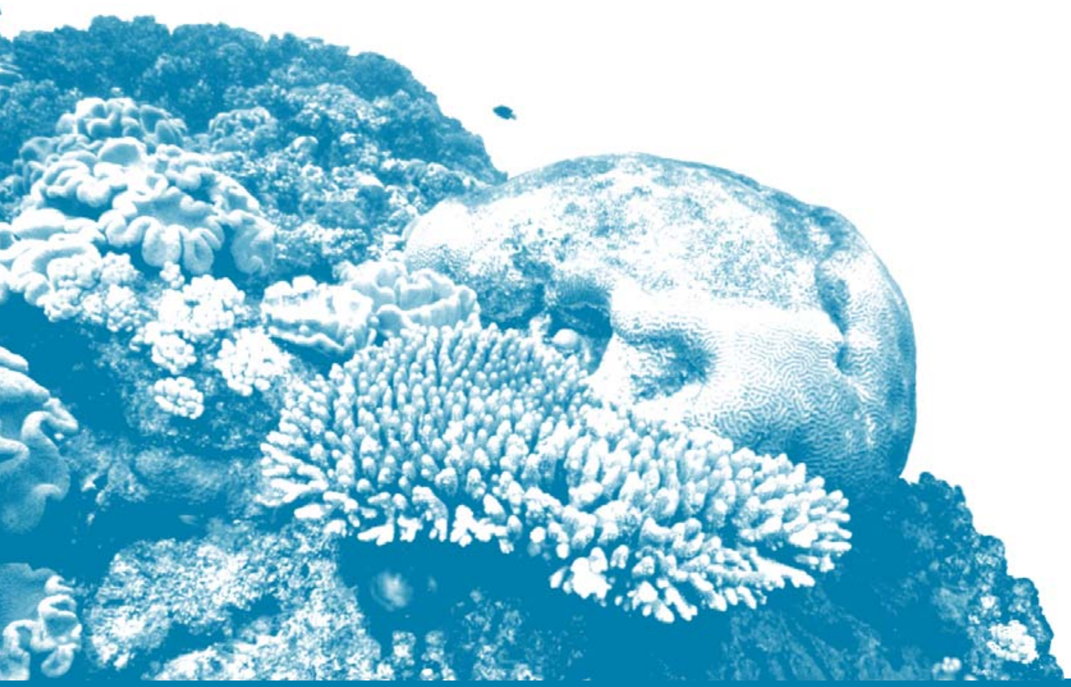
Australian Government
Great Barrier Reef
Marine Park Authority

RESEARCH PUBLICATION NO. 96

Population outbreaks and large aggregations of *Drupella* on the Great Barrier Reef



R.L. Cumming

RESEARCH PUBLICATION NO. 96

Population outbreaks and large aggregations of *Drupella* on the Great Barrier Reef

R.L. Cumming
Liquiddity Environmental Consulting
Cairns QLD 4879

Australian Government
Great Barrier Reef
Marine Park Authority

PO Box 1379
Townsville QLD 4810

Telephone: (07) 4750 0700
Fax: (07) 4772 6093
Email: info@gbrmpa.gov.au

www.gbrmpa.gov.au

Published by the Great Barrier Reef Marine Park Authority

ISBN 978 1 876945 87 9 (pdf)

The National Library of Australia Cataloguing-in-Publication entry :

Cumming, R. L.

Population outbreaks and large aggregations of drupella on the Great Barrier Reef [electronic resource] / R. L. Cumming.

ISBN 978 1 876945 87 9 (pdf)

Research publication (Great Barrier Reef Marine Park Authority. Online) ; 96.

Bibliography.

Drupella--Control--Environmental aspects--Queensland—Great Barrier Reef.
Great Barrier Reef Marine Park Authority.

594.3209943

Requests and inquiries concerning reproduction and rights should be addressed to:

Australian Government

Great Barrier Reef
Marine Park Authority
Director, Communication and Education Group
2-68 Flinders Street
PO Box 1379
TOWNSVILLE QLD 4810
Australia
Phone: (07) 4750 0700
Fax: (07) 4772 6093
info@gbrmpa.gov.au

Comments and inquiries on this document are welcome and should be addressed to:

Chief Scientist, Director Science Coordination
stig@gbrmpa.gov.au

www.gbrmpa.gov.au

ACKNOWLEDGMENTS

The author thanks all those who assisted in the collection, analysis and interpretation of the information in this report.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

EXECUTIVE SUMMARY

Drupella spp. are marine snails that feed exclusively on reef-building corals in the Indo-Pacific region. Since the early 1980s, numerous reports of large aggregations and population outbreaks of *Drupella* killing corals and damaging coral reefs have lead to the perception that population outbreaks of *Drupella* are common, widespread and destructive.

To date, *Drupella* have not been problematic on the Great Barrier Reef, but a concern to management is whether population outbreaks could occur here, and how we might identify and manage them. This report addresses the following questions:

1. How can a population outbreak of *Drupella* be distinguished from a normal population?
2. What abundance of *Drupella* would constitute a population outbreak on the Great Barrier Reef?
3. What indicators could be used to identify a potential problem population of *Drupella*?

The approach taken was to:

- Highlight the differences between large aggregations and population outbreaks of *Drupella*
- Collate all available estimates of density, and look for patterns that distinguish elevated densities from normal
- Make a comparison with the crown-of-thorns starfish (COTS), for which densities typical of outbreak and non-outbreak populations have been refined by a number of scientific studies
- Outline indicators of problem *Drupella* populations, and aspects of sampling design to specifically target *Drupella*, should a situation need monitoring.

The major results are:

- Evidence exists for population outbreaks of *Drupella* in only three broad locations: Japan, the northern Red Sea, and Ningaloo Reef in Western Australia. These are the only locations where *Drupella* densities of >3/m^2 have been recorded. All three locations include some sites with >5/m^2.
- *Drupella cornus* is the problem species at Ningaloo Reef and the northern Red Sea, and has reached a density of 19/m^2 at Ningaloo Reef.
- *Drupella fragum* is the problems species in Japan, for which the highest record is 5/m^2,
- *Drupella rugosa* has not been implicated in population outbreaks.
- The COTS comparison suggests the density that distinguishes non-outbreak from outbreak populations of *Drupella* lies between 1.4 and 6.4 *Drupella*/m^2.
- Large aggregations, involving hundreds or thousands of *Drupella* clumped on just one or a few adjacent coral colonies, have been observed in many reef locations and are different from population outbreaks.
- Reports of large aggregations have most often involved *D. rugosa*.

- *D. cornus* and *D. fragum*, or both together, appear to be more often associated with harsher environments such as shallow reef flats, and reef crests and slopes exposed to wave action, whilst *D. rugosa* has been recorded more often in sheltered reef slope environments.

It is not currently known whether large aggregations of *Drupella* could lead to increased reproduction and ultimately to population outbreaks, and/or are the first signs of elevated population densities.

Based on the information presented in this report, the following are scenarios that may indicate problem populations of *Drupella* and should be recorded and monitored if possible:

1. Any broad-scale variation on the species distribution amongst reef zones as described above
2. Concentration or conspicuous presence of *Drupella* on reef crests or other high energy environments
3. *Drupella* attacking small colonies <10cm diameter
4. *Drupella* occupying a high proportion of coral colonies
5. Presence of large aggregations, especially of *D. cornus* or *D. fragum*
6. Presence of large aggregations of juveniles
7. *Drupella* congregating on broken coral
8. *Drupella* congregating on stressed coral, for example colonies that are bleached or diseased.

INTRODUCTION

Drupella are predators of reef-building corals that are widespread on Indo-Pacific coral reefs, and are best known as potential problem species because population outbreaks of *Drupella* have been associated with considerable death of corals. This is significant because corals build the basic structure of coral reefs and provide habitat for reef organisms. Past outbreaks of the crown-of-thorns starfish (COTS) and *Drupella* have degraded reefs by drastically reducing coral cover. Since these predators tend to have prey preferences and choose the fast-growing branching species that often dominate reefs, they can also alter the basic structure of reefs.

