

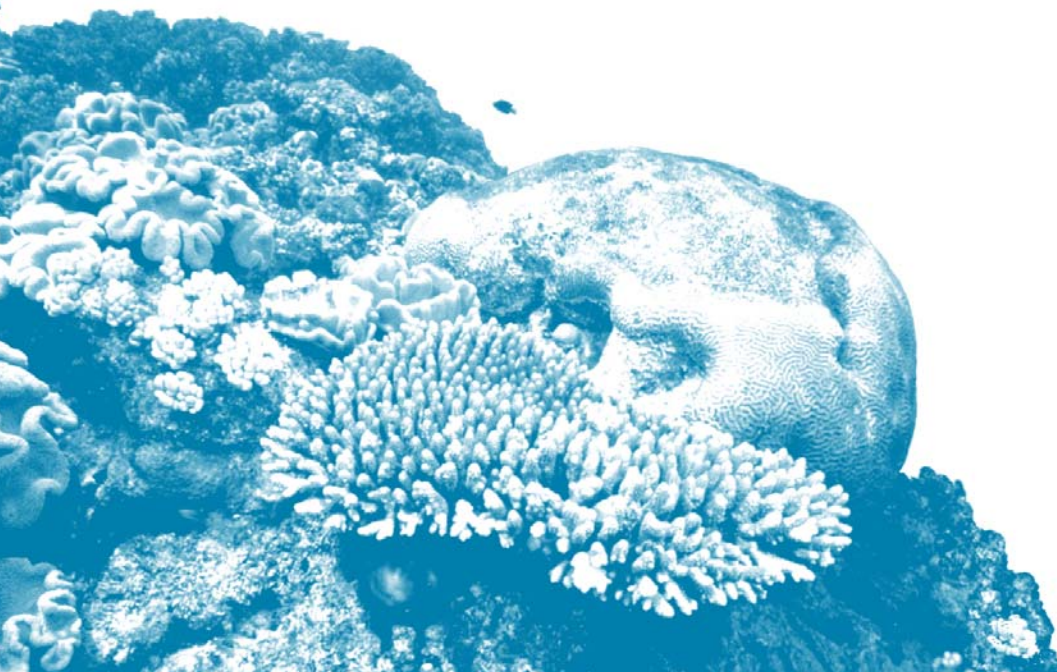


Australian Government
Great Barrier Reef
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RESEARCH PUBLICATION NO. 97

**Case study: impact of *Drupella* spp.
on reef-building corals of the
Great Barrier Reef**

R.L. Cumming



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EXECUTIVE SUMMARY

Drupella spp. are marine snails that feed exclusively on reef-building corals and occur on coral reefs throughout the Indo-Pacific. They are best known as agents of reef destruction, based on published reports of large aggregations and population outbreaks feeding on corals and leaving dead corals in their wake. Most publicized are outbreaks of *Drupella cornus* at Ningaloo Reef, Western Australia, where coral cover was reduced by up to 85 per cent during the 1980s and early 1990s, and *Drupella* densities at some sites reached 19/m².

Drupella densities on the Great Barrier Reef are typically less than 2/m² and population outbreaks are not known to have occurred here. The data presented in this report were collected from 1991 to 1994 at Lizard Island, Great Barrier Reef, where *Drupella* occurred in densities of 1-2/m². The Lizard Island fringing reefs were typical of the Great Barrier Reef in having a low-density assemblage of *Drupella* spp. and a coral community dominated by branching corals of the genus *Acropora* and family Pocilloporidae, that are the preferred prey of *Drupella*.

Several related studies were designed to address the question: How much damage do *Drupella* do on the Great Barrier Reef under conditions that are typical of the Great Barrier Reef?

Four separate studies were conducted:

- Prey choice was investigated using field survey data
- Residence times on individual coral colonies were monitored in permanently marked sites over two years
- Feeding rates were measured in laboratory aquaria
- The surface area of four preferred prey coral species was measured, for comparison with feeding rates to estimate the standing crop that was consumed.

These four studies were used to quantify the following:

- The mobility and movements of *Drupella* amongst coral colonies
- The typical damage to individual colonies, and the likelihood of death versus injury of colonies
- The damage to populations, i.e. the proportion of the standing crops of species consumed over time.

The data collected, and presented in this report, are those required to develop predictive models of the damage that *Drupella* could do under a variety of conditions, for example increased *Drupella* density, or decreased coral density on reefs affected by bleaching or other stressors.

The major results are:

- *Drupella* density remained constant at 1-2/m² over the course of the study (1991-1994), and the rate of attack remained constant at 2-4 per cent of prey colonies under attack at any time
- In seven censuses spaced three to four months apart, more than half of *Acropora* colonies larger than 40cm in diameter, and more than a quarter of smaller colonies, were attacked at least once
- Groups of *Drupella* vacated live prey, leaving colonies injured but not dead, which is contrary to initial appearances that suggested long-term residence, perhaps until the colony was completely devoured
- The likelihood of attack increased with colony size, and large arborescent thickets were the most preferred prey, harbouring one-third of all *Drupella*,
- Small colonies less than 10cm in diameter were rarely attacked and had an effective size refuge from attack
- 72 per cent of *Drupella* groups were small (1-3 *Drupella*) with short residence times of a few days to 2 to 3 weeks; 6 per cent were large (>10 *Drupella*) and could remain on a colony for several months, which amplified the difference in impact between heavily and lightly attacked colonies
- Mean feeding rate was 1.806 cm² of coral tissue/snail/night
- In 1992, *Drupella* consumed 1-12 per cent of the standing crop of four prey species, and in 1993 this more than doubled for three of the four prey species studied.

INTRODUCTION

Drupella are predators of reef-building corals that are best known as potential problem species, based on several reports of population outbreaks associated with coral damage (Turner 1994a; Cumming under review). Consequently, *Drupella* are perceived as a potential threat to the Great Barrier Reef that could have a similar impact to that of the crown-of-thorns starfish if outbreaks occurred here. To date, however, no population outbreaks of *Drupella* are known to have occurred on the Great Barrier Reef.

Drupella spp. occur on coral reefs throughout the Indo-Pacific. They usually occur as a multi-species assemblage (Cernohorsky, 1969; Cumming 1999; Fellegara 1996, Fujioka 1984; Fujioka and Yamazato 1983; Johnson & Cumming 1995; Page 1987; Taylor 1976, 1978), though nomenclature and species number has varied between reports. Johnson and Cumming (1995) identified three species of *Drupella* with broad geographic ranges around the Indo-Pacific: *D. cornus*, *D. fragum* and *D. rugosa*. However, only *D. cornus* is known from Ningaloo Reef, Western Australia (Armstrong 2007; Turner 1992, 1994a) and the Red Sea (Al-Moghrabi 1997; Schuhmacher 1992; Shafir et al. 2008), and these are locations of reported population outbreaks of *D. cornus*. *D. fragum* appears to predominate in Japan, although other species coexist (Fujioka and Yamazato 1983; Johnson & Cumming 1995).

On the Great Barrier Reef, *D. cornus*, *D. fragum* and *D. rugosa* co-occur in a multi-species assemblage (Cumming 1999; Johnson & Cumming 1995;), with possibly other species as well (e.g. Fellegara 1996). The assemblage of three *Drupella* species described at Lizard Island by Cumming (1999) is probably typical of much of the Great Barrier Reef. Ayling and Ayling (1992) made a strong case for the ubiquity of a multi-species assemblage on the Great Barrier Reef; they found three morphological entities in total, with more than one on every reef in a survey of almost 100 reefs.

These three species are characterized by large variations in density at both small and large scales (Cumming 1999, under review; Turner 1994b), and each can form large aggregations of hundreds or thousands of individuals clumped on one or a few adjacent coral colonies (Cumming 1999; Cumming & McCorry 1998). Large aggregations of *D. rugosa* have been observed on the Great Barrier Reef (Baird 1999; Cumming 1999; Fellegara 1996). These are distinguishable from population outbreaks as they represent unusually large groupings of individuals rather than high density populations over whole reef areas (Cumming 1999). Large aggregations have now been observed at many reef locations and are uncommon.

The purpose of this report is to address the question of how much damage *Drupella* do in a typical scenario on the Great Barrier Reef. *Drupella* abundance (for all species combined) on the Great Barrier Reef is typically in the range 0-2/m² (Cumming under review). This case study was conducted on the sheltered fringing reef slopes at Lizard Island, that supported a *Drupella* assemblage of 1-2m², and that were dominated by a diverse assemblage of branching corals of the genus *Acropora* and family Pocilloporidae, the preferred prey of *Drupella*.

Preliminary surveys of these reefs revealed less than 6 per cent of prey corals being grazed at any given time, and under these conditions it was expected that *Drupella* grazing on corals would have a low-level, chronic impact on the coral community. However, there is evidence that this kind of day-to-day feeding by predators of corals is not trivial and can cause greater tissue loss than severe storms (Bythell et al. 1993; Knowlton et al. 1988). In addition, there can be significant demographic consequences of tissue loss, such as reduced size (Hughes 1980, 1984), growth (Kobayashi 1984, Meesters et al. 1994) and reproduction (Rinkevich & Loya 1989; Van Veghel & Bak 1994; Wahle 1983), and an increased chance of outright colony death (Cumming 2002).

In this case study, distributions of both *Drupella* and corals were surveyed to determine prey preferences, feeding rates were measured in laboratory aquaria, and residence times of groups of *Drupella* on corals under natural conditions were monitored over a two year period. The end product was a model which combined these results to estimate the amount of tissue consumed annually by *Drupella*. To estimate the standing crop consumed for four coral species, the surface areas of branching corals were measured and extrapolated to estimate the standing crop of prey available to *Drupella*.

Description of the sheltered reef slopes at Mermaid Cove and Granite Bluff

The prey coral assemblage

This study was conducted on shallow, sheltered, fringing reef slopes at 5-8m depth. The study sites were on the leeward, north-east side of Lizard Island, Great Barrier Reef (14°40'S, 145°27'E), at Mermaid Cove and Granite Bluff (Figure 1). This sheltered location is protected from the prevailing south-easterly trade winds during the dry season, and receives occasional swells from the north-west monsoon in the wet season (December to February/March).

Four 30m² study sites were permanently marked, two at Granite Bluff and two at Mermaid Cove. These locations occupied the same continuous stretch of fringing reef, but opposite sides of a headland.

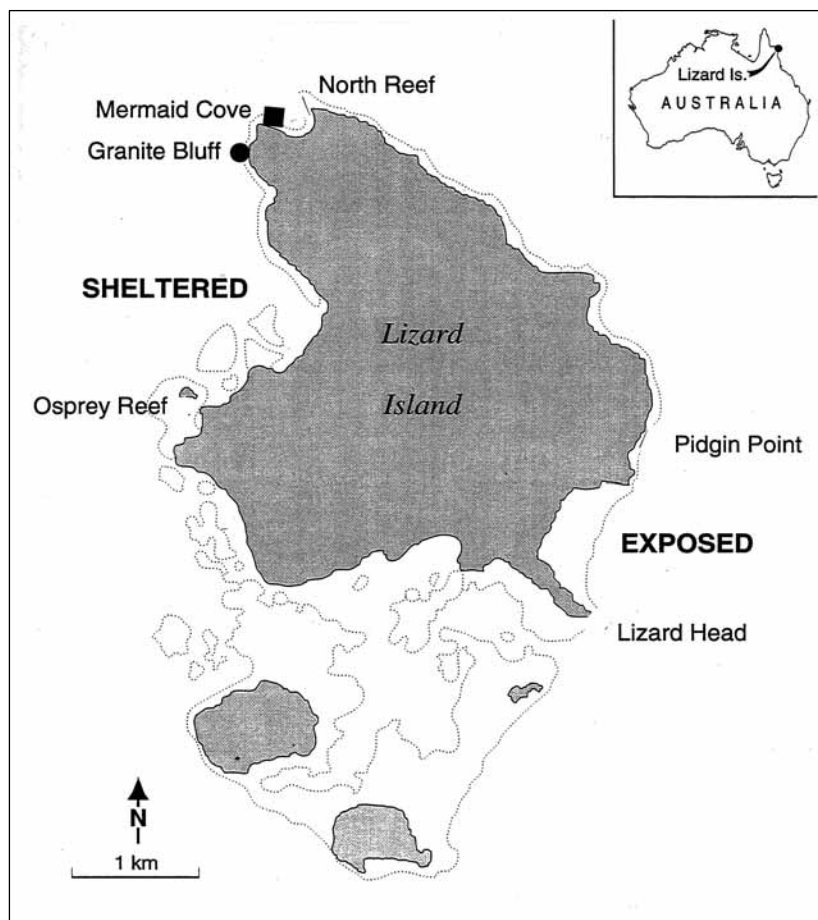


Figure 1. Lizard Island, showing locations of the sheltered fringing reefs at Mermaid Cove and Granite Bluff.

Table 1. Number of coral colonies monitored, by species, in each 30m² permanently marked site, in seven censuses between February 1992 and February 1994. A: number present in the first census in February 1992., B: number present in at least one census. Asterisks indicate species that were occupied by *Drupella*. 'Colonies' include loose fragments and pieces.

