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Coral-eating snail *Drupella cornus* population increases in Kenyan coral reef lagoons

T. R. McClanahan

The Wildlife Conservation Society, Coral Reef Conservation Project, PO Box 99470, Mombasa, Kenya

ABSTRACT: Data from a study of corallivorous snails in 8 Kenyan coral-reef lagoons sampled at 3 time intervals over a 6 yr period suggest that *Drupella cornus* populations have increased on Kenyan reefs. This increase was greatest in heavily fished reefs and a transition reef (converted to a park in about 1990) but less pronounced in the unfished parks and a reserve (restricted fishing). The abundance of corallivorous snails was better predicted by the abundance of their predators than the abundance of their coral food. The 2 most abundant species, *Coralliophila violacaea* and *D. cornus*, were associated with the coral genus *Porites* although *D. cornus* was found on a wider variety of coral genera than *C. violacea*. *D. cornus* was most abundant on fished reefs with the exception of 1 reef where *C. violacea* was dominant and persisted at high population densities over the study period. Observed population increases in Kenya and western Australia may be due to oceanic conditions which improved *D. cornus* recruitment success during the late 1980s.

KEY WORDS: Fishing · Marine protected areas · Population dynamics · Prosobranch snails

INTRODUCTION

Benthic invertebrates such as coral-eating starfish (Moran 1986), prosobranch snails (Moyer et al. 1982, 1985, Turner 1992a), and sea urchins (Lessios et al. 1984, McClanahan & Kurtis 1991, Glynn & Colgan 1992) frequently exhibit periods of stability punctuated with rapid population increases and decreases. These population changes are frequently associated with major changes in the ecological structure and processes of the coral-reef ecosystem. The causes of these fluctuations in population abundance are seldom known and it is frequently asked whether humans have had an influence in these population 'outbreaks' and 'mass mortalities'. Determining the causes of these population fluctuations is often difficult due to high spatial variability in coral reefs and the lack of replicate human management 'treatments' which allow for the statistical detection of human influence apart from the frequently synergistic influences of natural events. Separating human-influenced sources of variation from the natural ones, and how they interact is, therefore, one of the major challenges of both theoretical and applied marine ecology.

Corallivorous snails such as *Drupella cornus* (synonymous with *Morula* or *Drupella elata*; Spry 1961, Wilson 1992), *Coralliophila violacea* (= *C. neritoidea*; Abbott & Dance 1986) and other members of the Thaidinae and Coralliophilidae are ubiquitous members of the coral reef. Coral-reef snails are most frequently found at low population densities (i.e. <1 per 10 m^2; McClanahan 1990, McClanahan & Muthiga 1992). However, outbreaks or exponential population increases of *Drupella* snails have been recorded in Japan (Moyer et al. 1982, 1985) in the period 1976 to 1980, Enewetak (Boucher 1986), and in western Australian reefs during the late 1980s until the present (Turner 1992a, 1994). At high population densities, the snails' scars, left from their feeding on living coral, can kill extensive coral areas leaving reefs to be colonized by filamentous algae. Coral mortality in some areas of Japan and Enewetak, originally attributed to *Acanthaster planci* feeding, was later discovered to be created by *Drupella* swarms, which feed at night and was, therefore, less obvious to daytime observers (Moyer et al. 1982, 1985, Boucher 1986).

The causes of these large population increases and whether they are spreading in extent and intensity are largely unknown. Here I report on what appears to be the initial stages of a large increase in *Drupella cornus* populations in Kenyan coral reef lagoons. By comparing the management history and abundance of coral and predatory fishes on studied reefs, I attempt a partial explanation of the factors which may contribute to successful *D. cornus* population outbreaks.

METHODS

Collection of data included (1) coral cover to the genus level, (2) finfish to the family level and (3) snails (prosobranch gastropods) to the species level. Complete surveys were undertaken in 6 Kenyan coral reef lagoons in 1987 and again in 1992 and 1993. Snails were surveyed in 2 additional reefs [Kisite Marine National Park (MNP) and Mpunguti Marine National Reserve (MNR)] but other field measurements were not made on these 2 reefs. Data collection followed previously described methods (McClanahan & Muthiga 1989, McClanahan 1990, McClanahan & Shafir 1990). Coral cover estimates are based on 9 to 27 10-m line transects per site where coral is identified to the genus.