Reports of coral destruction by *Drupella* began in 1982 when Moyer et al. (1982) reported having observed "population explosions" of *D. fragum* since 1976 in the Izu Islands of southern Japan. Further reports of outbreaks of *D. fragum* in the southern regions of Okinawa, Shikoku and Kyushu followed through the 1980s and 1990s (Fujioka & Yamazato 1983; Awakuni 1989; Kimura et al. 2005). Some of these areas reportedly still had a large number of *D. fragum* in 2004 (Kimura et al. 2005). A mixture of *Drupella* species occurred, dominated by *D. fragum* (Fujioka and Yamazato 1983; Johnson and Cumming 1995; Moyer et al. 1982), in average densities of up to 5.12/m^2 for all species combined (Fujioka & Yamazato 1983).

In 1987, Ayling & Ayling (1987) discovered high densities of *Drupella cornus* at Ningaloo Reef, Western Australia, with densities up to 18.5/m^2 and high coral mortality. Monitoring over the following years (Ayling & Ayling 1992; Osborne 1992; Osborne & Williams 1995; Turner 1994a,b), revealed that the full 260km length of this reef was affected, with the outbreak beginning in the north and moving south over time, in much the same way as crown-of-thorns starfish (COTS) outbreaks do on the Great Barrier Reef (Sweatman et al. 2008). With up to 75 per cent reduction in live coral cover attributed to *D. cornus*, and average *Drupella* densities of up to 19.4/m^2, this is the largest and most well-known outbreak of *Drupella*.

In the mid 1990s, independent reports of outbreaks of *Drupella cornus* in the Red Sea came from Eilat in Israel and the Gulf of Aqaba (Antonius & Riegl 1997; Loya & Gur 1996; Al-Moghrabi 1997). Average densities of up to 12.24 *D. cornus*/m^2 were recorded at Aqaba (Al-Moghrabi 1997). Shafir et al. (2008) reported an outbreak of *D. cornus* on an artificial limestone quay from 1999 to 2004 that killed most of the coral colonies on the quay.

Thus three broad locations have each been the subject of multiple reports of high density populations of *Drupella* and associated coral damage: Ningaloo Reef, Japan and the northern end of the Red Sea. A characteristic common to all of these is that of associated and significant coral damage. To date, no population outbreaks of *Drupella* have been reported on the Great Barrier Reef, or in areas of Australia other than Ningaloo Reef, although numerous accounts exist of large aggregations in both Western Australian and the Great Barrier Reef.

Large aggregations are a different phenomenon from population outbreaks, and involve hundreds or thousands of *Drupella* clumped together on a single coral colony or a few adjacent colonies. Large aggregations were first documented in 1982 by Moyer et al. (1982) who described the phenomenon for both *D. fragum* (in Japan) and *D. rugosa* (in the Philippines), and Ayling & Ayling (1987) who described it for *D. cornus*. These have been followed by periodic observations of large aggregations of *D. rugosa* (Baird 1999; Boucher 1986; Cumming 1999, 2000; Cumming & McCorry 1998; Fellegara 1996; Harborne et al. 2000; Loch 1987) and *D. cornus* (Armstrong 2005) and it is now apparent that large aggregations are a widespread feature of the population dynamics of *Drupella*.

Large aggregations have complicated our ability to distinguish between outbreak and non-outbreak populations, and may have been mistaken for population outbreaks in the absence of any useful definition to distinguish population outbreaks from large aggregations.

The purpose of this report is to:

1. Highlight the differences between large aggregations and population outbreaks of *Drupella*
2. Define population outbreaks of *Drupella* in terms of density, as far as is possible, so that we can assess how frequent outbreaks have been and are likely to be in the future, and in particular the likelihood of outbreaks on the Great Barrier Reef
3. Define a potential problem population of *Drupella* on the Great Barrier Reef, and how it might be identified with the methods currently used for monitoring *Drupella* (given that most data on *Drupella* are currently collected as a side to other studies)
4. Elucidate aspects of a good sampling design to specifically target *Drupella*, should a situation need monitoring.

DEFINING POPULATION OUTBREAKS OF *DRUPELLA*

Definition of an outbreak of *Drupella*

The provisional definition of an outbreak of *Drupella* to be used in this report is "any population of elevated density that causes extensive mortality of corals and persists for months or years over large areas of reef". This definition emphasises the important aspects of temporal persistence and large spatial scale, and follows closely Potts' (1981) definition of a population outbreak of the crown-of-thorns starfish. Since a lower absolute density of *Drupella* could cause "extensive mortality" in an area with sparse coral growth, or damaged by bleaching or other stressors, the definition of "elevated density" must be a range. It is the intention of this report to identify this range of *Drupella* densities.

Temporal persistence and large spatial scale are key aspects that distinguish population outbreaks of *Drupella* from large aggregations. Large aggregations typically occupy a small spatial scale (one or a few adjacent coral colonies), and the few that have been monitored have not persisted for longer than a few months (e.g. Boucher 1986; Cumming 1999).

Trends in *Drupella* abundance

A summary of data from replicated surveys is given in table 1. Since *Drupella* density is very patchy on small scales (Cumming 1999; Turner 1994b), high densities recorded with small sampling effort (single quadrats or transects, or a small number of preliminary quadrats) are not included in Table 1. Thus, the highest density recorded to date, nearly 20/m^2 at Low Isles, Great Barrier Reef, was not considered an outbreak by Ayling & Ayling (1992) because they sampled only a small number of preliminary quadrats.

It is clear from table 1 and figure 1 that it is only *Drupella cornus* that has occurred in densities >3/m^2 (except the single site at Sesoko Island, Japan). All of the densities of >3/m^2 are from the outbreak locations of Ningaloo, Aqaba and Japan, although there is only one site at Sesoko Island, Japan, that is in this group (5.12/m^2). Table 1 also clearly shows that although all three of these locations have very high densities at some sites (in some years), they all include sites with densities equal to or lower than those from non-outbreak populations. This reflects the great spatial and temporal variation which characterises *Drupella* densities and highlights the importance of sampling replicate sites.

Densities at the non-outbreak sites, Bundegi Reef, Murion Islands, Hong Kong, Sanganeb Atoll and the Great Barrier Reef, all fall within the range of 0-2/m^2, except one site at Bundegi Reef and two sites at Lizard Island. Apart from the two Lizard Island sites, all estimates for the Great Barrier Reef are less than 1/m^2.

The densities in Table 1 form an almost unbroken continuum up to the value of 7.4 (figure 1). Values greater than 7.4 include just 13 of the 130 sites, or 10 per cent, and they are all at Ningaloo and Aqaba. 37 per cent of the sites had less than 1 *Drupella*/m^2 and 69 per cent had less than 3 *Drupella*/m^2.

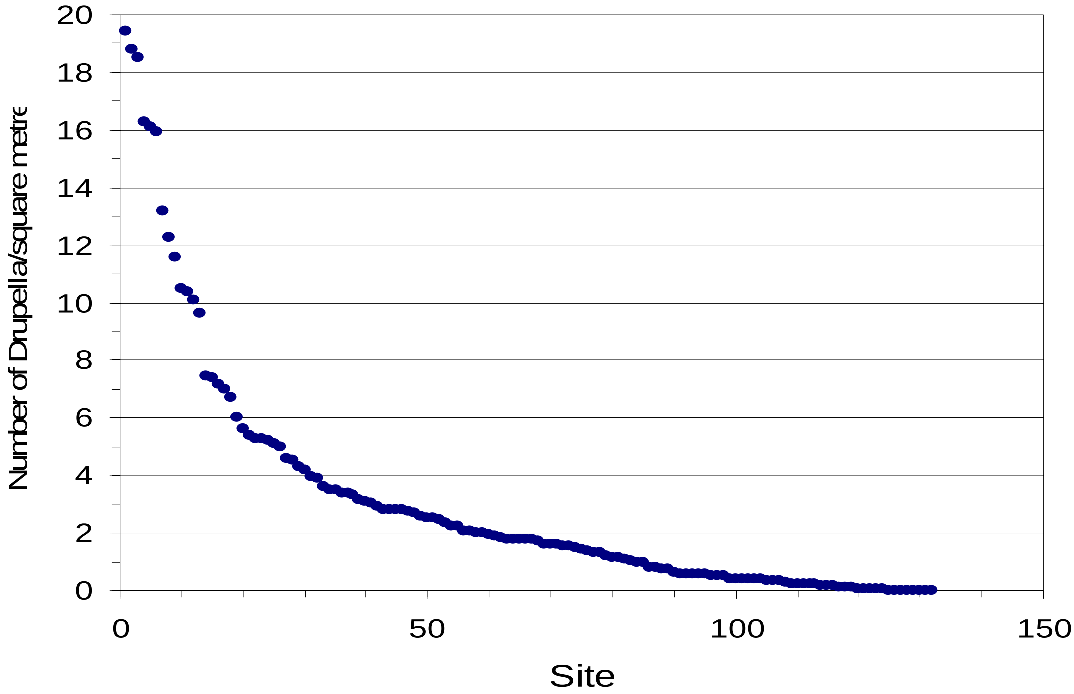


Figure 1. Density estimates for 130 sites, in descending order (all *Drupella* species combined). Data are from Table 1.