GROWTH FORM	SPECIES	SITE								TOTAL	
		Mermaid #1		Mermaid #2		Granite #1		Granite #2			
		A	B	A	B	A	B	A	B	A	B
ACROPORA											
Hispidose	<i>A. carduus</i>	0	0	0	0	0	0	1	3	1	3
	<i>A. echinata*</i>	3	3	0	0	0	0	1	3	4	6
	<i>A. elseyi*</i>	1	2	3	8	4	6	8	17	16	33
	<i>A. longicyathus*</i>	5	7	5	9	2	2	2	2	14	20
	<i>A. loripes*</i>	40	57	30	42	64	78	57	72	191	249
	Unidentified	0	0	0	0	1	2	0	0	1	2
Corymbose	<i>A. aculeus</i>	1	2	2	2	0	4	1	4	4	12
	<i>A. caroliniana</i>	0	0	3	3	0	0	4	4	7	7
	<i>A. cerealis*</i>	11	13	2	3	13	16	10	13	36	45
	<i>A. divaricata*</i>	9	16	11	11	15	16	25	31	60	74
	<i>A. latistella</i>	0	1	0	0	1	2	0	0	1	3
	<i>A. millepora*</i>	9	13	8	11	9	13	3	5	29	42
	<i>A. nasuta*</i>	16	21	4	5	12	15	15	17	47	58
	<i>A. sarmentosa*</i>	12	14	10	14	24	27	30	35	76	90
	<i>A. secale*</i>	4	4	1	1	6	7	6	6	17	18
	<i>A. selago*</i>	10	16	18	20	8	9	21	30	57	75
	<i>A. tenuis*</i>	9	14	3	8	5	9	4	9	21	40
	<i>A. valida*</i>	28	36	18	27	30	43	35	49	111	155
Digitate	<i>A. digitata</i>	2	3	0	0	0	0	0	0	2	3
	<i>A. gemmifera</i>	0	0	0	0	2	3	0	0	2	3
	<i>A. humilis</i>	3	5	2	2	2	2	5	5	12	14
Plate	<i>A. cytherea*</i>	6	7	6	7	18	18	15	16	45	48
	<i>A. hyacinthus*</i>	17	21	1	1	12	16	3	3	33	41
	<i>A. paniculata*</i>	0	0	0	0	2	4	6	7	8	11
Arborescent	<i>A. austera*</i>	0	0	0	0	2	2	0	0	2	2
	<i>A. brueggmanni</i>	2	3	1	1	0	0	0	0	3	4
	<i>A. florida</i>	0	0	3	3	2	4	0	0	5	7
	<i>A. formosa*</i>	22	35	15	21	37	49	18	23	92	128
	<i>A. grandis*</i>	6	6	5	6	3	3	4	4	18	19
	<i>A. microphthalma*</i>	4	5	11	21	12	18	2	5	29	49
	<i>A. nobilis*</i>	5	8	1	2	3	3	1	3	10	16
	<i>A. yongei*</i>	1	1	2	2	1	1	2	2	6	6
Submassive	<i>A. palifera</i>	0	1	2	2	0	1	0	0	2	4
Unidentified	fragment	1	4	0	0	2	9	1	3	4	16
	recruit*	10	94	23	86	70	179	125	241	228	600
POCILLOPORIDAE											
Bushy	<i>Pocillopora damicornis*</i>	29	74	17	45	8	17	23	45	77	181
	<i>Pocillopora edouxi*</i>	0	0	0	0	4	4	0	0	4	4
	<i>Pocillopora verrucosa</i>	2	3	2	2	5	6	4	4	13	15
	<i>Seriatopora histrix</i>	3	4	2	4	3	7	0	1	8	16
	<i>Stylophora pistillata*</i>	19	45	27	53	44	79	32	55	122	232
Unidentified	recruit	0	4	0	8	0	1	0	3	0	16
TOTAL COLONIES MONITORED		290	542	238	430	426	675	464	720	1418	2367

The coral community was dominated by a diverse assemblage of fast-growing, branching corals of the genus *Acropora* and family Pocilloporidae (Figure 2). At least 32 *Acropora* species were present (Table 1), and they comprised approximately 20 per cent of the substrate cover (Figure 3). The most abundant species (each with more than 50 colonies monitored in this study; Table 1) were: *A. divaricata*, *A. formosa*, *A. loripes*, *A. nasuta*, *A. sarmentosa*, *A. selago* and *A. valida*. Very large thickets of *A. microphthalma* and *A. elseyi* (>1m² diameter) contributed substantially to substrate cover in some areas, even though they were not particularly abundant in terms of colony numbers. The other common group of branching corals were the pocilloporids and two species, *Pocillopora damicornis* and *Stylophora pistillata*, were amongst the most common branching species (Table 1). *Drupella* preyed almost exclusively on these two groups of branching corals.

The remainder of the coral community was comprised of encrusting, foliaceous and massive corals, the most common of which were encrusting *Montipora* spp., massive *Porites* spp. and a variety of small massive faviids (Figure 3). Although alternative prey were abundant, especially encrusting *Montipora* spp., *Drupella* were associated with these so rarely (only a few occasions in thousands of observations) that they were not included in any analyses. Approximately 35 to 40 per cent of the substrate was hard reef rock substrate with turf algae. Most of the substrate was consolidated; there was little coral rubble or sand cover (Figure 3).

Granite Bluff and Mermaid Cove had about the same cover of *Acropora* and pocilloporids (Figure 3) and the same prey species dominated at each site (Table 1). Nevertheless, there were some distinct differences in the coral community between the two locations. There were more colonies at Granite Bluff than at Mermaid Cove, due largely to higher abundance of some of the most common prey species; *A. loripes*, *A. divaricata*, *A. sarmentosa*, *A. valida*, *A. cytherea*, *A. formosa* and *Stylophora pistillata* (Table 1). At Mermaid Cove, massive *Porites*, faviids and encrusting *Montipora* contributed similar proportions of the cover, whereas Granite Bluff had few *Porites* or faviids but a very high cover of encrusting *Montipora* spp.; at site one this contributed more cover than the *Acropora* spp. (Figures 3A,B).

To determine whether the permanently marked study sites were representative of the general coral community on these sheltered fringing reefs, haphazardly placed 20m transects were sampled and compared to the study sites. These resembled the study sites, and the differences between Mermaid Cove and Granite Bluff also occurred in these transects (Figure 3).

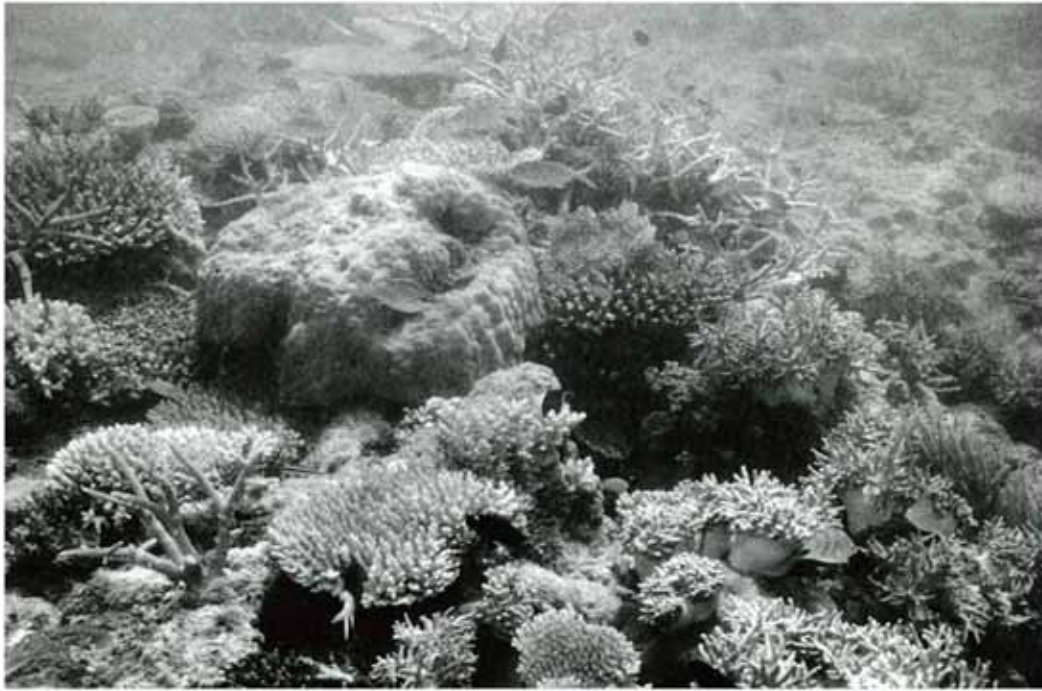


Figure 2. The sheltered fringing reef slope at Mermaid Cove, Lizard Island.

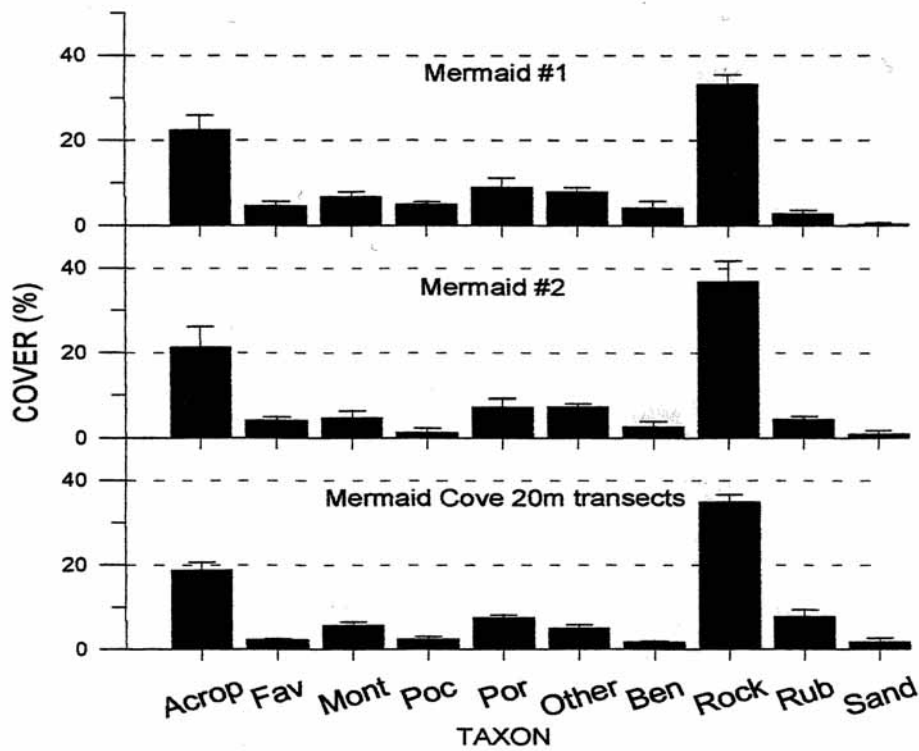


Figure 3A. Composition of the coral community on the reef slopes at Mermaid Cove, December 1992. Data are the per cent of the substrate covered by each taxon under four parallel 10m transects through each permanently marked 30m² study site, and eight haphazardly placed 20m transects on the reef adjacent to the study sites. For taxon key see Figure 3B.

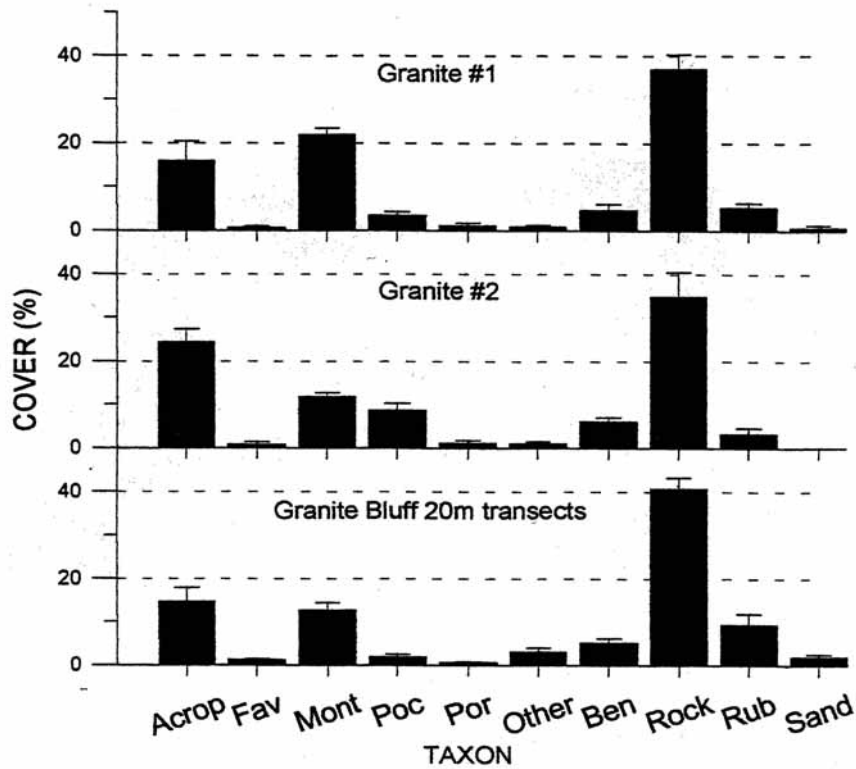


Figure 3B. Composition of the coral community on the reef slopes at Granite Bluff, December 1992. Data are the per cent of the substrate covered by each taxon under four parallel 10m transects through each permanently marked 30m² study site, and four haphazardly placed 20m transects on the reef adjacent to the study sites. Acrop = *Acropora*; Fav = family Faviidae (massive only): *Barabattoia*, *Cyphastrea*, *Diploastrea*, *Favites*, *Favia*, *Goniastrea*, *Montastrea* and *Platygyra*; Mont = *Montipora*; Poc = family Pocilloporidae: *Pocillopora*, *Seriatopora* and *Stylophora*; Por = massive *Porites*; Other = all other hermatypic corals and branching faviids: *Echinopora*, *Caulastrea*, *Australogyra*; Ben = all other benthic organisms: algae, anemones, ascidians, clams, gorgonians, hydroids, *Millepora*, sponges, whips, zooanthids; Rock = hard reef rock substrate; Rub = unconsolidated coral rubble; Sand = sand.

