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DYNAMICS OF *DRUPELLA CORNUS* POPULATIONS ON KENYAN CORAL REEFS

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ABSTRACT

In the central Pacific and western Australia the coral-eating snail *Drupella cornus* has been reported to exhibit large population increases or 'outbreaks' (>10 snails/m^2) that result in the loss or devastation of their coral prey. In Kenya, a large population increase of *Drupella cornus* was recorded from the early 1990's where D. *cornus* increased from a rare species in the mid 1980's to among the most common prosobranch snail by 1995 (~0.2 snails/m^2). Population increases were most commonly observed in a section of reef that had experienced heavy fishing and loss of the durophagous predators such as triggerfish, but still maintained a high abundance of the branching coral *Porites nigrescens.* In unfished reefs, the population increases of D. *cornus* were less pronounced despite an abundance of their preferred coral prey - branching *Acropora, Montipora,* and *Pocillopora.* In one heavily fish reef, with a high abundance of another coral-eating snail, *Coralliophila neritoidea,* and low abundance of branching corals, few D. *cornus* were observed. Consequently, the success of D. *cornus* appears to be related to a complex interaction between appropriate environmental conditions for settlement success, the existence of branching corals, a low abundance of predators and the lack of other competitors such as C. *neritoidea.* An alternate hypothesis is that D. *cornus* settlement is patchy in space and time and the patterns observed in Kenya simply reflect this patchiness.

INTRODUCTION

The coral-eating snail *Drupella cornus* displays periodic population increases throughout the central Pacific (Moyer et al. 1982; 1985; Boucher 1986; papers in Turner 1992a), Indian Ocean (McClanahan 1994) and the Red Sea (Hillman, J.C. personal communication). In some cases D. cornus populations increase such that living coral is reduced greatly along with these population 'outbreaks'

This has occurred in Japan, Philippines, and Enewetak in the 1970' sand 1980' s (Moyer et al. 1982; 1985; Boucher 1986). More recently *D. cornus* outbreaks have occurred in western Australia where snail abundance has increased over 4 orders of magnitude since the mid 1980's (Turner 1994). A more modest increase was reported in Kenya during the early 1990's (McClanahan 1994) where D. *cornus* populations increased from a rare species in 1987 to the second most commonly observed prosobranch by 1993. Observations on Tanzanian and Madagascan reefs in 1995 and 1996 also indicate that D. *cornus* is among the most common snail species on these reefs (McClanahan personal observation). Reports from the southern Red Sea in 1995 also indicate an increase in D. *cornus* populations off of the coast of Eritrea that may be having detrimental effects on coral populations (Hillman, personal communication). Consequently, from existing studies and data, D. *cornus* has been a very successful snail during the last 3 decades and, although originally widespread (Abbott and Dance 1986), outbreak population may be spreading or arising at similar times throughout the central and western Indo-Pacific. Despite increased research on this snail the causes of these population outbreaks remain mysterious as multiple factors may interact to create appropriate conditions for outbreaks (McClanahan 1994).

The taxonomy, biology and ecology of D. *cornus* has only recently begun to receive attention as reported population outbreaks have stimulated researchers to understand the factors that influence their populations (Turner 1992a,b; Johnson et al. 1993; Black and Johnson 1994; McClanahan 1994; Turner 1994; Johnson and Cumming 1995). These studies have found that D. *cornus* has been given numerous names in the taxonomic literature (Wilson 1992; Johnson et al. 1993; Johnson and cumming 1995), has small variation in allelic frequencies (Holborn et al. 1994), has widespread planktotrophic larvae with a larval stage of about 30 days (Turner 1992b; Holborn et al. 1994), sexual maturity occurs between 2.5 and 3.5 years, and, on average, individuals can live for more than 5 but can reach their asymptotic size as late as 45 years (Blac_ and Johnson 1994). D. *cornus* feeds exclusively on corals and although it is often associated with *Acropora, Montipora, Seriatopora,* and *Pocillopora* (Moyer et al. 1982; Turner 1994; Cumming personal communication) this would seem to be more of a preference for branching coral forms than a dietary restriction (MCClanahan 1994). Cohorts from the same reef show similar genetic composition while comparisons of different cohorts in the same reef indicate low between-cohort genetic similarity (Johnson et al. 1993). Consequently, most mixed-cohort populations in a reef may come from different sources but some evidence suggests that outbreak populations are successful populations that have spread from a single source where a number of factors have interacted to create successful survival and reproduction (Holborn et al. 1994).