Thus, the high densities of *D. cornus* at Aqaba and Ningaloo distinguish these locations quite clearly. The highest density recorded to date is 19.4 /m^2 at Ningaloo in 1990/1991. The third outbreak location, Japan, is less clearly defined as an outbreak in terms of absolute density, despite numerous reports of high *D. fragum* densities and associated coral mortality. Nevertheless, 3.37/m^2 is the highest density of *D. fragum* on record, and 5.12/m^2 for all species combined is in the top 15 per cent of all records, and is above the range of 0-3/m^2 that includes all of the non-outbreak locations.

We can tentatively define a non-outbreak *Drupella* assemblage as having densities in the range 0-2/m^2. Densities in non-outbreak areas greater than 2/m^2 may be worth monitoring as they fall at the high end of the range suggested as normal in non-outbreak densities. The major problem species is *D. cornus* and since large aggregations of *D. cornus* have only been recorded in the outbreak locations, a large aggregation of *D. cornus* occurring in non-outbreak locations might be worth monitoring. In all cases, densities should be considered in light of the nature of the coral community, so that a severely depauperate coral assemblage, or one under pressure from other stressors such as bleaching or disease, may be susceptible to significant damage from lower densities of *Drupella*.

Table 1. Estimates of *Drupella* population densities. '-' = information not available to the author. 'Back reef' = sheltered side of the reef crest. 's.e.' = standard error of the mean.

Location	Reef site/date	*Drupella*/m²		Species	Sampling effort	Source
		Mean	s.e.			
Ningaloo Reef, WESTERN AUSTRALIA	Back reef, 1987	5.3	1.70	*D. cornus*	10-30 5x0.5m transects	Ayling and Ayling (1987)
		16.1	3.41	"	"	
		10.4	2.45	"	"	"
		18.5	7.74	"	"	"
		9.6	3.33	"	"	"
		16.3	6.24	"	"	"
		7.0	2.69	"	"	"
		7.4	1.58	"	"	"
	Lagoon, 1987	5.0	1.01	"	"	"
	Outer slope, 1987	1.6	1.03	"	5 5x0.5m transects	"
	Reef crest, 1987	1.3	0.45	"	"	"
"	Back reef, 1989	2.6	-	*D. cornus*	34 20x0.5m transects	Forde (1992)
		6.7	-	"	"	"
"	Lagoon, 1989	2.80	1.38	*D. cornus*	9 5x5m quadrats	Osborne (1992)
		2.26	0.90	"	"	"
		0.09	0.07	"	"	"
	Back reef, 1989	0.21	0.10	"	"	"
		0.38	0.28	"	"	"
		0.05	0.04	"	"	"
		1.78	1.70	"	"	"
		0.56	0.13	"	"	"
		0.02	0.01	"	"	"
		1.82	0.85	"	"	"
		3.36	1.69	"	"	"
		15.95	0.78	"	"	"
"	Reef flat, 1990/1991	5.2	4.47	*D. cornus*	5 1x1m quadrats	Turner (1994b)
		0.0	0.00	"	"	"
		4.2	4.20	"	"	"
		2.8	1.39	"	"	"
		3.6	1.86	"	"	"
		5.4	2.69	"	"	"
		4.6	2.20	"	"	"
		6.0	4.28	"	"	"
		5.6	0.68	"	"	"
	Back reef, 1990/1991	1.0	0.77	"	"	"
		1.8	1.36	"	"	"
		2.8	1.39	"	"	"
		13.2	12.46	"	"	"
		11.6	3.46	"	"	"
		19.4	5.01	"	"	"

Table 1. cont'd

Location	Reef site/date	*Drupella*/m²		Species	Sampling effort	Source
		Mean	s.e.			
Ningaloo Reef, WESTERN AUSTRALIA (cont'd)	Lagoon, 1991	3.04	-	*D. cornus*	9 5x5m quadrats	Osborne and Williams (1995)
		3.49	-	"	"	
		0.60	-	"	"	"
	Back reef, 1991	0.30	-	"	"	"
		0.39	-	"	"	"
		0.05	-	"	"	"
		2.01	-	"	"	"
		0.83	-	"	"	"
		0.02	-	"	"	"
		2.04	-	"	"	"
		3.93	-	"	"	"
		18.77	-	"	"	"
	Lagoon, 1994	2.72	-	"	"	"
		3.30	-	"	"	"
		0.22	-	"	"	"
	Back reef, 1994	0.05	-	"	"	"
		0.51	-	"	"	"
		1.56	-	"	"	"
		1.00	-	"	"	"
		0.33	-	"	"	"
		1.01	-	"	"	"
		3.48	-	"	"	"
		1.60	-	"	"	"
		10.06	-	"	"	"
"	2005	1.3	0.27	"	9 0.5x20m transects	Armstrong (2005)
		2.33	0.67	"	"	
		3.13	0.38	"	"	
		2.01	0.54	"	"	
		1.47	0.29	"	"	
		1.37	0.18	"	"	
		3.38	0.62	"	"	
		2.53	0.46	"	"	
		1.72	0.17	"	"	
		2.44	0.32	"	"	
		2.26	0.74	"	"	
		5.25	0.89	"	"	
"	2006	1.87	0.39	"	9 0.5x20m transects	Armstrong (2007)
		1.77	0.26	"	"	
		2.80	0.70	"	"	
		7.44	1.35	"	"	
		1.79	0.25	"	"	
		3.89	0.72	"	"	
		1.93	0.27	"	"	
		4.30	-	"	3 0.5x20m transects	

Table 1. cont'd

Location	Reef site/date	*Drupella*/m² Mean	s.e.	Species	Sampling effort	Source
Bundegi Reef, WESTERN AUSTRALIA	1989	2.90	-	*D. cornus*	6 20x0.5m transects	Forde (1992)
	1989	1.45	0.67	*D. cornus*	9 5x5m quadrats	Osborne (1992)
	1990/1991	0.4 0.4 0.0	0.24 0.40 0.00	*D. cornus* " "	5 1x1m quadrats " "	Turner (1994b) " "
	1991 1994	1.62 1.77	0.37 -	*D. cornus* "	9 5x5m quadrats "	Osborne and Williams (1995)
	2005	0.2	0.04	*D. cornus*	9 0.5x20m transects	Armstrong (2007)
Murion Islands, WESTERN AUSTRALIA	2006	0.21 1.19	0.02 0.18	" "	9 0.5x20m transects "	Armstrong (2007)
Akajima Island, Okinawa, JAPAN	1991 1992 1993 1994	0.10 0.29 0.39 0.32 0.74 1.16 0.25 0.48 0.73 0.33 0.78 1.11	0.07 0.15 - 0.11 0.35 - 0.07 0.25 - 0.06 0.31 -	*D. cornus* *D. fragum* All species *D. cornus* *D. fragum* All species *D. cornus* *D. fragum* All species *D. cornus* *D. fragum* All species	4 50x2m transects " " 12 50x2m transects " " 12 50x2m transects " " 11 50x2m transects " "	Shimoike (1995) " " " " " " " " " "
Sesoko Island, Okinawa, JAPAN	Reef flat	1.30 3.37 0.41 0.04 5.12 0.74 0.63 0.04 1.14	0.76 2.31 0.22 0.04 - 0.44 0.38 0.04 -	*D. cornus* *D. fragum* *D.dealbata* *D.concatena ta* All species *D. cornus* *D. fragum* *D.dealbata* All species	27 1x1m quadrats " " " " " " " "	Fujioka and Yamazato (1983) " " " " " " "
Tung Tau Chau, HONG KONG		0.6	-	*D. rugosa*	-	Taylor (1980)
RED SEA SanganebAtoll, Sudan	**Reef flat** **Upper reef slope**	1.55 0.57	0.50 0.32	*D. cornus* "	4 10x1m transects 3 10x1m transects	Schuhmacher (1992)
RED SEA Aqaba, Jordan	**Reef flat** **Upper reef slope** **Lower reef slope** **Thermal Power Plant**	0.07 12.24 2.73 7.16	0.05 3.62 0.85 2.05	*D. cornus* " " "	90 1x1m quadrats 75 1x1m quadrats 80 1x1m quadrats 75 1x1m quadrats	Al-Moghrabi (1997) " "

