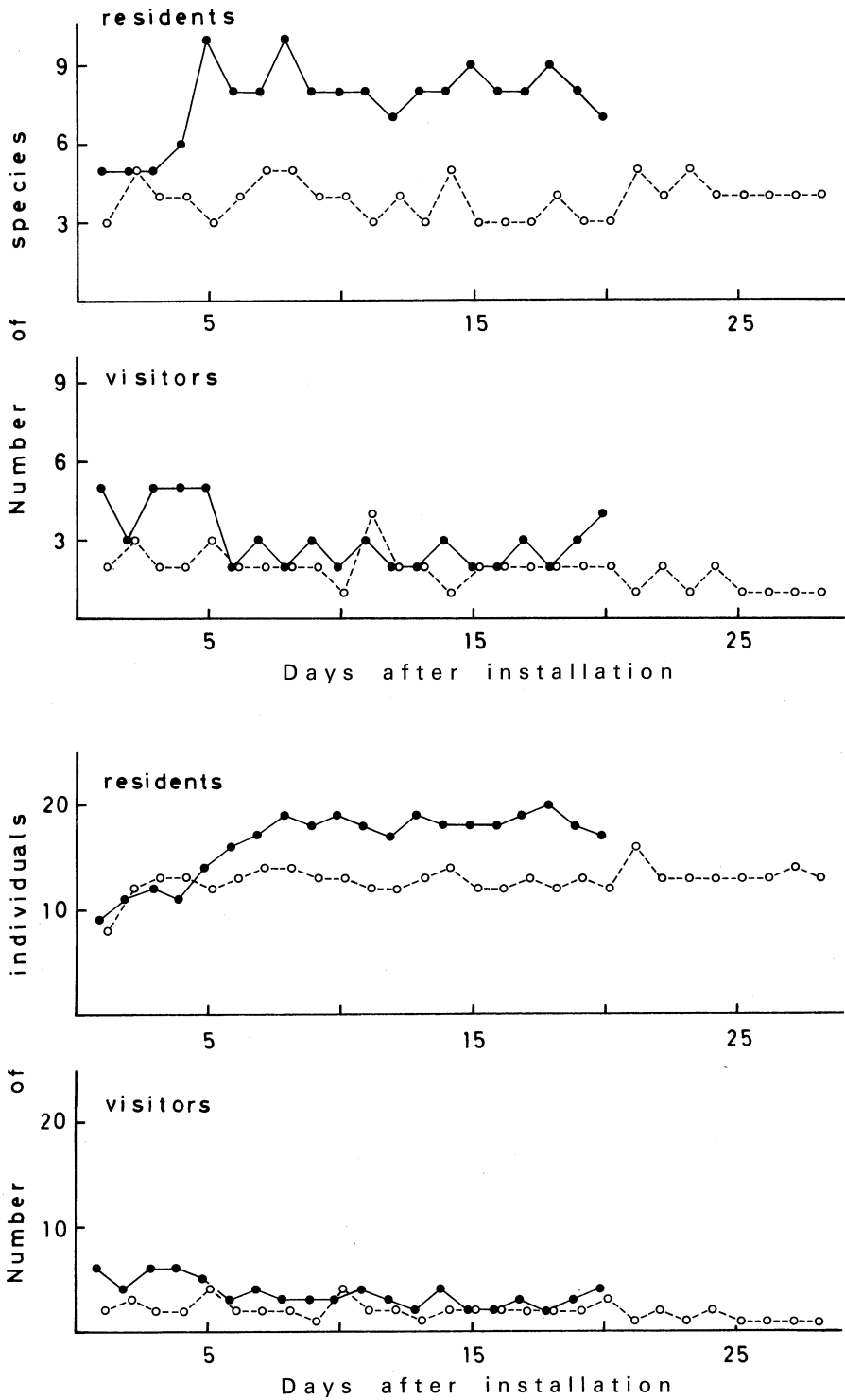


FIGURE 14. Numbers of species and of individuals for each group, residents and visitors, on the coral colonies of 95% (closed circle) and 70% (open circle) coverage in Experiment  $S_1$  during the study period.