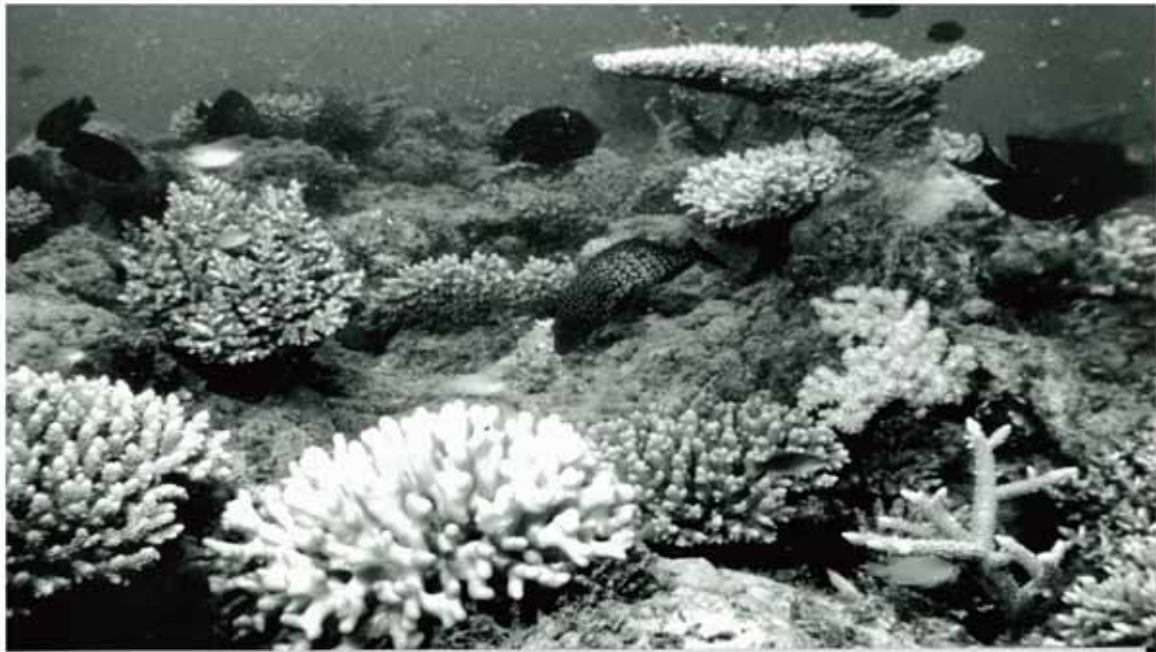
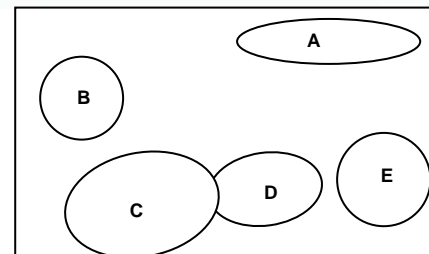


Figure 4. Representative section of the study sites showing the five growth forms of the dominant branching corals. **A:** plate *Acropora* (*A. hyacinthus*); **B:** hispidose *Acropora* (*A. loripes*); **C:** bushy (*Stylophora pistillata*); **D:** corymbose *Acropora* (*A. nasuta*); **E:** arborescent *Acropora* (*A. formosa*).



Colony growth form

Acropora are classified into growth forms based on colony shape and mode of branching (Wallace 1999). Four *Acropora* growth forms dominated the prey assemblage on these reefs: hispidose, corymbose, arborescent and plate (Figure 4; Table 1).

Hispidose colonies have secondary branches (branchlets) projecting out from the main branch ('Christmas tree' morphology) (Figure 4). Corymbose colonies have horizontal branches with short vertical branchlets, forming thick plates 6 to 8cm in height (Figures 5,6,7). Arborescent colonies have large, tree-like branches (Figure 8), and plate colonies have horizontal branches with very short vertical branchlets, forming thin tables (Figure 4).

A. divaricata is caespito-corymbose (Wallace 1999); it resembled a corymbose form with larger branches and branchlets than the other species (Figures 9,10), and is grouped with the corymbose colonies in analyses where colonies are grouped by growth forms (Table 1). Pocilloporids have very variable growth forms (Veron 1986) but on these shallow, sheltered fringing reefs they all formed compact bushes like the *Stylophora pistillata* colony shown in Figures 4 and 11.

The corymbose form was the most abundant in terms of species and number of colonies (Table 1) and they contributed about half of the entire *Acropora* assemblage in terms of substrate cover (approximately 10 per cent; Figure 12). Dead standing *Acropora* contributed more substrate cover than most growth forms at each site (Figure 12).

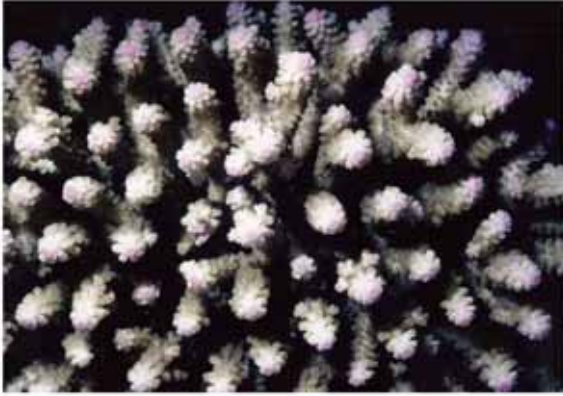


Figure 5. Top view of *Acropora nasuta*, a corymbose species, showing the regularly spaced branchlets.

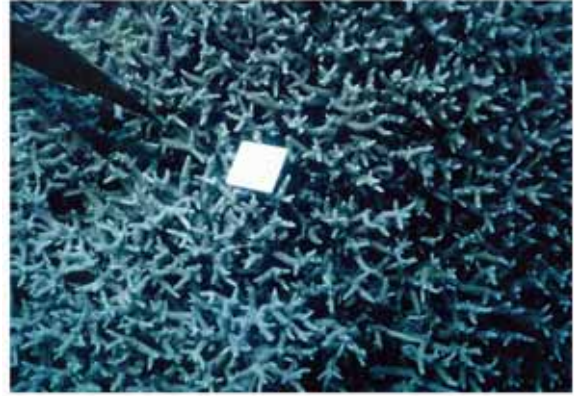


Figure 8. A large *Acropora microphthalmal* thicket. The white tile is 10cm square.



Figure 6. Side view of *A. nasuta*, showing the complex branching pattern.



Figure 9. A typical *Acropora divaricata* colony at Mermaid Cove. The white tile is 10cm square.



Figure 7. Top view of *A. valida*, a corymbose species.



Figure 10. Close-up of *Acropora civaricata* branching pattern.



Figure 11. *Stylophora pistillata*. This colony has been occupied by a large group of *Drupella*. The bases of about half the vertical branchlets were grazed, leaving the tips with live tissue.

The Drupella assemblage

Three species of *Drupella* from the Lizard Island reefs have been genetically distinguished: *D. cornus*, *D. fragum* and *D. rugosa* (Johnson & Cumming 1995). These three species coexisted in the study sites, usually in small groups with conspecifics but sometimes in multi-species groups (Cumming 1999). Relative abundance of the three species varied significantly between sites around Lizard Island, but on the sheltered reef slopes used in the present study *D. rugosa* was the most abundant and *D. fragum* the least abundant (Cumming 1999).

Drupella occurred in small, well-camouflaged groups between dead branches of corals, or in crevices in the substrate. Their shells were often covered with a pink calcareous alga like that which grows on dead coral branches, providing good camouflage. They were active only at night, and fed at night, and were immobile during the day. At night, they could venture to relatively exposed branches to feed, especially the larger adults (personal observation; Page 1987).

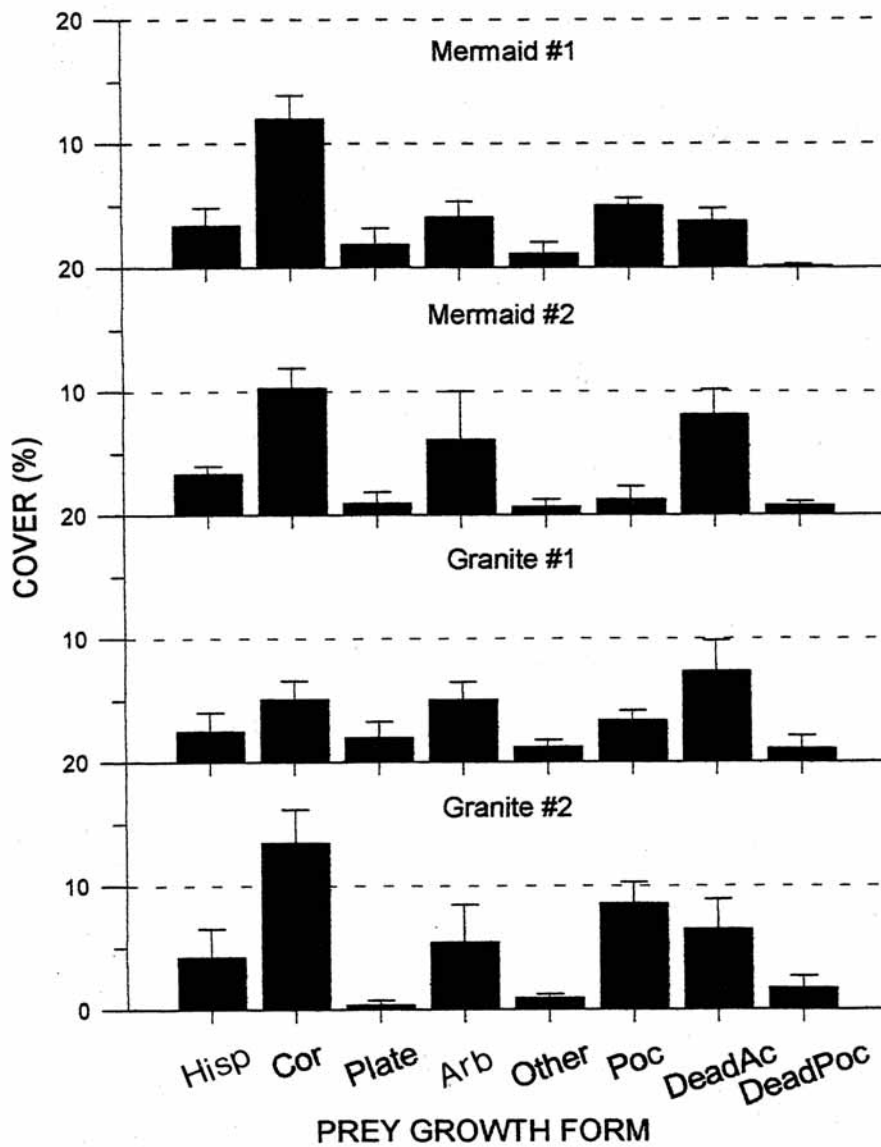


Figure 12. Composition, by growth form, of the prey coral assemblage in each permanently marked study site in December 1992. Data are the per cent of the substrate covered by each growth form under four parallel 10m transects through each site. Hisp = hispidose; Cor = corymbose; Plate = plate; Arb = arborescent; Other = unidentified recruits and fragments, massive, digitate; Poc = pocilloporid; DeadAc = dead standing *Acropora*; DeadPoc = dead standing pocilloporid.

Drupella feed exclusively on live coral tissue, rasping it from the skeleton using a specialised radula (Cernohorsky 1969). Page (1987) observed that *D. cornus* first rasped tissue from the epitheca, then placed its proboscis (and therefore mouth) into the mouth of the corallite. Coral polyp tissue appears to be selectively digested, with nematocysts and zooxanthellae passing through the gut undigested (Page 1987).

Drupella appear to be sensitive to the sting of corals' defence cells, the nematocysts, as they avoid contact with live coral. They clump on dead branches of their prey, or recently scarred areas, and not on live branches. Page (1987) observed that *Drupella cornus* tests a coral host by probing with its foot and proboscis. It sits at the live/dead tissue interface and reaches to the live polyps with the proboscis. In this way, it minimises contact with live coral tissue.

When *Drupella* feed, the skeleton is cleared of living tissue, leaving the skeleton exposed and a radiantly white feeding scar (Figure 13) which becomes discoloured by settling algae after a few days. However, Morton *et al.* (2002) reported that *Drupella rugosa* in laboratory feeding experiments fed on the coenenchyme and rarely ate the coral polyps of *Acropora pruinose*. The coenenchyme then regenerated.

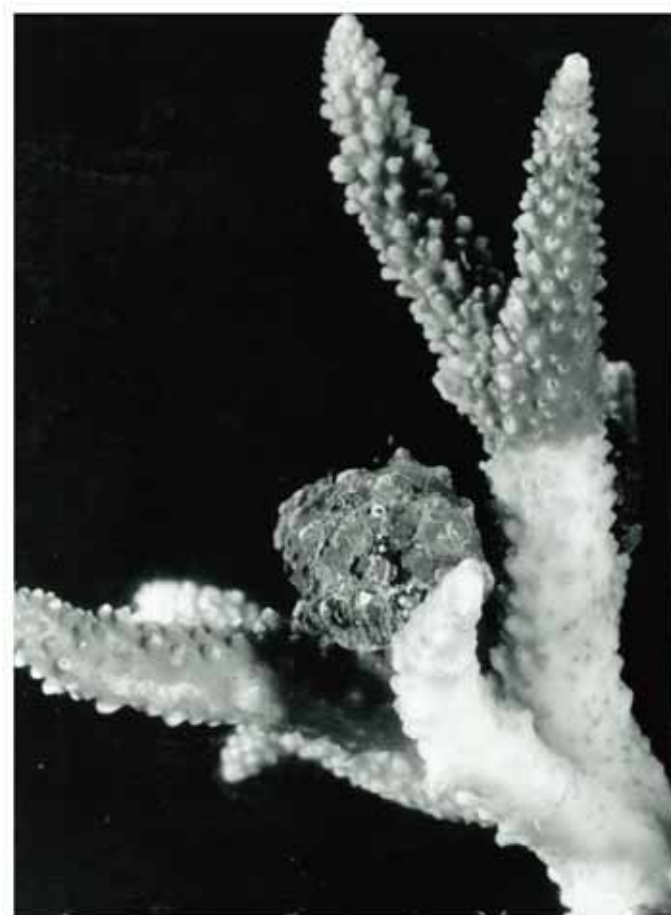


Figure 13. A solitary *Drupella cornus* feeding on *Acropora formosa*. The lower white section is feeding scar, showing exposed white calcium carbonate skeleton.