Table 1. cont'd

Location	Reef site/date	*Drupella*/m² Mean	s.e.	Species	Sampling effort	Source
GREAT BARRIER REEF	**Heron Island**					
	North Heron Reef	0.05	0.01	*D. cornus* adults	20 20x1m transects	Fellegara (1996)
		0.005	0.005	*D. eburnea* adults	"	
		0.01	0.01	*D. fragum* adults	"	"
		0.01	0.005	*D. rugosa* adults	"	"
	South Heron Reef	0.075	-	All species adults	"	"
		0.03	0.01	*D. cornus* adults	"	"
		0.05	0.005	*D. eburnea* adults	"	"
		0.02	0.01	*D. fragum* adults	"	"
	North Wistari Reef	0.07	0.02	*D. rugosa* adults	"	"
		0.17	-	All species adults	"	"
		0.08	0.02	*D. cornus* adults	"	"
		0.05	0.01	*D. eburnea* adults	"	"
	Heron Reef Flat	0.02	0.01	*D. fragum* adults	"	"
		0.10	0.03	*D. rugosa* adults	"	"
		0.25	-	All species adults	"	"
		0.01	0.02	*D. cornus* adults	"	"
		0.005	0.005	*D. eburnea* adults	"	"
		0	0	*D. fragum* adults	"	"
		0.10	0.03	*D. rugosa* adults	"	"
		0.115	-	All species adults	"	"
"	**Lizard Island**					
	Corner Beach	0.77		All species	10 10x2 m transects	Sutton (1996)
	Horseshoe Reef	0.49		"	"	"
	North Reef	0.01		"	"	"
"	**Lizard Island**					
	Exposed reef crests	0.64	0.13	D. cornus	32 2x2m quadrats	Cumming (1999)
		1.91	0.47	D. fragum	"	
		2.55	-	All species	"	"
	Exposed reef slopes	0.16	0.06	D. cornus	"	"
		0.05	0.02	D. fragum	"	"
		0.01	0.01	D. rugosa	"	"
		0.22	-	All species	"	"
	Sheltered reef crests	0.05	0.02	D. cornus	"	"
		0.14	0.06	D. fragum	"	"
		0.15	0.05	D. rugosa	"	"
		0.34	-	All species	"	"
	Sheltered reef slopes	0.33	0.08	D. cornus	"	"
		0.13	0.06	D. fragum	"	"
		1.62	0.42	D. rugosa	"	"
		2.08	-	All species	"	"
"	**8 reefs of the Great Barrier Reef, 1987**	0.61	-	All species	110 10x1m transects	Oxley (1988)

Table 1. cont'd

Location	Reef site/date	*Drupella*/m²		Species	Sampling effort	Source
		Mean	s.e.			
GREAT BARRIER REEF (cont'd)	**53 reefs of the Great Barrier Reef, 1993-2000,** surveyed by the Australian Institute of Marine Science long-term monitoring program.	Min: 0 Max: 0.299	-	All species	15 50x2m transects at each reef, on the north-east flank	I. Miller (personal communication)
"	**45 reefs of the Great Barrier Reef, in 2006,** surveyed by the Australian Institute of Marine Science long-term monitoring program.	Min: 0 Max: 0.055	-	All species	15 50x2m transects at each reef, on the north-east flank	Sweatman et al. (2008)
"	**43 reefs of the Great Barrier Reef, in 2007,** surveyed by the Australian Institute of Marine Science long-term monitoring program (all except two are different reefs from those surveyed in 2006)	Min: 0 Max: 0.065	-	All species	15 50x2m transects at each reef, on the north-east flank	Sweatman et al. (2008)
"	**16 reefs of the Great Barrier Reef, in 2008**, surveyed by Reef Check	Min: 0 Max: 0.02	-	All species	4 20x5m transects at each reef	Stella et al. (2008)

Alternate measures: the frequency of damage

***The proportion of colonies under attack by* Drupella**

Absolute density is difficult to measure by quick surveys. The assessment below addresses whether a population outbreak of *Drupella* could be identified by an elevated proportion of colonies under attack at any given time. Such a measure takes into account the nature of the coral community and the relative abundance of preferred prey corals. Since the impact of *Drupella* on coral communities must depend on the status of the coral community itself rather than just absolute density of *Drupella*, this measure is intuitively reasonable. However, the proportion of colonies under attack has not been measured in conjunction with most *Drupella* surveys.

Cumming (1999) recorded 0-6.9% of prey colonies (the branching species of *Acropora* and pocilloporids) occupied by *Drupella* in four different reef habitats at Lizard Island where *Drupella* density was 0.15-3.28/m^2, and percentage of prey corals occupied tended to increase with increasing *Drupella* density (figure 2). More data are needed over a wider range of *Drupella* densities. The two highest densities in Figure 2 are from the exposed reef crests that supported an assemblage of only *D. cornus* and *D. fragum*, and had the highest density of all habitats surveyed at Lizard Island (Cumming 1999).

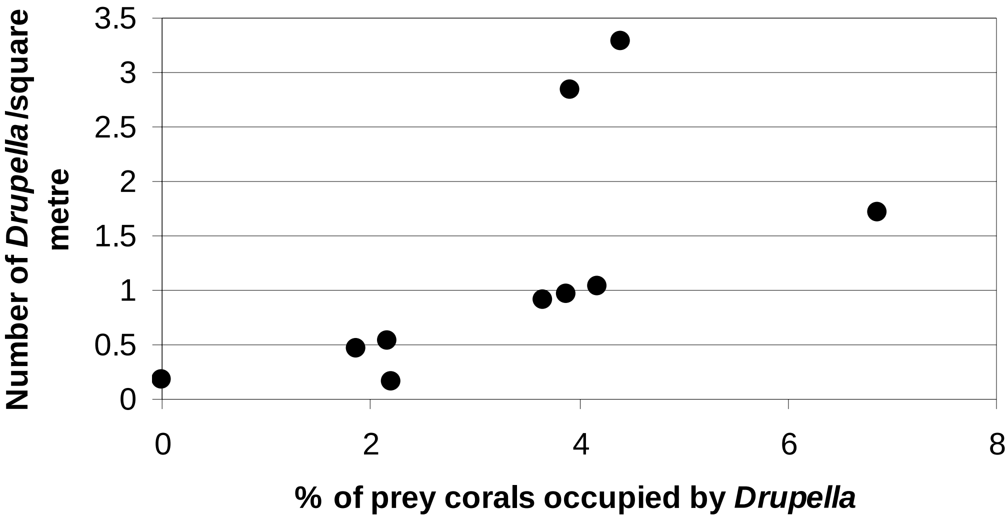


Figure 2. Percentage of prey colonies occupied by *Drupella* in relation to *Drupella* density. The relationships is not significant at the 5 per cent level (ANOVA , $F_{1,8}$= 4.80, p=0.06). Data are from Cumming (1999).

***The proportion of colonies damaged by* Drupella**

Ayling (2000) surveyed the percentage of colonies that had been damaged by *Drupella* (not necessarily currently occupied) on 47 reefs on the Great Barrier Reef in 1991 (funded by Great Barrier Reef Marine Park Authority) with 24 30x1m transects on each reef. Reef-wide damage ranged from 0.4 per cent to over 26 per cent of coral colonies, with a grand mean of 6.6 per cent.

Shafir et al. (2008) described an artificial quay at Eilat with *D. cornus* on 100 per cent of coral colonies of several branching coral species. Clearly, such a high proportion of colonies under attack would signify a problem, but the exact percentage that we may define as the cut-off point between what is normal and what is not, is a subject that requires more data for a range of *Drupella* densities.