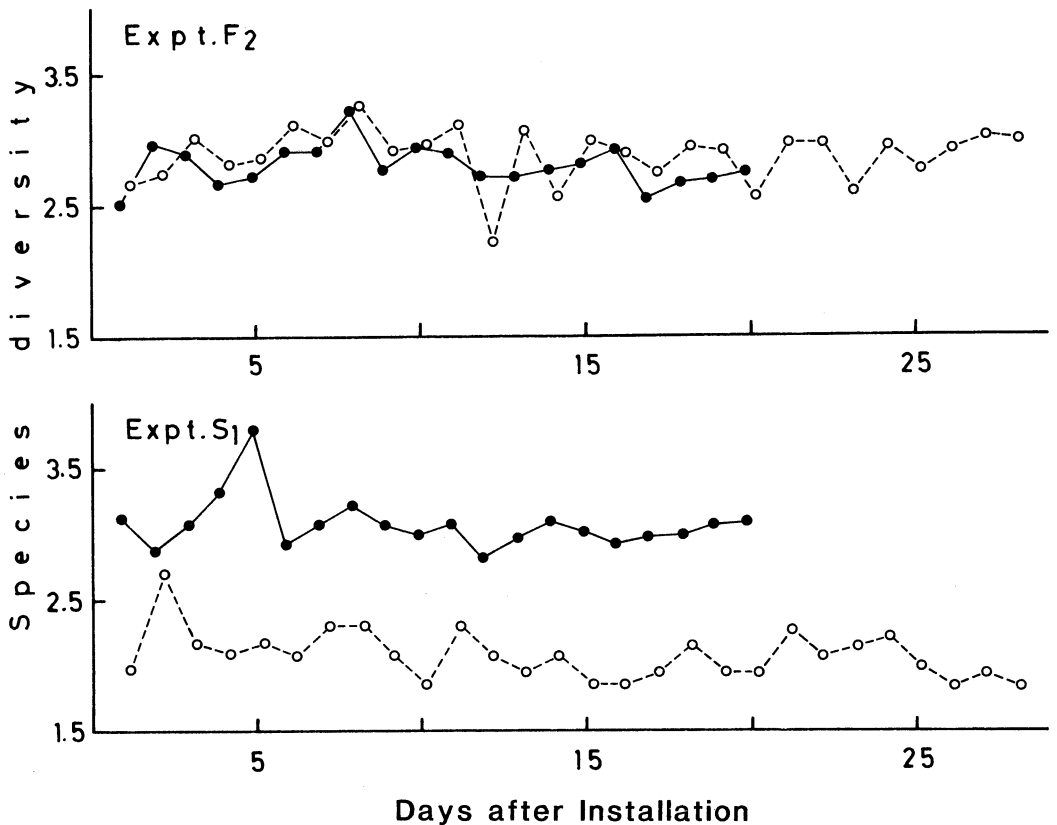


FIGURE 15. Species diversity of fishes on the coral colonies in Experiments  $F_2$  and  $S_1$  during the study period. In Experiment  $F_2$ , closed and open circles indicate the living and the dead coral colonies, respectively. In Experiment  $S_1$ , they indicate the coral colonies of 95% and 70% coverage, respectively.

colonies with 95% coverage and significantly greater numbers of visitor species were seen on the same colonies in both experiments (Mann-Whitney's  $U$ -test,  $p < 0.01$ ). However, the difference in the number of visitors between the two kinds of colonies was small compared with that of residents. Similar results were found for the numbers of individuals.