Studies on Kenyan reefs suggest that population increases have occurred throughout the entire stretch (-250 km) of fringing reef but that the highest populations have been found on reefs with a history of intense fishing and that the snail's preference for particular coral prey is less a factor in controlling populations (McClanahan 1994). Consequently, although fishing and removal of snail predators may not cause population outbreaks, predator removal can exacerbate the effects of these outbreaks.

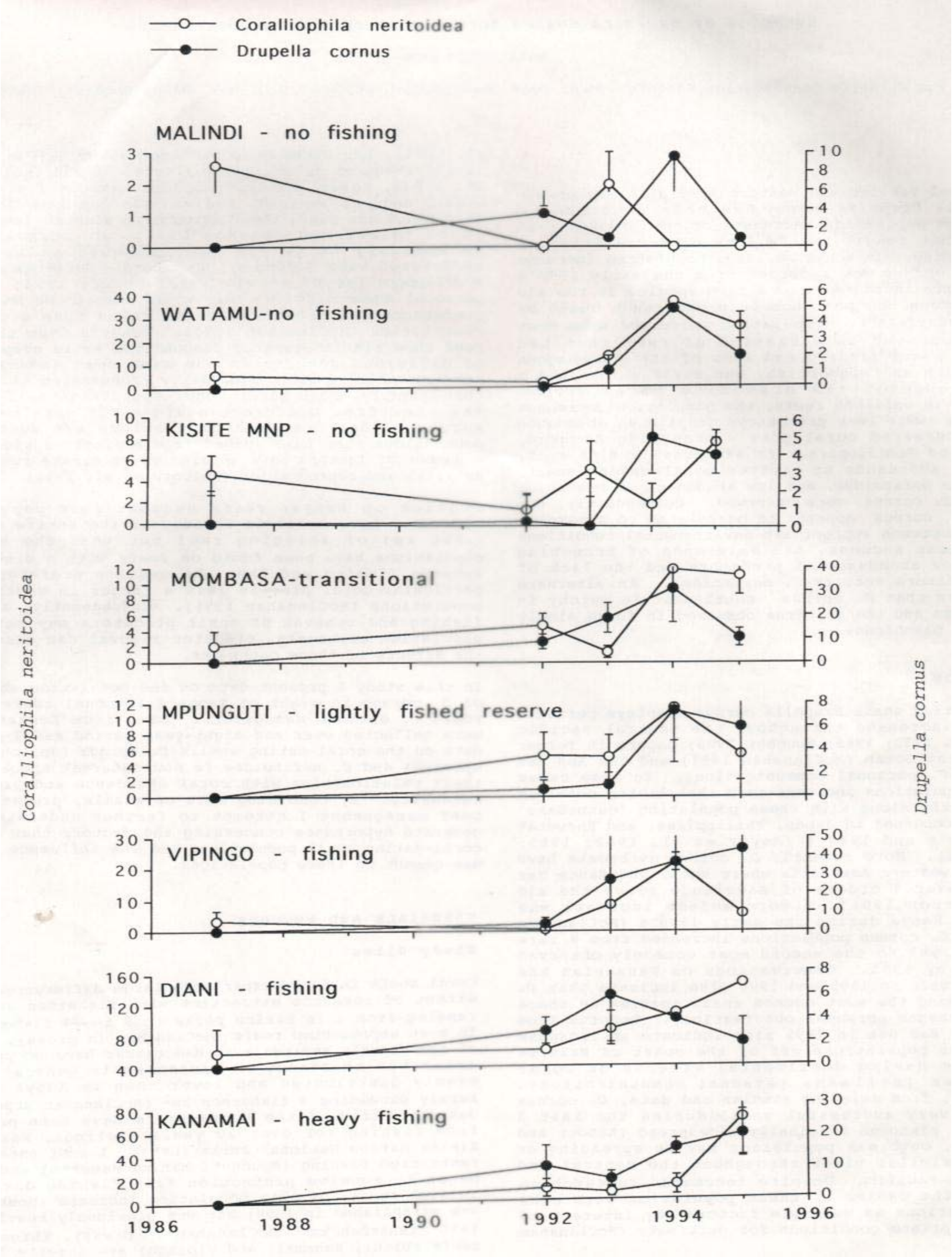
In this study I present data on the population abundance of D. *cornus* in eight of Kenya's lagoonal reefs and 15 reefs of eastern Madagascar. Data from Kenyan reefs were collected over and eight-year period and I present data on the coral-eating snails D. *cornus* (an 'outbreak' species) and C. *neritoidea* (a non outbreak species) and their relationships with coral abundance and predation intensity. By combining data on snails, predation and reef management I attempt to further understand and generate hypotheses concerning the factors that control coral-eating snail populations and the influence of reef management on these populations.