A crown-of thorns starfish comparison

The first attempt to distinguish between outbreaking and non-outbreaking crown-of-thorns starfish (COTS) populations in terms of density was given by Pearson &Endean (1969) who suggested >400/hectare for outbreaking populations and <100/hectare for non-outbreaking populations. Subsequently, reef ecologists calculated various definitions for non-outbreaking populations. All were less than 100/hectare except Endean & Stablum (1975) who suggested a cut-off point of 140/hectare. A full list of these estimates is provided by Moran & De'ath (1992).

Moran & De'ath (1992) fine-tuned the cut-off point to 15/hectare (0.22 COTS/2-minute manta-tow), using Australian Institute of Marine Science (AIMS) long-term monitoring manta-tow data in conjunction with intensive underwater surveys. This was subsequently revised by Lassig & Engelhardt (1995) and Engelhardt et al. (1997) to 68/hectare (1 COTS/2-minute manta-tow) as a starfish density that is 'highly likely to cause net decline in corals' (Sweatman et al. 2008). Currently, the AIMS long-term monitoring program uses this definition of outbreaks, and defines a COTS density in the range 15-68/hectare as an "incipient outbreak". Thus, the current AIMS working definition of COTS outbreak and non-outbreak densities closely resembles those initially offered in the 1970s (see Moran & De'ath 1992).

Glynn (1973) calculated that 65 COTS/hectare could be maintained on a pocilloporid reef in Panama, including reef growth in the calculation. Keesing & Lucas (1992), however, calculated that significant coral mortality could occur on reefs with low coral cover (20%) when COTS densities exceed 10/hectare and highlighted the importance of taking into account characteristics of the coral community as well.

The above COTS densities were converted to *Drupella* densities using mean feeding rate measurements for *Drupella* spp. (1.806 cm^2/day; Cumming under review) and COTS (238 cm^2/day on the Great Barrier Reef, Keesing & Lucas 1992; and 148 cm^2/day in Panama, Glynn 1973). COTS feeding rates were measured as the surface area of reef consumed per day, whereas *Drupella* feeding rates were measured as the surface area of coral branches consumed per day (a 3-dimensional measures vs. a 2-dimensional measure), so a conversion rate was used. To estimate the branch area available to *Drupella* for a given surface of reef, regression relationships between the projected area (a 2-dimensional measure equivalent to the surface area of reef) and branch surface area were used (Figure 3). These were available for three different growth forms of the preferred prey species of COTS and *Drupella*; corymbose *Acropora* colonies (fine-branched, thick plates 6-8cm in

height), caespito-corymbose colonies (thicker-branched, thicker plates) and the bushy growth forms typical of pocilloporids, *Stylophora pistillata* (Cumming under review). For the corymbose colonies, projected area was on average only 10.3 per cent of the surface area available to *Drupella* grazing, for caespito-corymbose it was 17.6 per cent, and for *S. pistillata*, it was 14.04 per cent. Therefore, for three of the common prey types on the Great Barrier Reef, the surface area of reef was less than 20 per cent of the actual surface area available to *Drupella* grazing.

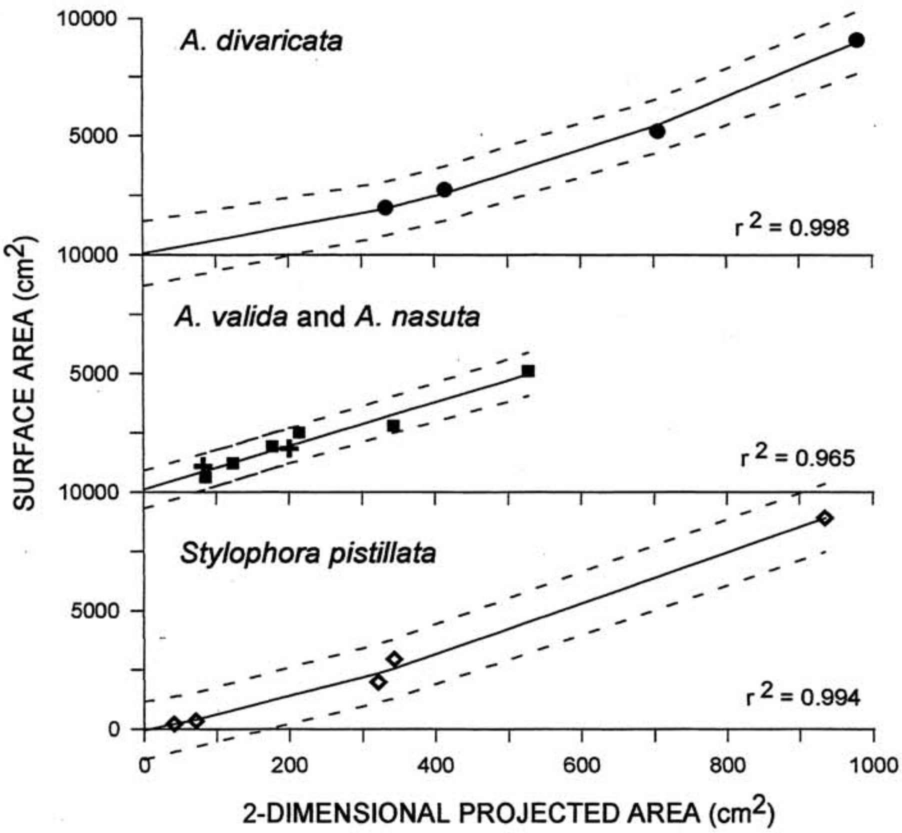


Figure 3. The relationship between the two-dimensional projected area and surface area of four common prey species. Projected area was calculated with the formula for an ellipse: area = $\prod d_1/2.d_2/2$. Crosses: *A. nasuta*; squares: *A. valida*. Regression equations: *A. divaricata*: $y = 54.0058 + 3.895x + 0.0053x^2$; *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 (cm^2) and y=surface area (cm^2). *A. nasuta* and *A. valida* were pooled to increase sample size. Dotted lines are 95 per cent confidence intervals.

For a comparison between COTS and *Drupella* on the Great Barrier Reef, a conversion rate of 14.0 per cent was used, which is the average of the three conversion rates calculated from Figure 3, since Great Barrier Reef reefs usually support a combination of growth

forms. For the Panama pocilloporid reefs that Glynn calculated could support 65 COTS per hectare, and the conversion rate of 14.0% for *S. pistillata* alone was used.

These calculations estimate that 68 COTS/hectare consume coral tissue at the same rate as 6.40 *Drupella*/m^2, 100 COTS/hectare are equivalent to 9.41 *Drupella*/m^2, 15 COTS/hectare are equivalent to 1.41*Drupella*/m^2 and 10 COTS/hectare were equivalent to 0.94 *Drupella*/m^2 (Table 2).

The 65 COTS/hectare in Panama were calculated as equivalent to 3.80 *Drupella*/m^2, whereas 65 COTS on the Great Barrier Reef would be equivalent to 6.1 *Drupella*/m^2. The difference is that the bushy growth form of pocilloporids provides less surface area of tissue than some of the other prey growth forms, particularly corymbose *Acropora*.

The results of these calculations coincide well with the analysis of *Drupella* density above. Thus, 1.4 *Drupella*/m^2 is within the range of what we have tentatively defined as non-outbreak, and the corresponding 15 COTS/hectare is also considered non-outbreak (Sweatman et al. 2008). Between 15-68 COTS/hectare is a 'grey' area, which is currently defined as incipient outbreak by Sweatman et al. (2008). A density of 6.4 *Drupella*/m^2, would be defined as an outbreak, along with densities considerably lower than this. In agreement with the density analysis, Table 2 suggests the density that distinguishes non-outbreak from outbreak populations of *Drupella* lies between 1.4 and 6.4 *Drupella*/m^2.

Finally, as with Keesing & Lucas' (1992) calculations for COTS, it is recognised that significant coral mortality could result from as few as 0.9 *Drupella/* m^2 in areas of low coral cover. As an example, Ningaloo Reef had low densities of *Drupella* in the early 1990s compared with high densities in 1987, but also very low remaining coral cover (Osborne 1992).

Table 2. COTS densities considered significant in defining population outbreaks of COTS on the Great Barrier Reef, and corresponding *Drupella* densities calculated using regression relationships between surface area of reef and surface area of coral branches, given in Figure 3.