METHODS

Species identification

Drupella specimens were identified on the basis of morphological characters. Descriptions of these, and photographs, are given in Johnson & Cumming (1995). Voucher specimens are deposited in the Australian Museum (numbers C169228-C169230). Coral species identification followed Veron (1986) and Veron & Wallace (1984). Specimens are deposited in the Museum of Tropical North Queensland, Townsville, Australia (numbers G48292-G48328 and G49225-G49245). Three pairs of coral species that are difficult to distinguish in the field were pooled: *A. caroliniana* & *A. granulosa*, *P. edouxi* & *P. edwardsi* and *P. verrucosa* & *P. meandrina* (Table 1). These species were all quite rare, with only a few colonies present in the study sites.

Measuring colony size

Colonies were recorded in size classes based on the largest diameter, i.e. the largest distance across if the colony was not circular, and the diameter at right angles to this. All observations were done by SCUBA, and this technique proved to be very fast and efficient; an experienced diver would learn to recognise size classes rapidly and direct measurements were only needed for borderline cases. Borderline cases were classified by averaging both diameters. The accuracy of this method was tested using the formula for an ellipse (because most of the monitored *Acropora* and pocilloporids were approximately ellipsoid or spherical):

$$2\text{-dimensional (projected) area} = \pi \cdot d_1/2 \cdot d_2/2$$

Where: π = pi,

d_1 = the largest diameter (the length), and

d_2 = the diameter at right angles to this (the width).

This worked because an ellipse always has a smaller area than a circle with diameters that average the same (a circle encloses optimum area for its circumference). If an ellipse's average diameter only slightly exceeds a circle's diameter, the ellipse has a larger area than the circle unless the ellipse is very close to being circular. In practice, these conditions were rare so problems rarely arose with borderline cases.

Size #1=0-5cm; Size #2=>5-10cm; Size #3=>10-20cm; Size #4=>20-30cm; Size #5=>30-40cm, and Size #6=>40cm. The first two size classes were half the width of the others to distinguish small recruits.

Distribution of *Drupella* amongst prey colonies (prey preferences)

Prey choice was investigated with quadrat sampling, in which the growth form, species and size of occupied corals, and the species of their resident *Drupella*, were recorded. Data were collected in September 1991, December 1991, February 1992, December 1992, March 1993, July 1993 and December 1993. In September 1991, December 1991 and February 1992, 5x5m quadrats were sampled. An area was haphazardly chosen, its boundaries marked with measuring tapes, then searched for approximately 45 minutes. These large quadrats proved too cumbersome, and a comparison of 1x1m and 2x2m quadrats lead to 2x2m quadrats being used in 1993. A total of 74 2x2m, 20 1x1m and 14 5x5m quadrats were sampled between September

1991 and December 1993. In a subset of these, in December 1992, July 1993 and December 1993, all unoccupied colonies of the prey assemblage were also recorded, to assess the *proportion* of colonies that were occupied.

Feeding rates

Laboratory measurements

Feeding rates were measured in outdoor aquaria at the Lizard Island Research Station. The aquaria measured 30x20x18cm and received flowing seawater, pumped from the adjacent lagoon at the rate of one litre per 25 seconds. A shade cloth roof over the aquaria reduced the irradiance to 20per cent of outside irradiance, a level equivalent to that at about 5m depth on the adjacent reef, the natural habitat of the corals used in the experiments.

Corals offered to the *Drupella* were carefully chosen to reflect natural field conditions as closely as possible. Two characteristics of the prey colony were considered to be particularly important. First, it should be large enough for groups of *Drupella* to cluster together. Second, it should have some dead skeleton to allow snails to crawl onto the colony and establish residence. Snails do not crawl over live coral and without some dead section may clump underneath the coral, but would not establish themselves on it.

Thirty-seven groups of 5 to 20 *Drupella* were kept for 3 to 17 days in aquaria with whole coral pieces (Table 5). *Drupella* used in these observations were either collected from the same species of prey in the field or held with that species in aquaria for several days prior to observations, to minimise any bias created by a sudden enforced switch to a different food species.

Groups, rather than individuals, were used for two reasons. First, *Drupella* naturally cluster into groups of 5 to 20 individuals (Cumming 1999), so using groups reflected natural conditions. Second, pilot observations showed that feeding by individual snails is not constant over time; some individuals may not feed at all on some nights. Since the focus of this study was the impact of *Drupella* on their prey, using groups helped to average out this variation.

Feeding rates were measured as the total surface area of tissue devoured per snail per night. Areas of devoured tissue were clearly distinguishable by the bared white skeleton (Figure 13). Feeding rates were measured separately for different sizes and species of *Drupella* (Table 5), and for two types of adults, thick-shelled adults and thin-shelled adults. Thick-shelled adults had a thickened aperture and apertural nodules, indicating that they had neared their maximum size and were growing very little (R. Cumming, unpublished data), and were usually totally covered in a pink calcareous alga. Thin-shelled adults were approximately adult size but did not have thickening around the aperture. 'Juveniles' were smaller, thin-shelled snails 14 to 18cm long.

D. fragum were not used in the laboratory feeding measurements because this species was uncommon on the sheltered reef slopes that were the focus of this study. *D.*

fragum was abundant on the exposed reef crests of Lizard Island that were inaccessible most of the time due to weather conditions and wave action (see Cumming 1999).

An independent measure of feeding rates: scar sizes on the reef

To determine how feeding rates observed in laboratory aquaria compared with those on the reef, the sizes of fresh feeding scars on occupied colonies were recorded during field sampling. A fresh feeding scar is defined as an area of bare white skeleton not yet discoloured by the turf algae that settles on exposed skeleton. To determine the age of fresh feeding scars, the rate of colonisation of turf algae on fresh scars was measured by monitoring freshly grazed branches of the arborescent coral *Acropora formosa* kept at 3m depth. After 3 to 5 days, the scars were discoloured by algae and were clearly distinguishable from fresh scars.

Scar sizes are more difficult to measure in the field than in the laboratory because they often occur on the closely packed branchlets of coral with complex growth forms. They are also often underneath snails. Therefore the scar sizes were recorded in size categories of 5cm². For colonies with more than one scar, total scarred area was calculated by adding the midpoints of size categories.

Residence times

Three separate studies were used to investigate the time spent by groups of *Drupella* on colonies and their movements between colonies:

- (a) Monitoring corals in permanently marked 30m² sites at 3 to 5 month intervals
- (b) Monitoring the same corals over shorter intervals (3 to 15 days)
- (c) Monitoring additional tagged colonies over shorter intervals (14 to 15 days).

Groups of *Drupella* were classified into three size-classes: 'small'=1 to 3 snails; 'medium'=4 to 9 snails; 'large'= ≥ 10 snails, with class borders derived from the size-frequency distribution of *Drupella* group sizes in the permanently marked sites (Cumming 1999). Individual snails were not marked or identified, because the focus of this study was the impact of the corals.

Monitoring corals in permanently marked 30m² sites at 3 to 5 month intervals

In each of four permanently marked sites, all *Acropora* spp. and pocilloporids were mapped, totalling 1418 colonies in 37 taxa across all sites (Table 1). The number and species of *Drupella* occupying each colony was recorded at seven censuses at 3 to 5 month intervals from February 1992 to February 1994.

Monitoring the same corals over shorter intervals (3 to 15 days)

Four-monthly monitoring soon revealed that the identity of occupied colonies changed markedly between censuses, indicating that groups moved on a scale of less than four months. Several short-term censuses were then conducted, monitoring every few days for 2 to 3 week stretches. Table 2 shows details of these censuses.

Monitoring additional tagged colonies over shorter intervals (14 to 15 days)

Because only about 5 per cent of colonies were occupied at any one time, and only 6 per cent of these were large groups of ≥ 10 *Drupella* (see Results), monitoring the 30m² sites

provided low sample sizes of large groups. Therefore, 60 additional colonies occupied by *Drupella* were tagged with flagging tape and re-censused 14 to 15 days later, in February 1994. These included 11 different species of *Acropora* and pocilloporids. This was a non-random sample with preference given to corals harbouring large groups of *Drupella*.

Table 2. Details of short-term monitoring of permanently marked sites.

Date	Site	Census period	# days between censuses
December 1992	Granite Bluff site #2	5 Dec - 10 Dec	5
		10 Dec - 14 Dec	4
		14 Dec - 17 Dec	3
March 1993	Granite Bluff site #2	3 Mar - 9 Mar	6
		9 Mar - 13 Mar	4
		13 Mar - 21 Mar	8
December 1993	Mermaid Cove site #1	5 Dec - 11 Dec	6
	Mermaid Cove site #2	10 Dec - 14 Dec	4
	Granite Bluff site #1	9 Dec - 14 Dec	5
	Granite Bluff site #2	7 Dec - 11 Dec	4
February 1994	Mermaid Cove site #1	11 Feb - 26 Feb	15
	Mermaid Cove site #2	13 Feb - 27 Feb	14
	Granite Bluff site #2	14 Feb - 26 Feb	12

Impact on corals

Colony surface area measurements

Surface area measurements of coral colonies were required in order to estimate the proportion of coral tissue that was consumed by *Drupella*. Surface area was measured for four common species that were frequently preyed on by *Drupella*: *Acropora nasuta* (Figures 5,6), *A. valida* (Figure 7), *A. divaricata* (Figures 9,10) and *Stylophora pistillata* (Figure 11). These species all have vertical branchlets which bifurcate at irregular distances along the branchlet, and they include three of the most complex coral growth forms: corymbose (*A. valida* and *A. nasuta*), caespito-corymbose (*A. divaricata*) and bushy (*S. pistillata*) (Figure 4; Table 1).

Pieces of paper were wrapped around the branches, then digitised. The technique was very time-consuming; one branch could take up to one hour to measure. To reduce the time commitment, a sub-sample of 1 to 3 branches from each colony was selected randomly and measured, and the whole-colony surface area calculated using the following methodology. Only branches that grew from the very base of the colony were used. Although these began at the base as a single branch, they bifurcated repeatedly (see Figure 6), so that the complete 'branch' was highly complex and

included branchlets and sub-branchlets. By counting the number of vertical branchlets reaching to the top surface of the colony on both the measured branches and the parent colony, the surface area measurements were converted to values for the whole colony.

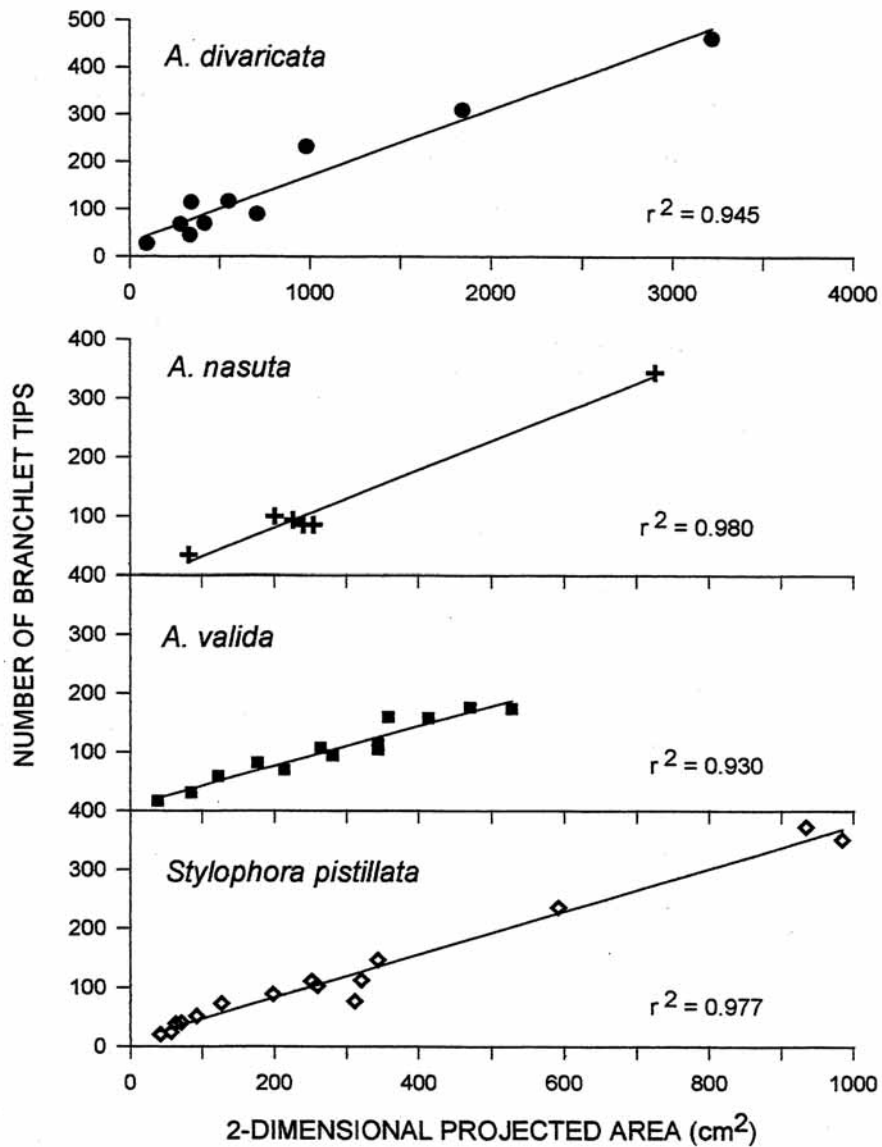


Figure 14. Relationship between colony size and the number of branchlet tips for four common reef slope corals. Branchlets were counted if they were $>x$ cm long; $x=3$ for *A. divaricata*, $x=2$ for *A. nasuta* and *A. valida*, $x=1$ for *Stylophora pistillata*. The slopes of all regression lines were significantly different from 0 ($p \leq 0.0001$ for all species), and all constants were not significantly different from 0 ($p > 0.05$ for all species). Regression equations: *A. divaricata*: $y = 0.14x + 30.38$; *A. nasuta*: $y = 0.49x - 17.02$; *A. valida*: $y = 0.348x + 9.049$; *Stylophora pistillata*: $y = 0.364x + 10.79$; $x=2$ -dimensional projected area, y =number of branchlet tips.