Fish population estimates are based on 3 to 9 replicate 5 × 100 m belt-transects per reef per sampling period where individuals were identified to the family and to the nearest 10 cm length-class interval (McClanahan & Shafir 1990). Data are presented for members of 4 durophagous families (Balistidae, Diodontidae, Labridae and Lutjanidae) known to feed on snails and other hard-bodied invertebrates (Randall 1967, McClanahan & Shafir 1990). Abundance of species within each family category are presented in McClanahan (in press a). Members of the 'Lutjanidae' group are actually a combination of species in the Lutjanidae, Lethrinidae and Haemulidae as taxonomically organized by Nelson (1984). The reasons for this grouping are that (1) some species in these families are difficult to distinguish in the field and (2) the family-subfamily taxonomy of these groups has been unstable in field guides (e.g. compare Carcasson 1977 with Nelson 1984).

The wet weights (i.e. kg ha^{-1}) of fish were calculated for each family using length-weight relationships established at a local landing site (Kenyatta Beach; McClanahan unpubl. data). Lengths and weights were taken for many individuals and species and then grouped into the above family categories for calculating length-weight relationships. From these relationships an appropriate length to weight conversion factor was applied to each family and size-class group. Biomass of each family was then estimated by summing the weight estimates in each length category.

Estimates of prosobranch population densities were made on the above 6 reefs and 2 additional protected reefs (Kisite MNP and Mpunguti MNR). All reefs are similar in being shallow (<3 m at low tide) coral reef areas protected from wave exposure and dominated by hard coral and algal cover. Of these 8 study sites, 5 received some protective management. Three reefs (Malindi, Watamu and Kisite MNPs) have been successfully protected from fishing and other resource removal for over 20 yr with infrequent poaching (author's pers. obs., Marine Park wardens pers. comm.). One reef experienced low levels of line and trap fishing (Mpunguti MNR) for over 5 yr (A. Kaka, warden, pers. comm.) Another reef, Mombasa MNP, had a history of intense fishing but was converted into a marine park in 1990, and excluded fishermen shortly thereafter. Three reefs (Diani, Kanamai and Vipingo) had a long history of exposure to fishing and shell and coral collection.

Prosobranch snails were surveyed in the 8 reefs using a time-sampling technique where the number of species and individuals of each species are tallied during a 1 h daylight search period. The method has been described previously in more detail (McClanahan 1989, 1992a), tested against a quadrat method, and found to be superior for species with low population densities (McClanahan & Muthiga 1992) — common to the studied Kenyan reef lagoons (McClanahan 1990). Search sampling in the coral-reef habitat covers approximately 500 m^2 h^{-1} (Kohn 1968, McClanahan & Muthiga 1992).

Data were analyzed in 2 ways. Data from hourly samples tended to be right-skewed and, therefore, the nonparametric Mann-Whitney *U*-tests or Wilcoxon signed-rank test were used on hourly samples for comparisons with the older marine parks and the unprotected reefs. Data analysis based on hourly samples may be considered a 'pseudoreplicated' design (Hurlburt 1984). Because there are only a few marine parks and hourly samples are most frequently from different sites within individual marine parks, the scale-dependent definition of pseudoreplication is a dubious criticism of this analysis. Therefore, in addition to the above analyses, 2-way ANOVAs were performed on data using sites as the basis for replication — based on hourly samples within each site. This design is not pseudoreplicated but suffers from the unavoidable low number of replicate (n = 3) older protected areas.

RESULTS

Field studies indicate a lower abundance and more diverse fauna of corallivores in protected than unprotected reefs (Table 1, Fig. 1). In 1987, *Coralliophila violacea* was by far the most common corallivore in the 8 studied reefs by around a factor of 70 while *Drupella*

Table 1. Coral abundance, potential snail predators from durophagous fish families, and the abundance of the 2 most common coral-eating snails *Drupella cornus* and *Coralliophila violacea* in 6 of the 8 studied reef lagoons during the 3 sampling periods. Values are $\bar{x}$ ± SE (sample size). Protected reefs are indicated by the MNP after the site's name and sites are ordered from north on the left to south on the right of the table. Two protected areas not shown (Kisite and Mpunguti MNP) have low snail population densities and high fish population densities and are located to the south of Diani. UP: unprotected