COTS density per hectare	Equivalent *Drupella* density per m^2
10	0.9
15	1.4
68	6.4
100	9.4
140	13.2
400	37.6

SPECIES DISTRIBUTION PATTERNS BETWEEN LOCATIONS AND REEF HABITATS

Table 1 shows some geographic differences between *Drupella* species. Although some of the locations only have data for one *Drupella* species, other species have been observed at

some of these locations, for example *D. rugosa* occurs at Bundegi Reef (S. Armstrong, personal communication), and *D. cornus* occurs in Hong Kong (R. Cumming, unpublished data).

Four datasets in Table 1 distinguish between *Drupella* species, and include locations in Japan (Fujioka & Yamazato 1993; Shimoike 1995) and the Great Barrier Reef (Cumming 1999; Fellegara 1996). Based on these data, *D. fragum* is the dominant species for the Japanese sites, with *D. cornus* the second most abundant, and this is supported by various studies and accounts of population outbreaks of *D. fragum* (Awakuni 1989; Fujioka 1984; Kimura et al. 2005). This same 'partnership' of *D. fragum* and *D. cornus*, with *D. fragum* dominating, occurred on exposed reef crests at Lizard Island, Great Barrier Reef (Cumming 1999).

Taken together, these trends suggest that *D. cornus* and *D. fragum* could predominate in more exposed environments such as shallow reef flats, and reef crests and slopes exposed to wave action, dominated by wave resistant and exposure resistant corals with short, thick branches. The back-reef zone at Ningaloo Reef is dominated by these types of corals (Forde 1992; Osborne 1992; Turner 1994b), and is the location of *D. cornus* recruitment (Osborne 1992; Forde 1992; Turner 1994b). In addition, the highest *D. cornus* densities at Ningaloo Reef (refer to table 1) have all been on the "back reef" or reef flat areas on the sheltered side of the reef crest.

Cumming (1999) compared four reef habitats: exposed reef crests, exposed reef slopes, sheltered reef crests and sheltered reef slopes, and found different *Drupella* assemblages in each. The exposed reef crests had only *D.cornus* and *D. fragum*, dominated by *D. fragum*, the exposed reef slopes had all three species dominated by *D. cornus*, and both the sheltered reef crests and slopes had all three species dominated by *D. rugosa.* At Heron and Wistari Reefs, *D. rugosa* was the most abundant and *D. fragum* was less abundant than *D. cornus* and *D. rugosa* (Fellegara 1996), which corresponds with the Lizard Island sheltered habitats. *D. rugosa* aggregations were observed in sheltered lagoonal patch reefs in the Marshall Islands (Boucher 1986), and Moyer et al. (1982) also found *D. rugosa* in shallow, sheltered reef environments (1-2m). The dominant species in Hong Kong was *D. rugosa*, occurring amongst corals on shallow rocks in sheltered areas (Cumming and McCorry 1998). These trends suggest that *D. rugosa* could predominate in more sheltered environments such as sheltered reef slopes, where branching coral species dominate.

A survey of several reefs is needed to assess the generality of these patterns.

Large Aggregations

How common are they?

After numerous reports of large aggregations of *Drupella*, involving hundreds or thousands of *Drupella* on a single coral colony or a few adjacent colonies, it is clear that this phenomenon occurs in *D. rugosa*, *D. fragum* and *D. cornus*. Large aggregations of *D. cornus* are commonly seen at Ningaloo Reef (Armstrong, personal communication; Ayling &

Ayling 1987), and Loya & Gur (1996) and Shafir et al. (2008) have reported aggregations of more than 200 *D. cornus* in the northern Red Sea. Large aggregations of *D. fragum* are a feature of the *D. fragum* populations in Japan, for example Moyer et al. (1982) reported several large aggregations of *D. fragum* moving through a small reef. Records of large aggregations of these two species are restricted to the outbreak populations.

On the other hand, large aggregations of *D. rugosa* occur in normal, low-density populations and do not represent population outbreaks, or even high density within the local site. The numerous reports of large aggregations of *D. rugosa* (Baird 1999; Boucher 1986; Cumming 1999, 2000; Cumming & McCorry 1998; Fellegara 1996; Loch 1987) have not been associated with outbreaks of *D. rugosa* or high local density. Moyer et al. (1982) likened the *D. rugosa* aggregations at Mactan Island, Philippines, to biological control agents and noted that coral death was restricted to localised areas. Cumming (1999) surveyed a reef on which four large aggregations were found, with four 20m line transects, and found 4.5 per cent of colonies under attack by *Drupella*, which were dispersed in clusters of less than 10, which was not different from other nearby reef sites that were not supporting large aggregations. A large *D. rugosa* aggregation in Hong Kong (Cumming & McCorry 1998) existed in an area where the *Drupella* density was so low that zero were recorded in all transect sampling (R. Cumming, unpublished data).

Are large aggregations related to population outbreaks?

Marine snails aggregate for a variety of reasons, such as protection from physical stress or predation, increased feeding efficiency or reproductive opportunity (e.g. Caterall & Poiner 1983; Chapman 1985; Garrity & Levings 1984). Several species of *Thais*, a fellow muricid, form reproductive swarms of hundreds and thousands each year as part of their annual cycle (Feare 1971; Seed 1969; Tong 1988). Possibly, *Drupella* also aggregate periodically for reproductive or other purposes. Moyer et al. (1982) reported a *D. fragum* aggregation breaking up as waters cooled toward winter, and Boucher (1986) observed aggregations breaking up into several smaller groups. Cumming (1999) revisited four *D. rugosa* aggregations after two months; two had dispersed and two remained on the same coral colonies.

Whether large aggregations are the initial stage of population outbreaks is not known, but they could contribute to outbreaks if they enhance recruitment or reduce mortality. Cumming (1999) suggested that large aggregations of *Drupella* are transient reproductive swarms, like the annual swarms of *Thais*. Fellegara (1996) observed copious eggs laid in a large aggregation of approximately 3000 *D. rugosa* at Heron Island. If large aggregations are reproductive swarms, they form through the movement of adults, but this has not been observed directly. Alternatively, if they represent high density local recruitment events (followed by lack of dispersal) we should be seeing large aggregations of recruits as well.

Cumming (2000) observed three large aggregations of juvenile *D. rugosa* on a shallow fringing reef at Puerto Galera, Mindoro Island, the Philippines, at 1to 2m depth. They

were in the rubble at the bases of large staghorn thickets, the preferred prey of *D. rugosa* (Cumming under review). One of the aggregations was approximately 100 juveniles, one was several hundred adults and juveniles, the third was several thousand adults and juveniles, and more than half were juveniles. On the surrounding reef, *D. rugosa* was not very common, and so the local population was concentrated in these large aggregations. Small groups of *D. cornus* were common.

The fact that the juveniles were associated with large numbers of adults suggests a link between large aggregations of adults and recruitment events. Free swimming planktonic larvae could be attracted to the presence of adults and other recruits, or, alternatively, egg masses actually laid by the large aggregation could have restricted dispersal and recruit within the adult population. The hypothesis of restricted dispersal is supported by the work of Johnson et al. (1993) who found that *D. cornus* recruits inhabiting the same coral colony at Ningaloo Reef were genetically related. Little is known about natural mortality rates of *Drupella*, for any of the species or any of the life-history stages, and it is therefore not clear how large aggregations of juveniles might translate to adult numbers. Estimates of the life-span of *Drupella* are up to 20 years (Black and Johnson 1994).

To date, large aggregations have not been monitored over time spans long enough to address these important questions, but evidence from sampling data does not support the idea that outbreaks are simply accumulations of large aggregations; Turner (1994b) found *D. cornus* at Ningaloo Reef were dispersed primarily in small groups even though some large aggregations occurred and overall density was high.

RECOMMENDATIONS

Protocols for sampling *Drupella*

Since *Drupella* are small benthic organisms occupying a complex three-dimensional habitat, they are difficult and time-consuming to count. Several aspects of their life history, behaviour and ecological interactions with corals contribute to this.

1. Their cryptic behaviour and appearance makes individuals and small aggregations difficult to detect
2. Preferences for branching corals with complex three-dimensional structures keeps them well hidden within the reef matrix – in some locations they congregate in staghorn thickets and cannot be seen at all by a diver swimming over the top of the thicket
3. They occupy branch bases rather than branch tips, and so are often hidden deep within colonies
4. Their tendency to aggregate into small groups, sitting on top of each other, makes them difficult to count because many individuals are obscured from view
5. At least three different species are involved and they look different. Surveyors need to have a search image for more than one species and an understanding of the morphological range of species (see Johnson and Cumming 1995)
6. Surveyors need a search image which distinguishes *Drupella* from other gastropods of similar appearance. *Drupella* closely resemble some other muricid gastropods, particularly *Cronia margariticola* which preys facultatively on reef-building corals (Cumming and McCorry 1998)
7. Videos and still photographs are not appropriate for reliable estimates of *Drupella* abundance because *Drupella* can rarely be seen under these circumstances.