Species diversity measured for each day in Experiments  $F_2$  and  $S_1$  is shown in Figure 15 and mean daily species diversity during the stable period in each experiment in Table 6. In Experiments  $F_1$  and  $F_2$  species diversity during the stable period showed no significant difference between the living and the dead colonies ( $t$ -test,  $p > 0.20$ ). However, in Experiments  $S_1$  and  $S_2$  species diversity was

higher on the colonies with 95% coverage than on the colonies with 70% coverage.

#### DISCUSSION

Coral reef fishes that coexist within reef habitats utilize two main resources, food and living space. The availability of these resources declines in *Acanthaster*-damaged reef areas, and as a result the associated fish communities are altered. We first analyze the results of the field experiments to examine the effects on the fishes and then predict the possible changes in the structure of fish communities on natural dead coral colonies. We then analyze the observations of the natural coral colonies to see if the predicted changes actually occurred.

TABLE 6

MEAN DAILY SPECIES DIVERSITY ( $H'$ ) OF FISHES ON THE COLONY IN EACH EXPERIMENT DURING THE STABLE PERIOD

EXPERIMENT		$H'$
Expt. F1	Living coral colony	2.670 $\pm$ 0.132
	Dead coral colony	2.636 $\pm$ 0.146
Expt. F2	Living coral colony	2.804 $\pm$ 0.086
	Dead coral colony	2.875 $\pm$ 0.096
Expt. S1	Coral colony of 95% coverage	2.999 $\pm$ 0.052
	Coral colony of 70% coverage	2.027 $\pm$ 0.066
Expt. S2	Coral colony of 95% coverage	2.989 $\pm$ 0.119
	Coral colony of 70% coverage	2.453 $\pm$ 0.076

NOTE: Values are mean  $\pm$  95% confidence limits of the mean.

The effects of coral death on the fish communities were examined in Experiments F1 and F2 in which structural complexity of the coral colonies was preserved. In these experiments coral polyp feeders were markedly reduced in numbers by coral death. They inevitably disappeared from the experimental dead coral colonies because of the absence of food. Endean and Stablum (1973) also reported from the Great Barrier Reef, Australia, that coral hunting fishes such as chaetodontids and pomacentrids remained in the vicinity of dead coral skeletons initially, but disappeared when the skeletons were covered with a hard coating of algae.

On the other hand, it was expected that greater numbers of species and of individuals of both herbivores and omnivores would appear on the experimental dead coral colonies in both Experiments F1 and F2 because of the increase in food in the form of the heavy growth of filamentous algae on the dead coral skeletons. These expected changes did not always occur. A greater number of species of herbivores appeared on the experimental dead coral colony in Experiment F1 but not in Experiment F2, and there was a greater number of species of omnivores on the experimental dead coral colony in Experiment F2 but not in Experiment F1. Similarly, the numbers of individuals of both herbivores and omnivores were greater on the experimental dead coral colony in Experiment F1 but not in Experiment F2. In addition, even when the numbers of species and of individuals of both

herbivores and omnivores increased on the dead coral colonies, the increase was very small. Thus, considering these results synthetically, we conclude that the quantitative increase in filamentous algae has little or no effect on the species and fish numbers in both categories. The reason may be that intra- and interspecific territoriality and agonistic encounters among resident herbivores and omnivores already occupying the colonies prevent neighboring herbivores and omnivores from intruding into the experimental dead colonies even if their food is more abundant (Low 1971). For example, we actually observed the resident herbivore *Atrosalarias fuscus holomelas* and the resident omnivore *Pomacentrus flavicauda* attacking intruders of the same trophic category on and near the dead colonies.

It is noteworthy that Coles (1980), investigating decapod communities on living and dead colonies of the reef coral *Pocillopora meandrina* in Hawaii, found that the numbers of species and individuals and species diversity of decapods on the dead colonies, where structural complexity was preserved, were substantially greater than those on the living colonies. Coles' observation thus is quite different from the results of our studies on fish communities.