	Malindi MNP	Watamu MNP	Vipingo-UP	Kanamai-UP	Mombasa MNP	Diani-UP
Coral cover (%)						
Jul 1987	17.6 ± 3.3 (15)	30.0 ± 8.2 (9)	18.1 ± 2.6 (27)	12.7 ± 1.8 (27)	8.9 ± 1.4 (24)	4.6 ± 1.1 (18)
Feb 1992	20.8 ± 4.0 (18)	29.2 ± 3.3 (12)	22.0 ± 2.5 (27)	17.7 ± 2.6 (27)	31.1 ± 2.4 (27)	6.4 ± 1.9 (18)
Nov 1992	20.4 ± 4.5 (18)	29.6 ± 3.1 (12)	16.6 ± 1.9 (27)	13.4 ± 1.6 (27)	29.7 ± 2.2 (27)	6.9 ± 1.1 (18)
Predators (kg ha^{-1})						
Balistidae, 1988	31.73 ± 15.48 (5)	5.26 ± 2.54 (3)	2.05 ± 1.62 (5)	0.00 ± 0.00 (3)	2.09 ± 1.62 (5)	1.68 ± 1.68 (5)
1992	22.33 ± 6.62 (5)	9.00 ± 0.62 (3)	3.35 ± 2.05 (5)	2.93 ± 2.39 (5)	11.89 ± 5.68 (9)	0.00 ± 0.00 (5)
1993	39.83 ± 3.82 (5)	40.23 ± 15.85 (3)	8.75 ± 2.95 (5)	4.54 ± 4.50 (5)	1.68 ± 1.68 (5)	0.00 ± 0.00 (5)
Diodontidae, 1988	0.00 ± 0.00	6.94 ± 6.94	4.55 ± 2.93	2.84 ± 2.84	4.17 ± 4.17	0.00 ± 0.00
1992	2.84 ± 2.84	0.00 ± 0.00	1.71 ± 1.71	0.00 ± 0.00	16.57 ± 7.67	1.71 ± 1.71
1993	0.78 ± 0.78	0.00 ± 0.00	1.57 ± 0.96	1.71 ± 1.71	1.71 ± 1.71	0.00 ± 0.00
Labridae, 1988	68.84 ± 12.88	84.48 ± 3.90	32.48 ± 4.06	11.70 ± 2.59	9.17 ± 1.56	4.11 ± 0.85
1992	55.18 ± 6.56	67.53 ± 17.94	30.36 ± 2.29	21.00 ± 2.69	31.00 ± 4.07	4.81 ± 0.86
1993	70.58 ± 6.18	63.37 ± 13.34	33.62 ± 5.12	19.45 ± 1.98	29.27 ± 13.77	1.82 ± 0.32
Lutjanidae, 1988	32.27 ± 9.70	158.76 ± 99.07	0.00 ± 0.00	0.00 ± 0.00	0.91 ± 0.91	0.00 ± 0.00
1992	159.33 ± 69.14	195.71 ± 35.12	0.38 ± 0.23	0.19 ± 0.19	33.82 ± 12.68	0.93 ± 0.90
1993	91.53 ± 44.95	263.66 ± 47.12	2.81 ± 1.73	22.91 ± 9.81	144.26 ± 63.52	1.21 ± 0.59
Drupella cornus (no. h^{-1})						
1987	0.00 ± 0.00 (6)	0.00 ± 0.00 (5)	0.00 ± 0.00 (3)	0.40 ± 0.24 (6)	0.00 ± 0.00 (5)	0.60 ± 0.60 (5)
1992	3.50 ± 0.77 (4)	0.00 ± 0.00 (3)	3.70 ± 2.67 (3)	10.80 ± 6.72 (4)	8.60 ± 3.14 (5)	3.00 ± 1.15 (3)
1993	1.00 ± 0.00 (2)	1.00 ± 1.00 (2)	27.00 ± 8.00 (2)	6.50 ± 2.50 (2)	13.80 ± 5.03 (6)	6.00 ± 4.00 (2)
Coralliophilia violacea (no. h^{-1})						
1987	2.16 ± 1.38	4.68 ± 4.58	3.33 ± 3.33	0.00 ± 0.00	2.00 ± 2.00	59.20 ± 32.00
1992	0.00 ± 0.00	1.67 ± 0.88	0.66 ± 0.33	9.75 ± 6.40	4.60 ± 1.63	60.30 ± 0.88
1993	2.00 ± 1.00	13.00 ± 0.00	8.50 ± 0.50	6.00 ± 4.00	1.50 ± 0.56	71.20 ± 15.06

cornus was the most abundant of the uncommon Thaidinae (Tables 1 & 2). However, *D. cornus* populations increased by a factor of 40 between 1987 and 1992 and a factor of 75 between 1987 and 1993.