A potential problem was that branchlets bifurcate at irregular intervals along their length; some divide close to the top, forming a single vertical branchlet with a cluster of tips around it, and some divide much lower down, forming two distinct vertical

branchlets. The following rule was used to define a branchlet: it must reach to the top surface of the colony and be $>x$ cm long, where $x=3$ for *A. divaricata*, $x=2$ for *A. nasuta* and *A. valida*, $x=1$ for *Stylophora pistillata*. This was based on colony height and the branching pattern of each species. To test this rule, colony size was measured and branchlet tips were counted *in situ* for a range of colony sizes for each species. This revealed a very close relationship between colony size and branchlet number for each species (Figure 14), and validated the technique of using branchlet counts to predict surface area measurements.

The advantage of the paper wrapping technique was that it required no special equipment and was quite accurate, provided the coral was broken into small cylindrical pieces with simple shapes, so that paper could be wrapped around them accurately. The repeatability of the technique was tested by measuring six branches twice. These measurements were all within 10 per cent of each other. Whilst the end result, a relationship between size and surface area for each species, was time-consuming to construct, once established it provides a time-efficient way to convert size measurements of colonies into surface areas. Although the sample sizes were small, new data can easily be inserted into the model as they become available.

Calculating the proportion of the standing crop consumed by *Drupella*

The proportion of the standing crops of *A. divaricata*, *A. nasuta*, *A. valida* and *S. pistillata* consumed annually by *Drupella* was calculated with the following formula:

$$\text{Per cent consumed} = \frac{365 \cdot D \cdot F}{S}$$

where D = the mean number of *Drupella* occupying the species, averaged over all four permanently marked sites and all three censuses in the year

F = the mean feeding rate for all *Drupella* types and all observations (1.803 cm² tissue/snail/night)

and S = the mean standing crop of the species (cm²), averaged over all censuses for the year

$$S = \frac{\sum (a_i N_{iT})}{T}$$

where $i=1...6$,

a_i = the mean surface area of size class i

N_{iT} = the number of colonies in size class i at census T .

Surface areas used in the calculations were mid points of size classes, for example calculations for size class three used the surface area of a colony of 15cm diameter.

Data were pooled for all four permanently marked study sites. Separate calculations were made for each prey species and for 1992 and 1993. Standing crop was averaged over two censuses in 1992 (February and December; colony sizes were not recorded in the July 1992 census) and three in 1993 (February, July and December). Colonies in size class one were not included in the analysis because they were often not identifiable to species and were almost never occupied by *Drupella*.

RESULTS

Abundance of *Drupella* spp. on the study reef

Drupella abundance in each permanently marked site varied between 14 and 90 over the seven censuses, which is equivalent to 0.5 to 3 per m² (Figure 15). Numbers in each site fluctuated widely from one census to the next (Figure 9), but average density over a larger area of reef (4 sites pooled = 120 m²) was constant at 1 to 2 snails/m² over the whole two years. No site was consistently more heavily occupied; Mermaid Cove site #2 had the largest number most often and this was due to a single large staghorn thicket, comprised of the arborescent species *A. microphthalma*, being heavily utilized by *D. rugosa*.

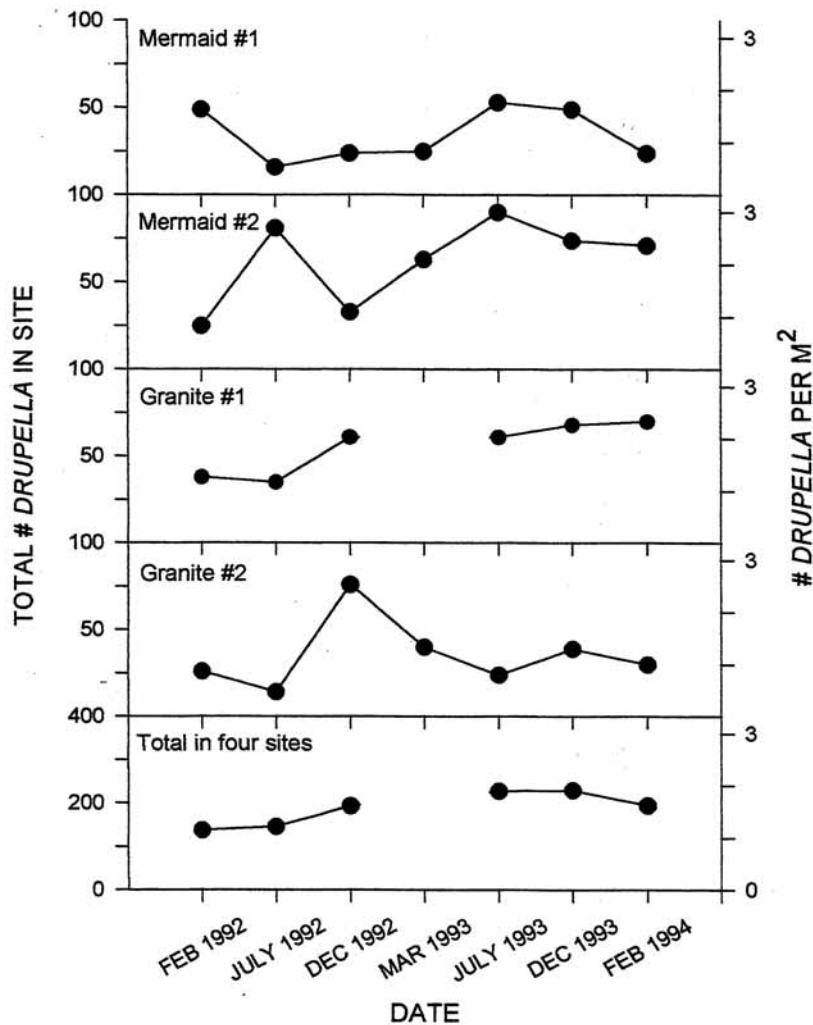


Figure 15. Total number of *Drupella* spp. and number per m² in each permanently marked 30m² site at each census. Granite Bluff site #1 was not censused in March 1993.

Distribution of *Drupella* amongst prey colonies (prey preferences)
Colony growth form and colony size

The null hypothesis that *Drupella* were distributed amongst colony growth forms in proportion to their availability was rejected (homogeneity test, $\chi^2=23.87$, $df=4$, $p<0.001$). More arborescent colonies and less pocilloporids were occupied than if they were occupied in proportion to availability (Figure 16). There were no differences between preferences of the *Drupella* species; growth forms were occupied by each species in similar proportions (homogeneity test comparing the number of each growth form occupied by each species, $\chi^2=8.335$, $df=8$, $p=0.40$).

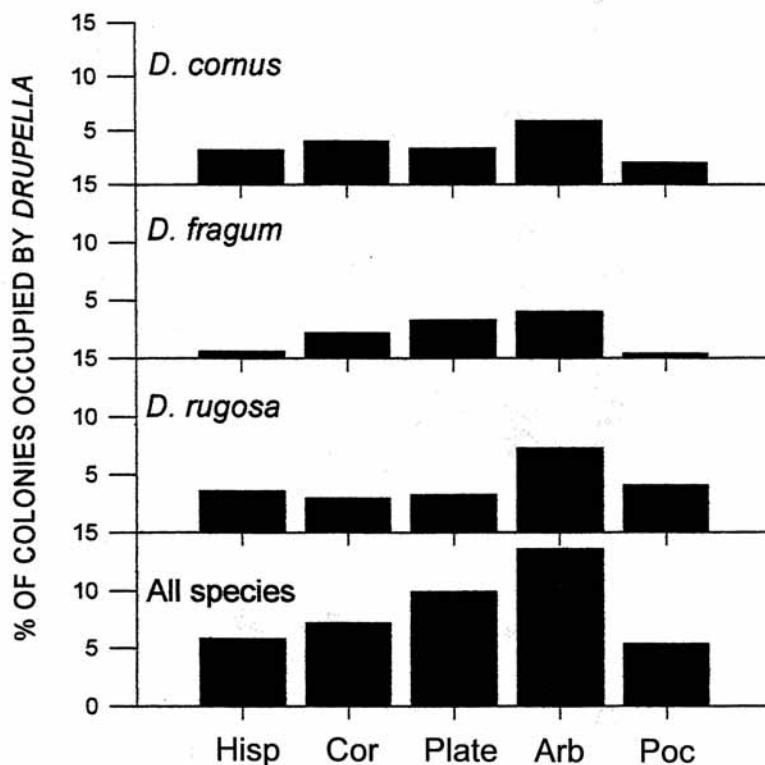


Figure 16. The percentage of the five dominant growth forms occupied by *Drupella*. Data are from quadrats sampled between September 1991 and December 1993. HISP = hispidose (n=309); COR = corymbose (n=501); PLATE = plate (n= 91); ARB = arborescent (n=273); POC = pocilloporids (n=244).

Larger colonies were more often occupied by *Drupella*, and the frequency of occupation increased with colony size (figure 17). These increases were statistically significant for all growth forms except plates (table 3). Small colonies <10cm in diameter were almost entirely avoided; the two cases in figure 17 were both occupied by solitary adult *D. cornus*. In contrast, 32% of the largest *Acropora* (>40cm diameter) were occupied, four times higher than average. The very high value of 50% for pocilloporids may be an artifact of the small sample size in this size class (N=2). The opposite trend occurred for dead corymbose *Acropora*; occupation rate significantly declined with colony size (figure 17; table 3).

The relative importance of colony growth form and size in frequency of occupation by *Drupella* were compared using a log-linear model (see Cumming 2002 for details of methodology). The model investigates the value of adding each factor to the model after the other has been included (Caswell 1989). Colony size was highly significant ($G^2=89.230$, $df=4$, $p<0.0001$), whereas growth form was not significant ($G^2=2.905$, $df=4$, $p=0.574$), indicating that growth form lost its importance in describing *Drupella* occupation patterns once colony size was accounted for.

***Drupella* group size: *Drupella* concentrated in large staghorn thickets**

In addition to being more often occupied, larger colonies supported significantly larger group sizes of *Drupella* (Figure 18). The net effect of these two factors is that 44.7% of the *Drupella* spp. in the community occupied colonies >40cm in diameter (Table 4).

Sixty per cent of coral colonies >40cm diameter (size #6) were arborescent (Figure 17), and many of these were large staghorn thickets up to 1m² or more in diameter (Figure 8). Almost one third (29 per cent) of the *Drupella* collected in the quadrat sampling occupied these thickets; all other growth forms and size classes each harboured <10 per cent of the *Drupella* (Table 4). Several species of arborescent acroporids occurred in this coral community (Table 1) but only two species were common; *A. formosa* and *A. microphthalma* made up 83 per cent (quadrat sampling) and 77 per cent (permanently marked sites; Table 1) of the arborescent colonies and formed almost all of the large staghorn thickets. However, only one of these two species, *A. microphthalma*, was heavily utilised by *Drupella*, even though it was less abundant than *A. formosa* (Table 1). Size #6 *A. microphthalma* thickets harboured 20.89 per cent of the *Drupella* collected in quadrat sampling, whereas size #6 *A. formosa* thickets harboured only 2.16 per cent. *A. microphthalma* thickets were clearly the most preferred prey, harbouring about one fifth of the *Drupella* on these reefs. *A. microphthalma* has a more compact growth form with thinner and shorter branches and smaller spaces between the branches, forming denser thickets (Figures 4,8; Veron 1986).