MATERIALS AND METHODS

Study sites

Coral reefs in Kenya experience large differences in the extent of resource extraction with fishermen abundance ranging from 0 in marine parks to 8 to 20 -fishermen/km^2 in most unprotected reefs (McClanahan in press). Reefs of the Masoala Peninsula in Madagascar have no protected areas but abundance of fishermen is generally more evenly distributed and lower than in Kenya reefs rarely exceeding 3 fishermen/km^2 (McClanahan unpublished data). Three of the Kenya reefs have been protected from fishing for over 20 years (Malindi, Watamu and Kisite Marine National Parks (MNP», 1 reef experiences restricted fishing (Mpunguti Marine Reserve) and 1 reef began to receive protection from fishing during the initial stages of this population increase (Mombasa MNP was established in 1990) but was previously heavily fish (>10 fishermen/km^2; McClanahan in press). Three Kenyan reefs (Diani, Kanamai, and Vipingo) are heavily fish (>8 fishermen/km^2/day). In seven of the studied Kenyan reefs data were collected on 1) predation intensity, 2) coral abundance to the genera, 3) coral-eating snail abundance, and 4) the type of coral or substrate on which D. *cornus* was resting or feeding.

Methods used for estimating coral abundance (McClanahan and Shafir 1990), predation (McClanahan and Muthiga 1989) and snails and their resting positions (McClanahan and Muthiga 1992; McClanahan 1994) are presented in more detail in previous publications. Briefly, the abundance



_: Time series of *Drupella cornus* and *Coralliophila neritoidea* populations *in* the studied reefs, Error bars are standard errors of the mean, Please note variable scales, of coral genera was estimated using 9 to 27 10 m line transects in each study site and by measuring the length of corals to the nearest cm underneath the transect line. Coral abundance was calculated as the centimeters of each genera per meter of line transect. Predation intensity was estimated by tethering the sea urchin Echinometra *mathaei* and recording the number of missing individuals over a three day period. Predation on this urchin appears to be one of the best measures of predation by durophagous predators which are often difficult to count using line transects (MCClanahan unpublished data). A predation index is calculated from the average survival rate (predation Intensity = (3S)/3, where S = survival, days). Snails were sampled by a time-sampling procedure where the number of individuals of each species is recorded during a onehour daylight search interval. Two to seven hours were completed per study site per year of sampling. The search-sampling method covers about 500 m^2 per hour but can vary between 150 and 800 m2 per hour depending on the cryptic nature of the individuals (McClanahan and Muthiga 1992). Data were collected during 1987 and annually from 1992 to 1996. Data on snails and their positions are presented as time series for each of the studied reefs and abundance for each year are then correlated with the yearly predation index, competitor abundance, and coral abundance data to determine factors that may most influence their populations.