Drupella epitomize the need for rigorous sampling because of the above issues and also their highly clumped dispersion patterns. These logistics mean that it is not ideal to survey *Drupella* abundance as an addition to surveys planned for other purposes. However, it is recognised that funding and resources dictate that this may occur, and in these cases sampling for *Drupella* should be done using visual surveys.

There are different species of *Drupella*, and it appears that these are not equal in terms of the threat of population outbreaks. Thus, it will be useful for surveyors to be able to identify the species of *Drupella* and to have an understanding of which species to expect in different types of reef habitats. Specifically, they are more likely to find *D. cornus* and *D. fragum* in harsher environments such as reef crests and reefs exposed to wave action. They are more likely to find *D. rugosa* in more sheltered reef sites. *D. cornus* and *D. fragum* are the species that have a record of population outbreaks at other locations, whereas there are no records of population outbreaks of *D. rugosa.* If large aggregations are encountered, members are likely to be *D. rugosa.*

Reef crests should be monitored where possible. Although it can be difficult to access reef crests because of tides and wave action, these could be the sites of highest density of both *D. cornus* and *D. fragum*. The 'back-reef', the sheltered side of the reef crest at Ningaloo Reef, was the place of recruitment of *D. cornus*, where recruits were concentrated in the upright fingers of digitate *Acropora* colonies.

Indicators of problem *Drupella* populations

The following is a list of scenarios that may indicate *Drupella* populations of elevated density, or that may be unsustainable or abnormal for a particular coral community. These are the types of scenarios that should be recorded, and, if possible, monitored with further visits and more intensive surveys.

1. *Drupella* attacking small colonies <10cm diameter. Cumming (1999) reported that at Lizard Island, Great Barrier Reef, this small size class of coral colonies was almost entirely avoided by all species of *Drupella*, affording an effective size refuge from predation pressure.
2. *Drupella* occupying a high proportion of coral colonies. Scant data to date suggest that higher *Drupella* density will lead to a higher proportion of colonies being occupied and damaged by *Drupella*, and that up to 6 per cent of coral colonies may typically be occupied by *Drupella* in non-outbreak situations.
3. Presence of large aggregations. Since it is possible that large aggregations are connected to population outbreaks in a variety of ways (see above), they could indicate future population increases and should be monitored if possible.
4. Presence of large aggregations or high densities of juveniles. These could be especially indicative of future population increases. These have been found in the following reef areas: thick-fingered digitate acroporids on shallow reef flats or reef crests, rubble underneath large staghorn thickets, and on a very large, very finely-branched *Acropora* colony. The site of recruitment of *D. cornus* juveniles at Ningaloo Reef was digitate corals on the shallow back-reef, the sheltered side of the reef crest. The only large aggregations of *D. rugosa* juveniles recorded to date were in rubble underneath staghorn thickets (Cumming 2000). A large hispidose colony (>1m^2), *Acropora elseyi* was the site of the largest groups of juveniles found by Cumming (1996) at Lizard Island. On reef slopes, the most likely locations for juveniles are in rubble under staghorn thickets, in staghorn thickets, or on very finely branched corals such as *Acropora* colonies with hispidose (or "bottlebrush") growth forms. *Drupella* congregate on larger colonies, so large staghorn and hispidose thickets are likely sites.
5. Large aggregations of *D. cornus* and *D. fragum*. Large aggregations of these two species are only known from outbreak locations. In non-outbreak locations, they occur in small groups and have not been recorded in the occasional large aggregations typical of *D. rugosa*.
6. *Drupella* congregating on broken coral. Experiments and observations indicate that *Drupella* are attracted to broken coral (Cumming, personal observation; Forde 1992;

Morton et al. 2002), and this behavioural trait could lead to increased tendency to form larger aggregations, and possibly other demographic changes. Therefore, particular attention should be paid to sites where breakage is a significant factor, for example after storms or in high use tourist areas.

7. *Drupella* congregating on stressed coral, for example colonies that are bleached or diseased. On reefs already under such pressures, the densities of *Drupella* that are sustainable could be considerably reduced. A relationship between *Drupella* and disease raises the question of the potential of *Drupella* to transmit disease.

REFERENCES

Al-Moghrabi, S.M. 1997, 'Bathymetric distribution of *Drupella cornus* and *Coralliophila neritoidea* in the Gulf of Aqaba (Jordan)', *Proceedings of the 8th International Coral Reef Symposium*, 2:1345-1350.

Antonius, A. & Riegl, B. 1997, 'A possible link between coral diseases and a corallivorous snail (*Drupella cornus*) outbreak in the Red Sea', *Atoll Research Bulletin*, 447:1-9.

Armstrong, S.J. 2005, '*The abundance and distribution of* Drupella *corallivorous gastropods at Ningaloo Reef, Western Australia*', Honours thesis, Southern Cross University, Lismore, New South Wales.

Armstrong, S.J. 2007, *Ningaloo Marine Park Drupella long term monitoring program: results of the 2006 survey*. Data Report: NIN/NMP-2007/03, Marine Science Program, Department of Environment and Conservation, Perth, Western Australia (unpublished report).

Awakuni, T. 1989, '*Reproduction and growth of coral predators* Drupella fraga *and* Drupella cornus *(Gastropoda: Muricidae)*', Honours thesis, University of the Ryukyus, Japan.

Ayling, A.M. & Ayling, A.L. 1987, *Ningaloo Marine Park: preliminary fish density assessment and habitat survey, with information on coral damage due to* Drupella *grazing*, Report to the Department of Conservation and Land Management, Western Australia.

Ayling, A.M. & Ayling, A.L. 1992, 'Preliminary information on the effects of *Drupella* grazing on the Great Barrier Reef', pp. 37-42 in Drupella cornus*: a synopsis. Proceedings of a Workshop held at the Department of Conservation and Land Management (CALM), Western Australia, 1991*, ed. S. Turner, CALM Occasional Paper 3/92.

Ayling, A.M. 2000, 'The effects of *Drupella* spp. grazing on coral reefs in Australia', http://www.searesearch.com.au/reports/drupella/drupella.html

Baird, A. 1999, 'A large aggregation of *Drupella rugosa* following the mass bleaching of corals on the Great Barrier Reef', *Reef Research* 9: 6-7.

Black, R. & Johnson, M.S. 1994, 'Growth rates in outbreak populations of the corallivorous gastropod *Drupella cornus* (Röding, 1798) at Ningaloo Reef, Western Australia', *Coral Reefs*, 13:145-150.

Boucher, L.M. 1986, 'Coral predation by muricid gastropods of the genus *Drupella* at Enewetak, Marshall Islands', *Bulletin of Marine Science*, 38: 9-11.

Caterall, C.P. & Poiner, I.R. 1983, 'Age- and sex-dependent patterns of aggregation in the tropical gastropod *Strombus luhuanua*', *Marine Biology*, 77:171-182.

Chapman, M.G. 1995, 'Aggregation of the littorinid snail *Littorina unifasciata* in New South Wales, Australia', *Marine Ecology Progress Series*, 126: 191-202.

Cumming, R.L. 1996, '*The corallivorous gastropods* Drupella cornus, D. fragum *and* D. rugosa*: ecology and impact on coral communities at Lizard Island, Great Barrier Reef*', Ph.D. Thesis, James Cook University, Australia.

Cumming, R.L. 1999, 'Predation on reef-building corals: multiscale variation in the density of three corallivorous gastropods, *Drupella* spp.', *Coral Reefs* 18:147-157.

Cumming, R.L. 2000, 'Do large aggregations of *Drupella* lead to population outbreaks?', *Reef Encounter*, 27:13-15.

Cumming, R.L. (2009), '*Case study: impact of* Drupella *spp. on reef-building corals of the Great Barrier Reef*', Report to the Great Barrier Reef Marine Park Authority, Townsville, Australia.

Cumming, R.L. & McCorry, D. 1998, 'Corallivorous gastropods in Hong Kong', *Coral Reefs*, 17:178.