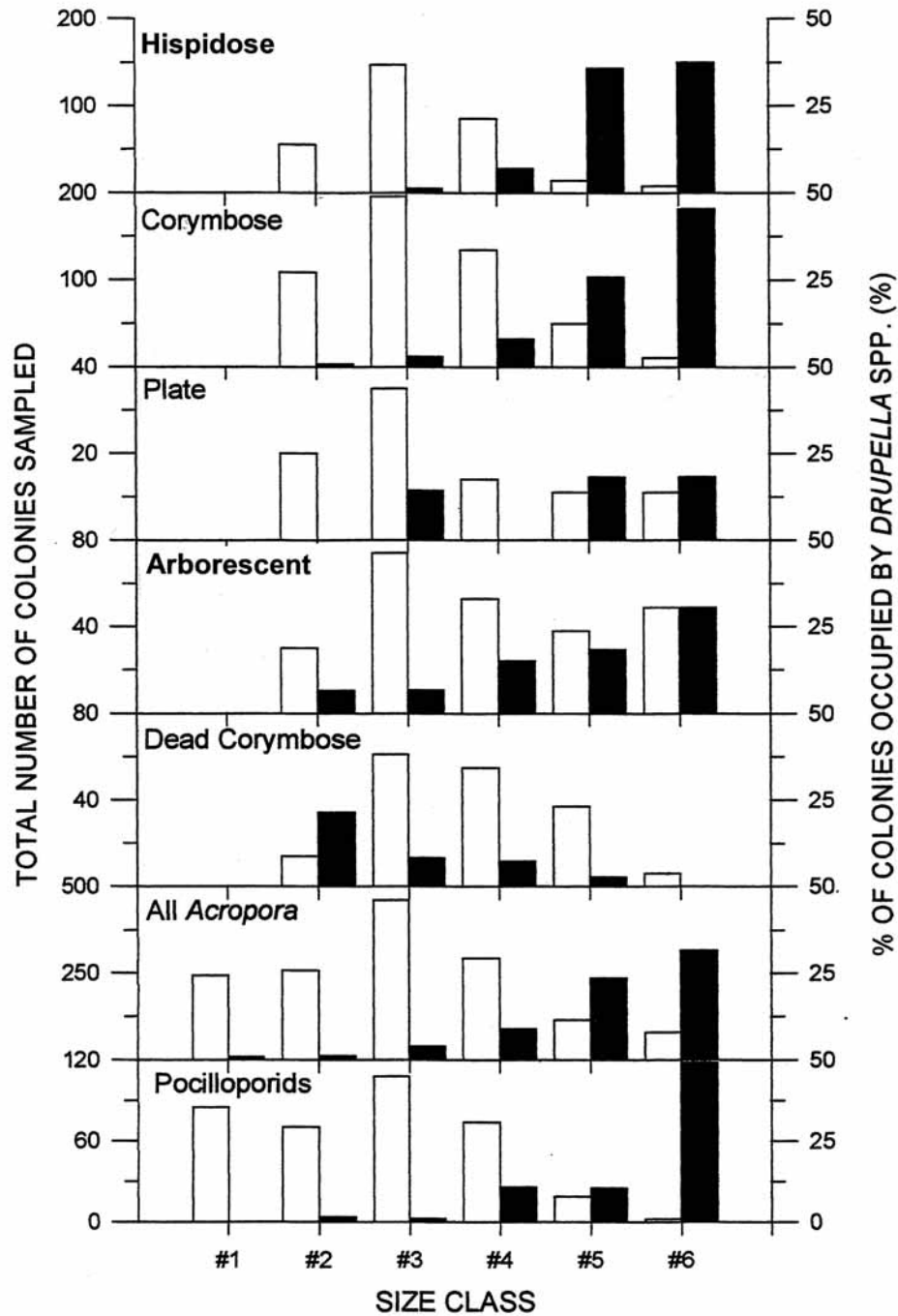


Figure 17. The proportion of colonies occupied by *Drupella* spp. and the total number of colonies sampled, by growth form and size. Open bars are the number of colonies sampled, filled bars are the proportion occupied. Maximum diameters of size classes are: #1=5cm; #2=10cm; #3=20cm; #4=30cm; #5=40cm, and #6>40cm. Size class #1 is not included for the individual *Acropora* growth forms because many could not be reliably assigned to growth form; therefore a distribution with all *Acropora* pooled is included. Data are from quadrats sampled in December 1992, July 1993 and December 1993.

Table 3. Results of homogeneity tests comparing the size distributions of colonies occupied and not occupied by *Drupella* spp., for each coral type shown in figure 17. Significant effects ($\alpha=0.05$) are in bold.

Growth form	χ^2	df	p
Hispidose	51.589	4	<0.0001
Corymbose	62.301	4	<0.0001
Plate	6.188	4	0.186
Arborescent	15.153	4	0.004
Dead Corymbose	63.960	4	<0.0001
All <i>Acropora</i>	151.062	5	<0.0001
Pocilloporids	32.202	5	<0.0001

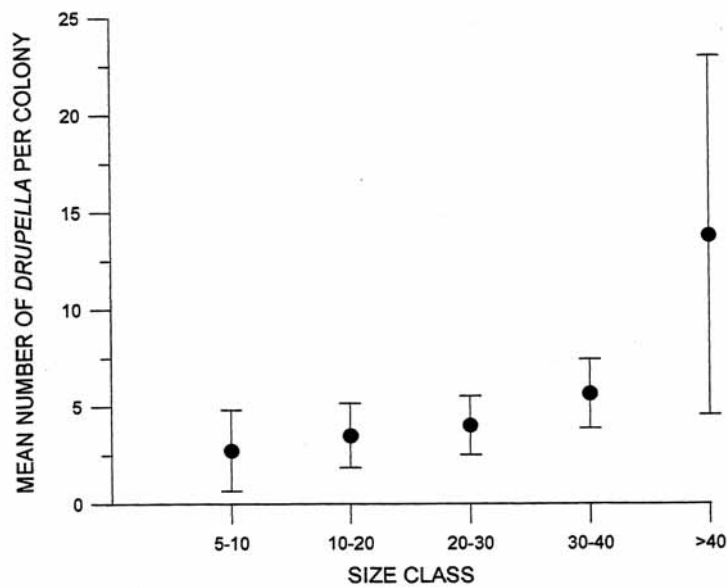


Figure 18. Mean numbers of *Drupella* occupying each colony size class, in quadrat samples. The means are significantly different (Kruskal-Wallis nonparametric test, $\chi^2=21.04$, $df=4$, $p<0.001$). Size class #2: N=8; #3: N=36; #4: N=66; #5: N=52; #6: N=46. Vertical bars are 95 per cent confidence limits.

Table 4. The per cent of all *Drupella* spp. found on each prey growth form and colony size.

Growth form	Size class					
	1	2	3	4	5	6
Hispidose	0.38	0	3.21	1.89	3.77	5.09
Corymbose	0	0.38	5.47	6.04	8.68	8.87
Plate	0	0	1.13	0	1.7	1.51
Arborescent	0	0.57	1.7	2.08	3.4	29.1
Dead corymbose	0	0.19	0.75	1.7	0.75	0.57
All living <i>Acropora</i>	0.38	0.94	11.5	10.2	17.5	44.5
Pocilloporids	0	0.38	0.19	3.96	0.38	0.19

Feeding Rates

Laboratory measurements

Feeding rate was highest for the largest type, *D. cornus*, and lowest for the smallest, *D. rugosa* juveniles 14-18mm long (Figure 19). However, results for individual groups were highly variable, even though groups rather than individuals were used to account for individual variability, and there was no statistical difference in feeding rates between the different types, between dates or between prey species (Tables 5, 6). The mean rate of tissue removal, averaged over all observations and *Drupella* types, was 1.806cm² tissue/snail/night.

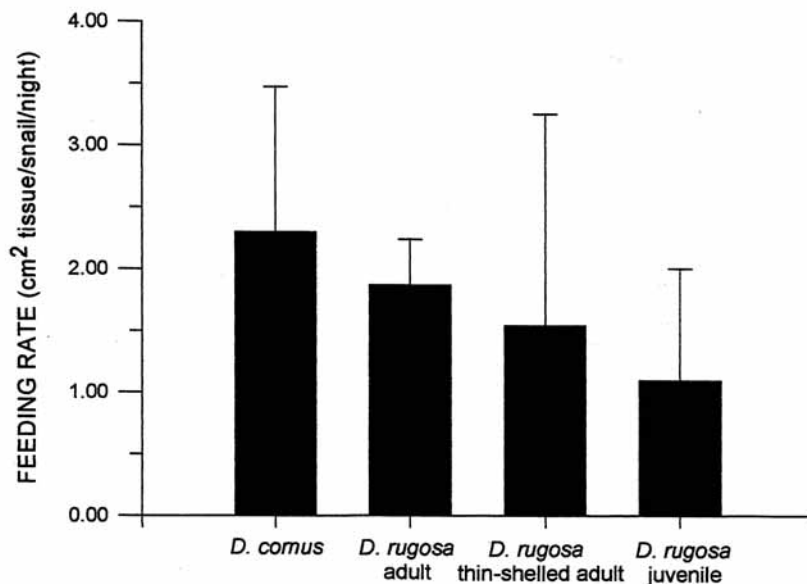


Figure 19. Mean feeding rates of each *Drupella* type, over all trials, as shown in Table 5. Vertical bars are 95 per cent confidence intervals.

Table 5. Feeding rates of groups of *Drupella* kept in outdoor aquaria. 'Juveniles' were 14 to 18mm long, 'thin-shelled adults' were approximately adult size but without the thickened apertures characteristic of adults, 'adults' had thickened apertures and apertural nodules; adult *D. rugosa* were 24 to 29mm long, adult *D. cornus* were 28 to 35mm long.

Date	Species	Type	Prey species	# Snails	# Nights	cm ² tissue/ snail/night
Aug 1994	<i>D. rugosa</i>	adult	<i>A. nasuta</i>	5	7	2.11, 2.31
	<i>D. rugosa</i>	adult	<i>A. valida</i>	5	7	3.83, 1.94
	<i>D. rugosa</i>	adult	<i>S. pistillata</i>	5	7	2.11, 2.41
	<i>D. rugosa</i>	adult	<i>A. microphthalma</i>	5	7	1.76, 1.89
	<i>D. rugosa</i>	thin-shelled adult	<i>A. microphthalma</i>	5	7	1.73, 0.77
	<i>D. rugosa</i>	adult	<i>A. microphthalma</i>	15	7	1.31, 1.28
Feb 1994	<i>D. rugosa</i>	thin-shelled adult	<i>A. microphthalma</i>	10	17	2.11
	<i>D. rugosa</i>	adult	<i>A. microphthalma</i>	10	17	2.09
	<i>D. rugosa</i>	adult	<i>A. elseyi</i>	10	3	3.03, 2.27
	<i>D. rugosa</i>	juvenile	<i>A. microphthalma</i>	10	7	1.44, 0.91
Oct 1993	<i>D. cornus</i>	adult	<i>A. microphthalma</i>	10	7	3.36, 2.24, 1.79
	<i>D. rugosa</i>	adult	<i>A. microphthalma</i>	10	7	1.59, 1.79, 2.13
	<i>D. rugosa</i>	adult	<i>A. microphthalma</i>	64	3	2.18
	<i>D. rugosa</i>	adult	<i>A. microphthalma</i>	81	7	1.48
Mar 1993	<i>D. rugosa</i>	adult	<i>A. microphthalma</i>	20	14	1.04
	<i>D. cornus</i>	adult	<i>A. microphthalma</i>	15	14	1.81
Feb 1992	<i>D. rugosa</i>	adult	<i>A. loripes</i>	5	8	2.88, 3.92, 0, 0, 1.02
	<i>D. rugosa</i>	juvenile	<i>A. loripes</i>	5	8	0.375, 1.65
	<i>D. rugosa</i>	adult	<i>A. formosa</i>	10	4	0.775, 1.375

Table 6. Results of one-way analyses of variance comparing feeding rates. Data were approximately normal and were not transformed prior to analysis. For comparison between the four types of *Drupella*, data were combined for all dates. The comparison between dates includes data for *D. rugosa* on *A. microphthalma* only: August 1994 (n=6), February 1994 (n=2) and October 1993 (n=5). The comparison between prey species includes the August 1994 trials only for groups of 5 adult *D. rugosa* (see Table 5).

Comparison	N	df	p
Between 'types' of <i>Drupella</i>	37	3,33	0.255
Between dates	13	2,10	0.091
Between prey species	8	3,4	0.543

An independent measure of feeding rates - natural scar sizes

So much variation occurred in the relationship between the number of *Drupella* and the area of fresh injuries on a colony on the reef (Figure 20) that it was not useful for assessing feeding rates of *Drupella*. With the constant movements of *Drupella* individuals and groups between colonies, even over short time-scales of a few days (see below; Figure 21), the number of *Drupella* resident on a colony may not be the number that produced the feeding scars. Decoupling of *Drupella* and their feeding scars is indicated in Figure 20 by the numerous colonies with *Drupella* but no feeding scars (25.5 per cent of colonies), and with injuries resembling feeding scars but no *Drupella* (55.7 per cent of colonies). In particular, about half the smallest injuries (<10cm²) were not associated with *Drupella* whereas all larger injuries were more likely than not to have associated *Drupella* (Figure 20). Another reason for the limited usefulness of field measurements is that scar sizes are more difficult to measure in the field, and it was necessary to use scar size categories.

Thus, due to the dynamic nature of the interaction between *Drupella* and their prey and the limited accuracy of measuring scar sizes in the field, the best estimates of feeding rates were made in laboratory aquaria, with attention to keeping conditions as natural as possible.

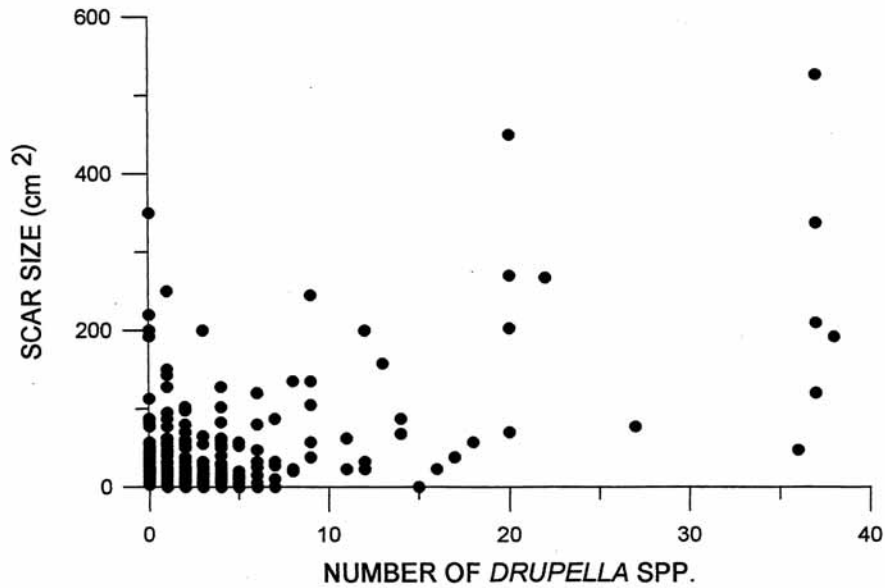


Figure 20. The relationship between the number of *Drupella* residents and the size of fresh injuries on a prey colony.

Residence times

Drupella typically occur on corals in small or large groups, which often include two or three *Drupella* species. In this study, 70.2 per cent of all groups sampled had 1 to 3 snails, 23.6 per cent had 4 to 9 snails, and 6.23 per cent had 10 or more snails.

Groups of all sizes vacated live colonies; 69 per cent of occupied colonies were alive and unoccupied 3 to 5 months later (Figure 21A). This included colonies harbouring large groups (>10 *Drupella*); though these were more likely to be occupied 3 to 5 months later than colonies harbouring small groups, 38 per cent were unoccupied 3 to 5 months later. Thus colonies were typically injured rather than killed.