Decrease in structural complexity of coral branches in Experiments S1 and S2 resulted in a decrease in the number of species, in the number of individuals, and in species diversity in the fish communities associated with the corals. These decreases in numbers and diversity were due to the reduction in shelter for residential species that are dependent on coral for cover. The numbers of visitors also decreased significantly but the decrease was small compared with that of the residents (Table 5, Figure 14). Visitors were not greatly affected by the decrease in structural complexity because they utilize home ranges much larger than the areas of the experimental colonies and can easily move to more suitable space. Clarke (1977) reported similar observations at South Bimini, Bahamas: species diversity of resident pomacentrids, *Stegastes* (as *Eupomacentrus*), is closely tied to habitat structural complexity, whereas that



of visitor chaetodontids, *Chaetodon*, is not so tied. However, if an entire coral reef is killed and the structural complexity is decreased, visitors might also be negatively affected because of the collapse of their refuge and resting sites.

Fish species diversity on coral reefs has been positively correlated with reef surface complexity (Risk 1972, Alevizon and Brooks 1975, Luckhurst and Luckhurst 1978, Gladfelter, Ogden, and Gladfelter 1980), and Kohn (1967) has reported a similar observation for assemblages of the gastropod genus *Conus* on tropical Indo-west Pacific reef platforms. Experiments S1 and S2 provide further confirmation of these observations as they do the theory of spatial heterogeneity of species diversity of Pianka (1966).

The experiments enable us to predict the course of events in the structure of coral reef fish communities when corals are killed. Coral polyp feeders disappear because of the absence of their food, but representatives of other trophic categories remain as long as the structural complexity of the coral is retained. When structural complexity is decreased by bio- and physical erosion, species diversity and the number of resident species and individuals decrease.

Fish community structure on the natural dead coral colonies was qualitatively and quantitatively different from that on natural living coral colonies. The numbers of resident species and individuals decreased markedly on the dead corals with low structural complexity, but visitors did not show the same pattern (although the number of species in spring slightly decreased). These observations are similar to those recorded in Experiments S1 and S2, and we again conclude that the numbers of residents decrease on the dead coral colonies when structural complexity diminishes. Visitors, on the other hand, are not substantially affected by the destruction of the colonies because of their larger home ranges. Sale and Dybdahl (1975) reported a similar result from an experiment at Heron Reef, Great Barrier Reef, Australia, in which patterns of distribution of residents on small living colonies (25 to 30 cm in diameter) of *Acropora pulchra* were compared with those on similar size pieces of eroded coralline rock.

Greater numbers of species and of individuals were collected from the topographically heterogeneous living colonies than from the more homogeneous pieces of coralline rock.

Coral polyp feeders were most negatively affected by destruction of the coral and completely disappeared from the dead coral colonies. A similar phenomenon was observed on the experimental dead colonies in Experiments F1 and F2. Therefore, we again conclude that, due to the absence of food, coral polyp feeders inevitably disappear from dead coral colonies.

The numbers of species and individuals of other trophic categories decreased on the dead coral colonies. Zooplankton feeders and omnivores decreased both in numbers of species and of individuals, and herbivores decreased in number of individuals. However, representatives of these categories did not decrease on the experimental dead coral colonies where structural complexity was preserved (Experiments F1 and F2). To explain this apparent contradiction, we examined abundance of food for each category on the living and dead colonies. Demersal zooplankton is considered the main food resource for zooplankton feeders and for some omnivores censused in the present study, but biomass of demersal zooplankton is not significantly different on the L- and D-Sts (Sano 1982). Algal biomass, the main food resource for herbivores and omnivores, increased on the dead colonies as the coral skeletons exposed by the attack of *Acanthaster* were overgrown with tufts of filamentous algae. Thus, zooplankton feeders, herbivores, and omnivores on dead corals cannot be limited by their food. Rather, they must be limited by living space because of the decrease in the structural complexity of the dead coral colonies.

