

Recruitment of juvenile corals onto coral tables preyed upon by *Acanthaster planci*

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ABSTRACT: Corals of 3 table-forming species of the genus *Acropora*, whose tissues had been removed by the seastar *Acanthaster planci* (L.) during 2 mo prior to a major annual coral-spawning season, acted as substrata onto which juvenile corals settled. Juvenile corals were detected microscopically in the laboratory on samples taken from tables 10 wk after spawning time (mean diameter of juveniles 1.3 mm; density 3.5 per 100 cm²). Previously it had been thought that a delay of at least 1 yr was necessary before corals would settle after predation by *A. planci*. The same tables were sampled again after the next coral-spawning season (1 yr later). Despite the presence of algae and other colonizing organisms, new corals had settled at a density of 2.8 per 100 cm². About 34 % of the previous year's juveniles had survived, and mean diameter of these was now 7.24 mm. When tables were searched closely in the field, surviving juveniles and some new recruits (with diameters down to 2.00 mm) could be detected. These results indicate that apparent delay in settlement after predation by *A. planci* can be due to the small size of newly settled corals, which can only be seen by careful inspection of the substratum during the first year after settlement, and which do not achieve 3-dimensional structure until some time later. *A. planci* was still present at the site when these observations were made. Thus re-establishment of the coral community on this reef had begun during the time that the adult community was being preyed upon.

INTRODUCTION

The predatory seastar *Acanthaster planci* (Linnaeus) removes the tissues of its coral prey, leaving the skeleton bare. When seastars are numerous, few corals escape predation (e.g. Chesher 1969, Pearson & Endean 1969, Branham 1973, Endean 1973, review in Potts 1981) and afterwards new scleractinian corals do not become evident for some years (Endean 1973, 1974, 1976, Endean & Stablum 1973b, Randall 1973, Birke-land unpubl. report 1979). Although no detailed studies exist for recruitment of coral larvae immediately after such an event, several generalizations based on field observations have been made, in particular: (a) there is a lag period of at least a year before coral larvae can settle, some sort of preconditioning being required before the substratum is suitable (Pearson 1981 [review], Colgan 1982); (b) rapid coverage of coral skeletons by algal growth or soft corals creates a barrier to settlement of coral larvae (Endean 1973, 1976, Potts 1981); (c) even if larvae do settle on skele-

tons of corals killed by *Acanthaster planci*, subsequent growth of algae or soft corals, or other factors such as break-up and movement of the skeletal material, cause early mortality (Endean 1973, 1976).

Similar delays have been seen before settlement of corals onto artificial substrata (Schuhmacher 1974, 1977, Loya 1976) and to new surfaces provided by volcanic material (Grigg & Maragos 1974). Recent findings on recruitment to experimentally placed settlement plates, examined microscopically after a few months, offer some explanations for these patterns. Apparent delay in settlement is likely to be an observational error, due to the small size of juvenile corals, and a time lag due to the seasonal nature of availability of coral larvae. Juveniles of most species of corals are recognised only with difficulty before 1 yr old (Wallace 1983, 1985a, Babcock 1985, Harriott 1985) and their censusing requires close scrutiny of the substratum (e.g. Bak & Engel 1979, Sakai & Yamazato 1984). On the Great Barrier Reef, the greatest number and variety of larvae are available in summer, after the major coral-spawning season (Harrison et al. 1984, Wallace 1985b, Willis et al. 1985, Babcock et al. 1986). Although heavy algal cover may affect survival of

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juvenile corals (Birkeland 1977), algae have been shown not to inhibit settlement (Sammarco 1980, Sammarco & Carleton 1982).