Large groups were temporally more stable than small groups (1 to 3 *Drupella*). Small groups had short residence times of a few days to a few weeks, and large groups had much longer residence times, from two weeks up to several months or even longer. Only 24 per cent of colonies with small groups, but 67 per cent of colonies with large groups, were occupied four months later (Figure 21A). Medium-sized groups (4 to 9 *Drupella*) exhibited intermediate properties (Figure 21). On short time scales, most large groups changed little, whereas small groups had about equal chances of remaining or vacating a colony (Figure 21B,C). Groups grew and shrank in size frequently, indicating at least partially independent movement of members (Figure 21B,C). There was >40 per cent chance that a colony occupied by a small to medium group of *Drupella* (1 to 9) would be unoccupied within 3 to 8 days (Figure 21C).

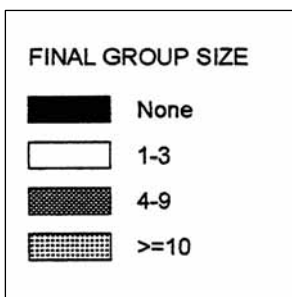
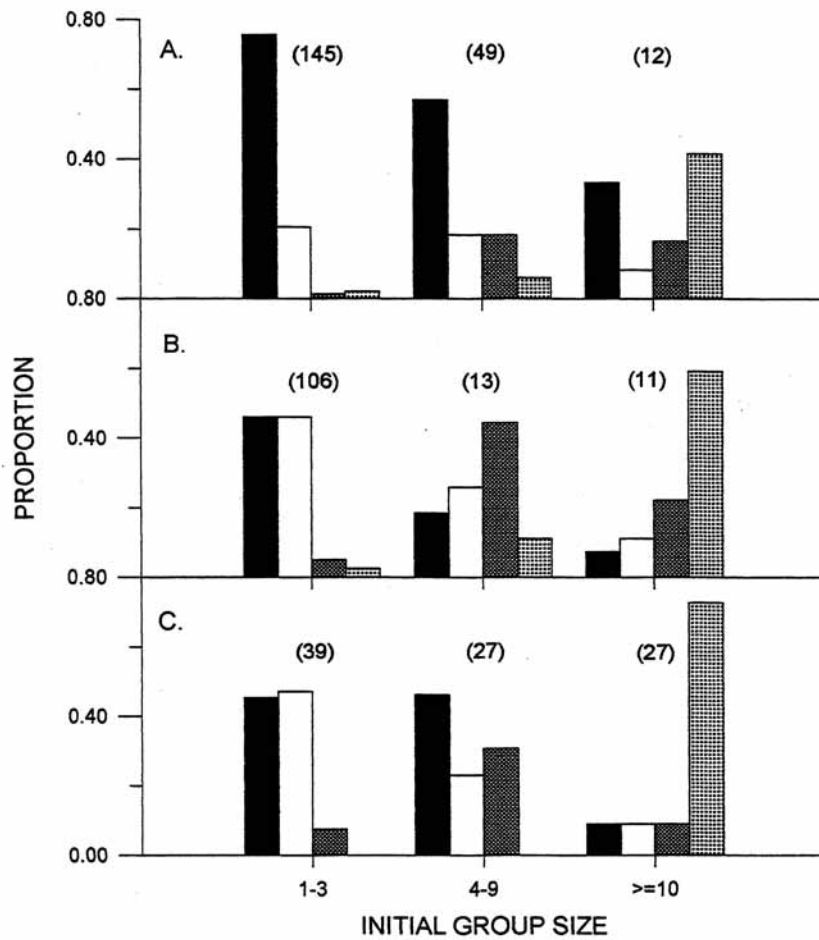


Figure 21. Group residence times: changes in the number of *Drupella* on monitored corals from one census to the next. Time between censuses was **A**: 3 to 5 months (permanently marked sites), **B**: 12 to 16 days (tagged colonies February 1994 and 30m² sites February 1994), **C**: 3 to 8 days (30m² sites). Data are pooled for all sites and all censuses and include only colonies that were alive at both censuses. Numbers in parentheses are sample sizes.

The proportion of colonies injured by *Drupella*

The results from the 3 to 5 month censuses of the permanently marked sites produced a total of 9721 records, with 305 cases of *Drupella* occupation. Whilst 2 to 4 per cent of prey corals were occupied by *Drupella* at each census, ten times this figure, 30.8 per cent, were occupied on at least one of the censuses (Figure 22). This pattern is even more striking for large colonies; more than 50 per cent of the large hispidose, corymbose, and arborescent acroporids and more than 25 per cent of colonies in size classes #3 to #4 were occupied by *Drupella* on at least one census (Figure 22).

However, the evidence from the short-term monitoring (Figure 21) suggests that these high occupation rates are underestimates. As an example, in two of the short-term monitoring series in which the same permanently marked site was monitored every few days for two weeks (Granite Bluff site #2; Table 2), 22 colonies were occupied initially and 16 became occupied during this period. Therefore, only 58 per cent of the colonies that were occupied within a two week period were actually recorded in the 3 to 5 monthly census.

Impact on corals

Colony surface area measurements

A strong relationship exists between the 2-dimensional projected area and the 3-dimensional surface area of the four coral species measured: *A. divaricata*, *A. nasuta*, *A. valida* and *S. pistillata*. The 2-dimensional area accounts for more than 96 per cent of the variation in surface area for each species (Figure 23).

The relationship is linear over the size ranges measured for the corymbose species *A. nasuta* and *A. valida*, which have a standard height of 6 to 8cm and grow by adding branchlets horizontally (Figures 5,6,7). The relationship is quadratic for *A. divaricata* and *S. pistillata* which have a more 3-dimensional growth form and grow vertically as well as horizontally (Figures 9,10,11). All relationships were highly significant ($p < 0.001$) and constants were not significantly different from zero for all three relationships. Thus, as predicted by the regularity of the branching patterns, colonies have a highly predictable surface area and area of consumable tissue, for a given size.

For these complex branching corals, the projected area is only 10 to 20 per cent of the actual surface area. For colonies of size #4 and smaller (<30cm diameter), *A. nasuta* and *A. valida* have the highest surface area and *A. divaricata* the lowest (Figure 23). This is because *A. nasuta* and *A. valida* have the most closely-packed branchlets while *S. pistillata* and *A. divaricata* have more open-branching morphologies and larger branches (Figures 5,6,7,9,10,11). But for large colonies of size #6 (>40cm diameter), both *S. pistillata* and *A. divaricata* have higher surface areas, due to their growth in height as well as diameter, as reflected in the curved relationship (Figure 23).

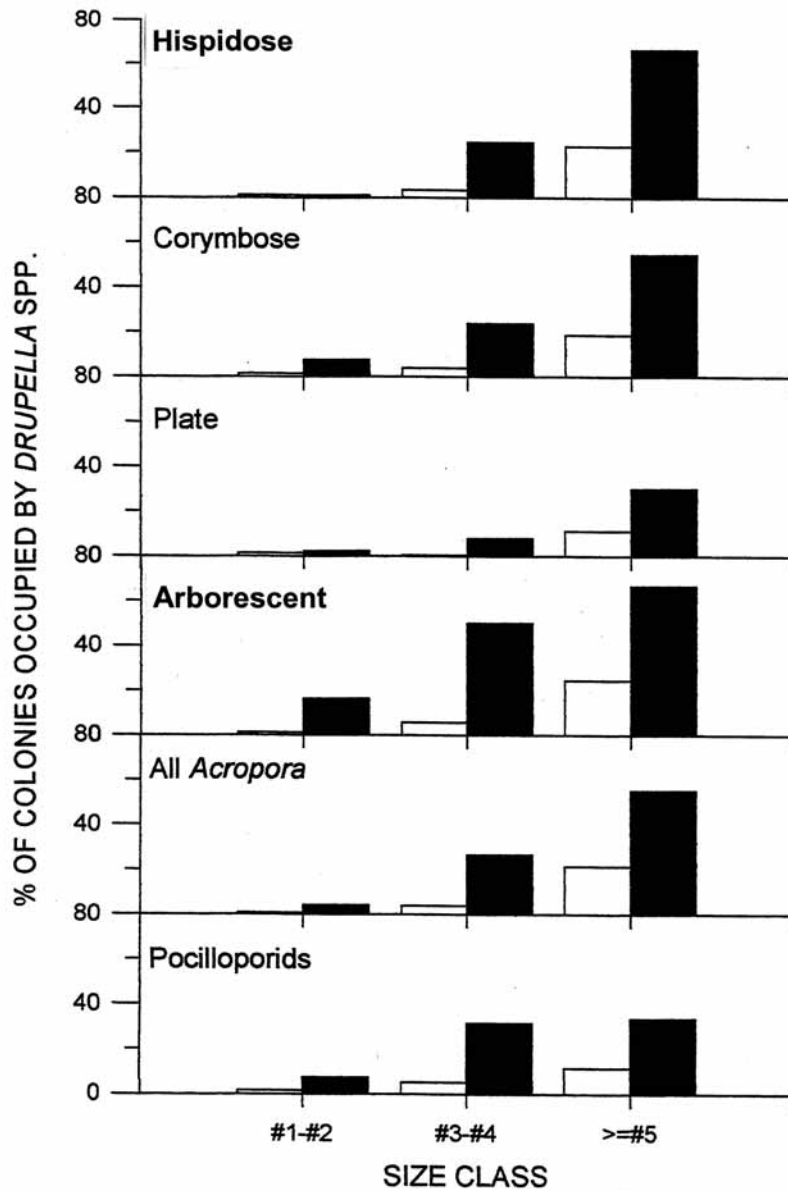


Figure 22. Temporal patterns of occupation, by growth form and size. Open bars are the proportion occupied at any single census, filled bars are the proportion occupied at least once in seven censuses over two years. Only colonies present at the start of the census period, February 1992, are included. Data are pooled for four 30m² sites and all censuses. Size #1 is included because records often pooled sizes #1 and #2.

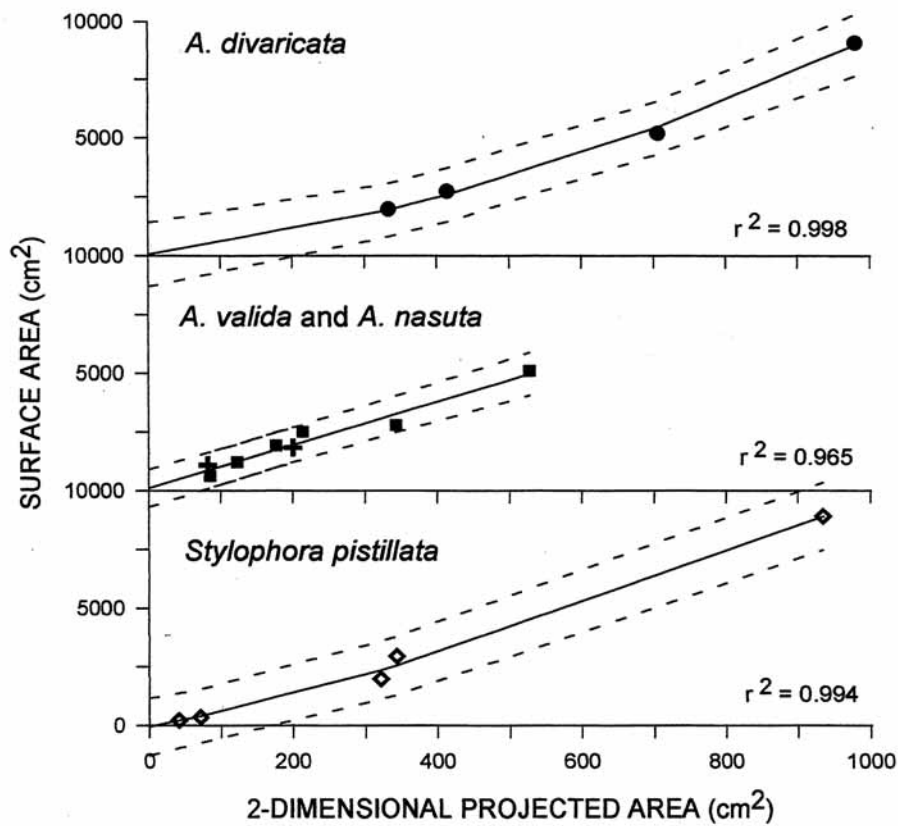


Figure 23. The relationship between the 2-dimensional projected area and surface area of four common prey species. Projected area was calculated with the formula for an ellipse: $\text{area} = \pi [d_1/2 \cdot d_2/2]$. Crosses: *A. nasuta*; squares: *A. valida*. Regression equations: *A. divaricata*: $y = 54.0058 + 3.895x + 0.0053x^2$; *A. nasuta* and *A. valida*: $y = 107.065 + 9.2336x$; *Stylophora pistillata*: $y = -64.8722 + 6.4589x + 0.0034x^2$ where $x=2$ -dimensional projected area (cm²) and y =surface area (cm²). *A. nasuta* and *A. valida* were pooled to increase sample size. Dotted lines are 95 per cent confidence intervals.

Impact on individual colonies

Drawing together residence times, feeding rates of *Drupella* and surface area of the prey colonies, the expected proportion of a colony's living tissue lost to *Drupella* can be calculated (Table 7). These calculations show that over normal expected residence times, colonies would usually be injured, not killed, by their *Drupella* residents. For example, it would take a group of 30 *Drupella* about six months to completely devour a size #5 *A. valida* colony and to devour approximately half of a 45cm diameter colony (Table 7).

An important result of these calculations is that the small groups that roam around and remain on colonies for short periods are not necessarily having a trivial impact. Smaller colonies (sizes #2 and #3) occupied by three *Drupella* for three weeks can lose approximately 8 (size #3) to 43 (size #2) per cent of their living tissue (Table 7).