RESULTS

Drupella cornus was very rare in the first sampling period in 1987 and its numbers have increased in most reef lagoons (Fig. 1). The largest population increases occurred on the three adjacent reefs of vipingo, Kanamai and Mombasa. Numbers continue to rise on the Vipingo and Kanamai reefs while there appears to be a reduction in numbers in the Mombasa reef beginning in 1994. The Parks experienced a modest increase in D. cornus numbers but there is also an indication of reduced numbers after 1994. *Coralliophila neritoidea* numbers were originally high and have remained higher or in some cases increased over the study period.

There are large differences in the resting positions of D. cornus in protected compared to unprotected reefs. Over 55% of the D. cornus in protected reefs were found on Acropora compared to <5% in unprotected reefs. In contrast in unprotected reefs most D. cornus were found on *Porites* with about 45% on branching *Porites* (mostly *P. nigrescens)* and around 25% on massive *Porites* (mostly *P. luted).* More than 85% of the C. *neritoidea* were found on massive *Porites* with some individuals being found on *Acropora, Pocillopora,* and branching *Porites.* Some of the differences in resting positions may be due to the relative abundance of the different corals in the protected and unprotected reefs (Table I). *Acropora* is the most abundant coral in the protected reefs but very rare in unprotected reefs while branching *Porites* is most abundant in the unprotected reefs.

Resting position and association with corals over the study period (Fig. 2b) changed but it is difficult to determine if there were any trends with only three years of data. Associations with the two species of *Galaxea and* with *Montipora* declined consistently.

Scatterplots of the relationships between coral-eating snails and coral cover, predation and competitors suggests that some of these variables may constrain but do not strictly control populations (Fig. 3). The relationship with coral cover is very poor and perhaps negative because many of the high coral cover areas are protected and also have a high abundance of predators (McClanahan 1994). The unprotected site of Diani has low numbers of D. *cornus* which may be partly attributable to the low coral cover in this reef «12%). Predation seems to constrain populations but there is also a great deal of variation suggesting multiple influences in population control. Finally, the two coral-eating snail species appear to reach their highest population densities when the other species does not reach high numb,rs. For example, Diani has the highest C. *neritoidea* populations but of the unprotected reefs it also has the lowest D. *corn* us number. Again, the relationship suggests constraint and not a high degree of interdependence.