Availability of coral larvae has been noted as a further factor potentially limiting recruitment after predation by *Acanthaster planci*, usually in the context of reduced local coral populations (Randall 1973, Endean & Stablum 1973b, Pearson 1981). These authors assumed dependence on localized recruitment, since most corals were thought to release brooded larvae. The possibility that coral populations may derive recruits from non-localized sources of larvae is indicated by recent findings that the majority of corals are broadcast spawners, whose offspring do not settle until 4 to 17 d after release (Kojis & Quinn 1981, Harrison et al. 1984, Schlesinger & Loya 1985, Babcock & Heyward in press).

Such findings suggested a reappraisal of settlement and survival of juvenile corals after predation by *Acanthaster planci*. An opportunity was presented by a population increase of the seastar, and subsequent demise of coral populations, on a reef where experimental studies of coral recruitment were underway (Wallace & Bull 1982, Wallace 1985a, 1985b).

The study reef (Big Broadhurst Reef) was not damaged by *Acanthaster planci* during the population outbreaks in the late 1960s (Pearson & Endean 1969 as 'Shinbun Reef'; Endean & Stablum 1973a as 'Lynch Reef'), although its close neighbour, Broadhurst Reef, suffered a heavy infestation (Pearson & Endean 1969, Endean & Stablum 1973a). In the next outbreak (1979 to present, see Anonymous 1985), of the 2 reefs only Big Broadhurst Reef has thus far been damaged. In mid 1981, large (> 40 cm) and small (6 to 22 cm) individuals of the seastar were present at densities of 1 and up to

8 per 50 m² respectively (small seastar information from T. Walker pers. comm.). By October 1984, large seastars were present at an estimated density of 5 per 50 m². During 1981 and 1982, individual seastars were killing small coral colonies and portions of larger colonies (Wallace 1985c). By late 1983, whole large coral tables were being killed, and their skeletons stood out clearly amongst the live or algae-covered corals of the reef front (Fig. 1). About 60 % of the previously present coral cover remained alive, and colonies of many species contained ripe gonads and spawned during the mass spawning event during the week following the November full moon (Wallace 1985c, Willis et al. 1985, Babcock et al. 1986). One yr later (October 1984), only an estimated 10 to 20 % of the coral cover remained alive, as patches of flourishing corals on the reef top.

We followed recruitment to tables denuded in late 1983, asking: (a) did juvenile corals settle during the first season after predation, when tables had been dead for less than 2 mo? (b) did newly settled corals survive beyond 1 yr? (c) did new corals settle after the following reproductive season, 1 yr later, when tables already had 1 yr's growth of benthic organisms and when few live corals remained as a source of local recruitment?

METHODS

Study sites. Coral tables used in this study were located around the edges of 2 adjacent surge channels on the SW front of Big Broadhurst Reef off the Queensland coast (see Wallace 1985b for map). These channels were flanked by 2 buttresses where recruitment of juvenile corals to settlement plates has been



Fig. 1 Reef front near study sites in Oct 1983, showing white skeletons of freshly killed *Acropora* colonies interspersed amongst darker living and dead colonies

studied for 2 and 5 yr, respectively (by 1985). During a visit to these sites to study spawning of corals in late November 1983, we noted the positions of 11 large tables, freshly killed since a visit in early October. The tables were from 3 species, *Acropora hyacinthus* Dana 1846, *A. cytherea* Dana 1846 and *A. clathrata* Brook 1891 (see Wallace 1978). All were at 3 to 5 m depth on the slopes and base of the reef buttresses.

Study of recruitment immediately after predation. To determine whether coral larvae from the 1983 spawning event settled on these tables, we took a sample from each table (total 11 samples) in February 1984, 10 wk after the time of major offshore spawning (Table 1). This was long enough for recruits to develop