Coralliophila violacea populations doubled over the sampling period (Table 2, Fig. 1). Comparing hourly samples of *C. violacea*, over the 3 sampling periods, indicated a significant increase ($p < 0.05$) between 1987 and 1992. Comparisons based on hourly samples also indicated higher population numbers in unprotected than protected reefs. However, the protected-unprotected population differences were not statistically significant in 1993 due to the snails' patchy spatial distributions (i.e. high variation; Tables 1 & 2).

Changes in *Drupella cornus* populations in Kenya's southern fringing reef lagoons did not occur in all reefs with equal intensity. Increases in the 3 marine parks (Malindi, Watamu and Kisite) and the Reserve (Mpunguti) were modest — increasing from unrecorded in 1987 to ~1 h^{-1} in 1992 and 1993 (Table 1, Fig. 1). In contrast the unprotected reefs experienced a large increase in *D. cornus* over the sampling period, as did the reef in transition from heavy fishing to total protection (Mombasa MNP). Combining *D. cornus* data for all sites by years and performing a Wilcoxon signed-rank test with the hourly samples as replicates produced statistically significant differences for these temporal comparisons between 1987 and 1992 and 1993 (1987 vs 1992, $p < 0.003$; 1987 vs 1993, $p < 0.008$; 1992 vs 1993, statistically insignificant, ns).

Table 2. Comparison of the abundance ($\bar{x}$ ± SE, no. h^{-1}) of the 2 most common coral-eating snails in the protected (i.e. Marine Parks, no fishing or collection) and unprotected reefs. Wilcoxon signed-rank test compares protected versus unprotected for each year. ns: not significant

Year	Protected reefs	Unprotected reefs	p
Drupella cornus			
1987	0.00 ± 0.00	0.38 ± 0.23	ns
1992	1.27 ± 0.60	6.30 ± 2.84	0.06
1993	0.57 ± 0.30	13.16 ± 4.99	0.03
Coralliophila violacea			
1987	3.13 ± 1.30	14.77 ± 8.52	ns
1992	1.00 ± 0.59	22.20 ± 8.82	0.04
1993	6.57 ± 2.02	34.00 ± 17.84	ns

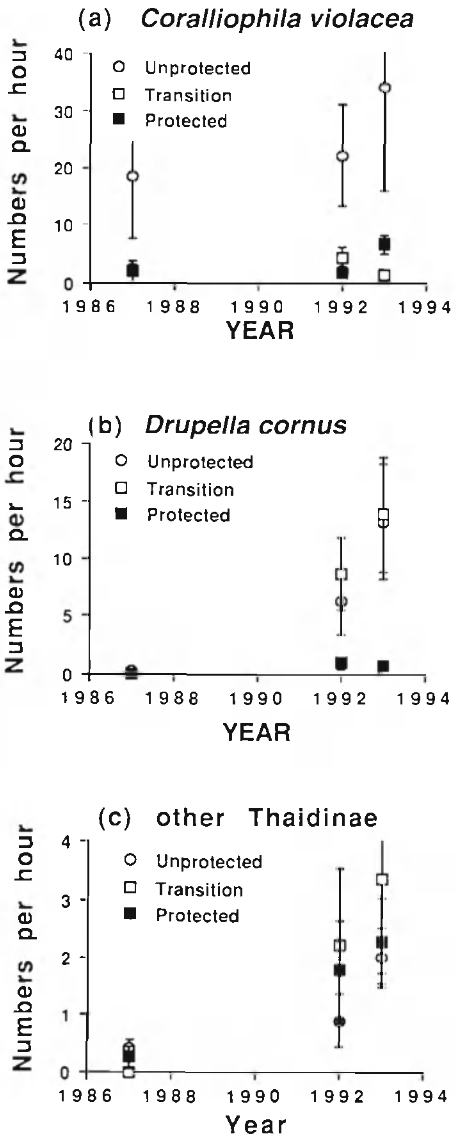

Fig. 1. Abundance ($\bar{x} \pm$ SE) of (a, b) the 2 dominant species of coral-eating snails and (c) other members of the Thaidinae as a function of the 3 sampling intervals. Data combine reefs into 3 reef categories where unprotected reefs are reefs exposed to unregulated fishing, the transition reef is Mombasa MNP which was converted into a marine park around 1990, and protected reefs include Kenya's other 3 marine parks and the Mpunguti Marine Reserve which experiences light and controlled fishing. See Table 1 for sample sizes of reef categories and years