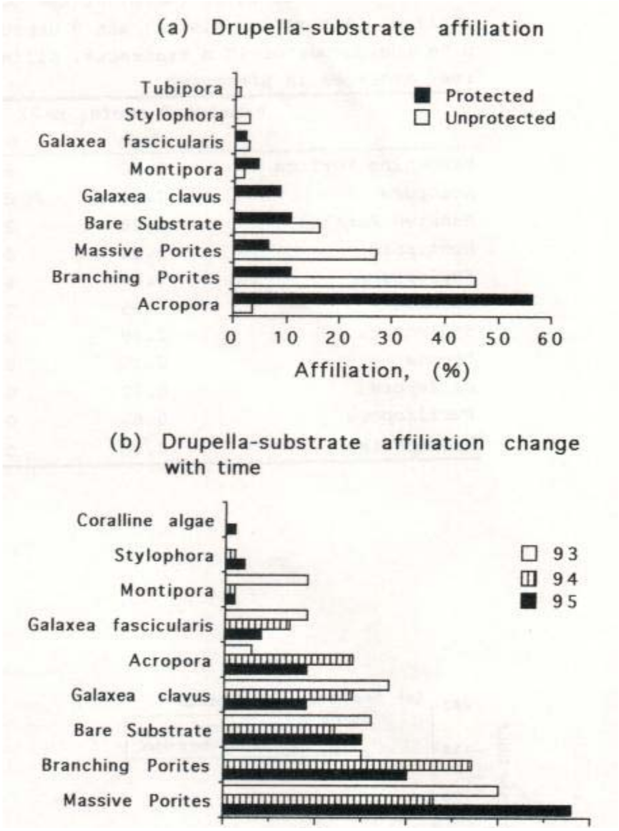


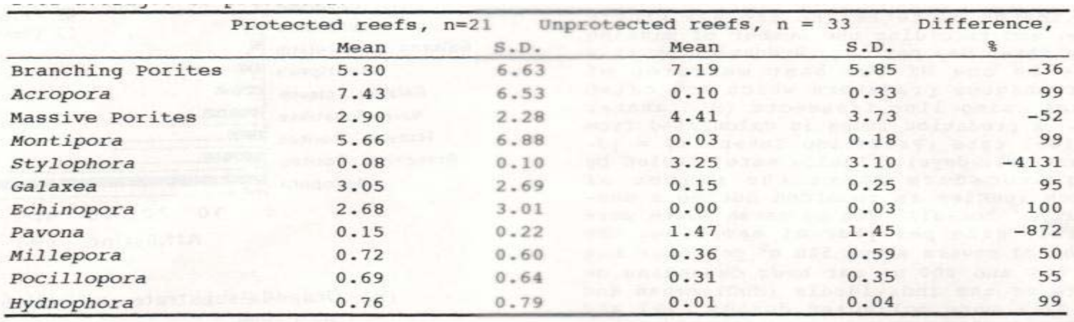
FiG. 2: Resting positions of D. *cornus* in (a) protected (Malindi, Watamu and Kisite) and unprotected reefs (Vipingo, Kanamai and Diani) and (b) the changes in resting position over the 1993-95 study period. C. *neritoidea* are largely found in the crevices of massive *Porites* heads (i.e. *Porites luted).*

Summarizing D. *cornus* and C. *neritoidea* population densities over the study period 1992 to 1996 by the management or fishing intensity of the reef suggests a relationship between management and population numbers (Fig. 4). The older unprotected reefs clearly have maintained the lowest populations while two unprotected reefs have had the highest numbers. The low numbers at the Diani site keep the overall number of the unprotected site lower than the Mombasa site which was in transition from no protection to full protection from fishing. The reefs of the lightly fished Masoala peninsula of Madagascar had moderate populations of D. *cornus* similar to the Mpunguti Marine Reserve in Kenya and low levels of C. *neritoidea.*

DISCUSSION

This study followed the population abundance of two coral-eating snail species over a eight-year period in reefs experiencing different levels of fisheries management. The study collected data on the abundance of their coral food, resting positions, and predation intensity on hard-shelled invertebrates. *Coralliophila neritoidea* was and presently is the most abundant species of prosobranch in these reefs (McClanahan 1990; unpublished data) and largely lives in the crevices of massive *Porites.* Its populations are greater in the unprotected than protected reefs. Unprotected reefs have lower overall coral cover but a greater absolute and relative abundance of massive *Porites* (Table 1; McClanahan and Mutere 1994). Numbers of C. *neritoidea* appear to be rising over time, particularly in unprotected reefs, and may be due to reduced predation intensity in these reefs. This hypothesis needs further testing.

Table 1. Absolute cover (cm/m) of the most abundant coral genera in 3 protected (Malindi, Watamu and Kisite) and 3 unprotected reefs (Vipingo, Kanamai and Diani). n is the number of 10 m transects. Difference between the protected and unprotected reef averages is presented.