Table 1. Sequence of relevant events and sampling times

| Date | Event |
|----------------|--|
| Oct–Nov 1983 | Tables killed |
| 23–26 Nov 1983 | Mass offshore coral spawning event |
| 7 Feb 1984 | Tables sampled for lab. study |
| 3 Oct 1984 | Juveniles photographed <i>in situ</i> |
| 11–14 Nov 1984 | Mass offshore coral spawning event |
| 12 Feb 1985 | Tables sampled for lab. study; juveniles measured in field |

a recognizable skeleton. Samples with top and bottom surface areas of 150 to 200 cm² were removed carefully with a hacksaw. They were fixed in 10 % formalin for 1 wk and then air-dried. They were then marked with 10 squares, each of 10 cm², on each of the upper and lower surfaces, giving a total sampling surface of 200 cm² per sample. They were searched twice (by 2 different examiners) under a binocular microscope lit by a fibre optic light source. All corals found within the squares were marked, photographed, measured for diameter (see Wallace 1985a), and identified to family.

Coral tables provide a natural, irregular surface of short branchlets interspersed with depressions, so that alternately exposed and protected positions occur in roughly equal proportions over the surface. Juvenile corals were recorded as occupying 'exposed' or 'protected' sites. Because of the anastomosing branching patterns, some depressions contained holes connecting to the other side of the table.

Study of recruitment during second year after predation. To determine whether coral larvae from the 1984 coral-spawning event settled on the tables, we took samples again in February 1985, following the same procedures and examining the samples as before. During this and the previous sampling time, settlement of larvae onto settlement plates was being monitored at 10 sites on the 2 nearby buttresses (Wallace 1985b, Wallace & Watt unpubl. data).

Survival. Survival of the first year's recruits was

examined (a) by recognizing older juveniles from size classes of juveniles on the second year's samples, and (b) by examination of the tables *in situ*. Tables were examined in early October 1984, when they had been dead for 12 mo, to see whether recruits had become visible. In February 1985, visible recruits were measured for maximal and median diameter.

RESULTS

Settlement immediately after predation

On the first samples, taken 4 mo after predation (Table 1), 78 juvenile corals were found (7.00, SE \pm 2.02, per 200 cm²). Significantly more (53) were on lower surfaces than on upper surfaces (25) (chi-square test, $p < 0.05$). Those on lower surfaces were distributed randomly between exposed and protected positions, but those on upper surfaces were situated preferentially in protected positions. Most recruits (68.8 %) were from the family Acroporidae, with the remainder from Pocilloporidae (18.2 %), Poritidae (1.3 %) and other families (10.4 %) (Fig. 2); 1.3 % were unidentifiable because of extremely small size or damaged condition. Diameters ranged from 0.50 to 3.80 mm, with a mean of 1.34 mm SE \pm 0.07 (Fig. 3).

Settlement during second recruitment season

On the second set of 11 samples, taken 1 yr later in February 1985, 88 corals were found (8.1 per 200 cm², SE \pm 2.1), and 2 size categories could be detected (Fig. 3). One category, with a range of diameters from 0.60 to 2.50 mm and a mean of 1.33 mm SE \pm 0.05, consisted of 61 new recruits from the 1984–5 recruitment season. The other, with a range of 4.00 to 16.00 mm and a mean diameter of 7.24 mm SE \pm 0.07, consisted of surviving juveniles from the 1983–4 season, plus any which might have settled during the intervening year. The 61 new recruits showed no significant difference in numbers settled on upper and lower surfaces (chi-square test, $p > 0.05$).

Survival of recruits and visibility in the field

Survival of recruits, based on the density of large juveniles on the second set of samples, was approximately 34 %. Of 27 survivors on 11 samples taken after 16 mo, 16 were on the upper surfaces of tables. Nine of the 11 survivors on lower surfaces were from the ahermatypic genera *Tubastrea* and *Dendrophyllia*, and the other 2 were hermatypic corals.