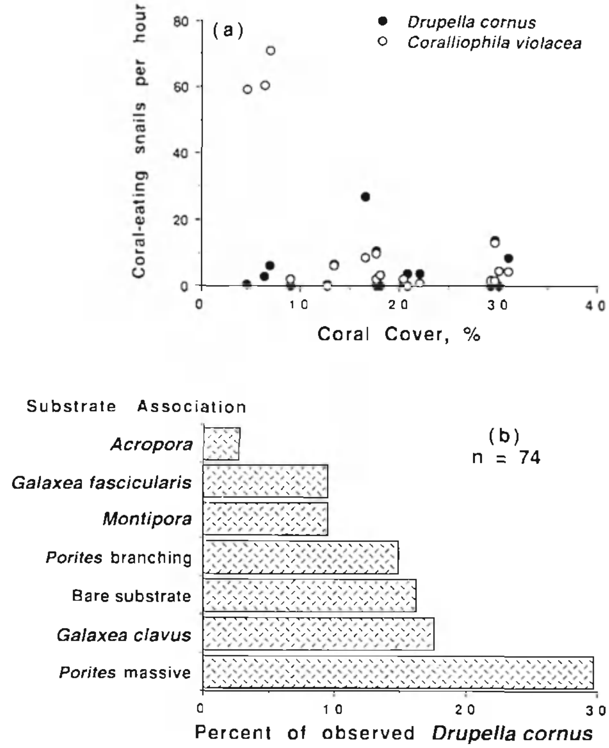

Fig. 2. (a) Abundance of coral-eating snails *Drupella cornus* and *Coralliophila violacea* as a function of coral cover in 6 studied reefs where coral cover was measured during the 3 sampling intervals (1987, 1992, 1993). (b) Association of *D. cornus* with coral and substrate types in 3 studied reefs (Mombasa, Diani and Vipingo). *C. violacea* was found nearly exclusively on massive *Porites*

Comparison of *Drupella cornus* population estimates between protected and unprotected reefs indicated significantly higher population densities in unprotected than protected reefs in 1992 and 1993 but not in 1987. If data are combined such that the older marine parks (n = 3) and unprotected reefs (n = 3) are the replicates and a 2-way ANOVA, with protection and time as the treatments, is performed, then only protection is statistically significant for *D. cornus* (at $p < 0.05$; Table 3). Neither time nor protection are significant predictors of population numbers at $p < 0.05$ for *Coralliophila violacea* by the 2-way ANOVA procedure.

Previous studies suggested that outbreaks or high population densities are most common on reefs with abundant coral (Osborne 1992). Preferred corals are reported to be from the genus *Acropora* and the family Pocilloporidae (Moyer et al. 1982, Boucher 1986, Ayling & Ayling 1992, Cumming 1992, pers. comm.). However, scatterplots of the abundance of *Coralliophila violacea* and *Drupella cornus* with coral abundance (Fig. 2a) suggest no relationship ($r = 0.07$, $n = 6$ reefs × 3 sampling periods = 18, ns) with *D. cornus* and a negative relationship for *C. violacea* ($r = -0.63$, $p < 0.05$).

During a portion of the final survey I recorded the species or genus of coral on which I found *Drupella cornus* and *Coralliophila violacea* resting or feeding. *C. violacea* was found nearly exclusively (i.e. >95%) in the crevices of the massive *Porites lutea* or other

Table 3. Two-way ANOVA analysis of *Drupella cornus* and *Coralliophila violacea* abundance with reef protection (using only the older marine parks, n = 3) and time (3 sampling periods) being the treatments

Source of variation	df	MS	*F*	p
***Drupella cornus* abundance**				
Protection	1	153.13	5.51	0.04
Time	2	68.35	2.46	0.13
Interaction	2	57.04	2.05	0.17
Within	12	27.79		
Total	17			
***Coralliophila violacea* abundance**				
Protection	1	1916.01	3.25	0.10
Time	2	60.46	0.10	0.90
Interaction	2	10.56	0.02	0.98
Within	12	589.63		
Total	17			

species of massive *Porites* with juveniles occasionally found on acroporids and branching *Porites*. *Porites* was also the single most dominant genus occupied by *D. cornus* but was also found with a greater variety of coral genera and species (Fig. 2b). However, there were no significant correlations between the abundance of corallivorous snails and the abundance of either branching or massive *Porites* — the *D. cornus*-branching *Porites* relationship was just short of statistical significance (r = 0.76, p = 0.07). However, the similar coral association among studied snail species suggests the potential for competition for food, or perhaps more importantly, competition for crevices near a food source.