To provide a partial test of this explanation, fishes known to be zooplankton feeders and omnivores were grouped as either resident or visitor, and the total number of species of each group was plotted against the volume of each coral colony (Figures 16 and 17). Among the zooplankton feeders, residents showed significantly greater numbers of species on the living coral colonies compared with those on the dead colonies in spring and summer

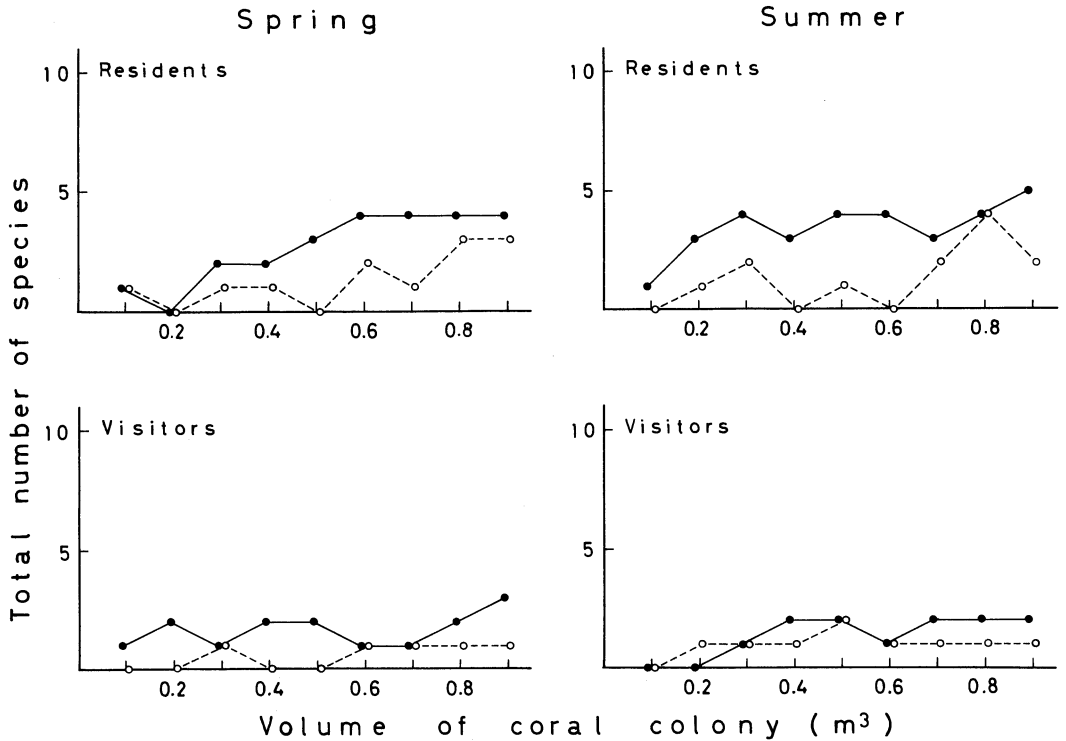


FIGURE 16. Total numbers of species of resident and visitor zooplankton feeders on each living (closed circle) and dead (open circle) coral colony in spring and summer.

(Wilcoxon's test,  $p < 0.02$  for spring and  $p < 0.01$  for summer). Visitors showed slightly greater numbers on the living coral colonies in spring ( $p < 0.05$ ), but no significant difference in summer ( $p > 0.05$ ). On the other hand, among the omnivores, there was a significantly greater number of resident species on the living corals in both seasons ( $p < 0.01$  for spring and  $p < 0.05$  for summer). There was no significant difference in visitors between the two kinds of colonies in either season ( $p > 0.10$  for spring and  $p > 0.05$  for summer). Therefore, we conclude that the decrease in the numbers of species of these two trophic categories on the dead coral colonies was mainly due to the decrease in the residents in each of the trophic categories except for the visitor zooplankton feeders in spring.