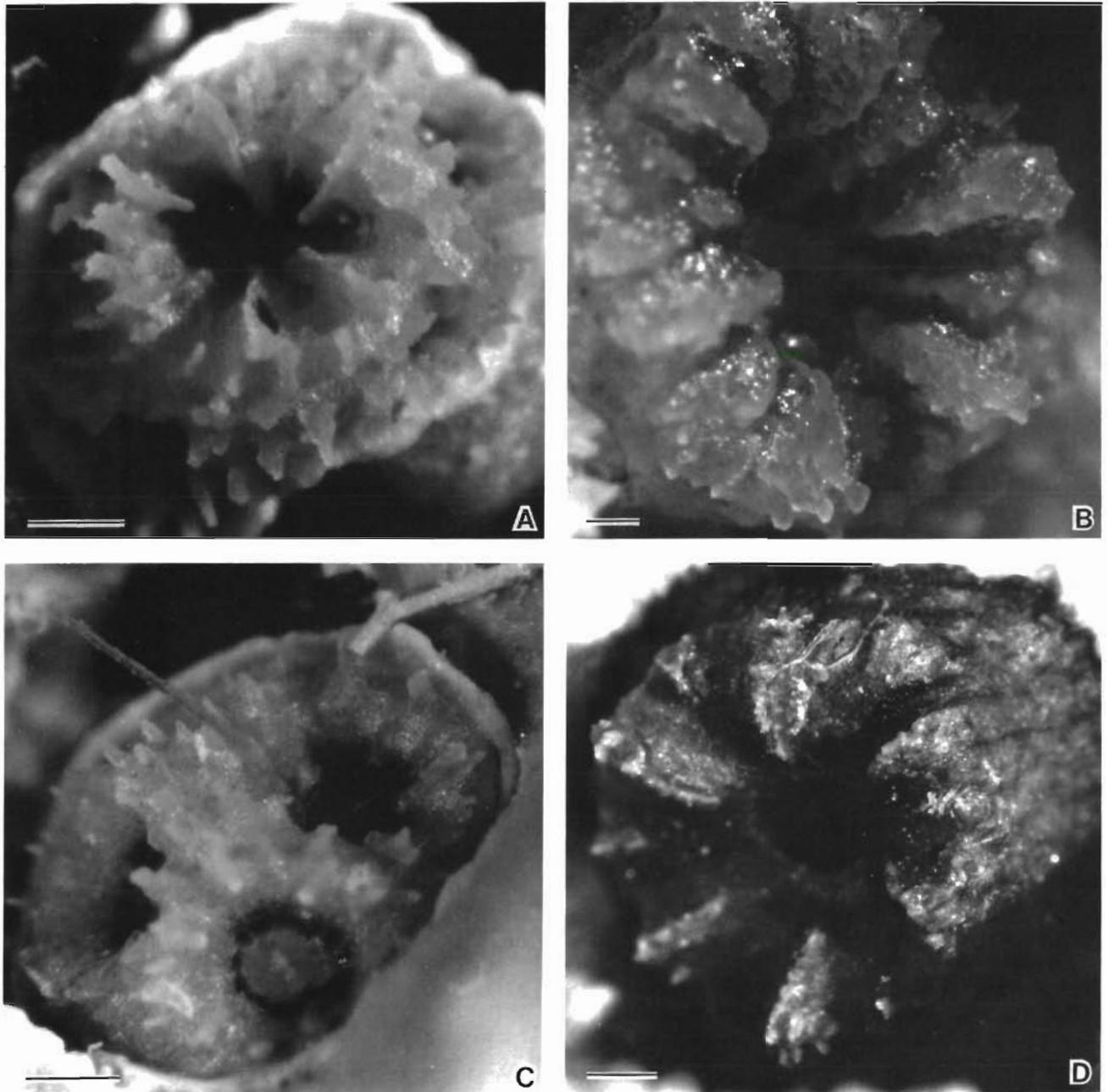


Fig. 2. Ten-week-old coral recruits from coral tables sampled in Feb 1984. (A) Acroporidae; (B) Faviidae ('other'); (C) Pocilloporidae; (D) Dendrophylliidae ('other'). Scale bars: 0.200 mm