Predation in these reef lagoons has been studied previously in some detail (McClanahan 1989, 1992b, McClanahan & Muthiga 1989, McClanahan & Shafir 1990). An analysis of fish population numbers and biomass estimates (Table 4) suggests that balistids (largely *Balistapus undulatus* and *Rhinecanthus aculeatus*) and lutjanids are significantly more abundant in protected than unprotected reefs regardless of the method of analysis. Diodontids are similar in protected and unprotected reefs while labrids have similar numbers but lower biomass in unprotected reefs.

To determine the possible effects of predation I calculated average biomasses of fish families for the 6 intensively studied sites based on the 3 sampling periods. I then plotted these biomass averages with average *Coralliophila violacea* population estimates for the 3 sampling periods and *Drupella cornus* populations for the last 2 sampling periods (Fig. 3). No relationship was found between the corallivorous snails and diodontid populations and a poor but negative relationship between the corallivorous snails and lutjanid abundance (Fig. 3c). However, *C. violacea* abundance appears to decrease steeply with increasing labrid and balistid abundance, whereas *D. cornus* exhibits a peak at a low to intermediate abundance of these 2 families (Fig. 3a, b).

DISCUSSION

This study presents a retrospective analysis of corallivorous snail population changes over a 6 yr period where the second most abundant snail, *Drupella cornus*, has experienced large population increases par-

Table 4. Comparison of the population density ($\bar{x}$ ± SE) and biomass of members of 4 families of durophagous fish (potential snail predators) in the protected (i.e marine parks, no fishing or collection) and unprotected reefs during the 3 sampling periods

Year	Density (no. per 500 m^2)			Biomass, wet wt (kg ha^{-1})		
	Protected reefs	Unprotected reefs	p	Protected reefs	Unprotected reefs	p
Balistidae						
1988	3.50 ± 0.71	0.23 ± 0.12	0.012	21.801 ± 10.47	1.43 ± 0.86	0.012
1992	2.75 ± 0.68	0.60 ± 0.32	0.025	17.33 ± 4.65	2.09 ± 1.22	0.012
1993	4.50 ± 0.78	0.47 ± 0.22	0.017	39.985 ± 5.66	4.4 ± 1.92	0.017
Diodontidae						
1988	0.13 ± 0.13	0.23 ± 0.12	1.000	2.60 ± 2.60	2.41 ± 1.32	0.655
1992	0.13 ± 0.13	0.13 ± 0.09	1.000	1.78 ± 1.78	1.14 ± 0.78	0.655
1993	0.13 ± 0.13	0.20 ± 0.11	1.000	0.49 ± 0.49	1.17 ± 0.68	1.000
Labridae						
1988	56.75 ± 8.26	56.46 ± 12.86	0.012	74.70 ± 8.31	16.78 ± 4.00	0.012
1992	62.88 ± 7.73	74.80 ± 10.98	0.036	59.81 ± 7.41	18.73 ± 3.04	0.012
1993	74.00 ± 4.47	74.87 ± 14.96	0.889	67.88 ± 5.87	18.30 ± 3.87	0.012
Lutjanidae						
1988	16.00 ± 9.65	0.00 ± 0.00	0.012	79.70 ± 40.20	0.00 ± 0.00	0.012
1992	21.32 ± 5.47	0.33 ± 0.13	0.012	172.98 ± 43.40	0.50 ± 0.31	0.012
1993	20.00 ± 5.57	6.67 ± 2.39	0.017	156.08 ± 44.18	8.98 ± 4.06	0.012