	Protected reefs, n=21		Unprotected reefs, n = 33		Difference,
	Mean	S.D.	Mean	S.D.	%
Branching Porites	5.30	6.63	7.19	5.85	-36
Acropora	7.43	6.53	0.10	0.33	99
Massive Porites	2.90	2.28	4.41	3.73	-52
Montipora	5.66	6.88	0.03	0.18	99
Stylophora	0.08	0.10	3.25	3.10	-4131
Galaxea	3.05	2.69	0.15	0.25	95
Echinopora	2.68	3.01	0.00	0.03	100
Pavona	0.15	0.22	1.47	1.45	-872
Millepora	0.72	0.60	0.36	0.59	50
Pocillopora	0.69	0.64	0.31	0.35	55
Hydnophora	0.76	0.79	0.01	0.04	99

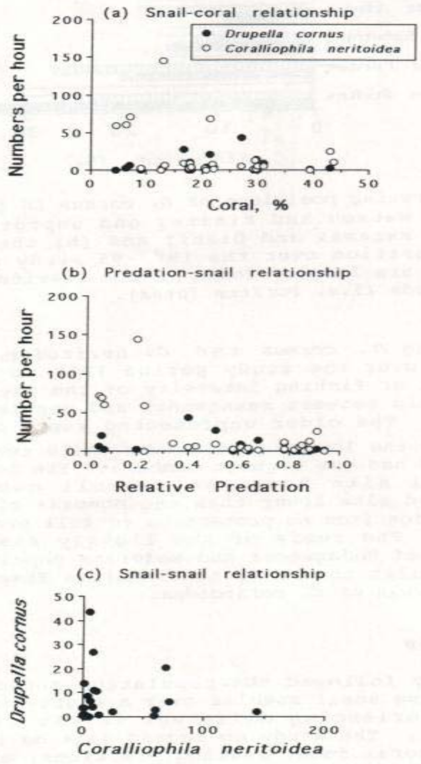


Fig. 3: Scatterplots of the abundance pf coral-eating snails and the abundance of (a) coral, (b) predation intensity on hard-shelled invertebrates, and (c) the two competing species. Units for snail abundance are number of snails found per hour.

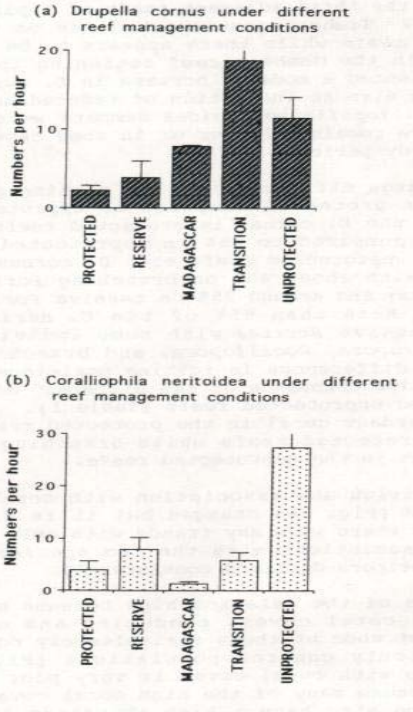


Fig. 4: Comparison of the population abundance of (a) D. *cornus* and (b) C. *neritoidea* in Kenya under different reef management conditions and from the lightly fished Masoala Peninsula in north-eastern Madagascar.

Table 2. Summary of Drupella sp. population abundance in previously studied reefs. Assumes a one hour search is equal to 500 m2. n.d. = no data given

Location	Population density,# m^{2} Range	Mean	Reference
Ningaloo Reef, Western Australia	0.3–63	14.7	Turner 1994
Ningaloo Reef, Western Australia	5.3-175	12	Ayling and Ayling 1987
Pilbara, Western Australia	0.2->6.0	n.d.	Hilard and Chalmer 1992
Norman Reef, Great Barrier Reef	n.d.	1.1	Ayling and Ayling 1987
Lizard Island, Great Barrier Reef	n.d.	1.3	Cumming, R. pers. comm.
Enewetak, Marshall Islands	7-150	n.d.	Boucher 1986
Miyake-jima, Japan	n.d.	5.1	Moyer et al. 1982
Mactan Island, Philippines	7-3000	n.d.	Moyer et al. 1982
Kenyan fringing reefs	0-0.2	0.17	This study
Masoala, Madagascar	0-0.2	0.015	McClanahan, unpublished