Small corals could be detected in the field on close examination of the tables in October 1984 (Fig. 4). By that time, and in the following February when diameters were measured in the field, growth was encrusting. Only 1 of the tables had broken from its stalk by February 1985, and it had fallen about 0.5 m without overturning. Field examination of tables in February 1985 yielded 47 juvenile corals which could be measured. (Others, because of their position within crevices or on undersurfaces, were not accessible.) The mean diameter of recruits measured in the field was

8.9 mm ($SE \pm 0.64$). Five of the recruits measured were under 4 mm diameter, and the smallest was 2 mm; these were thus likely to be recruits from the November 1984 spawning season.

DISCUSSION

Since recruitment occurred during the first 4 mo after predation, we conclude that coral tables freshly killed by *Acanthaster planci* act as substrata for settle-

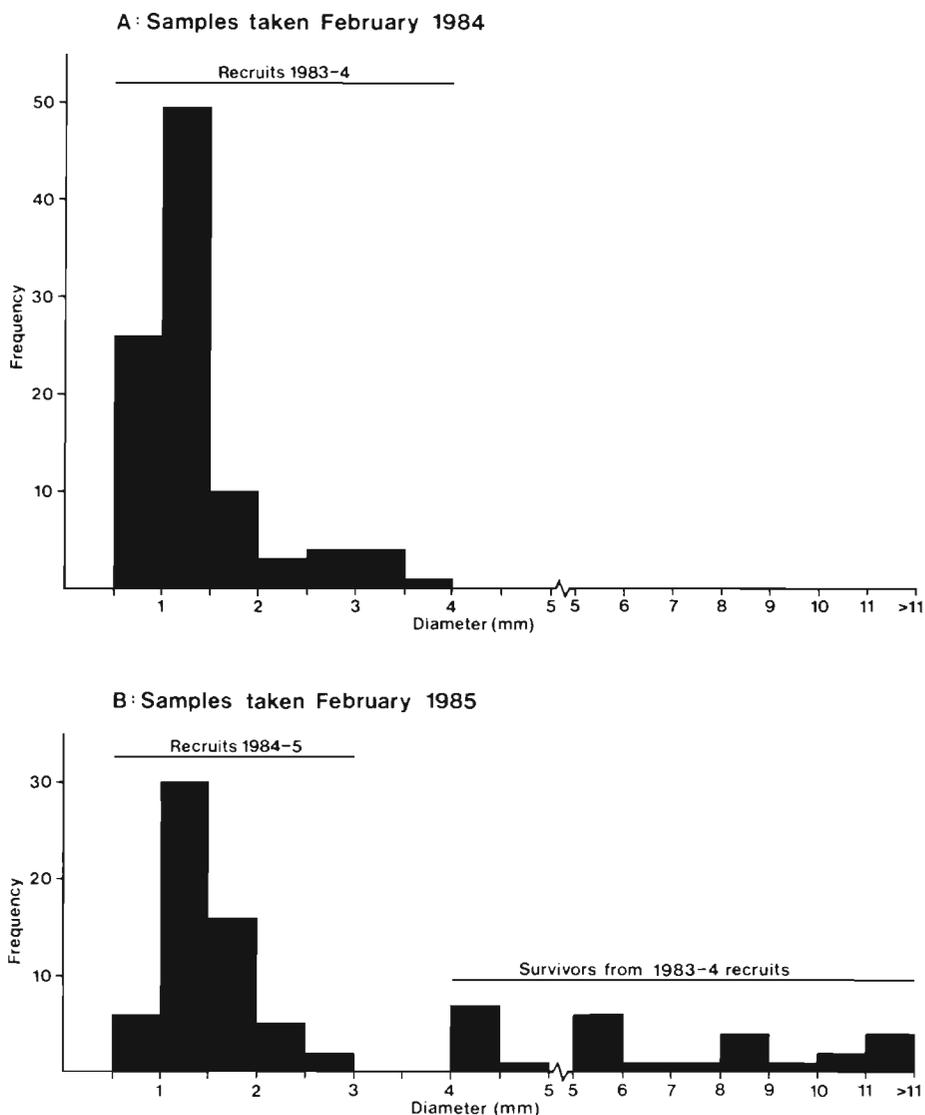


Fig. 3. Size distribution of juvenile corals found on samples from 11 *Acropora* tables. Total area sampled 2200 cm². (A) Feb 1984, 4 mo after predation; (B) Feb 1985, 16 mo after predation