Endean, R. & Stablum, W. 1975, 'Population explosions of *Aeanthaster planci* and associated destruction of the hard coral cover of reefs of the Great Barrier Reef, Australia', *Envionmental Conservation* 2:247-256.

Engelhardt, U., Miller, I., Lassig, B., Sweatman, H. & Bass, D. 1997, 'Crown-of-thorns starfish (*Acanthaster planci*) populations in the Great Barrier Reef World Heritage Area: status report 1995-1996', pp. 158-184 in *State of the Great Barrier Reef World Heritage Area Workshop. Proceedings of a technical workshop held in Townsville, Qld, 27-29 November 1995 (GBRMPA Workshop Series 23)*, eds. Wachenfeld, D., Oliver, J. & Davis, K., Great Barrier Reef Marine Park Authority, Townsville, Australia.

Feare, C.J. 1971, 'The adaptive significance of aggregation behaviour in the dogwhelk *Nucella lapillus* (L.)', *Oecologia*, 7:117-126.

Fellegara, I. 1996, '*On some aspects of the ecology and biology of the coral eating* Drupella *(Mollusca, Gastropoda) from Heron and Wistari Reefs (southern Great Barrier Reef)*', M.Sc. Thesis, University of Queensland, Australia.

Forde, M.J. 1992, 'Populations, behaviour and effects of *Drupella cornus* on the Ningaloo Reef, Western Australia', pp. 45-50 in Drupella cornus*: a synopsis: Proceedings of a Workshop held at the Department of Conservation and Land Management (CALM), Western Australia, 1991*, ed. S. Turner, CALM Occasional Paper 3/92.

Fujioka, Y. & Yamazato, K. 1983, 'Host selection of some Okinawan coral associated gastropods belonging to the genera *Drupella*, *Coralliophila* and *Quoyula*' , *Galaxea*, 2: 59-73.

Garrity, S.D. & Levings, S.C. 1984, 'Aggregation in a tropical neritid', *Veliger*, 27:1-6.

Glynn, P.W. 1973, '*Acanthaster*: effect on coral reef growth in Panama', *Science*, 180: 504-506.

Harborne, A., Fenner, D., Barnes, A., Beger, M., Harding, S. & Roxburgh, T. 2000, '*Status report on the coral reefs of the east coast of peninsula Malaysia*', Coral Cay Conservation Ltd., London.

Johnson, M.S. & Cumming, R.L. 1995, 'Genetic distinctness of three widespread and morphologically variable species of *Drupella* Thiele, 1925 (Gastropoda, Muricidae)', *Coral Reefs*, 14:71-78.

Johnson, M.S.,Holborn, K. & Black, R. 1993, 'Fine-scale patchiness and genetic heterogeneity of recruits of the corallivorous gastropod *Drupella cornus*', *Marine Biology*, 117: 91-96.

Keesing, J.K. & Lucas, J.S. 1992, 'Field measurement of feeding and movement rates of the crown-of-thorns starfish *Acanthaster planci* (L.)', *Journal of Experimental Marine Biology and Ecology*, 156:89-104.

Kimura, T., Hasegawa, H., Igarashi, T. Inaba, M., Iwao, K., Iwase, F., Kajiwara, K., Matsumoto, H., Nakai, T., Nojima, S., Nomura, K., Nonaka, M., Oki, K., Sakai, K., Seino, S., Shimoike, K., Sugihara, K., Ueno, M., Ueno, S., Yamano, H., Yokochi, H. & Yoshida, M. 2005, 'Status Of Coral Reefs In Northeast Asian Countries: Japan', pp. 165-182 in *Status of Coral Reefs in East Asian Seas Region: 2004*, ed. Japan Wildlife Research Centre, Ministry of Environment, Tokyo, Japan.

Lassig, B.R. & Engelhardt, U. 1995, 'COTS comms', *Reef Research*, 5(1):18-23.

Loch, I. 1987, 'Whodunnit? - COT death versus the dastardly *Drupella*', *Australian Shell News*, 58:1-2.

Loya, Y. & Gur, O. 1996, 'Life history and population dynamics of the predatory snail *Drupella cornus* at Eilat, Red Sea', *Abstract*, *8th International Coral Reef Symposium*, Panama, July 1996.

Moran, P.J. & De'ath, G. 1992, 'Estimates of the abundance of the crown-of-thorns starfish *Acanthaster planci* in outbreaking and non-outbreaking populations on reefs within the Great Barrier Reef', *Marine Biology*, 113:509-515.

Morton, B., Blackmore, G. & Kwok, C.T. 2002, 'Corallivory and prey choice by *Drupella rugosa* (Gastropoda: Muricidae) in Hong Kong', *Journal of Molluscan Studies*, 68:217-223.

Moyer, J.T., Emerson, W.K. & Ross, M. 1982, 'Massive destruction of scleractinian corals by the muricid gastropod *Drupella* in Japan and the Philippines', *The Nautilus*, 96: 69-82.

Osborne, S. 1992, 'A preliminary summary of *Drupella cornus* distribution and abundance patterns following a survey of Ningaloo Reef in spring 1991', pp. 11-17 in Drupella cornus*: a synopsis: Proceedings of a Workshop held at the Department of Conservation and Land Management (CALM), Western Australia, 1991*, ed. S. Turner, CALM Occasional Paper 3/92.

Osborne, S. & Williams, M.R. 1995, *Status of* Drupella cornus *outbreak at Ningaloo Reef*, Unpublished report, Australian Nature Conservation Agency.

Oxley, W.G. 1988, '*A sampling study of a corallivorous gastropod Drupella, on inshore and midshelf reefs of the Great Barrier Reef*'. Honours thesis, James Cook University, Townsville.

Pearson, R.G. & Endean, R. 1969, 'A preliminary study of the coral predator *Acanthaster planci* (L.) (Asteroidea) on the Great Barrier Reef', *Qld Dep Harb Mar Fish Not* 3:27-55.

Potts, D.C. 1981, 'Crown-of-thorns starfish - man-induced pest or natural phenomenon?', pp. 55-86 in *The ecology of pests*, eds. Kitching, R.L. & Jones, R.E., CSIRO, Melbourne.

Schuhmacher, H. 1992, 'Impact of some corallivorous snails on stony corals in the Red Sea', *Proceedings of the 7th International Coral Reef Symposium* 2:840-846.

Seed, R. 1969, 'The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. I. Breeding and settlement', *Oecologia***,** 3:277-316.

Shafir, S., Gur, O. & Rinkevich, B. 2008, 'A *Drupella cornus* outbreak in the northern Gulf of Eilat and changes in coral prey', *Coral Reefs*, 27(2):379.

Shimoike, K. 1995, 'Gametogenesis of the corallivorous gastropods (*Drupella cornus* and *D. fragum*) and their habitat in Akajima Island', *Midoriishi (Reports of the Akajima Marine Science Laboratory)*, 6:12-16.

Stella, J., Prutzman, S., Swansborough, T. & Hill, J. 2008, '*2008 site report, Great Barrier Reef project*', Reef Check Australia.

Sutton, K.A. 1996, '*The abundance, spatial distribution, and feeding ecology of* Drupella *at Lizard Island*', Honours Thesis, James Cook University, Australia.

Sweatman, H., Cheal, A., Coleman, G., Emslie, M., Johns, K., Jonker, M., Miller, I. & Osborne, K. 2008, '*Long term monitoring of the Great Barrier Reef, status report number 8, 2008*', Australian Institute of Marine Science, Australia.

Taylor, J.D. 1980, 'Diets and habitats of shallow water predatory gastropods around Tolo Channel, Hong Kong', in *The Malacofauna of Hong Kong and Southern China. Proceedings of the First International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong, 1977*', ed. Morton, B., University of Hong Kong Press, Hong Kong.

Tong, L.K.Y. 1988, 'The reproductive biology of *Thais clavigera* and *Morula musiva* (Gastropoda: Muricidae) in Hong Kong', *Asian Marine Biology*, 5:65-75.

Turner, S.J. 1994a. 'The biology and population outbreaks of the corallivorous gastropod *Drupella* on Indo-Pacific reefs', *Oceanography and Marine Biology Annual Review*, 32:461-530.

Turner, S.J. 1994b, 'Spatial variability in the abundance of the corallivorous gastropod *Drupella cornus*', *Coral Reefs*, 13: 41-48.