Drupella cornus was rare in 1987 but its numbers rose in the early 1990s until at present it is among the most abundant prosobranchs on Kenyan reefs. These population increases were not uniform among the reefs and factors of patchy recruitment, reef management, the presence of branching corals, predation and competition may have all played a role in these differences. Patchy recruitment may be responsible for the large increases in the three adjacent reefs of Vipingo, Kanamai and Mombasa (Sheppard 1985). Nonetheless, the presence and rise of *D. cornus* in other Kenyan reefs and their relatively high relative abundance in Masoala, Madagascar and Tanzania suggest that the recorded increase in Kenya may have been part of a larger scale increase that affected much of the East African region and even the Red Sea (Hillman personal communication). D. *cornus* populations continue to rise or level on the two unprotected reefs while the Mombasa reef, which has received protection from fishing, is experiencing a decline in numbers since 1994. Further monitoring is required to determine if this decline in population numbers will continue in the protected reefs. Consequently, patchy recruitment may playa role in D. *cornus* success but post-recruitment processes may also be important in determining the success of recruits.

Branching corals seem to be important for the success of *D. cornus* but there is less dependence on the particular branching species or on total coral cover. The lack of fidelity for particular branching coral species is reflected in the large differences in coral affiliations between protected and unprotected reefs. Kenya's unprotected reefs have much lower abundance of *Acropora* due to coral collection and trampling by fishermen (McClanahan and Mutere 1994; McClanahan et al. 1996). Nonetheless, this does not appear to restrain D. *cornus* which is able to use other branching and columnar species such has *Porites nigrescens, Stylophora* pistillata, and *Galaxea clavus.* In general, *D. cornus* appears to be most strongly associated with the most abundant branching species at a reef. Nonetheless, these associations may change over time as D. cornus individuals grow. One plausible hypotheses is that branching corals are important in the early life stages of *D.* cornns for protection from predators but as individuals grow, beyond the stage that they are _usceptible to predators, they may move onto less protective prey such as massive *Porites.* Further experimental work is required to determine the sizedependent role of prey preference and refuge from predators in determining the foraging sites of D. *cornus.* C. *neritoidea* also prefers massive *Porites* in its later stages of growth and the potential for interspecific competition for food or a resting spot on massive *Porites* among these species remains a factor also needing further investigation.

Reef management probably plays its greatest role in controlling coral-eating snail popula_ions by controlling the abundance of durophagous predators such as triggerfish, wrasses and scavengers (McClanahan and Shafir 1990; McClanahan 1994). The protected reefs have the highest abundance of these predators (McClanahan 1994) and this may be largely responsible for constraining population outbreaks on these reefs and for the early demise cc these populations as noted in a number of the protected reefs. Unprotected reefs, except for the Diani site, experienced the greatest population increases and also the lack of a reduction in these reefs in the last few years. D. *cornus* populations have now reached large sizes and reproductive age (Black and Johnson 1994) in unprotected reefs and may, therefore, form a source of propagules in the future. The consequences of this persistence to D. *cornus* success and the reefs in the region requires further monitoring and research. Nonetheless, this study suggests that management and protection of durophagous predators may play an important role in the control of pest populations such as *D. cornus.*

Comparisons with other studies sites suggest that Kenyan D. *corn* us has not reached the 'outbreak' levels reported on other reefs (Table 2). D. *corn* us 0 n Kenyan and Masoala, Madagascar reefs are one fifth lower than found in the Great Barrier Reef and perhaps one to four orders of magnitude lower than 'outbreak' populations reported from Western Australia and the central Pacific. The effect of D. *cornus* on living coral in Kenya is still very small at present and is not a major force in controlling coral populations to the extent of collection, trampling, competition with algae, and perhaps sea urchin grazing (McClanahan and Mutere 1994; McClanahan et al. 1996). Consequently, although populations have increased greatly there is still no evidence of a population outbreak and its destructive effects on corals. The factors that create outbreak populations still remains mysterious but studies on Kenya's fringing ref suggest that fisheries management may playa role in controlling and recovering from these outbreaks.

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