ment of coral larvae, as would be predicted by recruitment to similar substrata used in experimental studies (e.g. Sammarco 1980, 1983, Sammarco & Carleton 1982, Wallace & Bull 1982, Harriott 1985, Wallace 1985a,b). Thus no perceptible time lag (as measured here) occurs before coral larvae can settle after predation by *A. planci*. Two factors contribute to an apparent lag before settlement. Firstly, most corals grow very slowly during the first year of life. At 1 yr they are encrusting only. Although they can be seen easily by a diver scrutinizing the coral surface, they cannot be seen by larger-scale censusing methods, such as photographic or manta-tow surveys (Fig. 5). Three-dimensional, readily visible colonies such as those reported by Endean & Stablum (1973a: Fig. 20) are probably 3 yr old or more. Secondly, larvae of most corals are available only during a limited summer period, so recruits will become obvious 1 yr after this period (Harriott 1985, Wallace 1985a).

Approximately 34 % of the settled juveniles survived beyond 1 yr. Thus we conclude that death of early colonizing larvae due to overgrowth by algae and other organisms is not responsible for the apparent lack of new corals after predation by *Acanthaster planci*. Grazing animals may have removed newly settled juveniles from the upper surfaces of tables, as few juveniles were found in exposed positions on upper surfaces. With 1 exception, coral tables did not break up and fall during the 16 mo of our observations. Breakage and redistribution of coral tables apparently is very dependent on cyclonic influences in the locality (Wallace 1985c). Such influences did not occur during the study. Should the tables have been overturned, at least in the first few months after settlement (the most likely time of the year for cyclonic weather on the Great Barrier Reef), a different set of juveniles might have survived, namely those on undersurfaces rather than upper surfaces.

Recruitment rates in first versus second year

Although recruitment occurred in the second year, when tables had a considerable covering of algae and benthic invertebrates, including other corals, the rate of recruitment was less than that in the first year. Such a reduction might be attributed to exclusion by competition for space from other organisms. This conclusion, however, relies on an assumption of equal availability of larvae in the 2 yr. Before making this assumption, we examined our own data on recruitment to settlement plates placed on an adjacent reef buttress. We have been monitoring recruitment to experimentally placed settlement plates since 1980/81 (Wallace & Bull 1982, Wallace 1985a, b, Wallace & Watt unpubl. data). In 1983/84, mean recruitment to a set of 4 sites arranged down the reef front from 0 to 12 m was 20.1 (SE \pm 3.1) per 200 cm². Recruitment in that year to a reef shoulder site, which was the most similar location in depth to that of the tables, was 7.2 (SE \pm 3.7) per 200 cm² (Wallace 1985b). In the following year, both mean recruitment to all sites and that to the reef shoulder were significantly less (16.80 SE \pm 1.77 and 3.13 SE \pm 0.69 respectively). The lowered recruitment rate on the *Acropora* tables preyed upon by *Acanthaster planci*, from 7.00 per 200 cm² in 1983/84 to 5.6 per 200 cm² in 1984/85 is within the range of variability expected because of lowered availability of larvae in the second year. Thus there is no basis for a hypothesis of competitive exclusion in the second year.