On larger colonies, small groups have a more trivial impact, usually removing less than 1 per cent of the tissue (Table 7). Since large groups are likely to reside for several months, however, colonies occupied by large groups can lose at least 10 per cent of their living tissue before the group vacates the colony (Table 7). Even brief periods of occupation by a large group can have significant impact on a colony; a size #4 *S. pistillata* colony occupied for two weeks by 30 *Drupella*, for example, would lose approximately 18 per cent of its tissue.

Table 7. Estimates of the percentage of a colony devoured for given *Drupella* group sizes and residence times, for four common prey species.

A. ACROPORA DIVARICATA						
# <i>Drupella</i>	Residence time (weeks)	Size Class				
		#2	#3	#4	#5	#6
1	1	4.73	1.19	0.36	0.14	0.06
	2	9.46	2.38	0.71	0.27	0.12
3	1	14.19	3.57	1.07	0.41	0.18
	2	28.37	7.15	2.14	0.81	0.36
	3	42.56	10.72	3.21	1.22	0.55
4	1	18.91	4.76	1.43	0.54	0.24
	4	75.66	19.05	5.70	2.17	0.97
	8	100	38.11	11.40	4.34	1.95
9	1	42.56	10.72	3.21	1.22	0.55
	4	100	42.87	12.83	4.89	2.19
	8	100	85.74	25.65	9.77	4.38
10	2	94.50	23.82	7.13	2.71	1.22
	8	100	95.27	28.50	10.86	4.86
	16	100	100	57.01	21.72	9.73
	24	100	100	85.51	32.58	14.59
20	2	100	47.75	14.25	5.43	2.43
	8	100	100	57.01	21.72	9.73
	16	100	100	100	21.72	9.73
	24	100	100	100	65.16	29.18
30	2	100	71.50	21.38	8.14	3.65
	8	100	100	85.51	32.58	14.59
	16	100	100	100	21.72	9.73
	24	100	100	100	97.74	43.77

Table 7. cont'd.

B. ACROPORA VALIDA & ACROPORA NASUTA						
# <i>Drupella</i>	Residence time (weeks)	Size Class				
		#2	#3	#4	#5	#6
1	1	2.18	0.63	0.25	0.13	0.08
	2	4.35	1.27	0.51	0.27	0.16
3	1	6.53	1.90	0.76	0.40	0.24
	2	13.06	3.81	1.52	0.80	0.49
	3	19.59	5.71	2.28	1.20	0.73
4	1	8.71	2.54	1.01	0.53	0.33
	4	34.83	10.15	4.05	2.13	1.30
	8	69.66	20.31	8.10	4.26	2.61
9	1	19.59	5.71	2.28	1.20	0.73
	4	78.37	22.85	9.11	4.79	2.93
	8	100	45.70	18.22	9.58	5.87
10	2	43.50	12.69	5.06	2.66	1.63
	8	100	50.77	20.24	10.64	6.52
	16	100	100	40.48	21.28	13.03
	24	100	100	60.73	31.92	19.55
20	2	87.00	25.50	10.12	5.32	3.26
	8	100	100	40.48	21.28	13.03
	16	100	100	80.97	42.56	26.07
	24	100	100	100	63.84	39.10
30	2	100	38.00	15.18	7.98	4.89
	8	100	100	60.73	31.92	19.55
	16	100	100	100	63.84	39.10
	24	100	100	100	95.76	58.65

Table 7. cont'd.

C. <i>STYLOPHORA PISTILLATA</i>						
#<i>Drupella</i>	Residence time (weeks)	Size Class				
		#2	#3	#4	#5	#6
1	1	4.69	0.91	0.30	0.13	0.06
	2	9.37	1.83	0.59	0.26	0.13
3	1	14.06	2.74	0.89	0.38	0.19
	2	28.12	5.48	1.78	0.77	0.38
	3	42.18	8.23	2.67	1.15	0.58
4	1	18.75	3.66	1.19	0.51	0.26
	4	74.98	14.62	4.75	2.05	1.02
	8	100	29.25	9.50	4.10	2.05
9	1	42.18	8.23	2.67	1.15	0.58
	4	100	32.90	10.69	4.61	2.30
	8	100	65.80	21.37	9.23	4.61
10	2	93.75	18.28	5.94	2.56	1.28
	8	100	73.12	23.75	10.25	5.12
	16	100	100	47.49	20.50	10.24
	24	100	100	71.24	30.75	15.36
20	2	100	36.50	11.87	5.13	2.56
	8	100	100	47.49	20.50	10.24
	16	100	100	94.98	41.00	20.48
	24	100	100	100	61.50	30.72
30	2	100	54.75	17.81	7.69	3.84
	8	100	100	71.24	30.75	15.36
	16	100	100	100	61.50	30.72
	24	100	100	100	92.25	46.08

Impact on population standing crops

The percentage of the standing crop of the four coral species that was devoured by *Drupella* spp. annually ranged between 0.96 per cent and 11.6 per cent (Figure 24), and the mean percentage lost was 6.28 per cent. For three of the four species it more than doubled from 1992 to 1993, but it decreased for *A. divaricata* (Figure 24). This was due to two factors: there were more *Drupella* in the sites in 1993 (Figure 15) and the standing crops were reduced in 1993.

As a first approximation, these results suggest that the general prey community in the study sites lost between two and twelve per cent of its standing crop per year to *Drupella* grazing. The four species used in this case study were not selected because they were the most commonly occupied. To the contrary, the many other prey species in the community (Table 1) probably lost a similar portion of their standing crop to *Drupella* because the number of *Drupella* occupying them was within the same range, i.e. up to 50.

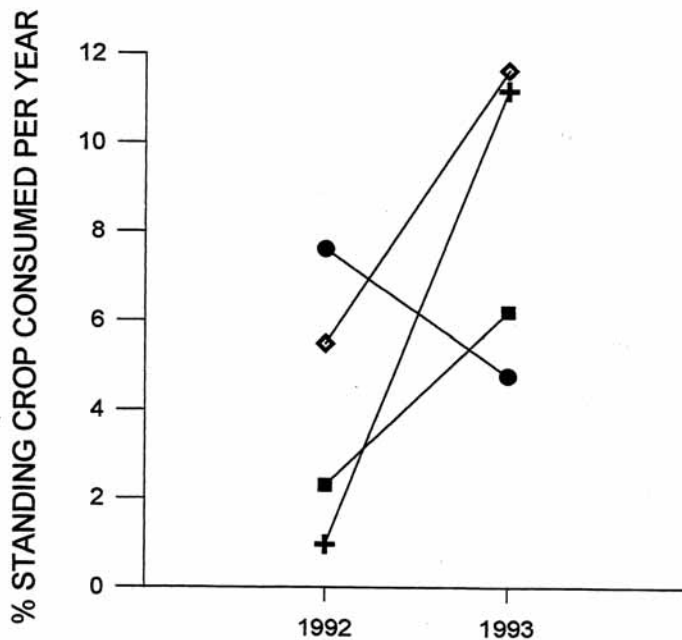


Figure 24. The percentage of the standing crop of four common prey species consumed annually by *Drupella* spp. Circles: *A. divaricata*; crosses: *A. nasuta*; squares: *A. valida*; diamonds: *Stylophora pistillata*. The total number of colonies present in the sites changed between censuses; population sizes in February 1992 are shown in Table 1.

DISCUSSION

Modelling the impact of *Drupella*

Three parameters of the coral/*Drupella* interaction were measured and drawn together into preliminary estimates of colony and population damage attributable to *Drupella*. These are prey selection, residence times and feeding rates. These data are preliminary estimates and represent the first step toward modelling the impacts of *Drupella* under a variety of scenarios of *Drupella* abundance and coral community types. The purpose of this report is to present data as a first step in this modelling process, and issues of accuracy, precision and confidence are for the next stage in the modelling process. The input data can be updated and fine-tuned as more data become available.

Prey selection, residence times and feeding rates were the three parameters required to understand the distribution of damage amongst individual coral colonies due to *Drupella*. Measuring the surface area of a subset of hosts provided an estimate of the amount of tissue available to *Drupella* and therefore the proportion of the standing crop consumed.

On the sheltered reef slopes at Mermaid Cove and Granite Bluff, where *Drupella* abundance was constant at 1 to 2 per m² over the two years of this study, and the percentage of prey colonies occupied remained constant at 2 to 4 per cent, *Drupella* spp. consumed up to 12 per cent annually of the standing crop of the species investigated. Since *Drupella* are ubiquitous inhabitants of most Indo-Pacific coral reefs, and numbers on many reefs are similar to or higher than those in the present study (Cumming under review), these levels of tissue loss are probably widespread.

The level of tissue loss calculated in this study is within the same range as the proportion consumed by insect herbivores in terrestrial forests (Mattson & Addy 1975; Landsberg & Ohmart 1989).

Feeding rates

Feeding rates measured in this study using laboratory aquaria for *Drupella cornus* (2.3cm² per day) are similar to field estimates for *Drupella cornus* by Ayling & Ayling (1987), who estimated 2.6cm² per day for plate acroporids at Ningaloo Reef, Western Australia. They used the same technique of averaging feeding rates out over individuals in a group and over several days of feeding. Their estimate was based on revisiting groups of *Drupella* feeding on plate corals after seven days and using photographs to estimate the amount of tissue consumed over that period.

Prey choice

The tendency of *Drupella* to hide in crevices or amongst coral branches suggests a pressure to seek substrates that provide protection from predators such as fish, crabs, octopus or other molluscs. By nestling deep between the branchlets of branching coral colonies, with little excess space, they limit the size of predators that can reach them. Their cryptic behaviour is assisted by the camouflage of the pink calcareous alga that covers their shells and blends with dead coral branches and rubble.

The importance of prey colonies with previous injuries

Drupella avoid contact with live coral branches, perhaps because they are not immune to the nematocysts (Cumming 1996; Page 1987; Turner 1994a). This has two important effects: first, they prey on a colony from the edge of the live tissue and never remove flesh from areas surrounded by live tissue (unless they can reach it from some other perch), and second, dead branches that represent previous unregenerated injuries probably make it easier for *Drupella* to occupy a colony. Exemptions could include if a dead branch of one coral touches a live branch of another, or if coral tissue can be reached from a crevice in the substrate.

Dead branches, evidence of previous unregenerated injuries, appear to add to the attractiveness of a colony by providing suitable substrate, but this was not tested explicitly. Presence of *Drupella* already on a colony may also influence prey choice because *Drupella* are attracted to other *Drupella* in forming aggregations. Morton et al. (2002) observed that the feeding activity of *D. rugosa* in laboratory aquaria stimulated other conspecifics to feed, thus forming feeding aggregations.

Preference for larger prey colonies

The log-linear model identified colony size as a more important characteristic in prey choice than growth form, indeed growth form lost its importance after size was included in the log-linear model. The likelihood of occupation increased with colony size, and up to 50 per cent of colonies >40cm diameter were occupied at any time, while small colonies <10cm diameter had a size refuge; they were rarely occupied. Large colonies also supported significantly larger group sizes, resulting in 45 per cent of *Drupella* occupying colonies >40cm diameter. This increase in occupation rate with colony size is not adequately explained by predator avoidance. Once a colony is greater than a threshold size, say 10cm diameter, there should be little difference between the degree of protection offered by it and larger colonies, especially for corymbose forms for which branchlet spacing and height is no different in larger colonies (Figures 5,6,7,9,10). A possible explanation is that small colonies were less likely to have suffered previous injury and have dead branches. Demographic studies of corals have reported the likelihood of injury increasing with colony size (Babcock 1991; Hughes & Jackson 1985).

A second explanation involves optimal foraging; theory predicts that predators will aggregate in areas of high prey density. Large staghorn thickets (Figure 8), which represent local patches of high prey density, harboured almost a third of all *Drupella* on the study reefs. In addition, the two largest aggregations of *Drupella* observed at Lizard Island by Cumming (1996), with >2000 snails each, were both in large staghorn thickets. These thickets provide excellent cover; a large group of resident *Drupella* can be invisible. These two explanations are not mutually exclusive, and it is possible that both influence prey choice.

Impact of *Drupella* on prey colonies

The *Drupella* assemblage on these sheltered fringing reef slopes was organised into many small groups that changed colonies frequently and a few large groups that were temporally more stable and remained on colonies for several months or longer. Hence,

large groups of *Drupella* had an amplified impact on their prey colonies because they also resided for longer.

By extrapolating estimates from different time scales, it was estimated that most of the large colonies more than 40cm diameter on these reefs were occupied and injured by *Drupella*. Many colonies were lightly injured by small groups, a few were heavily injured by large groups and some were occupied repeatedly. But while the proportion of colonies injured by *Drupella* was high, little surface area of many was consumed because most groups were small and transient.

However, scientific studies of injury to reef-building corals have shown detrimental effects of injuries, such as decreased growth and reproduction and increased death of injured colonies (Hall 1998; Kobayashi 1984; Meesters et al. 1994; Rinkevich & Loya 1989; van Veghel & Bak 1994). Injuries may also provide establishment opportunities for bioeroders, pathogens or competing organisms.

Regeneration of injuries drains energetic resources. Injuries to coral colonies are not always fully regenerated and the rate of regeneration slows over time until it finally stops with incomplete recovery of the wound (Hall 1998; Meesters 1994). This suggests a finite energetic resource, so regeneration may have little ability in the long-term to compensate for chronic or repeated injuries, even if they are small. No studies have to date addressed the effect of low-level repeated injuries of the type typical of small groups of *Drupella*.

Cumming (2002) recorded the injuries on all prey corals in the permanently marked sites at each census and compared them with subsequent growth, shrinkage or death of the colonies. The data showed a strong relationship between injuries and subsequent colony shrinkage and death, and larger injuries had a stronger effect (for corymbose, hispidose and pocilloporid colonies). In addition, 43 per cent of the heavily injured corymbose colonies (with old, unregenerated injuries covering more than 5 per cent of the colony, as well as fresh new injuries) were dead within 3 to 5 months. Arborescent colonies, however, were relatively immune to the impact of injuries from *Drupella* grazing and other sources; injured arborescent colonies were not more likely to decline or die.

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