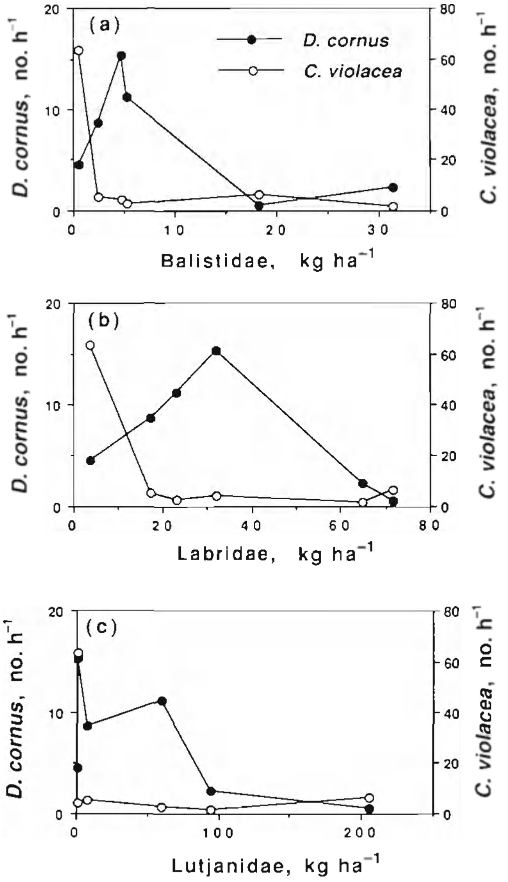

Fig. 3. Scatterplots of the abundance of coral-eating snails *Drupella cornus* and *Coralliophila violacea* as a function of (a) Balistidae (triggerfish), (b) Labridae (wrasses) and (c) the 'Lutjanidae' = Lutjanidae, Haemulidae and Lethrinidae

ticularly in 2 unprotected reefs and a reef recently closed from fishing. Populations of *D. cornus* have not reached the high levels reported in Japan and western Australia but have simply increased from a rare species to among the most abundant prosobranch species. However, the influence of *D. cornus* on living coral is largely unnoticeable, at present, and the relationship between coral and *D. cornus* abundance is weak (i.e. branching *Porites*) to nonexistent (total coral cover) at the given level of sampling. Heavily fished reefs, with the lowest fish biomass, have a coral assemblage largely composed of massive and branching *Porites* (McClanahan & Mutere 1994) and *Coralliophila violacea* appears to be the most successful species under these conditions. *D. cornus* is most abundant at low to intermediate predator abundance and is associated with more diverse coral assemblages.

Existing correlational data and the experimental conditions of fished and unfished reefs would suggest that high *Drupella cornus* populations may be affected by the abundance of the invertebrate predator guild such as balistids (i.e. *Balistapus undulatus*) and perhaps some species of labrids (McClanahan in press b). Yet, unless further experimental studies are completed and the possibility of other factors associated with low predator abundance are discounted, this conclusion remains tentative.

Is this population change in *Drupella cornus*, over the 6 yr of study, part of a population expansion from western Australia (Turner 1992a), a cyclic pattern compounded by human influences, a result of increasing eutrophication of nearshore waters (Moyer et al. 1982), or the long-term consequence of overfishing (Aronson 1990)? The nearshore eutrophication hypothesis is not supported by the Kenya, Enewetak or western Australia observations and data (Boucher 1986, Turner 1992a, 1994). In Kenya, Malindi reef waters were colored by river discharge for ~1 mo yr^{-1} (Brakel 1984) but have maintained low *D. cornus* populations over the study period. The cyclic pattern may be supported by the coincidence between population increases and peak sunspot activity and heating of Indo-Pacific waters in 1987 (Yan et al. 1992). Reported population increases in western Australia and Kenya have occurred during a similar time and may be part of a similar response to global oceanic conditions. Alternatively, population increases in Kenya may be an expansion of large populations from western Australia. However, larval development of *D. cornus* in the plankton requires about 30 d (Turner 1992b). Oceanic currents in the Indian Ocean are on the order of 1 m s^{-1} (Deutsches Hydrographisches Institut 1960) or ~2600 km per 30 d. The distance from western Australia to Kenya is about 9000 km, suggesting that dispersal from Australia is an unlikely cause for population changes in Kenya.

It is most likely that multiple factors interact to create conditions appropriate for population increases. Our study suggests that reef management (i.e. no fishing) is likely to play an important role in the intensity of these population increases. However, studies in the Mombasa MNP suggest that fishing regulations instigated at or after the time of population outbreaks may not control population increases of *Drupella cornus*. The Mpunguti MNP, which has light and controlled fishing, had lower *D. cornus* populations than Mombasa MNP. Yet the lack of replication of these management conditions make this conclusion tentative. Clearly the interactions between reef management, coral abundance, predators, competition among corallivores, and oceanographic conditions need to be studied in more detail before a more robust understanding of population outbreaks can be obtained.

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