Pattern of predation and coral recruitment

Invasion of a reef by *Acanthaster planci* and subsequent re-establishment of the coral community usually are considered as 2 separate events: *A. planci* appears in large numbers, kills most of the corals, and disappears; after this, recruitment of new corals and regrowth of partially-dead corals begins (Colgan 1982, Endean 1976, Pearson 1974, 1981). Our results indicate a more integrated process. Small, then increasingly larger patches of corals were killed by the seastar over a period of more than 4 yr. By the time the corals of the reef front were killed by *A. planci*, patches potentially carried up to 4 year-classes of juvenile corals. Our sampling demonstrates that at least 2 year-classes of young corals existed on the reef before the *A. planci* population had abated in the area. Thus the recolonization of this reef had commenced well ahead of the demise of the previously existing populations.

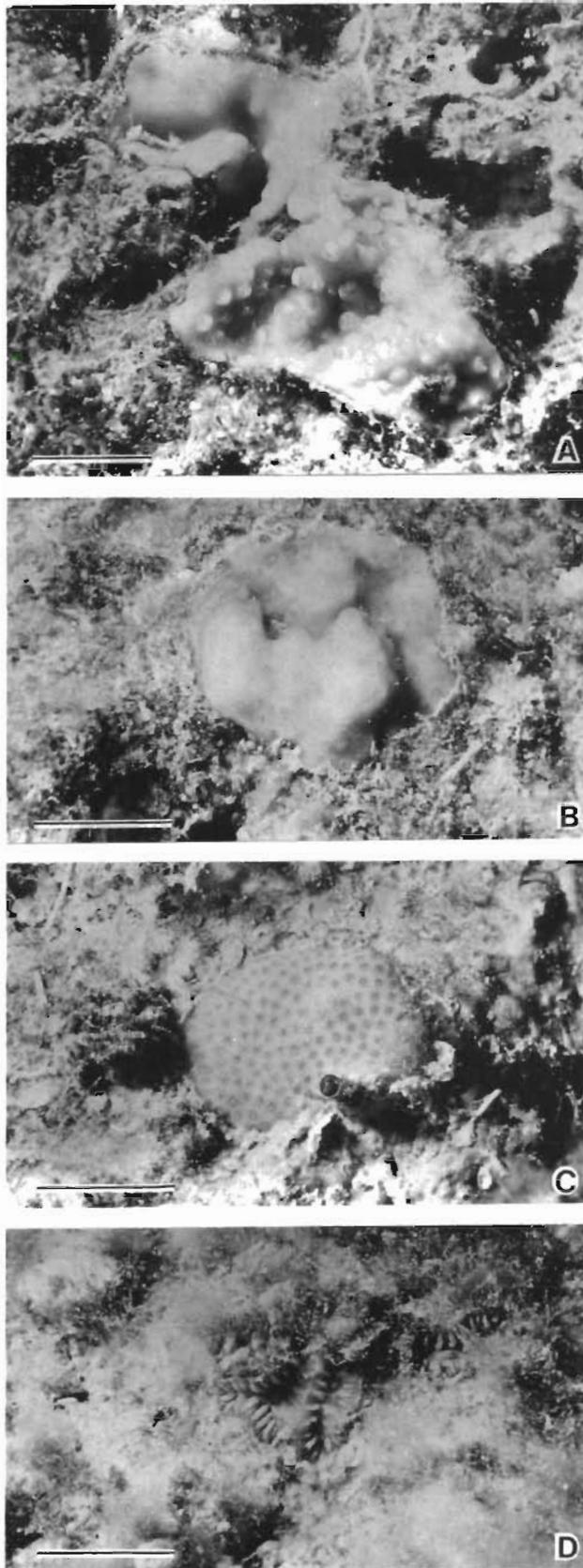


Fig. 4. Juvenile corals estimated to be 10 mo old, photographed *in situ* 12 mo after predation of coral tables by *Acanthaster planci*. (A) *Acropora* (2 colonies); (B) *Acropora*; (C) *Porites*; (D) cf. *Leptastrea*. Scale bars: 10 mm