When examining the decrease in numbers of individuals of the three trophic categories on the dead corals, our attention was drawn to

species which were abundant on the living colonies but markedly less numerous on the dead colonies. These species included *Atriosalaria fuscus holomelas* among the herbivores, *Apogon nubilus* (only summer) of the zooplankton feeders, and *Dascyllus aruanus*, *Pomacentrus moluccensis*, *Chrysiptera cyanea*, and *Asterropteryx semipunctatus* (only summer) among the omnivores. All were residents. Here again, we reach the same conclusions.

The changes in structure of fish communities on dead corals generally agree with those predicted in the field experiments. That is, on the dead corals, coral polyp feeders disappear due to the absence of food, and the numbers of species and individuals of residents decrease due to decrease in living space or shelter associated with the reduction in structural complexity. Fish species diversity also markedly decreases.

There remain, however, some anomalies

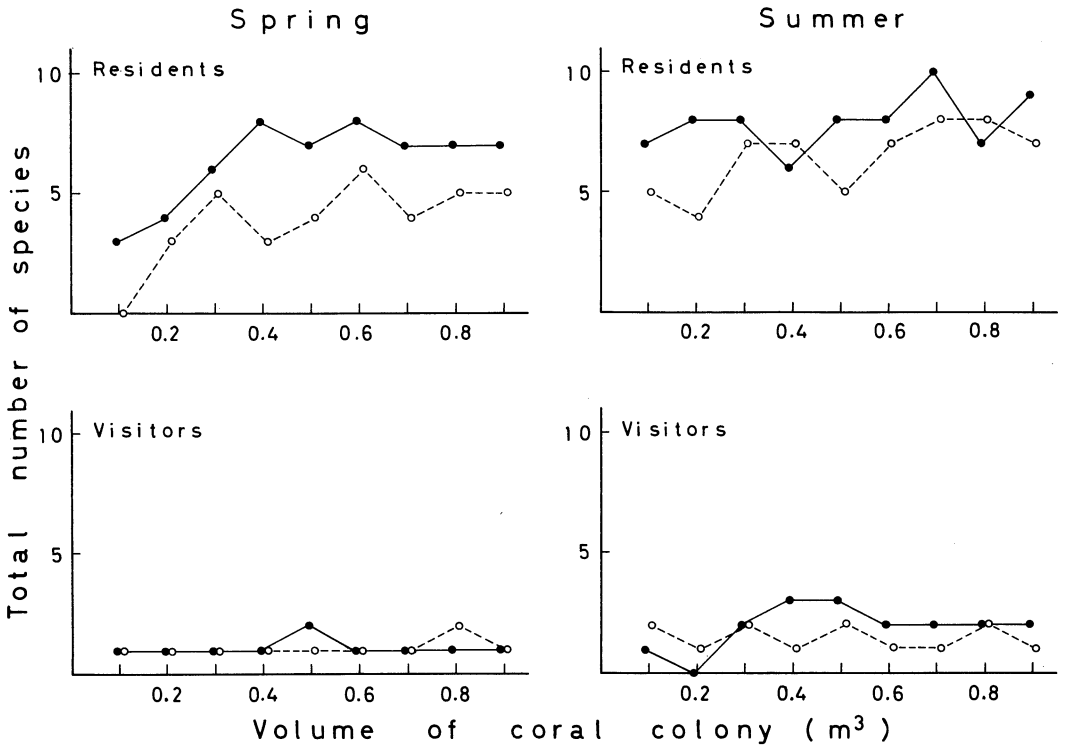


FIGURE 17. Total numbers of species of resident and visitor omnivores feeders on each living (closed circle) and dead (open circle) coral colony in spring and summer.

among our observations. Unexpectedly, one resident omnivore, *Pomacentrus littoralis*, showed a remarkable increase in number of individuals on the dead corals. We are unable to explain this observation. Nor can we explain the small and/or inconsistent increases in numbers of individuals some species showed on the dead corals (Table 1).

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