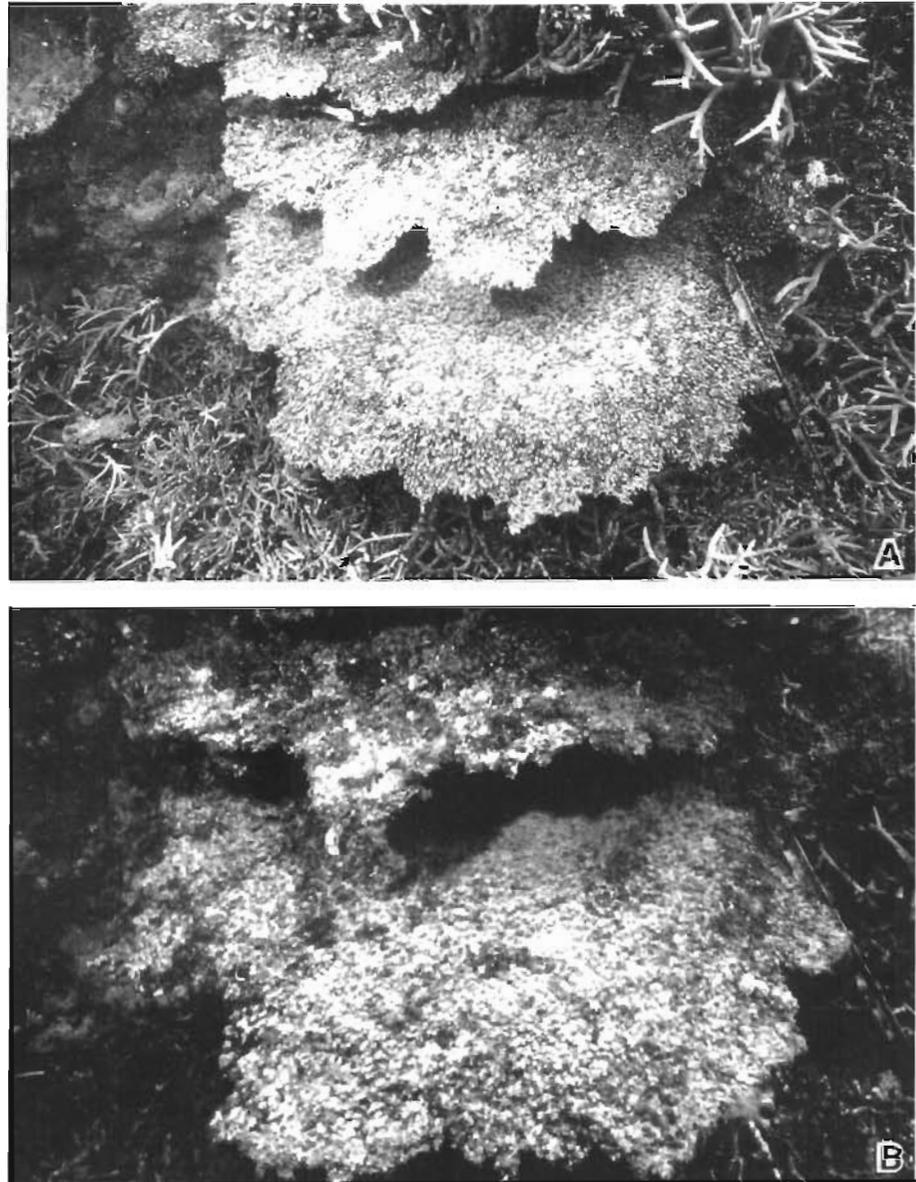


Fig. 5. Dead *Acropora* tables photographed (A) in Feb 1984, 4 mo after predation by *Acanthaster planci* and (B) in Feb 1985. Samples taken at both times had new recruits and (B) also had surviving juveniles, approximately 15 mo old. Even on (B) these were only obvious on close examination of the surface, because of their small size and encrusting nature

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